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**SYSTEMATICS AND DISTRIBUTION OF FISHES OF THE ASIAN
GOBY GENERA *CHAENOGOBius* GILL AND *GYMNOGOBius* GILL
(PERCIFORMES: GOBIIDAE), WITH COMMENTS ON THE
RELATIONSHIPS OF THE *CHASMICHTHYS* GROUP**

Duane E. Stevenson

A dissertation submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

University of Washington

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Program Authorized to Offer Degree: School of Aquatic and Fishery Sciences

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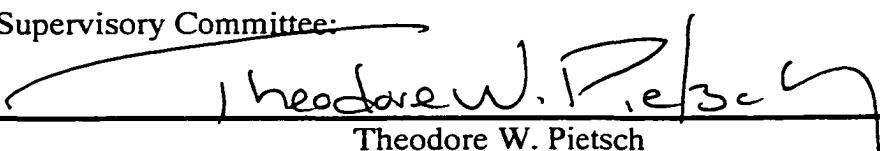
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Chair of Supervisory Committee:


Theodore W. Pietsch

Reading Committee:


Theodore W. Pietsch


James W. Orr


Paul Bentzen

Date: 11 January 2002

University of Washington

Abstract

Systematics and distribution of fishes of the Asian goby genera *Chaenogobius* Gill and *Gymnogobius* Gill (Perciformes: Gobiidae), with comments on the relationships of the *Chasmichthys* Group

Duane E. Stevenson

Chair of the Supervisory Committee:

Professor Theodore W. Pietsch

School of Aquatic and Fishery Sciences

The gobiid *Chasmichthys* Group includes two genera found in the western North Pacific and another six genera found in the eastern North Pacific along the coast of North America. Within the *Chasmichthys* Group, the taxonomy of the genus *Chaenogobius* Gill, 1859, has been unclear for over a century, at least partially due to the apparent absence of a type specimen for its type species, *Chaenogobius annularis* Gill. The latest revisions of this genus include at least one undescribed species and several points of disagreement among authors. Furthermore, the phylogenetic relationships among the species of the genus are largely unknown, as is the relationship of this genus to the rest of the *Chasmichthys* Group. This study reports the discovery of the holotype of *Chaenogobius annularis* in the collection of the U. S. National Museum of Natural History. Having established the identity of this specimen, a complete systematic revision of the Asian *Chasmichthys* Group, including the genera *Chaenogobius* and *Gymnogobius*, is presented, with the description of a new species,

keys to the species of both genera, and numerous taxonomic clarifications. In addition to the taxonomic problems in this group, the phylogenetic relationships among the species included in these genera and their relationship to the North American members of the *Chasmichthys* Group have not been established. This study presents a detailed osteological examination of *Gymnogobius macrognathos* (Bleeker), and an osteological comparison with other species of *Gymnogobius*, as well as all other genera of the *Chasmichthys* Group. A hypothesis of phylogenetic relationships within the group is presented based on this comparison. Finally, DNA sequence data from the mitochondrial ND2 gene is presented for several species of the *Chasmichthys* Group. The evolutionary dynamics of the sequenced region are discussed, and the sequence data are used to construct a hypothesis of phylogenetic relationships among the species of *Gymnogobius* and among the genera of the *Chasmichthys* Group.

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INTRODUCTION

The Gobioidei is among the largest of teleost suborders, containing an estimated 2,120 species of marine, estuarine, and freshwater fishes (Birdsong, 1975; Hoese, 1984; Harrison, 1989). There is considerable debate about exactly how this suborder should be divided. Miller (1973) recognized two gobioid families: the monotypic Rhyacichthyidae and the Gobiidae (divided into seven subfamilies). Hoese (1984) recognized six gobioid families (Rhyacichthyidae, Eleotrididae, Xenisthmidae, Microdesmidae, Gobiidae, and Kraemeriidae), and Nelson (1984) added another by splitting Xenisthmidae into Gobiodidae and Trypauchenidae. More recently, Hoese and Gill (1993) have proposed a three-family classification, recognizing Rhyacichthyidae, Odontobutidae, and Gobiidae (including the subfamilies Butinae, Eleotridinae, and Gobiinae). Pezold (1993) has advocated retention of the six-family classification of Hoese (1984), and Nelson (1994) and Akihito et al. (2000) have advocated an eight-family classification (Rhyacichthyidae, Odontobutidae, Eleotridae, Xenisthmidae, Microdesmidae, Gobiidae, Kraemeriidae, and Schindleriidae). The large number of species and an evolutionary tendency toward reduction and loss of skeletal elements have significantly impeded higher-level classification of the Gobioidei (Birdsong et al., 1988). No sister group for the suborder has ever been proposed, although Winterbottom (1993) explored some candidates and found that hoplichthyids, trachinoids, and the gobiesocid/callionymoid lineage have much in common with gobies.

Regardless of how the gobioid fishes are classified, the Gobiidae is by far the most speciose family, containing nearly 2,000 species. Gobies are found throughout the tropical and subtropical regions of the world, and many species range into temperate latitudes. They inhabit coral reefs, mangroves, estuaries, oceanic islands, rivers, and mountain streams, and some species spend extended periods of time on land (Nelson, 1984). The gobioid fauna of eastern Asia and the western North Pacific includes approximately 62 genera, most of which are also found in the Indo-west Pacific (Birdsong et al., 1988). In contrast, the eastern North Pacific supports only 13 gobioid genera, two of which are exotics recently introduced from Asia.

The *Chasmichthys* Group of Birdsong et al. (1988) was included in the gobiid subfamily Gobionellinae by Pezold (1993). This group is diagnosed by the insertion of the anteriormost pterygiophore of the first dorsal fin in the fourth or fifth interneural space. It includes two genera found exclusively in the western North Pacific (*Chaenogobius* and *Chasmichthys*) and six genera found along the Pacific coast of North America (*Clevelandia*, *Eucyclogobius*, *Gillichthys*, *Ilypnus*, *Lepidogobius*, and *Quietula*). The Asian genera are found throughout Japan and along the coast of Asia from the Amur River basin to the mouth of the Yangtze River. They inhabit a wide range of aquatic habitats, including shallow marine, brackish, and fresh waters. Ecological and life history information on these fishes is scarce, but they can be quite common and may represent important components of aquatic ecosystems in these regions (Pinchuk, 1984).

The organization and scope of the Asian genus *Chasmichthys* has remained unchanged for nearly a century. In contrast, the genus *Chaenogobius* has been significantly altered several times within the 20th century (e.g., Tomiyama, 1936; Takagi, 1966a; Pinchuk, 1984) and has been considered synonymous with *Gymnogobius* and *Chloea* by many authors. The instability of *Chaenogobius* has resulted from the near certainty that the holotype of the type species, *Chaenogobius annularis* Gill, has not been examined since Gill (1859) erected the genus. Because this specimen has not been examined, *Chaenogobius* has not been clearly defined by recent authors and a number of taxonomic problems have resulted, including nominal species and genera of questionable validity, identification difficulties, and undescribed species.

The species of this group are distinguished primarily on the basis of differences in head morphology and meristic counts. The most diagnostic character complex is the pattern of pores and sensory papillae on the head, or cephalic lateral line system, which was first formally proposed for use as a taxonomic character for gobies by Takagi (1957), although Schmidt (1904) had mentioned it briefly a half a century earlier. The cephalic lateral line system has been extensively mapped for the *Chasmichthys* Group (Macdonald, 1972; Akihito et al., 1984) and the utility of this character complex in the classification of gobioid fishes has been demonstrated (Hoese, 1984; Gill et al., 1992). In addition to the cephalic lateral line system, various fin-ray counts, vertebral counts, scale counts, gross morphology, and coloration can be used to distinguish some species of the *Chasmichthys* Group. With the exception of two studies (Aizawa et al., 1994; Suk et al., 1996), molecular techniques have not been used to distinguish these fishes.

Aizawa et al. (1994) provided some allozyme characters that distinguish a few species of *Chaenogobius*, as well as evidence that at least one undescribed species should be recognized. That study, while including only seven species, indicated that molecular markers can be quite useful in determining phylogenetic relationships among species of *Chaenogobius* and the rest of the *Chasmichthys* Group. Suk et al. (1996) provided additional allozyme evidence indicating that an undescribed species of *Chaenogobius* should be recognized.

Although much taxonomic work has been done, a comprehensive and detailed morphological study of the entire genus *Chaenogobius* has never been attempted. Therefore, the first major objective of this project was to clarify the taxonomy of the genus through a comprehensive and detailed study of the external and internal morphology of all potential members of the genus. This work has resulted in significant nomenclatural changes, a new species description, and new type specimen designations (Chapters I and II). Detailed synonymies, distributions, and a key to the species of both western North Pacific genera are also included in this work.

In addition to the taxonomic problems, the evolutionary relationships among species of the genus *Chaenogobius* are virtually unknown and monophyly has never been demonstrated for the genus. Aizawa et al. (1994) published the only attempt to produce a species phylogeny for *Chaenogobius*, but they included only seven species and based their hypothesis only on allozyme characters. The evolutionary placement of this genus relative to other gobiid genera is also unclear. Birdsong et al. (1988) and Pezold (1993) placed *Chaenogobius* in the *Chasmichthys* group based on morphological

characters, but made no attempt to determine relationships within this group. Comparisons of external morphology and osteology have proven very useful in the elucidation of the deep phylogenetic relationships of the Gobioidei (e.g., Miller, 1973; Birdsong, 1975; Birdsong et al., 1988; Harrison, 1989; Hoese and Gill, 1993; Pezold, 1993) as well as finer-scale relationships among genera (Takagi, 1950, 1988; Parenti and Thomas, 1998). These studies provide a guide to further investigation and a context in which new knowledge can be interpreted. Therefore, morphological characters exhibit a great deal of potential for resolving relationships within the *Chasmichthys* Group as well as higher level relationships.

One of the major impediments to the construction of a phylogeny of the *Chasmichthys* Group and the placement of this group within the Gobioidei has been the lack of a detailed osteological examination of any species within the group. Although several detailed osteological examinations of gobioids have been published (Miller, 1973; Birdsong, 1975; Springer, 1983; Murdy, 1985), none of them have treated any member of the Gobionellinae. This important gap in the gobioid literature is here addressed with a detailed osteological description of *Gymnogobius macrognathos*, thus providing a baseline for a comparative osteological examination of the *Chasmichthys* Group and insight into the placement of the group within the Gobionellinae (Chapter III).

Although morphological character comparisons are often useful, they may provide insufficient resolution for fine-scale phylogenies in cases of very recent divergence or in the presence of significant homoplasy. Several authors (Birdsong et al.,

1988; Harrison, 1989; Hoese and Gill, 1993) have remarked on the difficulties confronting the establishment of phylogenetic relationships within the Gobiidae, including the large number of taxa and their tendency toward reduction of skeletal elements. Furthermore, the species of the *Chasmichthys* Group display a great deal of morphological similarity, as indicated by the amount of taxonomic uncertainty surrounding these fishes. Therefore, morphology may not provide sufficient evidence to support a well-resolved phylogeny of this group. In anticipation of this possibility, the final portion of this project is a mitochondrial DNA sequencing study (Chapter IV). The aim of this portion of the study is to provide information on the evolutionary dynamics of the region chosen for study, as well as another data set upon which to base a hypothesis of the phylogenetic history of the group. The combination of a complete classical systematic revision with a detailed comparative osteological examination and a comparative DNA sequence study make this the most comprehensive systematic and phylogenetic investigation ever undertaken for this group of fishes.

CHAPTER I:

DISCOVERY OF THE HOLOTYPE OF *CHAENOGOBius ANNULARIS*

The gobiid genus *Chaenogobius* Gill, 1859, includes nearly 30 nominal species, of which about 14 have been recently recognized as valid (Akihito et al., 1984; Pinchuk, 1984). The genus was erected to accommodate a new species, *Chaenogobius annularis*, based on a single specimen collected in Japan, for which Gill (1859) gave neither size nor catalog number. Gill did not mention where this specimen was deposited; only that it was collected in "Hakodadi" Bay in Japan by W. Stimpson. The distinguishing characters of the genus included scales small and cycloid, mouth large extending to behind the eye, "maxillae equal," and "tongue slightly emarginate."

Günther (1861) did not recognize *Chaenogobius*, listing Gill's species as *Gobius annularis*, although he certainly did not see the type. He also placed several European and Asian species in the genus *Gobiosoma* Girard. Gill (1863:269) disagreed with this alignment, believing that *Gobiosoma* should remain a strictly North American genus and recommending removal of all European and Asian species and creation of a new genus for each of those species:

The genus *Gobiosoma* is apparently peculiar to North America, and is represented on both the Eastern and Western coasts. The foreign species referred to it belong to several genera, the *Gobius macrognathos* Blkr. of Japan, differing in the form of the head, &c., may be named *Gymnogobius*; the *G.*

ophiocephalus Jenyns, in form and development of fins, *Ophiogobius*; the *G. Nilssonii* D. & K., distinguished by the biradiate first dorsal, may take the name *Crystallogobius*, and *G. stuvitzii* D. & K., *Boreogobius*.

Gill (1863) thus erected four genera, including the Japanese genus *Gymnogobius*, in a single sentence. Counting *Gymnogobius* (see Chapter II), three of these genera are still considered valid today. Bleeker (1874) recognized *Gymnogobius* and augmented its description, adding details about the dentition, head characters, and fin ray counts.

In the next major treatment of this group, Jordan and Snyder (1901b) did recognize *Chaenogobius*, listing both *C. annularis* Gill and *C. macrognathos* (Bleeker). Although they did not examine the type specimen, they significantly modified Gill's (1859) description of the genus to accommodate *C. macrognathos*. They replaced Gill's phrase "maxillae equal" with "lower jaw projecting" (p. 75) and Gill's "scales cycloid, mostly small" with "scales very small, cycloid or weakly ctenoid" (p. 76). They also deleted from the original description the phrase "mouth large, greatly split, extending to behind the eyes" and added "gill opening continued forward below" (p. 76). They suggested that *Gymnogobius*, a genus that Gill (1863) had erected for *Gobius macrognathos* Bleeker under the impression that the species was scaleless, might be synonymous with *Chaenogobius*. However, "Not having seen the type of *Chaenogobius*" (p. 76), they could not be sure. In the same publication Jordan and Snyder (1901b) erected the genus *Chloea*, which differed from *Chaenogobius* in having

seven or eight first dorsal fin spines instead of six, and included four species: the type species *Chloea castanea* (O'Shaughnessy), plus *C. laevis* (Steindachner), *C. mororana* Jordan and Snyder, and *C. sarchynnis* Jordan and Snyder.

Tomiyama (1936) completely reorganized these taxa, synonymizing both *Gymnogobius* and *Chloea* with *Chaenogobius*. He recognized four species of *Chaenogobius*: *C. annularis* Gill, *C. heptacanthus* (Hilgendorf), *C. macrognathos* (Bleeker), and *C. cylindricus* Tomiyama. He divided the first two of these species into two “forms,” for which he provided trinomials. Again there is no indication that Tomiyama examined the type specimen of *C. annularis*. In fact, in his synonymy he referred to the type species as “*Gobius annularis*,” suggesting that he did not even see the original description. Fowler (1961) agreed with Tomiyama (1936) in recognizing *Gymnogobius* and *Chloea* as junior synonyms of *Chaenogobius*, and his description of the genus included all the changes that Jordan and Snyder (1901b) had made.

Whitley (1940) noted that *Chloea* Jordan and Snyder was preoccupied by *Chloeia* Savigny, in Lamarck, 1818 (Polychaeta). He therefore suggested the replacement name *Chloeichthys*, which apparently no subsequent author has used. Fowler (1961) noted that *Chloea* Jordan and Snyder is derived from a personal name, and therefore *Chloeia* Savigny has a different derivation and is not involved.

Takagi (1966a) realized that *Chaenogobius* was being discussed, redefined, and its contents modified by various authors without regard to the original description or type specimen. He assumed that the holotype of *Chaenogobius annularis* was lost or destroyed, because Jordan and Snyder (1901b) had not examined it in their review of

the genus, and Koumans (1940) had not listed it in his reexamination of gobioid types from around the world. Concentrating on the length of the upper jaw, Takagi (1966a) tried to determine whether *C. annularis* *sensu* Tomiyama (1936) was equivalent to *C. annularis* Gill. In his original description of the genus, Gill (1859:13) stated that the mouth extended “beyond the eye.” Takagi (1966a) found that *C. annularis* *sensu* Tomiyama had a much smaller mouth, the jaw (by which he presumably meant the maxilla) not extending to the posterior margin of the eye, and could therefore not be equivalent to *C. annularis* Gill. Based on this character and the fin ray counts given in Gill’s original description, Takagi (1966a) also concluded that *C. urotaenia* (Hilgendorf) is a junior synonym of *C. annularis* Gill. In a subsequent paper, Takagi (1966b) divided *C. annularis* *sensu* Tomiyama into two species.

Throughout most of the 20th century, Russian workers (Berg, 1916, 1933, 1949; Taranetz, 1933, 1934; Schmidt, 1950; Lindberg and Krasyukova, 1975) continued to recognize *Gymnogobius* and *Chloea* but not *Chaenogobius*. As Taranetz (1934) pointed out, the type species of *Chaenogobius* was in question and thus the status of *Chaenogobius* was uncertain. However, Pinchuk (1978, 1984) agreed with Japanese and American ichthyologists in synonymizing these two genera under *Chaenogobius*. He agreed with Takagi (1966a, b) in recognizing the heterogeneity of *C. annularis* *sensu* Tomiyama and considering *C. urotaenia* to be a junior synonym of *C. annularis*. Pinchuk (1992) also believed the type specimen of *C. annularis* to be lost.

The confusion surrounding the identity of *Chaenogobius annularis* was compounded when Nakanishi (1978a, b) and Ishino et al. (1983) recognized three

distinct forms of *C. annularis*, which they referred to as the “freshwater type,” “middle reach type,” and “brackish water type.” The original description lacked the details necessary to distinguish the three forms and the holotype of *C. annularis* was thought to be lost, so it was unclear which of these forms was represented by Gill’s original description. Following these additional complications, Akihito et al. (1984) and Pinchuk (1992) disregarded the name *C. annularis* altogether, using *C. urotaenia* for the “freshwater type” of *C. annularis*, and *Chaenogobius* sp. 1 and *Chaenogobius* sp. 2 for the “middle reach type” and “brackish water type,” respectively. Since then, the two latter species have remained undescribed in the literature due to the uncertainty surrounding the identity of *Chaenogobius annularis*. The “freshwater type” is still referred to as either *C. annularis* or *C. urotaenia* depending on the author.

Jordan and Snyder (1901a) erected the genus *Chasmias* to include *Gobius dolichognathus* Hilgendorf and to accommodate a new species, *Chasmias misakius*, collected from Japan. Distinguishing characters included scales minute and cycloid, mouth large with upper jaw projecting, maxilla extending beyond the eye, tongue “slightly notched” (p. 762) or “not notched” (p. 763), isthmus very broad with the gill openings restricted to the sides, and upper pectoral rays with “free silky tips” (p. 763). In a later publication, Jordan (1901) noted that *Chasmias* Jordan and Snyder was preoccupied, and substituted the name *Chasmichthys*. Two years later, Jordan (1903) recognized that *Chasmichthys misakius* was a junior synonym of *Saccostoma gulosum* Guichenot, in Sauvage (1882); but *Saccostoma* was also preoccupied, so Jordan recognized this species as *Chasmichthys gulosus*. *Chasmichthys* then included *C.*

gulosus (Guichenot, in Sauvage) and *C. dolichognathus* (Hilgendorf). Subsequent authors (Jordan et al., 1913; Tomiyama, 1936; Fowler, 1961; Lindberg and Krasyukova, 1975; Akihito et al., 1984) left the genus unchanged.

MATERIALS AND METHODS

Method of counting scales follows Akihito et al. (1984). Method of counting fin rays follows Hubbs and Lagler (1958). Dorsal pterygiophore formulae (DF), vertebral counts, and number of anal pterygiophores anterior to the first haemal spine (AP) follow Birdsong et al. (1988). Counts were made using a Zeiss SV-11 binocular microscope and radiographs. The posteriormost ray of the second-dorsal and anal fins is divided to its base, but counted here as one ray. Cephalic sensory pore symbols (B = posterior nasal, C = anterior interorbital, D = posterior interorbital, F = postorbital, G = intermediate otic, H = extreme otic) follow Akihito et al. (1984). Institutional abbreviations follow Leviton et al. (1985). Standard length (SL) is used throughout.

IDENTITY OF THE HOLOTYPE OF *CHAENOGOBius ANNULARIS*

From the beginning, attempts to revise *Chaenogobius* have been thwarted by the lack of a type specimen for *C. annularis*, the type species of the genus. Gill's (1859) description was based on a single specimen collected from "Hakodadi" by William Stimpson, but he gave no catalog number or even the institution in which the specimen was deposited (Appendix A). Subsequent authors either did not try to locate the specimen or assumed it was lost, and there is no indication that it was examined by

anyone after its original description in 1859. However, the specimen does indeed exist and was only lost in the sense that it was not labeled as the type.

The United States National Museum of Natural History, where Stimpson deposited most of his material and where he began processing his material after returning from Ringgold's North Pacific exploring expedition (Dall, 1888), holds a specimen collected by Stimpson (Fig. 1.1) labeled *Chaenogobius annularis* (USNM 6336). The stated locality is "Hakodadi, Japan," which is the same locality, including the alternate spelling of what is surely Hakodate, that Gill (1859) stated for the type of *C. annularis*. Although there is no collection date on the label, the USNM catalog number and ledger indicate that the specimen was collected before 1869 (Shirleen Smith, USNM, pers. comm., 25 February 1999).

Measurements of the specimen (Table 1.1) closely match those reported by Gill (1859) in the original description of *C. annularis*. The body height goes into standard length 6.5 times (Gill reported 7), head length is 0.23 body length (Gill reported 1/4), head width is 0.67 head length (Gill reported > 1/2), orbital diameter is 0.23 head length (Gill reported nearly 1/4), and the caudal fin is 0.17 total length (Gill reported 1/6).

Morphological details of the specimen also match Gill's description. The scales are small and all cycloid, the jaws are approximately equal, the maxilla extends beyond the posterior margin of the eye, and the gill opening is restricted to the sides of the head. All of these details match the original description but contradict Jordan and Snyder's (1901b) modifications of Gill's description. The color of the specimen also matches

Gill's description, although the second dorsal fin is so degraded that it is impossible to determine whether it has the three bands that Gill described.

Gill (1859) reported the following meristic counts for the type of *C. annularis*: D. VI–9, A. 8, C. 19. The dorsal- and anal-fin ray counts for USNM 6336 are D. VI–I,10, A. I,8, and the specimen has 9 + 8 principal caudal fin rays. If Gill was counting only soft rays in the second dorsal and anal fins, the counts for the first dorsal and anal fins match exactly those of the type of *C. annularis*, and the count for the second dorsal is off by one ray. If Gill was counting principal caudal rays, then the count for USNM 6336 differs from the count of the type by two. These two differences (one ray in the second dorsal fin and two in the caudal fin) are the only evidence that refutes the possibility that USNM 6336 is the holotype of *C. annularis*.

Considering the small size of the specimen (< 41 mm SL) and overall difficulty of counting these rays, even with modern equipment, it is reasonable to assume that Gill's dorsal-fin ray count may have erred by one element. In addition, this species (and indeed the vast majority of all gobies) has many dorsal and ventral procurent caudal-fin rays that are difficult to distinguish from principal rays without the aid of radiographs, an option that Gill did not have. Springer and Bauchot (1994) postulated a similar discrepancy in Kaup's (1858) description of *Xenocephalus armatus* from the same time period. Finally, the dorsal and caudal fins of USNM 6336 are now in poor condition. Although it is impossible to determine the condition of these fins at the time of Gill's examination, degraded fins would have increased the likelihood of a miscount. Based on the preceding evidence, USNM 6336 is herein recognized as the specimen

that Gill described as *Chaenogobius annularis*, and it therefore represents the holotype of the species.

With characters provided by the holotype of *Chaenogobius annularis*, it is possible to more precisely define *Chaenogobius* and determine which nominal species it should include. The holotype has small cycloid scales, jaws approximately equal, and maxilla extending past the posterior margin of the orbit, all of which were mentioned by Gill (1859). The specimen also has several free rays on the dorsal margin of the pectoral fin, gill opening confined to the side of the head, and a single medial pore in the posterior interorbital space. These characters agree fully with the original description of *Chaenogobius* Gill but not with Jordan and Snyder's (1901b) modifications, which have been accepted by most subsequent authors. Therefore, USNM 6336 does not represent the same species recognized as *C. annularis* throughout the 20th century, nor does it represent any species currently included in *Chaenogobius*. This refutes Takagi's (1966a) suggestion that *C. annularis* and *C. urotaenia* are synonymous. In fact, within the framework of the currently accepted taxonomy of Japanese gobies (Akihito et al., 1984), these characters suggest inclusion in *Chasmichthys* Jordan.

Chasmichthys can be distinguished from *Chaenogobius* by the presence of minute cycloid scales, gill opening restricted to the side of the head, and the presence of free silky tips on the upper pectoral fin rays (Jordan and Snyder, 1901a). Additionally, *Chasmichthys* can clearly be distinguished from *Chaenogobius* by the pattern of cephalic sensory canals and pores (Fig. 1.2). The paired oculoscapular canals of

Chasmichthys are connected in the posterior interorbital space by a commissure and open through paired B, F, and H pores and a single medial D pore. The oculoscapular canals of *Chaenogobius* are not connected by a commissure and open through paired C, D, F, and G pores (although some or all pairs of pores may be absent in some species). *Chasmichthys* includes two species: *C. dolichognathus* (Hilgendorf, 1879) and *C. gulosus* (Guichenot, in Sauvage, 1882). These two species differ in meristic counts, coloration, and maximum size (Akihito et al., 1984).

Several morphological characters of the holotype of *Chaenogobius annularis*, including the pectoral fins, gill openings, and cephalic sensory pore pattern, clearly differentiate *C. annularis* from *C. urotaenia* and indeed all other species of *Chaenogobius*, but not from either species of *Chasmichthys* (Table 1.2). Unfortunately, the holotype of *Chaenogobius annularis* is too damaged and fragile to allow an accurate determination of the overall sensory papillae pattern, with one exception (see below).

Fin ray counts are too variable and overlap too much to be useful in separating these species, but other meristic counts are useful (Table 1.3). Of the material examined in this study, only two specimens of *Chasmichthys dolichognathus* have the same vertebral count as the holotype of *Chaenogobius annularis*. Dorsal-fin pterygiophore formulae (DF) are fairly stable in the two species of *Chasmichthys*, and both match that of *Chaenogobius annularis*. Although the DF of *C. urotaenia* are more variable, none of the eight syntypes has the same pattern seen in *C. annularis*. Scale counts are variable in all four species, but their ranges appear to be completely disjunct in the two species of *Chasmichthys* (the syntypes of *Chaenogobius urotaenia* are too

small to obtain reliable scale counts). Both longitudinal and transverse scale counts of *C. annularis* are very close to the counts of *Chasmichthys dolichognathus* but well outside the ranges of *C. gulosis*. The predorsal scale count of *Chaenogobius annularis* is well below the range of that of *Chasmichthys gulosis* and also significantly lower than that of *C. dolichognathus*. The number of anal fin pterygiophores preceding the first haemal spine (AP) effectively separates *Chaenogobius annularis* from *Chasmichthys gulosis* and *Chaenogobius urotaenia* but not from *Chasmichthys dolichognathus*. Finally, the number of papillae in the symphyial line posterior to the mental flap clearly differentiates *Chaenogobius annularis* from *Chasmichthys gulosis*.

In summary, all available evidence indicates that USNM 6336 is the holotype of *Chaenogobius annularis*. A comparison of morphological and meristic characters of the holotypes of *C. annularis*, the two species of *Chasmichthys*, and *Chaenogobius urotaenia* reveals that *C. annularis* is clearly not synonymous with *C. urotaenia* but instead is a senior synonym of *Chasmichthys dolichognathus*.

TAXONOMIC CONSEQUENCES

The genus *Chasmichthys* has included two species since Jordan and Snyder (1901a) erected the genus: *C. dolichognathus* (= *Chaenogobius annularis*) and *C. gulosis*. These two species differ only in meristic counts and coloration, and share many characteristics (e.g., pectoral and pelvic fin morphology) to the exclusion of all other members of the *Chasmichthys* Group. Therefore, it seems most reasonable to keep them within the same genus. Since *C. annularis* is the type species of the genus

Chaenogobius, the species synonymy recognized herein forces recognition of *Chaenogobius* (including only *C. annularis* and *C. gulosus*) as a senior synonym of *Chasmichthys*.

The issue then remains of what to do with the other species formerly included in *Chaenogobius*. *Gymnogobius* Gill (1863) was erected for *Gobius macrognathos* Bleeker, a species originally described as scaleless and one that Gill considered similar to *Gobiosoma* Girard. Jordan and Snyder (1900:372) were convinced that *G. macrognathos* had been wrongly described as scaleless based on a letter they had received from Dr. Van Lidth de Jeude (University of Leiden) in which he stated:

I am rather inclined to think that the specimen must have had small scales. A careful microscopical examination exhibited on some parts of the body scale pouches about 0.28 mm wide, and after softly stroking the tail end with a small scalpel I succeeded in loosening a small scale about 0.25 mm wide.

Koumans (1931) studied Bleeker's type specimen (RMNH 4461) and concluded that it was indeed incorrectly described as scaleless.

Clearly, the specimen had scales at one time (Fig. 1.3), though few in number and not closely spaced. Thus, although the original description of this genus was inadequate and inaccurate, its type specimen represents a species that adequately represents this group of fishes. Therefore, *Gymnogobius* Gill is the next available name for these species. With the exception of *Chaenogobius annularis*, all species formerly included in *Chaenogobius* are here referred to *Gymnogobius* (see Stevenson, 2000).



Fig. 1.1. Photograph of the holotype of *Chaenogobius annularis* Gill, USNM 6336 (40.6 mm SL). Photograph by P. McGiffert.

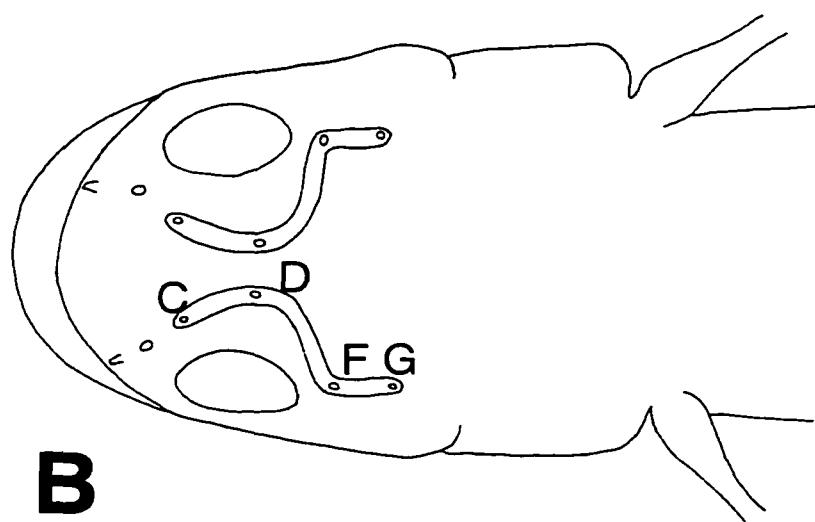
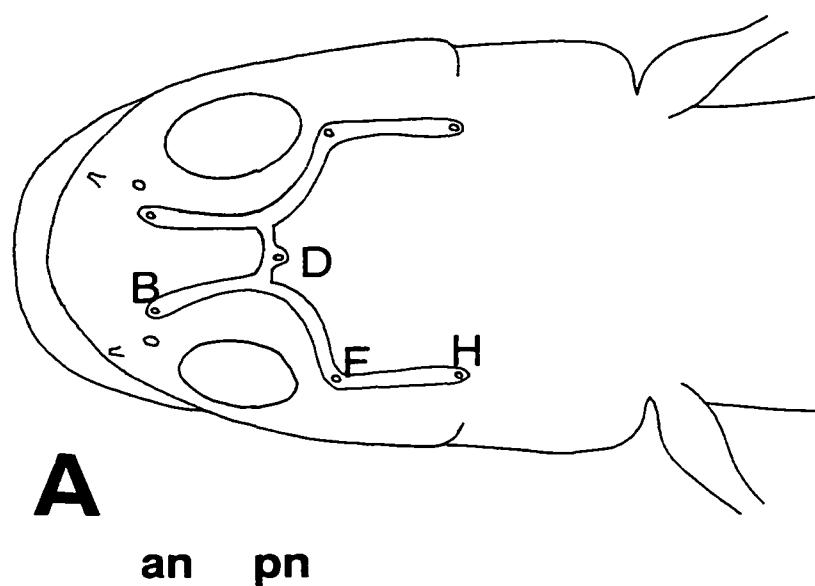


Fig. 1.2. Diagram of the dorsal aspect of the head of *Chasmichthys* (A) and *Chaenogobius* (B), showing placement of cephalic sensory canals and pores (cutaneous papillae not shown). Pore symbols follow Akihito et al. (1984), an = anterior naris, pn = posterior naris.



Fig. 1.3. Photograph of the holotype of *Gobius macrognathos* Bleeker, RMNH 4461 (35.5 mm SL). Photograph by P. McGiffert.

Table 1.1. Counts, measurements, and morphological characters for the holotype of *Chaenogobius annularis*, USNM 6336, published by Gill (1859) compared to those recorded here. Length of Gill (1859) is body length.

	Gill (1859)	Present findings
Measurements:		
Body depth	7 in length	6.4 in TL
Head length	4 in length	4.3 in TL
Head width	>1/2 HL	0.67 HL
Orbital diameter	4 in HL	4.3 in HL
Caudal fin length	6 in length	5.8 in TL
Morphology:		
Scales	cycloid	cycloid
Jaws	equal	equal
Maxillae	beyond orbit	beyond orbit
Meristics:		
Dorsal fin rays	"VI.9"	D ₁ :VI D ₂ :I,10
Anal fin rays	8	I,8
Caudal fin rays	19	9 + 8

Table 1.2. Comparison of morphological characters among species of *Chaenogobius* and *Chasmichthys*. D = posterior interorbital, G = intermediate otic, H = extreme otic.

	<i>Chaenogobius annularis</i>	<i>Chasmichthys dolichognathus</i>	<i>Chasmichthys gulosus</i>	<i>Chaenogobius urotaenia</i>
Free pectoral rays	present	present	present	absent
Gill opening	restricted to side	restricted to side	restricted to side	continued below head
D pore(s)	single	single	single	paired
G pores	absent	absent	absent	present
H pores	present	present	present	absent

Table 1.3. Comparison of meristic characters among species of *Chaenogobius* and *Chasmichthys*. Values for *C. urotaenia* are the mode of N = 8 syntypes. For *C. dolichognathus* and *C. gulosus* fin-ray counts, vertebral counts, and dorsal-fin pterygiophore formulae (DF) are given as mode followed in parentheses by holotype. Scale counts are given as holotype followed in parentheses by range. NC = scales not counted due to small size of specimens, AP = anal-fin pterygiophores preceding first

haemal spine

	<i>Chaenogobius annularis</i>	<i>Chasmichthys dolichognathus</i>	<i>Chasmichthys gulosus</i>	<i>Chaenogobius urotaenia</i>
N	1	11	12	8
First dorsal fin	VI	VI (VI)	VI (VI)	VI
Second dorsal fin	I,10	I,11 (I,10)	I,10 (I,10)	I,11
Anal fin	I,8	I,9 (I,9)	I,9 (I,9)	I,10
Vertebrae	14 + 18	14 + 19 (14 + 18)	14 + 19 (14 + 19)	16 + 18
DF	4-1211100	4-1211100 (4-1211100)	4-1211100 (4-1211100)	4-12201000
Longitudinal scales	65	66*	79 (78-83)	NC
Transverse scales	21	22*	29 (29-35)	NC
Predorsal scales	17	23*	32 (28-34)	NC
AP	2	2	3	3
Symphysial line papillae	2	2	6	2

*Data from holotype only.

CHAPTER II:

SYSTEMATICS AND DISTRIBUTION

With the identity of *Chaenogobius annularis* clearly established, the major barrier to a complete revision of the Asian *Chasmichthys* Group has been removed. Recent revisions of this group have included the genus *Chasmichthys*, containing two species, and *Chaenogobius*, containing 12 to 14 species (Akihito et al., 1984; Pinchuk, 1984). However, the finding that *Chaenogobius annularis* Gill is a senior synonym of *Chasmichthys dolichognathus* Hilgendorf forces recognition of the genus *Chaenogobius* as a senior synonym of *Chasmichthys*. The next available genus name for the species orphaned by this nomenclatural change is *Gymnogobius* Gill (see Chapter I). The following systematic account of the Asian *Chasmichthys* Group therefore includes the genera *Chaenogobius* and *Gymnogobius*. This account includes the description of a new species, as well as keys to both genera, the clarification of a number of long-standing taxonomic problems in the group, and a list of nominal species assigned to other genera.

MATERIALS AND METHODS

Methods of counting scales follow Akihito et al. (1984). Method of counting fin rays follows Hubbs and Lagler (1958). Dorsal pterygiophore formulae (DF), vertebral counts, and number of anal pterygiophores anterior to the first haemal spine (AP) follow Birdsong et al. (1988). The last ray of the second dorsal and anal fins is divided to its

base, but counted here as one ray. The first caudal vertebral centrum is defined as the anteriormost centrum with a complete haemal arch. Cephalic sensory pore symbols (B = posterior nasal, C = anterior interorbital, D = posterior interorbital, F = postorbital, G = intermediate otic, H = extreme otic) follow Akihito et al. (1984). Sensory papillae nomenclature and symbols (*n* = anterior transverse row of occipital series, *f* = mental row, *lm* = lateral midline series) follow Sanzo (1911), as modified by Wongrat and Miller (1991). Institutional abbreviations follow Leviton et al. (1985), with the exception of the Biological Laboratory of the Imperial Household in Tokyo, which is abbreviated BLIH. Measurements are straight-line distances determined using dial calipers or an ocular micrometer with a Zeiss SV-11 binocular microscope, and standard length (SL) is used throughout. Meristics in species accounts are given as ranges, with modal counts, when a clear mode exists, indicated in parentheses. For *Gymnogobius opperiens* n. sp. and *G. scrobiculatus*, meristics are given as ranges, with counts for the holotype (or neotype) in bold, followed by modal count in parentheses. Meristic frequency distributions for all species included in this study are given in Tables 2.2–2.4, and a summary of scale counts is given in Table 2.5.

SYSTEMATICS

Genus *Chaenogobius* Gill, 1859

Chaenogobius Gill, 1859:12 (type species *Chaenogobius annularis* Gill, 1859, by monotypy).

Saccostoma Guichenot, in Sauvage, 1882:171 (type species *Saccostoma gulosus*

Guichenot, in Sauvage, 1882, by monotypy, preoccupied by *Saccostoma* Fitzinger, 1843, a genus of Squamata).

Chasmias Jordan and Snyder, 1901a:761 (type species *Chasmias misakius* Jordan and Snyder, 1901a, by original designation, preoccupied by *Chasmias* Ashmead, 1901, a genus of Insecta).

Chasmichthys Jordan, 1901:941 (type species *Chasmias misakius* Jordan and Snyder, 1901a, by original designation).

Diagnosis.—Anteriormost pterygiophore of first dorsal fin inserted in fourth (rarely fifth) interneural space; tongue emarginate; cheeks and opercles without scales; predorsal scales extending anteriorly beyond posterior margin of opercle; posterior oculoscapular and preopercular canals absent; dorsal rays of pectoral fin divided into 10–20 fine filamentous projections free from fin membrane (Fig. 2.1); anterior oculoscapular canals present, connected in posterior interorbital space by short transverse commissure, opening through single medial D pore and paired B, F, and H pores; gill opening confined to side of head; scales cycloid (except in some specimens < 30 mm SL).

Description.—Body elongate, cylindrical anteriorly, becoming compressed posteriorly; scales small and cycloid (except in some specimens < 30 mm SL), covering entire body

including belly, extending anteriorly on dorsum beyond origin of first dorsal fin.

Genital papilla small and ovoid, with no apparent external sexual dimorphism.

Head broad, depressed, without barbels, its widest point near preopercle; snout rounded in dorsal profile, bluntly pointed in lateral profile. Head without scales. Eyes directed laterally and slightly upward, set anteriorly in head; interorbital space broad and flat. Anterior nares opening through short, tubular projections; posterior nares flush with snout. Mouth very large; upper jaw extending anteriorly beyond lower; maxilla extending posteriorly well beyond posterior margin of orbit; a fleshy flap overlapping middle third of maxilla. Premaxillary and dentary teeth conical, slightly curved, arranged in several irregular rows; canines absent; tongue emarginate. Anterior oculoscapular canals present, opening through minute pores; left and right canals connected by short transverse commissure in posterior interorbital space; posterior oculoscapular and preopercular canals and pores absent. Sensory papillae pattern invariable; four longitudinal rows of papillae on cheek, no transverse rows on cheek; no papillae in interorbital space. Gill opening short, vertical, extending anteroventrally just beyond base of pectoral fin; gill membranes attached at isthmus; branchiostegal rays five.

Two dorsal fins, separated, not connected by membrane, approximately equal in height. First dorsal fin short, somewhat rounded in profile, consisting of six spines (rarely five), anteriormost pterygiophore inserted in fourth (rarely fifth) interneural space; DF somewhat variable, most commonly beginning 4-1211100. Second dorsal fin with one spine and 9–11 soft rays, posteriormost ray divided to its base, anteriormost

pterygiophore usually inserted in interneural space 11. Anal fin approximately equal to second dorsal fin in height, its length somewhat shorter than second dorsal, its origin posterior to origin of second dorsal; consisting of one spine and 8–10 soft rays, posteriormost ray divided to its base; two or three anal fin pterygiophores preceding first haemal spine. Caudal fin rounded, consisting of 17 segmented rays (9 dorsal + 8 ventral), 15 of which are branched (8 dorsal + 7 ventral), and several dorsal and ventral unsegmented rays; epurals two. Pectoral fins large, rounded, extending posteriorly beyond midpoint of first dorsal fin, consisting of 21–24 rays; dorsalmost rays forming 10–20 fine filaments, each free from fin membrane. Pelvic fins short, rounded, completely fused to each other, consisting of one spine and five soft rays; pelvic frenum fleshy, its posterior margin concave, with a deep notch between spine and lateralmost soft ray on each side (Fig. 2.2A).

Two species, often found sympatrically in rocky tide pools along the coasts of Japan and Korea.

Key to Species of *Chaenogobius*

- 1A. Scales in longitudinal series 61–67, scales in transverse series 20–22, predorsal scales 17–24; one pair of sensory papillae in row *f* (Fig. 2.3A); modal second dorsal-fin ray count I,10; modal AP 2; modal vertebral count 14 + 18.....
.....*Chaenogobius annularis* Gill, p. 30

- 1B. Scales in longitudinal series 77–87, scales in transverse series 29–36, predorsal scales 28–44; three pairs of sensory papillae in row *f* (Fig. 2.3B); modal second dorsal-fin ray count I,11; modal AP 3; modal vertebral count 14 + 19.....
..... *Chaenogobius gulosus* (Guichenot, in Sauvage), p. 33

***Chaenogobius annularis* Gill, 1859**

Japanese name *agohaze*

Korean name *jeom-mang-dug*

Figs. 2.4A, 2.5

Chaenogobius annularis Gill, 1859:13–14 (original description, “Hakodadi” Bay, Japan); Jordan and Snyder, 1901b:76; Jordan et al., 1913:350.

Gobius annularis: Günther, 1861:65–66 (new combination).

Gobius dolichognathus Hilgendorf, 1879:108 (original description, Japan).

Chasmias dolichognathus: Jordan and Snyder, 1901b:764, fig. 16 (new combination).

Chasmichthys dolichognathus: Jordan, 1901:941 (replacement name for *Chasmias dolichognathus*); Jordan and Metz, 1913:57; Jordan et al., 1913:353, fig. 306; Mori, 1928:8; Mori and Uchida, 1934:30; Mori, 1952:144–145; Chyung, 1954:384; Matsubara, 1955:839, fig. 326; Okada, 1955:365; Fowler, 1961:49–51; Lindberg and Krasyukova, 1975:386–387; Akihito et al., 1984:275, fig. 172, pl. 252-C; Kim et al., 1987:538–539.

Chasmichthys dolichognathus dolichognathus: Tomiyama, 1936:93 (new subspecies); Chyung, 1977:484, pl. 102.3.

Diagnosis.—A species of *Chaenogobius* unique in having 61–67 scales in longitudinal series, 20–22 scales in transverse series, 17–24 predorsal scales; one pair of sensory papillae in row *f*; modal second dorsal-fin ray count I,10; modal AP 2; modal vertebral count 14 + 18; dorsal fins light brown with distinct wavy dark-brown longitudinal bands; caudal and pectoral fins light brown with distinct dark-brown transverse bands; body and head light brown with approximately six broad dark transverse bands, several small black spots, and a distinct dark blotch at caudal fin base.

Description.—Body robust, cylindrical anteriorly, becoming compressed posteriorly; caudal peduncle deep. Scales small, cycloid (except in some specimens < 30 mm SL possessing many ctenoid scales), covering entire body from posterior margin of opercle to caudal fin, extending anterior to first dorsal fin along dorsal midline; head naked; scales in longitudinal series 61–67, scales in transverse series 20–22, predorsal scales 17–24. Several rows of sensory papillae in abdominal region; approximately 28 vertical rows of sensory papillae in *lm* series.

Head broad and depressed, with broad bulge on snout; interorbital space broad and flat, its width greater than orbital diameter; mouth large, subterminal; upper jaw protruding beyond lower jaw; maxilla extending beyond posterior margin of orbit and beyond perimeter of gape, its posterior end not attached to cheek; small sharp conical premaxillary and dentary teeth in irregular rows; posterolateral end of mental flap indistinct, continuous posteriorly; no fleshy barbel-like processes behind chin; a single

pair of sensory papillae in row *f*; gill opening short, vertical, extending anteroventrally just beyond base of pectoral fin. Anterior oculoscapular canals connected by short transverse commissure in posterior interorbital space, opening through paired B, F, and H pores and a single medial D pore (Fig. 2.5); four suborbital rows of sensory papillae oriented longitudinally; a single sensory papilla in row *n*, directly dorsal to F pore.

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin V–VI (VI); DF somewhat variable, modally 4-1211100; second dorsal fin I,9–11 (I,10); anal fin I,8–10 (I,9); AP 2–3 (2); pectoral fins large, rounded, extending posteriorly beyond midpoint of first dorsal fin, consisting of 21–23 (22) rays; dorsalmost rays forming 10–20 fine filaments, each free from fin membrane; pelvic fins I,5, united with complete and fleshy frenum, a deep notch separating distal portion of spine and first soft ray; segmented caudal fin rays 9 + 8, branched caudal fin rays 8 + 7; vertebrae 14 + 18–19 (14 + 18).

Color in alcohol.—Head and body light brown, with small dark-brown or black spots, 5–7 broad dark-brown vertical bands, and a large dark blotch at base of pectoral and caudal fins. First dorsal fin light brown with several distinct dark-brown longitudinal bands and a large dark blotch near the posterior margin; second dorsal fin light brown with several distinct longitudinal wavy bands; anal fin medium brown with indistinct dark blotches; caudal and pectoral fins light brown with several transverse rows of distinct dark-brown speckles.

Distribution.—Specimens examined are from several localities on southern Hokkaido and western Honshu, as well as Okushiri Island (Fig. 2.6). Akihito et al. (1984) reported this species from Hokkaido to Tanegashima in Japan. Mori (1928) reported it from Wonsan in North Korea and Kim et al. (1987) reported it throughout the South Korean coast.

Remarks.—Since 1903, this species has been referred to as *Chasmichthys dolichognathus*, while the name *Chaenogobius annularis* has been incorrectly used for several different species (see species accounts under *Gymnogobius*). This confusion was the result of the brevity of the original description of *C. annularis* and the mistaken assumption that the holotype was lost. After discovering the holotype, Stevenson (2000) showed that *Chaenogobius annularis* Gill is a senior synonym of *Gobius dolichognathus* Hilgendorf (see Chapter I).

Comparative Remarks.—*Chaenogobius annularis* attains a much smaller maximum size than *C. gulosus*. The largest specimen examined in this study was under 56 mm. Large specimens have only cycloid scales, but some of the smaller individuals examined (< 30 mm) have many ctenoid scales, particularly on the caudal peduncle. *Chaenogobius annularis* can be distinguished from *C. gulosus* by color pattern, lower scale counts and meristics, and row of sensory papillae pattern.

***Chaenogobius gulosus* (Guichenot, in Sauvage, 1882)**

Japanese name *dorome*

Korean name *byeol-mang-dug*

Figs. 2.4B, 2.7

Saccostoma gulosus Guichenot, in Sauvage, 1882:171 (original description, Eloffe, Japan).

Chasmias misakius Jordan and Snyder, 1901a:761–764, pl. 36 (original description, Misaki, Sagami, Honshu, Japan); Jordan and Snyder, 1901b:86–88.

Chasmichthys misakius: Jordan, 1901:941 (replacement name for *Chasmias misakius*).

Chasmichthys gulosus: Jordan, 1903:696 (new combination); Jordan and Metz, 1913:57; Jordan et al., 1913:353; Jordan and Hubbs, 1925:308; Mori, 1928:8; Mori and Uchida, 1934:30; Uchida and Yabe, 1939:13; Mori, 1952:143; Chyung, 1954:384; Matsubara, 1955:839; Okada, 1955:366; Fowler, 1961:51–53; Lindberg and Krasnyukova, 1975:386–388; Akihito et al., 1984:275, pl. 252-D; Kim et al., 1987:538–539.

Chaemichthys gulosus: Wang and Wang, 1935:189–190, fig. 18 (typographical error).

Chasmichthys dolichognathus gulosus: Tomiyama, 1936:93 (new subspecies); Chyung, 1977:484–485, pl. 265.2–3.

Diagnosis.—A species of *Chaenogobius* unique in having 77–87 scales in longitudinal series, 29–36 scales in transverse series, 28–44 predorsal scales; three pairs of sensory papillae in row *f*; modal second dorsal-fin ray count I,11; modal AP 3; modal vertebral

count 14 + 19; dorsal fins dark brown with indistinct black blotches, second dorsal fin with white margin; caudal and anal fin dark brown with white margin; pectoral fin dusky without distinct bands; body and head dark brown, mottled with lighter areas and, in life, white spots; indistinct dark blotch at caudal fin base.

Description.—Body robust, cylindrical anteriorly, becoming compressed posteriorly; caudal peduncle deep. Scales small, cycloid, covering entire body from posterior margin of opercle to caudal fin, extending anterior to first dorsal fin along dorsal midline; head naked; scales in longitudinal series 77–87, scales in transverse series 29–36, predorsal scales 28–44. Several rows of sensory papillae in abdominal region; 28–30 vertical rows of sensory papillae in *lm* series.

Head broad and depressed, with broad bulge on snout; interorbital space broad and flat, its width greater than orbital diameter; mouth large, subterminal; upper jaw protruding beyond lower jaw; maxilla extending beyond posterior margin of orbit and beyond perimeter of gape, its posterior end not attached to cheek; small sharp conical premaxillary and dentary teeth in irregular rows; posterior end of mental flap indistinct, continuous posteriorly; no fleshy barbel-like processes behind chin; three pairs of sensory papillae in row *f*; gill opening short, vertical, extending anteroventrally just beyond base of pectoral fin. Anterior oculoscapular canals connected by short transverse commissure in posterior interorbital space, opening through paired B, F, and H pores and a single medial D pore (Fig. 2.7); four suborbital rows of sensory papillae oriented longitudinally; a single sensory papilla in row *n*, directly dorsal to F pore.

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin V–VI (VI); DF somewhat variable, modally 4-1211100; second dorsal fin I,9–11 (I,11); anal fin I,8–10 (I,9); AP 2–3 (3); pectoral fins large, rounded, extending posteriorly beyond midpoint of first dorsal fin, consisting of 21–23 (22) rays; dorsalmost rays forming 10–20 fine filaments, each free from fin membrane; pelvic fins I,5, united with complete and fleshy frenum, a deep notch separating spine and first soft ray; segmented caudal fin rays 9 + 8, branched caudal fin rays 8 + 7; vertebrae 14—15 + 18—19 (14 + 19).

Color in alcohol.—Head and body dark brown, with light brown mottling, becoming lighter on ventral surface, with a large indistinct dark blotch at base of caudal fin. First dorsal fin medium brown with indistinct dark-brown longitudinal bands and a large dark blotch near the posterior margin; second dorsal, anal, and caudal fins medium brown with narrow white margin; pectoral fin dusky brown.

Distribution.—Specimens examined are from southeastern Hokkaido, the Pacific side of central Honshu, and Okushiri Island (Fig. 2.8). Akihito et al. (1984) reported this species from Hokkaido to Kyushu in Japan. It has also been reported from Wonsan (Mori, 1928), Quelpart Island (Uchida and Yabe, 1939), throughout the coast of South Korea (Kim et al., 1987), and from Tsingtau on the Chinese coast (Wang and Wang, 1935).

Remarks.—The BMNH lot labeled “cotypes” of *Chasmias misakius* by Jordan is somewhat problematic. Jordan and Snyder (1901a) based their description of this species on ten specimens, one of which was established as the holotype (SU 6484). The BMNH lot of “cotypes” includes not nine, but 27 specimens, only the smallest of which is actually *Chaenogobius gulosus*. It is difficult to determine which specimens Jordan and Snyder were using in their description, but they did include the measurements of the types, and all are larger than the single specimen of *C. gulosus* that is now part of the BMNH lot. Therefore that specimen, and probably most of the others, was not part of the original type series.

Comparative Remarks.—The largest specimen of *C. gulosus* examined for this study was over 117 mm, and many specimens were significantly larger than the maximum size of *C. annularis*. Although several specimens < 30 mm were examined, ctenoid scales were not observed in this species, in contrast to *C. annularis*. In addition, *C. gulosus* generally has a darker body and fins than *C. annularis*, has higher scale counts and meristic counts, and a different row of sensory papillae pattern.

Genus *Gymnogobius* Gill, 1863

Gymnogobius Gill, 1863:269 (type species *Gobius macrognathos* Bleeker, 1860, by monotypy).

Chloea Jordan and Snyder, 1901b:78–79 (type species *Gobius castaneus* O’Shaughnessy, 1875, by original designation).

Chloeichthys Whitley, 1940:243 (replacement name for *Chloea* Jordan and Snyder 1901b).

Paleatogobius Takagi, 1957:117–118 (type species *Paleatogobius uchidai* Takagi, 1957, by monotypy).

Rhodonichthys Takagi, 1966b:39 (type species *Gobius laevis* Steindachner, 1880, by monotypy and by original designation).

Diagnosis.—Anteriormost pterygiophore of first dorsal fin inserted in interneural space 4 (rarely 5); tongue emarginate; cheeks and opercles without scales; extent of predorsal scales highly variable; posterior oculoscapular and preopercular canals absent; pectoral fin without filamentous projections; anterior oculoscapular canals present (except in *G. castaneus*), not connected by transverse commissure; when present, oculoscapular canals opening through as many as four pairs of pores (C, D, F, and G); gill opening not confined to side of head, but continuing forward below opercle; scales cycloid anteriorly and ctenoid posteriorly, but in some species very weakly so.

Description.—Body elongate, cylindrical anteriorly, becoming compressed posteriorly; anterior scales generally cycloid, in most species becoming increasingly ctenoid on posterior half of body, particularly on caudal peduncle. Genital papilla small and conical; slightly more broad and posteriorly rounded in females, but sexes generally difficult to differentiate when not in spawning condition.

Head narrow to broad, its widest point generally near preopercle; snout rounded in dorsal profile, bluntly pointed or rounded in lateral profile; head without scales. Eyes directed laterally and slightly upward, set anteriorly in head; interorbital space narrow to moderately broad and flat. Anterior nares opening through short, tubular projections; posterior nares flush with snout. Mouth terminal or subterminal, small to large, with maxilla in some species extending posteriorly only to anterior margin or midline of orbit, in other species extending well beyond posterior margin of orbit; usually directed slightly upward; no fleshy flap overlapping middle third of maxilla. Premaxillary and dentary teeth conical, slightly curved, arranged in several irregular rows; canines absent; tongue emarginate. Anterior oculoscapular canals, when present, not connected by short commissure; posterior oculoscapular and preopercular canals and pores absent. Sensory papillae pattern variable; 3-4 longitudinal rows of papillae on cheek, transverse rows absent on cheek (except in *G. uchidai*); interorbital portion of oculoscapular canal replaced by a longitudinal row of papillae in some species. Gill opening extending anteriorly below base of pectoral fin; gill membranes attached at isthmus; branchiostegal rays five.

Two dorsal fins, separated, not connected by membrane, approximately equal in height. First dorsal fin short, consisting of five to eight spines, anteriomost pterygiophore inserted in fourth (rarely fifth) interneural space; DF highly variable, most commonly beginning 4-122 or 4-121; second dorsal fin consisting of one spine and 9-14 soft rays, posteriormost ray divided to its base, anteriomost pterygiophore inserted in interneural space 11-13. Anal fin approximately equal to second dorsal in

height, its length shorter than or equal to second dorsal, its origin posterior to origin of second dorsal; consisting of one spine and 8–13 soft rays, posteriormost ray divided to its base; two to four anal-fin pterygiophores preceding first haemal spine. Caudal fin rounded or truncate, usually consisting of 17 segmented rays (9 dorsal + 8 ventral), usually 13 of which are branched (7 dorsal + 6 ventral), and several dorsal and ventral unsegmented rays; epurals two. Pectoral fins large, rounded, consisting of 16–23 rays; dorsal rays not forming filamentous projections. Pelvic fins elliptical, their length greater than their width, completely fused to each other, consisting of one spine and five soft rays; posterior margin of pelvic frenum slightly concave, with a small notch between spine and most lateral soft ray on each side (Fig. 2.2B).

Thirteen species, found in freshwater, estuarine, and coastal marine waters throughout Japan as well as the Russian Far East and southern Kuril Islands, North and South Korea, and in the Yellow Sea basin of China.

Remarks.—As here defined, the genus *Gymnogobius* is the only Asian member of Birdsong et al.'s (1988) *Chasmichthys* Group that has separate right and left oculoscapular canals, a characteristic that may represent a developmental truncation from the primitive condition. However, the North American genus *Eucyclogobius* (another member of the *Chasmichthys* Group) also has separate right and left oculoscapular canals, although the structure of the canals is slightly different from *Gymnogobius*, so this condition has likely arisen more than once. Therefore, it is possible that *Gymnogobius* is actually paraphyletic. Within the genus there are some

distinct species groups (e.g., the *G. castaneus*–*G. taranetzi*–*G. breunigii* Group), and one or several of these species groups may warrant generic status. However, like the genus itself, the species groups suggested in this study are also difficult to define with a convincing synapomorphy, and the relationships among the species groups are far from clear. Thus, it is premature to consider elevation of the species groups within *Gymnogobius* to generic status. A complete phylogenetic analysis of these species and several outgroups, probably including molecular data, is a necessary step to settle this question (see Chapters III and IV). The following 13 species are therefore retained in the genus *Gymnogobius*.

Key to Species of *Gymnogobius*

- 1A. Mouth small, maxilla not extending beyond midorbit and typically not beyond anterior margin of orbit 2
- 1B. Mouth moderate to large, maxilla extending beyond midorbit and typically beyond posterior margin of orbit..... 4
- 2A. Oculoscapular canals and pores present 3
- 2B. Oculoscapular canals and pores absent, replaced by rows of sensory papillae in interorbital space..... *Gymnogobius castaneus* (O'Shaughnessy), p. 45

- 3A. Oculoscapular canals not extending anteriorly through interorbital space, but replaced by rows of sensory papillae; C pores absent
..... *Gymnogobius taranetzi* (Pinchuk), p. 50
- 3B. Oculoscapular canals extending anteriorly through interorbital space; paired C pores present *Gymnogobius breunigii* (Steindachner), p. 54
- 4A. Oculoscapular canals present only in interorbital and postorbital region, opening through paired C, D, and F pores 5
- 4B. Oculoscapular canals extending posteriorly beyond postorbital region, opening through paired C, D, F, and G pores 8
- 5A. Upper jaw extending anteriorly beyond lower jaw; D pores very close together, often joined to form single opening 6
- 5B. Lower jaw extending anteriorly beyond upper jaw or jaws approximately equal; D pores close together but distinct, not forming a single opening 7
- 6A. Patches of pigment restricted to upper 2/3 of body and caudal fin; anal fin origin posterior to third soft ray of second dorsal; second dorsal fin I,11–13; anal fin I,10–11 *Gymnogobius cylindricus* (Tomiyama), p. 58

- 6B. Patches of pigment extending onto lower body and caudal fin, becoming distinct bands below lateral line; anal fin origin anterior to third soft ray of second dorsal; second dorsal fin I,10–11; anal fin I,8–10
 *Gymnogobius scrobiculatus* (Takagi), p. 62
- 7A. No barbel-like fleshy processes behind chin; scales on side of body loosely arranged, non-imbricate, and easily lost; anterior extent of jaws approximately equal *Gymnogobius macrognathos* (Bleeker), p. 66
- 7B. Distinct fleshy barbel-like processes behind chin; scales on side of body imbricate, not easily lost; lower jaw extending anteriorly beyond upper jaw
 *Gymnogobius uchidai* (Takagi), p. 72
- 8A. Head laterally compressed, its depth greater than or equal to its width; spines in first dorsal fin usually seven; second dorsal and anal fins usually I,12; vertebrae > 36 9
- 8B. Head broad and depressed, its width greater than its depth; spines in first dorsal fin usually six; second dorsal and anal fins usually I,10 or I,11; vertebrae < 36 10
- 9A. Three longitudinal rows of sensory papillae below eye; < 80 scales in longitudinal series; dark blotch on posterior margin of first dorsal fin in females; vertebrae usually 17 + 21 *Gymnogobius heptacanthus* (Hilgendorf), p. 75

- 9B. Four longitudinal rows of sensory papillae below eye; > 80 scales in longitudinal series; first dorsal fin without dark blotch; vertebrae usually 16 + 22
..... *Gymnogobius mororanus* (Jordan and Snyder), p. 80
- 10A. Scales extending above insertion of pectoral fin and onto dorsum with > 20 predorsal scales; sensory papillae on cheek oriented in four longitudinal rows ... 11
- 10B. No scales on dorsum anterior to first dorsal fin or on sides dorsal to insertion of pectoral fin; sensory papillae on cheek oriented in both longitudinal and transverse rows *Gymnogobius isaza* (Tanaka), p. 85
- 11A. First dorsal fin with indistinct bands or without bands, and a dark blotch on posterior margin; two to six sensory papillae in row *n*; second dorsal fin usually I,11; vertebrae usually 15–16 + 18 12
- 11B. First dorsal fin with several distinct indented bands, but no dark blotch on posterior margin; a single sensory papilla in row *n*; second dorsal fin usually I,10; vertebrae usually 15 + 17 *Gymnogobius petschiliensis* (Rendahl), p. 88

- 12A. Right and left D pores separated by less than one-third orbital diameter; dark y-shaped blotch at base of caudal fin; vertebrae usually 15 + 18; anal fin usually I,11; first dorsal fin with indistinct oblique dark bands; anteriomost pterygiophore of first dorsal fin usually inserted in interneural space 4; anteriomost pterygiophore of the second dorsal fin usually inserted in interneural space 11; in life, white spots on pectoral fin near its insertion
..... *Gymnogobius opperiens* Stevenson n. sp., p. 93
- 12B. Right and left D pores separated by more than one-third orbital diameter; dark wedge-shaped blotch at base of caudal fin; vertebrae usually 16 + 18; anal fin usually I,10; first dorsal fin predominantly dark, with no bands; anteriomost pterygiophore of first dorsal fin usually inserted in interneural space 5; anteriomost pterygiophore of the second dorsal fin usually inserted in interneural space 12; in life, no white spots on pectoral fin
..... *Gymnogobius urotaenia* (Hilgendorf), p. 99

Gymnogobius castaneus (O'Shaughnessy, 1875)

Japanese name *juzukakehaze*

Figs. 2.9A, 2.10

Gobius castaneus O'Shaughnessy, 1875:145 (original description, Aomori, Honshu, Japan).

Chloea nakamurae Jordan and Richardson, 1907:265–266, fig. 3 (original description, Nagaoka, Echigo, Japan); Jordan et al., 1913:352, Fig. 305; Mori, 1928:8; Mori and Uchida, 1934:30.

Chloea senbae Tanaka, 1916:228 (original description, Mito, Ibaraki Pref., Japan).

Chaenogobius annularis annularis: Tomiyama (in part), 1936:90–91 (new subspecies); Okada (in part), 1961:676–678.

Chaenogobius annularis: Chyung, 1954:380 (new combination); Fowler (in part), 1961:62–63.

Rhodonichthys laevis: Takagi, 1966b:39, fig. 2B, pl. I (C–E) (new combination); Pinchuk, 1978:11–12, fig. 3C, 1981:1513, fig. 1B3, 2Γ–E, 1984:68; Nikoforov et al., 1994:27; Reshetnikov et al., 1997:721.

Chaenogobius laevis: Akihito et al., 1984:276, fig. 174, pl. 252G–J; Pinchuk, 1992:130–131.

Gymnogobius laevis: Pietsch et al., 2001:146 (new combination).

Diagnosis.—A species of *Gymnogobius* unique in lacking oculoscapular canals and pores, which are replaced by rows of sensory papillae. *Gymnogobius castaneus* is further characterized by having the following combination of characters: head broad, its width greater than its depth; a single sensory papilla in row *n*; lower jaw extending anteriorly beyond upper; maxilla not extending beyond mid-orbit; posterolateral end of mental flap distinct; no fleshy barbel-like processes behind chin; dark pigment patches on sides forming a series of indistinct vertical bands, often extending below level of

vertebral column; caudal fin translucent or pale yellow, with dark blotches forming indistinct vertical bands; 0–7 predorsal scales; 60–69 scales in longitudinal series; modal vertebral count 16 + 20; first dorsal fin usually with seven spines, anteriormost pterygiophore inserted in fourth interneural space; modal second dorsal-fin ray count I,10, anteriormost pterygiophore usually inserted in interneural space 12; modal anal-fin ray count I,10, anal fin origin anterior to third soft ray of second dorsal fin; first dorsal fin with small dark blotches forming several oblique bands.

Description.—Body somewhat elongate, its depth approximately 5 in SL; caudal peduncle moderately deep, its depth approximately 8 in SL. Scales small, ctenoid, covering entire body from base of pectoral fin to caudal fin, on dorsum extending anterior to first dorsal fin in most specimens; head naked; scales in longitudinal series 60–69, scales in transverse series 15–18; predorsal scales 0–7. Several rows of sensory papillae in abdominal region; approximately 30 vertical rows of sensory papillae in l_m series.

Head somewhat broad, depressed, its width greater than its depth, with broad bulge on snout; eye diameter 4.5 to 5 in head length; interorbital space narrow, its width less than orbital diameter; mouth small, directed slightly upward; lower jaw protruding slightly beyond upper jaw; maxilla extending to anterior margin of orbit or midorbit; small conical premaxillary and dentary teeth in four irregular rows; posterolateral end of mental flap distinct, no fleshy barbel-like processes behind chin; gill rakers short, slender, without tooth patches, 2 + 9–10 (2 + 9). Anterior oculoscapular canals and

pores absent, each canal replaced by a row of sensory papillae (Fig. 2.10); four suborbital rows of sensory papillae oriented longitudinally; a single sensory papilla in row n .

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin VI–VIII (VII); DF highly variable, modally 4-12120100; second dorsal fin I,9–11 (I,10), anteriomost pterygiophore inserted in interneural space 11–13 (12); anal fin I,8–12 (I,10), its insertion ventral to or anterior to third soft ray of second dorsal; AP 2–4 (3); pectoral fin rounded, not extending to posterior margin of first dorsal fin, pectoral fin rays 19–21 (20); segmented caudal-fin rays 9 + 8, branched caudal-fin rays 7 + 6; vertebrae 15–16 + 18–21 (16 + 20).

Color in alcohol.—Head and body brown, becoming yellowish-white on ventral surface; tiny dark brown or black spots forming irregular blotches on dorsum and usually forming 5–7 broad, irregular, dorsoventrally oriented bands on sides of body, often extending below lateral line region; dark spots generally less dense, and often completely absent, on ventral surface. First and second dorsal fins with several distinct dark longitudinal wavy bands; first dorsal fin usually with a large dark blotch near the posterior margin; anal fin dusky, usually darker near base; caudal fin yellowish and translucent, with distinct dark-brown transverse bands; pectoral fin pale yellow with irregularly placed small dark-brown spots. Branchiostegal region, pelvic fins, and anal fin black in spawning females.

Distribution.—Specimens examined are from southwestern Hokkaido, western Honshu and the northern tip of Honshu, southern Sakhalin Island, and the islands of Zelionyi, Polonskogo, and Tanfilyeva in the Kuril Archipelago (Fig. 2.11). This species has been reported from Hokkaido to Kyushu in Japan (Akihito et al., 1984). *Gymnogobius castaneus* usually inhabits freshwater lakes and streams.

Remarks.—This species has been widely misunderstood for at least the past 50 years. Takagi (1966b) seems to have been the first to associate the lack of oculoscapular canals and pores with the nominal species *Gobius laevis* Steindachner, and subsequent authors have followed this alignment. However, the holotype of *Gobius laevis* clearly has oculoscapular canals and four pairs of pores, as well as a broad and depressed head and a jaw that extends well beyond the posterior margin of the eye. This specimen certainly does not represent the species that Takagi (1966b) and subsequent authors identified as “*Chaenogobius laevis*.” In fact, *Gobius laevis* Steindachner is synonymous with *Gobius urotaenia* Hilgendorf (see additional remarks under *G. urotaenia*). On the other hand, the two syntypes of *Gobius castaneus* O’Shaughnessy lack oculoscapular canals and have the anterior portion of these canals replaced by rows of sensory papillae (Fig. 2.10). Therefore, the species that has recently been known as *Chaenogobius laevis* is actually valid as *Gymnogobius castaneus*.

The type locality for this species was reported as Nagasaki, Japan (O’Shaughnessy, 1875). However, in the BMNH ledger the locality field for this specimen has “Nagasaki” crossed out and replaced by “Northern part of Japan

(Aomori)." The ledger also indicates that this specimen was "purchased of W. Higgins." One possible explanation for this change is that the specimen was purchased in a fish market in Nagasaki, and its origin was later determined to be Aomori in northern Japan.

In their study of allozyme polymorphisms, Aizawa et al. (1994) found that two populations of *Chaenogobius laevis* (= *Gymnogobius castaneus*), one from northern Honshu and one from central Honshu, did not form a monophyletic unit. This suggests the possibility that the species herein recognized as *G. castaneus* actually represents two distinct species. While specimens representing the two populations sampled by Aizawa et al. (1994) were not examined for this study, the results of Aizawa et al. (1994) clearly indicate the need for further detailed study of this species group, including extensive series of all three morphological species from throughout their respective ranges.

Comparative Remarks.—*Gymnogobius castaneus*, *G. taranetzi*, and *G. breunigii* are morphologically similar and form a distinct species group within *Gymnogobius* (hereafter referred to as the *G. castaneus* Group). They share a small mouth and their meristics are virtually identical (Tables 2.2–2.4). However, they can be distinguished on the basis of the oculoscapular morphology and, to a lesser extent, body coloration. Within this species group, *G. castaneus* has lost the oculoscapular canals and has the most prominent series of vertical bands on the body.

Gymnogobius taranetzi (Pinchuk, 1978)Japanese name *shinjikohaze*

Figs. 2.9B, 2.12

Chloea castanea: Tarantsov, 1933:85, 1934:398; Berg, 1949:1072–1073, fig. 801–803; Lindberg and Krasyukova (in part), 1975:384.

Chaenogobius taranetzi Pinchuk, 1978:10–11, fig. 3B (original description, Kedrovka River mouth, Primorski Krai, Russia), 1981:1511–1513, fig. 1B2, 2B; 1984:68; 1992:130; Reshetnikov et al., 1997:718.

Chaenogobius castaneus: Kim et al., 1987: fig. 2h.

Diagnosis.—A species of *Gymnogobius* unique in having only the posterior section of the interorbital oculoscapular canals opening through paired D and F pores.

Gymnogobius taranetzi is further characterized by having the following combination of characters: head broad, its width greater than its depth; right and left D pores distinct; a single sensory papilla in row *n*; lower jaw protruding anteriorly beyond upper; maxilla not extending beyond mid-orbit; posterolateral end of mental flap distinct; no fleshy barbel-like processes behind chin; dark pigment patches on sides forming a series of indistinct vertical bands, often extending below level of vertebral column; caudal fin translucent, pale yellow, with dark blotches forming indistinct vertical bands; 0–6 predorsal scales; 62–67 scales in longitudinal series; modal vertebral count 16 + 20; first dorsal fin usually with seven spines, anteriomost pterygiophore inserted in fourth interneural space; modal second dorsal-fin ray count I,10, anteriomost pterygiophore

usually inserted in interneural space 12; modal anal-fin ray count I,10, anal fin origin ventral or anterior to third soft ray of second dorsal fin; first dorsal fin with small dark blotches forming several oblique bands.

Description.—Body somewhat elongate, its depth approximately 5 in SL; caudal peduncle moderately deep, its depth approximately 8 in SL. Scales small, ctenoid, covering entire body from base of pectoral fin to caudal fin, on dorsum extending anterior to first dorsal fin in most specimens; head naked; scales in longitudinal series 62–67, scales in transverse series 17–21; predorsal scales 0–6. Several rows of sensory papillae in abdominal region; approximately 30 vertical rows of sensory papillae in *lm* series.

Head somewhat broad, depressed, its width greater than its depth, with broad bulge on snout; eye diameter 4.5 to 5.5 in head length; interorbital space narrow, its width less than orbital diameter; mouth small, directed slightly upward; lower jaw protruding slightly beyond upper jaw; maxilla extending to anterior margin of orbit or midorbit; small conical premaxillary and dentary teeth in four irregular rows; posterolateral end of mental flap distinct; no fleshy barbel-like processes behind chin; gill rakers short, slender, without tooth patches, 2–3 + 10–11 (2 + 10). Anterior oculoscapular canals restricted to posterior interorbital and postorbital region, opening through paired D and F pores, anterior interorbital portion of each canal replaced by a row of sensory papillae (Fig. 2.12); four suborbital rows of sensory papillae oriented longitudinally; a single sensory papilla in row *n*, directly dorsomedial to F pore.

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin VII–VIII (VII); DF highly variable, modally 4-12121000; second dorsal fin I,10–11 (I,10), anteriormost pterygiophore inserted in interneural space 11–13 (12); anal fin I,9–11 (I,10), its origin ventral or anterior to third soft ray of second dorsal; AP 2–3 (3); pectoral fin rounded, not extending to posterior margin of first dorsal fin, pectoral fin rays 19–21 (20); segmented caudal-fin rays 9 + 8, branched caudal-fin rays 7 + 6; vertebrae 15–16 + 19–21 (16 + 20).

Color in alcohol.—Head and body brown, becoming yellowish-white on ventral surface; tiny dark brown or black spots forming indistinct vermiculations on dorsum, a series of dark blotches in lateral line region, and often forming 5–7 obscure, broad, dorsoventrally oriented bands on sides of body, often extending below lateral line region; dark spots generally less dense, and often completely absent, on ventral surface. First and second dorsal fin with several distinct dark longitudinal wavy bands; first dorsal fin usually with a large dark blotch near the posterior margin; anal fin dusky, usually darker near base; caudal fin yellowish and translucent, with distinct dark-brown transverse bands; pectoral fin pale yellow with irregularly placed small dark-brown spots. Branchiostegal region, pelvic fins, and anal fin black in spawning females.

Distribution.—Specimens examined are from Shinji Lake in Japan, the southern part of the Maritime Territory (Primorski Krai) of the Russian Far East, and eastern North

Korea (Fig. 2.13). *Gymnogobius taranetzi* is a widely euryhaline species that has been collected in freshwater, brackish water, and in full marine habitats.

Remarks.—The distinguishing characteristic of this species – the configuration of the oculoscapular canals – was noted by Russian authors 45 years before the species was described. Taranetz (1933) was the first to note this canal configuration, but he identified his material as *Chloea castanea* and used the truncated oculoscapular canal pattern to define the genus *Chloea*, stating “The genus *Chloea* differs from *Gymnogobius* in the structure of the mucous canals on the upper part of the head” (p. 85). The genus remained thus defined by Russian authors for over four decades. When Pinchuk (1978) synonymized *Chloea* with *Chaenogobius*, he recognized *Chaenogobius castaneus*, with paired anterior interorbital, posterior interorbital, and postorbital pores, in agreement with Takagi (1966b). However, he also recognized that the species that Russian authors since Taranetz (1933) had been calling *C. castaneus*, with truncated oculoscapular canals and only two pairs of pores, was really a separate undescribed species. He described this species as *Chaenogobius taranetzi*, based on specimens from the southern Primorski Krai in Russia. Japanese authors (Koshikawa and Sato, 1986) later discovered this same species in Lake Shinji in Japan, but they were unable to determine its conspecificity. This investigation confirms that the species inhabiting Lake Shinji is indeed *Gymnogobius taranetzi*.

Comparative Remarks.—Within the *G. castaneus* Group, *G. taranetzi* is intermediate between the other two species. It has a more reduced oculoscapular canal pattern than *G. breunigii*, but not absent, as in *G. castaneus*. It also has dark vertical bands on the body, as in *G. castaneus*, but they are not as prominent.

***Gymnogobius breunigii* (Steindachner, 1880)**

Japanese name *biringo*

Figs. 2.9C, 2.14

Gobius breunigii Steindachner, 1880:138–140 (original description, Hakodate, Japan).

Chloea castanea: Jordan and Snyder, 1901b:79–80 (new combination); Jordan et al., 1913:351; Tanaka, 1927:700–704, pl. CLVIII, Figs. 443–444; Lindberg and Krasyukova (in part), 1975:384.

Aboma breunigi: Jordan and Snyder, 1901b:71 (new combination); Jordan et al., 1913:348.

Chloea castanaea: Jordan and Hubbs, 1925:307–308 (typographical error).

Chaenogobius annularis annularis: Tomiyama (in part), 1936:90–91 (new subspecies); Okada (in part), 1961:676–678.

Chaenogobius castanea: Matsubara, 1955:838 (new combination); Chyung, 1977:481.

Chaenogobius annularis: Fowler (in part), 1961:62–63.

Chaenogobius castaneus: Takagi, 1966b: fig. 1, 2A; Pinchuk, 1978:9–10, fig. 3A; 1981:1511, figs. 1B1, 2A–B; 1984:67, 1992:130; Akihito et al., 1984:276, fig.

173, pl. 252-E, F; Choi et al., 1990:207–208; Nikoforov et al., 1994:27;
Reshetnikov et al., 1997:717.

Gymnogobius castaneus: Pietsch et al., 2001:145 (new combination).

Diagnosis.—A species of *Gymnogobius* characterized by having the following combination of characters: head broad, its width greater than its depth; anterior oculoscapular canals extending only to postorbital region, opening through paired C, D, and F pores; right and left D pores distinct; a single sensory papilla in row n ; lower jaw protruding anteriorly beyond upper; maxilla not extending beyond mid-orbit; posterolateral end of mental flap distinct; no fleshy barbel-like processes behind chin; dark pigment patches forming reticulations on head, dorsum, and sides, extending below level of vertebral column, but usually not onto belly; caudal fin translucent, pale yellow, with dark blotches forming indistinct vertical bands; 3–8 predorsal scales; 60–71 scales in longitudinal series; modal vertebral count 16 + 20; first dorsal fin with seven spines, anteriormost pterygiophore inserted in fourth interneural space; modal second dorsal-fin ray count I,10, anteriormost pterygiophore usually inserted in interneural space 12; modal anal-fin ray count I,10, anal fin origin ventral or anterior to third soft ray of second dorsal fin; first dorsal fin with small dark blotches forming several oblique bands.

Description.—Body somewhat elongate, its depth approximately 5 in SL; caudal peduncle moderately deep, its depth approximately 8 in SL. Scales small, ctenoid,

covering entire body from base of pectoral fin to caudal fin, on dorsum extending anterior to first dorsal fin in many specimens; head, cheek, and opercle naked; scales in longitudinal series 60–71, scales in transverse series 16–19; predorsal scales 3–8. Several rows of sensory papillae in abdominal region; 29–31 vertical rows of sensory papillae in *lm* series.

Head somewhat broad, depressed, its width greater than its depth, with broad bulge on snout; eye diameter 4 to 5 in head length; interorbital space narrow, its width less than orbital diameter; mouth small, directed slightly upward; lower jaw protruding slightly beyond upper jaw; maxilla extending to anterior margin of orbit or midorbit; small conical premaxillary and dentary teeth in four irregular rows; posterolateral end of mental flap distinct; no fleshy barbel-like processes behind chin; gill rakers short, slender, without tooth patches, 2–3 + 9–11 (2 + 10). Anterior oculoscapular canals opening through paired C, D, and F pores (Fig. 2.14); four suborbital rows of sensory papillae oriented longitudinally; a single sensory papilla in row *n*, directly dorsomedial to F pore.

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin VII–VIII (VII); DF highly variable, modally 4-12121000; second dorsal fin I,9–11 (I,10), anteriormost pterygiophore inserted in interneural space 11–13 (12); anal fin I,9–11 (I,10), its origin ventral or anterior to third soft ray of second dorsal; AP 2–4 (4); pectoral fin rounded, not extending to posterior margin of first dorsal fin, pectoral fin rays 18–21 (20); segmented caudal-fin rays 9 + 7–8 (9 + 8), branched caudal-fin rays 7 + 6; vertebrae 15–16 + 19–21 (16 + 20).

Color in alcohol.—Head and body brown, becoming yellowish-white on ventral surface; tiny dark brown or black spots forming indistinct vermiculations on dorsum and on sides down to lateral line region; dorsoventrally oriented bands absent; dark spots generally less dense, and often completely absent, on ventral surface. First and second dorsal fin with several distinct dark longitudinal wavy bands; first dorsal fin usually with a large dark blotch near the posterior margin; anal fin dusky, usually darker near base; caudal fin yellowish and translucent, with distinct dark-brown transverse bands; pectoral fin pale yellow with irregularly placed small dark-brown spots. Branchiostegal region, pelvic fins, and anal fin black in spawning females.

Distribution.—Specimens examined are from southern Hokkaido, southern Sakhalin Island, and the islands of Shikotan, Iturup, and Kunashir in the Kuril Archipelago (Fig. 2.15). This species has been reported from Hokkaido to Yakushima in Japan (Akihito et al., 1984) and from the southern and eastern coasts of South Korea and Quelpart Island (Kim et al., 1987; Choi et al., 1990). *Gymnogobius breunigii* inhabits brackish water and freshwater lakes and streams.

Remarks.—This species has been incorrectly recognized as *Gymnogobius castaneus* by a number of authors, including all those treating this group in the last 30 years. However, neither of the syntypes of *Gobius castaneus* O’Shaughnessy has any oculoscapular canals or any remnants of canals, so that name cannot be applied to this

species. The nominal species *Gobius breunigii* Steindachner has been placed in *Aboma* (Jordan and Snyder, 1901b; Jordan et al., 1913), considered a junior synonym of *Chaenogobius annularis* (Tomiyama, 1936; Okada, 1961; Chyung, 1977), or completely ignored (Berg, 1949; Lindberg and Kras'yukova, 1975; Pinchuk, 1978, 1984). However, the syntypes of *G. breunigii* clearly have the small mouth characteristic of the *G. castaneus* species group, and all seven specimens have paired C, D, and F pores. Therefore, they do represent this species, and it is therefore valid as *Gymnogobius breunigii*.

Comparative Remarks.—Within the *G. castaneus* species group, *G. breunigii* has the most extensive oculoscapular canal pattern, with three pairs of pores. This species is also the only one in the group whose body coloration is dominated by dark vermiculations on the dorsal surface, and has only indistinct dark vertical bands if any at all.

***Gymnogobius cylindricus* (Tomiyama, 1936)**

Japanese name *kiseruhaze*

Figs. 2.16, 2.17

Chaenogobius cylindricus Tomiyama, 1936:92, fig. 39 (original description, Hiroshima, Japan); Matsubara, 1955:839; Pinchuk, 1978:9, 1984:65; Suzuki and Masuda, 1993:2–4, figs. 1–6.

Diagnosis.—A species of *Gymnogobius* characterized by having the following combination of characters: head somewhat broad, its width approximately equal to its depth; anterior oculoscapular canals extending only to postorbital region, opening through paired C, D, and F pores; right and left D pores adjacent to each other or fused to form single opening; a single sensory papilla in row n ; upper jaw protruding anteriorly beyond lower; maxilla extending beyond posterior margin of eye and beyond margin of gape; posterolateral end of mental flap distinct; no fleshy barbel-like processes behind chin; dark pigment patches on side forming vertical bands extending to lateral line region, but not onto belly; caudal fin translucent, pale yellow, with dark blotches forming distinct bands on upper and middle rays; predorsal scales absent; longitudinal series scale count approximately 50–60; vertebral count 15 + 18; first dorsal fin with six spines, anteriomost pterygiophore inserted in fourth interneural space; modal second dorsal-fin ray count I,13, anteriomost pterygiophore usually inserted in interneural space 11; modal anal-fin ray count I,10, anal fin origin posterior to third soft ray of second dorsal fin; first dorsal fin with small dark blotches forming several oblique bands.

Description.—Body elongate, its depth approximately 8 in SL; caudal peduncle slender, its depth approximately 13 in SL. Scales small, ctenoid, covering entire body from base of pectoral fin to caudal fin, but absent on dorsum anterior to second dorsal fin and on sides dorsal to pectoral fin base; head naked; scales in longitudinal series approximately

50–60, scales in transverse series approximately 10–12. Several rows of sensory papillae in abdominal region; *lm* series of sensory papillae obscure.

Head cylindrical, its width approximately equal to its depth, with broad low bulge on snout; eye diameter approximately 5 in head length; interorbital space narrow, its width less than orbital diameter; mouth large, directed slightly upward; upper jaw protruding slightly beyond lower jaw; maxilla extending beyond posterior margin of orbit and beyond perimeter of gape, its posterior end not attached to cheek; small conical premaxillary and dentary teeth in four irregular rows; posterolateral end of mental flap distinct; no fleshy barbel-like processes behind chin; gill rakers short, slender, without tooth patches, count unknown. Anterior oculoscapular canals opening through paired C, D, and F pores (Fig. 2.17); right and left D pores very close together, fused to create a single pore in some specimens; four suborbital rows of sensory papillae oriented longitudinally; a single sensory papilla in row *n*, posteromedial to F pore.

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin VI; DF modally 4-1220100; second dorsal fin I,11–13 (I,13), anteriormost pterygiophore inserted in interneural space 11–12 (11); anal fin I,10–11 (I,10), its origin posterior to third soft ray of second dorsal; AP 2; pectoral fin rounded, not extending to posterior margin of first dorsal fin, pectoral fin rays 16–18 (18); segmented caudal-fin rays 9 + 8, branched caudal-fin rays 7 + 6; vertebrae 15 + 18.

Color in alcohol.—Head and body brown, becoming yellowish-white on ventral surface; tiny dark brown or black spots forming distinct dorsoventrally oriented bands on sides down to lateral line region; dark spots generally less dense, and often completely absent, on ventral surface. First and second dorsal fin with translucent membranes and pigment concentrated along the spines and rays forming several distinct dark longitudinal bands; first dorsal fin with an indistinct dark blotch near posterior margin; anal fin dusky; caudal fin slightly yellowish, with translucent membrane and distinct dark-brown transverse bands on upper and middle rays; pectoral fin pale yellow with irregularly placed small dark-brown spots. In life, ventral surface of body white to bright yellow, lower opercula silvery.

Distribution.—Specimens examined are from southern Honshu in the Setonaikai Sea (Fig. 2.18). Akihito et al. (1984) reported this species from Shikoku, Tsushima, the Goto Islands, and Kyushu. However, at least some of their records, and perhaps all of them are misidentified specimens of *G. scrobiculatus*. Pinchuk (1978) and Sheiko (1983) reported this species from Peter the Great Bay, but the single specimen that Pinchuk examined (ZISP 9599) is no longer in the ZISP collection, nor is any other specimen of this species. *Gymnogobius cylindricus* inhabits shallow marine waters.

Remarks.—This species has commonly been confused with *Gymnogobius scrobiculatus*. In fact, Akihito et al. (1984) considered *G. cylindricus* and *G. scrobiculatus* to be synonymous (see below). However, as Suzuki and Masuda (1993)

pointed out, these two species can clearly be distinguished based on color pattern, anal-fin insertion, and meristics. Tomiyama's (1936:92, fig. 39) illustration accurately depicts these characteristics in *G. cylindricus* with the exception of the coloration of the caudal fin. The photographs of Suzuki and Masuda (1993, figs. 1–8) clearly illustrate the color differences between *G. cylindricus* and *G. scrobiculatus* (see Fig. 2.16).

Comparative Remarks.—*Gymnogobius cylindricus* is very similar to *G. scrobiculatus*, but can be distinguished from the latter by the lack of dark pigment patches on the lower body and lower part of the caudal fin. In addition, the anal fin origin of *G. cylindricus* is more posterior than that of *G. scrobiculatus* and the second dorsal-fin ray and anal-fin ray counts are higher.

Gymnogobius scrobiculatus (Takagi, 1957)

Japanese name *kubohaze*

Figs. 2.19, 2.20

Chaenogobius scrobiculatus Takagi, 1957:120–123, fig. 7 (original description, Muromi R., Fukuoka, Japan); Pinchuk, 1984:65; Suzuki and Masuda, 1993:4, figs. 7, 8.

Chaenogobius cylindricus Akihito et al., 1984:277–278, pl. 253-A.

Type Material.—Holotype apparently lost; not present in the BLIH or NSMT collections. Neotype hereby designated OMNH-P 11261, 29.9 mm, mouth of Asa

River, Ushirogata-kami, Nishi-Takadomari, Onoda, Yamaguchi Prefecture, Honshu, Japan.

Diagnosis.—A species of *Gymnogobius* unique in having five or six dark narrow vertical bands extending onto the belly. *Gymnogobius scrobiculatus* is further characterized by having the following combination of characters: head somewhat broad, its width approximately equal to its depth; anterior oculoscapular canals extending only to postorbital region, opening through paired C, D, and F pores; right and left D pores adjacent to each other or fused to form single opening; a single sensory papilla in row n ; upper jaw protruding anteriorly beyond lower; maxilla extending beyond posterior margin of eye and beyond margin of gape; posterolateral end of mental flap distinct; no fleshy barbel-like processes behind chin; caudal fin translucent, pale yellow, with dark blotches forming distinct bands on all rays; predorsal scales absent; longitudinal series scale count approximately 50–60; modal vertebral count 15 + 18; first dorsal fin with six spines, anteriormost pterygiophore inserted in fourth interneural space; modal second dorsal-fin ray count I,10, anteriormost pterygiophore usually inserted in interneural space 12; modal anal-fin ray count I,9, anal-fin origin anterior to third soft ray of second dorsal fin; first dorsal fin with small dark blotches forming several oblique bands.

Description.—Body elongate, its depth approximately 7.5 in SL; caudal peduncle slender, its depth approximately 12 in SL. Scales small, ctenoid, embedded, covering

entire body from base of pectoral fin to caudal fin, but absent on dorsum anterior to second dorsal fin and on sides dorsal to pectoral fin base; head naked; scales in longitudinal series approximately 50–60, scales in transverse series approximately 10–12. Several rows of sensory papillae in abdominal region; *lm* series of sensory papillae obscure.

Head cylindrical, its width approximately equal to its depth, with broad low bulge on snout; eye diameter approximately 5 in head length; interorbital space narrow, its width less than orbital diameter; mouth large, directed slightly upward; upper jaw protruding slightly beyond lower jaw; maxilla extending beyond posterior margin of orbit and beyond perimeter of gape, its posterior end not attached to cheek; small conical premaxillary and dentary teeth in four irregular rows; posterolateral end of mental flap distinct; no fleshy barbel-like processes behind chin; gill rakers short, slender, without tooth patches, 3 + 8. Anterior oculoscapular canals opening through paired C, D, and F pores (Fig. 2.20); right and left D pores very close together, fused to create a single opening in some specimens; four suborbital rows of sensory papillae oriented longitudinally; a single sensory papilla in row *n*, posteromedial to F pore.

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin VI; DF modally **4-12111000**; second dorsal fin **I,10-11** (I,10), anteriormost pterygiophore inserted in interneural space 12; anal fin I,8-**9-10** (I,9), its origin ventral or anterior to third soft ray of second dorsal; AP 2-3 (2); pectoral fin rounded, not extending to posterior margin of first dorsal fin, pectoral-fin rays 17-**18**

(18); segmented caudal-fin rays 9 + 8, branched caudal-fin rays 7 + 6; vertebrae 15 + 18.

Color in alcohol.—Head and body brown, becoming yellowish-white on ventral surface; tiny dark brown or black spots forming distinct narrow dorsoventrally oriented bands on sides down to lateral line region, extending onto belly as 5–6 distinct bands; dark spots generally less dense, and often completely absent, on ventral surface. First and second dorsal fins with translucent membranes and pigment concentrated along the spines and rays forming several distinct dark longitudinal bands; first dorsal fin with a vague dark blotch near posterior margin; anal fin dusky; caudal fin slightly yellowish, with translucent membrane and distinct dark-brown transverse bands on all rays; pectoral fin pale yellow with irregularly placed small dark-brown spots. In life, ventral surface of body white to bright yellow, especially in spawning females, and lower opercula silvery white.

Distribution.—Specimens examined are from western Shikoku and southwestern Honshu, and the type locality is on northern Kyushu (Fig. 2.21). Suzuki and Masuda (1993) reported this species from southern Honshu, Shikoku, Kyushu, and Tsushima in Japan. *Gymnogobius scrobiculatus* inhabits shallow marine and brackish waters.

Remarks.—In the original description of this species, Takagi (1957) stated that it differs from *Gymnogobius cylindricus* (Tomiyama) in that the scales are ctenoid and the

maxilla is longer. Akihito et al. (1984) believed these differences were attributable to the difference in size between the type specimens of the two species, and therefore synonymized the two, while Pinchuk (1984) continued to recognize both species. Tomiyama (1936) incorrectly believed the scales of *G. cylindricus* to be cycloid, as they are indeed finely ctenoid, but his scale counts could not be reliably verified with the specimens examined in this study. Suzuki and Masuda (1993) recognized differences in color pattern and anal-fin placement in the two species, providing excellent photos of each. Both of these species are poorly represented in collections, but clearly differences exist.

All the type material of *Chaenogobius scrobiculatus* (= *Gymnogobius scrobiculatus*) appears to be lost. Takagi (1957) described this species based on five specimens, which he transferred to the Imperial Household upon retirement (K. Takagi, pers. comm., 24 February 2000). It is the policy of the Imperial Household to transfer all holotypes to the National Science Museum, Tokyo (Y. Ikeda, Biol. Lab. Imperial Household, pers. comm., 28 February 2000). However, this specimen is not currently present in either the BLIH or NSMT collections. Therefore, there is some question whether Takagi was actually just re-describing *G. cylindricus*, since the characteristics that he used to differentiate the two species do not clearly distinguish them. However, the second-dorsal and anal-fin ray counts published in the description of *G. scrobiculatus* are below the range of *G. cylindricus*, so *G. scrobiculatus* (Takagi) is most likely not synonymous with *G. cylindricus* (Tomiyama). Due to the similarity of these two species and the taxonomic confusion surrounding their identity, a neotype is

herein chosen to represent *G. scrobiculatus*. The neotype was collected on 24 May 1998 by A. Notomo at the mouth of the Asa River, Ushirogata-kami, Nishi-Takadomari, Onoda, in Yamaguchi Prefecture, Honshu Island, Japan, along with one other specimen (OMNH-P 11262). The neotype locality is in the prefecture adjacent to Fukuoka Prefecture, where the original type specimen was collected.

Comparative Remarks.—*Gymnogobius scrobiculatus* can be distinguished from *G. cylindricus* by the presence of dark pigment patches on the lower body and lower part of the caudal fin. In addition, the anal fin origin of *G. scrobiculatus* is more anterior than that of *G. cylindricus* and the second dorsal-fin ray and anal-fin ray counts are lower.

Gymnogobius macrognathos (Bleeker, 1860)

Japanese name *edohaze*

Figs. 2.22, 2.23

Gobius macrognathos Bleeker, 1860:83–84, tab. II, fig. 1 (original description, Jeddo).

Gobiosoma macrognathos: Günther, 1861:86 (new combination).

Gymnogobius macrognathus: Gill, 1863:269 (new combination).

Gymnogobius raninus Taranetz, 1934:398 (original description, Peter the Great Bay, Russia); Berg, 1949:1075; Lindberg and Krasyukova, 1975:375.

Chaenogobius macrognathus: Tomiyama, 1936:89–90, fig. 37 (new combination);
Matsubara, 1955:838; Pinchuk, 1984:65; Akihito et al., 1984:278, fig. 180, pl.
253-B; Reshetnikov et al., 1997:717.

Chaenogobius macrognathos: Pinchuk, 1978:9; Suzuki and Masuda, 1993:4–6, figs. 10,
11.

Gymnogobius macrognathos: Pietsch et al., 2001:146 (new combination).

Diagnosis.—A species of *Gymnogobius* unique in having the anterior extent of the upper and lower jaws approximately equal and having loosely placed non-imbricate scales. *Gymnogobius macrognathos* is further characterized by having the following combination of characters: head somewhat broad, its width approximately equal to its depth; anterior oculoscapular canals extending only to postorbital region, opening through paired C, D, and F pores; right and left D pores distinct; a single sensory papilla in row n ; maxilla extending beyond posterior margin of eye and beyond margin of gape; posterolateral end of mental flap indistinct, continuous posteriorly; no fleshy barbel-like processes behind chin; dark pigment patches on side forming vertical bands extending to lateral line region, but not onto belly; caudal fin translucent, pale yellow, with dark blotches forming distinct bands on upper and middle rays; predorsal scales absent; scales on side of body loosely arranged and easily lost, approximately 45–50 in longitudinal series; modal vertebral count 16 + 19; first dorsal fin with six spines, anteriormost pterygiophore inserted in interneural space 4; modal second dorsal-fin ray count I,11, anteriormost pterygiophore usually inserted in interneural space 12; modal

anal-fin ray count I,10, anal-fin origin posterior to third soft ray of second dorsal fin; first dorsal fin with small dark blotches forming several oblique bands.

Description.—Body elongate, its depth approximately 7 in SL; caudal peduncle slender, its depth 12–13 in SL. Scales small, ctenoid, sparsely placed, not overlapping, easily lost, covering entire body from base of pectoral fin to caudal fin, but absent on dorsum anterior to second dorsal fin and on sides dorsal to pectoral fin base; head naked; scales in longitudinal series approximately 45–50, scales in transverse series approximately 10. Several rows of sensory papillae in abdominal region; *lm* series of sensory papillae obscure.

Head cylindrical, its width approximately equal to its depth, with broad low bulge on snout; eye diameter approximately 4 in head length; interorbital space narrow, its width less than orbital diameter; mouth large, directed slightly upward; upper jaw and lower jaw approximately equal in anterior extent; maxilla extending beyond posterior margin of orbit and beyond perimeter of gape, its posterior end not attached to cheek; small conical premaxillary and dentary teeth in four irregular rows; posterolateral end of mental flap indistinct, continuous posteriorly; no fleshy barbel-like processes behind chin; gill rakers short, slender, without tooth patches, 2 + 8. Anterior oculoscapular canals opening through paired C, D, and F pores (Fig. 2.23); right and left D pores well separated; four suborbital rows of sensory papillae oriented longitudinally; a single sensory papilla in row *n*, posteromedial to F pore.

Dorsal fins separated, not connected by membrane, the first somewhat higher than the second in females, equal in males; first dorsal fin V–VII (VI); DF highly variable, modally 4-12201000; second dorsal fin I,10–12 (I,11), anteriormost pterygiophore inserted in interneural space 11–13 (12); anal fin I,9–11 (I,10), its origin ventral or posterior to third soft ray of second dorsal; AP 2–3 (2); pectoral fin rounded, not extending to posterior margin of first dorsal fin, pectoral fin rays 20; segmented caudal-fin rays 9 + 8, branched caudal-fin rays 7 + 6; vertebrae 16 + 18–20 (16 + 19).

Color in alcohol.—Head and body brown, becoming yellowish-white on ventral surface; tiny dark brown or black spots forming distinct narrow dorsoventrally oriented bands on sides down to lateral line region; dark spots generally less dense, and often completely absent, on ventral surface. First and second dorsal fin with several distinct dark longitudinal bands; first dorsal fin with a vague dark blotch near posterior margin; anal fin dusky; caudal fin translucent, slightly yellow with distinct dark-brown transverse bands on upper and middle rays; pectoral fin pale yellow with irregularly placed small dark-brown spots. In life, abdominal area, prepectoral area and lower opercula white.

Distribution.—Specimens examined are from the Pacific side of central Honshu and eastern Shikoku Island in Japan, the southern Maritime Territory in Russia, and the Chinese coast along the Shandong Peninsula in the Yellow Sea (Fig. 2.24). Akihito et

al. (1984) and Suzuki and Masuda (1993) reported this species from Miyagi Prefecture on the northwestern side of Honshu south to Oita Prefecture on northwestern Kyushu.

Gymnogobius macrognathos inhabits brackish waters.

Remarks.—This species has been the source of a great deal of confusion. It was originally described as scaleless: “capite totoque corpore alepidotis et vestigiis squamarum nullis” (Bleeker, 1860:83). This description led Günther (1861) to place the species in *Gobiosoma*, and Gill (1863) to establish the genus *Gymnogobius*. Based on a communication from Van Lidth de Jeude of the University of Leiden, Jordan and Snyder (1900) began to doubt that this species was scaleless and included it in *Chaenogobius*. However, Jordan and Snyder (1901b) and several later authors (Berg, 1916; Jordan and Hubbs, 1925; Jordan and Tanaka, 1927; Mori, 1928) were clearly referring to a different species (*G. urotaenia*) in their discussions of *G. macrognathos*. Koumans (1931) examined the holotype and found that the specimen has obvious “pouches” that once held scales. Therefore, the species was not scaleless; the scales had simply fallen off. Tomiyama (1936) recognized that the *G. macrognathos* of Jordan and Snyder was not identical with *G. macrognathos* Bleeker and was the first to provide an accurate description (including scales) of the true *G. macrognathos*.

The original spelling of the specific name of this species was *macrognathos* (Bleeker, 1860). This spelling was retained by Günther (1861), but emended to *macrognathus* by Gill (1863) with no explanation. Subsequent authors have used both spellings, although *macrognathus* is more common. Although the Fourth Edition of the

ICZN (1999) allows for the maintenance of altered subsequent spellings if they are in prevailing usage (Art. 33.3.1), and it could be argued that *macrognathus* is in prevailing usage, I prefer to maintain the original spelling of *macrognathos*.

The distribution of *G. macrognathos* is poorly known. Specimens examined in this study are from three widely separated localities. Akihito et al. (1984) and Suzuki and Masuda (1993) reported this species from only the Pacific side of central Japan, yet Russian authors have collected confirmed specimens from Peter the Great Bay and the western Yellow Sea; there are no reports of this species in Korean waters. Therefore, either this species consists of several isolated relict populations or its distribution is much more extensive than currently believed. Additional collecting on the Korean Peninsula and the western side of Japan may eventually close these distribution gaps.

Comparative Remarks.—*Gymnogobius macrognathos* can be distinguished from *G. cylindricus* and *G. scrobiculatus* by the lack of an overhanging upper jaw and greater distance between posterior interorbital pores. Unlike *G. uchidai*, *G. macrognathos* has no barbel-like processes behind the chin.

Gymnogobius uchidai (Takagi, 1957)

Japanese name *chikuzenhaze*

Figs. 2.25, 2.26

Paleatogobius uchidai Takagi, 1957:118–120, fig. 6 (original description, Kanakuzu R., Fukuoka, Japan); Pinchuk, 1984:68.

Chaenogobius uchidai Akihito et al., 1984:278, pl. 253-C (new combination); Suzuki and Masuda, 1993:4, fig. 9.

Diagnosis.—A species of *Gymnogobius* unique in having a pair of distinct fleshy barbel-like processes behind chin. *Gymnogobius uchidai* is further characterized by having the following combination of characters: head somewhat broad, its width approximately equal to its depth; anterior oculoscapular canals extending only to postorbital region, opening through paired C, D, and F pores; right and left D pores distinct; a single sensory papilla in row n ; lower jaw protruding anteriorly beyond upper; maxilla extending beyond posterior margin of eye and beyond margin of gape; dark pigment patches forming vertical bands extending to lateral line region, but not onto belly; caudal fin translucent, pale yellow, with dark blotches forming distinct bands on upper and middle rays; predorsal scales absent; modal vertebral count 15 + 19; first dorsal fin with six spines, anteriormost pterygiophore inserted in interneural space 4; modal second dorsal-fin ray count I,11, anteriormost pterygiophore usually inserted in interneural space 12; modal anal-fin ray count I,10, anal-fin origin anterior to third soft ray of second dorsal fin, first dorsal fin with small dark blotches forming several oblique bands.

Description.—Body elongate, its depth approximately 6.5 in SL; caudal peduncle slender, its depth 11–12 in SL. Scales small, ctenoid, covering entire body from base of pectoral fin to caudal fin, but absent on dorsum anterior to second dorsal fin and on

sides dorsal to pectoral fin base; head naked; scales in longitudinal series approximately 45, scales in transverse series approximately 12. Several rows of sensory papillae in abdominal region; *lm* series of sensory papillae obscure.

Head cylindrical, its width approximately equal to its depth, with broad low bulge on snout; eye diameter approximately 4.5 in head length; interorbital space narrow, its width less than orbital diameter; mouth large, directed slightly upward; lower jaw protruding slightly beyond upper jaw; maxilla extending beyond posterior margin of orbit and beyond perimeter of gape, its posterior end not attached to cheek; small conical premaxillary and dentary teeth in four irregular rows; a pair of distinct fleshy barbel-like processes behind chin; gill rakers short, slender, without tooth patches, 2 + 10. Anterior oculoscapular canals opening through paired C, D, and F pores (Fig. 2.26); right and left D pores well separated; four suborbital rows of sensory papillae oriented longitudinally; a single sensory papilla in row *n*, posteromedial to F pore.

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin V–VI (VI); DF somewhat variable, modally 4-12201000; second dorsal fin I,10–11 (I,11), anteriormost pterygiophore inserted in interneural space 12; anal fin I,9–11 (I,10), its origin ventral or anterior to third soft ray of second dorsal fin; AP 2–3 (3); pectoral fin rounded, not extending to posterior margin of first dorsal fin, pectoral fin rays 18–20 (20); segmented caudal-fin rays 9 + 8, branched caudal-fin rays 7 + 6; vertebrae 15–16 + 18–19 (15 + 19).

Color in alcohol.—Head and body brown, becoming yellowish-white on ventral surface; tiny dark brown or black spots forming distinct narrow dorsoventrally oriented bands on sides down to lateral line region; dark spots generally less dense, and often completely absent, on ventral surface. First and second dorsal fin with several distinct dark longitudinal bands; first dorsal fin with a vague dark blotch near posterior margin; anal fin dusky; caudal fin translucent, slightly yellow with distinct dark-brown transverse bands; pectoral fin pale yellow with irregularly placed small dark-brown spots. In life, abdominal area, prepectoral area, and lower opercula silvery white. Posterior half of body somewhat translucent.

Distribution.—Specimens examined are from southern Hokkaido, the Pacific side of central Honshu, and northern Kyushu (Fig. 2.27). This species has been reported from Hokkaido to southern Kyushu in Japan (Akihito et al., 1984; Suzuki and Masuda, 1993). *Gymnogobius uchidai* inhabits brackish and shallow marine waters.

Remarks.—Takagi (1957) established the genus *Paleatogobius* to accommodate this species, believing that its most distinctive character (a pair of distinct fleshy barbel-like processes behind the chin) warranted placement of the species in a separate genus. Subsequent authors (e. g., Akihito et al., 1984; Suzuki and Masuda, 1993) have largely disagreed. *Gymnogobius uchidai* is very similar to the *G. macrognathos-cylindricus-scrobiculatus* group, sharing with them more characters than do other species in the genus. Therefore, although a phylogeny for this genus has not been hypothesized,

establishment of a separate genus for *G. uchidai* would most likely render *Gymnogobius* paraphyletic (see Chapters III and IV), and *Paleatogobius* is therefore considered a junior synonym.

Comparative Remarks.—*Gymnogobius uchidai* is the only species in this genus with fleshy barbel-like processes behind the chin. This species is most similar to *G. macrognathos*, but can be distinguished from the latter species by the presence of imbricate scales and the anterior extent of the lower jaw, in addition to the presence of the barbel-like processes.

***Gymnogobius heptacanthus* (Hilgendorf, 1879)**

Japanese name *nikuhaze*

Korean name *sal-mang-dug*

Fig. 2.28

Gobius heptacanthus Hilgendorf, 1879:110–111 (original description, “Jedo”).

Aboma heptacantha: Jordan and Snyder, 1901b:70–71 (new combination); Jordan et al., 1913:348.

Chloea sarchynnis Jordan and Snyder, 1901b:82–83, fig. 15 (original description, Wakanoura, Honshu, Japan); Jordan and Metz, 1913:56, fig. 53; Jordan et al., 1913:352; Mori, 1928:8; Mori and Uchida, 1934:30; Wang and Wang, 1935:186–187, fig. 16; Koumans, 1940:142.

Gymnogobius sarchynnis: Taranetz, 1934:397–399 (new combination).

Chaenogobius heptacanthus heptacanthus: Tomiyama, 1936:91–92 (new subspecies).

Chloea nigripinnis Wang and Wang, 1935:187–189, fig. 17 (original description, Chefoo, China).

Chaenogobius heptacanthus: Mori, 1952:143; Chyung, 1954:380–381, 1977:481, pl. 101.5; Matsubara, 1955:839; Fowler, 1961:64–66; Pinchuk, 1978:9, 1984:67; Akihito et al., 1984:276, fig. 175, pl. 252-K, L; Kim et al., 1987:538, fig. 2i.

Chaenogobius nigripinnis: Fowler, 1961:68–69, fig. 42 (new combination); Pinchuk, 1984:66.

Gymnogobius nigripinnis: Lindberg and Krasyukova, 1975:375–378 (new combination).

Gymnogobius heptacanthus: Lindberg and Krasyukova, 1975:382–383 (new combination).

Diagnosis.—A species of *Gymnogobius* unique in having only three longitudinal rows of sensory papillae below the eye. *Gymnogobius heptacanthus* is further characterized by having the following combination of characters: head narrow and laterally compressed, its depth greater than its width; anterior oculoscapular canals extending beyond postorbital region, opening through paired C, D, F, and G pores; right and left D pores distinct; a single sensory papilla in row *n*; lower jaw protruding anteriorly beyond upper; maxilla extending to posterior margin of eye and beyond margin of gape; posterolateral end of mental flap indistinct; no fleshy barbel-like processes behind chin; dark pigment patches concentrated on dorsum and around lateral line area, not

extending onto lower part of body; caudal fin dusky, with dark blotches forming indistinct bands; 1–3 predorsal scales; 67–75 scales in longitudinal series; modal vertebral count $17 + 21$; first dorsal fin with seven spines, anteriormost pterygiophore inserted in interneural space 4; modal second dorsal-fin ray count I,12, anteriormost pterygiophore usually inserted in interneural space 13; modal anal-fin ray count I,12, anal-fin origin anterior to third soft ray of second dorsal fin; first dorsal fin with small dark blotches forming several oblique bands, mature females with dark blotch near posterior margin of first dorsal fin.

Description.—Body elongate, its depth 7–8 in SL; caudal peduncle slender, its depth 11.5–12.5 in SL. Scales small, ctenoid, covering entire body from base of pectoral fin to caudal fin, on dorsum extending anterior to first dorsal fin in most specimens; head naked; scales in longitudinal series 67–75, scales in transverse series 17–19; predorsal scales 1–3. Several rows of sensory papillae in abdominal region; 32–34 vertical rows of sensory papillae in *lm* series.

Head narrow, somewhat laterally compressed, its depth greater than its width, with broad bulge on snout; eye diameter approximately 4 in head length; interorbital space narrow, its width less than orbital diameter; mouth large, directed slightly upward; lower jaw protruding slightly beyond upper jaw; maxilla extending beyond posterior margin of orbit and beyond perimeter of gape, its posterior end not attached to cheek; small conical premaxillary and dentary teeth in four irregular rows; lateral margins of mental flap continuous posteriorly, its lateral margins not produced into

fleshy barbel-like processes; gill rakers somewhat elongate, slender, without tooth patches, 6 + 18. Anterior oculoscapular canals opening through paired C, D, F, and G pores (Fig. 2.28); right and left D pores well separated; three suborbital rows of sensory papillae oriented longitudinally; a single sensory papilla in row *n*, directly dorsomedial to F pore.

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin VII; DF somewhat variable, modally 4-122110000; second dorsal fin I,10–12 (I,12), anteriormost pterygiophore inserted in interneural space 12–13 (13); anal fin I,11–13 (I,12), its origin ventral or anterior to third soft ray of second dorsal fin; AP 3–4 (3); pectoral fin rounded, not extending to posterior margin of first dorsal fin, pectoral fin rays 19–21 (19); segmented caudal-fin rays 9 + 8, branched caudal-fin rays 7 + 6; vertebrae 15–17 + 20–22 (17 + 21).

Color in alcohol.—Head and body light brown, becoming yellowish-white on ventral surface; tiny dark brown spots covering dorsal surface of head and forming a dark blotch anterior to eye; a series of dark patches on dorsal surface of body and in lateral line region, lateral dark patches often fused to form broad longitudinal stripe, becoming darker on posterior half of body and forming a triangular blotch at base of caudal fin; ventral surface without dark pigment. First and second dorsal fin with several distinct dark longitudinal bands; first dorsal fin in females with prominent dark blotch near posterior margin; anal fin dusky; caudal fin yellowish and translucent, with distinct

dark-brown transverse bands on all rays; pectoral fin pale yellow with irregularly placed small dark-brown spots.

Distribution.—Specimens examined are from the Pacific side of central Honshu, the waters surrounding the Tsugaru Strait, and western Hokkaido in Japan, as well as the southern Maritime Territory (presumably Peter the Great Bay) in the Russian Far East and in the Yellow Sea at Chefoo on the Chinese coast (Fig. 2.29). This species has been reported from Miyagi Prefecture on Honshu south to Kyushu in Japan (Akihito et al., 1984). It has also been reported from Wonsan, North Korea (Mori, 1928), and throughout South Korean coastal waters (Chyung, 1954, 1977; Kim et al., 1987).

Gymnogobius heptacanthus inhabits shallow marine waters.

Remarks.—The nominal species *Chloea nigripinnis* was described from eight specimens collected at Chefoo in the Yellow Sea. These specimens were deposited in the Museum of the Biological Laboratory of the Science Society of China, an institution which has not existed in China for some time, and the whereabouts of these and other specimens of this collection are unknown (He Shunping, pers. comm., 2 November 1998). In the original description of this species (Wang and Wang, 1935:189), the authors stated that “This new species is very closely related to *C. mororana* [= *Gymnogobius mororanus*] and *C. sarchynnis* [= *Gymnogobius heptacanthus*]; but it differs from the latter, by having [a] large mouth, and much dark[er] fins.” As we now know, the females of many if not all the species of this genus (including *G.*

heptacanthus) show dark coloration of the branchiostegal area and fins. That the authors were examining female specimens is evident by the statement (p. 188) "Seven cotypes from the same locality, and of about equal size, some ones with numerous eggs, that indicate the fishes are quite in maturity." The mouth of *G. mororanus* is not significantly larger than that of *G. heptacanthus*, which has the maxilla extending to or well beyond the posterior margin of the eye. In addition, all meristic values (with the exception of scale counts) fall within the observed range for *G. heptacanthus*, and *G. heptacanthus* has been collected at the same locality. Therefore, even without the type series, it can be reasonably concluded that *Chloea nigripinnis* is a synonym of *G. heptacanthus*.

Comparative Remarks.—*Gymnogobius heptacanthus* is very similar to *G. mororanus*. Both species have laterally compressed heads and elevated vertebral counts. However, *G. heptacanthus* is the only species in this genus with three longitudinal rows of sensory papillae below the eye. It can also be distinguished from *G. mororanus* by having fewer scales in longitudinal series, a dark blotch on the first dorsal fin in females, a vertebral count of 17 + 21, and a larger eye (4 in HL vs. 4.5-5.5 in HL).

***Gymnogobius mororanus* (Jordan and Snyder, 1901)**

Japanese name *hebihaze*

Korean name *eol-nug-mang-dug*

Fig. 2.30

Chloea mororana Jordan and Snyder, 1901:80–82, fig. 14 (original description, Mororan, Hokkaido, Japan); Jordan et al., 1913:351; Koumans, 1940:142.

Chloea bungei Schmidt, 1931:119–120, fig. 5 (original description, Port Shestakoff, North Korea).

Chloea bungeri: Mori and Uchida, 1934:30 (typographical error).

Gymnogobius mororanus: Taranetz, 1934:398 (new combination); Lindberg and Krasyukova, 1975:381–382; Pietsch et al., 2001:146.

Chaenogobius heptacanthus murorana: Tomiyama, 1936:92 (new subspecies).

Chaenogobius mororana: Mori, 1952:143 (new combination); Chyung, 1954:381–382, 1977:482, pl. 102.1; Fowler, 1961:69–70.

Chaenogobius murorana: Matsubara, 1955:839.

Gymnogobius bungei: Lindberg and Krasyukova, 1975:379–381 (new combination).

Chaenogobius mororanus: Pinchuk, 1978:9, 1984:67; Akihito et al., 1984:276, fig. 176, pl. 252-M; Kim et al., 1987:538, fig. 2j.

Chaenogobius bungei: Pinchuk, 1984:67 (new combination).

Diagnosis.—A species of *Gymnogobius* unique in having greater than 80 scales in longitudinal series. *Gymnogobius mororanus* is further characterized by having the following combination of characters: head narrow and laterally compressed, its depth greater than its width; anterior oculoscapular canals extending beyond postorbital region, opening through paired C, D, F, and G pores; right and left D pores distinct; a single sensory papilla in row n; lower jaw protruding anteriorly beyond upper; maxilla

extending beyond posterior margin of eye and beyond margin of gape; posterolateral end of mental flap indistinct; no fleshy barbel-like processes behind chin; dark pigment patches forming vermiculations on dorsum and vertical bands extending to lateral line area, but not extending onto lower part of body; caudal fin dusky, with dark blotches forming indistinct bands; 0–8 predorsal scales; 89–101 scales in longitudinal series; modal vertebral count 16 + 22; first dorsal fin usually with seven spines, anteriormost pterygiophore inserted in interneural space 4; modal second dorsal-fin ray count I,12, anteriormost pterygiophore usually inserted in interneural space 13; modal anal-fin ray count I,12, anal-fin origin anterior to third soft ray of second dorsal fin; first dorsal fin with small dark blotches forming several oblique bands.

Description.—Body elongate, its depth 6.5–7.5 in SL; caudal peduncle slender, its depth 11.5–14 in SL. Scales minute, very weakly ctenoid, covering entire body from base of pectoral fin to caudal fin, on dorsum extending anterior to first dorsal fin in most specimens; head naked; scales in longitudinal series 89–101, scales in transverse series 25; predorsal scales 0–8. Several rows of sensory papillae in abdominal region; 32–34 vertical rows of sensory papillae in *Im* series.

Head narrow, laterally compressed, its depth greater than its width, with broad bulge on snout; eye diameter 4.5–5.5 in head length; interorbital space narrow, its width less than orbital diameter; mouth large, directed slightly upward; lower jaw protruding slightly beyond upper jaw; maxilla extending beyond posterior margin of orbit and beyond perimeter of gape, its posterior end not attached to cheek; small conical

premaxillary and dentary teeth in four irregular rows; posterolateral end of mental flap indistinct; no fleshy barbel-like processes behind chin; gill rakers somewhat elongate, slender, without tooth patches, 4–7 + 16–17 (6 + 17). Anterior oculoscapular canals opening through paired C, D, F, and G pores (Fig. 2.30); right and left D pores well separated; four suborbital rows of sensory papillae oriented longitudinally; a single sensory papilla in row n , directly dorsomedial to F pore.

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin VII–VIII (VII); DF highly variable, modally 4-122110000; second dorsal fin I,10–14 (I,12), anteriormost pterygiophore inserted in interneural space 1214 (13); anal fin I,11–13 (I,12), its origin ventral or anterior to third soft ray of second dorsal fin; AP 3–4 (3); pectoral fin rounded, not extending to posterior margin of first dorsal fin, pectoral fin rays 21–23 (22); segmented caudal-fin rays 9 + 8, branched caudal-fin rays 7 + 6; vertebrae 16–17 + 21–23 (16 + 22).

Color in alcohol.—Head and body light brown, becoming yellowish-white on ventral surface; tiny dark-brown spots covering dorsal surface of head and forming a dark blotch anterior to eye; a series of dark vermiculations on dorsal surface of body, extending onto lateral line region as a series of broad, irregular dark vertical bars, lateral bars becoming less distinct on posterior half of body; ventral surface without dark pigment. First and second dorsal fins with several distinct dark longitudinal bands; anal fin dusky; caudal fin yellowish and translucent, with distinct dark-brown transverse

bands on all rays; pectoral fin pale yellow with irregularly placed small dark-brown spots.

Distribution.—Specimens examined are from both sides of central Honshu and from southwestern and eastern Hokkaido in Japan, as well as Shikotan in the Kuril Archipelago and Port Shestakoff (Seikoshin) on the North Korean coast (Fig. 2.31). This species has been reported from Hokkaido to Chiba Prefecture in Japan (Akihito et al., 1984) and throughout the South Korean coast (Chyung, 1954, 1977; Kim et al., 1987). *Gymnogobius mororanus* inhabits shallow marine and brackish waters.

Remarks.—The nominal species *Chloea bungei* Schmidt was described as having “Three rows of pores below eye” (Schmidt, 1931:119), which would indicate that it may be synonymous with *Gymnogobius heptacanthus*. However, all three syntypes actually have four rows of sensory papillae below the eye, as well as > 80 lateral scales in longitudinal series and small eye size in common with *G. mororanus*. Therefore, *Chloea bungei* is considered a junior synonym of *Gymnogobius mororanus*.

Comparative Remarks.—*Gymnogobius mororanus* is very similar to *G. heptacanthus*, but can be distinguished from the latter species by the presence of four longitudinal rows of sensory papillae below the eye, greater number of scales in longitudinal series, a vertebral count of 16 + 22, and smaller eye size. There is no dark blotch on the posterior margin of the first dorsal fin in the female.

Gymnogobius isaza (Tanaka, 1916)

Japanese name *isaza*

Figs. 2.32A, 2.33

Chaenogobius macrognathos: Jordan and Snyder, 1900:372.

Chaeuogobius isaza Tanaka, 1916:102–103 (original description, genus name is

typographical error; Lake Biwa, Honshu, Japan).

Chaenogobius annularis urotaenia: Tomiyama (in part), 1936:91 (new subspecies).

Chaenogobius isaza: Takagi, 1952:14–22; Matsubara, 1955:838; Okada, 1955:358, fig. 325, 1961:680–682, fig. 117; Pinchuk, 1984:66; Akihito et al., 1984:277, fig. 179, pl. 252-Q.

Diagnosis.—A species of *Gymnogobius* unique in having the sensory papillae of the cheek oriented in both longitudinal and transverse rows. *Gymnogobius isaza* is further characterized by having the following combination of characters: head broad and depressed, its width greater than its depth; anterior oculoscapular canals extending beyond postorbital region, opening through paired C, D, F, and G pores; right and left D pores distinct; several sensory papillae in row *n*; lower jaw protruding anteriorly beyond upper; maxilla extending to posterior margin of eye; posterolateral end of mental flap indistinct; no fleshy barbel-like processes behind chin; dark pigment patches forming broad bands on sides of body; caudal fin dusky, with dark blotches forming distinct bands; predorsal scales absent; 57–65 scales in longitudinal series; modal vertebral

count 15 + 18; first dorsal fin usually with six spines, anteriomost pterygiophore inserted in interneural space 4; modal second dorsal-fin ray count I,10, anteriomost pterygiophore usually inserted in interneural space 11; modal anal-fin ray count I,10, anal fin origin anterior to third soft ray of second dorsal fin; first dorsal fin predominantly dark with no bands or indistinct broad bands, and a dark blotch on posterior margin.

Description.—Body elongate, its depth approximately 7 in SL; caudal peduncle slender, its depth approximately 12 in SL. Scales small, weakly ctenoid anteriorly, becoming visibly ctenoid posteriorly, covering entire body from base of pectoral fin to caudal fin, but absent on dorsum anterior to space between dorsal fins and on sides dorsal to pectoral fin base; head naked; scales in longitudinal series 57–65, scales in transverse series 13–18. Several rows of sensory papillae in abdominal region; sensory papillae in *lm* series obscure.

Head broad and depressed, its width greater than its depth, with broad bulge on snout; eye diameter approximately 4 in head length; interorbital space narrow, its width less than orbital diameter; mouth large, directed slightly upward; lower jaw protruding slightly beyond upper jaw; maxilla extending to or beyond posterior margin of orbit; small conical premaxillary and dentary teeth in four irregular rows; posterolateral end of mental flap indistinct; no fleshy barbel-like processes behind chin; gill rakers short, slender, without tooth patches, 1–4 + 11–13 (3 + 12). Anterior oculoscapular canals opening through paired C, D, F, and G pores (Fig. 2.33); right and left D pores well

separated; four suborbital rows of sensory papillae oriented longitudinally and approximately six transverse rows of sensory papillae on cheek; several sensory papillae in row n , directly dorsomedial to F pore.

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin V–VII (VI); DF highly variable, modally 4-1211100; second dorsal fin I,10–12 (I,10), anteriormost pterygiophore inserted in interneural space 11–12 (11); anal fin I,9–11 (I,10), its origin ventral or anterior to third soft ray of second dorsal; AP 2–4 (3); pectoral fin rounded, not extending to posterior margin of first dorsal fin, pectoral fin rays 18–20 (19); segmented caudal-fin rays 9 + 8, branched caudal-fin rays 7 + 6; vertebrae 14–15 + 17–19 (15 + 18).

Color in alcohol.—Head and body brown, becoming yellowish-white on ventral surface; tiny dark brown or black spots covering most of dorsum, forming a series of broad vertical bands on sides and an indistinct dark blotch at base of caudal fin; dark spots generally less dense, and often completely absent, on ventral surface of body and on pelvic fins; first dorsal fin with dark margin, an unpigmented submarginal band, three indistinct dark transversely oriented bands, and a large dark blotch at posterior margin; second dorsal, caudal, and anal fins with small dark spots and several indistinct bands, but without spots along margins; pectoral fin heavily spotted near base, more sparsely spotted throughout. Branchiostegal region, pelvic fins, and anal fin black in spawning females.

Distribution.—This species is endemic to Lake Biwa on Honshu Island (Fig. 2.34).

Akihito et al. (1984) also reported that it has been introduced to Lake Kasumigaura and Lake Sagami.

Remarks.—At least some of the specimens that Dr. Kishinouye collected from Lake

Biwa (BMNH 1898.12.1.4–8), referred to by Jordan and Snyder (1900) as

Chaenogobius macrognathos (= *Gymnogobius macrognathos*), represent *G. isaza*.

However, they were not recognized as a distinct species at that time.

Comparative Remarks.—*Gymnogobius isaza*, *G. petschiliensis*, *G. opperiens*, and *G. urotaenia* form a very similar species group (hereafter referred to as the *G. urotaenia* species group). *Gymnogobius isaza* can be distinguished from the other members of this group by the lack of predorsal scales, the presence of transverse rows of sensory papillae on the cheek, and the comparatively narrow caudal peduncle.

Gymnogobius petschiliensis (Rendahl, 1924)

Japanese name *sumi-ukigori*

Figs. 2.32B, 2.35

Gobius petschiliensis Rendahl, 1924:20–22 (original description, Qinhuangdao, Shanghaiguan, Hebei Province, China).

Chaenogobius sp. 2 Akihito et al., 1984:277, fig. 178, pl. 252P; Pinchuk, 1992:129.

Chaenogobius transversefasciatus Wu and Zhou, 1990:144–148, fig. 1, 2 (original description, Cangnan Shuitou, Ao-jiang R., Zhejiang Province, China).

Diagnosis.—A species of *Gymnogobius* characterized by having the following combination of characters: head broad and depressed, its width greater than its depth; anterior oculoscapular canals extending beyond postorbital region, opening through paired C, D, F, and G pores; right and left D pores distinct, separated by more than one-third orbital diameter; a single sensory papilla in row n ; lower jaw protruding anteriorly beyond upper; maxilla extending to or beyond posterior margin of eye; posterolateral end of mental flap indistinct; no fleshy barbel-like processes behind chin; dark pigment patches forming a series of broad bands on side of body and a distinct wedge-shaped blotch at base of caudal fin; caudal fin dusky, with dark blotches forming broad distinct bands; 23–31 predorsal scales; 62–72 scales in longitudinal series; modal vertebral count $15 + 17$; first dorsal fin usually with six spines, anteriormost pterygiophore usually inserted in interneural space 4; modal second dorsal-fin ray count I,10, anteriormost pterygiophore usually inserted in interneural space 11; modal anal-fin ray count I,10, anal fin origin anterior to third soft ray of second dorsal fin; first dorsal fin with distinct wavy bands, and no dark blotch on posterior margin.

Description.—Body moderately elongate, its depth 4.5–6 in SL; caudal peduncle broad, its depth 7.5–9 in SL. Scales small, weakly ctenoid anteriorly, becoming clearly ctenoid posteriorly, covering entire body from base of pectoral fin to caudal fin, on

dorsum extending anterior to first dorsal fin; head naked; scales in longitudinal series 62–72, scales in transverse series 18–22; predorsal scales 23–31. Several rows of sensory papillae in abdominal region; 25–30 vertical rows of sensory papillae in *lm* series.

Head broad and depressed, its width greater than its depth, with broad bulge on snout; eye diameter 4.5–6 in head length; interorbital space broad and flat, its width equal to or greater than orbital diameter; mouth large, directed slightly upward; lower jaw protruding slightly beyond upper jaw; maxilla extending to or beyond posterior margin of orbit; small conical premaxillary and dentary teeth in four irregular rows; posterolateral end of mental flap indistinct; no fleshy barbel-like processes behind chin; gill rakers short, slender, without tooth patches, 3–4 + 8–9 (3 + 9). Anterior oculoscapular canals opening through paired C, D, F, and G pores (Fig. 2.35); right and left D pores well separated; four suborbital rows of sensory papillae oriented longitudinally; a single sensory papilla in row *n*, directly dorsomedial to F pore.

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin V–VII (VI); DF highly variable, modally 4-1220100; second dorsal fin I,9–11 (I,10), anteriormost pterygiophore inserted in interneural space 11–13 (11); anal fin I,9–11 (I,10), its origin ventral or anterior to third soft ray of second dorsal; AP 2–4 (3); pectoral fin rounded, not extending to posterior margin of first dorsal fin, pectoral fin rays 19–22 (21); segmented caudal-fin rays 9 + 8, branched caudal-fin rays 7–8 + 6–7 (7 + 6); vertebrae 14–17 + 16–18 (15 + 17).

Color in alcohol.—Head and body brown, becoming yellowish-white on ventral surface; tiny dark-brown or black spots covering most of dorsum, forming a series of broad vertical bands on sides and a distinct wedge-shaped dark blotch at base of caudal fin; dark spots generally less dense, and often completely absent, on ventral surface of body and on pelvic fins; first dorsal fin with dark margin, an unpigmented submarginal band, and three distinct dark transversely oriented wavy bands; second dorsal, caudal, and anal fins with small dark spots and several indistinct bands, but without spots along margins; pectoral fin heavily spotted near base, more sparsely spotted throughout. Branchiostegal region, pelvic fins, and anal fin black in spawning females.

Distribution.—Specimens examined are from the Yellow Sea coast in the Zhejiang and Hebei Provinces of China and from the Pacific side and southwestern tip of Honshu, Tsushima Island, and Yakushima Island in the northern Ryukyus (Fig. 2.36). Akihito et al. (1984) reported this species from Hokkaido to Amamioshima in the central Ryukyus and the Korean Peninsula, and Pinchuk (1992) reported questionable records from Sakhalin Island. *Gymnogobius petschiliensis* inhabits brackish and freshwater habitats near river mouths.

Remarks.—The nominal species *Gobius petschiliensis* has been largely ignored. Only Berg (1933) and Fowler (1961) listed it in synonymies of this genus (as a synonym of *Gymnogobius macrognathos*), and subsequent authors apparently did not consider it relevant to the taxonomy of the genus. Wu and Zhou (1990) redescribed it as

Chaenogobius transversefasciatus, but did not compare it with any of the most closely related species. They included only a brief comparison with *G. mororanus*, from which this species differs considerably, and did not mention any other nominal species in the description. Unfortunately, the holotype and most of the paratypes of *C. transversefasciatus* have been destroyed (H. L. Wu, personal communication, 2 June 2000). However, one paratype was transferred to the Biological Laboratory of the Imperial Household in Japan, and represents the only remaining member of the type series. This paratype clearly represents *G. petschiliensis*, agreeing with the syntypes of *G. petschiliensis* in oculoscapular canal and sensory papillae morphology, coloration, and meristics.

In Japan, this species was rediscovered by Nakanishi (1978a, b), who referred to it as the “brackish water type” of *Chaenogobius annularis* (by which he actually meant *G. urotaenia*). Subsequent Japanese and Russian authors (Akihito et al., 1984; Pinchuk, 1992) referred to this species as “*Chaenogobius* sp. 2,” with no reference to *G. petschiliensis*. Japanese specimens of this form (*Chaenogobius* sp. 2 of Akihito et al., 1984) and Chinese specimens (types of *G. petschiliensis* and *C. transversefasciatus*) have the same oculoscapular canal and sensory papillae morphology and coloration, including the distinctive coloration of the first dorsal fin and the presence of a single sensory papilla in row *n*. Morphometrics and most meristics for the Japanese and Chinese specimens are also identical. However, there are a few differences. The Chinese specimens tend to have a higher first dorsal-fin ray count (mode = VII vs. VI) and higher vertebral counts (mode = 16 + 18 vs. 15 + 17) than the Japanese specimens.

These discrepancies may represent ecophenotypic differences between these two populations, or it is possible that they represent different species. However, a large sample of specimens from Chinese and Japanese waters, as well as from the Korean peninsula, will be required for this question to be resolved. Because these two forms cannot be clearly diagnosed, and in the interest of preventing a continued proliferation of nominal species, the Chinese and Japanese forms are here provisionally considered synonymous.

Comparative Remarks.—*Gymnogobius petschiliensis* can be clearly distinguished from *G. opperiens* and *G. urotaenia* by the presence of distinct indented bands on the first dorsal fin, the lack of a dark blotch on the posterior margin of the first dorsal fin, the presence of a single sensory papilla in row *n*, and a vertebral count of 15 + 17.

***Gymnogobius opperiens*, new species**

Japanese name *shima-ukigori*

Figs. 2.32C, 2.37

Chaenogobius annularis (“middle reach type”): Nakanishi, 1978a, 1978b.

Chaenogobius sp. 1: Akihito et al., 1984:277, pl. 252-O; Pinchuk, 1992:129; Nikoforov et al., 1994:27.

Gymnogobius n. sp.: Pietsch et al., 2001:145.

Holotype.—NSMT-P 60922 (EX NSMT-P 14366), 67.0 mm, sex undetermined, Yurapu-gawa River, Yamagoe, Toshima, Hokkaido, Japan, N. Takeuchi, 8 August 1970.

Paratypes.—HUMZ 40721, 40723, 2 (66.3–70 mm), Zenibako Kangaiyosui, Japan, Tsumura and Kahata; HUMZ 42113, 42115, 42119, 42127, 42129, 42131, 42152, 42153, 42155, 42171, 10 (51.4–79.5 mm), Shiodomari River, Hakodate, Hokkaido, Japan; HUMZ 70173, 79.5 mm, Kunebetsu River, Hokkaido, Japan; NSMT-P 11055, 65.0 mm, Awaizumi, Komoto-gawa R., Iwate Pref., Honshu, Japan; NSMT-P 11090, 4 (58.0–64.0 mm), Kuji-gawa River, Iwate Pref., Honshu, Japan; NSMT-P 14366, 54.6 mm, collected with holotype; NSMT-P 14338, 55.6 mm, Mitsuishi-kawa River, Hourai, Mitsuishi, Hokkaido, Japan, Takeuchi; NSMT-P 14937, 3 (47.0–49.0 mm), Tuume-gawa River, Tugaru-gun, Aomori Pref., Honshu, Japan; NSMT-P 16210, 5 (43.0–52.0 mm), Sabaishi-gawa River, Kashiwazaki, Niigata Pref., Honshu, Japan; NSMT-P 18772, 3 (59.0–66.0 mm), Sanriku tyou, Kesen-gun, Iwate Pref., Honshu, Japan; NSMT-P 19291, 69.0 mm, Nishina River, Izu Peninsula, Honshu, Japan, Matsuura; UW 40100, 7 (49.2–81.5 mm), 44°00.47'N, 145°40.98'E, Kunashir, Kuril Archipelago, Pietsch et al.; UW 40113, 15 (42.2–62.7 mm) + 5 CS, 44°00.47'N, 145°40.98'E, Kunashir, Kuril Archipelago, Pietsch et al.; UW 42003, 11 (53.2–76.0 mm), 44°00.25'N, 145°40.34'E, Kunashir, Kuril Archipelago, López; UW 043542, 69 (42.0–75.0 mm), Kunashir, Kuril Archipelago, Stevenson; UW 044225, 22 (49.5–76.5 mm), Shamora River, near Vladivostok, Russia, Shedko.

Diagnosis.—A species of *Gymnogobius* unique in having a dark, y-shaped blotch at the base of the caudal fin and, in life, white spots on the pectoral fin near its insertion.

Gymnogobius opperiens is further characterized by having the following combination of characters: head broad and depressed, its width greater than its depth; anterior oculoscapular canals extending beyond postorbital region, opening through paired C, D, F, and G pores; right and left D pores distinct, separated by less than one-third orbital diameter; several sensory papillae in row *n*; lower jaw protruding anteriorly beyond upper; maxilla extending to or beyond posterior margin of eye; posterolateral end of mental flap indistinct; no fleshy barbel-like processes behind chin; dark pigment patches forming a series of broad bands on body; caudal fin dusky, with dark blotches forming distinct bands; 19–26 predorsal scales; 71–78 scales in longitudinal series; modal vertebral count 15 + 18; first dorsal fin usually with six spines, anteriomost pterygiophore usually inserted in interneural space 4; modal second dorsal-fin ray count I,11, anteriomost pterygiophore usually inserted in interneural space 11; modal anal-fin ray count I,11, anal-fin origin anterior to third soft ray of second dorsal fin; first dorsal fin with distinct oblique bands, and a dark blotch on posterior margin.

Description.—Body moderately elongate, its depth 5.5–8.5 in SL; caudal peduncle broad, its depth 8.5–10.5 in SL. Scales deeply embedded and small (will not stain with alizarin red S even in largest known specimens), very weakly ctenoid, covering entire body from base of pectoral fin to caudal fin, on dorsum extending anterior to first dorsal

fin; head naked; holotype with approximately 75 longitudinal row scales, approximately 21 transverse row scales, and approximately 21 predorsal scales. Several rows of sensory papillae in abdominal region, one row on either side of first dorsal fin and several rows on either side of dorsal midline anterior to first dorsal fin; 30–31–32 (31) vertical rows of sensory papillae in *lm* series; genital papilla broad and rounded to slightly pointed, sex could not reliably be determined in most specimens.

Morphometric character values are given in Table 2.6.

Head broad and depressed, its width greater than its depth, with broad bulge on snout; eye diameter 5–6.5 in head length; interorbital space broad and flat, its width equal to or greater than orbital diameter; mouth large, directed slightly upward; lower jaw protruding slightly beyond upper jaw; maxilla extending to or beyond posterior margin of orbit; small conical premaxillary and dentary teeth in four irregular rows; tongue emarginate with roughened dorsal surface; posterolateral end of mental flap indistinct; no fleshy barbel-like processes behind chin; gill rakers short, slender, without tooth patches, 2–3 + 7–8 (3 + 8). Anterior oculoscapular canals opening through paired C, D, F, and G pores (Fig. 2.37); right and left D pores separated by less than one-third orbital diameter; four suborbital rows of sensory papillae oriented longitudinally; two to six sensory papillae in row *n*, directly dorsomedial to F pore.

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin V–VI (VI); DF highly variable, modally 4-1220100, 4-1211100 in holotype; second dorsal fin I,10–11–12 (I,11), anteriormost pterygiophore inserted in interneural space 11–12 (11); anal fin I,9–11–12 (I,11), its origin ventral or

anterior to third soft ray of second dorsal; AP 2–3–4 (3); pectoral fin rounded, not extending to posterior margin of first dorsal fin, in life with several small white spots near the base, pectoral-fin rays 20–21–22 (21); segmented caudal-fin rays 9 + 8, branched caudal-fin rays 7–8 + 6–7 (7 + 6); vertebrae 15–16 + 18–19 (15 + 18).

Color in alcohol.—Head and body light brown, becoming yellowish-white on ventral surface; tiny dark-brown or black spots covering most of head and dorsum; forming several broad, irregular, dorsoventrally oriented bands on body and a dark y-shaped blotch near base of caudal fin; dark spots generally less dense, and often completely absent, on ventral surface of body and on pelvic fins; first dorsal fin with a dark margin, an unpigmented submarginal band, three indistinct dark transversely oriented bands, and a large dark blotch at posterior margin; second dorsal, caudal, and anal fins with small dark spots and several indistinct bands, but without spots along margins; pectoral fin heavily spotted near base, more sparsely spotted throughout. Branchiostegal region, pelvic fins, and anal fin black in spawning females.

Etymology.—The name *opperiens* is derived from the Latin verb *opperior*, meaning to wait or expect. The present participle, here used as a noun in apposition, therefore means “the one who waits,” alluding to the fact that this species, though recognized as new for more than 20 years, has long awaited formal description.

Distribution.—The specimens examined are from northeastern and central Honshu and southern Hokkaido in Japan, one locality on the island of Kunashir in the Kuril Archipelago, southern Sakhalin Island, and southern Primorski Krai in the Russian Far East (Fig. 2.38). This species has been reported from Hokkaido to the Ibaraki and Fukui Prefectures in Japan and the Korean Peninsula (Akihito et al., 1984).

Ecology.—*Gymnogobius opperiens* is generally found hidden among rocks in shallow, fast-moving, rock-bottom streams and rivers. At least one population of this species is notably tolerant of high water temperatures. This population inhabits a 1-km reach of an unnamed stream on the western side of Kunashir Island in the Kuril Archipelago. Specimens have been collected in the vicinity of a thermal spring that empties directly into this stream, and individuals have been found in water temperatures in excess of 30°C.

Remarks.—This species was first discovered by Nakanishi (1978a, b), who referred to it as the “middle reach type” of *Chaenogobius annularis*. Subsequent authors, including Akihito et al. (1984) and Pinchuk (1992) referred to it as “*Chaenogobius* sp. 1.” Presumably these authors were reluctant to describe the species without a clear definition of *Chaenogobius annularis* for comparison. The fact that this species is indeed distinct from *Gymnogobius urotaenia* and *G. petschiliensis* is further supported by the molecular evidence presented by Aizawa et al. (1994) and Suk et al. (1996).

Comparative Remarks.—*Gymnogobius opperiens* is very similar to *G. petschiliensis* and *G. urotaenia*. It can be distinguished from both species by the closely spaced posterior interorbital pores and dark y-shaped blotch at the base of the caudal fin. Additionally, *G. opperiens* can be distinguished from *G. petschiliensis* by the presence of a dark blotch on the posterior margin of the first dorsal fin and the presence of more than one sensory papilla in row n , and from *G. urotaenia* by vertebral count, dorsal-fin pterygiophore formula and, in life, the presence of white spots on the pectoral fin.

Gymnogobius urotaenia (Hilgendorf, 1879)

Japanese name *ukigori*

Figs. 2.32D, 2.39

Gobius urotaenia Hilgendorf, 1879:107–108 (original description, Japan).

Gobius laevis Steindachner, 1880:138–140 (original description, Japan).

Chaenogobius castaneus: Jordan and Snyder, 1900:372.

Aboma urotaenia: Jordan and Snyder, 1901b:71 (new combination); Jordan et al., 1913:348.

Chaenogobius macrognathos: Jordan and Snyder (in part), 1901b:76, fig. 13; Jordan et al., 1913:350–351, fig. 302; Jordan and Hubbs, 1925:307; Fowler, 1961:66–68.

Chloea laevis: Jordan and Snyder, 1901b:80 (new combination); Jordan et al., 1913:351; Wang and Wang, 1935:184–186, fig. 15.

Chloea aino Schmidt, 1904:207–208 (original description, Lake Tunaichi, Sakhalin Island, Russia); Jordan et al., 1913:351.

Chaenogobius macrognathus: Jordan and Metz, 1913:56; Jordan and Tanaka, 1927:276; Mori, 1928:8.

Gymnogobius macrognathus: Berg, 1916:424, fig. 313, 1949:1073–1075, figs. 804–807; Tarantsov, 1934:398; Schmidt, 1950:128; Nikolsky, 1956:438–439; Lindberg and Krasyukova, 1975:377–379.

Chaenogobius annularis urotaenia: Tomiyama (in part), 1936:91, fig. 38 (new subspecies); Mori, 1952:143; Chyung, 1954:381; Okada, 1961:678–680, fig. 116.

Chaenogobius urotaenia: Takagi, 1952:14–22 (new combination); Matsubara, 1955:838; Okada, 1955:359; Pinchuk, 1978:9; Akihito et al., 1984:276–277, fig. 177, pl. 252-N; Choi et al., 1990:206–207; Pinchuk, 1992:129; Nikoforov et al., 1994:27.

Chaenogobius annularis: Takagi, 1966a:17–27; Pinchuk, 1984:65–66; Kim et al., 1987:538, fig. 2g; Reshetnikov et al., 1997:717.

Gymnogobius urotaenia: Pietsch et al., 2001:146 (new combination).

Diagnosis.—A species of *Gymnogobius* unique in having the anteriormost pterygiophore of the first dorsal fin commonly inserted in interneural space 5.

Gymnogobius urotaenia is further characterized by having the following combination of characters: head broad and depressed, its width greater than its depth; anterior oculoscapular canals extending beyond postorbital region, opening through paired C, D, F, and G pores; right and left D pores distinct, separated by more than one-third orbital

diameter; several sensory papillae in row *n*; lower jaw protruding anteriorly beyond upper; maxilla extending to or beyond posterior margin of eye; posterolateral end of mental flap indistinct; no fleshy barbel-like processes behind chin; dark pigment patches forming a series of broad bands on body; caudal fin dusky, with dark blotches forming distinct bands; 20–30 predorsal scales; 66–76 scales in longitudinal series; modal vertebral count 16 + 18; first dorsal fin usually with six spines; modal second dorsal-fin ray count I,11, anteriomost pterygiophore usually inserted in interneural space 12; modal anal-fin ray count I,10, anal fin origin anterior to third soft ray of second dorsal fin; first dorsal fin predominantly dark with no bands or indistinct broad bands, and a dark blotch on posterior margin.

Description.—Body moderately elongate, its depth 4.5–6.5 in SL; caudal peduncle broad, its depth 8–11 in SL. Scales small, weakly ctenoid anteriorly, becoming clearly ctenoid posteriorly, covering entire body from base of pectoral fin to caudal fin, on dorsum extending anteriorly from first dorsal fin to posterior margin of opercle or beyond; head naked; scales in longitudinal series 66–76, scales in transverse series 19–22; predorsal scales 20–30. Several rows of sensory papillae in abdominal region; 29–32 vertical rows of sensory papillae in *lm* series.

Head broad and depressed, its width greater than its depth, with broad bulge on snout; eye diameter 4.5–6 in head length; interorbital space broad and flat, its width equal to or greater than orbital diameter; mouth large, directed slightly upward; lower jaw protruding slightly beyond upper jaw; maxilla extending to or beyond posterior

margin of orbit; small conical premaxillary and dentary teeth in four irregular rows; posterolateral end of mental flap indistinct; no fleshy barbel-like processes behind chin; gill rakers short, slender, without tooth patches, 1–3 + 6–8 (2 + 7). Anterior oculoscapular canals opening through paired C, D, F, and G pores (Fig. 2.39); right and left D pores well separated; four suborbital rows of sensory papillae oriented longitudinally; two to six sensory papillae in row n , directly dorsomedial to F pore.

Dorsal fins approximately equal in height and separated, not connected by membrane; first dorsal fin V–VII (VI); DF extremely variable, modally 5-2211000; second dorsal fin I,9–12 (I,11), anteriormost pterygiophore inserted in interneural space 11–13 (12); anal fin I,9–11 (I,10), its origin ventral or anterior to third soft ray of second dorsal; AP 2–4 (3); pectoral fin rounded, not extending to posterior margin of first dorsal fin, pectoral fin rays 19–22 (20); segmented caudal-fin rays 9–10 + 8 (9 + 8), branched caudal-fin rays 6–8 + 5–8 (7 + 6); vertebrae 15–17 + 16–19 (16 + 18).

Color in alcohol.—Head and body brown, becoming yellowish-white on ventral surface; tiny dark-brown or black spots covering most of dorsum, forming a series of broad vertical bands on sides and a distinct dark blotch at base of caudal fin; dark spots generally less dense, and often completely absent, on ventral surface of body and on pelvic fins; first dorsal fin with dark margin, an unpigmented submarginal band, a dark blotch on posterior margin, and usually indistinct dark transversely oriented bands; second dorsal, caudal, and anal fins with small dark spots and several indistinct bands, but without spots along margins; pectoral fin heavily spotted near base, more sparsely

spotted throughout. Branchiostegal region, pelvic fins, and anal fin black in spawning females.

Distribution.—Specimens examined are from northern and central Honshu and southern Hokkaido in Japan, the islands of Shikotan, Zelionyi, Kunashir, and Iturup in the Kuril Archipelago, southern Sakhalin Island, and southern Primorski Krai in the Russian Far East (Fig. 2.40). This species has been reported from Hokkaido to Kyushu (except Shikoku) in Japan (Akihito et al., 1984), Khabarovsk Province in Russia (Pinchuk, 1978), and the entire Korean Peninsula and Quelpart Island (Mori, 1928; Chyung, 1954, 1977; Kim et al., 1987; Choi et al., 1990). *Gymnogobius urotaenia* is found in freshwater, preferring the slow-moving waters of rivers and lakes.

Remarks.—This species was considered a synonym of *Gymnogobius macrognathos* or *Chaenogobius annularis* by many early authors. Tomiyama (1936) clearly distinguished it from *G. macrognathos*, but the lack of a satisfactory definition of *C. annularis* contributed to the continued confusion between these two species. Takagi (1966a) believed the type specimen of *C. annularis* was lost, and on the basis of the original description he suggested that *G. urotaenia* may be a synonym of *C. annularis*. However, this suggestion was not universally accepted and both names continued to be used for this species. Stevenson (2000) resolved this problem by clarifying the identity of *C. annularis*.

Another potential issue with this species is the status of the name *Gobius laevis* Steindachner. The species herein recognized as *Gymnogobius castaneus*, characterized by a lack of oculoscapular canals and pores, has widely been recognized by previous authors as *G. laevis*. However, the holotype of *Gobius laevis* has well-developed oculoscapular canals with four pairs of pores. It also has a large mouth, with the maxilla extending beyond the posterior margin of the eye, a broad and depressed head with widely separated posterior interorbital pores, and a conspicuous dark blotch on the posterior margin of the first dorsal fin. Therefore, *Gobius laevis* Steindachner is synonymous with *Gobius urotaenia* Hilgendorf.

The question is which name was published first. Hilgendorf presented the description of *Gobius urotaenia* on a Tuesday at the 15 July 1879 session of the *Gesellschaft Naturforschender Freunde zu Berlin*, and the description was published in the minutes of that meeting (*Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*) sometime later in 1879. Steindachner presented the description of *Gobius laevis* on Thursday of the same week at the 17 July 1879 session of the *Kaiserlichen Akademie der Wissenschaften der Wien*, and that description was published in Volume 80 of the *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften*, which appeared in early 1880. That description also appeared in an earlier separate (presumably in late 1879), but the precise publication date of the separate cannot be established (E. Mikschi, pers. comm., 20 October 2000). Lacking clear evidence that the description of *Gobius laevis* was published before that of *Gobius urotaenia*, and in

the interests of nomenclatural stability, *Gobius urotaenia* is herein considered the senior synonym.

Comparative Remarks.—*Gymnogobius urotaenia* is very similar to *G. petschiliensis* and *G. opperiens*, but is the only species in this genus with the anteriormost pterygiophore of the first dorsal fin commonly inserted in interneural space 5. It can further be distinguished from *G. petschiliensis* by the presence of more than one sensory papilla in row *n* and a dark blotch on the posterior margin of the first dorsal fin, and from *G. opperiens* by the widely spaced posterior interorbital pores and wedge-shaped dark blotch at the base of the caudal fin.

Nomen Dubium

Gobius (Chaenogobius) nigrimembranis Wu and Wang, 1931

Gobius (Chaenogobius) nigrimembranis Wu and Wang, 1931:4–6, fig. 3 (original description, Chefoo, China).

Chaenogobius nigripinnis: Wang and Wang, 1935:184 (error).

Chaenogobius nigrimembranis: Fowler, 1961:70–71 (new combination).

Gymnogobius nigrimembranis: Lindberg and Krasyukova, 1975:379, fig. 294 (new combination).

Remarks.—The two syntypes of this species were collected at Chefoo in the Yellow Sea and deposited in the Museum of the Biological Laboratory of the Science Society of

China. Their whereabouts are currently unknown (see remarks under *G. heptacanthus*). This species appears to have the second dorsal-fin and pectoral-fin ray counts of *G. mororanus*, and longitudinal series scale count and eye size between *G. mororanus* and *G. heptacanthus*. The first dorsal-fin ray count does not match that of either species, but all other characteristics seem to fit both *G. mororanus* and *G. heptacanthus*. This species is most likely a synonym of *G. mororanus*, but it is impossible to be certain without the type series.

Nominal Species Assigned to Other Genera

Parawaous megacephalus (Fowler, 1905)

Chaenogobius megacephalus Fowler, 1905:516–517, fig. 15 (original description, Borneo).

Awaous megacephalus: Koumans, 1940:134 (new combination).

Parawaous megacephalus: Watson, 1993:181–183, figs. 1–3 (new combination).

Remarks.—The genus *Parawaous* can be distinguished from *Chaenogobius* and *Gymnogobius* externally by the presence of posterior oculoscapular and preopercular canals. *Parawaous* also has the anteriormost pterygiophore of the first dorsal fin inserted in interneural space 3 and only 26 vertebrae (Watson, 1993).

***Bryaninops erythrops* (Jordan and Seale, 1906)**

Chaenogobius erythrops Jordan and Seale, 1906:404, Pl. XXXVII, fig. 3 (original description, Pago Pago, Samoa).

Bryaninops erythrops: Larson, 1985:74–77, fig. 9 (new combination).

Remarks.—The genus *Bryaninops* can be distinguished from *Chaenogobius* and *Gymnogobius* externally by the presence of canine teeth and a pocket in the pelvic frenum. *Bryaninops* also has only 26 vertebrae and a single epural (Larson, 1985).

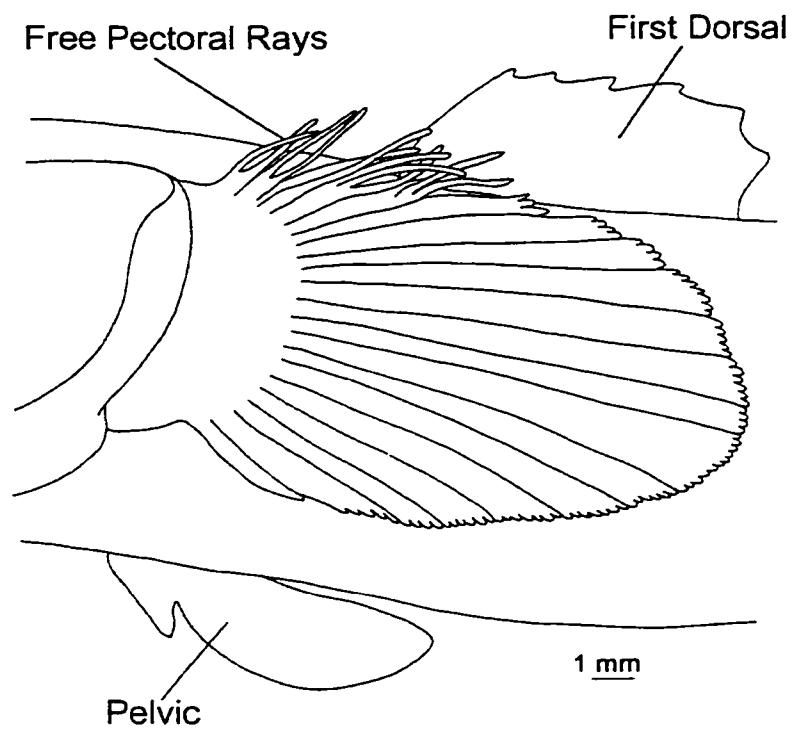


Fig. 2.1. Pectoral fin of *Chaenogobius annularis*, HUMZ 154885, 52.2 mm SL
(anterior to the left).

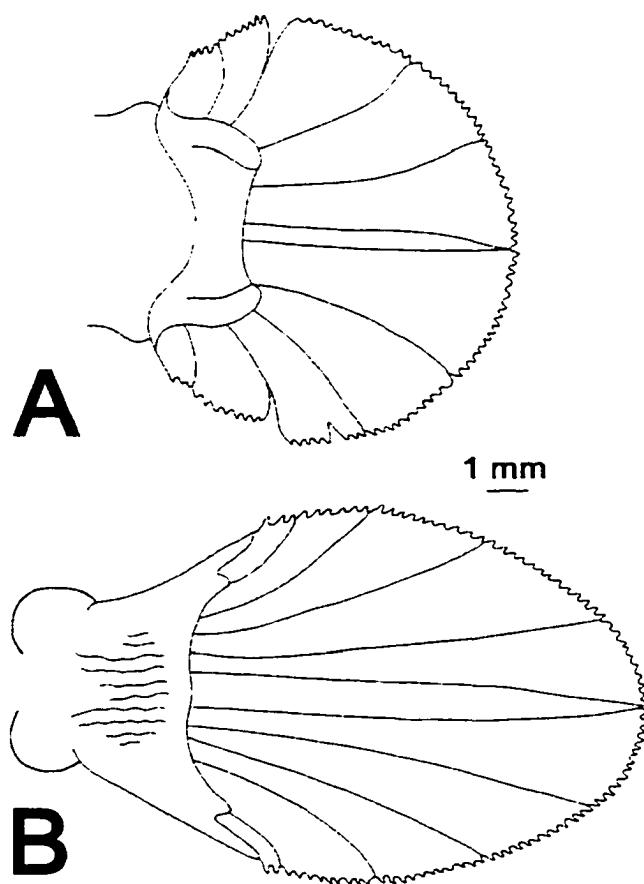


Fig. 2.2. Ventral view of pelvic fins of (A) *Chaenogobius gulosus*, HUMZ 99330, 75.9 mm SL; and (B) *Gymnogobius urotaenia*, HUMZ 40727, 91.1 mm SL.

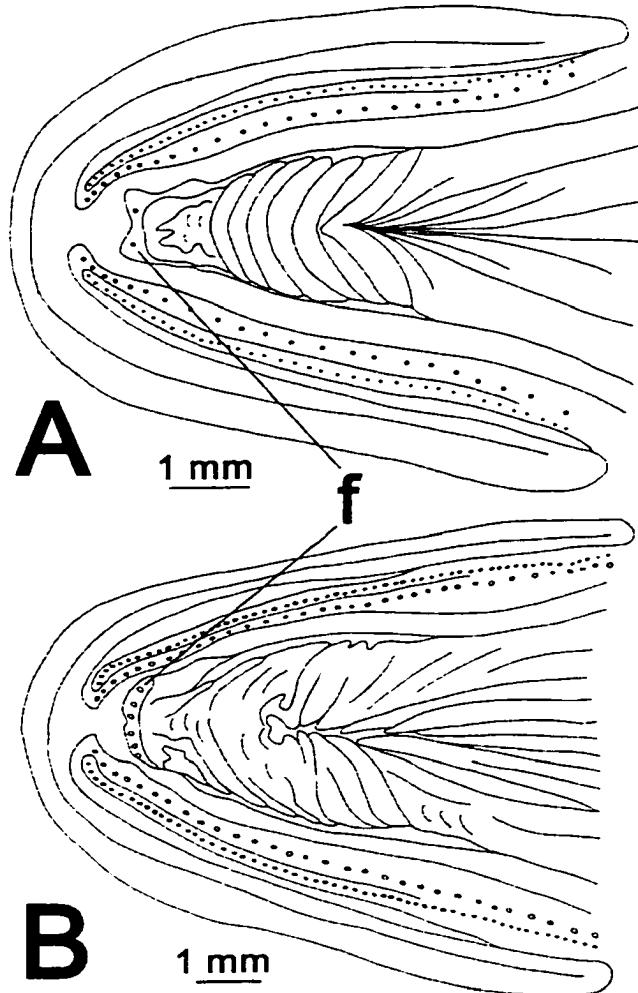


Fig. 2.3. Ventral aspect of chin of (A) *Chaenogobius annularis*, LACM 44905-2, 43.5 mm SL; and (B) *C. gulosus*, LACM 44905-2, 62.0 mm SL. *f* = mental row of sensory papillae.

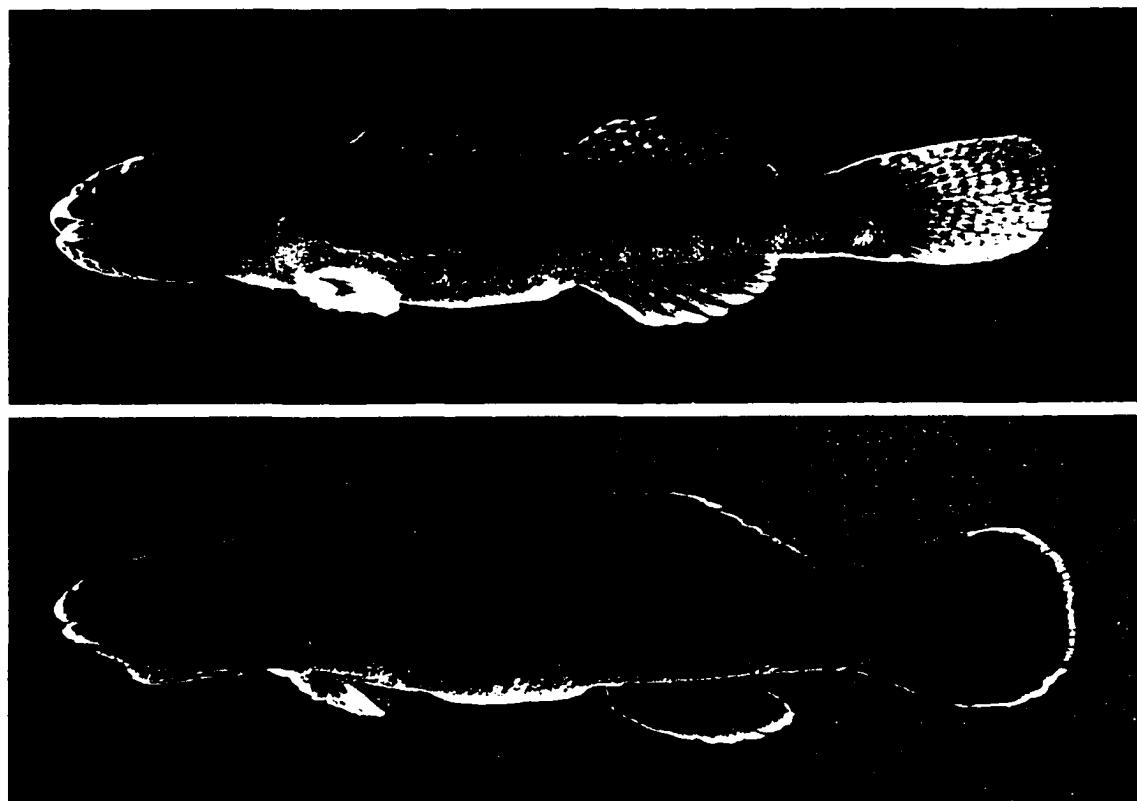


Fig. 2.4. Photographs of (A) *Chaenogobius annularis*, HUMZ 109687, 102.9 mm SL, and (B) *C. gulosus*, HUMZ 154885, 51.8 mm SL. Photographs: P. McGiffert.

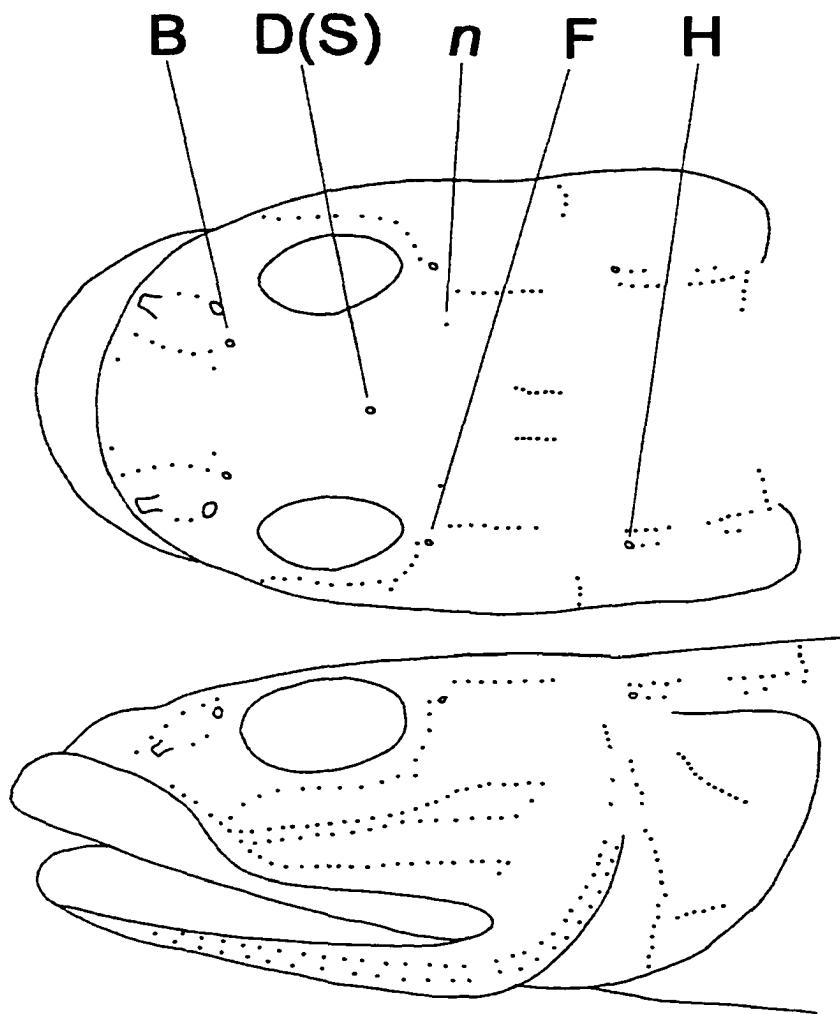


Fig. 2.5. Dorsal and lateral aspects of head of *Chaenogobius annularis*, HUMZ 154885, 52.2 mm SL, detailing oculoscapular canal pore and sensory papillae morphology; B = posterior nasal pores, D(S) = single medial posterior interorbital pore, F = postorbital pores, H = extreme otic pores, n = anterior transverse row of occipital series of sensory papillae.

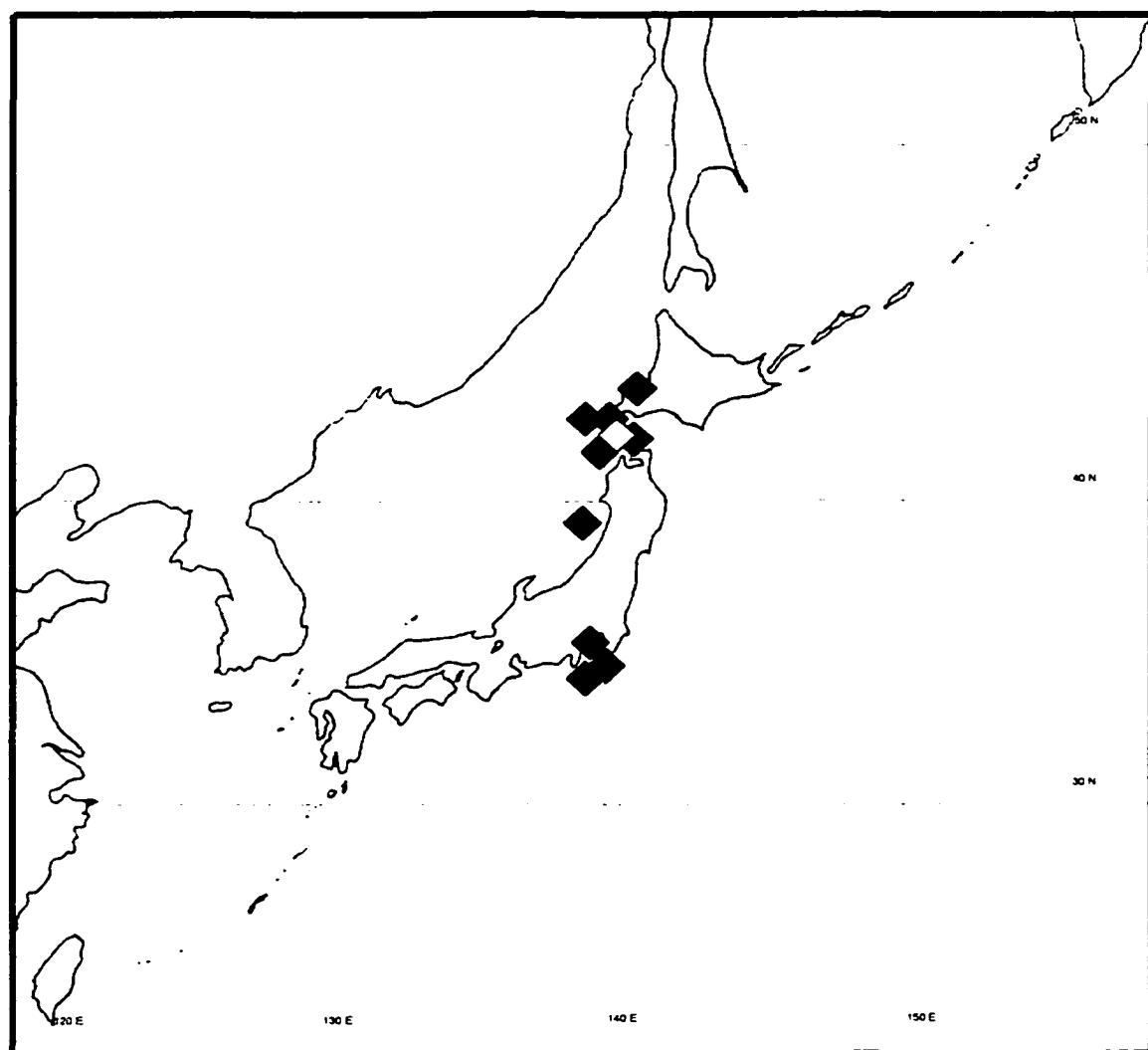


Fig. 2.6. Distribution of specimens examined for *Chaenogobius annularis*. Black diamonds indicate specimen locality; white diamond indicates type locality.

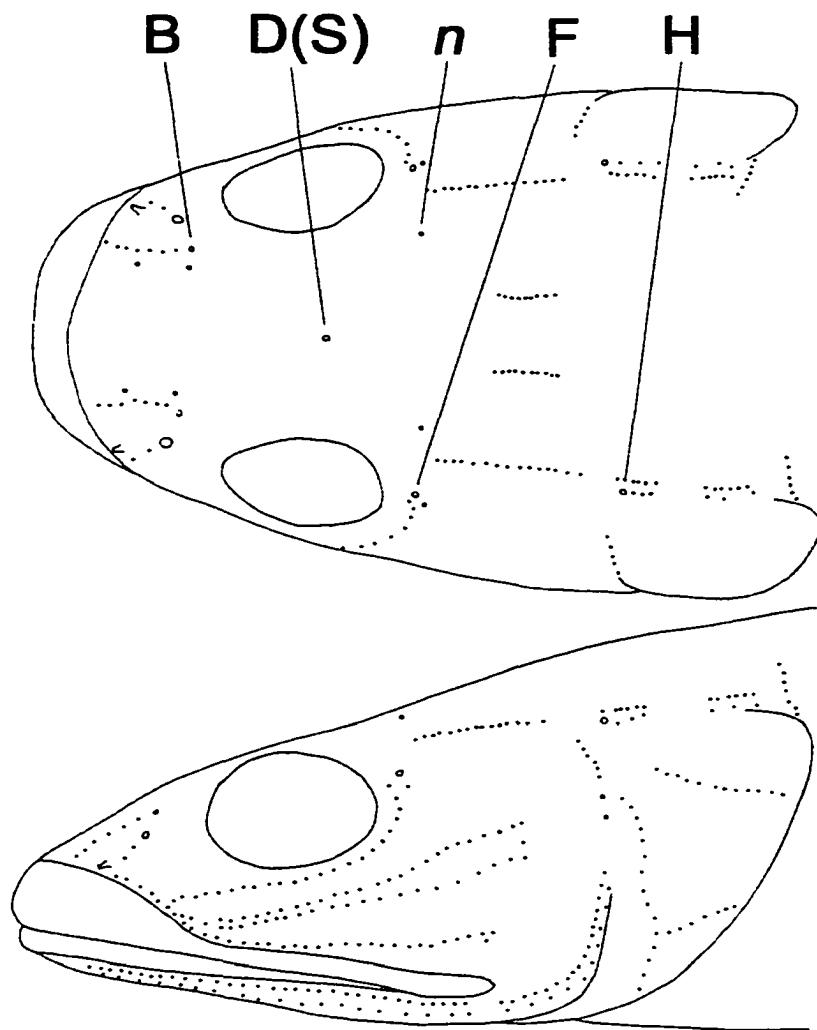


Fig. 2.7. Dorsal and lateral aspects of head of *Chaenogobius gulosus*, LACM 44905-2, 58.5 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. B = posterior nasal pores, D(S) = single medial posterior interorbital pore, F = postorbital pores, H = extreme otic pores, n = anterior transverse row of occipital series of sensory papillae.

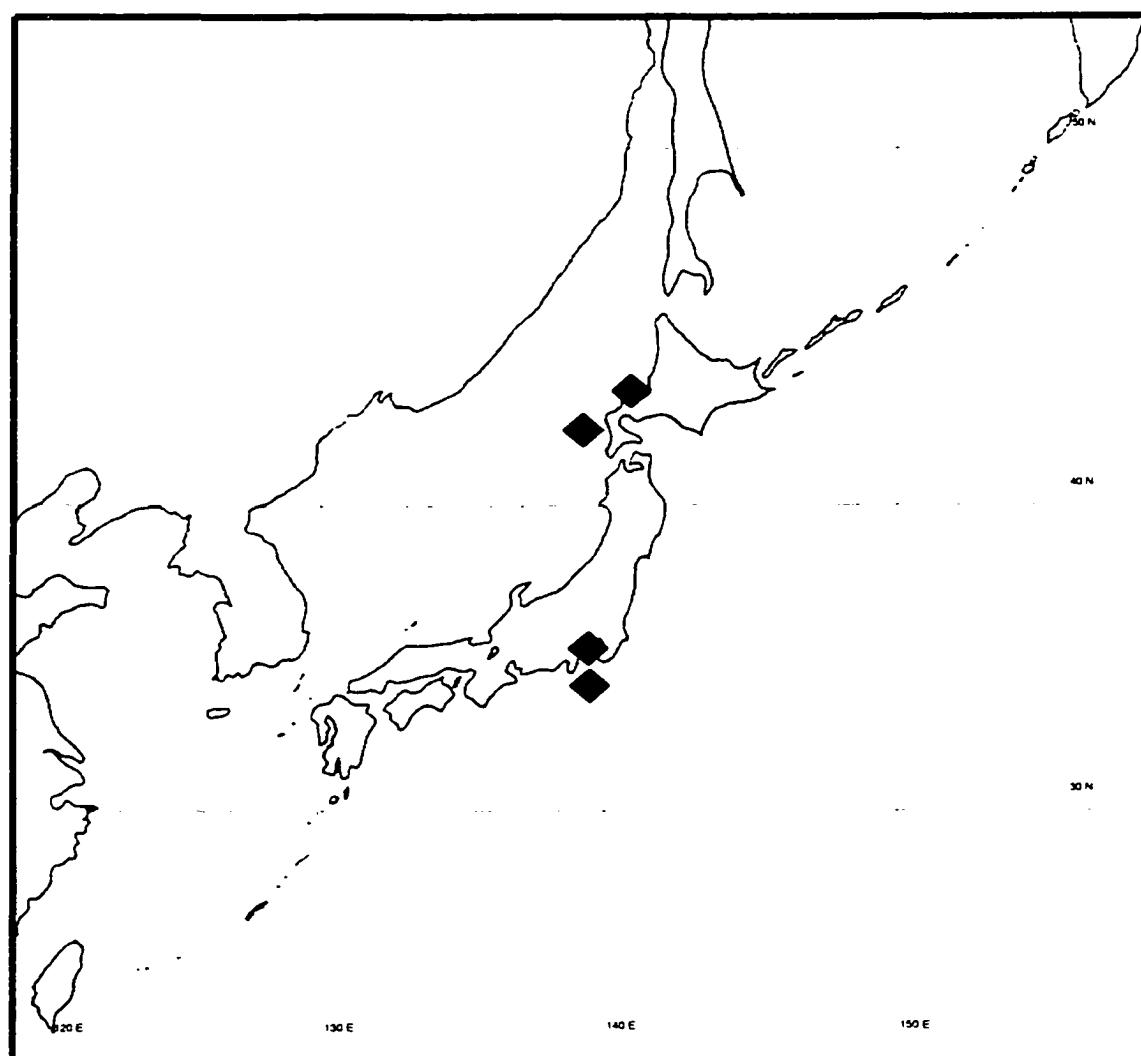


Fig. 2.8. Distribution of specimens examined for *Chaenogobius gulosus*. Black diamonds indicate specimen locality. Type locality: "Eloff, Japan."

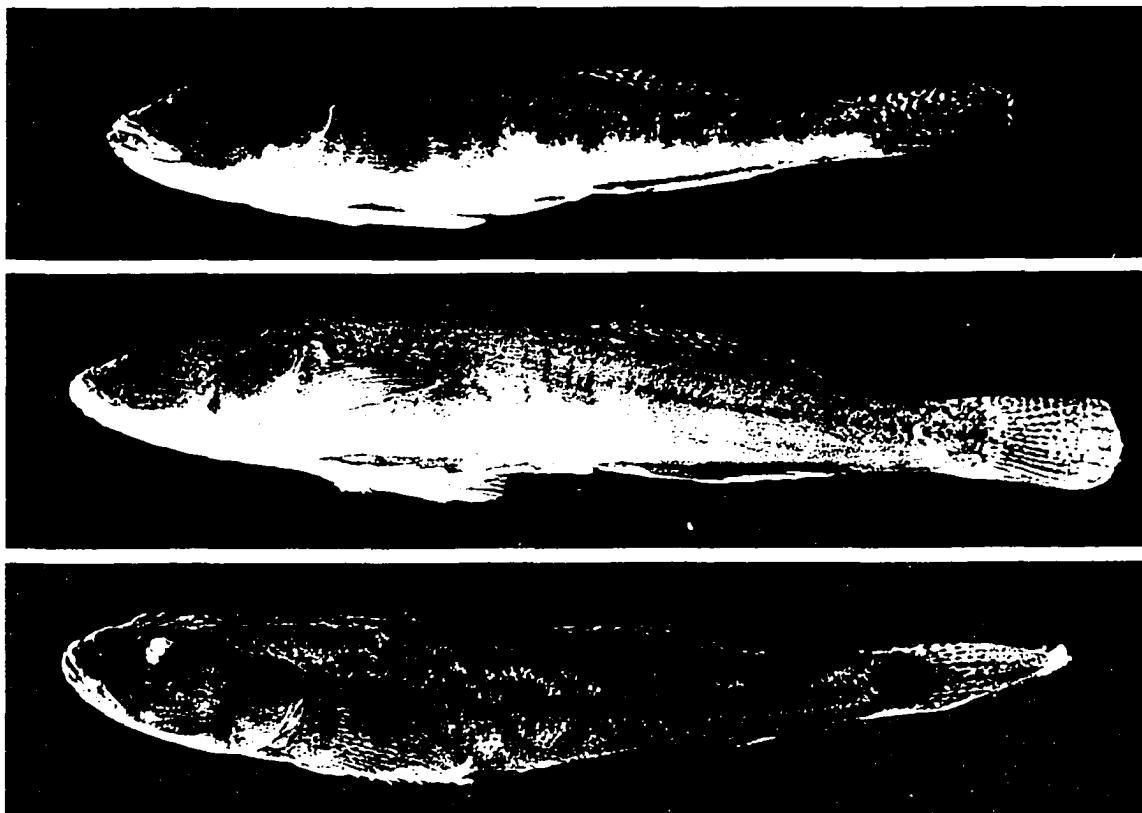


Fig. 2.9. Photographs of (A) *Gymnogobius castaneus*, UW 040521, 51.3 mm SL; (B) *G. taranetzi*, UW 044224, 61.5 mm SL; and (C) *G. breunigii*, UW 040527, 56.1 mm SL.
Photographs: P. McGiffert.

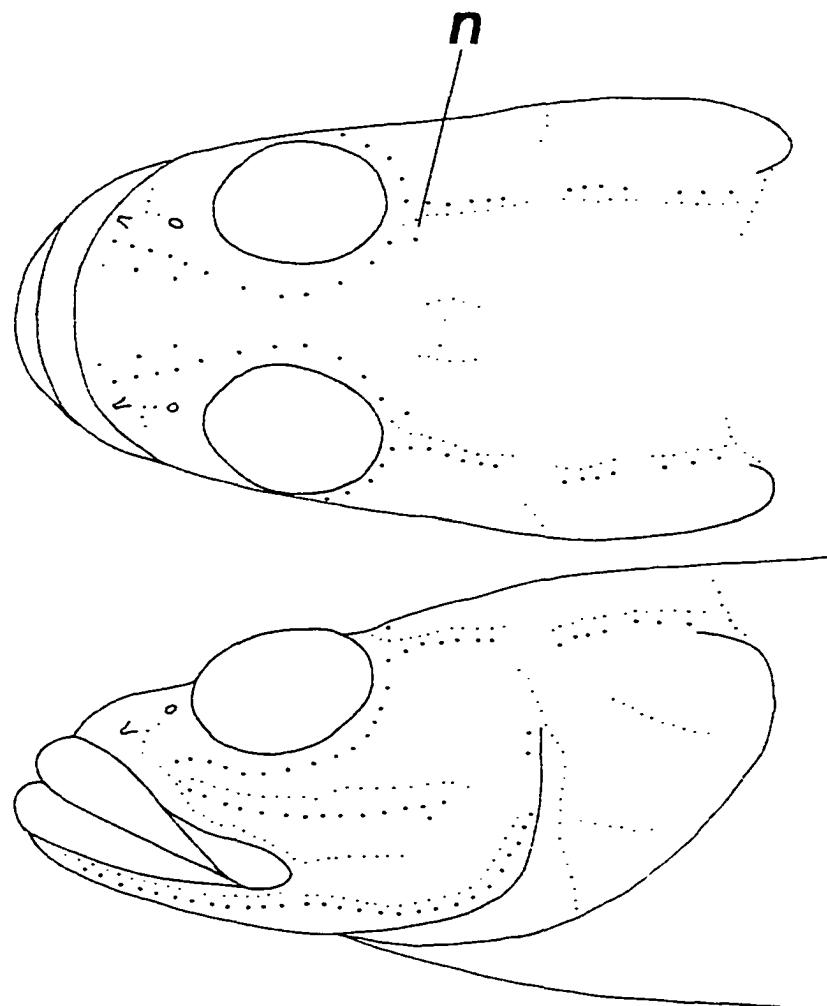


Fig. 2.10. Dorsal and lateral aspects of head of *Gymnogobius castaneus*, UW 029332, 40.4 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. *n* = anterior transverse row of occipital series of sensory papillae.

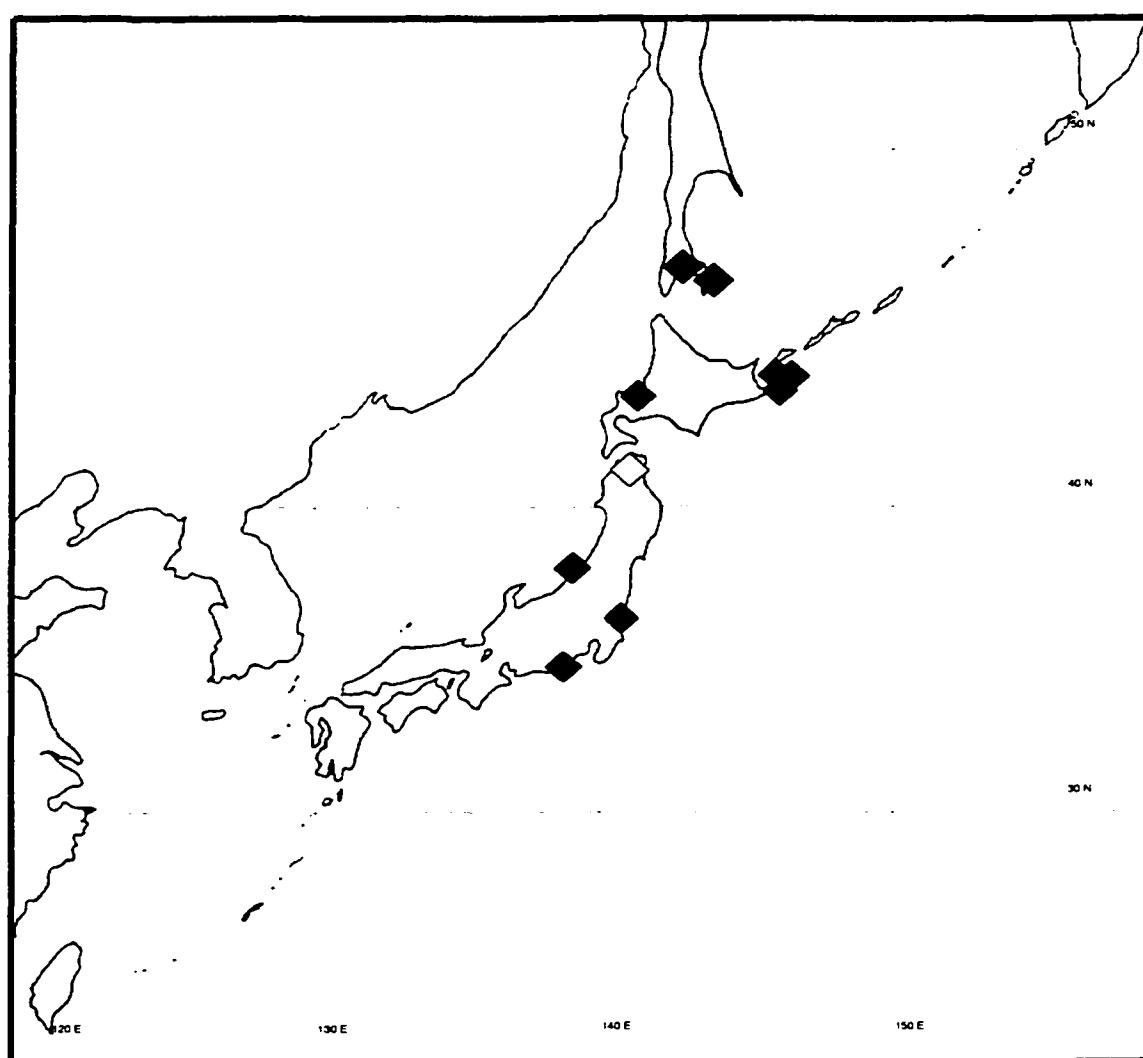


Fig. 2.11. Distribution of specimens examined for *Gymnogobius castaneus*. Black diamonds indicate specimen locality; white diamond indicates type locality.

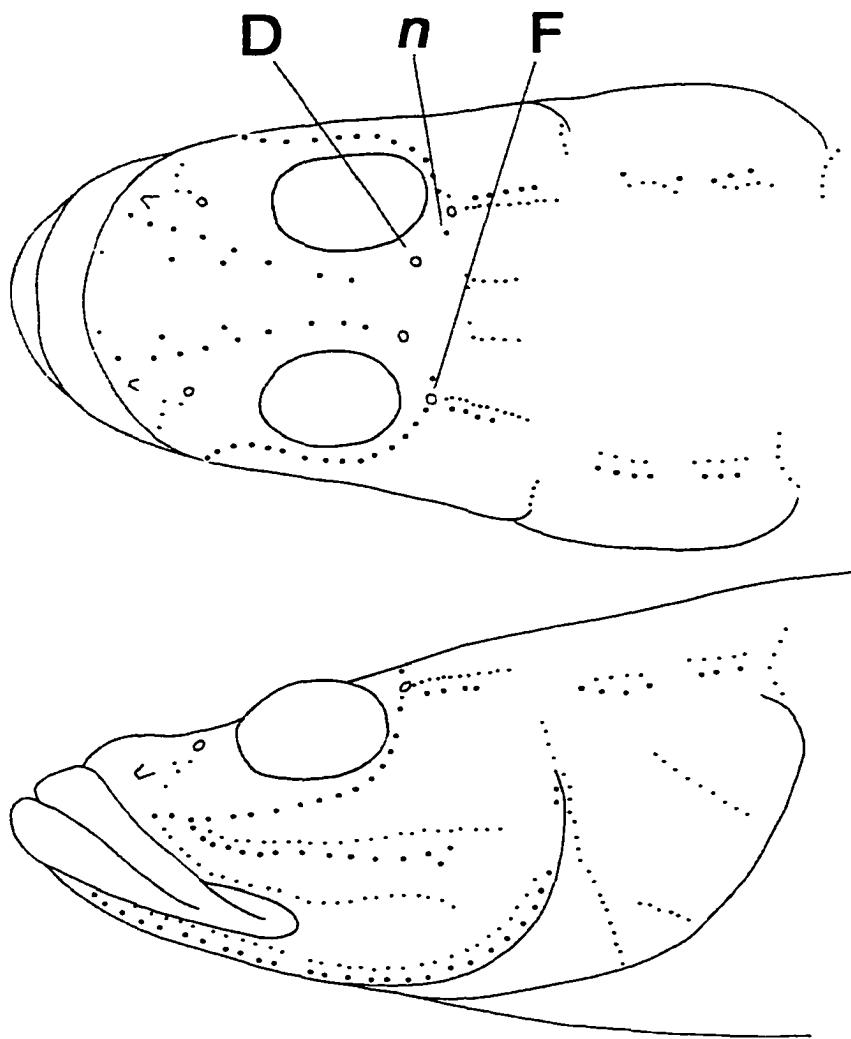


Fig. 2.12. Dorsal and lateral aspects of head of *Gymnogobius taranetzi*, UW 044224, 61.3 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. D = paired posterior interorbital pores, F = postorbital pores, n = anterior transverse row of occipital series of sensory papillae.

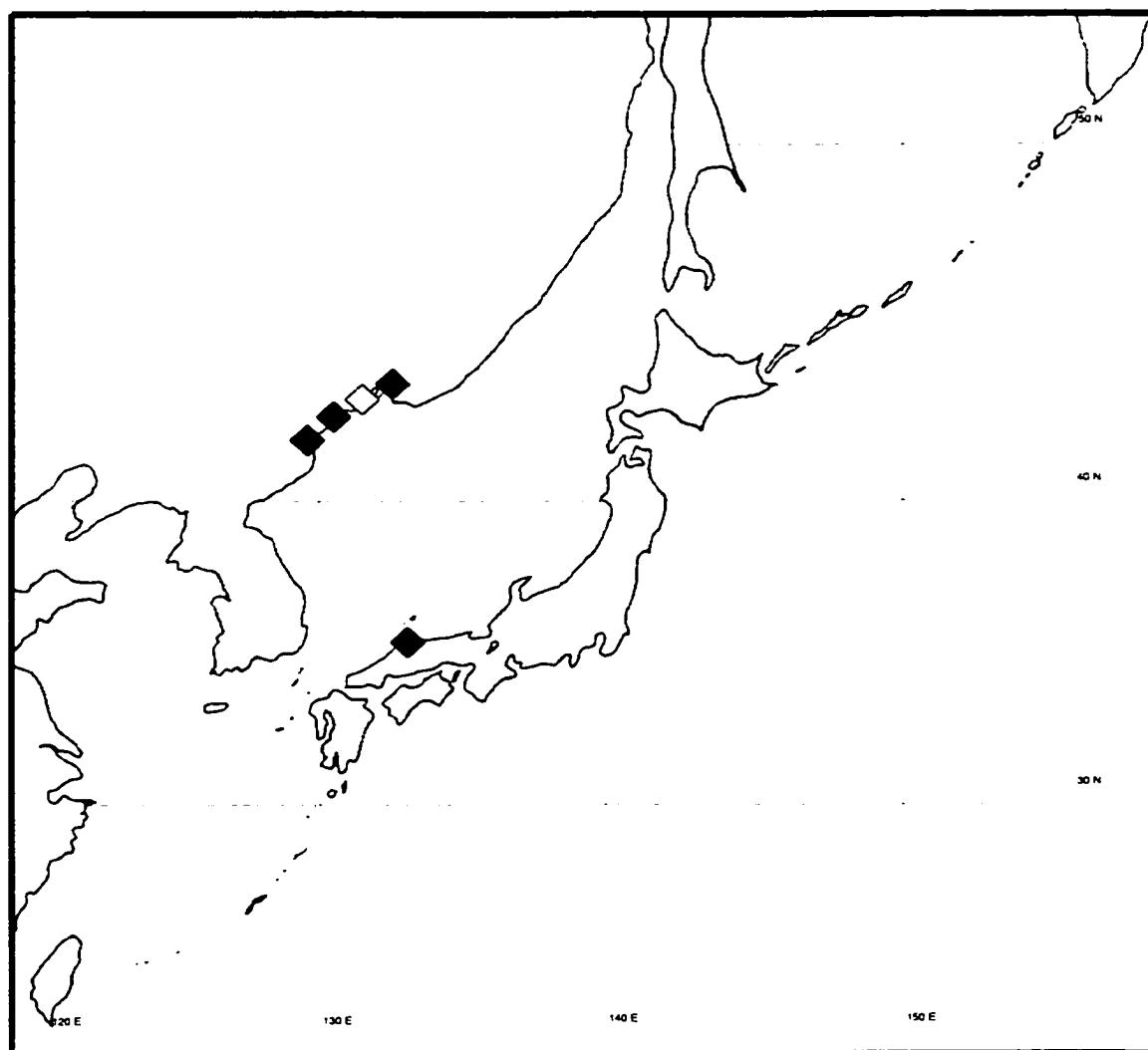


Fig. 2.13. Distribution of specimens examined for *Gymnogobius taranetzi*. Black diamonds indicate specimen locality; white diamond indicates type locality.

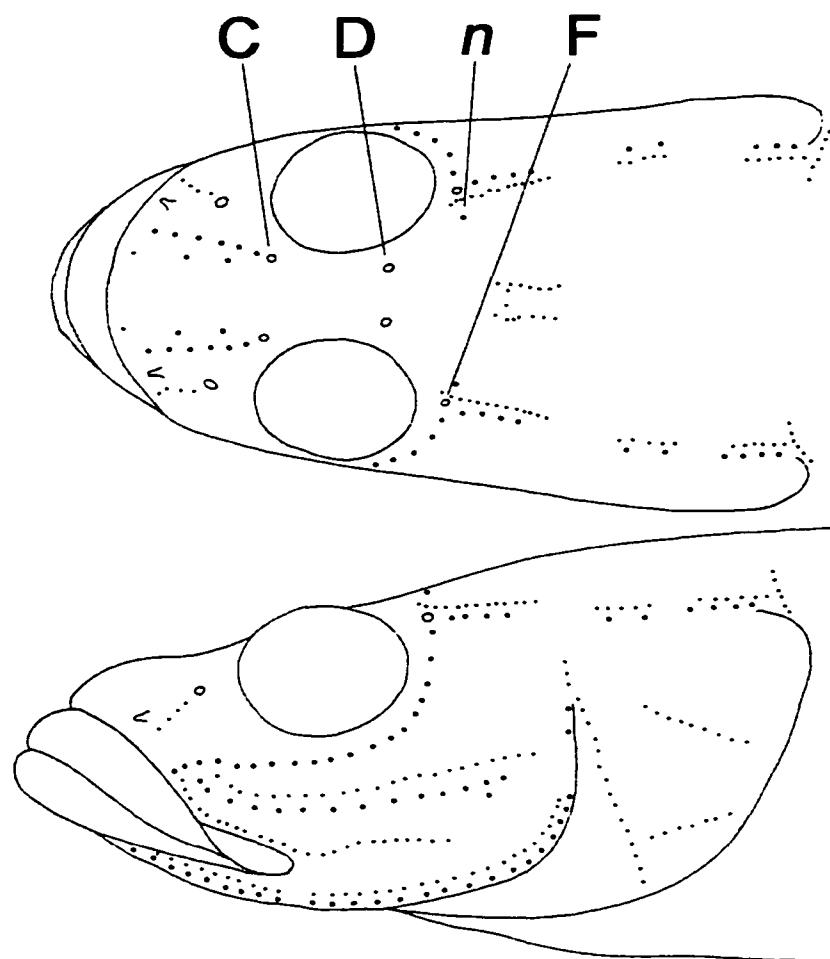


Fig. 2.14. Dorsal and lateral aspects of head of *Gymnogobius breunigii*, UW 029281, 42.5 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. C = anterior interorbital pores, D = paired posterior interorbital pores, F = postorbital pores, n = anterior transverse row of occipital series of sensory papillae.

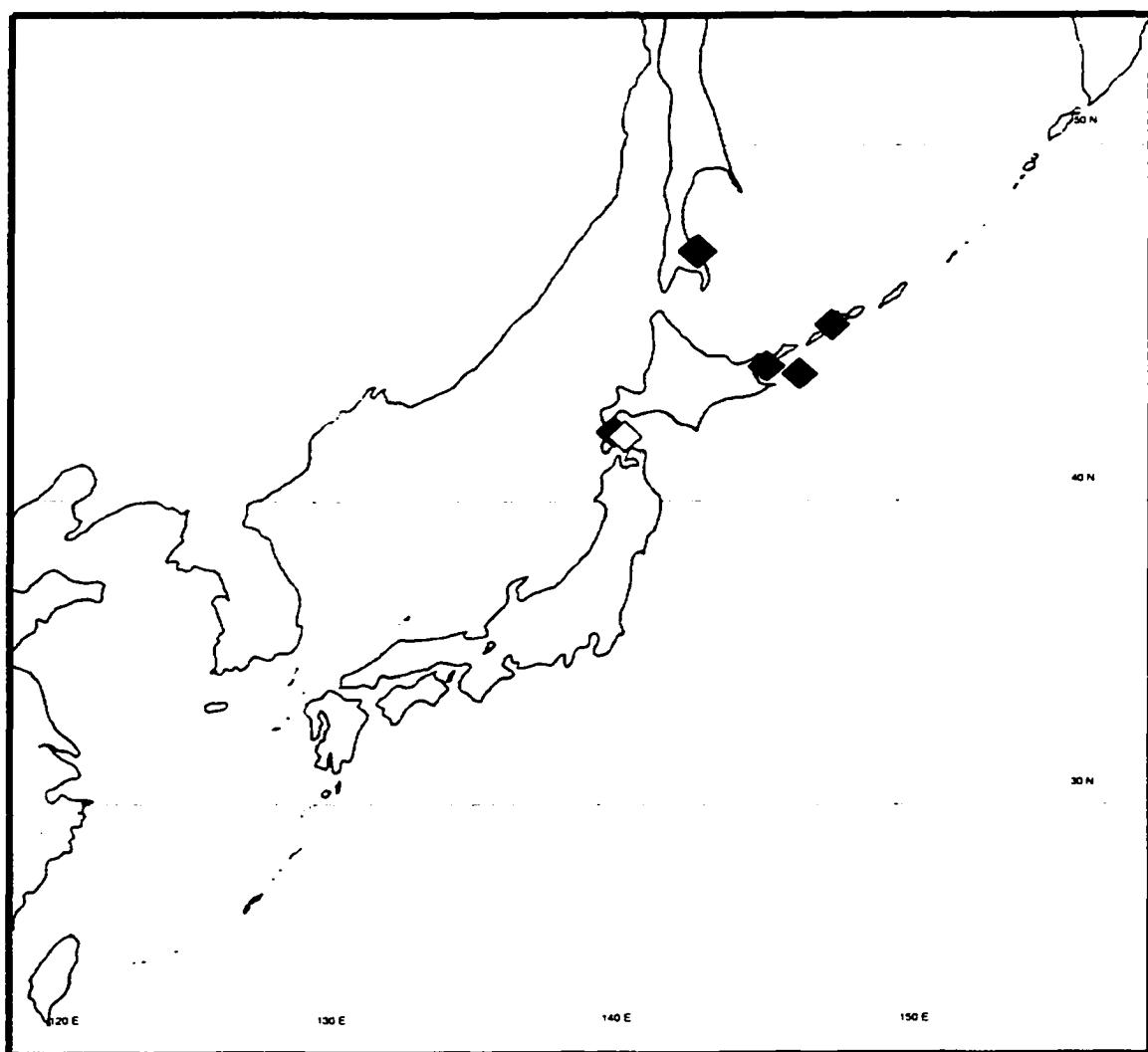


Fig. 2.15. Distribution of specimens examined for *Gymnogobius breunigii*. Black diamonds indicate specimen locality; white diamond indicates type locality.

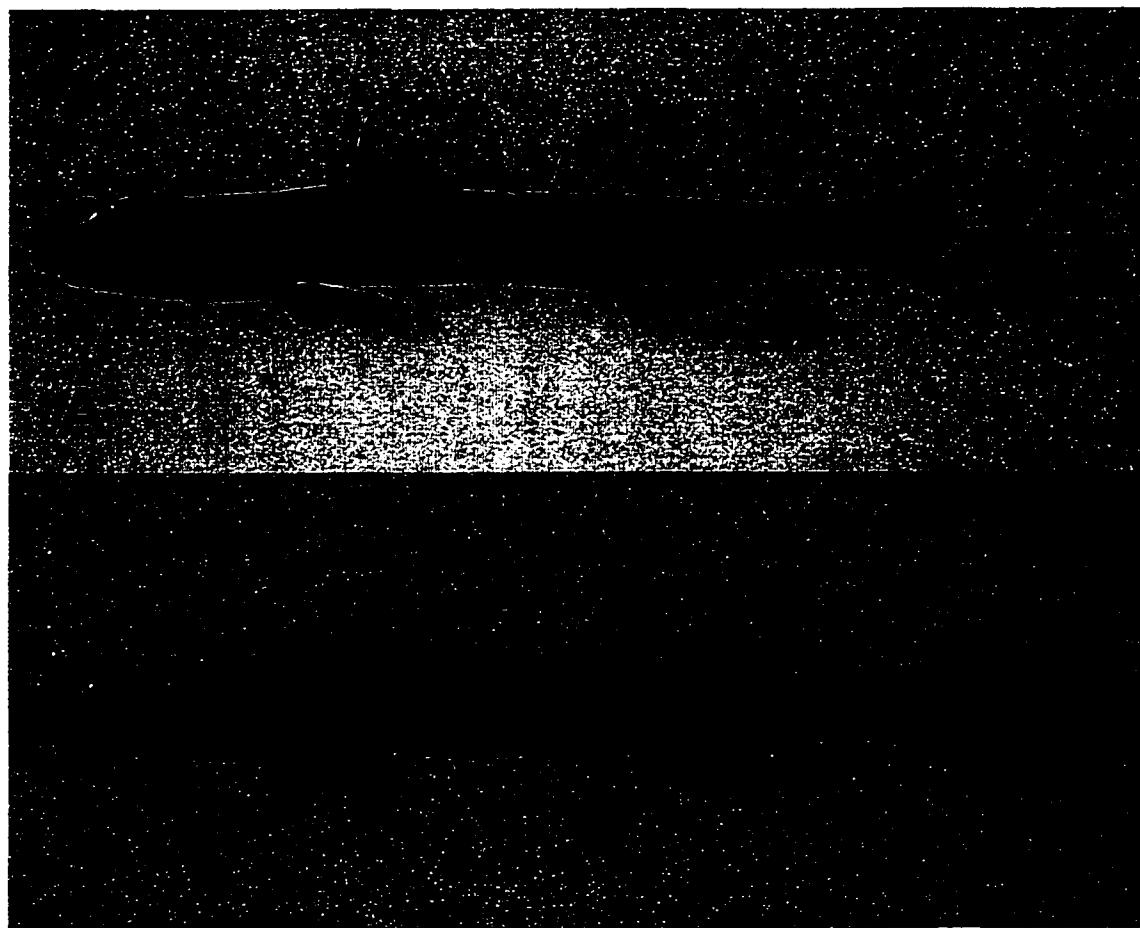


Fig. 2.16. Photographs of *Gymnogobius cylindricus*: (A) male, BLIH 1993001, 49.2 mm SL; (B) female, OMNH-P 3006, 54.1 mm SL. Photographs: T. Suzuki.

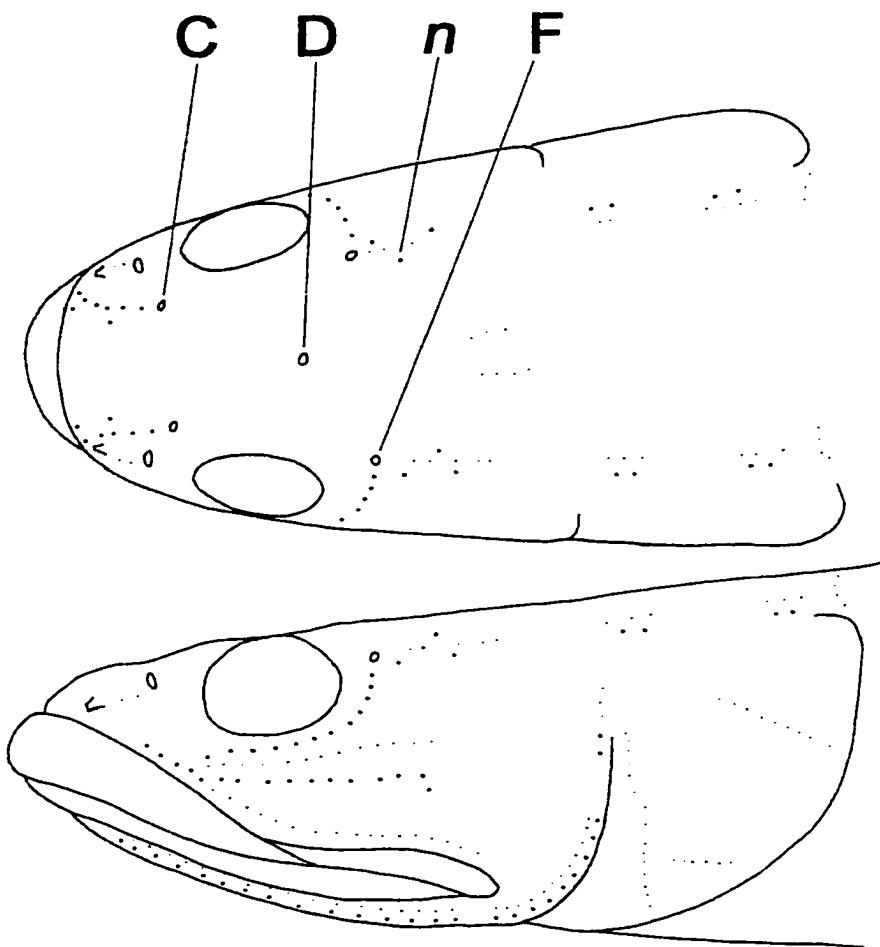


Fig. 2.17. Dorsal and lateral aspects of head of *Gymnogobius cylindricus*, BLIH 1993284, 52.0 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. C = anterior interorbital pores, D = paired posterior interorbital pores, F = postorbital pores, n = anterior transverse row of occipital series of sensory papillae.

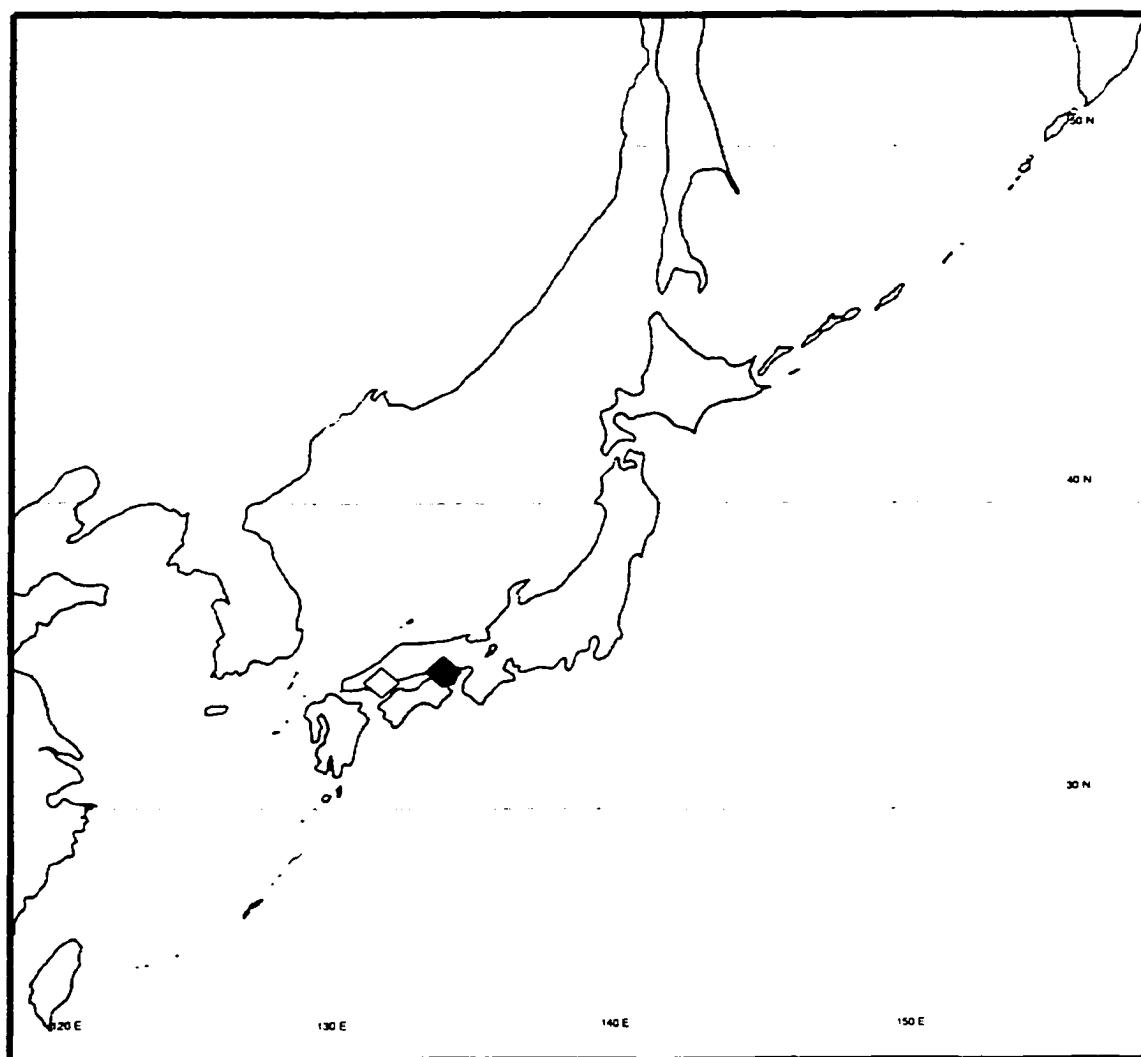


Fig. 2.18. Distribution of specimens examined for *Gymnogobius cylindricus*. Black diamonds indicate specimen locality; white diamond indicates type locality.

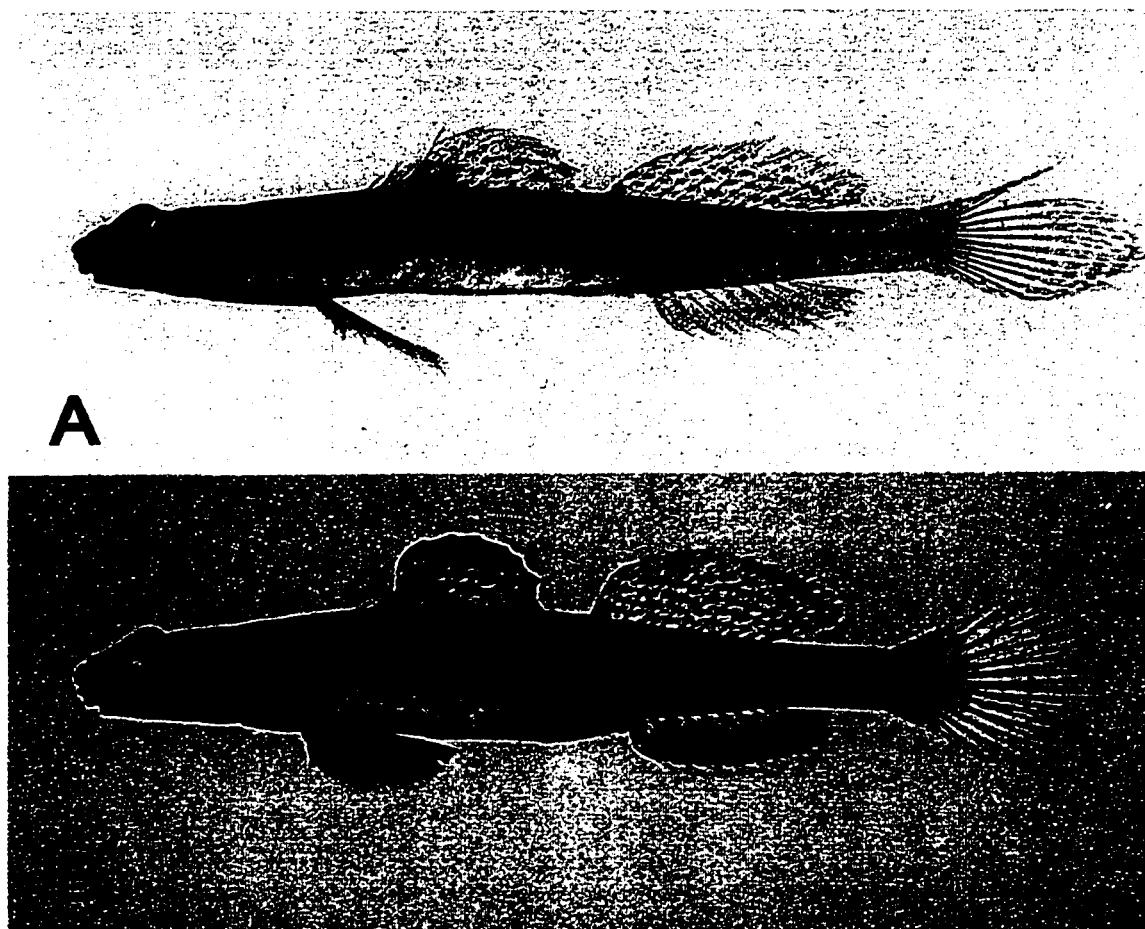


Fig. 2.19. Photographs of *Gymnogobius scrobiculatus*: (A) male, OMNH-P 11261, neotype, 29.9 mm SL; (B) female, BLIH 1990104-1. Photographs: M. Hatooka (A), and Y. Ikeda (B).

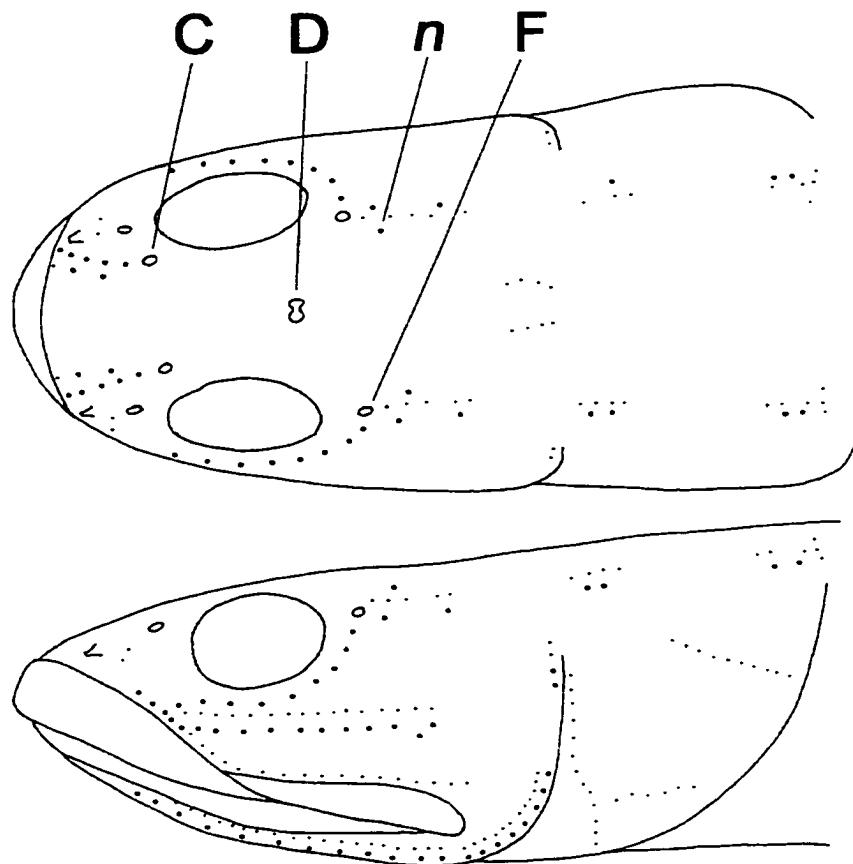


Fig. 2.20. Dorsal and lateral aspects of head of *Gymnogobius scrobiculatus*, BLIH 19891183, 33.8 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. C = anterior interorbital pores, D = paired posterior interorbital pores, F = postorbital pores, n = anterior transverse row of occipital series of sensory papillae.

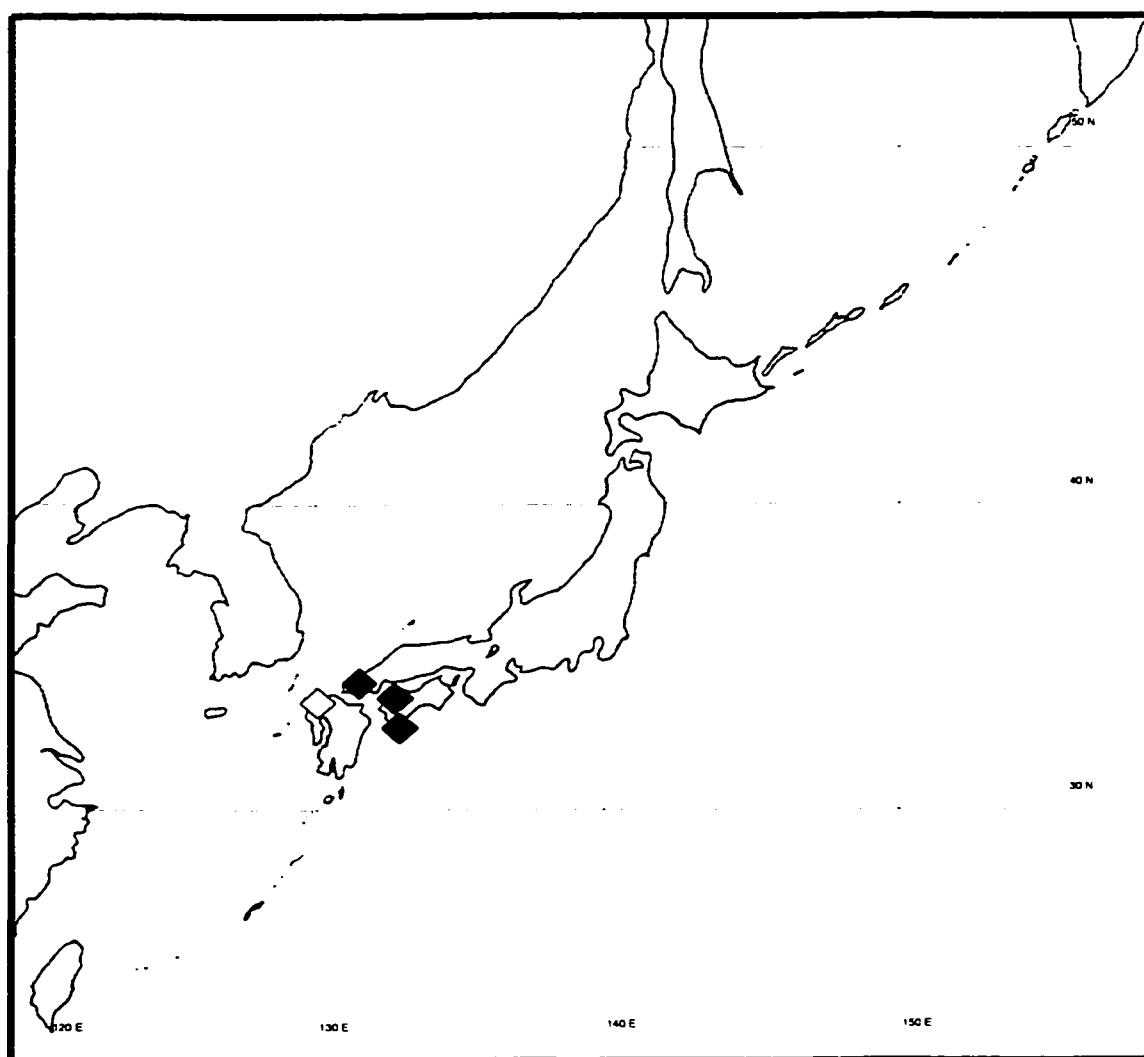


Fig. 2.21. Distribution of specimens examined for *Gymnogobius scrobiculatus*. Black diamonds indicate specimen locality; white diamond indicates type locality.

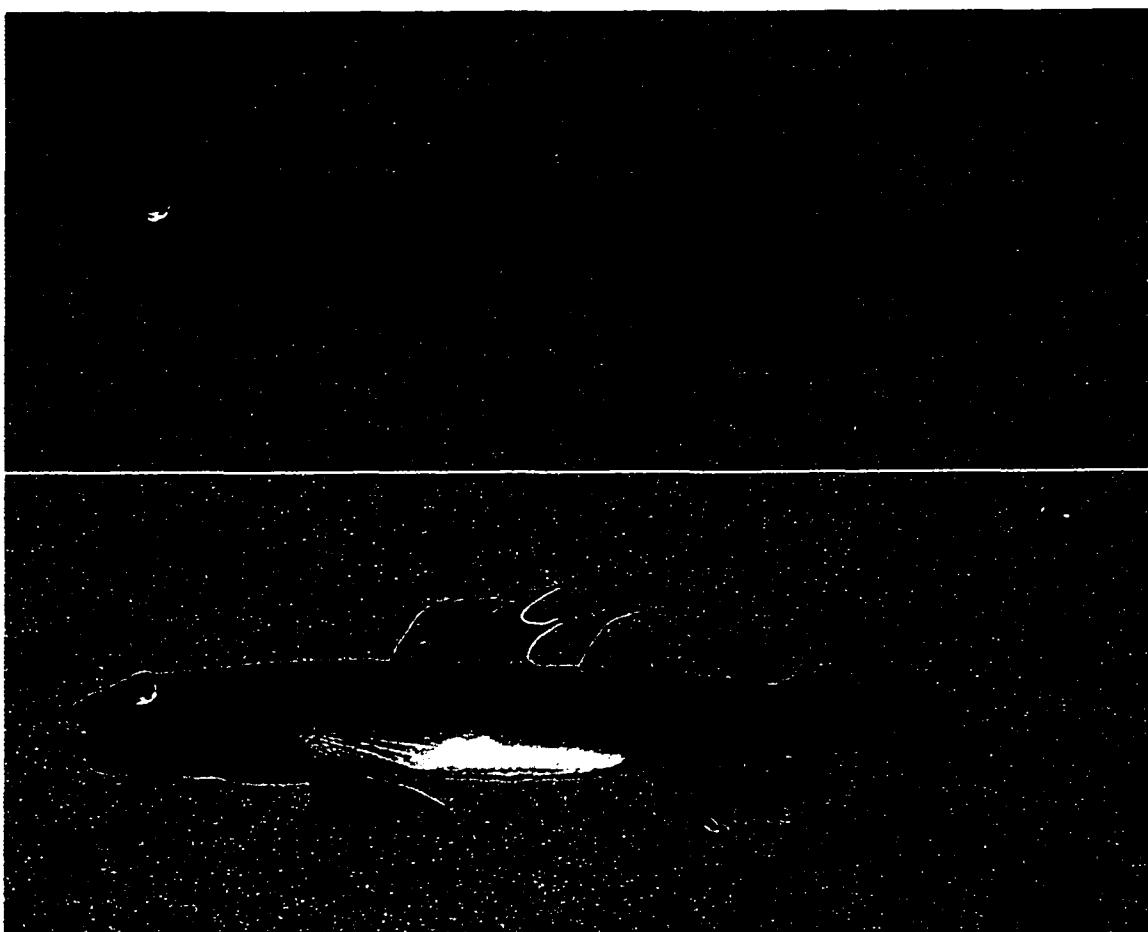


Fig. 2.22. Photographs of *Gymnogobius macrognathos*: (A) male, BLIH 1990007-3; (B) female, BLIH 1990007-4. Photographs: Y. Ikeda.

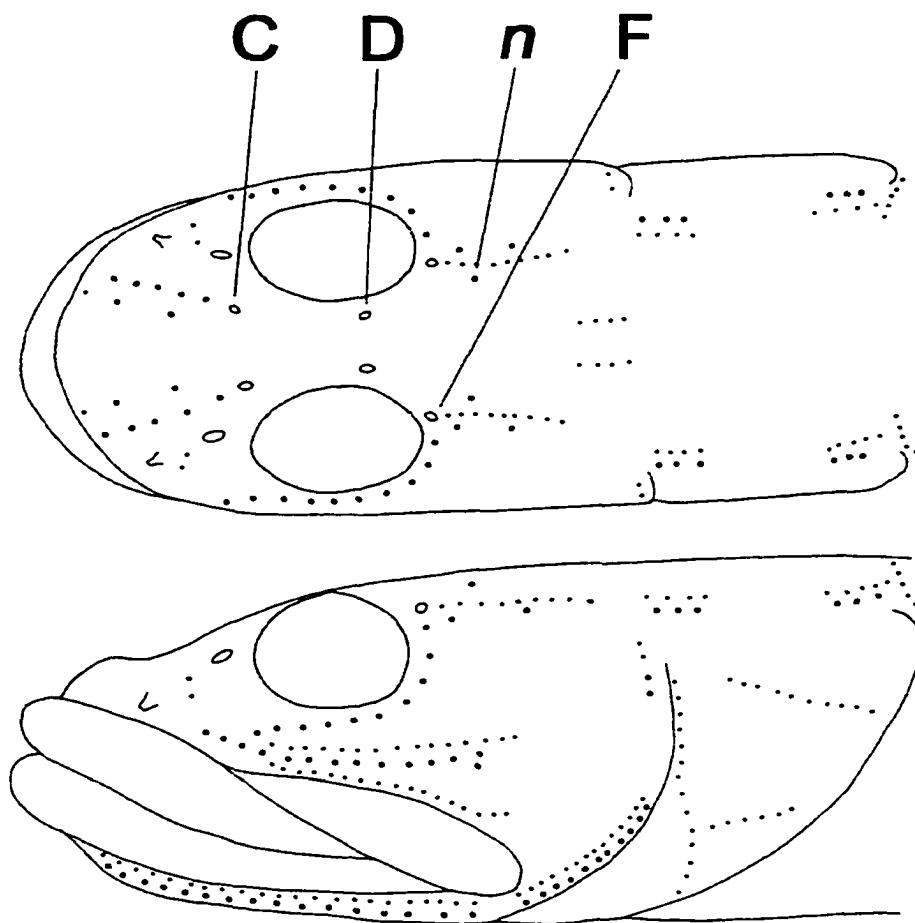


Fig. 2.23. Dorsal and lateral aspects of head of *Gymnogobius macrognathos*, NSMT SK 5002, 26.0 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. C = anterior interorbital pores, D = paired posterior interorbital pores, F = postorbital pores, n = anterior transverse row of occipital series of sensory papillae.

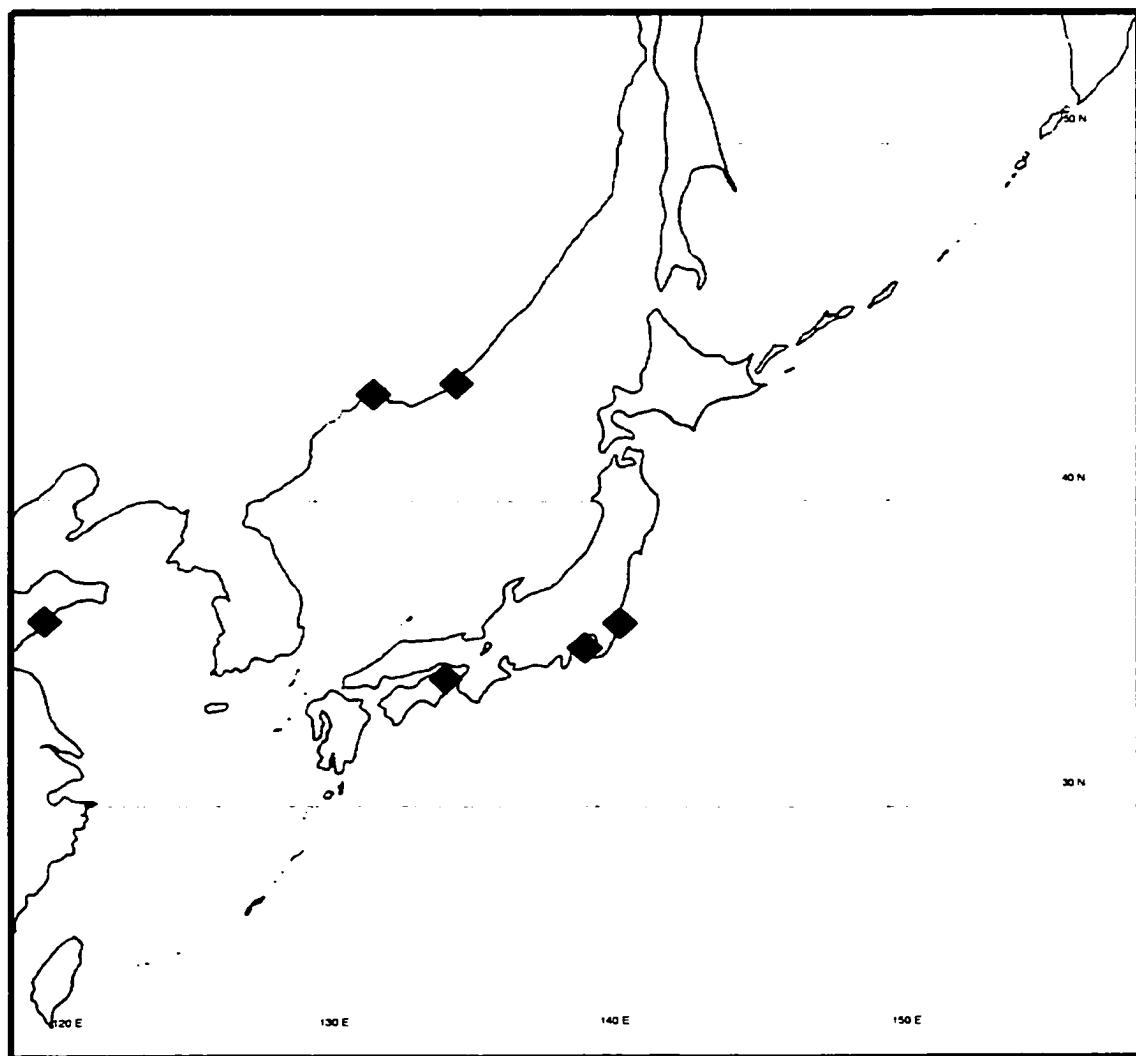


Fig. 2.24. Distribution of specimens examined for *Gymnogobius macrognathos*. Black diamonds indicate specimen locality. Type locality: "Jeddo."

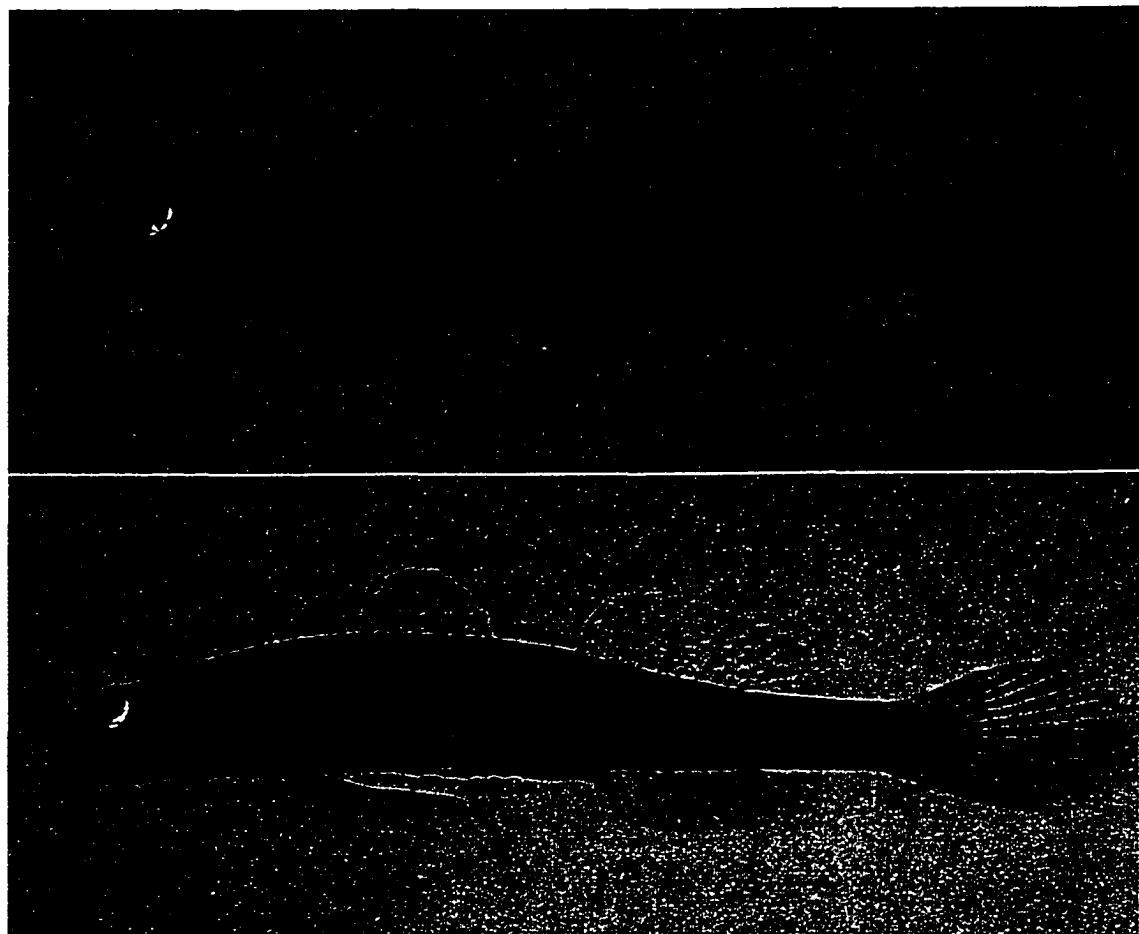


Fig. 2.25. Photographs of *Gymnogobius uchidai*: (A) male, BLIH 1990120-3; (B) female, BLIH 1990120-10. Photographs: Y. Ikeda.

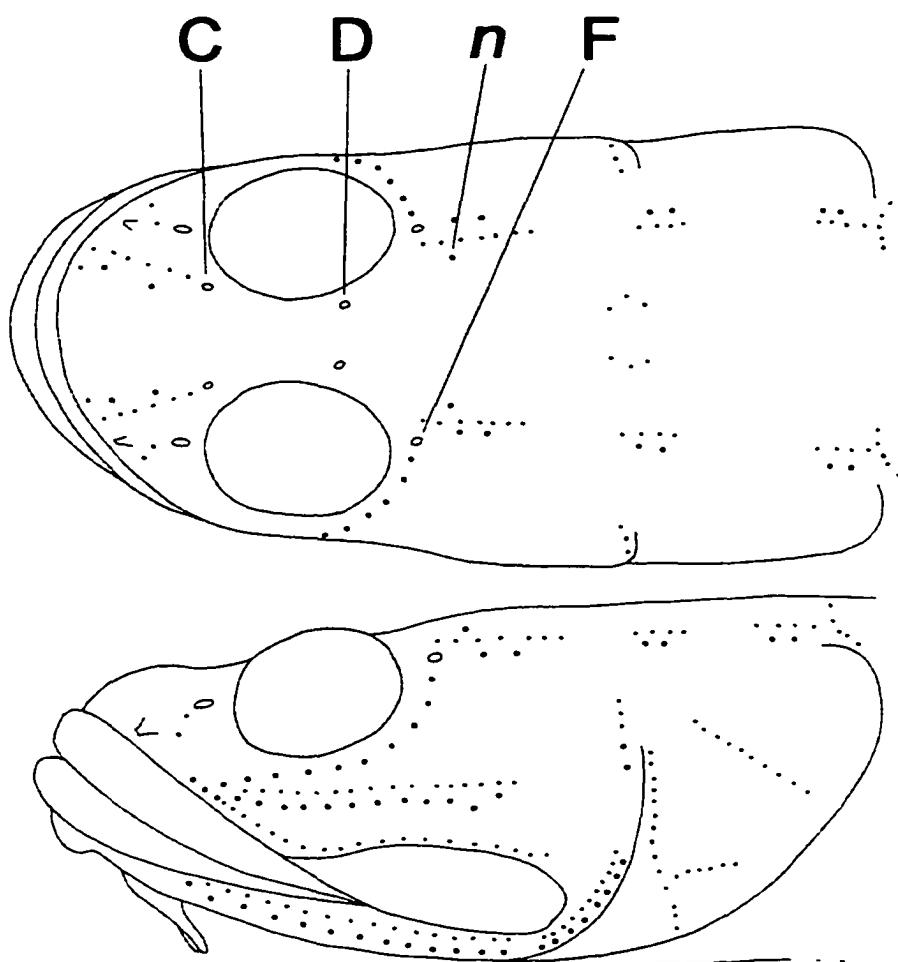


Fig. 2.26. Dorsal and lateral aspects of head of *Gymnogobius uchidai*, BLIH 1990120, 27.0 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. C = anterior interorbital pores, D = paired posterior interorbital pores, F = postorbital pores, n = anterior transverse row of occipital series of sensory papillae.

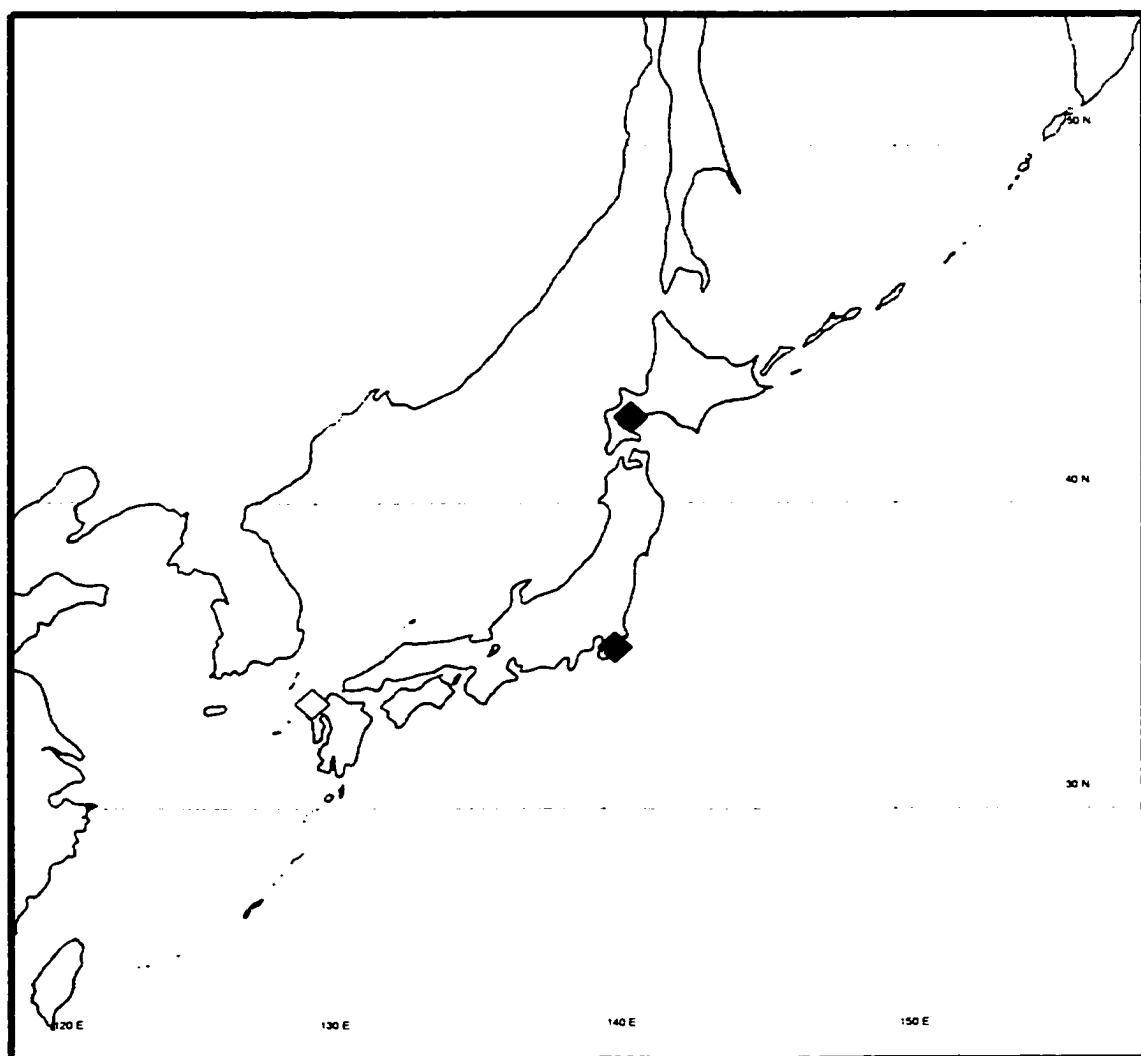


Fig. 2.27. Distribution of specimens examined for *Gymnogobius uchidai*. Black diamonds indicate specimen locality; white diamond indicates type locality.

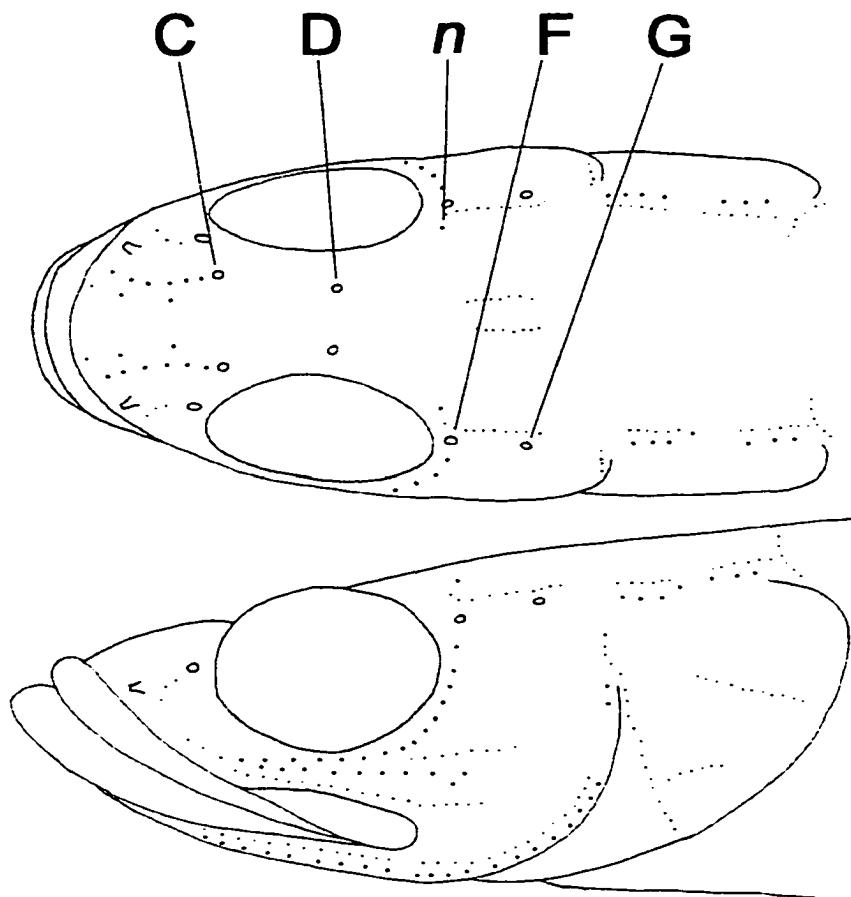


Fig. 2.28. Dorsal and lateral aspects of head of *Gymnogobius heptacanthus*, LACM 44370-2, 34.5 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. C = anterior interorbital pores, D = paired posterior interorbital pores, F = postorbital pores, G = intermediate otic pores, n = anterior transverse row of occipital series of sensory papillae.

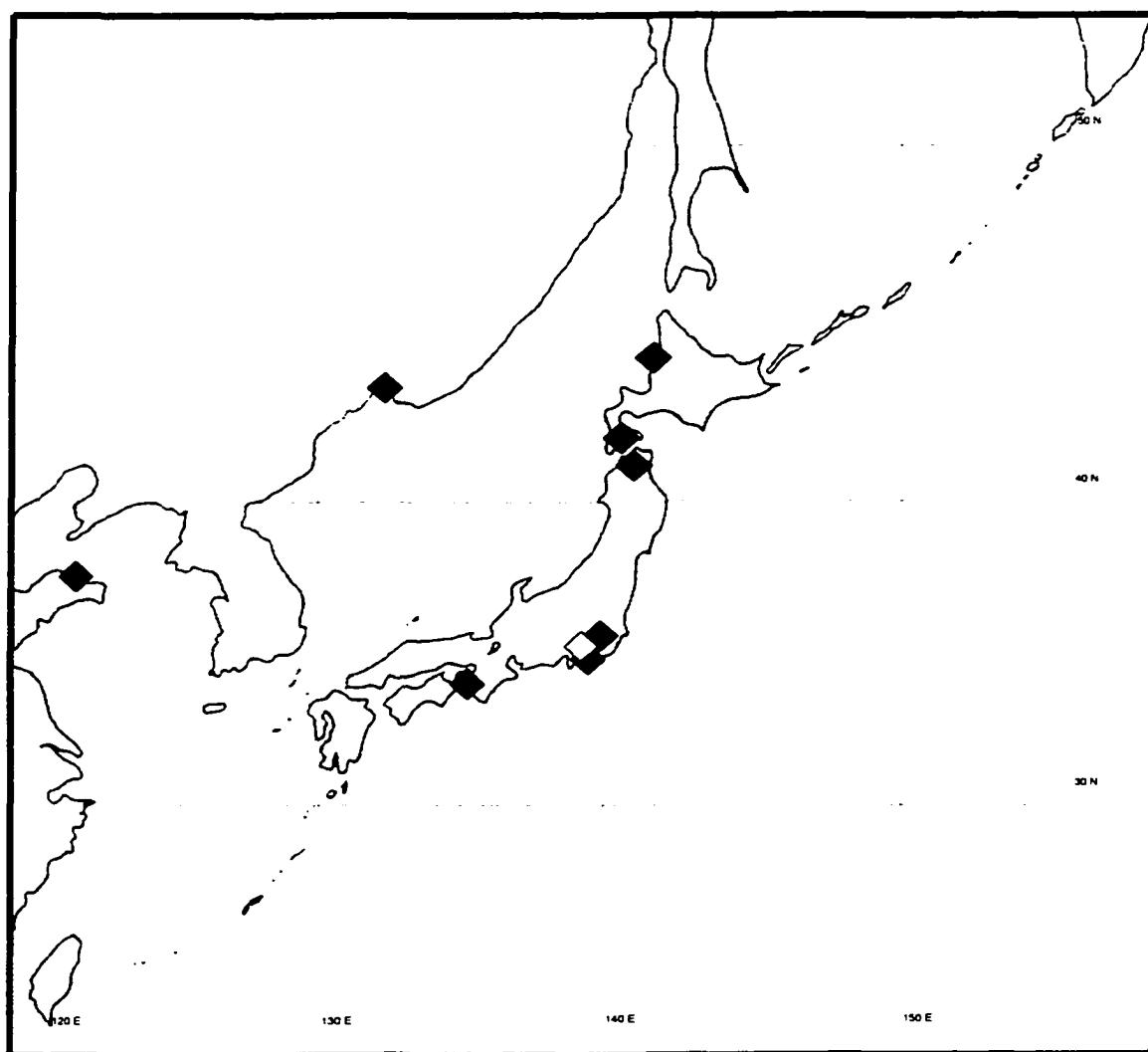


Fig. 2.29. Distribution of specimens examined for *Gymnogobius heptacanthus*. Black diamonds indicate specimen locality; white diamond indicates type locality.

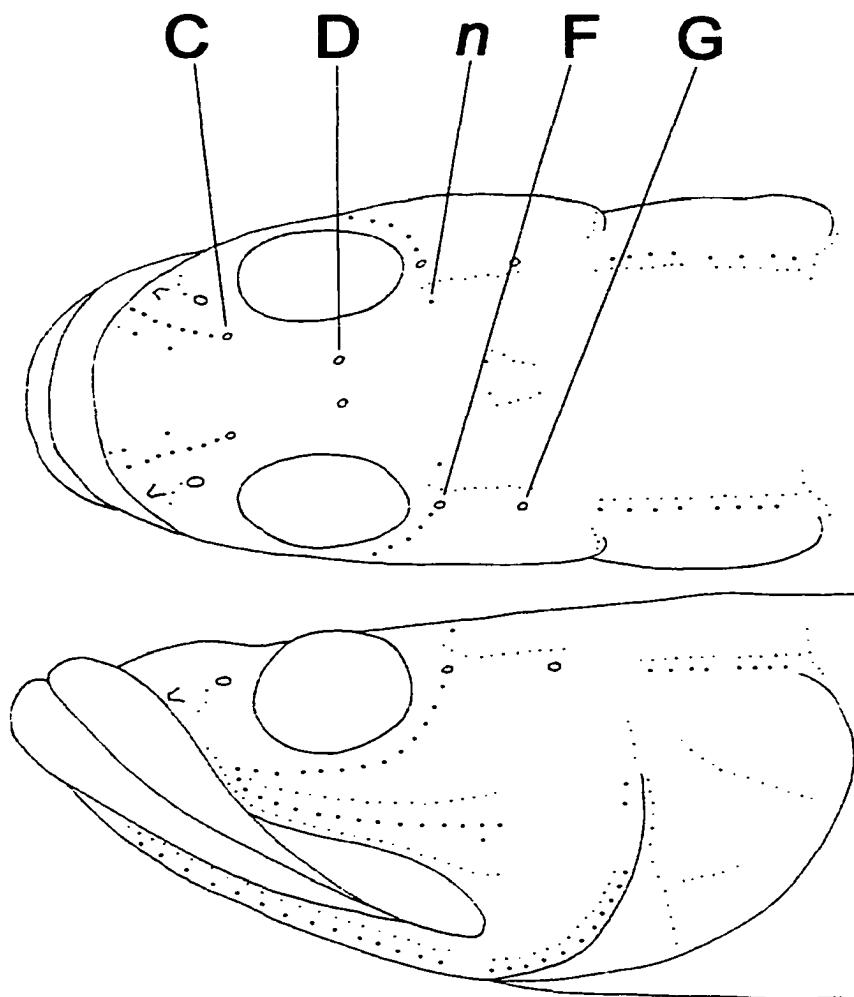


Fig. 2.30. Dorsal and lateral aspects of head of *Gymnogobius mororanus*, CAS 106619, paratype, 55.4 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. C = anterior interorbital pores, D = paired posterior interorbital pores, F = postorbital pores, G = intermediate otic pores, n = anterior transverse row of occipital series of sensory papillae.

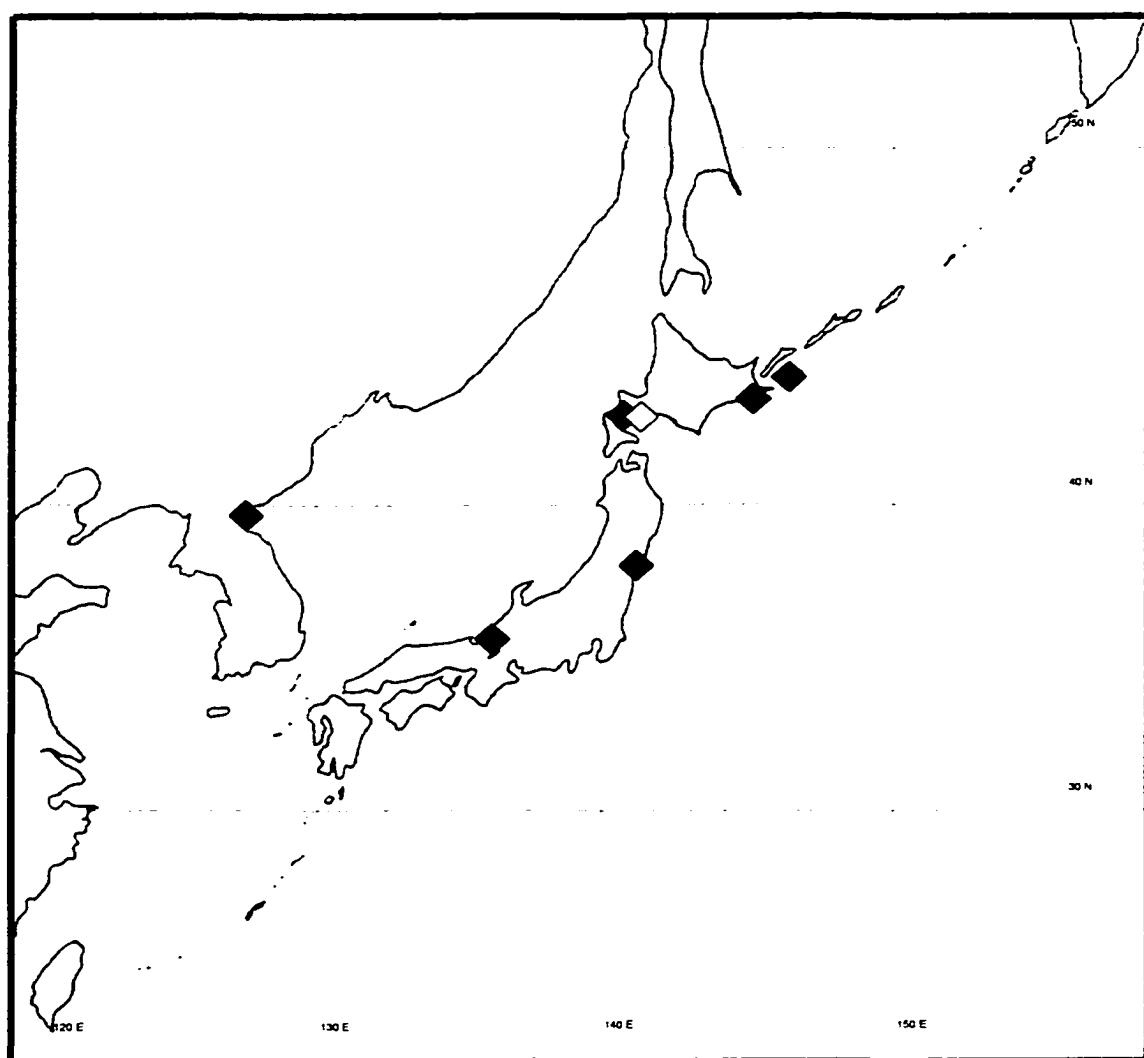


Fig. 2.31. Distribution of specimens examined for *Gymnogobius mororanus*. Black diamonds indicate specimen locality; white diamond indicates type locality.

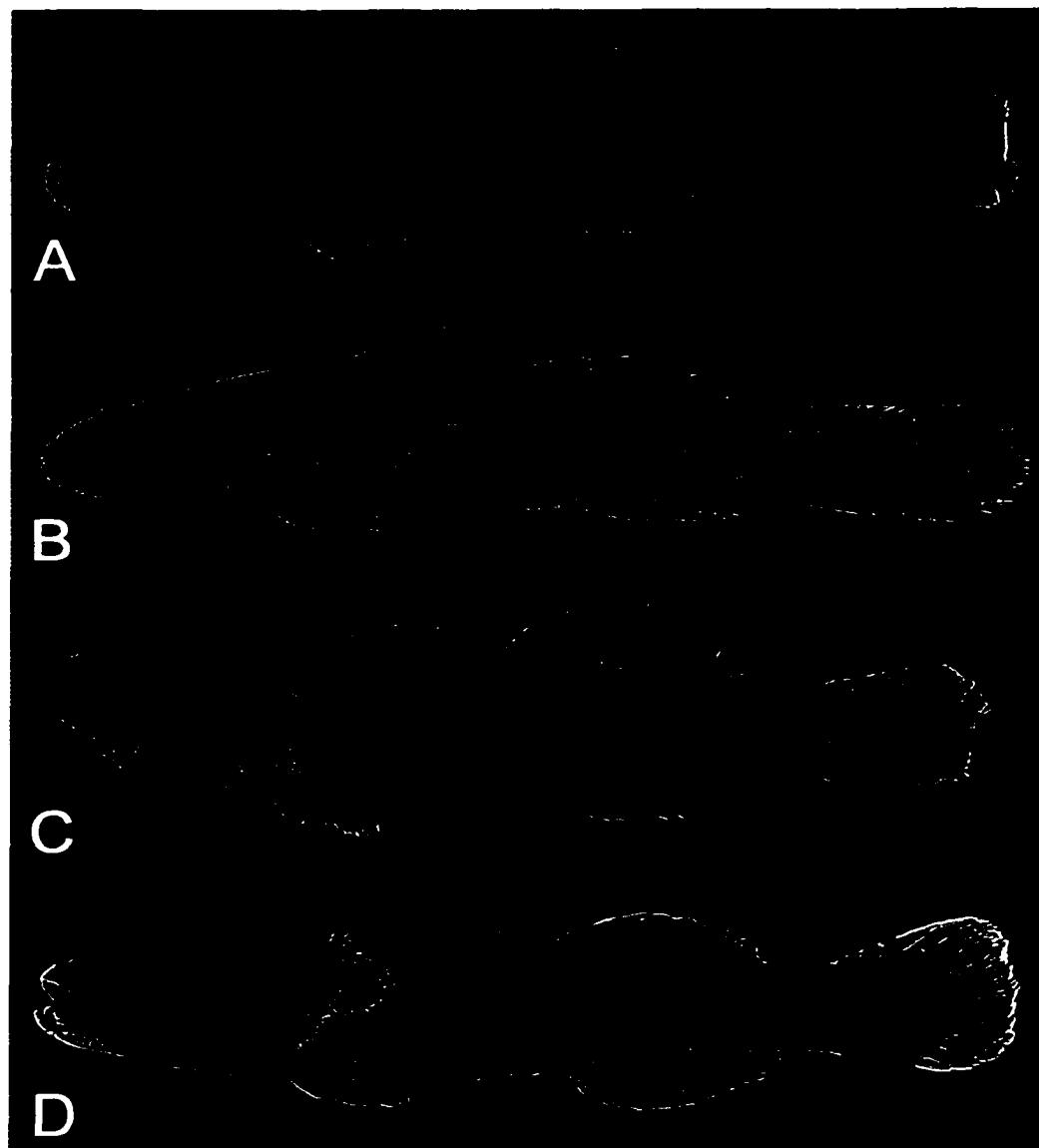


Fig. 2.32. Photographs of: (A) *Gymnogobius isaza*, NSMT-P 14242, 56.0 mm SL; (B) *G. petschiliensis*, NSMT-P 14396, 77.4 mm SL; (C) *G. opperiens* n. sp., NSMT-P 60922, holotype, 67.0 mm SL; and (D) *G. urotaenia*, HUMZ 40720, 92.5 mm SL. Photographs: P. McGiffert.

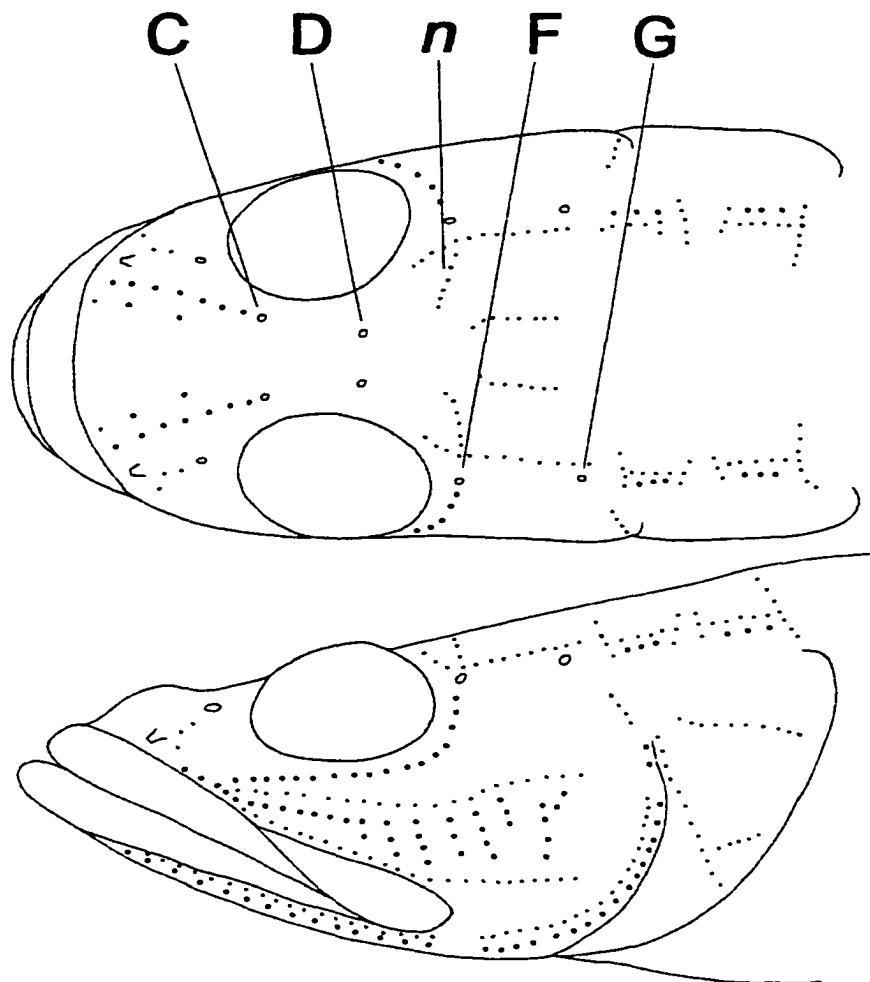


Fig. 2.33. Dorsal and lateral aspects of head of *Gymnogobius isaza*, UW 07817, 47.0 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. C = anterior interorbital pores, D = paired posterior interorbital pores, F = postorbital pores, G = intermediate otic pores, n = anterior transverse row of occipital series of sensory papillae.

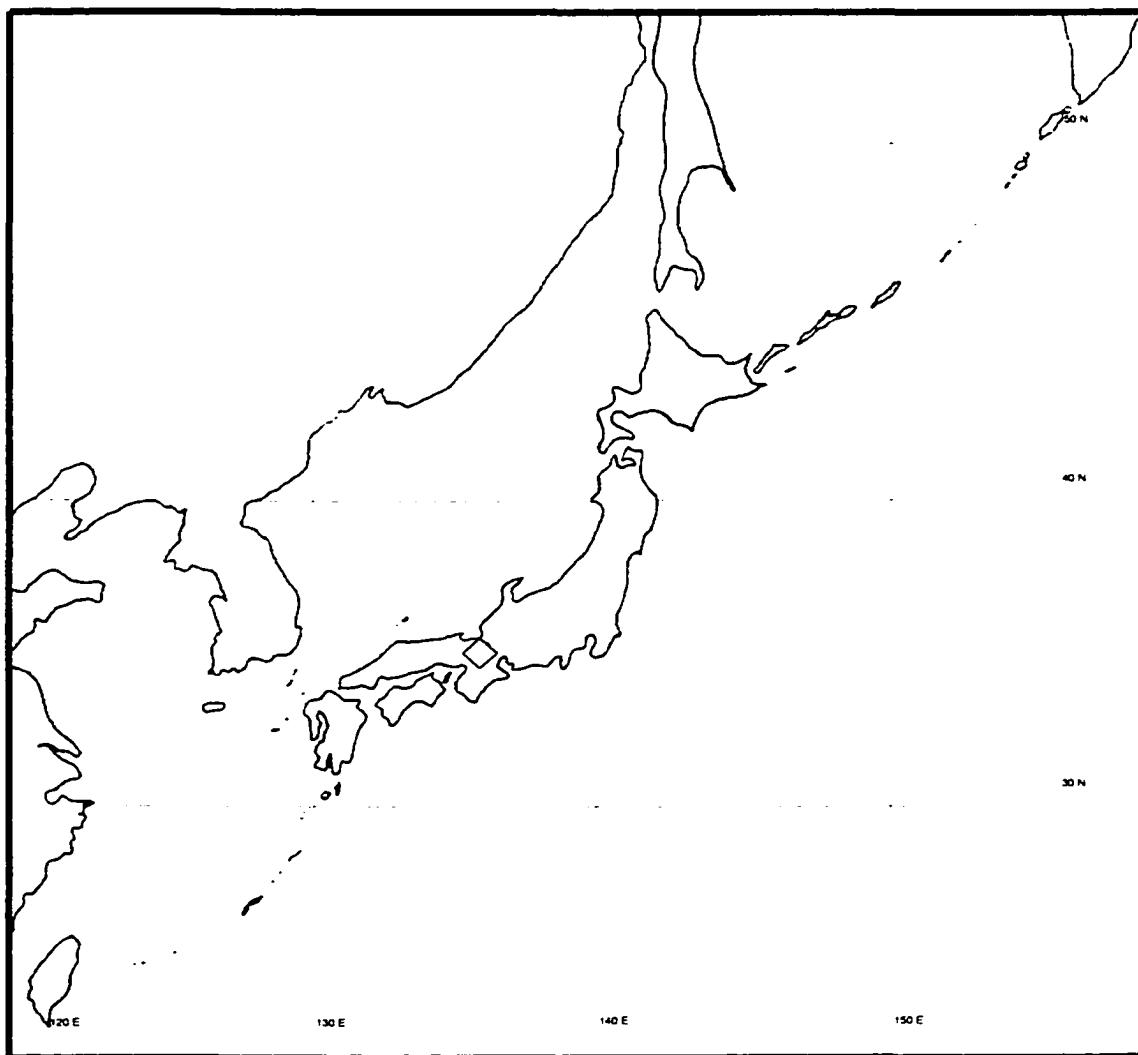


Fig. 2.34. Distribution of specimens examined for *Gymnogobius isaza*. All specimens examined were collected in Lake Biwa, indicated by the white diamond.

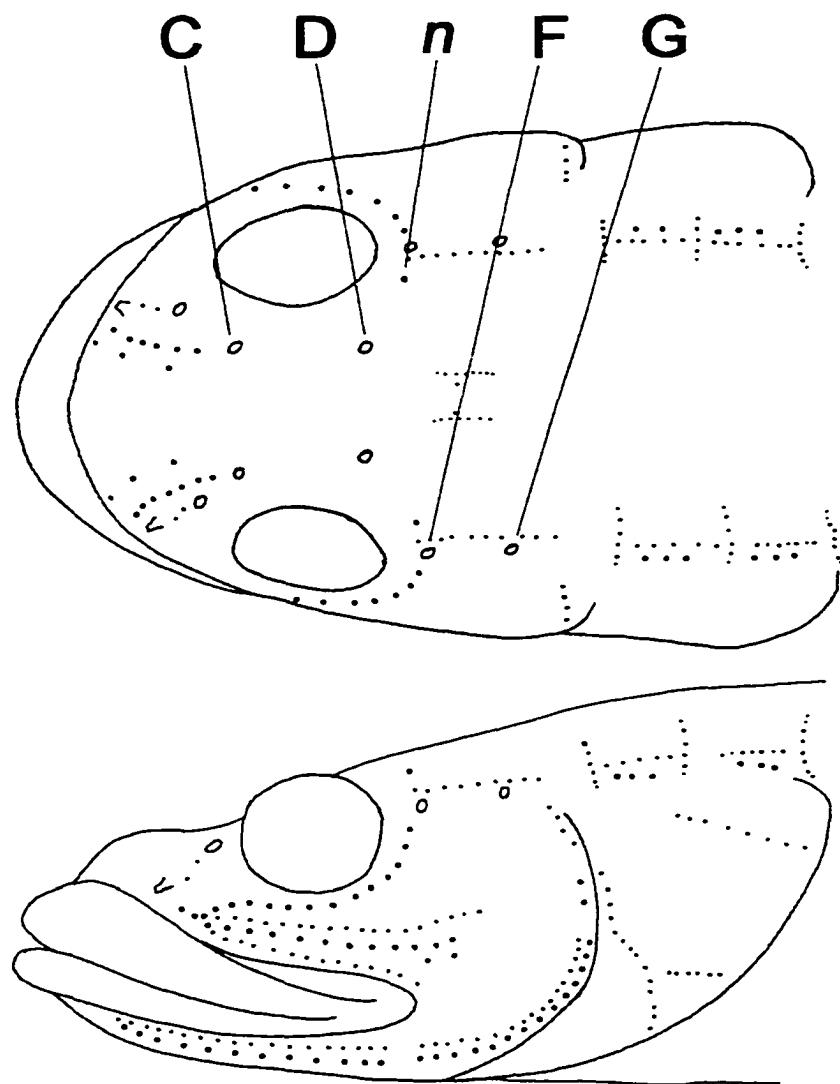


Fig. 2.35. Dorsal and lateral aspects of head of *Gymnogobius petschiliensis*, NSMT-P 14396, 60.8 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. C = anterior interorbital pores, D = paired posterior interorbital pores, F = postorbital pores, G = intermediate otic pores, n = anterior transverse row of occipital series of sensory papillae.

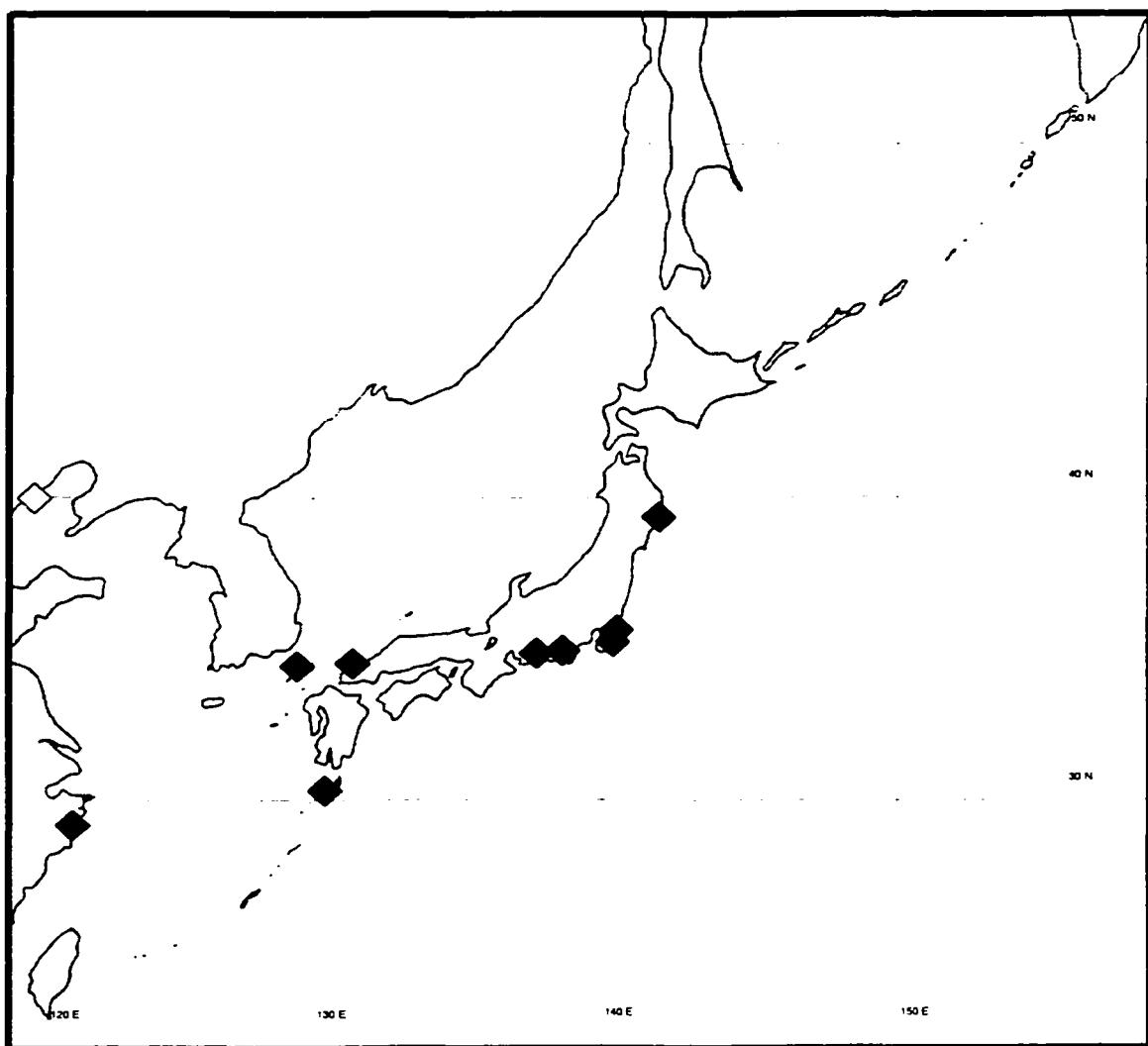


Fig. 2.36. Distribution of specimens examined for *Gymnogobius petschiliensis*. Black diamonds indicate specimen locality; white diamond indicates type locality.

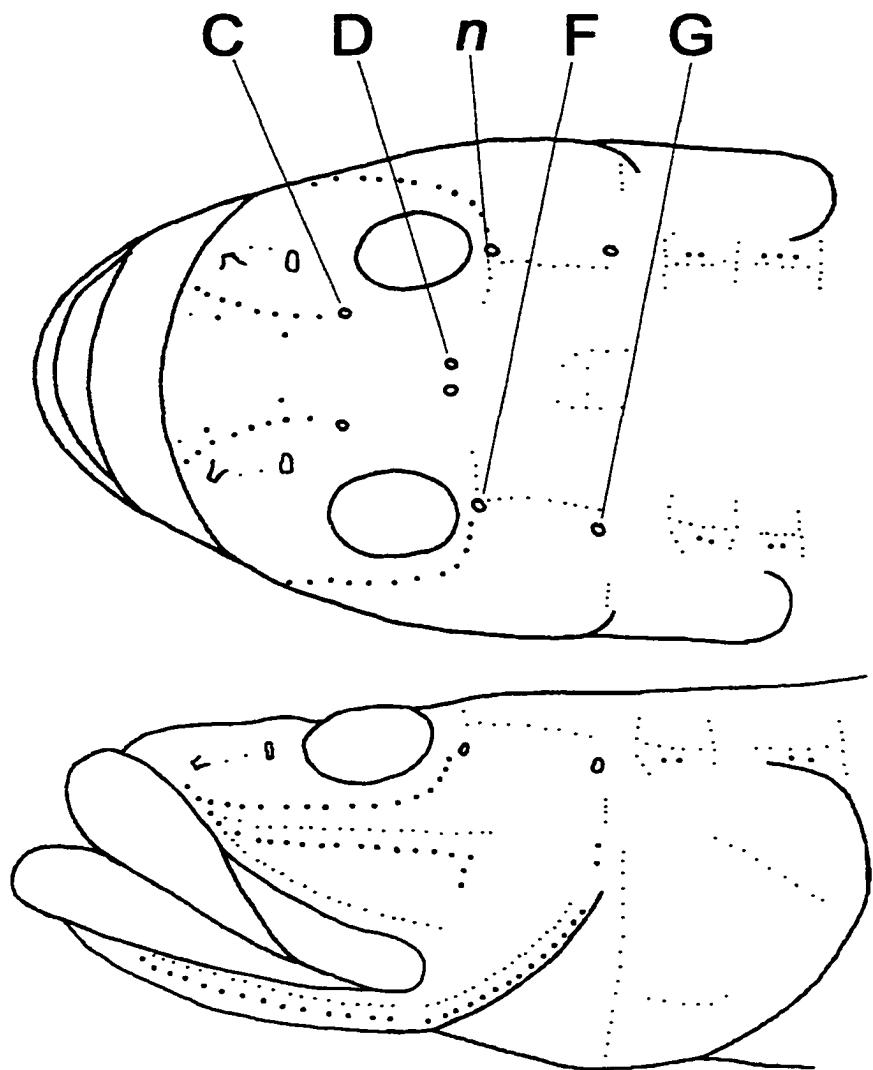


Fig. 2.37. Dorsal and lateral aspects of head of *Gymnogobius opperiens* n. sp., NSMT-P 60922, holotype, 67.0 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. C = anterior interorbital pores, D = paired posterior interorbital pores, F = postorbital pores, G = intermediate otic pores, n = anterior transverse row of occipital series of sensory papillae.

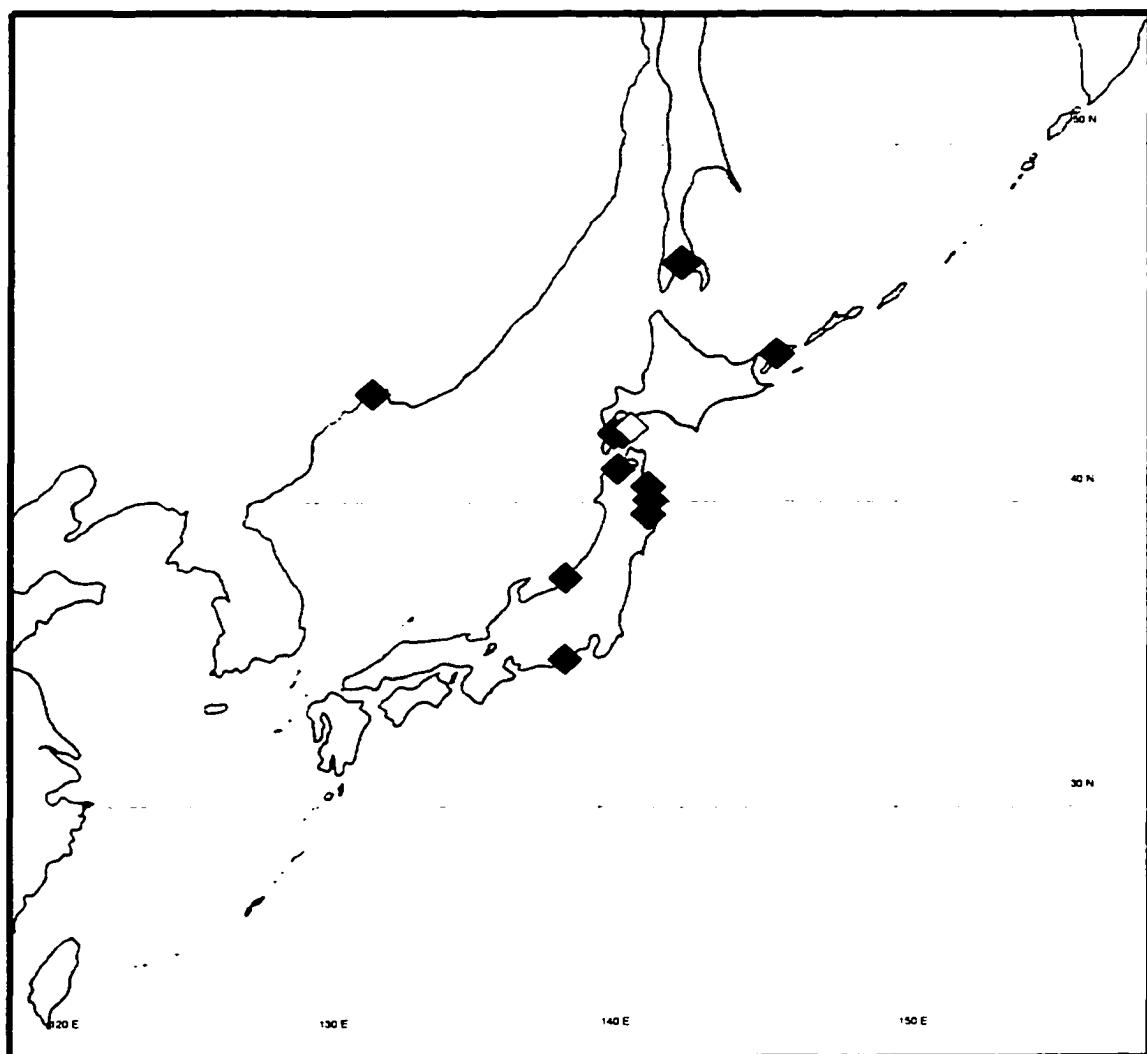


Fig. 2.38. Distribution of specimens examined for *Gymnogobius opperiens* n. sp.

Black diamonds indicate specimen locality; white diamond indicates type locality.

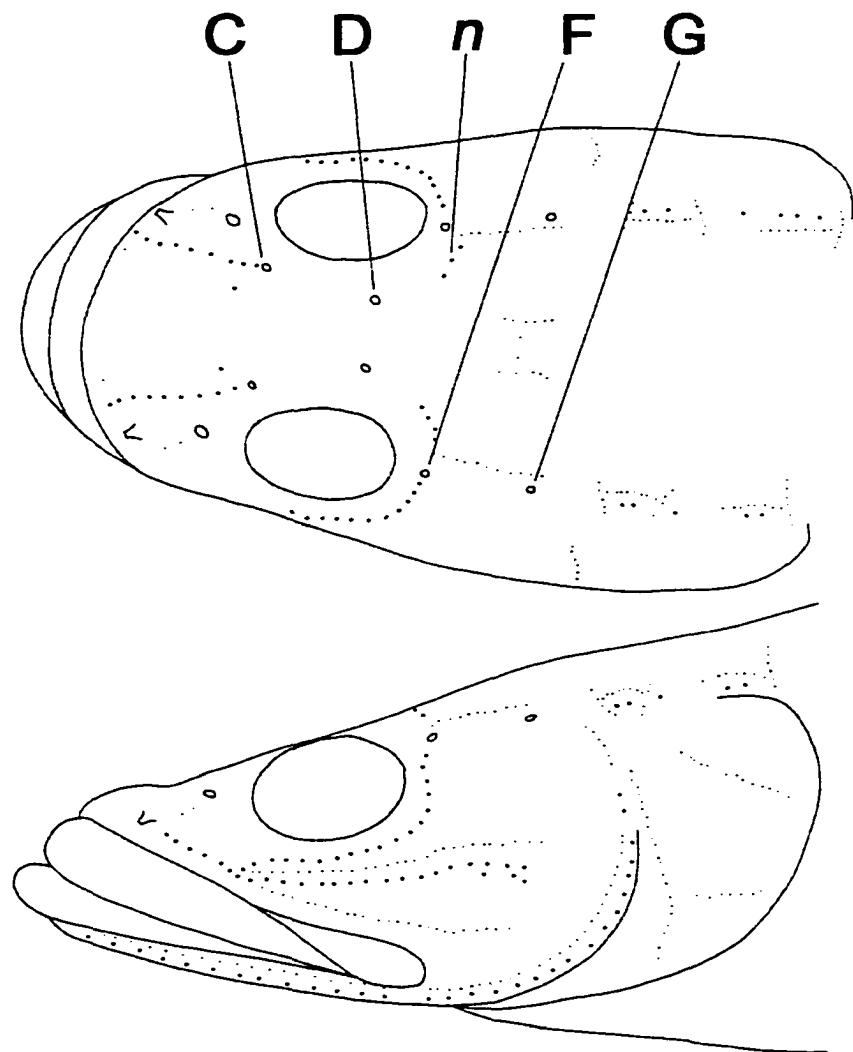


Fig. 2.39. Dorsal and lateral aspects of head of *Gymnogobius urotaenia*, UW 027494, 71.0 mm SL, detailing oculoscapular canal pore and sensory papillae morphology. C = anterior interorbital pores, D = paired posterior interorbital pores, F = postorbital pores, G = intermediate otic pores, n = anterior transverse row of occipital series of sensory papillae.

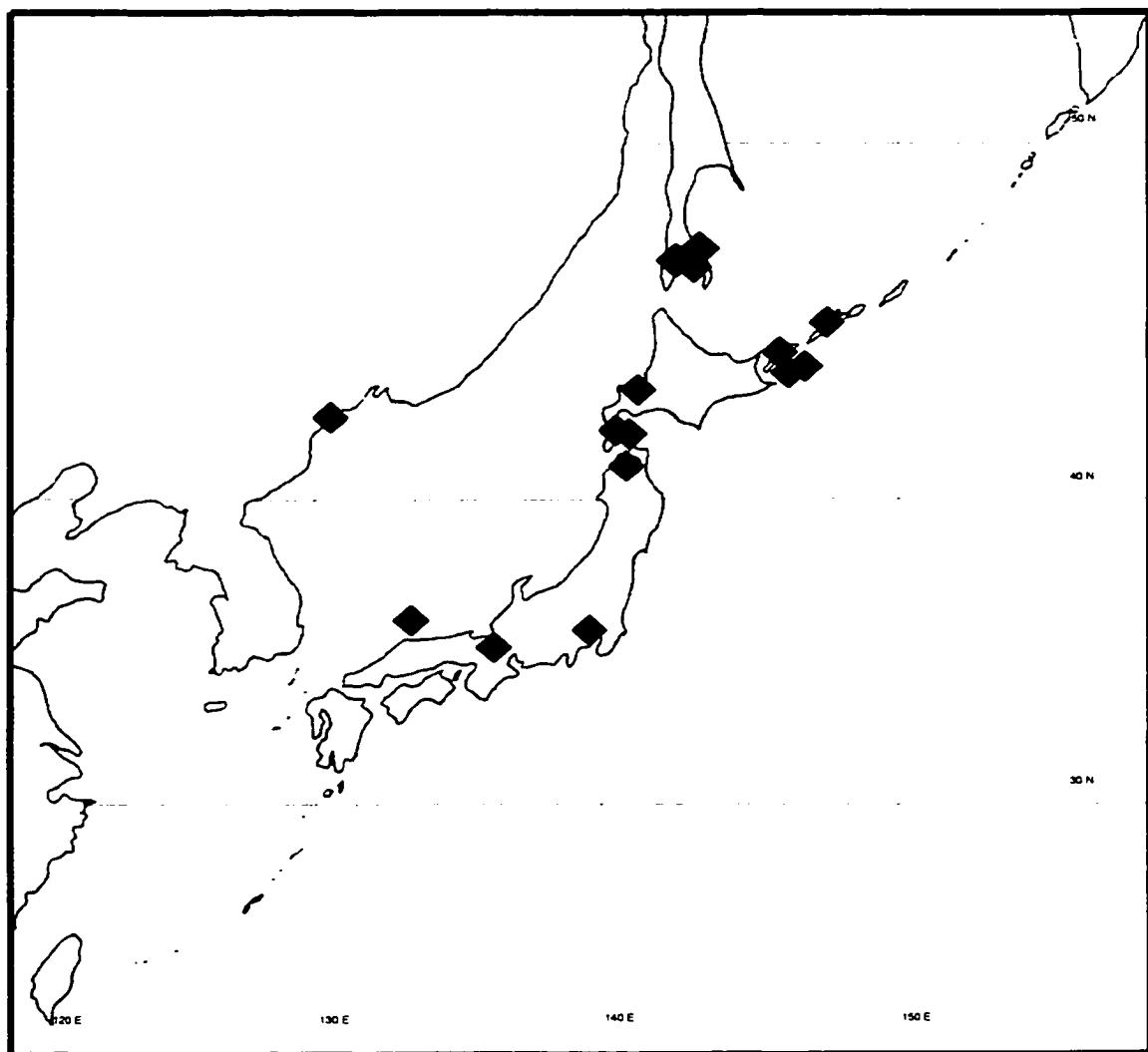


Fig. 2.40. Distribution of specimens examined for *Gymnogobius urotaenia*. Black diamonds indicate specimen locality. Type locality: "Japan."

Table 2.1. Species recognized in this study and their equivalents in Akihito et al. (1984) and Pinchuk (1984).

Akihito et al. (1984)	Pinchuk (1984)	This Study
<i>Chasmichthys dolichognathus</i>		<i>Chaenogobius annularis</i>
<i>Chasmichthys gulosus</i>		<i>Chaenogobius gulosus</i>
<i>Chaenogobius laevis</i>	<i>Rhodonichthys laevis</i>	<i>Gymnogobius castaneus</i>
	<i>Chaenogobius taranetzii</i>	<i>Gymnogobius taranetzii</i>
<i>Chaenogobius castaneus</i>	<i>Chaenogobius castaneus</i>	<i>Gymnogobius breunigii</i>
	<i>Chaenogobius cylindricus</i>	<i>Gymnogobius cylindricus</i>
<i>Chaenogobius cylindricus</i>	<i>Chaenogobius scrobiculatus</i>	<i>Gymnogobius scrobiculatus</i>
<i>Chaenogobius macrognathus</i>	<i>Chaenogobius macrognathus</i>	<i>Gymnogobius macrognathos</i>
<i>Chaenogobius uchidai</i>	<i>Paleatogobius uchidai</i>	<i>Gymnogobius uchidai</i>
<i>Chaenogobius heptacanthus</i>	<i>Chaenogobius heptacanthus</i>	<i>Gymnogobius heptacanthus</i>
<i>Chaenogobius mororanus</i>	<i>Chaenogobius mororanus</i>	<i>Gymnogobius mororanus</i>
<i>Chaenogobius isaza</i>	<i>Chaenogobius isaza</i>	<i>Gymnogobius isaza</i>
<i>Chaenogobius</i> sp. 2		<i>Gymnogobius petschiliensis</i>
<i>Chaenogobius</i> sp. 1		<i>Gymnogobius opperiens</i>
<i>Chaenogobius urotaenia</i>	<i>Chaenogobius annularis</i>	<i>Gymnogobius urotaenia</i>

Table 2.2. Frequency distribution of first dorsal fin, second dorsal fin, and anal fin ray counts for known species of *Chaenogobius* and *Gymnogobius*.

Species	First Dorsal Fin				Second Dorsal Fin					Anal Fin						
	V	VI	VII	VIII	I,09	I,10	I,11	I,12	I,13	I,14	I,08	I,09	I,10	I,11	I,12	I,13
<i>C. annularis</i>	3	41			5	29	9				5	35	2			
<i>C. gulosus</i>	3	31			1	11	21				2	23	8			
<i>G. castaneus</i>	2	56	16		16	46	11				1	20	40	12	1	
<i>G. taranetzi</i>		30	4		20	14					5	25	3			
<i>G. breunigii</i>		52	21		1	49	24				7	54	12			
<i>G. cylindricus</i>		4				1	1	2				3	1			
<i>G. scrobiculatus</i>		11				10	1				10	1				
<i>G. macrognathos</i>	2	21	3			3	14	9			2	13	10			
<i>G. uchidai</i>	2	16				8	10				4	11	3			
<i>G. heptacanthus</i>		23				1	4	17				3	11	9		
<i>G. mororanus</i>		48	7			2	31	19	2		1	4	36	15		
<i>G. isaza</i>	1	24	1			12	11	1			3	20	2			
<i>G. petschiliensis</i>	1	51	5		11	43	3				13	39	4			
<i>G. opperiens</i>	7	142	5			3	121	27	3		2	57	89	5	1	
<i>G. urotaenia</i>	17	101	11		7	52	64	6			7	89	32			

Table 2.3. Frequency distribution of abdominal vertebrae, caudal vertebrae, and AP (number of anal-fin pterygiophores preceding first haemal spine) counts for known species of *Chaenogobius* and *Gymnogobius*.

Species	Abdominal Vertebrae				Caudal Vertebrae							AP			
	14	15	16	17	16	17	18	19	20	21	22	23	2	3	4
<i>C. annularis</i>	34						24	10					17	2	
<i>C. gulosus</i>	23	5					3	25					9	19	
<i>G. castaneus</i>		8	51				3	20	33	3			2	41	14
<i>G. taranetzi</i>		2	31				8	23	2				1	31	
<i>G. breunigii</i>	17	40					15	36	6				3	24	29
<i>G. cylindricus</i>		4					4						4		
<i>G. scrobiculatus</i>	11						11						10	1	
<i>G. macrognathos</i>		25					2	19	4				20	4	
<i>G. uchidai</i>	17	1					1	17					5	13	
<i>G. heptacanthus</i>	1	6	16						6	16	1		8	3	
<i>G. mororanus</i>		42	10				1		7	34	10		30	3	
<i>G. isaza</i>	7	31					2	27	9				3	20	1
<i>G. petschiliensis</i>	3	40	4	1	1	40	7						1	45	2
<i>G. opperiens</i>	1	142	8				4	137	10				15	68	10
<i>G. urotaenia</i>		5	110	4	1	48	67	3					4	53	2

Table 2.4. Frequency distribution of first dorsal-fin pterygiophore formulae for known species of *Chaenogobius* and *Gymnogobius*.

Species	4-1221000	4-1221100	4-1221200	4-1221300	4-1221400	4-1221500	4-1221600	4-1221700	4-1221800	4-1221900	4-12211000	4-12212000	4-12213000	4-12214000	4-12215000
<i>C. annularis</i>															
<i>C. gulosus</i>															
<i>G. castaneus</i>	1			4			1	1	1	1	14	2	1		
<i>G. taranetzi</i>				1			1			1	1	7			
<i>G. breunigii</i>	1	1	1	1	1	1	7		1	2	1	1	4	11	1
<i>G. cylindricus</i>															
<i>G. scrobiculatus</i>						1									
<i>G. macrognathos</i>						2	1					2			
<i>G. uchidai</i>						1							1		
<i>G. heptacanthus</i>				1							3	11	1		
<i>G. mororanus</i>				5				1	1	1	1	2	30		
<i>G. isaza</i>					3		2				1				
<i>G. petschiliensis</i>					3							1	3		
<i>G. opperiens</i>	2				1	2		1				1		2	
<i>G. urotaenia</i>												1			

Table 2.4. Continued.

Species	4-1121000	4-11220100	4-11221000	4-11230100	4-11231000	4-11240100	4-11241000	4-11250100	4-11251000	4-11260100	4-11261000	4-11270100	4-11271000
<i>C. annularis</i>	4												
<i>C. gulosus</i>	9												
<i>G. castaneus</i>		1	4	1	1	9	11	2				1	1
<i>G. taranetzi</i>			2	1		12		2				4	1
<i>G. breunigii</i>				4	2	14						1	
<i>G. cylindricus</i>		2	1										
<i>G. scrobiculatus</i>			1					8					1
<i>G. macrognathos</i>	1	1	8	3			1		3	1	1		
<i>G. uchidai</i>			12								1		
<i>G. heptacanthus</i>					1	1						1	1
<i>G. mororanus</i>				1						1	1		3
<i>G. isaza</i>		3	1				8	3					1
<i>G. petschiliensis</i>		24				2	1	9	1	1	1		1
<i>G. opperiens</i>		72	13			1	27	3		3		1	6 4
<i>G. urotaenia</i>		4	9			1	1	5	9		1		4 17

Table 2.4. Continued

Species	6-221100	5-1121100	5-121100	5-1210100	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000	5-1211000				
<i>C. annularis</i>	1																													
<i>C. gulosus</i>																				1										
<i>G. castaneus</i>																														
<i>G. taranetzi</i>																														
<i>G. breunigii</i>																														
<i>G. cylindricus</i>																	1													
<i>G. scrobiculatus</i>																														
<i>G. macrognathos</i>																				1										
<i>G. uchidai</i>					2																1									
<i>G. heptacanthus</i>																														
<i>G. mororanus</i>			1					1																						
<i>G. isaza</i>				1																										
<i>G. petschiliensis</i>																														
<i>G. opperiens</i>	1	1	1																1											
<i>G. urotaenia</i>	1							1	2	2	5	20	2	1						2	4	1	3	1	1	2	2	9	2	1

Table 2.5. Summary of scale count ranges for known species of *Chaenogobius* and *Gymnogobius*. Asterisks (*) indicate that counts could not be reliably obtained for the material examined due to the small size, embedded position, or irregular placement of the scales.

Species	Lateral Scales	Transverse Scales	Predorsal Scales
<i>Chaenogobius annularis</i>	61–67	20–22	17–24
<i>Chaenogobius gulosus</i>	77–87	29–36	28–44
<i>Gymnogobius castaneus</i>	60–69	15–20	0–12
<i>Gymnogobius taranetzi</i>	62–67	17–21	0–6
<i>Gymnogobius breunigii</i>	60–71	16–19	0–9
<i>Gymnogobius cylindricus</i>	~50–60*	~10–12*	0
<i>Gymnogobius scrobiculatus</i>	~50–60*	~10–12*	0
<i>Gymnogobius macrognathos</i>	~45–50*	~8–12*	0
<i>Gymnogobius uchidai</i>	~45–50*	~10–15*	0
<i>Gymnogobius heptacanthus</i>	67–75	17–19	1–3
<i>Gymnogobius mororanus</i>	89–101	25	0–8
<i>Gymnogobius isaza</i>	57–65	13–18	0
<i>Gymnogobius petschiliensis</i>	62–72	18–22	22–31
<i>Gymnogobius opperiens</i>	71–78	20–21	19–26
<i>Gymnogobius urotaenia</i>	66–76	19–22	20–30

Table 2.6. Measurements of type specimens of *Gymnogobius opperiens* n. sp. Snout length, postorbital head length, interorbital width, orbital diameter, interdorsal fin space, and upper jaw length are expressed in percent of head length; distance between D (posterior interorbital) pores is expressed in percent of orbital diameter; all other measurements are expressed in percent of standard length. 1D = first dorsal fin, 2D = second dorsal fin, P1 = pectoral fin, P2 = pelvic fin, A = anal fin.

	Holotype	Range (N=41)	Mean
Standard length	67.0 mm	42.4–81.5 mm	58.4 mm
Body depth	18.4	11.9–18.5	16.3
Caudal peduncle depth	11.2	9.4–11.5	10.4
Caudal peduncle length	22.1	18.7–23.7	21.3
Predorsal length	36.6	36.5–42.7	40.3
Head length	28.7	28.7–33.8	31.3
1D origin to 2D origin	20.4	18.3–22.6	20.6
2D origin to A origin	17.3	13.7–17.6	16.2
P2 origin to A origin	32.8	31.8–37.1	34.1
Snout to P2 origin	31.5	28.6–36.4	31.3
1D origin to P2 origin	19.3	17.0–22.7	19.9
1D origin to A origin	31.2	26.7–31.2	28.9
P2 origin to 2D origin	34.3	31.4–36.3	34.1
Length of 1D base	17.2	13.3–17.6	15.8

Table 2.6. Continued.

	Holotype	Range	Mean
Length of 2D base	21.2	17.0–21.1	18.9
Length of A base	16.3	13.8–18.5	15.5
P2 length	14.9	13.1–18.6	15.6
P1 length	18.7	15.2–21.9	19.9
Caudal fin length	20.0	14.6–23.8	21.2
Snout length	31.3	24.5–34.9	28.9
Postorbital head length	52.6	47.5–56.3	52.6
Interorbital width	16.1	9.5–19.3	14.1
Orbital diameter	17.7	14.9–20.9	17.4
Interdorsal fin space	13.5	7.0–18.7	13.9
Upper jaw length	39.6	37.3–59.2	46.6
Distance between D pores	27.6	16.5–40.7	24.5

CHAPTER III:

DESCRIPTIVE OSTEOLOGY, COMPARATIVE OSTEOLOGY, AND MORPHOLOGICAL PHYLOGENY

Several recent studies have greatly advanced gobioid classification (Birdsong et al., 1988; Harrison, 1989; Pezold, 1993; Hoese and Gill, 1993), but there is still much to be done. The utility of osteological characters in the study of gobioid interrelationships has been recognized for nearly a century (Regan, 1911). Osteological studies focusing on gobies have generally fallen into two categories: broad surveys grouping genera and species based on specific osteological character complexes (Takagi, 1950; Akihito, 1969; Birdsong et al., 1988; Harrison, 1989; Parenti and Thomas, 1998), and detailed descriptions of the complete osteology of one or more species (Birdsong, 1975; Springer, 1983; Murdy, 1985). Using the classification of Pezold (1993) those studies in the latter group have treated members of the Xenisthmidae (Springer, 1983) and Gobiidae (Birdsong, 1975; Murdy, 1985), and both gobiid studies treated members of the subfamily Gobiinae. Pezold's (1993) proposed classification leaves only one gobiid subfamily, the Gobionellinae, without evidence of monophyly. To date, a complete osteological examination of a gobionelline species has not been published.

Within the Gobionellinae, Pezold (1993) followed the grouping of Birdsong et al. (1988), recognizing *Acanthogobius*, *Astrabe*, and *Chasmichthys* groups, but suggested that the synapomorphies used to define these groups "require further refinement and resolution" (p. 641). The *Chasmichthys* group is defined by one

synapomorphy – the insertion of the first spinous dorsal-fin pterygiophore in the fourth or fifth interneural space – and includes the western Pacific genera *Gymnogobius* and *Chaenogobius* as well as six eastern Pacific genera. The goal of this study is to provide a detailed description of the osteology of *Gymnogobius macrognathos*, and to compare it with other species of the genus *Gymnogobius*, other genera of the *Chasmichthys* Group, and previously published descriptions of *Microgobius signatus* (Birdsong, 1975) and *Istigobius ornatus* (Murdy, 1985). This study is the first detailed osteological description of a species within the Gobionellinae.

MATERIALS AND METHODS

Osteological observations are based on dissection of specimens cleared and stained using the method of Potthoff (1984). Meristic variation of the axial skeleton was determined using cleared-and-stained specimens and radiographs. Drawings were made using a Zeiss SV-11 binocular microscope with a camera lucida. Terminology for skeletal elements follows Springer (1983), and institutional abbreviations are as listed by Leviton et al. (1985). Stippled areas in the figures indicate cartilage, and a key to the abbreviations used in the figures may be found in Table 3.1.

Specimens representing a total of 21 species were cleared and stained and dissected to compare with *Gymnogobius macrognathos* (see Appendix B). The material examined includes nearly every species of *Gymnogobius* (suitable specimens of *G. cylindricus* and *G. scrobiculatus* could not be obtained), both species of *Chaenogobius*, at least one species from each of the other six genera included in the *Chasmichthys*

Group (*Clevelandia*, *Eucyclogobius*, *Gillichthys*, *Ilypnus*, *Lepidogobius*, and *Quietula*), and three species representing gobionelline genera outside the *Chasmichthys* Group (*Acanthogobius*, *Gnatholepis*, and *Tridentiger*). Comparisons with *Microgobius signatus* and *Istiogobius ornatus* are based on Birdsong (1975) and Murdy (1985), respectively. The taxonomic positions of these species according to Pezold (1993) are listed in Table 3.2 and a morphological character matrix is listed in Table 3.3. A complete list of characters used in the morphological character matrix can be found in Appendix C.

The phylogenetic analysis was performed using the MIX program of the PHYLIP software package (Felsenstein, 1995) and the Wagner parsimony algorithm. Multistate characters were factored into binary characters prior to the analysis and all characters were weighted equally. *Istiogobius ornatus* was used as the outgroup root.

DESCRIPTIVE OSTEOLOGY OF *GYMNOCOBIUS MACROGNATHOS*

Neurocranium.—(Figs. 3.1–3.5) The anterior region of the toothless vomer (VO) is laterally broad and dorsoventrally flattened. It bears two bulbous processes along its anterolateral margins and two short spine-like projections on its ventral surface. It also bears a single medial dorsal extension that rises to meet the anterior margin of the medial ethmoid. These two bones thus form a capsule that houses the ethmoid cartilage (EC), which extends posteriorly to form a septum between the orbits. Posteriorly the vomer extends as an elongate process tightly joined to the ventral surface of the parasphenoid.

The median ethmoid (ME) is a complexly folded, but primarily flat bone. Its dorsal surface is convex and bears two rounded extensions, which serve as attachment points for the maxillary-ethmoid ligaments. Its posterodorsal surface is overlain by the anterior extensions of the frontals, and its anterior extension is ventrally directed to meet the vomer. The anteroventral surface is concave, forming the roof of the capsule in which the ethmoid cartilage is housed. Lateral processes of the median ethmoid receive the anteromedial processes of the lateral ethmoids. The posteroventral region of the median ethmoid forms a wedge-shaped socket into which the ethmoid cartilage is inserted.

The lateral ethmoids (LE) are somewhat elongate elements extending laterally on either side of the median ethmoid. Each lateral ethmoid bifurcates medially into an anteromedial process, which is synchondrally joined to the median ethmoid, and a posteromedial process, which is connected to the ethmoid cartilage. The gap between the two medial processes serves as the olfactory nerve foramen. The anteroventral surface of the anteromedial process bears a small shelf that articulates with the ethmoid process of the palatine. The lateral cartilaginous extension of the lateral ethmoid articulates with the lacrimal. The posterior surface of the lateral ethmoid is flat and plate-like, forming the anterior wall of the orbital.

The frontals (FR) are somewhat broad and flat posteriorly, where they form the anterior roof of the cranium, and very narrow anteriorly, where they extend to meet the median ethmoid. Each frontal is tightly joined to its fellow along nearly its entire length. Laterally, the frontal overlaps the pterosphenoid, sphenotic, and pterotic.

Posteriorly it overlaps the supraoccipital and the anterior corner of the epioccipital. The frontal bears neither a sagittal crest nor supraorbital troughs. On its ventrolateral surface near midlength the frontal bears a socket, which receives the dorsal end of the pterosphenoid.

The sphenotics (SPH) form the anterolateral wall of the cranium and the posterior margin of the orbit. Each sphenotic is bounded anteriorly by the pterosphenoid, ventrally by the prootic, posteriorly by the pterotic, and dorsally by the frontal. The sphenotic bears a broad lateral shelf buttressed by two struts. A shallow depression posteroventral to the shelf receives the anterodorsal strut of the hyomandibula. Internally the sphenotic bears a narrow curved ridge running from its posterodorsal corner to its midventral margin. This ridge is continuous with a dorsoventrally oriented ridge on the internal surface of the prootic.

The pterotics (PTO) form the posterolateral wall of the cranium. Each pterotic is bounded dorsomedially by the supraoccipital and epioccipital, posteriorly by the exoccipital, ventromedially by the intercalar and subtemporal fossa (STF), anteroventrally by the prootic, and anterodorsally by the sphenotic. The pterotic bears a lateral shelf in line with, but not continuous with, that of the sphenotic. Just ventral to the anterior terminus of this shelf, the pterotic receives the posterodorsal strut of the hyomandibula. Internally the pterotic forms a large longitudinally oriented tube that houses the horizontal semicircular canal.

The epioccipitals (EPO) form the posterior roof of the cranium. Each epioccipital is bounded anteromedially by the supraoccipital, medially by its fellow,

posteriorly by the exoccipital, and laterally by the pterotic. The posterior extension of the supraoccipital overlies the epioccipital medially. Each epioccipital bears a broad, rounded, posterolaterally directed ridge corresponding to an interior tube that houses the posterior vertical semicircular canal. On this ridge is a small laterally directed spine, which receives the dorsal arm of the posttemporal.

The supraoccipital (SOC) is a single elongate bone with broad lateral extensions. Its anterolateral margins lie underneath the frontals. The supraoccipital is bounded laterally by the sphenotics, pterotics, and epioccipitals. The posterior extension of the supraoccipital overlies the medial margins of the epioccipitals and exoccipitals. Along its posterior midline the supraoccipital bears a low crest and internally it bears two elongate lateral depressions.

The exoccipitals (EXO) form the posterior wall of the cranium. Each exoccipital is bounded anterodorsally by the epioccipital and anterolaterally by the pterotic and intercalar. Along its dorsomedial margin the exoccipital is joined to its fellow. The dorsal junction lies deep to the supraoccipital, while the ventral margin lies deep to the basioccipital. The exoccipitals thus form the dorsal and lateral margins of the foramen magnum. Each exoccipital bears a posterolaterally directed condyle that articulates with the anterolateral processes of the atlas. The vagus nerve foramen lies at the anterior base of this condyle. The glossopharyngeal foramen, which is somewhat larger than the vagus, pierces the exoccipital anterolaterally to the condyle. Inferiorly, the exoccipitals each bear a thin anteroventrally directed bony strut that terminates ventrally as a bilobed “foot” straddling an internal ridge on the basioccipital.

The basioccipital (BO) forms the posteromedial floor of the cranium and the ventral margin of the foramen magnum. Anteriorly it lies dorsal to the posterior parasphenoid and is bounded by the prootics. Laterally it is overlapped by the intercalars. Its posterior extension lies ventral to the exoccipitals. It bears a small medial ridge on its ventral surface that culminates in a posterior condyle. This condyle articulates with the anteromedial process of the atlas. Baudelot's ligament attaches to the basioccipital on each side near the base of the condyle. Inferiorly, the basioccipital bears two longitudinally oriented low ridges. Each ridge bears a small notch that receives the base of the exoccipital strut.

The small, thin intercalars (INT) overlap the lateral margins of the basioccipital and the anteroventral margins of the exoccipitals. The intercalar forms the posteromedial boundary of the subtemporal fossa. It receives a ligament from the ventromedial arm of the posttemporal.

The prootics (PRO) form the anterolateral floor of the cranium. Each prootic is bounded and slightly overlapped medially by the parasphenoid. It is bounded anterodorsally by the sphenotic, posterodorsally by the pterotic and subtemporal fossa, and posteroventrally by the basioccipital. The prootic bears the large facial nerve foramen. Along its anterodorsal margin the prootic bears a notch that, in conjunction with a smaller notch in the anteroventral margin of the sphenotic, forms the trigeminal nerve foramen. The prootic bears a broad ridge near its internal posterior margin and a narrower Y-shaped ridge on its anterior internal surface. The posterior ridge is

continuous with the internal ridge of the basioccipital, and the anterior ridge is continuous with that of the sphenotic.

The small pterosphenoids (PTS) lie anterior and medial to the sphenotics, and ventral to the frontals. They form a portion of the posterior margin of the orbitals. Each pterosphenoid is bounded dorsally by the frontal, posteriorly by the sphenotic, and ventrally by the parasphenoid. The pterosphenoid is excluded from the margin of the trigeminal nerve foramen, but bears its own foramen visible in anterior view.

The parasphenoid (PS) is a large elongate bone along the ventral cranial midline. It is composed of a narrow anterior extension and a broad posterior section. The anterior extension terminates in the ethmoid region along the dorsal surface of the vomer, with which it forms a tight syndesmosis. Near the middle of its length, the parasphenoid begins to broaden to form the anterior floor of the cranium. Two lateral extensions rise dorsolaterally to meet the ventral margins of the pterosphenoids. The posterior margins of these lateral extensions and the lateral margins of the middle third of the parasphenoid are bounded by the prootics. Immediately posterior to the lateral extensions, the parasphenoid is deeply notched. The notches, along with the anteromedial margins of the prootics, circumscribe the internal carotid artery foramen. Posteriorly the parasphenoid narrows to a slightly emarginate apex. This posterior region overlaps and is posterolaterally bounded by the basioccipital. Internally the parasphenoid bears two lateral sockets along the posterior margins of its lateral extensions, which receive the ventral extensions of the pterosphenoids, and a single

medial socket near midlength that serves as the attachment point for the ocular rectus muscles.

The basisphenoid and parietals are absent.

Jaws, Suspensorium, and Opercular Series.—(Figs. 3.6, 3.7) The premaxilla (PMX) bears well-developed ascending, articular, and postmaxillary processes. The ascending processes of the left and right premaxillae are closely aligned and slide along the dorsal surface of the oval-shaped rostral cartilage (RC) that overlies the median ethmoid. Nasal bones are absent. The articular process receives the medial process of the maxilla, and the postmaxillary process is tucked under the maxilla as the jaw is closed. Sharp, conical, curved teeth are present along the entire length of the premaxilla. They are arranged in 3-4 indistinct rows, decreasing posteriorly to 2 rows, with the outer row bearing the largest teeth.

The maxilla (MAX) is an elongate bone, nearly twice the length of the premaxilla. Anteriorly it bears medial and lateral processes that straddle the articular process of the premaxilla. The anterolateral face of the lateral process of the maxilla articulates with the maxillary process of the palatine. The maxilla also bears a large triangular process along its dorsal margin at approximately mid-length. Posteriorly the maxilla extends well beyond its point of articulation with the dentary, nearly to the anteroventral terminus of the preopercle.

A thin, platelike, somewhat triangular lacrimal (LAC) lies along the dorsolateral surface of the maxilla. This is the only element of the infraorbital series present. It is joined at its anterodorsal margin to the lateral ethmoid and bears no foramen.

The dentary (DEN) bears sharp, conical, slightly curved teeth along the anterior two-thirds of its length. The teeth are arranged in 3-4 rows near the dentary symphysis, but decreasing posteriorly to a single row. Near its posterior end the dentary bears a well-developed coronoid process that projects posterodorsally between the palatine and maxilla. This process serves as a major attachment point for the adductor mandibulae. The medial surface of the dentary bears a groove that serves as the anterior insertion point for Meckel's cartilage. Anteriorly the dentary is bound to its fellow at the dentary symphysis. Posteriorly, the dentary is joined to the lateral surface of the articular.

The anguloarticular (ANG) is divided anteriorly into two elongate pointed processes. The anterodorsal process lies medial to the posterior half of the dentary. The long, narrow Meckel's cartilage originates on the medial surface of the anguloarticular just anterior to its articulation with the quadrate. It continues anteriorly beyond the anterior end of the anterodorsal process of the anguloarticular and inserts into a groove along the medial surface of the dentary. A small sesamoid articular (SES) lies along the Meckel's cartilage on the medial face of the anguloarticular. The anteroventral process of the anguloarticular runs parallel to the dentary slightly ventral to it. Along its posterodorsal surface the anguloarticular bears a circular socket that receives the anteroventral process of the quadrate.

The small L-shaped retroarticular (RET) is situated along the medial surface of the anguloarticular just ventral to its articulation with the quadrate. It is attached dorsally to the medial surface of the anguloarticular and ventrally to the interopercle via a ligament.

The hyomandibula (HYO) is a complex element with three cylindrical struts, each bearing a cartilaginous cap. The anteriormost strut, along the anterodorsal margin of the hyomandibula, articulates with the sphenotic. The middle strut, along the dorsal margin of the hyomandibula, articulates with the pterotic. The posteriormost strut lies along the posterior margin of the hyomandibula and articulates with a socket on the anterior margin of the opercle. The hyomandibula also bears a groove along the posterior margin into which the anterodorsal margin of the preopercle is inserted. Along its anterolateral surface, the hyomandibula is synchondrally attached to the dorsal end of the symplectic. A shallow depression on the lateral surface of the hyomandibula ventral to the anteriormost strut receives the dorsal end of the metapterygoid. Posterior to its junction with the metapterygoid, the hyomandibula bears a foramen through which the hyomandibular branch of the facial nerve passes.

The metapterygoid (MPT) is a large, flat bone that dominates the symplectic-metapterygoid strut. It is synchondrally attached to the lateral surface and dorsal margin of the quadrate along its anteroventral margin, and to the hyomandibula along its dorsomedial surface. The mesopterygoid is absent.

The symplectic (SYM) is approximately the same length as the metapterygoid, but is much narrower, particularly its ventral end. Its broad dorsal margin is bound

synchondrally to the hyomandibula, and the dorsal half of its anterior margin contacts the posterior margin of the metapterygoid. The ventral half of its anterior margin follows the posterior contour and medial surface of the quadrate. The ventral terminus of the symplectic is inserted into a pocket along the medial surface of the quadrate, just posterior to its articulation with the anguloarticular.

The large hatchet-shaped quadrate (QU) bears three processes: a knobby anteroventral process that forms a saddle joint with the anguloarticular; a flat dorsal process that provides attachment points for the metapterygoid along its dorsal margin and lateral surface, and for the ectopterygoid along its anterior margin; and an elongate posterior process that bears a groove along its ventral margin. The anterodorsal surface of the preopercle is inserted into this groove.

The ectopterygoid (PT) is long and slender, produced into a point at its anterior end. For the anterior half of its length it runs along the dorsomedial surface of the palatine, where it terminates anteriorly. Posteriorly it is synchondrally bound to the quadrate.

The palatine (PAL) is approximately equal to the ectopterygoid in length. Its posterior end is pointed and bound tightly to the lateral surface of the ectopterygoid. Anteriorly it bears two bulbous processes. The medially oriented ethmoid process articulates with the lateral ethmoid, while the laterally oriented maxillary process articulates with the lateral process of the maxilla.

The opercle (OP) is a large flat bone whose posterodorsal margin is very poorly ossified. Anteriorly it bears a well-developed socket that receives the posterior strut of

the hyomandibula. On the medial face of the opercle a strong ridge radiates posterodorsally from this process toward the margin.

The subopercle (SOP) is also a thin flat bone. Its posterior and ventral margins are poorly ossified. It is somewhat J-shaped with the ventral extension of the opercle inserted in its anterodorsal recess. The opercle overlies the subopercle along most of their common margin. The subopercle is attached ligamentously at its anteroventral extremity to the posterior end of the interopercle.

The preopercle (POP) is a heavy, well-ossified bone separated from the symplectic by a wide gap. It is tightly bound to the hyomandibula along its anterodorsal margin. The dorsal margin of its anteroventral extension lies in a groove along the ventral surface of the quadrate. The preopercle bears a prominent ridge along its lateral midline and a small foramen near its dorsal end.

The interopercle (IOP) is a small flat bone lying medial to the ventral extension of the preopercle. Ligaments at its posterior end bind it to the lateral surface of the posterior ceratohyal and to the subopercle, and a ligament at its anterior end binds it to the retroarticular.

Hyoid Arch.—(Fig. 3.8) The short interhyal (IH) connects the hyoid arch to the suspensorium. It is a small cylindrical element with anterior and posterior flanges and a small shelf on the lateral face. This shelf serves as the attachment point for a broad ligament that connects the interhyal with the posteromedial surface of the preopercle. Another ligament originating on the ventromedial face of the interhyal extends

dorsomedially, joining with the ligamentous extension of the anteromedial process of epibranchial 1 and then attaching to the prootic posterolateral to the internal carotid foramen. The cartilaginous dorsal end of the interhyal is attached to the medial surface of the preopercle and to the hyomandibula along its posteroventral connection to the preopercle. The cartilaginous ventral end of the interhyal articulates with the posterior ceratohyal.

The posterior ceratohyal (PC) is flat and triangular in shape, with a small socket on its posterodorsal margin. This socket receives the ventral end of the interhyal. The entire anterior margin of the posterior ceratohyal is synchondrally bound to the anterior ceratohyal.

The anterior ceratohyal (AC) is a long, hatchet-shaped bone that forms the bulk of the hyoid arch. Its posterior margin is tightly bound to the posterior ceratohyal. At its anterior end the anterior ceratohyal is capped dorsomedially and anteromedially by the dorsal and ventral hypohyals, respectively. The ventral margin of the broad posterior section is cartilaginous.

Five branchiostegal rays (BR) are present. The anteriormost ray is slender and nearly cylindrical, while the others are more flattened and broad; the posteriormost ray is the largest. The anteriormost branchiostegal ray is borne on the ventral surface of the elongate anterior process of the anterior ceratohyal. Branchiostegals 2–4 are borne on the ventrolateral face of the blade-like posterior process. The lateral surface of the posterior ceratohyal near its anteroventral apex bears the posteriormost branchiostegal ray.

The dorsal hypohyal (DH) lies on the anterior dorsomedial surface of the anterior process of the anterior ceratohyal. It is synchondrally bound to the ventral hypohyal and to its fellow by a ligament attached along its posterior margin. The ventral hypohyal (VH) is ligamentously bound on its dorsal surface to the posterolateral surface of the basihyal and along its anteromedial surface to the anterolateral surface of the urohyal.

The basihyal (BH) is broad, flat, and approximately Y-shaped. The anterior margins of its two broadly rounded anterior processes are cartilaginous, and a thin shelf of bone spans the deepest portion of the gap between these two processes. Ligaments on its posteromedial surfaces bind the basihyal to the ventral hypohyals and a ligament along its posterior margin binds it to the urohyal. A pair of long, stout ligaments on the lateral surfaces of the anterior processes bind the basihyal to the ventral hypohyals.

The urohyal (UH) lies along the midline between the hyoid arches. It is thin and flat, presenting a narrow dorsal profile in position ventral to the basibranchials. Its anterodorsal margin bears a dorsally flattened T-shaped process, which underlies the cartilaginous first basibranchial. Anteriorly this process bears a ligament attached to the basihyal. Along its anteroventral margin, the urohyal is produced into two small lateral lobes. Each of these lobes receives a ligament from its respective ventral hypohyal. The posterior margin of the urohyal is emarginate in lateral view.

Branchial Apparatus.—(Fig. 3.9) Four basibranchials (BB) are present. Basibranchial 1 is a peanut-shaped cartilaginous element lying on the dorsal surface of the anterodorsal

process of the urohyal. It is ligamentously attached to the cartilaginous anteromedial ends of hypobranchials 1. Basibranchials 2 and 3 are long rod-shaped elements that bear cartilaginous anterior and posterior tips. They are synchondrally joined to each other. Basibranchial 2 bears two small keels arranged in parallel along its ventral surface, while basibranchial 3 bears a single medial keel on its ventral surface. Basibranchial 4 is a diamond-shaped element completely composed of cartilage.

Three pairs of hypobranchials (HB) are present. Hypobranchials 1 and 2 are similarly shaped. They consist primarily of a main shaft, whose anterior half is directed laterally, then angled posterolaterally near midlength. The anteromedial and posterolateral ends of hypobranchial 1 and hypobranchial 2 are cartilaginous. The anteromedial end of hypobranchial 1 is slightly more broad, and that of hypobranchial 2 significantly more broad, than the rest of the shaft. Each element bears a strong anteroventrally directed spine along its anterior margin near midlength. Hypobranchial 1 is closely associated with its fellow along the midline, attached via a ligament to basibranchial 1. Its posterolateral tip articulates with ceratobranchial 1. Hypobranchial 2 articulates anterodorsally with basibranchial 2 and basibranchial 3 and posterolaterally with ceratobranchial 2. Hypobranchial 3 is a largely cartilaginous club-shaped element. Its cylindrical anterolateral process bears a rounded cartilaginous tip. The main body of hypobranchial 3 articulates with its fellow and with basibranchial 3 along its anteromedial surface, with basibranchial 4 along its posteromedial surface, and with ceratobranchial 3 along its posterolateral surface.

Five pairs of ceratobranchials (CB) are present, all bearing cartilaginous anteromedial and posterolateral tips. Ceratobranchial 1 bears eight slender pointed gill rakers. Each ceratobranchial articulates anteromedially with its respective hypobranchial and posterolaterally with its respective epibranchial, except ceratobranchial 4, which articulates anteromedially with basibranchial 4. There are no toothpatches on ceratobranchials 1–4. Ceratobranchial 5 bears the lower pharyngeal toothplate, which is somewhat perforated and bears approximately 50 sharp, slightly curved teeth. The toothplate and anteromedial extension of ceratobranchial 5 is closely associated with its fellow.

Epibranchials (EB) 1–4 are present, all with cartilaginous tips. Epibranchial 1 bears an uncinate process, which articulates with a small interarcual cartilage that in turn articulates with the anterior margin of infrapharyngobranchial 2. Along its lateral arm, epibranchial 1 bears 2–3 small slender gill rakers. Epibranchial 2 is simply rod-shaped, its medial tip articulating with the posterolateral margin of infrapharyngobranchial 2. Epibranchial 3 bears a small lateral uncinate process. It articulates laterally with ceratobranchial 3 and medially with the lateral margin of infrapharyngobranchial 3. Epibranchial 4 is an angled rod-shaped bone with a prominent rounded spine midway along its dorsal surface. Its medial end appears to articulate with the posterolateral margin of infrapharyngobranchial 3.

Infrapharyngobranchials (IPB) 2–4 are present, each fused with its respective pharyngeal toothplate. The toothplates are all highly perforated and bear sharp, slender, slightly curved teeth, while the supporting infrapharyngobranchials are greatly reduced,

consisting primarily of cartilaginous patches connected by a thinly ossified lamina.

Infrapharyngobranchial 3 is the largest of the three. It bears a large open space in the middle, an anterior patch of cartilage articulating with infrapharyngobranchial 2, and a posterolateral patch of cartilage articulating with infrapharyngobranchial 4 and epibranchials 3 and 4. Infrapharyngobranchial 2 bears an anterior cap of cartilage bound ligamentously to the interarcual cartilage and a posterolateral patch of cartilage that articulates with epibranchial 2. Infrapharyngobranchial 4 consists only of a small thin triangular lamina with a small posterolateral patch of cartilage.

Paired Fins.—(Figs. 3.10, 3.11) The posttemporal (PTM) is divided anteromedially into two elongate processes. The dorsal process is tightly bound to the epioccipital and the ventral process attaches via a ligament to the intercalar. The lateral surface is broadened near the junction of the anteromedial processes, forming a flat surface for muscle attachment. The posteromedial surface of the posttemporal articulates with the anterolateral surface of the supracleithrum. Oculoscapular canals are absent.

The supracleithrum (SCL) is a small, flattened rod. Its posterior end articulates with the dorsolateral surface of the cleithrum. Postcleithra are absent.

The cleithrum (CL) is a large, elongate bone that forms the structural base of the pectoral girdle. Dorsally it is split into a pair of processes. Baudelot's ligament passes between these processes and attaches on the medial surface of the supracleithrum. On its posteromedial surface the cleithrum bears a small knobby process that articulates with the anterior arm of the pelvic intercleithral cartilage, which in turn attaches the

pectoral girdle to the pelvic girdle. The right and left cleithra are joined near their ventral ends by the small ventral intercleithral cartilage.

The scapula (SCA) and coracoid (COR) are almost completely fused, nestled in a groove along the posteromedial surface of the cleithrum. The elongate scapula is almost completely cartilaginous, with apparent ossification only near its dorsal terminus, where it is pierced by a foramen. The coracoid is shorter, wider, and more completely ossified than the scapula and bears a narrow posteriorly directed process.

Along the posterior edges of the cleithrum, scapula, and coracoid lie four large flat cuboidal proximal radials (PR) almost completely sheathed in cartilage. The cartilaginous sheath enveloping the proximal radials is perforated by three large openings, one at each gap between adjacent radials. The cartilaginous sheath does not entirely envelop the ventral proximal radial. Twenty small, ovoid distal radials (DR) lie at the bases of the twenty segmented pectoral-fin rays along the posterior margin of the proximal radials. The pectoral girdle is joined to the pelvic girdle via the large butterfly-shaped pelvic intercleithral cartilage.

The pelvic fins are fused along the ventral midline. The large butterfly-shaped pelvic intercleithral cartilage (PIC) joins the two pelvic bones and connects the pelvic girdle to the cleithra. The pelvic intercleithral cartilage bears two anterior and two posterior extensions. The anterior extensions articulate with the cleithra, while the posterior extensions are inserted into cone-shaped recesses on the anterior pelvis.

The pelvis (PV) is a complex and delicate bone. Its anterior portion consists of the thinly ossified elongate processes that surround the pelvic intercleithral cartilage.

The most lateral of these processes bears a dorsally directed blade-like extension that is closely associated with the posterior process of the coracoid. Medial to the pelvic intercleithral cartilage, the pelvis bears a thin, flat process and a delicate ventrally directed extension. The posterior portion of the pelvis is more substantial, providing attachment points for the fin elements.

The pelvic fins are modified into an adhesive disk, with the segmented rays supporting the posterior and lateral margins of the disk and the spines supporting the anterior margin. The spine of each pelvic fin is therefore not in line with the segmented rays, but rather displaced ventrally and medially. Each pelvic fin consists of one spine (PVS) and five segmented rays (PVR). In each fin, a single large oval cartilaginous radial (PVC) supports the spine and four most lateral soft rays. A small circular cartilaginous radial supports the most medial soft ray. The pelvic spine bears a dorsally directed spur.

Vertebral Column, Medial Fins, and Caudal Skeleton.—(Figs. 3.12, 3.13) There are 16 abdominal and 20 caudal vertebrae (16 + 19 in 19 of 25 specimens), including the urostyle. Caudal vertebrae are defined as those bearing a closed haemal canal and an elongate haemal spine (in some specimens the posteriormost abdominal vertebra has an enclosed haemal canal but no haemal spine).

The abdominal vertebrae (VT 1–16) all bear strong neural spines (NS) and, except the atlas, all bear well-developed parapophyses (PAP). The parapophyses originate near the dorsal margin of the centrum on all abdominal vertebrae except

vertebrae 14–16, on which they originate near the ventral margin of the centrum. All abdominal vertebrae bear well-developed neural prezygapophyses (NEZ). Neural postzygapophyses (NOZ) are not present on the several anteriormost abdominal vertebrae but are present on the rest, becoming gradually more prominent among the posteriormost abdominal vertebrae. At least one lateral foramen pierces all abdominal vertebrae on each side of the neural arch, and vertebrae 1–4 bear two foramina on each side. Epineurals (EPN) are present on vertebrae 1–13, and pleural ribs (PLR) are present on vertebrae 3–14. Vertebra 15 bears a small pleural rib on the right side only (absent in comparative cleared-and-stained specimen). The first vertebra, or atlas, bears two anterolateral processes that articulate with the condyles of the exoccipitals. A Baudelot's ligament attaches to the posterolateral surface of each of these processes. Anteromedially the atlas presents a ventrally tilted face for articulation with the basioccipital.

All caudal vertebrae, except for the urostyle, bear well developed neural and haemal spines (HS). Neural prezygapophyses are prominent on several of the anteriormost and posteriormost caudal vertebrae but not on those near the center of the series. Neural postzygapophyses are prominent on vertebrae 17-29 but not on the others. Haemal pre- and postzygapophyses are absent. Vertebrae 17-32 bear a lateral foramen dorsal to the centrum.

The first dorsal fin consists of five to seven spines (six in 21 of 26 specimens). The five anteriormost spines are closely spaced, while the sixth is separated from the others by a larger gap. Each spine is associated with a single pterygiophore, which

consists of a fused proximal and medial radial (PR + MR). Distal radials are absent. Each proximal radial + medial radial element bears an anteroventrally directed process with anterior and posterior flanges (except the sixth pterygiophore, which bears only a posterior flange) and a posterodorsally directed process. Both the anteroventral and posterodorsal tips of each pterygiophore are cartilaginous. The anteriormost pterygiophore is inserted in the interneural space 4, and the first dorsal-fin pterygiophore formula is 4-12111000. There is some variation in first dorsal-fin pterygiophore formula, and most of the specimens examined (15 of 25) exhibited a formula beginning with 4-122.

The second dorsal fin consists of one spine and ten to twelve segmented soft rays (I,11 in 14 of 26 specimens). The anterior spine is supported by a single pterygiophore consisting of two parts: an elongate proximal radial + medial radial element with an anterior flange and a small knob-like distal radial (DR). The first soft ray is supported by a similar two-part pterygiophore, but the proximal radial + medial radial element lacks an anterior flange. Soft rays 2–11 are each supported by a single pterygiophore consisting of three parts: an elongate proximal radial, cartilaginously joined to an elongate medial radial, and a small knob-like distal radial that articulates with the fin ray via two lateral processes (Fig. 3.13 inset). The posteriormost ray is divided to its base but is supported by a single pterygiophore. This pterygiophore consists of a shortened proximal radial and an irregularly shaped medial radial that bears cartilaginous ventral and posterior processes. The distal radial is absent. The

anteriormost pterygiophore is inserted in interneural space 11, 12, or 13 (12 in 18 of 25 specimens).

The anal fin consists of one spine and nine to eleven segmented soft rays (I,10 in 13 of 25 specimens). The anterior spine and the first soft ray are both supported by a single pterygiophore. This pterygiophore consists of an elongate element (PR + MR) with an anterior flange and two small distal radials. The distal radial that articulates with the anterior spine is associated with the ventral surface of the proximal radial + medial radial, while that which articulates with the first soft ray is associated with its posteroventral edge. A single three-part pterygiophore identical to those in the second dorsal fin supports each of the soft rays 2–10. The posteriormost soft ray is also as in the first dorsal fin. Two anal-fin pterygiophores are inserted anterior to the first haemal spine (20 of 24 specimens).

Vertebra 34 is slightly modified, bearing somewhat flattened neural and haemal spines. Vertebra 35 is highly modified to support the caudal structure. Its neural spine is shortened and very broad. Its haemal spine is elongate and flattened, consisting of a cylindrical process flanked anteriorly by a bladelike flange, and its haemal canal bears a large lateral foramen on either side. The tip of the haemal spine of vertebra 35 is cartilaginous.

The posteriormost vertebra, or urostyle (US), consists of a half centrum fused with hypurals 3 and 4 (HYP 3-4). This element is closely associated with a broad and flat element consisting of the fused hypurals 1 and 2 (HYP 1-2). Hypurals 1-2 are inserted into a groove on the posteroventral surface of the urostyle near the point where

the centrum fuses with hypurals 3-4. The posterior margins of hypurals 1-2 and hypurals 3-4 are cartilaginous.

A small autogenous post-haemal spine cartilage (PHC) is present between the haemal spine of vertebra 35 and the parhypural. The parhypural (PHP) is elongate and cylindrical with small anterior and posterior flanges and a cartilaginous posteroventral margin. Hypural 5 (HYP 5) is somewhat cylindrical and club-shaped, with a cartilaginous posterodorsal margin. Two epurals (EPU) are present. The anterior epural is flat and plate-like, while the posterior epural is a cylindrical strut with a broad anterior flange.

Procurrent cartilaginous plates (PRC) support eleven dorsal (9-12 in comparative specimens) and ten ventral (9-11 in comparative specimens) procurrent rays. A single segmented but unbranched ray flanks the branched caudal rays ventrally, articulating with the haemal spine of vertebra 35. The 15 branched caudal rays (BCR 1-15) articulate as follows: the first with the post-haemal spine cartilage, the second with the parhypural, rays 3-7 with hypurals 1-2, rays 8-14 with hypurals 3-4, and ray 15 with hypural 5. Another segmented but unbranched ray articulates with the posterior epural. The total number of caudal elements is therefore 38 (35-40 in comparative specimens).

COMPARATIVE OSTEOLOGY

Neurocranium.—The gobioid neurocranium, like many other regions of the gobioid skeleton, is composed of a reduced number of elements relative to other

perciform groups. The parietals and basisphenoid are absent, the intercalar is reduced or lost, and the circumorbital series is represented only by the lacrimal (Springer, 1983). In general, the neurocrania of species examined in this study are somewhat elongate and depressed, particularly in comparison with *Microgobius signatus* and *Istigobius ornatus*. All gobionelline genera examined have a large ethmoid cartilage lying ventral to the median ethmoid (Character 1). In contrast, both *Microgobius signatus* and *Istigobius ornatus* have a more extensive median ethmoid, with the ethmoid cartilage lying anterior to it. Therefore, the position of the ethmoid cartilage may represent a synapomorphy for the Gobionellinae.

The *Chasmichthys* Group exhibits two very different types of vomer-ethmoid attachment (Character 2). The most common form of this attachment is exhibited by *Gymnogobius macrognathos* (Fig. 3.2). In this species, the vomer is attached to the median ethmoid by a single narrow bridge of bone overlying the ethmoid cartilage. The other form of this attachment consists of two struts of bone on the median ethmoid that form a more broad and robust bridge to the vomer. The latter condition is shared by four species of *Gymnogobius* (*G. mororanus*, *G. heptacanthus*, *G. castaneus*, and *G. breunigii*) and *Lepidogobius lepidus*. It almost certainly arose more than once, and is therefore of questionable phylogenetic utility.

Like previously surveyed gobiid species, those represented in this study all have a vertically oriented interorbital element bridging the gap between the anterior extensions of the frontals and the vomer-parasphenoid strut (Fig. 3.2). This is a posterior extension of the ethmoid cartilage, and in most of the species examined this

element is cartilaginous, similar to that of *Istigobius ornatus* and *Xenisthmus clarus*. However, in a few species (*Chaenogobius annularis*, *Gillichthys mirabilis*, *Gillichthys seta*, *Ilypnus gilberti*, *Quietula y-cauda*, and *Gnatholepis anjerensis*) this element is ossified, forming a bony division between the anterior portion of the orbitals, similar to that of *Microgobius signatus* (Character 3). However, this character may be somewhat dependent on the size of the specimen or be subject to intraspecific variation. Its phylogenetic utility can therefore not be clearly determined without examining a large series of specimens of each species.

Several features of the frontal bones are variable within this study group. First, nearly all of the species examined have a supraorbital groove on the lateral margin of the dorsal surface of the frontal (Character 4) that houses the posterior interorbital portion of the oculoscapular canal. This character has also been reported in *Microgobius signatus* and *Istigobius ornatus*. The exceptions in this group are two species of *Gymnogobius* (*G. macrognathos* and *G. uchidai*), which lack this groove entirely, despite the presence of interorbital oculoscapular canals (Fig. 3.2). This reduction is a synapomorphy for the *G. macrognathos* + *G. uchidai* clade, and if shared with *G. cylindricus* and *G. scrobiculatus*, may represent a synapomorphy uniting a *G. macrognathos* species group. Second, in some species of gobies, such as *Microgobius signatus*, the posteromedial margins of the frontals project dorsally to form a medial ridge (Birdsong, 1975). This ridge may extend posteriorly to meet the supraoccipital crest. Of the species examined in this study, only *Eucyclogobius newberryi* has such a frontal ridge (Character 5). Third, most species of gobies have the right and left frontals

tightly joined along nearly their entire length, diverging only near the anterior ends. This is also true of all of the species examined in this study except *Eucyclogobius newberryi*, in which the frontals are separated from each other along the anterior third of their length by a wide gap. This condition has never before been reported in gobies and its significance is uncertain, but is here considered autapomorphic in *Eucyclogobius*.

Previously published studies on the osteology of *Istiogobius ornatus* (Murdy, 1985) and *Microgobius signatus* (Birdsong, 1975) have reported the presence of a small anteroposteriorly oriented trough on the external surfaces of the sphenotic and pterotic. This trough houses the posterior portion of the oculoscapular canal. Members of the *Chasmichthys* Group lack posterior oculoscapular canals, and for the most part lack the sphenotic-pterotic trough as well (Character 6). However, there are exceptions to this pattern. Both species of *Chaenogobius* have the sphenotic-pterotic trough, and *Eucyclogobius newberryi* seems to have retained only the sphenotic portion of this trough. The gobionelline outgroup genera (*Acanthogobius* and *Tridentiger*) examined also share the presence of the sphenotic-pterotic trough. It therefore appears that the presence of this character is plesiomorphic for this group, and its loss represents a derived condition. However, the phylogenetic tree presented here indicates that the sphenotic-pterotic trough has been lost twice: in the genus *Gillichthys* and in the lineage leading to *Gymnogobius* and the remainder of the *Chasmichthys* Group.

The intercalars are small elements of the gobioid neurocranium, but are highly variable in size and morphology. Some gobies (e.g., *Istiogobius ornatus*) have fairly

large intercalars that completely cover the subtemporal fossa. While none of the species examined in this study exhibit that condition, many, including the gobionelline outgroups, have an intercalar that is large enough to overlap the prootic (Character 7). In contrast, many species of *Gymnogobius* (*G. macrognathos*, *G. uchidai*, *G. mororanus*, *G. heptacanthus*, and *G. breunigii*), as well as most other *Chasmichthys* Group genera (*Clevelandia*, *Eucyclogobius*, *Ilypnus*, *Lepidogobius*, and *Quietula*) have somewhat reduced intercalars that do not overlap the prootic. Reduced intercalars unite the *Clevelandia + Eucyclogobius + Ilypnus + Lepidogobius + Quietula* clade as well as the larger of the two *Gymnogobius* clades (with the exception of *G. castaneus*). Additionally, the intercalar may or may not bear a foramen (Character 8). Of the species examined in this study, only *Lepidogobius lepidus* bears an intercalar foramen. However, a number of species of *Gymnogobius* (*G. opperiens*, *G. mororanus*, *G. heptacanthus*, and *G. castaneus*) have a U-shaped notch in the anterior margin of the intercalar. The homology of this notch with the intercalar foramen of *Lepidogobius* and other gobies is uncertain.

The pterosphenoids are small bones on the anterolateral margins of the braincase. Previous studies have indicated that these bones may (Murdy, 1985) or may not (Birdsong, 1975) bear a foramen in gobies. Most of the species examined in this study have a pterosphenoid foramen, the only exception within the *Chasmichthys* Group being *Quietula y-cauda* (Character 9). However, in a few of the species examined, including *Gymnogobius mororanus*, *G. heptacanthus*, and *Acanthogobius flavimanus*, the foramen is not completely enclosed. The pterosphenoid is also present outside the

Chasmichthys Group and in at least one species outside the Gobionellinae (*I. ornatus*), so its distribution requires further investigation. The pterosphenoids in all species examined appear similar in shape and size to those of *Microgobius signatus* and *Istigobius ornatus*.

The small, flat lacrimal bone bears a foramen in *Microgobius signatus* and *Istigobius ornatus*, as well as in the gobionelline *Acanthogobius flavimanus* (*Tridentiger brevispinis* appears to lack a lacrimal). Though the shape and size of the lacrimal is similar in the *Chasmichthys* Group, none of the species examined within this group bear a lacrimal foramen (Character 10). However, *Gnatholepis anjerensis*, which is not a member of the *Chasmichthys* Group, also lacks a lacrimal foramen. Therefore, a more thorough survey of this character within the Gobionellinae is necessary before its phylogenetic utility can be realized.

Nasal bones, present in *Microgobius signatus*, *Istigobius ornatus*, and *Gnatholepis anjerensis*, are absent in all members of the *Chasmichthys* Group (Character 11). They are also absent in *Acanthogobius flavimanus* and *Tridentiger brevispinis*. The lack of nasal bones may therefore be a synapomorphy uniting a subset of the Gobionellinae, including the *Chasmichthys* and *Acanthogobius* Groups, or a redefined Gobionellinae excluding *Gnatholepis*.

Jaws, Suspensorium, and Opercular Series.—The gobioid suspensorium is considerably modified relative to other perciform groups. Most notably, there is a wide gap between the symplectic and the preopercle and the dorsal end of the interhyal does not meet the

dorsal end of the symplectic. In addition, the symplectic generally dominates the symplectic-metapterygoid strut and the mesopteryoid is reduced or absent (Springer, 1983).

In almost all members of the *Chasmichthys* Group, the maxilla is unremarkable relative to other gobioid species. However, in *Lepidogobius lepidus* the anteromedial process of the maxilla, which articulates with the articular process of the premaxilla, bears a large portal (Character 12). Although unique within the *Chasmichthys* Group, both *Acanthogobius flavimanus* and *Tridentiger brevispinis* share this condition. This also appears to be the case in *Istigobius ornatus*, based on Murdy's (1985) figure 6, although the author made no mention of it. Therefore, this maxillary portal appears to be widespread within the Gobiidae. The lack of such a portal can only be a useful synapomorphy uniting the *Chasmichthys* Group if its reappearance is hypothesized for *Lepidogobius*, or if *Lepidogobius* is removed from the group. In many species examined for this study, the maxilla also bears a triangular process about mid-length along its dorsal surface (Character 13). This process is present only in two species of *Gymnogobius*, both species of *Gillichthys*, and *Clevelandia ios* within the *Chasmichthys* Group, but is also found in two of the three gobionelline outgroups examined. Therefore, it has probably been lost multiple times. Posteriorly, the maxilla extends well beyond its point of articulation with the dentary in many of the species examined, including four species of *Gymnogobius*, both species of *Gillichthys*, *Clevelandia ios*, and *Quietula y-cauda* (Character 14). This posterior extension of the maxilla was not found outside the *Chasmichthys* Group, and therefore has potential utility for

diagnosing a subset of the group, though this would require a subsequent loss of the extension in at least *Gymnogobius*.

The jaws in species included in the study group are also relatively unspecialized and vary little. The one exception within the *Chasmichthys* Group is the dentition on the dentary (Character 15). In most members of the group the dentary bears teeth along at least 2/3 of its length. In these species, the teeth generally extend posterior to the coronoid process of the dentary. However, *Gymnogobius mororanus* and *G. heptacanthus* exhibit a reduced dentition pattern, with only the anterior half of the dentary bearing teeth. It is perhaps significant to note that these two species also have significantly longer, more numerous gill rakers than any other species in this group. This combination of reduced dentition with a proliferation of gill rakers may indicate a dietary preference that differs from other species in the group, and these characters are proposed as synapomorphies uniting these two species. Birdsong (1975) reported a foramen on the anguloarticular of *Microgobius signatus* just ventral to its articulation with the quadrate. That foramen is notably absent from all species examined in this study with the exception of *Acanthogobius flavimanus* and *Gnatholepis anjerensis* (Character 16).

Harrison (1989) published an extensive survey of the palatopteryquadrate complex (palatine, ectopterygoid, and quadrate) in gobioids, and discussed its relevance to gobioid systematics. Several members of the *Chasmichthys* Group ("*Chaenogobius annularis*," "*Chasmichthys dolichoya*," *Clevelandia ios*, and *Gillichthys mirabilis*) were included in Harrison's (1989) study. He concluded that all of these species exhibit

relatively unspecialized character states in this complex, characterized by a palatine extending half the length of the ectopterygoid, a quadrate with a long dorsal lamina, and an ectopterygoid joined to the vertical anterior edge of the quadrate. He was therefore unable to place them conclusively in his phylogeny. This study confirms that all members of the *Chasmichthys* Group share this unspecialized morphology of the palatoptyquadrade complex. However, there is some morphological variation in this study group. For instance, in the majority of the species examined the anteroposterior length of the ectopterygoid is approximately equal to that of the palatine (Character 17). However, in both species of *Chaenogobius* the ectopterygoid is considerably longer than the palatine, while in *Gnatholepis anjerensis* the ectopterygoid is greatly reduced, so that it is considerably shorter than the palatine. Therefore, the elongation of the ectopterygoid is here considered a synapomorphy of the genus *Chaenogobius*, while the reduction of the ectopterygoid is probably autapomorphic in *Gnatholepis*. As Springer (1983) pointed out, within the Gobioidei the symplectic is generally much larger and heavier than the metapterygoid and dominates the symplectic-metapterygoid strut. This is also true of the two non-gobionelline outgroups included in this study as well as the gobionelline *Gnatholepis* (Character 18). However, in all other species examined the symplectic and metapterygoid are approximately equal in size, and neither element can be said to dominate the symplectic-metapterygoid strut. This character requires further attention within the Gobionellinae, and may be useful as a synapomorphy uniting a portion of the subfamily. Finally, several of the gobionelline genera examined have a small spur extending from the posteroventral margin of the symplectic (Character 19).

This spur shows differing degrees of development, in some cases extending to meet a similar spur on the anterodorsal margin of the preopercle. Genera exhibiting this symplectic spur include all in the *Chasmichthys* Group, except *Ilypnus* and *Gymnogobius*, as well as *Tridentiger*.

In almost all surveyed species the preopercle bears some vestige of a preopercular canal (Character 20) ranging from a single foramen (completely absent in *Gymnogobius breunigii*) to a branched canal. Within *Gymnogobius* six species have only a preopercular foramen and four others have unbranched preopercular canals. Both species of *Chaenogobius* and both species of *Gillichthys* have branched preopercular canals, while all other members of the *Chasmichthys* Group have only a foramen. Of the outgroups included in this study, most do not have any enclosed preopercular canals, but instead have an open trough along the posterior margin of the preopercle. *Tridentiger* is the exception to this, having an unbranched preopercular canal. It should be noted that of the species examined in this study, only *Tridentiger brevispinis* and *Acanthogobius flavimanus* have external preopercular oculoscapular canals. The lack of a canal or groove in the preopercle was considered by Takagi (1988) to be derived among gobioid genera. Although it appears to involve a rather complex transformation series, it seems reasonable to consider the branched canal the primitive condition and further reductions in the canal as derived states, culminating in its representation by a single foramen and ultimately its complete absence in *Gymnogobius breunigii*.

In all gobionelline species examined except *Gnatholepis anjerensis*, the preopercle also bears a small anteriorly directed process along its anterodorsal margin (Character 21). In some species (*Chaenogobius annularis*, *Gillichthys mirabilis*, *Quietula y-cauda*, and *Tridentiger brevispinis*) this process contacts the posterior margin of the symplectic. In others (almost all species of *Gymnogobius*, *Clevelandia ios*, *Eucyclogobius newberryi*, *Lepidogobius lepidus*, and *Acanthogobius flavimanus*) this process is present, but does not extend to meet the symplectic. *Gnatholepis anjerensis* lacks this process entirely, as do *Istigobius ornatus* and *Microgobius signatus*.

Hyoid Arch.—Branchiostegal ray number in gobioids ranges from four to seven. The presence of six or seven branchiostegals is common in perciforms and is considered a primitive condition for gobioids (Springer, 1983). All of the specimens examined in this study, as well as *Microgobius signatus* and *Istigobius ornatus*, have five branchiostegals.

The anterior margin of the basihyal is deeply notched in all members of the *Chasmichthys* Group (Character 22). Conversely, in two of the three gobionelline outgroup species examined, and *Istigobius ornatus*, the anterior margin of this bone is rounded. Therefore, the notched condition could be a synapomorphy uniting the *Chasmichthys* Group. However, an anteriorly notched basihyal is not unique to the *Chasmichthys* Group. Takagi (1950) studied the shape of this bone (his glossohyal) in several species of Japanese gobioids. He found several species outside the

Chasmichthys Group that also have a notched basihyal. These included three species from the gobionelline *Astrabe* Group of Birdsong et al. (1988) (*Luciogobius guttatus*, *Astrabe lacticella*, and *Eutaeniichthys gilli*), the gobionellines *Mugilogobius abei* and *Awaous ocellaris*, and the oxudercines *Apocryptodon bleekeri* and *Boleophthalmus pectinirostris*. Using the notched basihyal as the derived condition, Takagi (1950) proposed two separate lineages for these species, both diverging from the *Leucopsarion* condition, in which there is only a very slight notch in the anterior margin of the basihyal. One lineage included *Luciogobius guttatus*, *Astrabe lacticella*, *Mugilogobius abei*, *Awaous ocellaris*, several species of *Gymnogobius*, *Apocryptodon bleekeri* and *Boleophthalmus pectinirostris*. In this lineage, *M. abei* was considered an intermediate and *A. bleekeri* the most specialized. The second lineage included *Eutaeniichthys gilli* and both species of *Chaenogobius*, with the *Chaenogobius* condition considered most specialized. Clearly these lineages do not reflect current theories on gobioid relationships, and it is therefore probable that the notched basihyal arose more than once in gobioid evolution.

Branchial Apparatus.—Springer's (1983) list of gobioid synapomorphies includes only one from the branchial apparatus: basibranchial 1 cartilaginous. This element is cartilaginous in all species examined in this study. Birdsong's (1975) description of *Microgobius signatus* does not show a basibranchial 1, but his specimens were not counterstained for cartilage, so he could have easily missed it.

Within the *Chasmichthys* Group there is some variation in the shape of hypobranchial 3 (Character 23). In most members of this group, as well as the gobionelline outgroups examined and *Microgobius signatus*, the third hypobranchial bears a conspicuous anterolateral extension with a cartilaginous tip. However, in *Gillichthys mirabilis* this bony extension is reduced, and in both species of *Chaenogobius* it is completely absent. It is difficult to evaluate this character in *Istigobius ornatus*, but it appears to represent the reduced condition, similar to that in *Gillichthys*. The reduction and loss of this anterolateral extension is interpreted as a derived condition.

Ceratobranchials 2–4 in both *Microgobius signatus* and *Istigobius ornatus* bear small toothpatches in series along their entire length (Character 24). No such toothpatches are present in any of the members of the *Chasmichthys* Group nor any of the gobionelline outgroups examined. Gill rakers in most of the species included in this study are of moderate length, well separated, and relatively few in number, ranging from 5 to 14 on the first arch (Character 25). However, in both *Gymnogobius heptacanthus* and *G. mororanus* in the *Chasmichthys* Group, as well as *Microgobius signatus*, the rakers are elongate, closely spaced, and numerous, ranging from 21 to 24 on the first arch. This proliferation of gill rakers was almost certainly independently derived in *Microgobius signatus*, but probably represents a synapomorphy uniting the two species of *Gymnogobius*.

In all species included in this study, the second infrapharyngobranchial bears a dorsolateral extension. However, there is some variation in the morphology of this

extension (Character 26). In many species this extension is nothing more than a cartilaginous cap on the margin of the infrapharyngobranchial. In others the extension is a more elongate bony process with a cartilaginous cap. The elongate form of this extension is present in both species of *Chaenogobius* and both species of *Gillichthys* as well as approximately half of the genus *Gymnogobius*, one of the three gobionelline outgroups, and *Istigobius ornatus*. The seemingly random distribution of this character is difficult to interpret, and it appears to be of little utility in the current context.

The pharyngeal teeth of nearly all species examined here are simple and conical. However, one of the species examined (*Gnatholepis anjerensis*) has nearly bifid pharyngeal teeth, with one curved main tip and one smaller accessory tip or bump a short distance down the shaft. Parenti and Thomas (1998) found this tooth shape on all five of the gobionelline genera they examined, indicating that this character may be useful for inferring relationships within the Gobionellinae. However, as this study shows, it is not universal among gobionelline genera, and within the current study group this character is autapomorphic for *Gnatholepis*.

Paired Fins.—The gobioid pectoral girdle is characterized by the same reductive trend observed in other functional units of the skeleton. All but the most primitive gobioids lack dorsal postcleithra and many also lack ventral postcleithra (Springer, 1983), and the scapula is reduced in most species, showing a tendency toward reduced ossification (Akihito, 1969). Springer (1983) predicted that the presence of a small ventral intercleithral cartilage would eventually be recognized as a gobioid synapomorphy.

The gobionelline outgroup species examined in this study (*Tridentiger brevispinis*, *Acanthogobius flavimanus*, and *Gnatholepis anjerensis*) all have a short canal on the broad lateral surface of the posttemporal bone housing the posterior portion of the oculoscapular canal (Character 27). This condition is also present in *Istigobius ornatus*. Comcomitant with their lack of posterior oculoscapular canals, no member of the *Chasmichthys* Group possesses a canal on the posttemporal bone, and this character may represent a synapomorphy for the group.

All species examined in this study lack dorsal postcleithra, and all the members of the *Chasmichthys* Group lack ventral postcleithra as well (Character 28). However, Murdy (1985) found a small ventral postcleithrum in *Istigobius ornatus*, and Akihito (1969) observed ventral postcleithra in most of the *Acanthogobius* Group as well as several other gobionelline genera. Of the species examined in this study, only *Tridentiger brevispinis* and *Acanthogobius flavimanus* have ventral postcleithra. The condition in *Gnatholepis anjerensis* could not be determined. The presence of ventral postcleithra may be a useful character for determining gobionelline relationships. Additionally, one of the gobionelline outgroup species examined (*Gnatholepis anjerensis*) possesses a small medially directed spur on the cleithrum just dorsal to its dorsoventral midpoint. This character has not been previously reported in the Gobiidae, and is absent in all other species examined here.

Akihito (1969) characterized the scapular development in a long list of gobiid species, dividing them by degree of ossification. He characterized several members of the *Chasmichthys* Group as having the “forked scapula” type (Akihito, 1969, fig. 6B),

in which the dorsal margin of the scapular foramen is ossified, but the ventral margin of the foramen and the main shaft of the scapula are composed of cartilage. This study confirms Akihito's conclusions and extends them to the entire *Chasmichthys* Group. All specimens examined, including gobionelline outgroups, may be characterized as having the "forked scapula" type. The ossification of the scapula is therefore not useful for elucidating the relationships among these species.

The gobioid pelvic girdle is dominated by the pelvic intercleithral cartilage, the presence of which has been proposed as a gobioid synapomorphy (Springer, 1983). The pelvic girdle in the *Chasmichthys* Group is remarkable only in one respect. All examined species of *Gymnogobius* and both species of *Chaenogobius* have two separate cartilaginous radials supporting each pelvic fin, one large and one very small (Character 29). The only other species examined with two pelvic radials on each side is *Lepidogobius lepidus*. All other members of the *Chasmichthys* Group, as well as the gobionelline outgroup taxa, have only one large radial on each side. The multiple-radial condition may be unique to the *Chasmichthys* Group, as there appears to be no other mention of it anywhere in the goby literature.

Vertebral Column, Medial Fins, and Caudal Skeleton.—Vertebral counts for members of the *Chasmichthys* Group (generally 32 or more) are somewhat high for gobies, but not strikingly so (Character 30). Birdsong et al. (1988) listed many other gobiid species with vertebral counts over 30, but the majority of those species are classified in the *Acanthogobius* Group and the *Astrabe* Group, which were included by Pezold (1993) in

the Gobionellinae along with the *Chasmichthys* Group. Therefore, elevated vertebral count may potentially be interpreted as a synapomorphy uniting these gobionelline groups. Pleural ribs are found on vertebrae 3–13 to 3–16 throughout the *Chasmichthys* Group. The gobionelline outgroup species have fewer ribs (on vertebrae 3–10 to 3–13), despite roughly similar vertebral counts, but intraspecific variability could easily blur this distinction.

Number of epineurals is quite variable in the *Chasmichthys* Group, ranging from 9 to 17. However, the placement of these epineurals is much less variable. Within the *Chasmichthys* Group most species have a pair of epineurals associated with the first vertebral centrum and a pair associated with each of the subsequent 11–15 centra. Epineurals are generally restricted to abdominal centra, but occasionally a pair is associated with the first 1 or 2 caudal centra. However, a subset of the *Chasmichthys* Group (*Clevelandia ios*, *Eucyclogobius newberryi*, *Ilypnus gilberti*, *Lepidogobius lepidus*, and *Quietula y-cauda*) lacks the anteriormost pair of epineurals (Character 31). In these species, epineurals are associated with the second thru 10th–18th centra. The absence of epineurals on the first vertebral centrum has not previously been reported in gobioids, with the exception of *Tyson belos* and *Rotuma lewisi*, which have only one pair of epineurals (Springer, 1988). Therefore, this character is interpreted as a synapomorphy uniting these five genera.

The anteriormost pterygiophore of the first dorsal fin is inserted in the fourth interneural space in the majority of the *Chasmichthys* Group, and in the fifth interneural space in *Gymnogobius urotaenia*, *Clevelandia ios*, and *Eucyclogobius newberryi*.

(Character 32). This character was the justification for creating the *Chasmichthys* Group in the first place (Birdsong et. al, 1988), as the typical gobioid condition is for this pterygiophore to be inserted in the third interneural space. Pezold (1993) hypothesized that insertion of this pterygiophore beyond the fourth interneural space is a derived characteristic, but that the polarity of insertion in the fourth interneural space is uncertain. The gobionelline outgroup species examined all have the typical gobioid condition.

Members of the *Chasmichthys* Group also appear to have a posterior displacement of the second dorsal fin (Character 33). All species examined have the anteriormost pterygiophore of the second dorsal fin inserted in interneural space 11, 12, or 13. The gobionelline outgroup species examined have this pterygiophore inserted in interneural space 8–10, as do *Microgobius signatus* and *Istigobius ornatus*. Although Birdsong et al. (1988) did not explicitly report this character in their extensive survey, it can be derived from their first dorsal-fin pterygiophore formulae. Derivation of this character for the genera surveyed by Birdsong et al. (1988) confirms that the overwhelming majority of gobiid genera have the anteriormost pterygiophore of the second dorsal fin inserted in the eighth or ninth interneural space. The posterior displacement of the second dorsal fin could be a simple consequence of the posterior displacement of the first dorsal fin in the *Chasmichthys* Group. However, the second dorsal fin also appears to be posteriorly displaced relative to the first dorsal fin in these genera. The survey of Birdsong et al. (1988) shows that the majority of gobiid genera have a single interneural gap between the posteriormost pterygiophore of the first dorsal

fin and the anteriormost pterygiophore of the second dorsal fin. This is also true of the gobionelline outgroup species examined in this study and of *Microgobius signatus* and *Istigobius ornatus*. In contrast, members of the *Chasmichthys* Group have two, three, or even four interneural gaps between the two dorsal fins. This indicates that the posterior displacement of the second dorsal fin may be independent of the posterior displacement of the first dorsal fin, and therefore represents an additional derived character uniting the *Chasmichthys* Group.

The number of anal-fin pterygiophores preceding the first haemal spine (AP) ranges from one to eleven in the Gobioidei, but is most commonly two, three, or four (Birdsong et al., 1988). For the species surveyed here, AP is either two or three (Character 34). However, this character does not vary in any obvious pattern, and its phylogenetic significance is questionable.

There is little variation in the caudal skeletons of the species examined in this study. Pezold (1993) used the presence of one epural as a diagnostic character for the Gobiinae, which excluded the *Chasmichthys* Group and the rest of the Gobionellinae. The results of this study are consistent with his classification, as all of the gobionelline species examined have two epurals, while the non-gobionelline *Microgobius signatus* and *Istigobius ornatus* each have only one (Character 35). There is some variation in the presence of small autogenous cartilages dorsal and ventral to the hypural plate. The only one of these elements that is consistently present is found posterior to the posteriormost haemal spine. This cartilage appears to support the first branched caudal ray, and is present in most species of *Gymnogobius*, as well as *Chaenogobius annularis*,

Lepidogobius lepidus, and *Ilypnus gilberti*. It is also present in the gobionelline outgroup species. However, there seems to be intraspecific variation in this element, as Fujita (1990) found it (labeled as CPHPU 2) in both species of *Chaenogobius* (his *Chasmichthys*) and all three of the species of *Gymnogobius* (his *Chaenogobius*) that he surveyed. Therefore, the small autogenous cartilages of the caudal skeleton are probably too variable to be useful in determining interspecific relationships, even within genera.

Additional Characters.—Several external morphological characters of the scales, cephalic lateralis system, and fins are also included in the data matrix. Scale type (Character 36) is generally ctenoid within the study group. However, two species of *Gymnogobius* (*G. opperiens* and *G. mororanus*) and *Chaenogobius annularis* have visibly ctenoid scales only when young, with larger specimens having very weakly ctenoid or cycloid scales. In addition, *Chaenogobius gulosus* and nearly all of the North American genera in the *Chasmichthys* Group have cycloid scales. Ctenoid scales are widespread within the Gobioidei, and probably represent the primitive condition for this group.

The morphology of the cephalic lateralis system can be quite complex in the Gobioidei. However, it is generally accepted that primitive gobioids have a more extensive cephalic lateralis system, and that the evolutionary trend within the suborder has been toward reduction (Miller, 1973; Springer, 1983; Hoese and Gill, 1993). Therefore, the presence or absence of sections of the oculoscapular canal system may

give an indication of the relative phylogenetic position of goby species, particularly within closely related subgroups. With the exception of *Gymnogobius castaneus*, all species within the current study group have interorbital canals, but there are differences in their extent and morphology. Several of the genera within the *Chasmichthys* Group as well as all three gobionelline outgroup genera have oculoscapular canals extending forward of the eyes and ending in pores in the posterior nasal position (Character 37). In contrast, all species of *Gymnogobius* and *Ilypnus gilberti* lack the posterior nasal portion of the oculoscapular canals, and the anterior terminus of the canal in these species is the anterior interorbital or posterior interorbital pore. The morphology of the interorbital portion of the oculoscapular canals is also variable in this group (Character 38). All outgroup genera and most of the genera in the *Chasmichthys* Group have the right and left oculoscapular fused along the midline in the interorbital space. In *Chaenogobius* and *Gillichthys*, the right and left oculoscapular canals are separate but connected by a short commissure in the posterior interorbital space. Only in *Gymnogobius* and *Eucyclogobius* are the right and left oculoscapular canals separate, without any connection in the interorbital space. Additionally, the otic portion of the oculoscapular canals may be present or absent in this group (Character 39), and this otic portion of the canal may terminate in either intermediate or extreme otic pores. For this character, the genera *Chaenogobius* and *Gillichthys* share the most primitive condition, which is the presence of the otic portion of the canal terminating in extreme otic pores, with the three gobionelline outgroup genera. Several members of *Gymnogobius* have the otic canals reduced, so that they terminate in intermediate otic pores. Other species

of *Gymnogobius*, as well as the remaining *Chasmichthys* Group, lack the otic portion of the oculoscapular canal entirely.

Finally, two features of the fins are shared by the two species of *Chaenogobius* to the exclusion of all other species examined. First, the uppermost pectoral-fin rays end in filamentous projections free from the fin membrane (Character 40, see Fig. 2.1). This characteristic has been reported in other goby groups (Winterbottom, 1976), but is absent in all other members of the Gobionellinae. The shape of the pelvic fins is also unique in *Chaenogobius* (Character 41). They are anteroposteriorly short and rounded, with a deep notch lateral to the pelvic spine (see Fig. 2.2), in contrast to all other species examined here, which have elongate, oval pelvic fins with a very shallow notch lateral to the pelvic spine.

The morphological character matrix resulting from the comparative osteological survey detailed above is presented in Table 3.3, and a complete list of characters may be found in Appendix C.

PHYLOGENETIC IMPLICATIONS

The maximum parsimony analysis of the morphological character matrix resulted in 100 most parsimonious trees of 108 steps. The majority rule consensus of these trees (Fig. 3.14) represents the topology with the most support ($CI = 0.398$). This reconstruction features a monophyletic *Chasmichthys* Group, present in all most parsimonious trees and supported by a high bootstrap value, and a monophyletic *Gymnogobius*, which is present in 70% of the most parsimonious trees, but supported

by a relatively low bootstrap value. However, the consensus tree does not support monophyletic North American and Asian clades within the *Chasmichthys* Group, nor does it recover a monophyletic Gobionellinae.

The *Chasmichthys* Group + *Tridentiger* + *Acanthogobius* form a clade supported by five unequivocal synapomorphies, including position of the ethmoid cartilage (1), absence of nasal bones (11), dominant bone of the metapterygoid-synplectic strut (18), presence of a preopercular spur (21), and vertebral count (31). This clade is recovered in all of the most parsimonious trees, and includes all of the gobionelline genera examined in this study except for *Gnatholepis*. This indicates that *Gnatholepis* is only distantly related to the *Chasmichthys* Group, which is not unexpected. Harrison (1989) suggested that *Gnatholepis* may be part of a gobionelline “*Ctenogobius* lineage” along with *Ctenogobius*, *Evorthodus*, *Gobionellus*, *Gobiooides*, and *Oligolepis*, while Parenti and Thomas (1998) suggested that *Gnatholepis*, *Awaous*, and *Stenogobius* may be closely related to the Sicydiinae. Although not conclusive, the results of this study add to the growing body of evidence that the Gobionellinae is not monophyletic, and that *Gnatholepis* belongs to a lineage that is not closely related to other gobionelline groups.

The *Chasmichthys* Group is supported in this reconstruction by two unequivocal synapomorphies, including the posterior displacement of the anteriormost pterygiophore of the first dorsal fin (33) and the posterior displacement of the second dorsal fin (34), and is represented in all most parsimonious reconstructions. The first of these characters was used by Birdsong et al. (1988) as a rationale for proposing the group in the first place. The posterior displacement of the second dorsal fin, if indeed it

represents an independent synapomorphy, adds support for the monophyly of this lineage. Within the surveyed Gobionellinae, the *Chasmichthys* Group is supported by two additional characters, which it shares with the gobiine *Microgobius signatus*. These are the absence of a canal on the posttemporal (28) and the absence of ventral postcleithra (29). These character states were probably independently derived in *Microgobius*, and may therefore represent synapomorphies within the Gobionellinae, but additional taxa must be surveyed before these characters can be confidently interpreted.

Within the *Chasmichthys* Group, *Chaenogobius* and *Gillichthys* form a distinct lineage, which is sister to the remaining genera of the group. The *Chaenogobius* + *Gillichthys* clade is supported by one unequivocal plesiomorphic character, the presence of a branched canal on the preopercle (20). This clade is recovered in 70% of the most parsimonious reconstructions, but is supported by a relatively low bootstrap value. The other clade, which includes all species of *Gymnogobius* and the other five genera in the *Chasmichthys* Group, is supported by one unequivocal synapomorphy, the reduction of the otic portion of the oculoscapular canal (40). This clade is recovered in all of the most parsimonious constructions, but again is supported by only a moderate bootstrap value. The significance of this arrangement is that it precludes the separation of the *Chasmichthys* Group into monophyletic Asian and North American clades. This indicates that the North American members of this group are not simply derivatives of an Asian species that colonized the North American coast and then subsequently

speciated, nor is the reverse true. A more complex explanation must be formulated to account for the biogeographic history of the group.

The clade containing the majority of the *Chasmichthys* Group consists of two lineages. One of these lineages consists of a monophyletic *Gymnogobius*, and the other includes the five remaining genera of the *Chasmichthys* Group (*Ilypnus*, *Eucyclogobius*, *Lepidogobius*, *Clevelandia*, and *Quietula*). The latter clade is supported by one unequivocal synapomorphy, the loss of epineurals on the first vertebral centrum (32), and is represented in 90% of most parsimonious topologies. This lineage represents the major North American radiation of gobies in the *Chasmichthys* Group. None of the nodes within this clade is supported by an unequivocal synapomorphy, and bootstrap support is low at each of the nodes. Therefore, although all three nodes are represented in at least 90% of most parsimonious reconstructions, support for this particular topology is not necessarily strong.

The genus *Gymnogobius* forms a monophyletic clade in 70% of the most parsimonious topologies, although it is not supported by any unequivocal characters and bootstrap support is low. The absence of the posterior nasal portion of the oculoscapular canal (38) and the presence of separated right and left oculoscapular canals (39) are derived conditions shared by all species of *Gymnogobius*. The former character state is also exhibited by *Ilypnus gilberti*, and the latter by *Eucyclogobius newberryi*. Both character states most likely represent developmental truncations of the cephalic lateral line system (Takagi, 1988; Pezold, 1993), and may have been independently derived. Support for nodes within the *Gymnogobius* clade is generally

low, which is to be expected given the relatively small number of characters and presumably close relationship of the species. The genus is split into two clades, one containing the *Gymnogobius urotaenia* species group (*G. urotaenia*, *G. opperiens*, *G. petschiliensis*, and *G. isaza*), and the other containing the remainder of the genus. Although neither of these clades is supported by an unequivocal character and statistical support is not strong for either clade, this separation is consistent with the topology obtained by Aizawa et al. (1994) using allozyme data.

Within the *G. urotaenia* clade all nodes are poorly supported, indicating a lack of fine-scale resolution within this data set. The topology presented here is not consistent with that of Aizawa et al. (1994) in this region of the tree. Their topology depicts *G. opperiens* as the sister group to the remaining three species, and *G. petschiliensis* as the sister group to *G. urotaenia* + *G. isaza*. The topology presented here reverses the positions of *G. opperiens* and *G. isaza*. Considering the lack of support for this portion of the topology, the relationships within the *G. urotaenia* species group are best considered unresolved by this data set.

The clade containing the remaining species of *Gymnogobius* does contain two clades represented in all most parsimonious reconstructions and each supported by an unequivocal synapomorphy. The *G. uchidai* + *G. macrognathos* clade is supported by the absence of a groove on the frontal (4), in which the interorbital portion of the oculoscapular canal rests. The two species of *Gymnogobius* not dissected in this study (*G. cylindricus* and *G. scrobiculatus*) are externally very similar to *G. uchidai* and *G. macrognathos*, so it seems reasonable to speculate that these two species would also be

included in this clade had specimens been available for dissection. None of these four species were included in the allozyme study of Aizawa et al. (1994). The *G. mororanus* + *G. heptacanthus* clade is supported unequivocally by a reduction in dentition on the dentary (15), and also by a proliferation of gill rakers (25), a character shared only with the outgroup species *Microgobius signatus*. These two species are externally very similar, and it is therefore not surprising that they form a well-supported clade. The placement of the other three species in this clade (*G. castaneus*, *G. taranetzi*, and *G. breunigii*), which intuitively form a closely related lineage, is poorly resolved. These three species were recovered as a monophyletic lineage by Aizawa et al. (1994). However, their data set did not include *G. macrognathos* or *G. uchidai*. If those two species were removed from this data set, then the three-species *G. castaneus* lineage would appear monophyletic in the current reconstruction as well. Thus, the current data set provides convincing evidence for a monophyletic *G. mororanus* + *G. heptacanthus* clade and a monophyletic *G. uchidai* + *G. macrognathos* clade (which may also include *G. cylindricus* and *G. scrobiculatus*), but not for a monophyletic *G. castaneus* + *G. taranetzi* + *G. breunigii* clade. The placement of these groups relative to each other is not convincingly resolved by this data set.

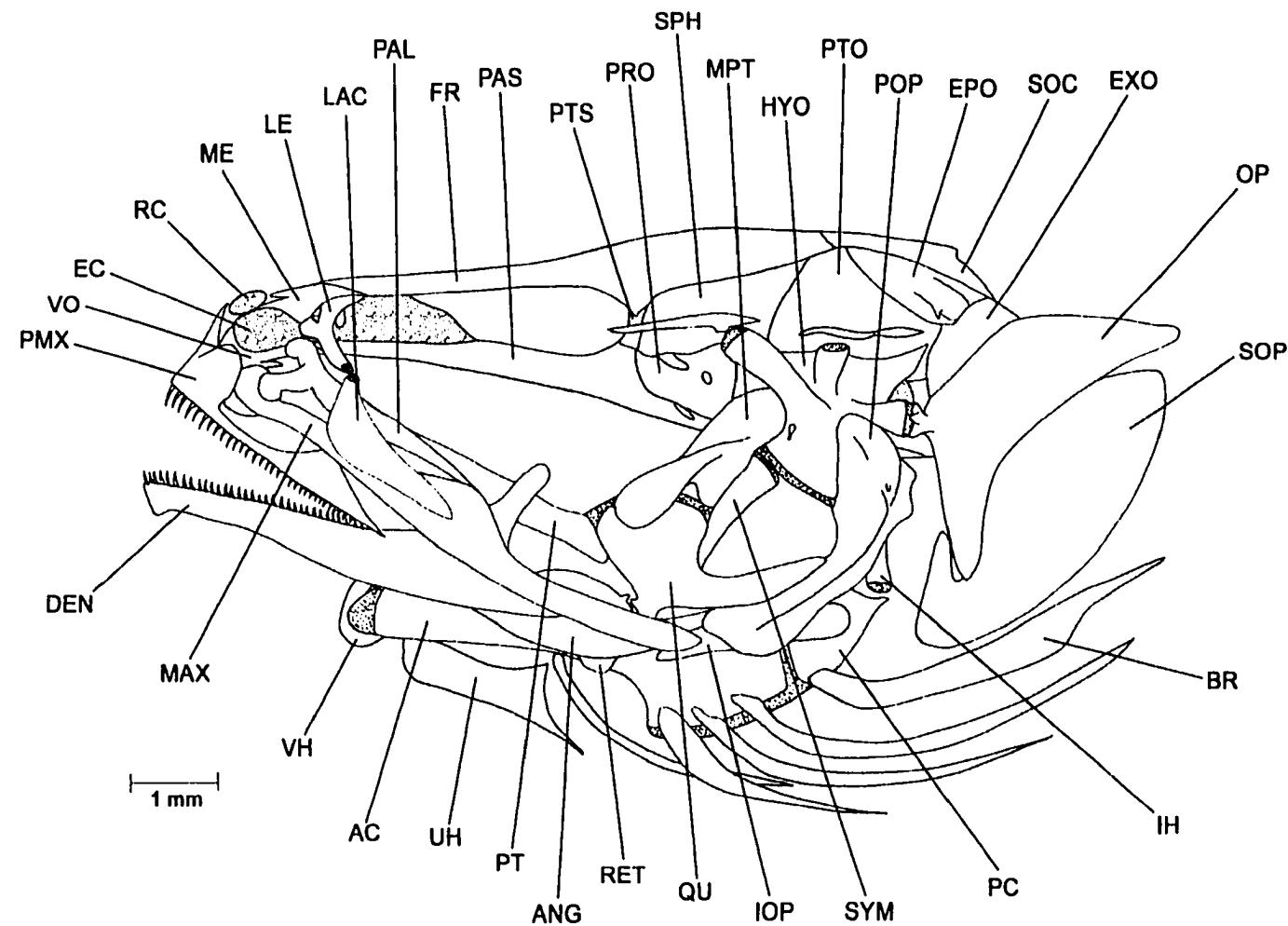


Fig. 3.1. Composite of all elements of the head of *Gymnogobius macrognathos*. For a key to abbreviations, see text and Table 3.1.

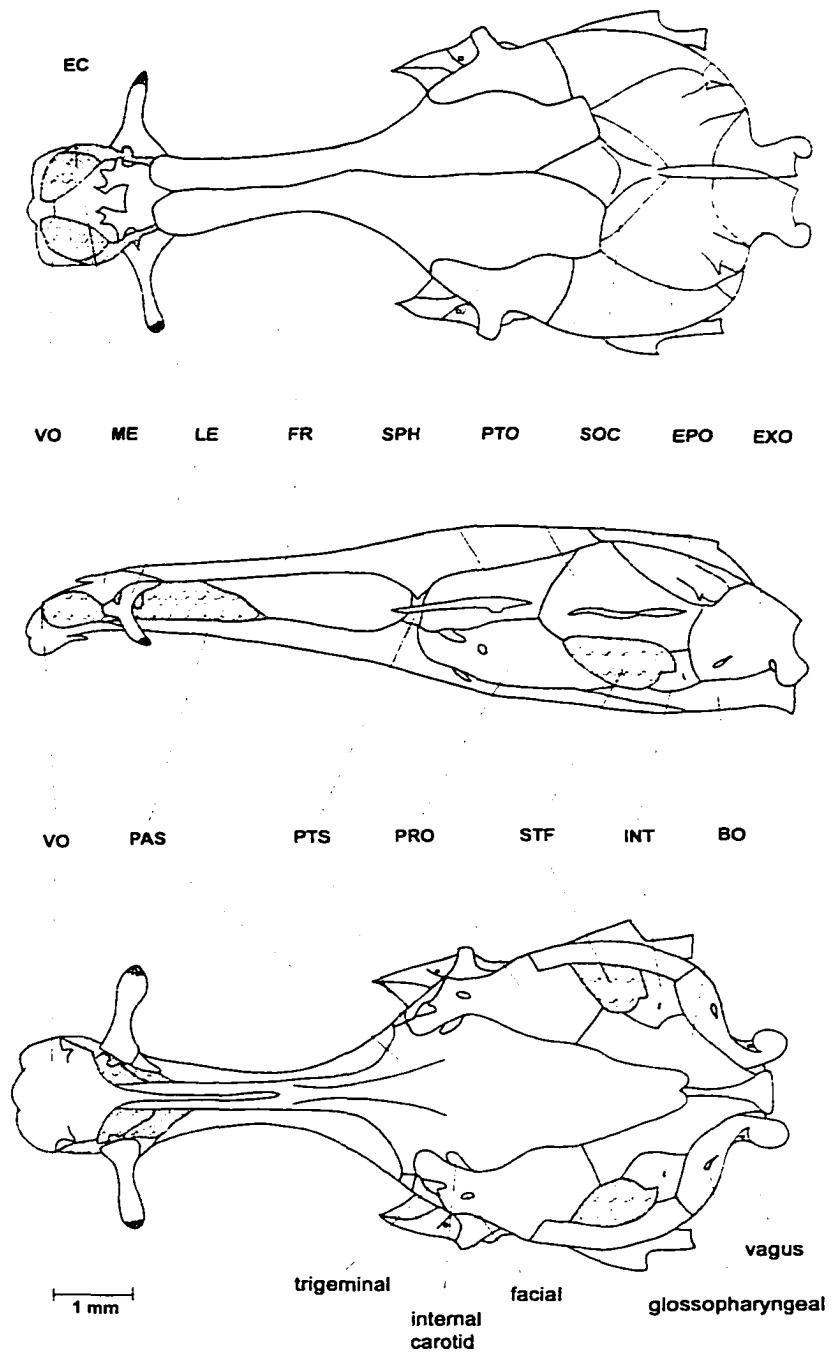


Fig. 3.2. Neurocranium of *Gymnogobius macrognathos*; top, dorsal view; middle, lateral view; bottom, ventral view. For key to abbreviations, see text and Table 3.1.

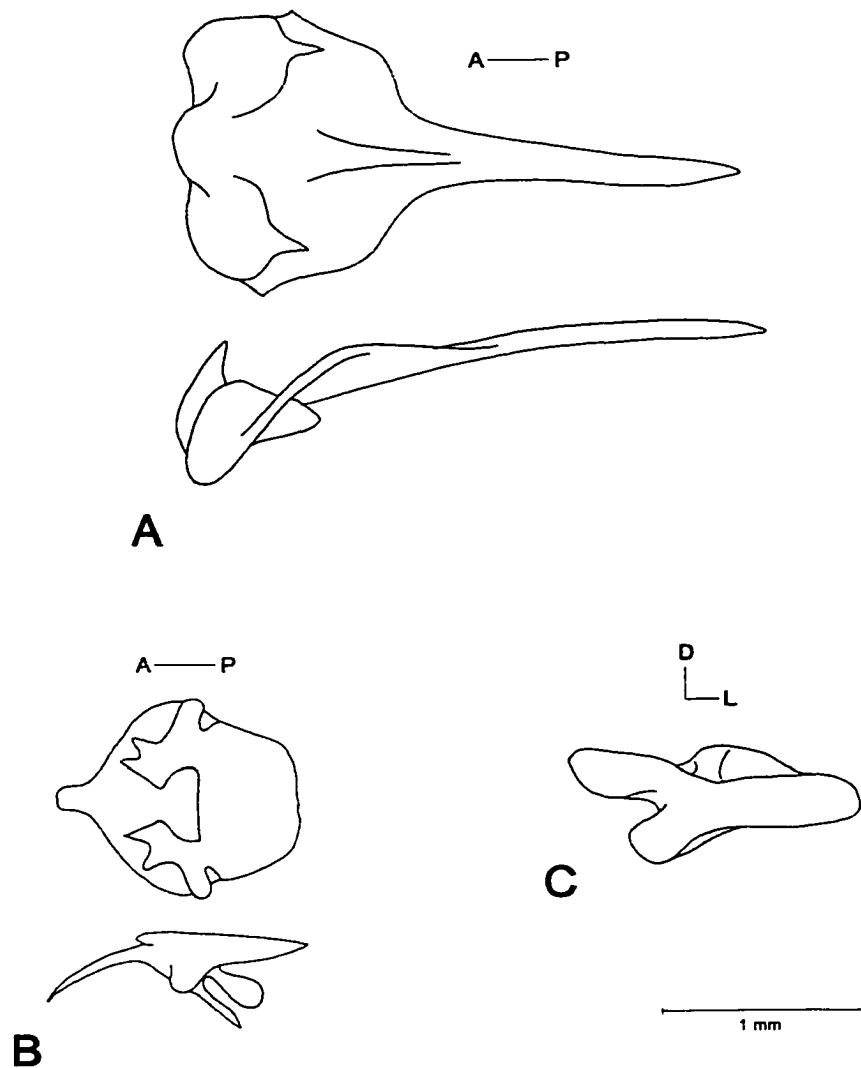


Fig. 3.3. Bones of the ethmoid region of *Gymnogobius macrognathos*: (A) Vomer, (B) Median ethmoid, (C) Lateral ethmoid.

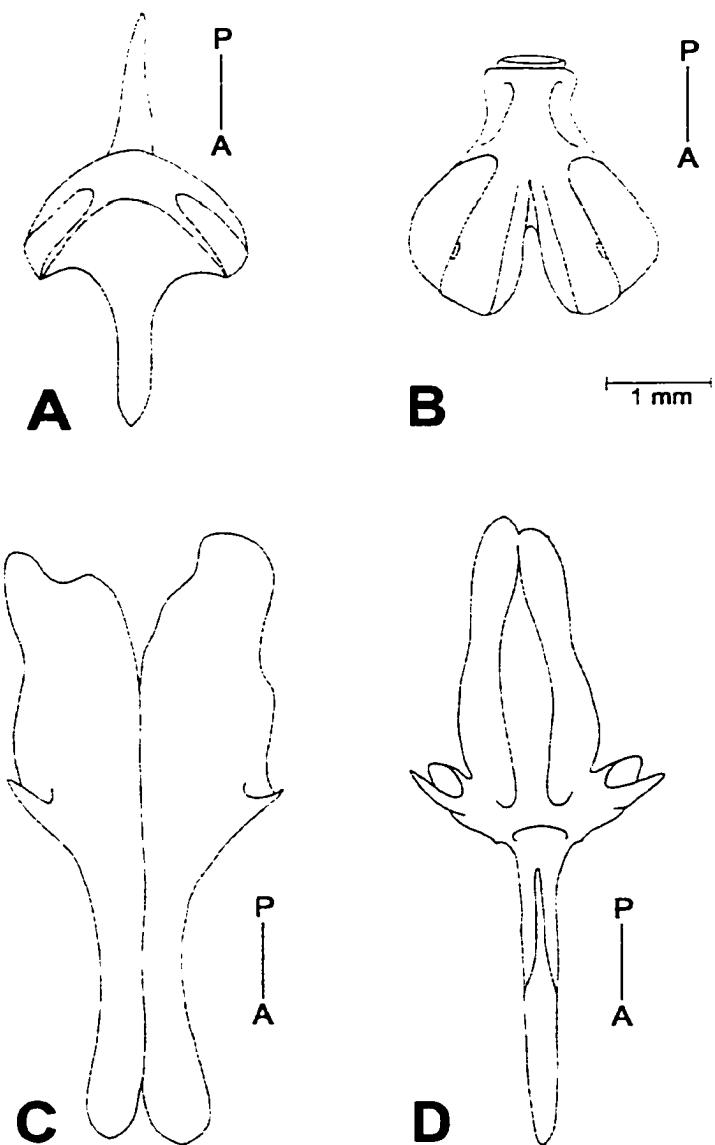


Fig. 3.4. Disarticulated medial bones of the neurocranium of *Gymnogobius macrognathos*: (A) Supraoccipital, (B) Basioccipital, (C) Frontals, (D) Parasphenoid.

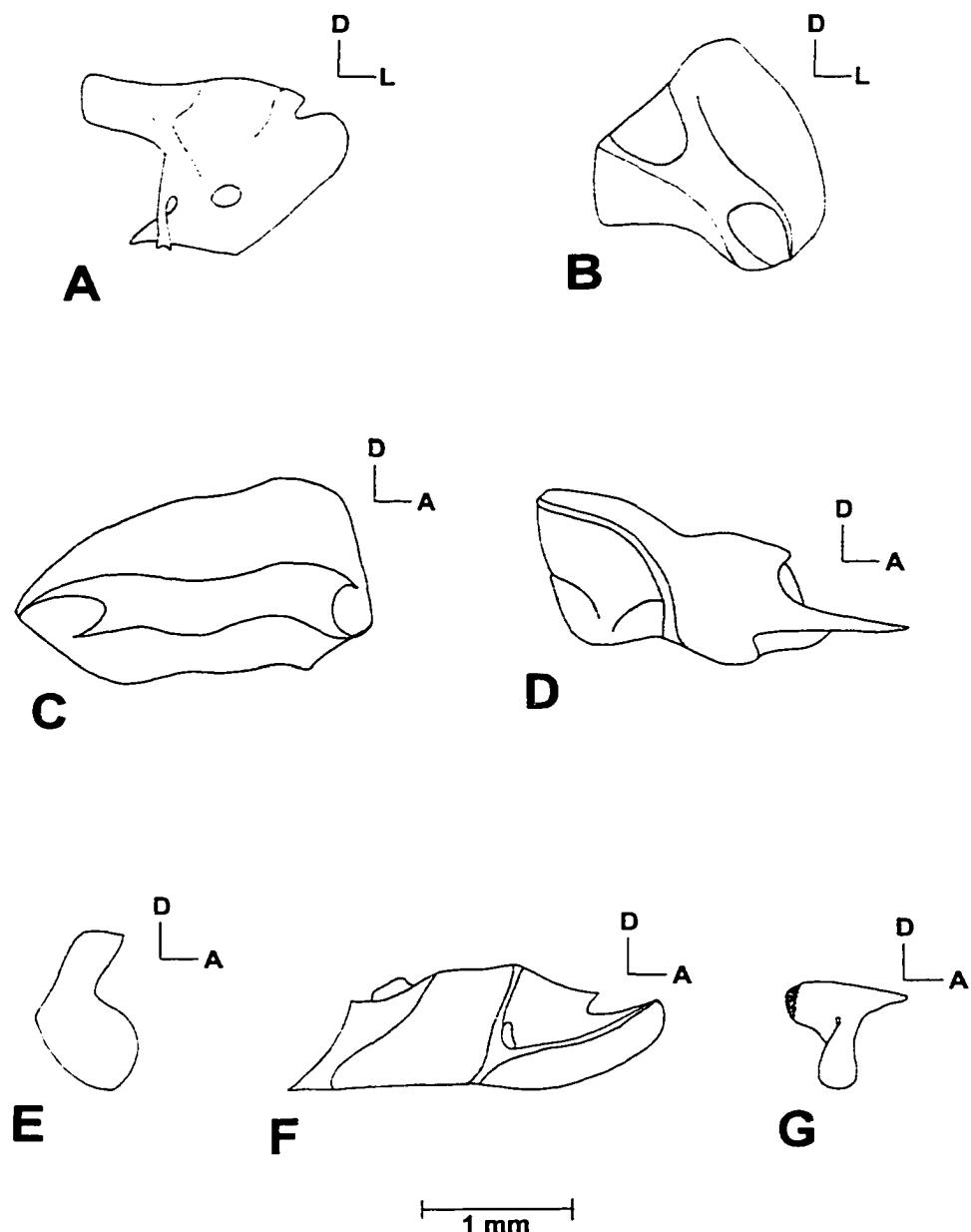


Fig. 3.5. Disarticulated lateral bones of the neurocranium of *Gymnogobius macrognathos*: (A) Exoccipital, (B) Epioccipital, (C) Pterotic, (D) Sphenotic, (E) Intercalar, (F) Prootic, (G) Pterosphenoid.

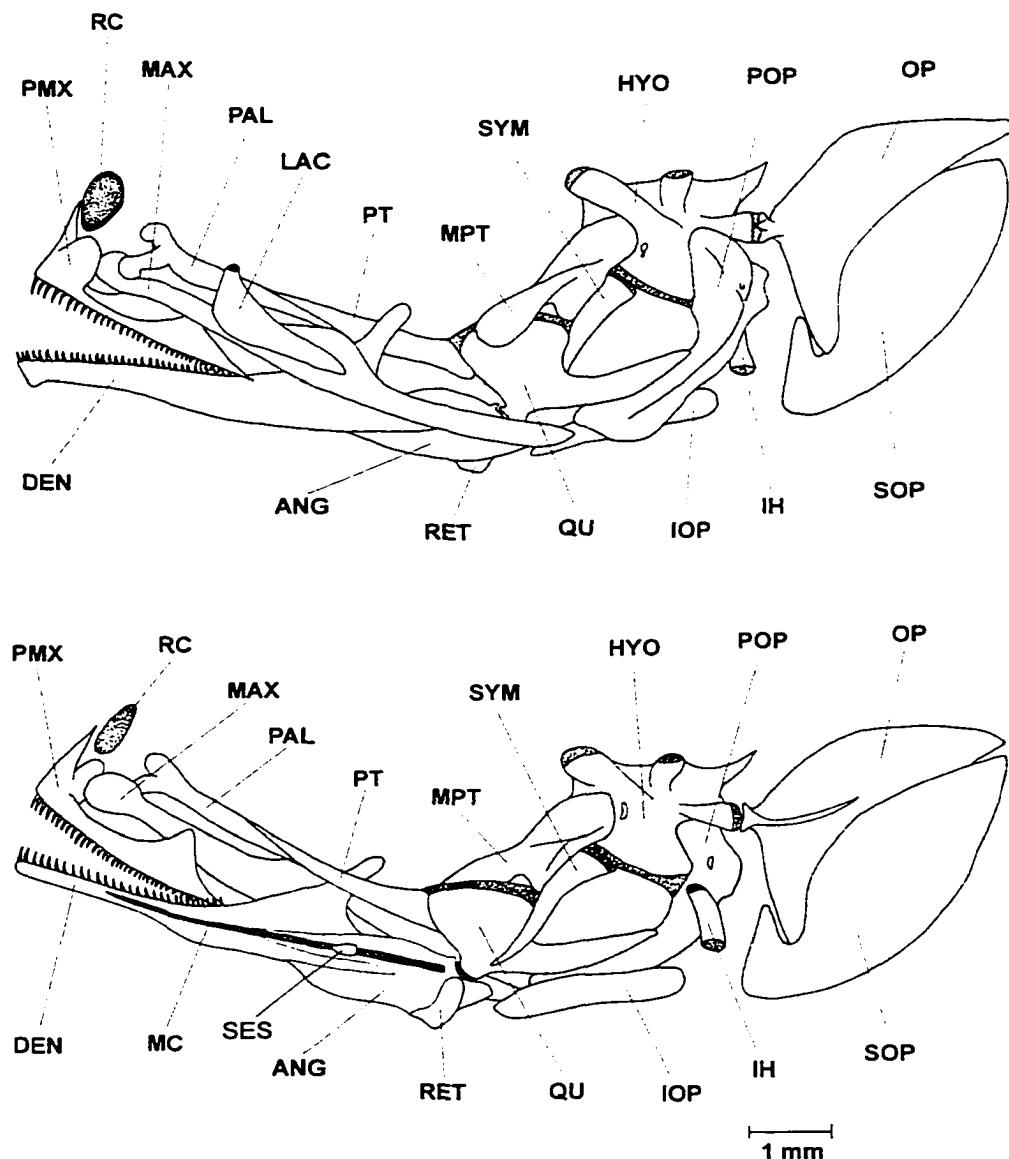


Fig. 3.6. Jaws, suspensorium, and opercular bones of *Gymnogobius macrognathos*; top, lateral view; bottom, medial view. For key to abbreviations, see text and Table 3.1.

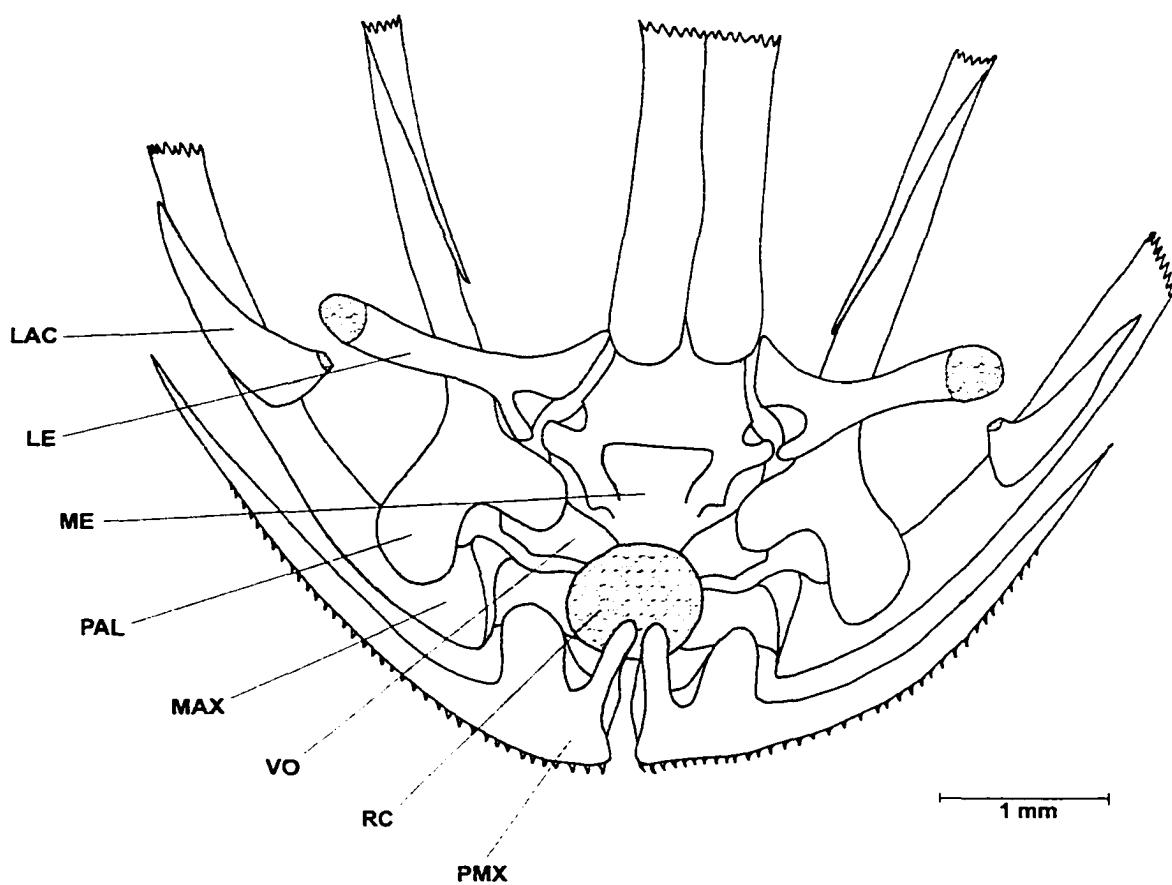


Fig. 3.7. Anterodorsal view of the snout of *Gymnogobius macrognathos* (frontals, ectopterygoids, and maxillae truncated). For key to abbreviations, see text and Table 3.1.

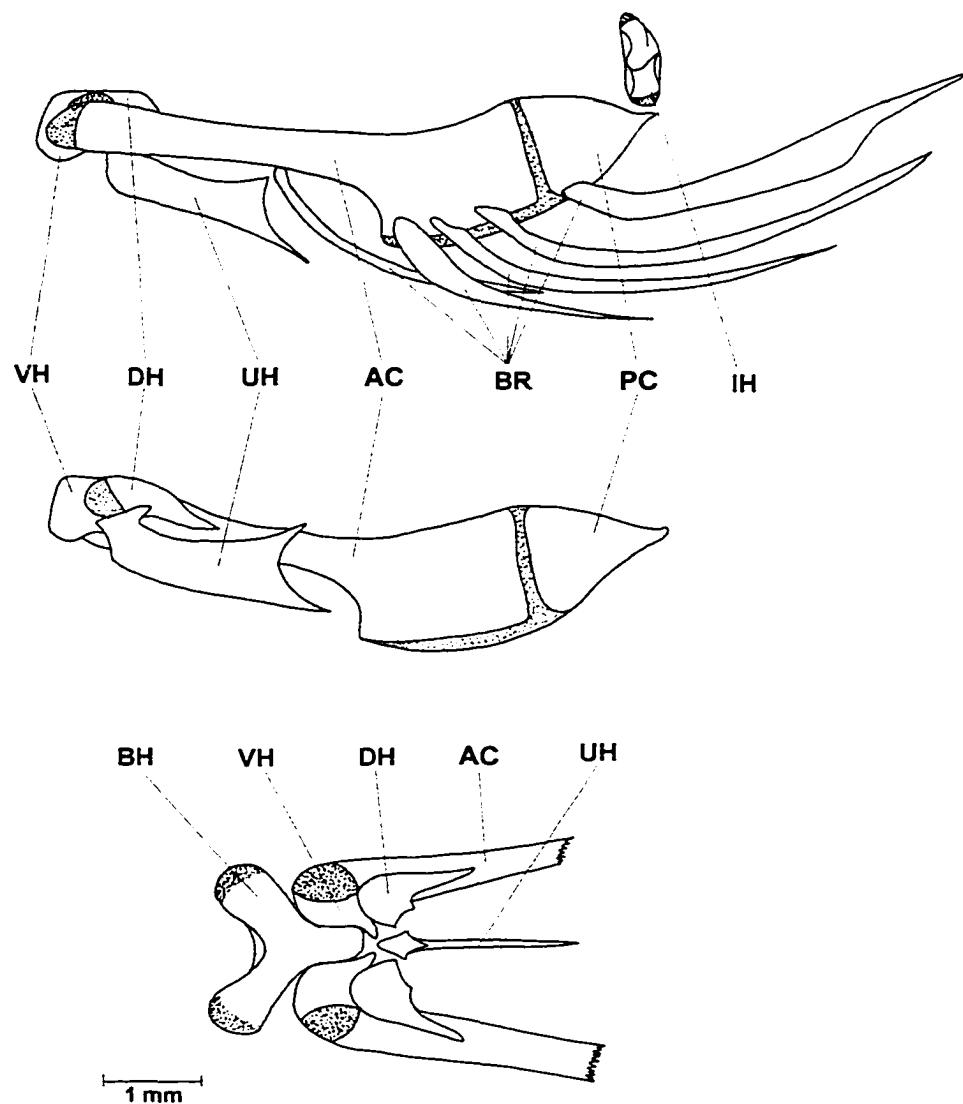


Fig. 3.8. Hyoid arch of *Gymnogobius macrognathos*; top, lateral view; middle, medial view (branchiostegals removed); bottom, dorsal view (anterior ceratohyals truncated).
For key to abbreviations, see text and Table 3.1.

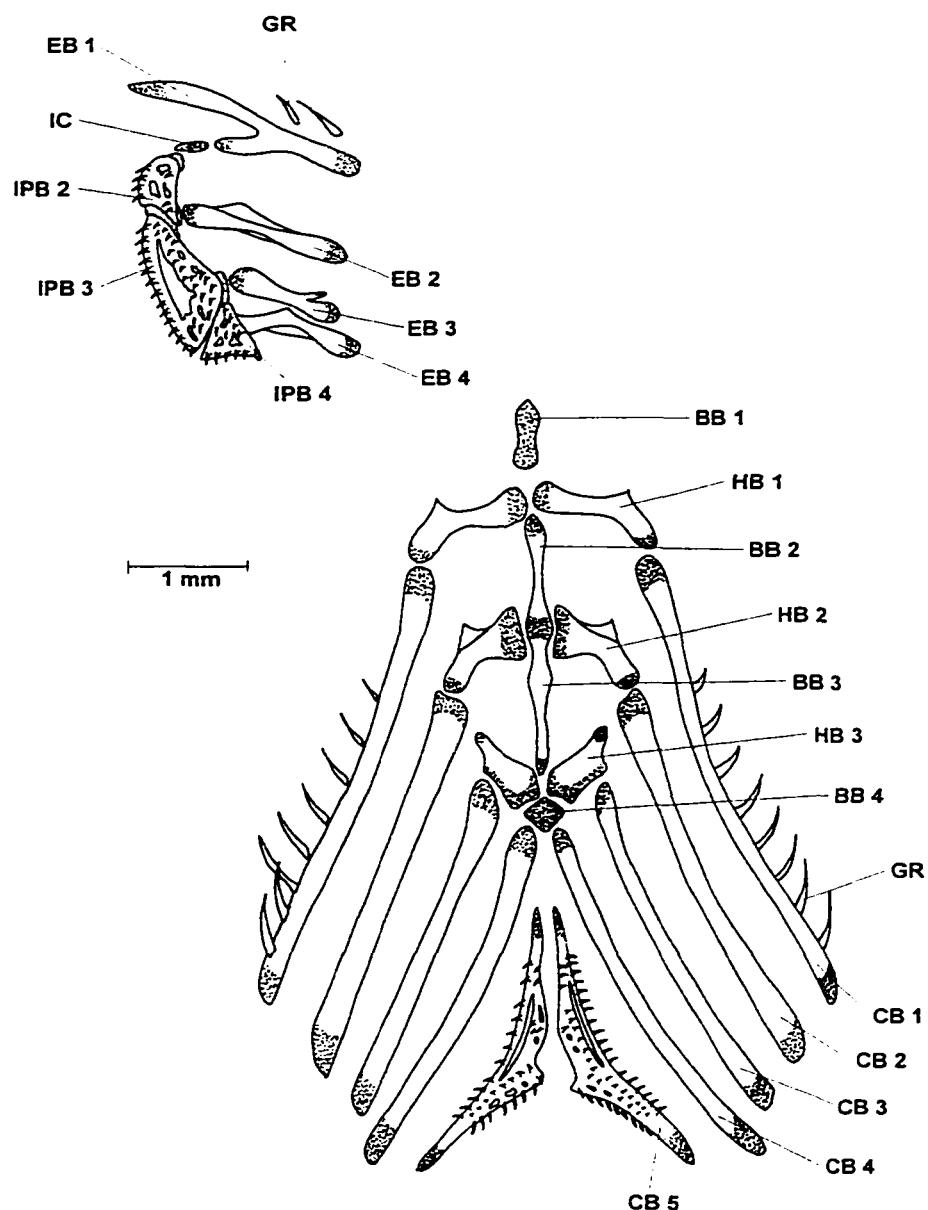


Fig. 3.9. Branchial apparatus of *Gymnogobius macrognathos*; upper left, ventral view of left upper pharyngeals; lower right, dorsal view of lower pharyngeals. For key to abbreviations, see text and Table 3.1.

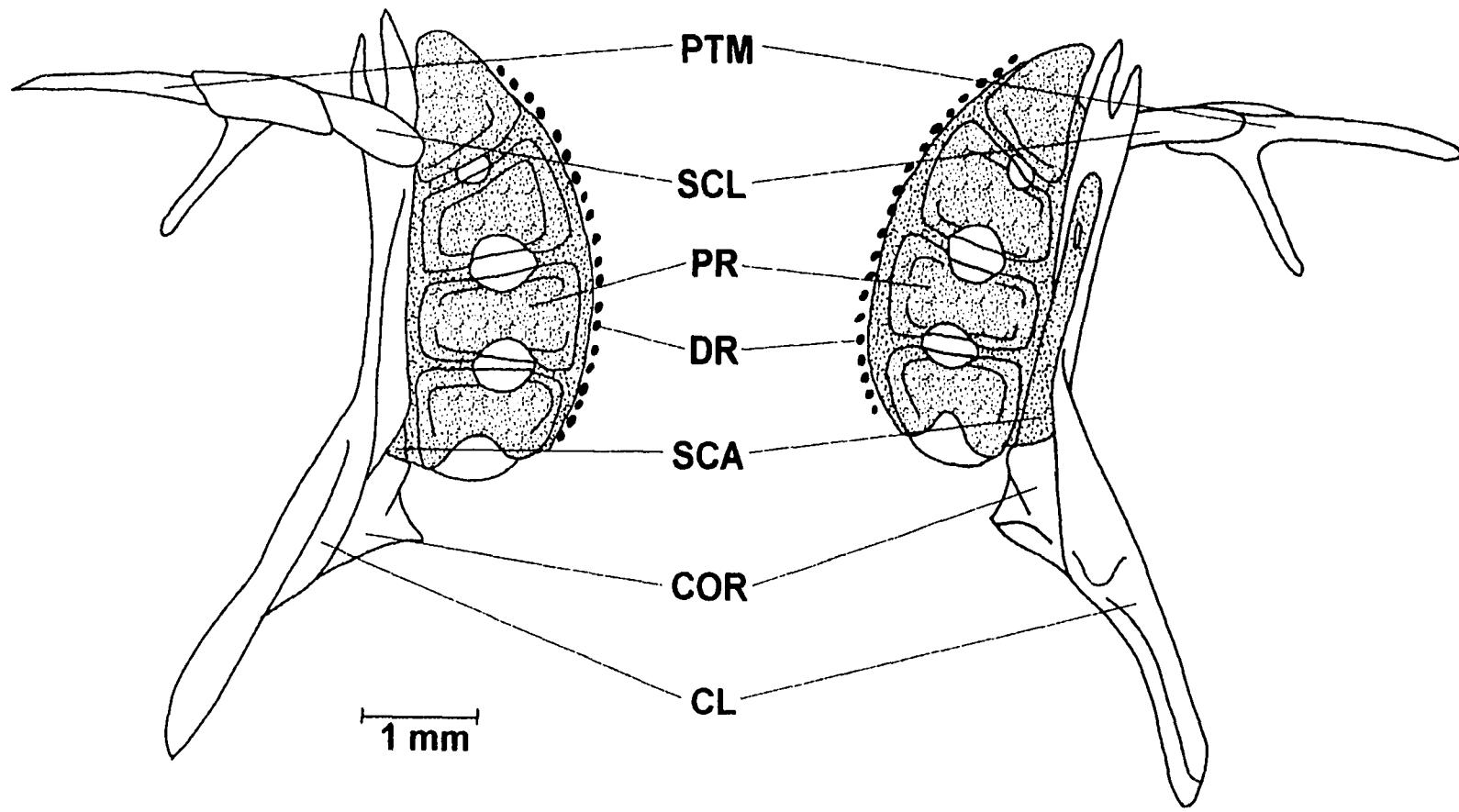


Fig. 3.10. Pectoral girdle of *Gymnogobius macrognathos*; left, lateral view; right, medial view. For key to abbreviations, see text and Table 3.1.

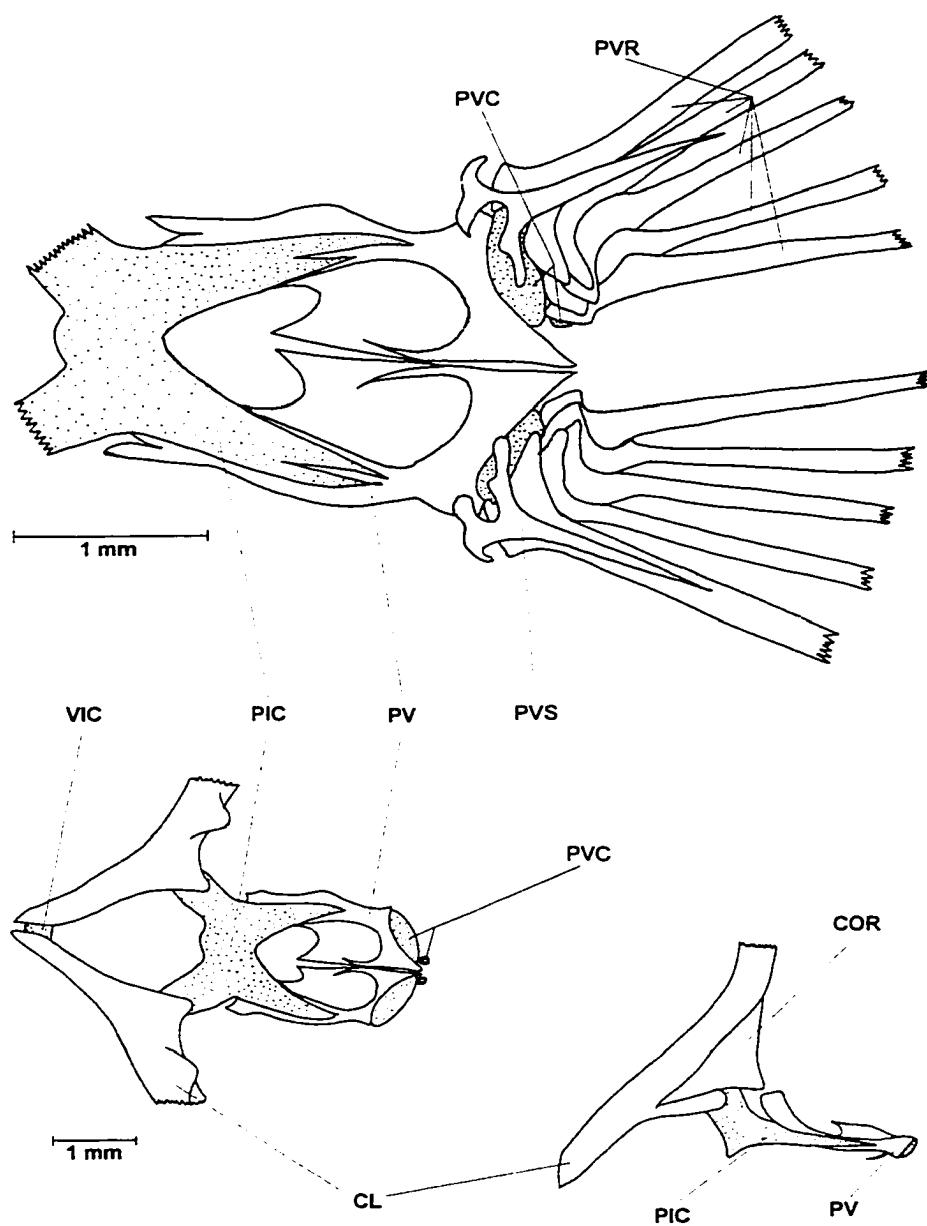


Fig. 3.11. Pelvic girdle of *Gymnogobius macrognathos*; top and bottom left, ventral view; bottom right, lateral view (pelvic fin rays truncated in top, not shown in bottom).
For key to abbreviations, see text and Table 3.1.

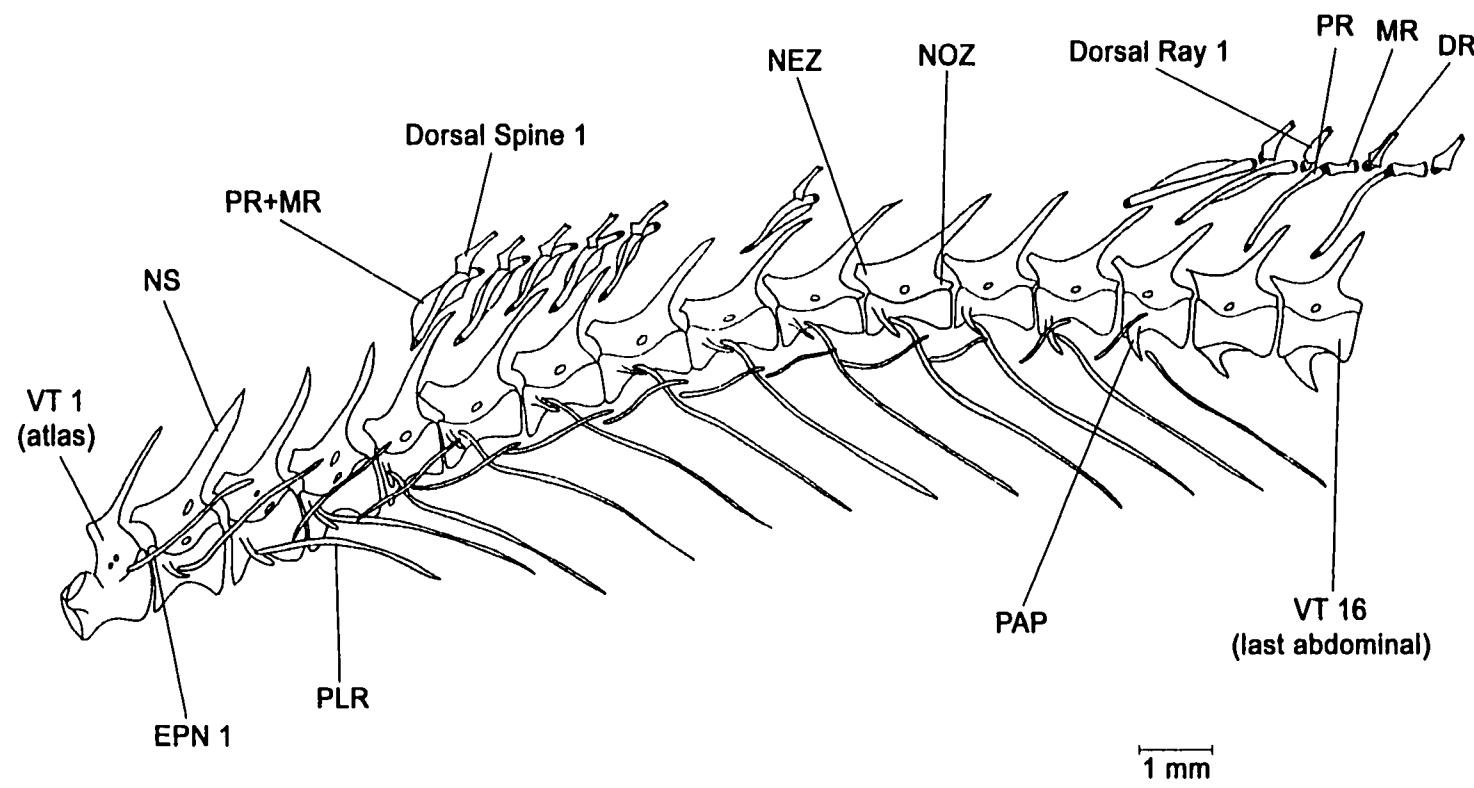


Fig. 3.12. Anterior half of vertebral column of *Gymnogobius macrogynathos*, including abdominal vertebrae and associated elements (fin rays truncated). For key to abbreviations, see text and Table 3.1

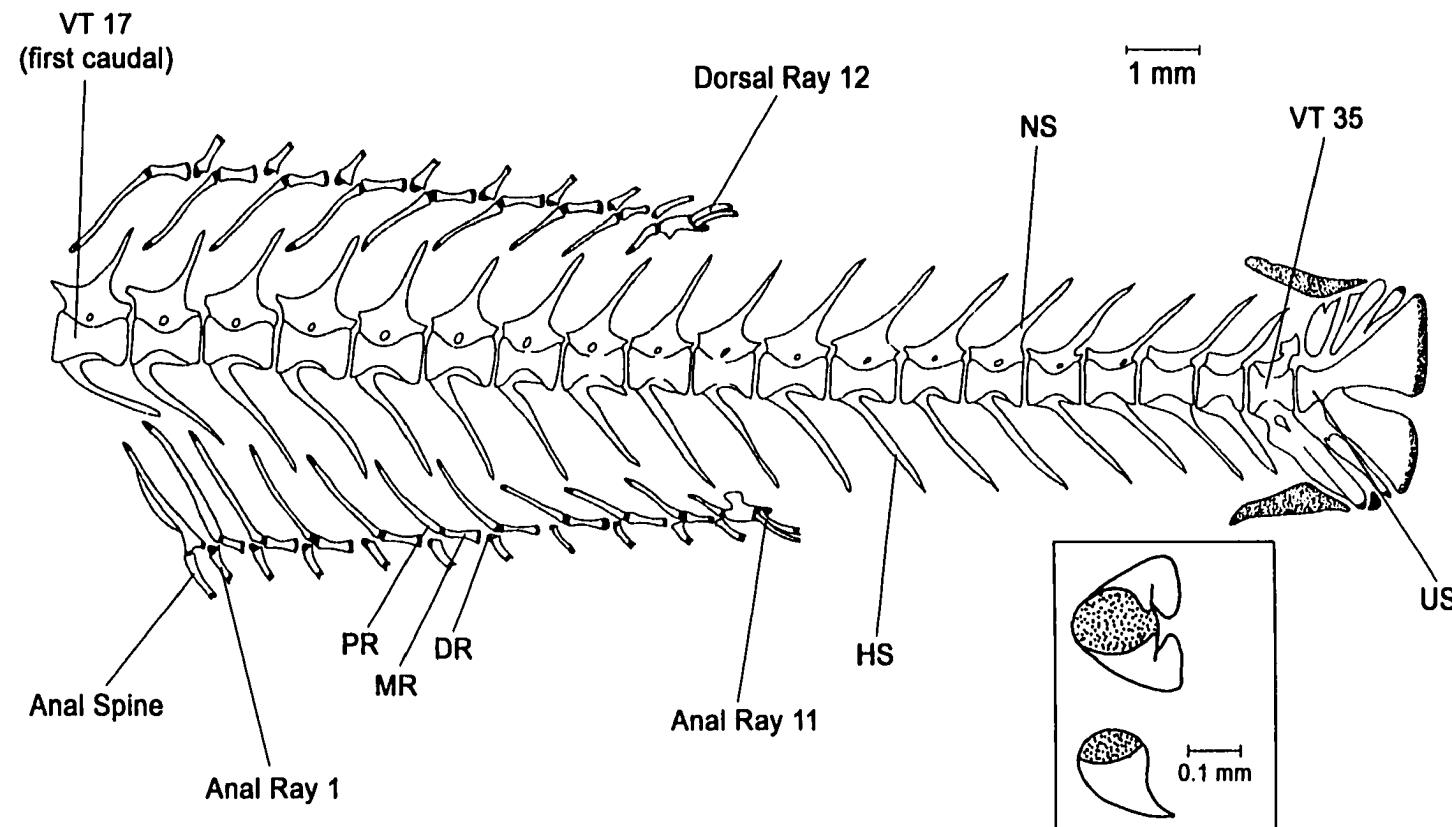


Fig. 3.13. Posterior half of vertebral column of *Gymnogobius macrognathos*, including caudal vertebrae and associated elements (caudal fin-rays not shown, all other fin rays truncated). Inset: dorsal (above) and lateral view (below) of anal-fin distal radial. For key to abbreviations, see text and Table 3.1.

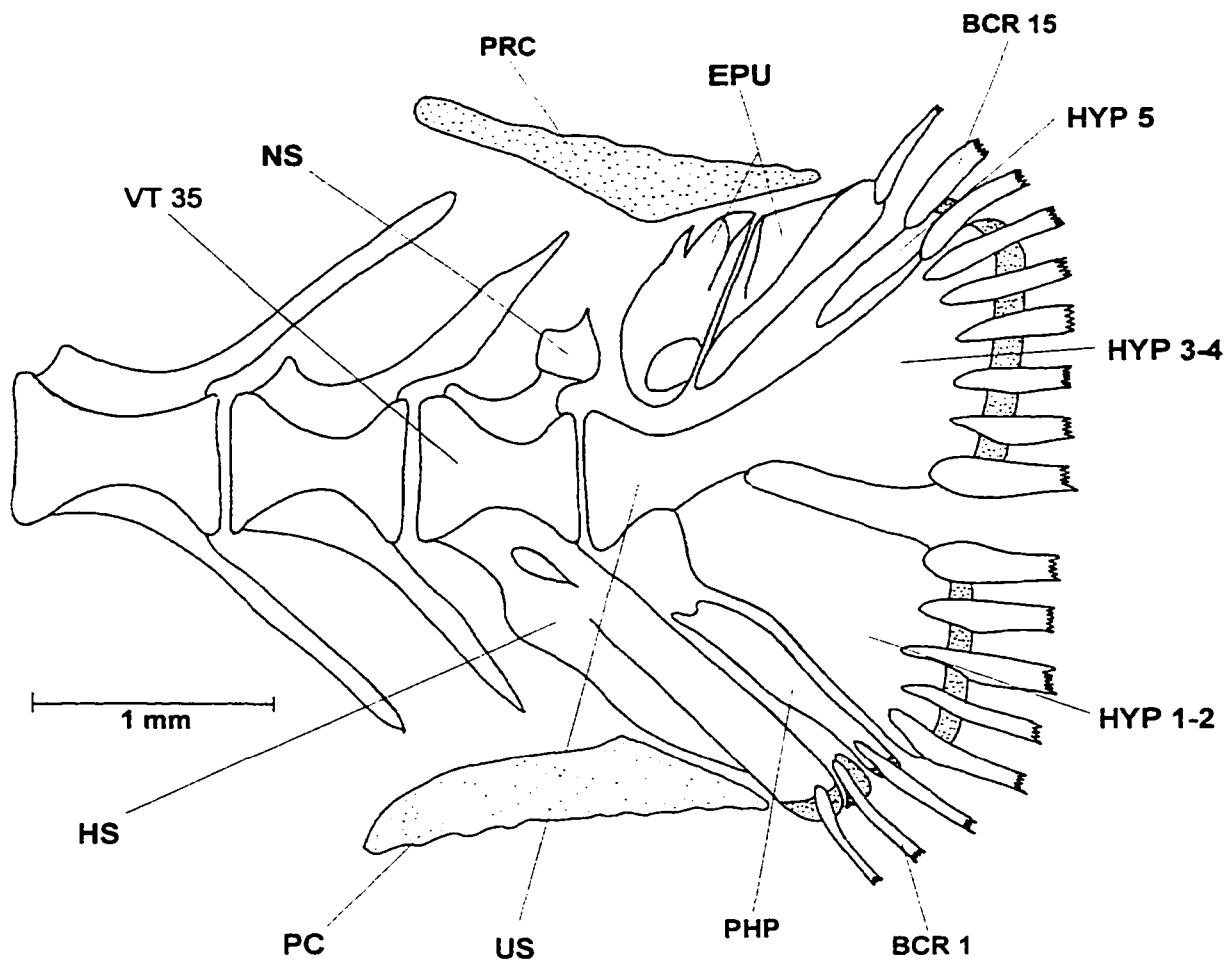


Fig. 3.14. Caudal skeleton of *Gymnogobius macrognathos* (procurent caudal rays not shown, segmented caudal rays truncated). For key to abbreviations, see text and Table 3.1.

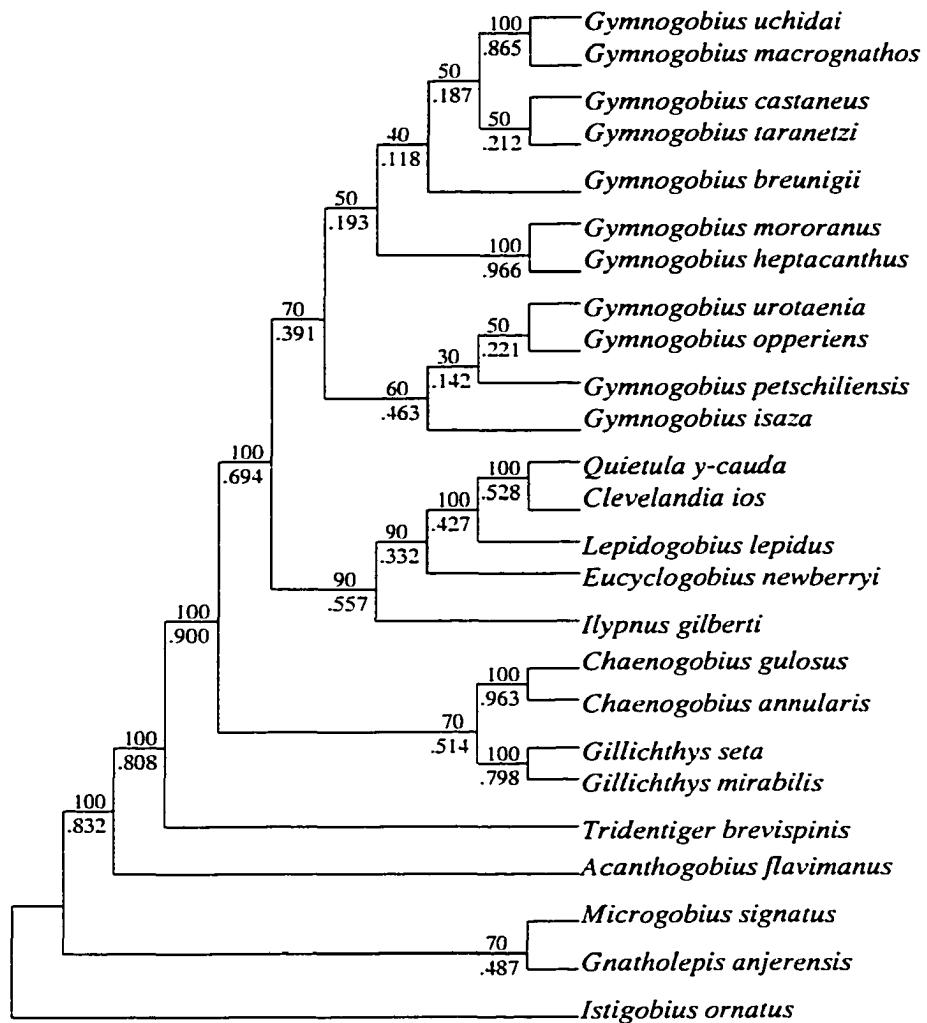


Fig. 3.15. Majority rule consensus of 100 most parsimonious trees (length = 108, CI = 0.398) generated with the morphological data set. Upper numbers at nodes represent the percentage of trees in which each clade is represented, lower numbers represent bootstrap support (1000 replicates). See Table 3.3 and text for characters.

Table 3.1. Abbreviations for skeletal elements.

AC—anterior ceratohyal	NS—neural spine
ANG—anguloarticular	OP—opercle
BB—basibranchial	PAL—palatine
BCR—branched caudal ray	PAP—parapophysis
BO—basioccipital	PAS—parasphenoid
BH—basihyal	PC—posterior ceratohyal
BR—branchiostegal ray	PHP—parhypural
CB—ceratobranchial	PIC—pelvic intercleithral cartilage
CL—cleithrum	PLR—pleural rib
COR—coracoid	PMX—premaxilla
DEN—dentary	POP—preopercle
DH—dorsal hypohyal	PR—proximal radial
DR—distal radial	PRC—procurent cartilage
EB—epibranchial	PRO—prootic
EC—ethmoid cartilage	PT—ectopterygoid
EPN—epineurial	PTM—posttemporal
EPO—epioccipital	PTO—pterotic
EPU—epural	PTS—pterosphenoid
EXO—exoccipital	PV—pelvis
FR—frontal	PVC—pelvic radial
GR—gill rakers	PVR—pelvic ray
HB—hypobranchial	PVS—pelvic spine
HS—haemal spine	QU—quadrate
HYO—hyomandibula	RC—rostral cartilage
HYP—hypural	RET—retroarticular
IC—interarcual cartilage	SCA—scapula
IH—interhyal	SCL—supracleithrum
INT—intercalar	SES—sesamoid articular
IOP—interopercle	SOC—supraoccipital
IPB—infrapharyngobranchial	SOP—subopercle
LAC—lacrimal	SPH—sphenoid
LE—lateral ethmoid	STF—subtemporal fossa
MAX—maxilla	SYM—symplectic
MC—Meckel's cartilage	UH—urohyal
ME—median ethmoid	US—urostyle
MPT—metapterygoid	VH—ventral hypohyal
MR—medial radial	VIC—ventral intercleithral cartilage
NEZ—neural prezygapophysis	VO—vomer
NOZ—neural postzygapophysis	VT—vertebra

Table 3.2. Taxonomic position of the species included in the comparative osteology section of this study, according to Pezold (1993).

Family Gobiidae	
Subfamily Gobiinae	
	<i>Istigobius ornatus</i>
Tribe Gobiosomini	
	<i>Microgobius signatus</i>
Subfamily Gobionellinae	
	<i>Gnatholepis anjerensis</i>
	<i>Tridentiger brevispinis</i>
	<i>Acanthogobius</i> Group
	<i>Acanthogobius flavimanus</i>
	<i>Chasmichthys</i> Group
	<i>Chaenogobius annularis</i>
	<i>Chaenogobius gulosus</i>
	<i>Gymnogobius breunigii</i>
	<i>Gymnogobius castaneus</i>
	<i>Gymnogobius heptacanthus</i>
	<i>Gymnogobius isaza</i>
	<i>Gymnogobius macrognathos</i>
	<i>Gymnogobius mororanus</i>
	<i>Gymnogobius opperiens</i>
	<i>Gymnogobius petschiliensis</i>
	<i>Gymnogobius taranetzi</i>
	<i>Gymnogobius uchidai</i>
	<i>Gymnogobius urotaenia</i>
	<i>Clevelandia ios</i>
	<i>Eucyclogobius newberryi</i>
	<i>Gillichthys mirabilis</i>
	<i>Gillichthys seta</i>
	<i>Ilypnus gilberti</i>
	<i>Lepidogobius lepidus</i>
	<i>Quietula y-cauda</i>

Table 3.3. Morphological character matrix for all species included in this study. For explanation of characters, see text and Appendix C.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<i>G. macrognathos</i>	1	0	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	0	1	0	1
<i>G. uchidai</i>	1	0	0	1	1	0	1	1	0	1	1	1	1	1	1	0	1	0	1	0	1
<i>G. opperiens</i>	1	0	1	0	0	1	0	0/1	1	1	1	1	0	0	0	1	0	1	0	2	1
<i>G. urotaenia</i>	1	0	1	0	0	1	0	0	1	1	1	1	0	0	0	1	0	1	0	2	1
<i>G. petschiliensis</i>	1	0	1	0	0	1	0	0	1	1	1	1	0	0	0	1	0	1	0	2	1
<i>G. isaza</i>	1	0	1	0	0	1	0	0	1	1	1	1	0	0	0	1	0	1	0	2	1
<i>G. mororanus</i>	1	1	1	0	0	1	1	0/1	0/1	1	1	1	1	0	1	1	0	1	0	2	1
<i>G. heptacanthus</i>	1	1	1	0	0	1	1	0/1	0/1	1	1	1	1	0	1	1	0	1	0	2	1
<i>G. castaneus</i>	1	1	1	0	0	1	0	0/1	1	1	1	1	0	0	0	1	0	1	0	1	1
<i>G. breunigii</i>	1	1	1	0	0	1	1	0	1	1	1	1	0	0	0	1	0	1	0	2	1
<i>G. taranetzi</i>	1	1	1	0	0	1	1	0/1	1	1	1	1	0	0	0	1	0	1	0	1	1
<i>C. annularis</i>	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	1	1	0	1
<i>C. gulosus</i>	1	0	1	0	0	0	0	0	1	1	1	1	0	0	0	1	1	1	1	0	1
<i>G. mirabilis</i>	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	0	1	0	1	1	0
<i>G. seta</i>	1	0	0	0	0	1	0	1	1	1	1	1	1	0	1	0	1	0	1	1	0
<i>E. newberryi</i>	1	0	1	0	1	0/1	1	0	1	1	1	1	0	0	0	1	0	1	1	2	1
<i>L. lepidus</i>	1	1	1	0	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	2	1
<i>C. ios</i>	1	0	1	0	0	1	1	0	1	1	1	1	1	0	1	0	1	1	1	2	1
<i>I. gilberti</i>	1	0	0	0	0	1	1	0	1	1	1	1	0	0	0	1	0	1	0	2	1
<i>Q. y-cauda</i>	1	0	0	0	0	1	1	0	0	1	1	1	1	0	0	1	0	1	1	2	1
<i>T. brevispinis</i>	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	1	1	1
<i>A. flavimanus</i>	1	0	1	0	0	0	0	0	0/1	0	1	0	0	1	0	0	0	1	0	2	1
<i>G. anjerensis</i>	0	?	0	0	0	0	0	0/1	1	1	0	0	0	1	0	0	?	0	0	2	0
<i>I. ornatus</i>	0	?	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	2	0
<i>M. signatus</i>	0	?	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	
<i>G. macrognathos</i>	1	0	0	0	0	1	1	1	1	0	1	1	0	0	0	1	1	2	0	0	
<i>G. uchidai</i>	1	0	0	0	0	1	1	1	1	0	1	1	1	0	0	1	1	2	0	0	
<i>G. opperiens</i>	1	0	0	0	1	1	1	1	1	0	1	1	1	0	0/1	1	1	1	0	0	
<i>G. urotaenia</i>	1	0	0	0	1	1	1	1	1	0	1	1	1	0	0	1	1	1	0	0	
<i>G. petschiliensis</i>	1	0	0	0	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	0	
<i>G. isaza</i>	1	0	0	0	1	1	1	1	1	0	1	1	1	0	0	1	1	1	0	0	
<i>G. mororanus</i>	1	0	0	1	0	1	1	1	1	0	1	1	1	0	0/1	1	1	1	1	0	
<i>G. heptacanthus</i>	1	0	0	1	0	1	1	1	1	0	1	1	1	0	0	1	1	1	0	0	
<i>G. castaneus</i>	1	0	0	0	0	1	1	1	1	0	1	1	1	0	0	0	1	1	2	0	
<i>G. breunigii</i>	1	0	0	0	0	1	1	1	1	0	1	1	1	0	0	0	1	1	2	0	
<i>G. taranetzi</i>	1	0	0	0	1	1	1	1	1	0	1	1	1	0	0	1	1	2	0	0	
<i>C. annularis</i>	1	1	0	0	1	1	1	1	1	0	1	1	1	0	0/1	0	0	1	1	1	
<i>C. gulosus</i>	1	1	0	0	1	1	1	1	1	0	1	1	1	0	1	0	0	0	1	1	
<i>G. mirabilis</i>	1	1	0	0	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	
<i>G. seta</i>	1	0	0	0	1	1	1	0	1	1	1	1	1	0	1	0	0	0	0	0	
<i>E. newberryi</i>	1	0	0	0	0	1	1	0	1	1	1	1	1	0	1	0	1	2	0	0	
<i>L. lepidus</i>	1	0	0	0	0	1	1	1	1	1	1	1	1	0	0	1	0	0	2	0	
<i>C. ios</i>	1	0	0	0	0	1	1	1	?	1	1	1	1	0	0	1	0	0	2	0	
<i>I. gilberti</i>	1	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	0	2	0	0	
<i>Q. y-cauda</i>	1	0	0	0	0	1	1	0	1	1	1	1	1	0	0	1	0	0	2	0	
<i>T. brevispinis</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	
<i>A. flavimanus</i>	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>G. anjerensis</i>	1	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>I. ornatus</i>	0	1	1	0	1	0	0	0	0	0	0	0	0	1	?	?	?	?	0	0	
<i>M. signatus</i>	1	0	1	1	0	1	1	0	0	0	0	0	1	?	?	?	?	0	0	0	

CHAPTER IV:

MOLECULAR PHYLOGENY

In recent years the comparison of DNA sequence data has become a powerful method for constructing species phylogenies. Due to several aspects of its evolutionary dynamics (Stepien and Kocher, 1997), the mitochondrial genome is the most common source of sequences for these comparisons. Mitochondrial DNA (mtDNA) has been extensively studied in fishes and a large library of potential primers for use in PCR amplification has been generated. Rates of evolution vary widely among regions of the mitochondrial genome, making it possible to choose an appropriate region based on anticipated divergence levels to be studied (Stepien and Kocher, 1997). Some mitochondrial genes, such as the cytochrome *b* and NADH dehydrogenase genes, code for transmembrane proteins. These regions can be particularly useful for phylogenetic studies because different portions of their protein products may be subjected to different selective pressures, and therefore exhibit different rates of nucleotide substitution (Irwin et al., 1991; Kocher and Carleton, 1997).

The mitochondrial NADH dehydrogenase subunit 2 (ND2) gene has been used in many studies of fish phylogeny. It has proven effective for elucidating phylogenetic relationships among species and closely related genera in cichlids (Cichlidae; Kocher et al., 1995), mollies (Poeciliidae; Ptacek and Breden, 1998), mackerels (Scombridae; Banford et al., 1999), and minnows (Cyprinidae; Broughton and Gold, 2000). This

gene codes for a section of the hydrophobic protein fraction of the NADH ubiquinone oxidoreductase complex, and although the exact function of its polypeptide product is unclear, it appears to be a transmembrane protein (Cantatore and Sacccone, 1987; Kocher et al., 1995). This region appears to evolve at a high rate compared to other mitochondrial genes, such as cytochrome *b* and cytochrome oxidase. It has been suggested that the mitochondrial ND subunits may play only a limited role in cellular respiration, and therefore may be subject to less stringent evolutionary constraints and exhibit higher levels of variation (Cantatore and Sacccone, 1987; Naylor et al., 1997).

Species of *Gymnogobius*, and indeed all members of the *Chasmichthys* Group, are morphologically very similar. It is therefore possible that short genetic distances separate them and that an investigation of their molecular phylogeny will require a high-resolution tool. Because it is a highly variable region of the mitochondrial genome that has been studied extensively in fishes, the ND2 gene is ideally suited for use in the current study. The objectives of this portion of the study were to sequence the mitochondrial ND2 region for all available species of the *Chasmichthys* Group in order to: 1) compare the evolutionary dynamics of this gene in gobiids with those of the ND2 gene in other fishes, and 2) elucidate the phylogenetic relationships of the genus *Gymnogobius* and the *Chasmichthys* Group.

MATERIALS AND METHODS

Sequence Generation and Alignment.—For the molecular analysis, small fin clips were taken from the right pectoral fin of specimens fixed and preserved in ethanol. Total

genomic DNA extractions were performed using the DNeasy Kit (Qiagen) protocol for animal tissues with a single final elution of 50 µl. The mitochondrial ND2 gene was amplified in two fragments using the following primer sets, made available by Christine Thacker (Los Angeles County Museum of Natural History): gobyL4919 (5'-
CCCATACCCGAAAATGATG-3') / gobyH5513 (5'-
GAGTAGGCTAGGATTTWCGAAGYTG-3') and gobyL5464 (5'-
GGTTGAGGRGGCCTMAACCARAC-3') / goby H6064 (5'-
CTCCTACTTAGAGCTTGAAAGGC-3'). Typical reaction parameters were: 20 seconds at 93°C, 20 seconds at 56°C, 35 seconds at 72°C, 35 cycles. Reactions contained one unit Taq DNA polymerase (PGC Scientific), 10X PCR buffer (100 mM Tris-HCl pH 8.3, 500 mM KCl, 15 mM MgCl₂, 1% Triton X-100), 2mM dNTPs, 2.5 mM MgCl₂, 0.3 µM primers, and an undetermined amount of DNA template. PCR products were then visualized on 2% agarose gels and the target fragment was excised using a wide-bore micropipet tip. Excised gel plugs were incubated in 50 µl low TE buffer (10mM Tris-HCl pH 8.0, 0.1mM EDTA) overnight and then used to seed another PCR with conditions identical to the first. PCR products were then purified using ExoSAP-IT enzyme (USB Corp.) and cycle-sequenced using the DYEnamic ET Dye Terminator Cycle Sequencing Kit for MegaBACE (Amersham Pharmacia Biotech, Inc.) with the same primers and the following profile: 20 seconds at 95°C, 15 seconds at 56°C, 1 minute at 60°C, 40 cycles. Cycle-sequencing products were ethanol-precipitated and loaded onto a MegaBACE 1000 sequencing instrument MegaBACE (Amersham Pharmacia Biotech, Inc.).

DNA sequences were aligned by eye using the *Rhinogobius giurinus* sequence (GenBank Accession # AB018982) as a reference. When possible, two specimens were sequenced from each species, and sequences were verified in the forward and reverse direction. Differences between sequences for a species were resolved conservatively, meaning that retention of consensus sequence was favored over substitution and silent substitution was favored over nonsilent substitution. When differences could not be resolved conservatively, the base was called ambiguous.

Molecular Analysis.—Nucleotide composition statistics, tests of heterogeneity among taxa, and transition/transversion saturation curves were generated using the DAMBE software package (Xia, 2000). Genetic distances are presented as both pairwise uncorrected distances (# site differences / # bases compared) and Tamura – Nei Gamma (TN 93) distances (Tamura and Nei, 1993). For TN 93 distances, the alpha parameter of the gamma distribution was determined using the “baseml” program of the PAML software package (Yang, 2001). The alpha parameter was estimated using both F84 and HKY 85 substitution models, each with 3, 10, and 25 rate categories. Kappa parameters were simultaneously estimated with “baseml.” The pairwise distance matrix was then generated using the mean of all six alpha estimates with the MEGA software package (Kumar et al., 2000). Maximum likelihood (ML) distance matrices were also generated by the DNADIST program in the PHYLIP software package (Felsenstein, 1995). These were generated using one category of substitution rates and transition/transversion ratios of 1, 2, and 5. In order to more closely model different

substitution rates at the three different codon positions, another ML distance matrix was generated assuming three categories of substitution rates with equal probability and relative rates of 5:1:10.

Phylogenetic trees were generated using the neighbor-joining clustering algorithm of Saitou and Nei (1987) and two different optimality criteria: maximum parsimony and maximum likelihood. Neighbor-joining (NJ) trees were generated using TN 93 and ML pairwise genetic distances. NJ trees using TN 93 distances were generated using the MEGA software package, with pairwise deletion of missing data and 1000 bootstrap replications. NJ trees were also generated using the NEIGHBOR program in PHYLIP and 1000 bootstrap replications. Maximum parsimony trees were generated using the MEGA program with three data sets: all sites, first and second codon positions only, and amino acid residues. Tree searches were performed with the close-neighbor interchange option at default values and 1000 bootstrap replications. The relative likelihood scores of the most parsimonious trees generated by the "all sites" data set were then assessed using a Student-Newman-Keuls test performed by the DAMBE software package. Maximum likelihood trees were generated using the DNAML program in the PHYLIP package. Trees were generated under the assumption of equal substitution rates among all sites with transition/transversion ratios of 1.0, 2.0, and 5.0, as well as under the assumption of three rate categories (equal probability, relative rates of 5:1:10) with transition/transversion ratios of 1.0, 2.0, and 5.0. The parameters that generated the tree with the best likelihood score were then used to produce a final maximum likelihood tree with 500 bootstrap replications.

RESULTS

A segment of the mitochondrial ND2 gene beginning at the ATG start codon was sequenced for 12 species, including seven species of *Gymnogobius*, two species of *Acanthogobius*, and one species each of *Chaenogobius*, *Eucyclogobius*, and *Gillichthys*. For the majority of the species included, the sequenced region is 923 bp in length, but in five cases the segment is shorter (532 bp in *Gymnogobius isaza*, 536 bp in *Gillichthys seta*, 683 bp in *Eucyclogobius newberryi*, 856 bp in *Acanthogobius flavimanus*, and 912 bp in *Gymnogobius urotaenia*). A sequence obtained from GenBank (Accession AB018982) for *Rhinogobius giurinus* is also included in the data set (Appendix D).

Nucleotide frequencies for A (0.262), C (0.296), and T (0.290) are nearly equal, while the frequency of G (0.152) is much lower. Heterogeneity among taxa in nucleotide frequency distribution is not significant in the total data set ($P = 0.889$), nor is it significant either at the first ($P = 0.999$) or second ($P = 0.999$) codon position. However, heterogeneity at the third codon position is significant ($P = 0.003$). Heterogeneity is not significant at the third codon position when the *Rhinogobius* sequence is removed from the data set ($P = 0.0867$).

The data set contains 551 variable sites, of which 427 are parsimony informative for the analysis. Putative mutations consist only of single nucleotide substitutions; no insertions or deletions were detected. Variation was found in 51.0% of first codon position sites, 30.5% of second codon position sites, and 95.4% of third codon position sites. Site variation does not appear to be clustered in any particular portion of the

sequence, as indicated by the plot of entropy vs. sequence position (Fig. 4.1). Uncorrected pairwise genetic distances (Table 4.1) range from 0.058 to 0.366, and Tamura-Nei distances range from 0.066 to 1.162. For both distance measures the smallest value is for the *Gymnogobius breunigii* – *G. castaneus* pair, while the largest distance value is for the *Gymnogobius castaneus* – *Acanthogobius lactipes* pair. A scatter plot of transversions vs. genetic distance shows a linear relationship, while a scatter plot of transitions vs. genetic distance shows a slightly curvilinear relationship (Fig. 4.2). Estimates of transition/transversion ratio range from 2.00 to 2.12, with a mean of 2.08. Estimates of the α -parameter range from 0.472 to 0.525, with a mean of 0.503.

Phylogenetic trees generated using the neighbor-joining clustering algorithm exhibit similar topology regardless of the rate assumptions used (Fig. 4.3). All three of the NJ trees generated recover a monophyletic *Gymnogobius urotaenia* species group (*G. urotaenia*, *G. petschiliensis*, *G. opperiens*, and *G. isaza*) as well as a monophyletic *Gymnogobius* and a monophyletic *Chasmichthys* Group. However, two of the three NJ trees (generated using ML distances with one substitution rate and ML distances with three substitution rates) recover a monophyletic *Chaenogobius* + *Gymnogobius* clade, while the other (generated using Tamura-Nei gamma distances) recovers a *Chaenogobius* + *Gillichthys* clade as the sister group of *Gymnogobius*. The relationships of *Chaenogobius* and *Gillichthys* are the only source of conflict among the NJ trees, and bootstrap support for these nodes is relatively low in all cases.

The maximum parsimony analysis of the entire data set recovers five most parsimonious trees of 1380 steps. The log-likelihood score of the best of these five trees is -6963.8, but none of the other four trees has a significantly lower score ($p > 0.5$ in all cases). The topology with the highest log-likelihood (Fig. 4.4) includes a monophyletic *G. urotaenia* species group, a monophyletic *Gymnogobius*, and a monophyletic *Chasmichthys* Group, with a consistency index of 0.64. In contrast to the NJ trees, the parsimony tree includes a *Chaenogobius* + *Gillichthys* + *Eucyclogobius* clade, which forms the sister group of *Gymnogobius*. However, bootstrap support for this clade and many of the other clades in this tree is relatively low. Removal of the third codon position sites changes the tree topology significantly. This tree includes a monophyletic *G. urotaenia* species group and a monophyletic *Chasmichthys* Group, but the genus *Gymnogobius* is rendered paraphyletic by the insertion of the *Chaenogobius* + *Gillichthys* + *Eucyclogobius* clade. Again, bootstrap support for many of the clades is very weak. The length of this tree is 458 steps and the consistency index is 0.74. The maximum parsimony tree generated using the amino acid data is almost completely unresolved, but still recovers a monophyletic *Chasmichthys* Group.

All maximum likelihood trees generated with this data set exhibit the same topology, regardless of assumed transition/transversion ratio or rate equality assumptions (Fig. 4.5). A ts/tv ratio of 2.0 improves the overall likelihood of the tree relative to ts/tv ratios of 1.0 and 5.0, and the assumption of unequal substitution rates (3 rate categories) improves the overall likelihood relative to an assumption of equal rates. This topology includes a monophyletic *G. urotaenia* species group, a monophyletic

Gymnogobius, and a monophyletic *Chasmichthys* Group. Like the parsimony tree, the ML tree includes a *Chaenogobius* + *Gillichthys* + *Eucyclogobius* clade, which is sister to *Gymnogobius*. However, the structures of the *G. urotaenia* species group and the *Chaenogobius* clade are slightly different than in the parsimony tree. Overall, this tree exhibits relatively high bootstrap support.

DISCUSSION

The ND2 gene in the *Chasmichthys* Group exhibits evolutionary dynamics similar to those reported for other fishes. The anti-G bias found in this study is comparable in magnitude to that found in this region by other workers (Kocher et al., 1995; Naylor et al., 1997; Ptacek and Breden, 1998; Banford et al., 1999; Broughton and Gold, 2000). Kocher et al. (1995) pointed out that this bias may be partially because hydrophobic amino acids correspond to codons with the nucleotides C and T in the second codon position. Because the ND2 gene codes for a hydrophobic membrane-spanning protein, hydrophobic amino acids such as threonine are disproportionately represented in the polypeptide. The significance of this anti-G bias is that it may cause the ND2 gene to reach substitution saturation more quickly than other mtDNA regions. The nucleotide bias may also influence the nucleotide substitution model that is most appropriate for use in phylogenetic reconstructions based on this gene.

Nucleotide frequency distributions are relatively homogeneous across taxa, a condition known as stationarity. Chi-square tests reveal significant deviation from stationarity only among third codon position sites, and even that significant result

disappears when the *Rhinogobius* sequence is removed. A lack of stationarity among third codon position sites has also been reported in cichlids (Kocher et al., 1995) and sharks (Naylor et al., 1997), but explanations for this pattern have not been postulated. The effects of deviations from stationarity on phylogenetic reconstruction are unknown, but the data indicate that nucleotide substitution dynamics at the third codon position may differ from those at the other positions in complex and currently unexplained ways. Therefore, caution must be exercised in the interpretation of phylogenetic patterns gleaned from these sites.

The pattern of variation exhibited by the sequences obtained in this study is also similar to those previously reported for this gene. Nearly all third codon position sites are variable, while the second position sites are the most conserved. This is the typical pattern seen in mitochondrial genes coding for proteins, and has been reported for cichlids (Kocher et al., 1995) and minnows (Broughton and Gold, 2000) in the ND2 gene. The relative variability of the three codon positions is an indication of the rate of nucleotide substitution at each position, and reflects the redundancy of the code. The fact that variation is not concentrated in any particular region of the gene indicates that there are no large portions of the polypeptide that are either particularly free of evolutionary constraints nor are there large regions that are particularly conserved. A similar result was reported in cichlids (Kocher and Carleton, 1997), although some short conserved segments in the gene have been detected (Kocher et al., 1995). The curvilinear relationship in the plot of transitions vs. genetic distance indicates that substitution saturation may be occurring among the more distantly related taxa, which

may cause those distances to be underestimated if not taken into account in the nucleotide substitution model. Transition/transversion ratios obtained in this study reflect the well-documented transition bias commonly seen in animal mtDNA, but are somewhat low compared with previously reported values for this gene in fishes, which typically range from 3:1 to 5:1 (Naylor et al., 1997; Banford et al., 1999). Alpha-parameter estimates obtained in this study averaged approximately 0.5. The alpha parameter indicates the shape of the gamma distribution used in modeling substitution rate variation among sites. When α is greater than 1, the gamma distribution is bell shaped, indicating that rate variation among sites is minimal. When α is less than 1 the distribution is L-shaped, indicating that rate variation among sites is considerable. The estimates of α obtained for this data set indicate that there may be a considerable amount of rate variation among sites, and therefore a gamma distribution may be more appropriate for modelling rate variation in this case than the poisson distribution assumed by many phylogenetic inference algorithms.

Overall, the properties of the sequences in this data set are consistent with those previously reported for the ND2 gene in fishes. This information about the evolutionary dynamics of the ND2 gene may provide some insight into the properties of the nucleotide substitution model that is most likely to retrieve an accurate phylogenetic reconstruction from this data set. The anti-G bias indicates that an assumption of equal nucleotide frequencies may be violated. The lack of stationarity, the pattern of variation among codon positions, and the estimates of the α -parameter indicate that an assumption of equal substitution rates may be violated. Finally, ts/tv ratios indicate that

differential weighting of transitions and transversions may be appropriate, but their small magnitude suggests that differential weighting may not be critical to performance of the model.

The phylogenies generated using this DNA sequence data set all have similar topologies. In every case the *Chasmichthys* Group is monophyletic, and in every case but one the genus *Gymnogobius* is monophyletic. In each of the recovered topologies the *Gymnogobius* is separated into two clades, one consisting of the *G. urotaenia* species group and the other of *G. breunigii* + *G. castaneus* + *G. heptacanthus*. The topology within the *G. urotaenia* species group and that of the remaining *Chasmichthys* Group is much less consistent across reconstructions.

Although all reconstructions recover the *Chasmichthys* Group as monophyletic, this result must not be overstated. Several of the genera included in the *Chasmichthys* Group were not included in the data set due to sequencing difficulties, and only two outgroup genera were successfully sequenced. Therefore, a convincing demonstration of the monophyly of this group will require additional sequencing work, including the other genera within the group and an assortment of additional gobionelline outgroup genera.

The consistent monophyletic recovery of *Gymnogobius* is a more significant result. In neighbor-joining and maximum likelihood reconstructions, *Gymnogobius* forms a monophyletic clade with high bootstrap support. The maximum parsimony reconstruction using the entire data set also includes a monophyletic *Gymnogobius*, but with somewhat lower bootstrap support. The only reconstruction that does not include a

monophyletic *Gymnogobius* (maximum parsimony with only first and second codon positions) has a number of nodes supported by very low bootstrap values, indicating that the structure is not stable. The instability of this topology is probably due to the reduction in the size and variability of the data set caused by the removal of the third codon position sites, over 90% of which are variable. Thus, the overall indication is that the genus is monophyletic within this data set. However, this result must also be viewed with caution. None of the species of the *G. macrognathos* species group were successfully sequenced, nor were several genera of the *Chasmichthys* Group, due to lack of availability of suitable specimens. It is possible that the inclusion of these species would render *Gymnogobius* non-monophyletic.

The genus *Gymnogobius* is consistently separated into two clades, one consisting of the *G. urotaenia* + *G. opperiens* + *G. isaza* + *G. petschiliensis* group and the other of *G. breunigii* + *G. castaneus* + *G. heptacanthus*. Both of these clades are generally supported by bootstrap values above 0.5. This result is consistent with the morphological data, as well as the result Aizawa et al. (1994) obtained using allozyme data.

The placement of *Chaenogobius*, *Gillichthys*, and *Eucyclogobius* is very inconsistent across reconstructions, and in no case is the placement of these genera supported by high bootstrap values. This may be partially due to the relatively small amount of sequence data obtained for *Eucyclogobius*. Unfortunately, a sister group of *Gymnogobius* cannot be confidently hypothesized in the face of this inconsistency. The two Asian genera in the *Chasmichthys* Group form a monophyletic clade only in the

neighbor-joining tree generated using maximum likelihood distances, and even in that case the clade is not well supported. Therefore, like the morphological data, the molecular data indicate that the *Chasmichthys* Group is not clearly separated into Asian and North American clades.

Within *Gymnogobius*, the relative placement of the members of the *G. urotaenia* species group is inconsistent across reconstructions. The results of Aizawa et al. (1994) indicate that *G. opperiens* forms the sister group of the remaining three species in this clade, and that *G. petschiliensis* forms the sister group of *G. urotaenia* + *G. isaza*. The three-species tree (*G. urotaenia*, *G. petschiliensis*, *G. opperiens*) of Suk et al. (1996) is consistent with Aizawa et al.'s (1994) topology. In this study, the maximum parsimony (entire data set) and maximum likelihood methods recover the same topology obtained by Aizawa et al. (1994) for this species group, although bootstrap support for the *G. urotaenia* + *G. isaza* clade is relatively low in both cases. In contrast, neighbor-joining reconstructions reverse the placement of *G. petschiliensis* and *G. isaza*, forming a *G. petschiliensis* + *G. urotaenia* clade with *G. isaza* as its sister group. The entire construction is well supported in both neighbor-joining trees. The inconsistency in this group may be partially due to the fact that a relatively small amount of sequence data was obtained for *G. isaza*. None of the topologies discussed here is consistent with that obtained in this study using morphological data.

Overall, the molecular data presented in this study support the phylogenetic hypotheses of previous authors, and are largely consistent with the morphological phylogeny presented in the previous chapter. These data support the conclusion that the

genus *Gymnogobius* consists of two separate clades of several species, one of which includes the *G. urotaenia* species group. They also support, albeit incompletely, the conclusions that both the *Chasmichthys* Group and the genus *Gymnogobius* are monophyletic. Finally, they suggest that the *Chasmichthys* Group does not consist of distinct Asian and North American clades. Future addition of sequence data from the remaining species of the genus *Gymnogobius* as well as the remaining members of the *Chasmichthys* Group and additional gobionelline outgroup genera will help to clarify the phylogenetic history of this group.

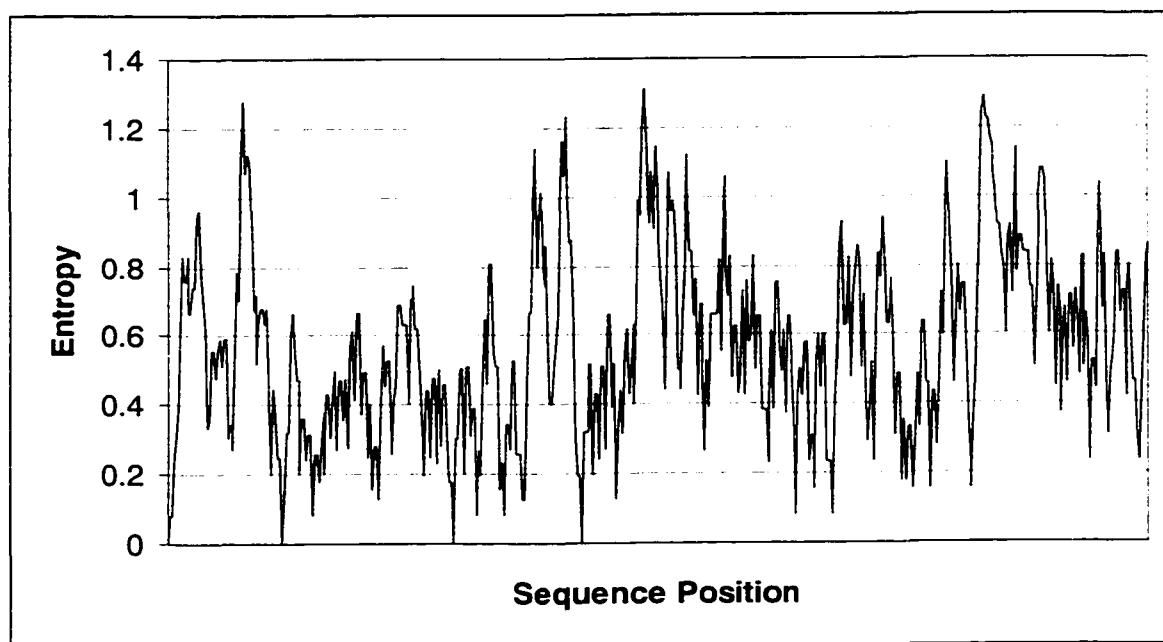


Figure 4.1. Line graph of relative entropy vs. sequence position for species included in this study.

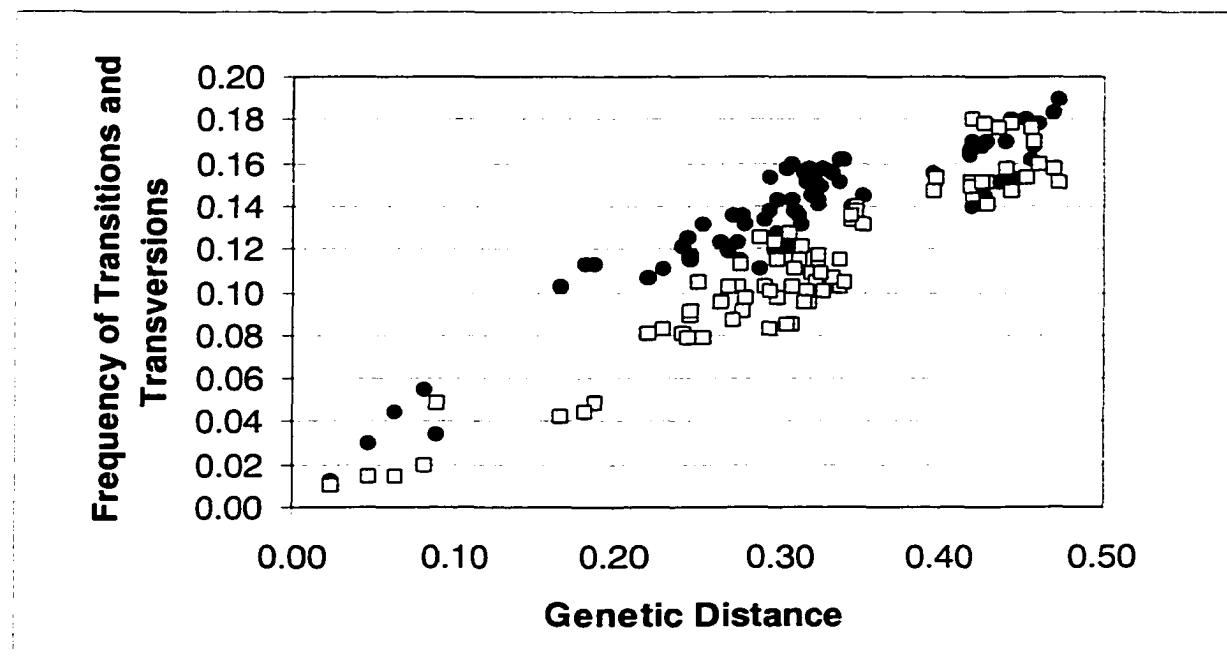


Fig. 4.2. Scatterplot of transition (closed circles) and transversion (open squares) frequency versus pairwise genetic distance (F84) for all taxa included in this study.

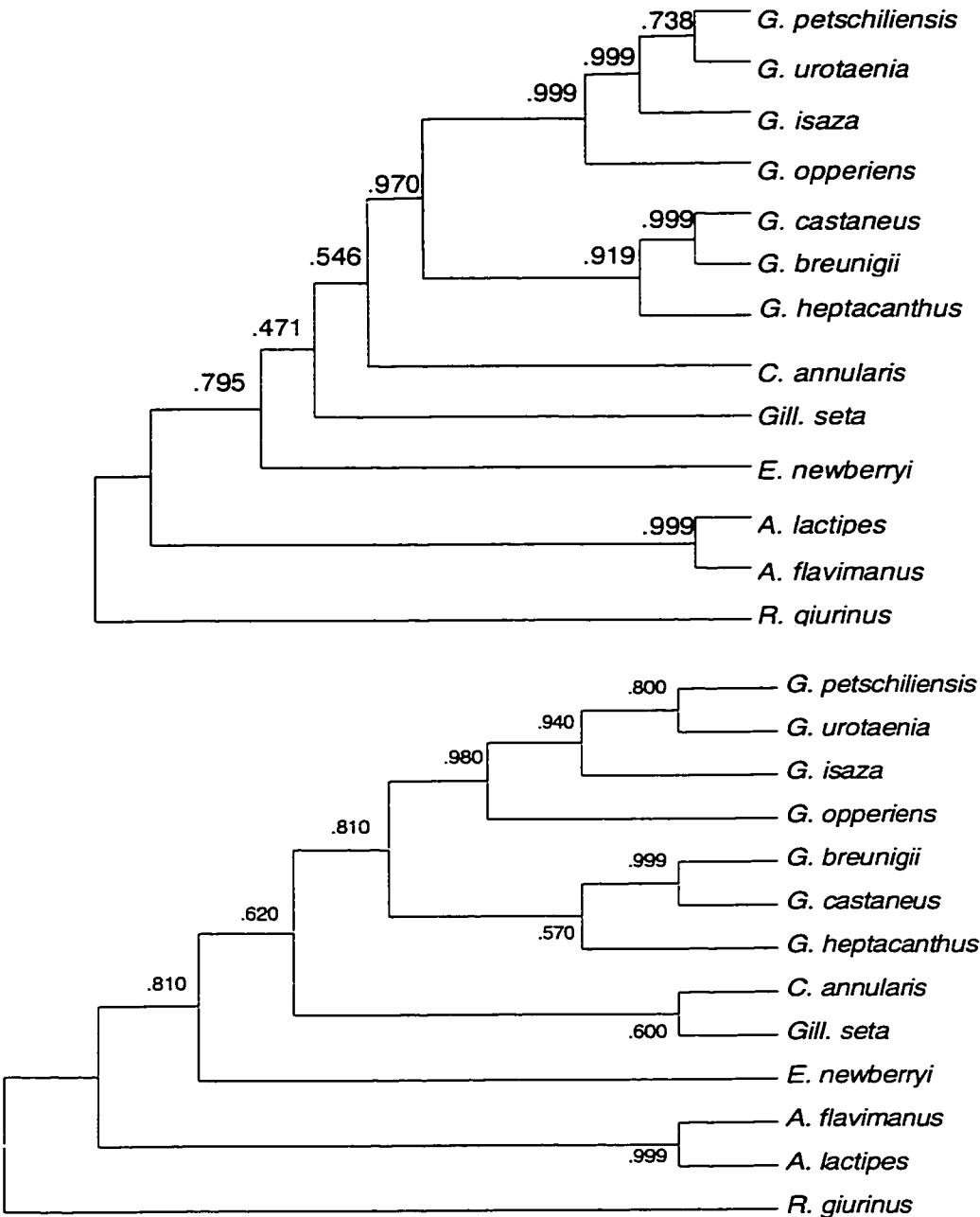


Fig. 4.3. Neighbor-joining trees generated using maximum likelihood distances (above) and Tajima-Nei gamma distances (below) for gobionelline species included in this study. Numbers at nodes indicate proportion of bootstrap support (1000 replicates).

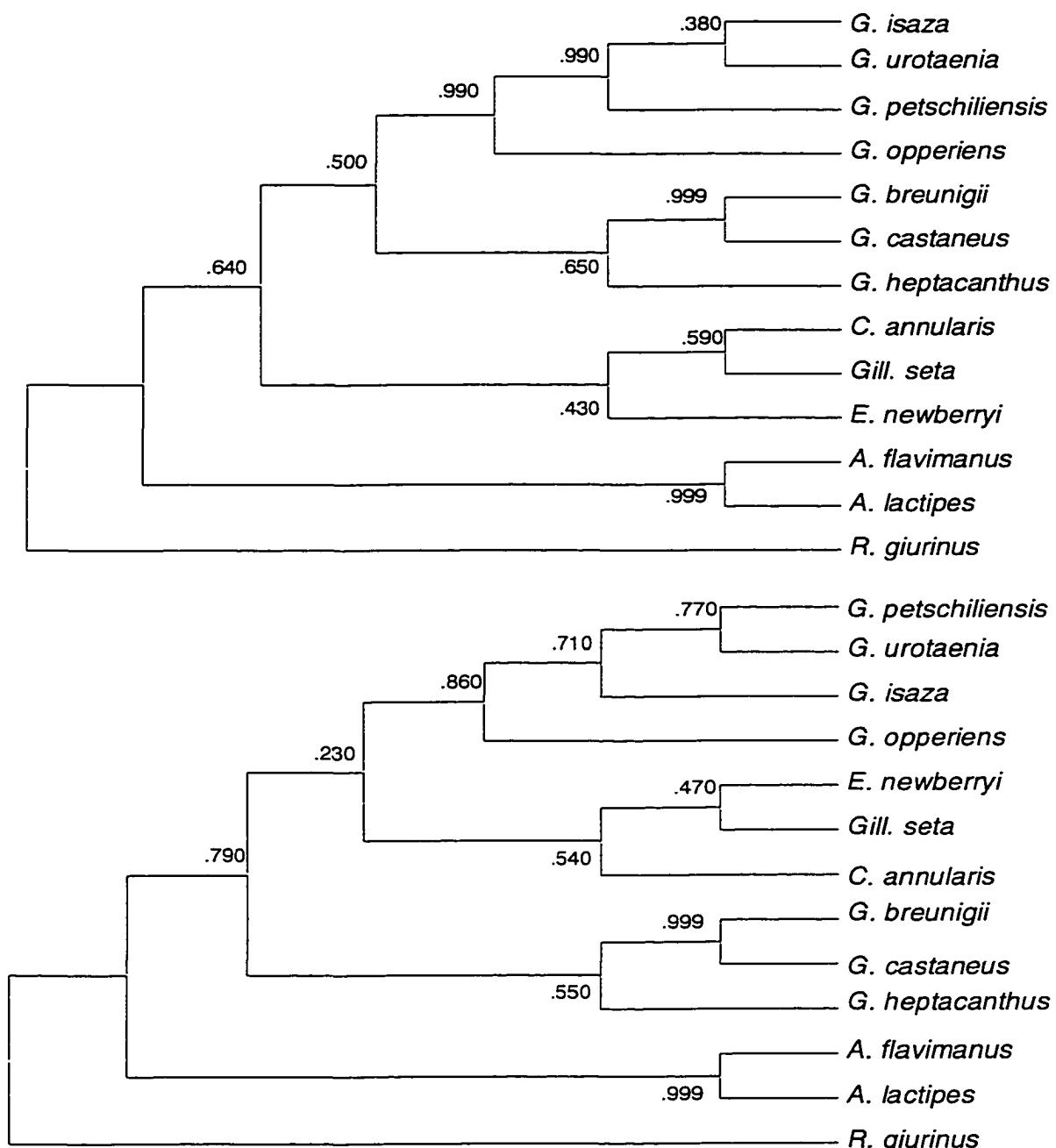


Fig. 4.4. Maximum parsimony trees generated using the entire data set (above) and first and second codon positions only (below) for gobionelline species included in this study. Numbers at nodes indicate proportion of bootstrap support (1000 replications).

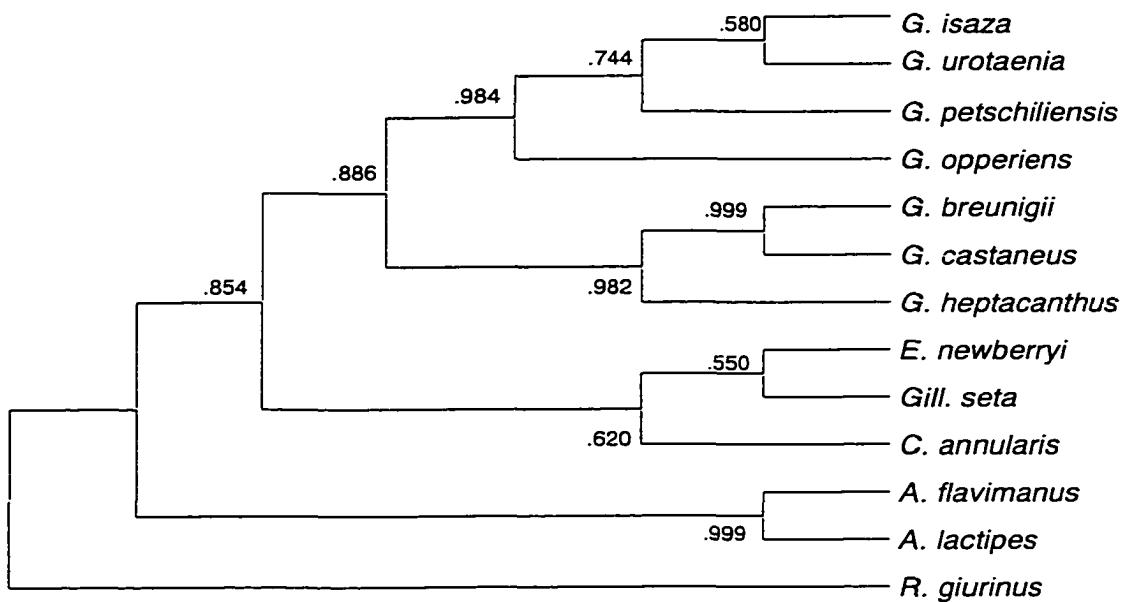


Fig. 4.5. Maximum likelihood tree generated using a ts/tv ratio of 2.0 and three rate categories for gobionelline species included in this study. Numbers at nodes indicate proportion of bootstrap support (500 replicates).

Table 4.1. Uncorrected pairwise genetic distances (above the diagonal) and Tamura-Nei Gamma distances (below the diagonal) among all taxa included in this study.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1 <i>Gymnogobius breunigii</i>		0.058	0.240	0.223	0.250	0.252	0.245	0.278	0.307	0.294	0.351	0.365	0.287
2 <i>Gymnogobius castaneus</i>	0.066		0.223	0.214	0.235	0.242	0.231	0.260	0.296	0.285	0.353	0.366	0.276
3 <i>Gymnogobius heptacanthus</i>	0.495	0.450		0.200	0.236	0.250	0.227	0.256	0.284	0.270	0.355	0.346	0.262
4 <i>Gymnogobius isaza</i>	0.411	0.392	0.342		0.076	0.168	0.049	0.251	0.239	0.272	0.328	0.324	0.235
5 <i>Gymnogobius petschiliensis</i>	0.527	0.473	0.473	0.093		0.156	0.070	0.260	0.271	0.273	0.348	0.341	0.271
6 <i>Gymnogobius opperiens</i>	0.523	0.496	0.528	0.272	0.250		0.155	0.248	0.280	0.259	0.345	0.352	0.268
7 <i>Gymnogobius urotaenia</i>	0.520	0.477	0.437	0.056	0.084	0.238		0.260	0.265	0.270	0.354	0.353	0.264
8 <i>Chaenogobius annularis</i>	0.616	0.551	0.529	0.532	0.574	0.502	0.576		0.271	0.251	0.346	0.344	0.275
9 <i>Eucyclogobius newberryi</i>	0.752	0.725	0.648	0.486	0.586	0.626	0.573	0.613		0.270	0.332	0.337	0.277
10 <i>Gillichthys seta</i>	0.687	0.684	0.581	0.633	0.617	0.545	0.603	0.498	0.608		0.352	0.344	0.264
11 <i>Acanthogobius flavimanus</i>	1.015	1.039	1.062	0.908	1.040	1.016	1.106	1.033	0.910	1.112		0.121	0.320
12 <i>Acanthogobius lactipes</i>	1.148	1.162	0.986	0.887	0.977	1.087	1.074	1.001	0.952	1.064	0.164		0.306
13 <i>Rhinogobius giurinus</i>	0.663	0.620	0.545	0.471	0.610	0.594	0.568	0.612	0.625	0.563	0.826	0.746	

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APPENDIX A:**English Translation of Gill's (1859) Original Latin Description of *Chaenogobius***

(D. E. Stevenson, 1998)

Advance description of a subfamily of Gobiid fishes with cycloid scales, collected by

W. Stimpson in the Pacific Ocean

Theodore Gill

Read 20 December 1858

Chaenogobius, Gill

Body elongate, slender, subcylindrical in front, narrower toward the caudal fin. Scales cycloid, mostly small. Head subconical, forehead lines nearly straight, depressed from above, broad, subrotund: crown and opercula without scales: anterior dorsum and sides naked, moderate patches of scales extending from dorsal fin to the nape. Eyes oblique, small, placed in the anterior part of the head. Mouth large, greatly split, extending behind the eye, slightly oblique. Maxillae equal. Tongue slightly emarginate. Teeth medium, subcylindrical, recurved. Dorsal fins two, entirely distinct. Anal fin opposite the second dorsal fin. Caudal fin rounded. Pectoral fins rounded. Ventral fins small, interspinous membrane shallow.

Chaenogobius annularis, Gill

Anterior of body nearly cylindrical, height greatest near dorsal fin, equal to one-seventh of the length, height similar near caudal; posterior compressed. Line from dorsal fin to rostrum nearly straight. Head awkward, laterally semiconical, below almost horizontal; depressed flat from above, slowly sloping toward the rounded rostrum. Nape slightly constricted. Head length from snout to opercular margin not longer than one quarter body length; head height nearly half head length; head width near nucham slightly more than half head length. Eyes completely in the front part of the head, orbit diameter nearly one quarter in head length; interorbital space equal to 3/5 diameter. Caudal fin small, rounded, about one sixth total length. First dorsal fin spines six, the last removed; second dorsal fin inserted in the posterior half of the length.

D. VI. 9. A. 8. C. 19.

Color brownish, with closely placed dark spots above, sides behind anus with nearly ocellate spots. Vent almost pointed, yellowish. Second dorsal fin with three bands.

Habitat: in "Hakodadi" Bay in Sea of Japan. W. Stimpson (single specimen).

APPENDIX B:**Material Examined*****Chaenogobius annularis***

Type Material.—*Chaenogobius annularis*, USNM 6336, holotype, 40.6 mm, “Hakodadi” Bay, Japan, Stimpson. *Gobius dolichognathus*, ZMB 10651, holotype, 44.0 mm, Japan, Hilgendorf; ZMB 10654, paratypes, 9 (27.5-55.9 mm), Japan, Hilgendorf.

Additional Material.—BMNH 1903.5.14.65-74, 38.0 mm, Misaki, Sagami, Honshu, Japan, Jordan; HUMZ 99287, 44.3 mm, Oshoro, Japan, Izutsu; HUMZ 99333, 47.1 mm, Oshoro, Japan, Izutsu; HUMZ 103018, 47.1 mm, Horonai, Okushiri Island, Japan, Miki, Nishida, and Maeda; HUMZ 152150, 42.1 mm, Cape Shiokubi, Toi, Hokkaido, Japan, Okada; HUMZ 152153, 41.2 mm, Cape Shiokubi, Toi, Hokkaido, Japan, Okada; HUMZ 152155, 46.5 mm, Kaminokuni, Hokkaido, Japan, Okada; HUMZ 152156, 42.5 mm, Kaminokuni, Hokkaido, Japan, Okada; HUMZ 152338, 45.0 mm, Cape Shirakami, Matsumae, Hokkaido, Japan, Okada; HUMZ 152339, 40.7 mm, Cape Shirakami, Matsumae, Hokkaido, Japan, Okada; HUMZ 154885, 52.2 mm, Anama, Hakodate, Hokkaido, Japan; HUMZ 154887, 30.4 mm, Anama, Hakodate, Hokkaido, Japan; HUMZ 154889, 26.4 mm, Kandahama, Okushiri Island, Japan; HUMZ 154894, 25.5 mm, Kandahama, Okushiri Island, Japan; HUMZ 154916, 38.5 mm, Cape Shiokubi, Toi, Hokkaido, Japan; HUMZ 154918, 39.0 mm, Cape Shiokubi, Toi, Hokkaido, Japan; LACM 44905-2, 43.5

mm, Misaki, Japan; NMW 30768, 40.6 mm, Hakodate, Hokkaido, Japan, Steindachner; NSMT-P 19363, 24 (40.5-52.5 mm), Tsumakizaki, Izu Peninsula, Honshu, Japan, Matsuura; NSMT-P 23159, 48.0 mm, Yamagata Pref., Tobi-shima Island, Japan, Arai, Matsuura, and Aizawa; NSMT-P 45880, 2 (44.5-44.6 mm), Izu, Miyake-jima Island, Japan, Shibukawa; NSMT-P 56774, 8 (29.0-57.0 mm), Iwai-zaki Point, Kesennuma, Miyagi, Honshu, Japan, Matsuura and Shibukawa.

Chaenogobius gulosus

Type Material.—*Saccostoma gulosus*, MNHN 5121, holotype, 117.1 mm, Eloffe, Japan. *Chasmias misakius*, BMNH 1903.5.14.65–74, “cotypes,” 26 (38.5-103.0 mm), Misaki, Sagami, Honshu, Japan, Jordan.

Additional Material.—HUMZ 99296, 76.2 mm, Oshoro, Japan, Izutsu; HUMZ 99330, 75.9 mm, Oshoro, Japan, Izutsu; HUMZ 99331, 78.0 mm, Oshoro, Japan, Izutsu; HUMZ 99332, 80.5 mm, Oshoro, Japan, Izutsu; HUMZ 100392, 77.6 mm, Oshoro, Japan, Izutsu; HUMZ 103008, 45.0 mm, Horonai, Okushiri Island, Japan, Miki, Nishida, and Maeda; HUMZ 103011, 39.4 mm, Horonai, Okushiri Island, Japan, Miki, Nishida, and Maeda; HUMZ 103012, 39.0 mm, Horonai, Okushiri Island, Japan, Miki, Nishida, and Maeda; HUMZ 103013, 39.5 mm, Horonai, Okushiri Island, Japan, Miki, Nishida, and Maeda; HUMZ 154908, 26.5 mm, Kandahama, Okushiri Island, Japan; HUMZ 154909, 30.5 mm, Kandahama, Okushiri Island, Japan; HUMZ 154910, 26.2 mm, Kandahama, Okushiri Island, Japan; LACM 1063, 89.6 mm, Misaki, Japan; LACM 44905-1, 2 (31.5-74.5 mm), Misaki, Japan; LACM 44905-2, 9 (58.0-87.5 mm),

Misaki, Japan; NSMT-P 23147, 5 (33.4-44.2 mm), Tobi-shima Island, Japan, Arai; NSMT-P 50675, 16 (34.3-83.9 mm), NE coast of Hegura-jima Island, Japan, Matsuura.

Gymnogobius castaneus

Type Material.—*Gobius castaneus*, BMNH 1870.12.2.1-2, syntypes, 2 (43.5-43.6 mm), Aomori, Honshu, Japan. *Chloea nakamurae*, USNM 61680, paratypes, 2 (32.5-39.2 mm), Nagaoka, Japan, Nakamura. *Chloea senbae*, ZUMT 57518, syntype, 55.6 mm, Mito, Ibaraki Pref., Japan, Tanaka. *Chloea senbae*, ZUMT 57519, syntype, 49.5 mm, Mito, Ibaraki Pref., Japan, Tanaka.

Additional Material.—BMNH 1903.5.14.58-59, 2 (50.0-51.1 mm), Niigata, Honshu, Japan, Jordan; HUMZ 2537, 61.5 mm, Sapporo, Hokkaido, Japan; HUMZ 2538, 56.7 mm, Sapporo, Hokkaido, Japan; HUMZ 2542, 58.0 mm, Sapporo, Hokkaido, Japan; HUMZ 2543, 58.2 mm, Sapporo, Hokkaido, Japan; HUMZ 2545, 61.8 mm, Sapporo, Hokkaido, Japan; HUMZ 2551, 57.0 mm, Sapporo, Hokkaido, Japan; HUMZ 2552, 61.4 mm, Sapporo, Hokkaido, Japan; HUMZ 2554, 59.2 mm, Sapporo, Hokkaido, Japan; HUMZ 2556, 64.3 mm, Sapporo, Hokkaido, Japan; HUMZ 2558, 66.4 mm, Sapporo, Hokkaido, Japan; HUMZ 2560, 63.8 mm, Sapporo, Hokkaido, Japan; HUMZ 2561, 59.4 mm, Sapporo, Hokkaido, Japan; HUMZ 2563, 56.5 mm, Sapporo, Hokkaido, Japan; HUMZ 2566, 61.0 mm, Sapporo, Hokkaido, Japan; HUMZ 2567, 57.6 mm, Sapporo, Hokkaido, Japan; UW 029184, 5 (37.0-44.0 mm), Zelionyi, Kuril Archipelago, Russia, Pietsch; UW 029332, 20 (32.1-45.5 mm), Zelionyi, Kuril Archipelago, Russia, Pietsch; UW 040520, 9 (35.0-52.0 mm), Tanfilyeva, Kuril Archipelago, Russia, Stevenson; UW 040531, 10 (17.0-27.0 mm), Polonskogo, Kuril

Archipelago, Russia, Stevenson; UW 044745, 85 (22.0-62.0 mm), Lake Barguzinskoye, southern Sakhalin Island, Russia, Stevenson, Woods, and Reimer; UW 044751, 51.5 mm, Cape Menaputsy, southern Sakhalin Island, Russia, Jensen; UW 044860, 3 (37.1-53.0 mm), Mereya River, southern Sakhalin Island, Russia, Stevenson, Woods, and Reimer.

Gymnogobius taranetzi

Type Material.—*Chaenogobius taranetzi*, ZISP 42342, holotype, 66.6 mm, Kedrovka River mouth, Primorski Krai, Russia, Pinchuk.

Additional Material.—LACM 44902-1, 42.5 mm, Shinji Lake, Japan, Hubbs; LACM 44902-2, 3 (20.0-38.0 mm), Shinji Lake, Japan, Hubbs; UW 044224, 29 (35.2-61.5 mm), Artemovka River, near Vladivostok, Russia, Shedko; HUMZ 43081, 64.0 mm, Chonchin, Kita-chosen, North Korea; ZISP 16967, 5 (39.3-46.1 mm), Tumangan River mouth, Primorski Krai, Russia; ZISP 17479, 6 (37.1-45.8 mm), Lake Kasan, Primorski Krai, Russia; ZISP 25497, 26 (20.2-40.3 mm), Rozanovskoye Lake, Primorski Krai, Russia.

Gymnogobius breunigii

Type Material.—*Gobius breunigii*, NMW 30276, syntypes, 7 (31.2-47.8 mm), Hakodate, Hokkaido, Japan.

Additional Material.—BMNH 1907.12.23.271, 41.2 mm, Toshi Island, Japan, Smith; HUMZ 43250, 51.5 mm, Usu, Hokkaido, Japan; HUMZ 67073, 38.5 mm, Moheji, Hokkaido, Japan; HUMZ 68919, 34.5 mm, Daitobetsu, Hakodate Bay, Hokkaido, Japan; HUMZ 154943, 43.3 mm, Kattoshi, Kamiiso, Hokkaido, Japan; HUMZ 154944,

42.5 mm, Kattoshi, Kamiiso, Hokkaido, Japan; HUMZ 154945, 40.0 mm, Kattoshi, Kamiiso, Hokkaido, Japan; HUMZ 154946, 39.2 mm, Kattoshi, Kamiiso, Hokkaido, Japan; HUMZ 154947, 38.0 mm, Kattoshi, Kamiiso, Hokkaido, Japan; HUMZ 154948, 36.4 mm, Kattoshi, Kamiiso, Hokkaido, Japan; HUMZ 154949, 36.0 mm, Kattoshi, Kamiiso, Hokkaido, Japan; HUMZ 154950, 37.9 mm, Kattoshi, Kamiiso, Hokkaido, Japan; HUMZ 154951, 37.4 mm, Kattoshi, Kamiiso, Hokkaido, Japan; HUMZ 154952, 37.4 mm, Kattoshi, Kamiiso, Hokkaido, Japan; UW 029160, 15 (41.5-54.5 mm), Iturup, Kuril Archipelago, Russia, Pietsch; UW 029163, 15 (31.0-49.0 mm), Iturup, Kuril Archipelago, Russia, Pietsch; UW 029281, 5 (40.0-45.0 mm), Kunashir, Kuril Archipelago, Russia, Pietsch; UW 040527, 21 (41.0-56.0 mm), Shikotan, Kuril Archipelago, Russia, Stevenson; UW 044782, 46.5 mm, Lake Dolgoye, southern Sakhalin Island, Russia, Stevenson, Woods, and Reimer; ZISP 40942, 28.2 mm, Shikotan, Kuril Archipelago, Russia, Turyanova.

Gymnogobius cylindricus

Type Material.—*Chaenogobius cylindricus*, ZUMT 30386, holotype, 44.0 mm, Hiroshima, Japan, Shiga Fisheries Station.

Additional Material.—LIAIP 1993001, 49.2 mm, Chigusa River, Ako, Honshu, Japan, Suzuki; LIAIP 1993284, 2 (50.0-52.0 mm), Chigusa River, Ako, Honshu, Japan, Suzuki.

Gymnogobius scrobiculatus

Type Material.—Holotype apparently lost; not present in the BLIH or NSMT collections. Neotype hereby designated: OMNH-P 11261, 29.9 mm, mouth of Asa

River, Ushirogata-kami, Nishi-Takadomari, Onoda, Yamaguchi Prefecture, Honshu, Japan.

Additional Material.—BLIH 19891183, 5 (28.6-33.8 mm), Hake River, Ohmishima Island, Ehime Prefecture, Japan; BILH 1990103, 2 (29.8-30.4 mm), Shimanto River, Nakamura, Kochi Prefecture, Shikoku, Japan, Kinoshita; BILH 1990104, 3 (28.2-33.4 mm), Shimanto River, Nakamura, Kochi Prefecture, Shikoku, Japan, Kinoshita; OMNH-P 11262, 24.0 mm, collected with neotype; OMNH-P 13484, 27.3 mm, mouth of Imadu River, Aihara, Yamaguchi City, Yamaguchi Prefecture, Honshu, Japan.

Gymnogobius macrognathos

Type Material.—*Gobius macrognathos*, RMNH 4461, holotype, 35.5 mm, Jeddo.

Gymnogobius raninus, ZISP 25485, lectotype, 29.7 mm, Shiauodem River mouth, Peter the Great Bay, Russia, Taranetz; ZISP 35325, paralectotype, 26.5 mm, Olga Bay, Primorski Krai, Russia, Tarasov.

Additional Material.—NSMT-P 35574, 4 (18.8-29.5 mm), Yoshino River, Shikoku, Japan, Sato and Aizawa; NSMT-SK 4947, 3 (30.2-31.0 mm), Tone-gawa River, Ibaraki Prefecture, Honshu, Japan, Nakamura; NSMT-SK 5002, 2 (26.0-28.3 mm), Tone-gawa River, Ibaraki Prefecture, Honshu, Japan, Nakamura; NSMT-SK 6490, 16 (25.5-37.0 mm), Tone-gawa River, Ibaraki Prefecture, Honshu, Japan, Nakamura; ZISP 36409, 3 (33.7-37.0 mm), Tsingtao, Yellow Sea, China, Turyanova.

Gymnogobius uchidai

Type Material.—*Paleatogobius uchidai*, USNM 215275, paratype, 29.0 mm, Kanakuzu R., Fukuoka, Japan, Ootu.

Additional Material.—HUMZ 88096, 25.1 mm, Usu Bay, Hokkaido, Japan; HUMZ 89734, 28.5 mm, Usu Bay, Hokkaido, Japan, Sawada; HUMZ 89735, 27.8 mm, Usu Bay, Hokkaido, Japan, Sawada; LIAIP 1990120, 10 (24.5-29.0 mm), Obitu River, Kisarazu, Chiba Prefecture, Honshu, Japan, Hosoya and Ikeda.

Gymnogobius heptacanthus

Type Material.—*Gobius heptacanthus*, ZMB 10656, holotype, 42.0 mm, Jedo, Japan, Hilgendorf. *Chloea sarchynnis*, CAS 106463, holotype, 31.5 mm, Wakanoura, Honshu, Japan, Jordan and Snyder; CAS 106653, paratypes, 4 (26.3-28.3), Wakanoura, Honshu, Japan, Jordan and Snyder.

Additional Material.—HUMZ 70706, 48.1 mm, Kamiiso, Hokkaido, Japan; HUMZ 132979, 26.7 mm, Obira, Rumoi, Hokkaido, Japan, Muto; HUMZ 132980, 24.5 mm, Obira, Rumoi, Hokkaido, Japan, Muto; HUMZ 132995, 27.0 mm, Obira, Rumoi, Hokkaido, Japan, Muto; LACM 44370-2, 7 (26.7-34.5 mm), Mutsu Bay, Japan, McLean; NSMT-P 18709, 7 (30.8-36.7 mm), Hakodate Bay, Hokkaido, Japan; NSMT-P 34354, 50.0 mm, Sagami Bay, Japan, Aizawa; NSMT-P 34355, 47.0 mm, Sagami Bay, Japan, Aizawa; NSMT-P 34356, 44.4 mm, Sagami Bay, Japan, Aizawa; ZISP 22172, 3 (34.0-40.0 mm), Vladivostok market, Russia, Rutenberg; ZISP 35624, 2 (38.3-38.6 mm), Chefoo, Yellow Sea, China.

Gymnogobius mororanus

Type Material.—*Chloea mororana*, CAS 106452, holotype, 61.8 mm, Mororan, Hokkaido, Japan, Jordan and Snyder; CAS 106619, paratypes, 19 (33.0-55.4),

Matsushima Bay, Honshu, Japan, Jordan and Snyder. *Chloea bungei*, ZISP 23107, syntypes, 3 (41.0-59.3 mm), Port Shestakoff, North Korea, Bunge.

Additional Material.—HUMZ 43158, 64.5 mm, Usu, Hokkaido, Japan; HUMZ 43203, 63.3 mm, Usu, Hokkaido, Japan; HUMZ 43226, 52.8 mm, Usu, Hokkaido, Japan; HUMZ 43237, 65.2 mm, Usu, Hokkaido, Japan; HUMZ 43264, 51.3 mm, Usu, Hokkaido, Japan; NSMT-P 45256, 7 (54.0-63.0 mm), Chikara-kotan, Akkeshi Lake, Hokkaido, Japan, Yabe and Muto; NSMT-P 45430, 70.5 mm, Akkeshi Lake, Hokkaido, Japan, Minami; NSMT-P 45537, 2 (35.6-42.5 mm), Akkeshi Lake, Hokkaido, Japan, Minami; USNM 71424, 21 (23.5-45.3 mm), Shiogama Rikuzen, Honshu, Japan; ZISP 40951, 2 (66.8-74.0 mm), Shikotan, Kuril Archipelago, Russia, Rutenberg.

Gymnogobius isaza

Type Material.—*Chaenogobius isaza*, ZUMT 57520, holotype, 49.3 mm, Lake Biwa, Honshu, Japan.

Additional Material.—BMNH 1898.12.1.4-8, 5 (41.0-42.5 mm), Lake Biwa, Honshu, Japan, Kishinouye; LACM 44899-1, 3 (30.0-51.1 mm), Lake Biwa, Japan; NSMT-P 14242, 8 (46.3-64.8 mm), Lake Biwa, Japan; NSMT-SK 3053, 13 (46.3-64.9 mm), Lake Biwa, Japan; UW 07817, 18 (21.0-50.0 mm), Lake Biwa, Japan.

Gymnogobius petschiliensis

Type Material.—*Gobius petschiliensis*, NRM 10621, syntypes, 4 (56.8-80.0 mm), Qinhuangdao, Shanghaiguan, Hebei Province, China. *Chaenogobius transversefasciatus*, LIAIP 1984387, paratype, 49.5 mm, Cangnan Shuitou, Ao-jiang R., Zhejiang Province, China.

Additional Material.—HUMZ 50578, 45.6 mm, Hikken River, Ishimiyokota, Masuda, Shimane Honshu, Japan, Sawada; HUMZ 50579, 41.0 mm, Ishimiyokota, Masuda, Shimane, Honshu, Japan, Sawada; HUMZ 50582, 35.1 mm, Ishimiyokota, Masuda, Shimane, Honshu, Japan, Sawada; HUMZ 50648, 42.5 mm, Oomisawa River, Kominato, Chiba, Honshu, Japan, Sawada; NSMT-P 5605, 56.7 mm, Izumi-kawa River, Tsushima Island, Japan; NSMT-P 11067, 2 (86.4-99.1 mm), Akka River, Iwate, Honshu, Japan; NSMT-P 14373, 5 (49.3-79.5 mm), Okawa-kawa River, Shizuoka, Honshu, Japan, Takeuchi; NSMT-P 14396, 9 (36.6-97.2 mm), Nishina-kawa River, Shizuoka, Honshu, Japan, Takeuchi; NSMT-P 20966, 3 (52.9-67.1 mm), Inasa, Shizuoka, Honshu, Japan; NSMT-P 21267, 58.8 mm, Amatsukominato-cho, Chiba, Honshu, Japan; NSMT-P 29077, 5 (49.6-74.6 mm), Nagata-gawa River, Kamikaya, Yakushima Island, Japan; NSMT-P 29082, 47.9 mm, Nagata-gawa River, Kamikaya, Yakushima Island, Japan; NSMT-P 29091, 4 (40.2-45.3 mm), Nagata-gawa River, Kamikaya, Yakushima Island, Japan; NSMT-SK 2701, 10 (36.3-72.2 mm), Japan; NSMT-SK 4542, 80.5 mm, Japan; NSMT-P 59485, 75.0 mm, Ibaraki Prefectural Nature Museum.

***Gymnogobius opperiens* n. sp.**

Holotype.—NSMT-P 14366-1, 67.0 mm, Yurapu-gawa River, Yamagoe, Toshima, Hokkaido, Japan, N. Takeuchi, 8 August 1970.

Paratypes.—NSMT-P 11090, 4 (58.0-64.0 mm), Kuji-gawa River, Iwate Pref., Honshu, Japan, 1967; NSMT-P 14366, 2 (54.6-67.0 mm), collected with holotype; NSMT-P 14338, 55.6 mm, Mitsuishi-kawa River, Hourai, Mitsuishi, Hokkaido, Japan, Takeuchi,

1970; UW 40100, 7 (49.2-81.5 mm), 44°00.47'N, 145°40.98'E, Kunashir, Kuril Archipelago, Russia, Pietsch et al., 1995; UW 40113, 15 (42.2-62.7 mm) + 5 CS, 44°00.47'N, 145°40.98'E, Kunashir, Kuril Archipelago, Russia, Pietsch et al., 1995; UW 42003, 11 (53.2-76.0 mm), 44°00.25'N, 145°40.34'E, Kunashir, Kuril Archipelago, Russia, López, 1996; UW 044225, 22 (48.5-76.5 mm), Shamora R., near Vladivostok, Russia, Shedko, 1995.

Additional Material.—Meristics and measurements not taken from 837 additional specimens (UW 029290, 040101, 040103, 040104, 040106, 040109, 040111, 040115, 040116, 040118, 040195, 040512, 040532, 041387, 042000, 042001, 042007, 042009, 042034, 042036, 042045, 042049, 042223, 042225, 042226, 042229, 043542, 043553) (17-81 mm) from the western side of central Kunashir, Kuril Archipelago, Russia, 1995-1999; UW 044808, 2 (54.3-57.3 mm), Lyutoga River, southern Sakhalin Island, Russia, Stevenson, et al.; UW 044820, 7 (49.8-62.2 mm), Lyutoga River, southern Sakhalin Island, Russia, Stevenson et al; HUMZ 70575, 52.5 mm, Mihogawa, Aomori, Honshu, Japan.

Gymnogobius urotaenia

Type Material.—*Chaenogobius urotaenia*, ZMB 10644, syntypes, 8 (24.3-31.4 mm), Japan, Hilgendorf. *Gobius laevis*, NMW 29508, holotype, 69.0 mm, Hakodate, Hokkaido, Japan, Steindachner. *Chloea aino*, ZISP 13106, syntypes, 3 (40.3-44.9 mm), Lake Tunaichi, Sakhalin Island, Russia, Brazhnikov; ZISP 13133, syntypes, 8 (59.7-110.3 mm), Arakul River, Sakhalin Island, Russia, Schmidt; NMW 82275, syntype? (possibly ex-ZISP 13133), 89.2 mm, Aniva Bay, Sakhalin Island, Russia.

Additional Material.—BMNH 1900.9.29.17-19, 3 (64.3-85.8 mm), Tokyo, Japan, Otaki; BMNH 1903.5.14.60-62, 3 (36.9-73.6 mm), Chikugo River, Japan, Jordan; BMNH 1907.12.23.268, 74.0 mm, Oki Island, Japan, Smith; HUMZ 40719, 77.3 mm, Zenibako Kangaiyosui, Hokkaido, Japan, Tsumura and Kahata; HUMZ 40720, 92.4 mm, Zenibako Kangaiyosui, Hokkaido, Japan, Tsumura and Kahata; HUMZ 40722, 80.0 mm, Zenibako Kangaiyosui, Hokkaido, Japan, Tsumura and Kahata; HUMZ 40724, 87.8 mm, Zenibako Kangaiyosui, Hokkaido, Japan, Tsumura and Kahata; HUMZ 40725, 78.9 mm, Zenibako Kangaiyosui, Hokkaido, Japan, Tsumura and Kahata; HUMZ 40727, 91.1 mm, Zenibako Kangaiyosui, Hokkaido, Japan, Tsumura and Kahata; HUMZ 40728, 75.0 mm, Zenibako Kangaiyosui, Hokkaido, Japan, Tsumura and Kahata; HUMZ 42111, 70.4 mm, Shiodomari River, Hakodate, Hokkaido, Japan; HUMZ 42117, 50.2 mm, Shiodomari River, Hakodate, Hokkaido, Japan; HUMZ 42132, 53.4 mm, Shiodomari River, Hakodate, Hokkaido, Japan; HUMZ 42135, 72.5 mm, Shiodomari River, Hakodate, Hokkaido, Japan; HUMZ 42136, 46.3 mm, Shiodomari River, Hakodate, Hokkaido, Japan; HUMZ 42144, 69.2 mm, Shiodomari River, Hakodate, Hokkaido, Japan; HUMZ 42157, 52.0 mm, Shiodomari River, Hakodate, Hokkaido, Japan; HUMZ 42165, 47.8 mm, Shiodomari River, Hakodate, Hokkaido, Japan; HUMZ 42166, 68.4 mm, Shiodomari River, Hakodate, Hokkaido, Japan; HUMZ 42167, 51.4 mm, Shiodomari River, Hakodate, Hokkaido, Japan; HUMZ 42173, 54.0 mm, Shiodomari River, Hakodate, Hokkaido, Japan; HUMZ 42174, 56.8 mm, Shiodomari River, Hakodate, Hokkaido, Japan; HUMZ 69474, 57.1 mm, Oono River, Hokkaido, Japan; HUMZ 70091, 75.5 mm, Lake Biwa, Honshu, Japan; HUMZ

70112, 98.4 mm, Onuma, Hokkaido, Japan; HUMZ 70116, 87.7 mm, Onuma, Hokkaido, Japan; HUMZ 70122, 92.7 mm, Onuma, Hokkaido, Japan; HUMZ 70126, 108.9 mm, Onuma, Hokkaido, Japan; HUMZ 70128, 88.9 mm, Onuma, Hokkaido, Japan; HUMZ 70131, 92.6 mm, Onuma, Hokkaido, Japan; HUMZ 70172, 91.3 mm, Kunebetsu River, Hokkaido, Japan; HUMZ 70714, 86.7 mm, Moibe River, Aomori, Japan; HUMZ 132693, 78.0 mm, Hakodate, Hokkaido, Japan; HUMZ 133442, 49.8 mm, Hakodate, Hokkaido, Japan; HUMZ 135093, 51.8 mm, Hakodate, Hokkaido, Japan; NMW 30767, 87.5 mm, Jesso, Japan, Steindachner; NSMT-P 27289, 18 (40.4-74.6 mm), Japan; NSMT-P 59486, 77.0 mm, Ibaraki Prefectural Nature Museum; UW 027488, 44.0 mm, Shikotan, Kuril Archipelago, Russia, Pietsch; UW 027494, 8 (50.3-84.5 mm), Zelionyi, Kuril Archipelago, Russia, Pietsch; UW 028208, 4 (67.3-82.8 mm), Iturup, Kuril Archipelago, Russia, Pietsch; UW 029254, 5 (39.1-92.2 mm), Kunashir, Kuril Archipelago, Russia, Pietsch; UW 029311, 93.2 mm, Shikotan, Kuril Archipelago, Russia, Pietsch; UW 044767, 10 (29.0-111.0 mm), Lake Barguzinskoye, southern Sakhalin Island, Russia, Stevenson, Woods, and Reimer; UW 044780, 8 (46.0-91.0 mm), Lake Dolgoye, southern Sakhalin Island, Russia, Stevenson, Woods, and Reimer; UW 044822, 2 (70.0-93.0 mm), Lyotoga River, southern Sakhalin Island, Russia, Stevenson, Woods, and Reimer; UW 044859, 2 (46.0-69.0 mm), Mereya River, southern Sakhalin Island, Russia, Stevenson, Woods, and Reimer; UW 044887, 4 (28.0-80.0 mm), Lake Lebyazhye, southern Sakhalin Island, Russia, Stevenson et al.; ZISP 16837, 55.1 mm, Tumangan River, Primorski Krai, Russia, Chersky; ZISP 17454, 6 (45.9-55.9 mm), Tumangan River, Primorski Krai, Russia, Chersky; ZISP 49204, 48.7

mm, Kunashir, Kuril Archipelago, Russia, Kusakin; ZISP 49205, 103.5 mm, Iturup, Kuril Archipelago, Russia, Makushok; ZISP 49924, 8 (43.2-95.0 mm), Lake Tunaichi, Sakhalin Island, Russia, Nikoforov.

Parawaous megacephalus

Type Material.—*Chaenogobius megacephalus*, ANSP 114891, holotype, 71.7 mm, Borneo, W. H. Furness.

Bryaninops erythrops

Type Material.—*Chaenogobius erythrops*, USNM 51781, holotype, 11.8 mm, Pago Pago, Samoa, Jordan and Kellogg.

***Cleared-and-Stained Material Used for Comparative Osteology.*—**

Acanthogobius flavimanus: UW 011692, 3 (67.0-73.0 mm), Nakatsu River, Japan, Ueno.

Chaenogobius annularis: NSMT P56774, 2 (54.8-56.9 mm), Iwai-zaki Point, Kesennuma, Miyagi Pref., Japan, Matsuura and Shibukawa.

Chaenogobius gulosus: LACM 44905-1, 31.5 mm, Misaki, Japan, Hubbs; NSMT-P 23147, 2 (42.5-43.5 mm), Tobi-shima Island, Japan, Arai.

Clevelandia ios: UW 042995, 45.8 mm, Rivers Inlet, Taylor Bay, British Columbia, Canada.

Eucyclogobius newberryi: UW 042984, 3 (31.0-38.4 mm), Carlsbad Bird Sanctuary, San Diego, California, USA, Paris and Powell.

Gillichthys mirabilis: LACM 39778-4, 57.0 mm, Ballona Marsh, Los Angeles County, California, USA, Swift.

Gillichthys seta: LACM W50-193, 2 (49.8-54.3 mm), South of San Felipe, Baja California, Gulf of California, Mexico, Limbaugh.

Gnatholepis anjerensis: UW 013914, 29.5 mm, Kailua, Hawaii, Gosline and Brock.

Gymnogobius breunigii: UW 029281, 2 (41.0-46.2 mm), Kunashir, Kuril Archipelago, Russia, Pietsch et al.

Gymnogobius castaneus: UW 029332, 2 (40.8-42.5 mm), Zelionyi, Kuril Archipelago, Russia, Pietsch et al.

Gymnogobius heptacanthus: NSMT P18709, 2 (35.7-36.2 mm), Hakodate Bay, Hokkaido, Japan.

Gymnogobius isaza: UW 007817, 3 (47.0-49.3 mm), Chikubu Island, Lake Biwa, Kyoto Pref., Honshu, Japan.

Gymnogobius macrognathos: NSMT-P SK4947, 3 (30.3-33.5 mm), Tone-gawa River, Ibaraki Pref., Honshu, Japan, Nakamura.

Gymnogobius mororanus: NSMT P45256, 2 (54.0-63.9 mm), Chikara-kotan, Akkeshi Lake, Hokkaido, Japan, Yabe and Muto.

Gymnogobius opperiens: UW 043524, 2 (47.3-50.0 mm), Kunashir, Kuril Archipelago, Russia, Stevenson et al.

Gymnogobius petschiliensis: NSMT P29077, 2 (50.4-56.0 mm), Nagata-gawa River, Kamikaya, Yakushima Island, Japan.

Gymnogobius taranetzi: UW 044224, 2 (44.2-48.7 mm), Artemovka River, near Vladivostok, Russia, Shedko.

Gymnogobius uchidai: HUMZ 89735, 27.8 mm, Usu, Hokkaido, Japan, Sawada.

Gymnogobius urotaenia: UW 043710, 3 (51.1-66.7 mm), Iturup, Kuril Archipelago, Russia, Stevenson et al.

Ilypnus gilberti: LACM 38547-6, 33.4 mm, Newport Bay, Orange County, California, USA, Horn.

Lepidogobius lepidus: UW 025207, 71.5 mm, Willapa Bay, Washington, USA, Jensen.

Quietula y-cauda: UW 042991, 3 (34.8-37.8 mm), Newport Bay, Orange County, California, USA, Arai.

Tridentiger brevispinis: UW 029233, 3 (49.2-58.6 mm), Iturup, Kuril Archipelago, Russia, Pietsch et al.

APPENDIX C:**List of Morphological Characters and Coding of Character States**

1. Position of ethmoid cartilage: 0 = anterior to median ethmoid, 1 = ventral to median ethmoid.
2. Attachment of vomer to ethmoid: 0 = narrow, 1 = broad.
3. Development of interorbital septum: 0 = ossified, 1 = cartilaginous.
4. Groove on lateral margin of frontals: 0 = present, 1 = absent.
5. Ridge on posteromedial margin of frontals: 0 = absent, 1 = present.
6. Sphenotic and pterotic trough: 0 = present, 1 = absent.
7. Intercalar: 0 = overlaps prootic, 1 = does not overlap prootic.
8. Intercalar foramen: 0 = absent, 1 = present.
9. Pterosphenoid foramen: 0 = absent, 1 = present.
10. Lacrimal foramen: 0 = present, 1 = absent.
11. Nasal bones: 0 = present, 1 = absent.
12. Maxillary portal: 0 = present, 1 = absent.
13. Posterior extension of maxilla: 0 = absent, 1 = present.
14. Medial process of maxilla: 0 = absent, 1 = present.
15. Teeth on dentary: 0 = present on anterior 3/4 of bone, 1 = reduced, present only on anterior 1/2 of bone.
16. Anguloarticular foramen: 0 = present, 1 = absent.

17. Anteroposterior length of ectopterygoid: 0 = equal to palatine, 1 = longer than palatine.
18. Dominant bone of the metapterygoid-symplectic strut: 0 = symplectic, 1 = elements approximately equal in size.
19. Symplectic spur: 0 = absent, 1 = present.
20. Development of canal on preopercle: 0 = branched canal, 1 = unbranched canal, 2 = absent.
21. Preopercle spur: 0 = absent, 1 = present.
22. Anterior margin of basihyal: 0 = rounded, 1 = notched.
23. Anterolateral extension of hypobranchial 3: 0 = present, 1 = absent.
24. Ceratobranchial toothpatches: 0 = absent, 1 = present.
25. Gill raker number: 0 = less than 15, 1 = greater than 20.
26. Dorsolateral extension of infrapharyngobranchial 2: 0 = small, consisting of only a cartilaginous cap, 1 = large, consisting of a bony extension with a cartilaginous cap.
27. Posttemporal canal: 0 = present, 1 = absent.
28. Ventral postcleithrum: 0 = present, 1 = absent.
29. Spur on medial surface of cleithrum: 0 = absent, 1 = present.
30. Number of pelvic radials on each side: 0 = one radial, 1 = two radials.
31. Number of vertebral centra: 0 = less than 30, 1 = greater than 30.
32. Pair of epineurals associated with anteriormost vertebral centrum: 0 = present, 1 = absent.

33. Insertion of anteriormost pterygiophore of first dorsal fin: 0 = third interneural space, 1 = fourth or fifth interneural space.
34. Posterior displacement of second dorsal fin: 0 = absent, 1 = present.
35. Number of anal-fin pterygiophores preceding first haemal spine: 0 = two, 1 = three.
36. Number of epurals: 0 = two epurals, 1 = one epural.
37. Scale morphology: 0 = ctenoid, 1 = cycloid.
38. Posterior nasal portion of oculoscapular canals: 0 = present, 1 = absent.
39. Posterior interorbital pore(s): 0 = single, 1 = paired.
40. Otic portion of oculoscapular canal: 0 = extreme; 1 = intermediate; 2 = otic canal absent.
41. Filamentous projections on pectoral fin: 0 = absent, 1 = present.
42. Pelvic fin shape: 0 = oval, 1 = round.

APPENDIX D:**DNA Sequence Data**

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G. breunigii ATG AAC CCT TAC AT? TTA ATC CTA CTT TCT GAT GG? CTG GCA CTA GGT
G. castaneus ATG AAA CCT TA? ATT TA? ATC CTA CTT TTC TT? GGC T?G GCA CTA GGT
G. heptacant ATG AAG ACC TAC ATT TTA CTC TTG CTT TTT CTT GGC TTA ?CG CTA GGC
G. isaza ATG AAC CCT TAT ATT TTA GTC CTC TTT TTT GGC CTA GCA CTA GGA
G. petschili ATG AAC CCA GAC ATA TTA GTC TTC CTT TTC TTT GGC TTA GCA CTA GGA
G. opperiens ATG AAC CCC TAC ATT TTA ATT CTC CTT TTC TTT GGC CTT GCA CTA GGA
G. urotaenia ATG AAC CCG TAC ATT TTA GTC CTC CTT TTC TTT GGC TTA GCA ATA GGA
C. annularis ATG AAC CTT A?A TTA TAT A?C TTT TTT TTC TTT GG? C?? A?? CTA GGA
E. newberryi ATG AAC CCT TAT AT? TTT AAC CTT CTT TTT GGC CTA GTC TTG GGC
G. seta ATG CAC CCC TAC ACA CTT A?C CTC CTT TTC TTT GG? CTT ATT CTA GGC
R. giurinus ATG AAC CCC TAC ATC TTG GCA CTC CTC TTT TTT GGC CTA GCC CTA GGA
A. flaviman ATG AAC CCT AGC ATT ATT CCA CTA TTT TTT CTT GGC ATC ?TA TTA GGA
A. lactipes ATG AAC CCC TAC AT? TAT ?TC CCT TTT TTT GGC ATC CTA TTA GGA

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G. breunigii ACA TGA CAT ATT ACT GCC ACC TCC CAC TGG TTG CTT GCT TGA ATG GGT
G. castaneus ACT ACT ATT ACT GCA ??C AGC TCC CAC TGG TTG CTT GCT TGA ATG GGT
G. heptacant ACA ACT ATT ACT GCA ACC AGC TCA CAC TGG CTG CTT GCA TGA ATG GGC
G. isaza ACC ACT ATA ACT GCA ACC AGC TCA CAC TGA TTG CTT GCA TGA ATG GGC
G. petschili ACC ACT ATT ACT GCA ACC AGC TCA CAC TGG TTG CTT GCG TGA ATG GGC
G. opperiens ACT ACC ATT ACT GCA ACC AGC TCA CAC TGG TTG CTT GCA TGA ATG GGC
G. urotaenia ACC ACT ATT ACT GCA ACC AGC TCA CAC TGA TTG CTT GCA TGA ATA GGC
C. annularis ACT ACC ATC ACT GCC ACT AGT TCC CAC TGG CTC GTC GCA TGA ATG GGC
E. newberryi ACT ACT ATC ACT ATA TCT AGC TCA CAC TGG CTG CTC GCG TGA ATA GGC
G. seta ACC ACC ATT ACT GCT ACT AGT TCC CAC TGG CTA CTT GCA TGG ATG GGC
R. giurinus ACC GGG GTA GCT GCC ACC AGC TCT CAC TGG CTA CTT GCA TGA ATG GGC
A. flaviman ACT GGA CTA GTT GCT TCT AGC TCA CAC TGG CTC CTT GCA TGA ATA GGC
A. lactipes ACT GGA CTA GTT GCT TCT AGC TCA CAC TGG CTC CTT GCA TGA ATA GGC

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G. breunigii CTC GAG ATC AAC ACC CTT GCT ATT ATT CCC CTA ATA GCA CAA CAA CAC
G. castaneus CTC GAG ATC AAC ACC CTT GCT ATT ATT CCC CTA ATA GCA CAG CAA CAC
G. heptacant CTG GAA ATT AAC ACT CTT GCC ATC ATT CCA TTA ATA GCA CAA CAG CAC
G. isaza CTG GAG ATC AAC ACC CTT GCT ATT ATC CCT TTA ATA GCA CGA CAG CAC
G. petschili CTG GAG ATC AAC ACC CTT GCT ATT ATT CCT TTA ATA GCA CGA CAG C?C
G. opperiens CTG GAA ATT AAT ACC CTT GCT ATT ATT CCT TTA ATG GCA CAA CAA CAC
G. urotaenia CTG GAG ATC AAC ACC CTT GCT ATT ATC CCT TTA ATA GCA CAA CAG CAC
C. annularis CTG GAA GTT AAT ACT CTT GCT ATT ATT CCC CTA ATG GCT CAA CAC CAT
E. newberryi TTG GAG ATT AGT ACT CTA GCT ATT ATT CCT CTG ATA ACA CAT CAA AAC
G. seta CTC GAA ATC AAC ACT CTG GCA ATT ATT CCC CTA ATA GCA CAA CAA AAT
R. giurinus CTA GAA ATT AAT ACT CTA GCC ATT ATT CCC TTA ATA GCC CAA CAA CAT
A. flaviman CTG GAG ATT AAT ACA TTA GCC ATC ATT CCC TTA ATG ATT CAA AAC CGT
A. lactipes CTG GAG ATT AAT ACA TTA GCC ATC ATT CCC TTA ATG ATT CAA AAC CGT

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G. breunigii CAC CCC CGC GCA ATT GAA GCC ACC ACA AAA TAT TTA TTG ACA CAA GCC
G. castaneus CAC CCC CGG GCA ATT GAA GCC ACC ACT AAA TAT TTC TTG ACA CAA GCC
G. heptacant CAC CGG CGA GCC ATT GAA GCT ACA ACT AAA TAC TTT TTA ACA CAA GCA
G. isaza CAC CCT CGA GCA ATT GAA GCC ACC ACA AAA TAT TTT TTA ACA CAA GCA
G. petschili CAT CCT CGA GCA ATT GAA GCC ACC ACA AAA TAT TTT TTG ACA CAA GCA
G. opperiens CAT CCT CGA GCA ATT GAA GCA ACC ACA AAA TAT TTT TTA ACA CAA GCA
G. urotaenia CAC CCT CGA GCA ATT GAA GCC ACC ACA AAA TAT TTT TTA ACA CAG GCA
C. annularis CAC CCC CGG GCA ATT GAA GCT ACT ACT AAA TAT TTT CTT ACA CAA GCA
E. newberryi CAC CCC CGA GCA ATC GAA GCC ACC ACC AAA TAC TTT TTG ACA CAA GCA
G. seta CAT CCC CGA GCA ATT GAA GCA ACC ACC AAG TAT TTC TTG ACA CAA GCA
R. giurinus CAC CCC CGG GCG ATC GAA GCA ACT ACC AAA TAC TTC TTA ACC CAA GCC
A. flaviman CAT CCC CGA GCA GTC GAA GCT ACC ACC AAA TAC TTC ATC ACC CAA GCG
A. lactipes CAT CCC CGA GCA GTC GAA GCT ACC ACC AAA TAC TTC ATC ACC CAA GCG

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G. breunigii ACC GC? GCT GCC ACT CTC CT? CTT GCA GCC GTC ACA AAT GCA TGA CTT
G. castaneus ACC GCG GCT GCC ACT CTC CTC TTC GCC AGC GTC ACA AAT GCA TGA CTT
G. heptacant ACC GCA GCT GCC ACC TTA CTC TTT GCA GGT ATC ACA AAT GCA TGG CTC
G. isaza ACA GCC GCT GCC ACC CTT TTG TTT GCC AGT ACA ACA AAT GCC TGG CTA
G. petschili ACA GCC GCT GCA CCC CTT CTG TTT GCC AGY ACT ACC AAT GCC TGA CTA
G. opperiens ACA GCT GCT GCA ACC CTT CTG TTT GCT AGC ACT ACC AAT GCC TGG CTA
G. urotaenia ACA GCC GCT GCC ACC CTT CTG TTT GCC AGT ACT ACA AAT GCC TGG CTA
C. annularis ACC GCT GCA GCT ACT ATC TTG TTT GCA GGT ATT ACA AAT GCG TGA CTA
E. newberryi ACT GCA GCA GCT ACA TTG TTG TTT GCC AGT GTG ACA AAT GCA TGG CTA
G. seta ACC GCT GCT GCC ACT TTC CTT TTT GCT AGT GTA ACA AAT GCT TGA CTC
R. giurinus ACA GCC GCT GCC ACC CTA CTC TTT GCC AGT ATT ACC AAT GCA TGA CTA
A. flaviman ACC GCG GCT GCG GTC CTC TTA GCT GCT GCA ACA GCC AAT GCC TGA CTA
A. lactipes ACC GCG GCT GCG GTC CTC TTA GCT GCT GCA ACA GCC AAT GCC TGA CTA

288

G. breunigii ACC GGA CAA TGA GAT ATT CAG CTT ATA ATA CAT CCT GTC CCT ACA ACG
G. castaneus ACC GGA CAA TGA GAT ATT CAG CTT ATA ATA CAT CCT GCC CCT ACA ACG
G. heptacant ACT GGT CAG TGG GAC ATC CAA CTT ATA CTC CAC CCC CTT CCA ACC ACA
G. isaza ACA GGA CAA TGG GAT ATT CAG TTG ATA GTT CAT CCC ATC CCT ACA ACC
G. petschili ACA GGA CAA TGG GAT ATT CAG TTG ATG GTT CAT CCC GTC CCT ACA A?C
G. opperiens ACA GGG CAA TGA GAT ATC CAA TTA ATG GTA CAC CCG ATT CCT ACG ACC
G. urotaenia ACA GGG CAA TGG GAT ATT CAG TTG ATG GTT CAT CCC ATC CCT ACA ACC
C. annularis ACA GGC CAG TGG GAC CTA CAA CTG ATA ACG CAC CCT ATT CCA ACC ACC
E. newberryi ACG GGC CAA TGA GAG ATT CAA AAC ATA ACC CAC CCA ATC CCC ACG ACC
G. seta ACA GGT CAA TGA GAC ATT CAA ATG ATA ACC CAC CCC CTC CCT A?C AAT
R. giurinus ACA GGT CAA TGA GAT ATT CAA CTA ATA ACA CAC CCA ATC CCC ACG ACC
A. flaviman ACA GGC CAA TGA AAT ATT TAT GAA CAA CCC CAC GAA ATC CCC ACT CTT
A. lactipes ACA GGC CAA TGA AAT ATT TAT GAA CAA CCC CAC GAA ATC CCC ACT CTT

336

G. breunigii ATG GTC ATT CTT GCT TTA GCC CTT AAA ATT GGC CTA GCC CCC CTT CAT
G. castaneus ATG GTC ATT CTT GCT TTA GCC CTT AAA ATT GGT CTA GCC CCC CTT CAT
G. heptacant ATG GTC ATT CTT GCT TTG GCC CTT AAA ATC GGT TTA GCC CCC TTA CAC
G. isaza ATG ATT ATT CTT GCT TTA GCC CTC AAG ATT GGC CTA GCA CCT TTA CAC
G. petschili ATA ATT ATT CTT GCT TTA GCC CTC AAG ATT GGC CTA GCA CCT TTA CAC
G. opperiens ATA ATT ATT CTT GCC CTC GCC TTA AAA ATT GGC CTA GCC CCT CTA CAC
G. urotaenia ATA ATT ATT CTT GCT TTA GCC CTC AAG ATC GGC CTA GCA CCT TTA CAC
C. annularis ATG CTC ATT TTG GCA CTC TCC CTC AAA CTT GGC TTA GCC CCT TTA CAC
E. newberryi ATA ATA ATT TTA GCC CTC TCG CTT AAG ATT GGA ATT GCC CCC CTG CAC
G. seta ATA ATC ATT TTG GCC CTT TCC CTA AAA GTG GGG TTA GCT CCC CTC CAC
R. giurinus ATA ATC ATT CTT GCA TTA GCC TTA AAA CTA GGC CTC GCC CCC CTC CAC
A. flaviman ATG ATT ATT ACA GCT GTT GCA CTT AAA CTG GGC CTA GCC CCC CTG CAC
A. lactipes ATG ATT ATT ACA GCT GTT GCA CTT AAA CTG GGC CTA GCC CCC CTG CAC

384

G. breunigii ACA TGA CTA CCA GAG GTC CTT CAA GGA CTA GAT TTG ACC ACG GGC CTC
G. castaneus ACA TGA CTA CCA GAG GTC CTT CAA GGA CTA GAT CTG ACC ACA GGC CTC
G. heptacant ACC TGA CTG CCA GAA GTT CTT CAA GGA CTT GAC CTA ACC ACG GGA CTA
G. isaza ACA TGA CTG CCA GAA GTA CTT CAA GGG TTG GAT TTA ACC ACA GGC CTT
G. petschili ACA TGA CTG CCA GAA GTA CTT CAA GGA TTG GAT TTA ACC ACA GGC CTT
G. opperiens ACA TGA CTG CCT GAA GTA CTT CAG GGG TTA GAC TTG ACC ACC GGC CTT
G. urotaenia ACA TGA CTG CCA GAA GTA CTT CAA GGG TTG GAT TTA ACC ACA GGC CTT
C. annularis ACC TGG CTT CCA GAA GTA CTT CAA GGC CTG GAC TTG TTT ACA GGC ATG
E. newberryi ACA TGA CTG CCA GAG GTG CTC CAA GGC CTC GAC CTA ACT ACG GGC CTT
G. seta ACC TGA CTC ACA GAA GTT CTT CAA GGC TTG GAC TTT AAT ACA GGC CTT
R. giurinus ACC TGA CTT CCA GAA GTA TTA CAA GGG CTT AAC CTT ACC ACC GGC TTA
A. flaviman CTG TGA CTT CCT GAA GTG CTT CAA GGA CTA GAT CTT AGC ACG GGC CTG
A. lactipes CTG TGA CTT CCT GAA GTG CTT CAA GGA CTA GAT CTT AGC ACG GGC CTR

432

G. breunigii ATC T?A TCC ACC TGA CAA AAA TTG GCC CCT TTT ACA CTC CTC CTT ?AG
G. castaneus ATC TTA TCC ACC TGA CAA AAA TTG GCC CCT TTT ACA CTC CTC CTT CAG
G. heptacant GTC TTG TCC ACA TGA CAA AAA TTG GCC CCC TTT GCC CTT CTC CTT CAA
G. isaza ATC CTC TCC ACC TGA CAA AAA TTG GCC CCC TTT GCT CTT CTA CTT CAA
G. petschili ATC CTC TCC ACC TGG CAA AAA TTG GCC CCC TTT GCT TTT CTA ATT CA?
G. opperiens ATT CTT TCT ACC TGG CAG AAA TTA GCC CCT TTT GCC CTC CTA CTT CAG
G. urotaenia ATC CTC TCC ACC TGA CAA AAA TTG GCC CCC TTT GCT CTT CTA CTT CAA
C. annularis ATC CTA TCG ACC TGG CAG AAG TTA GCT CCT TTT ACC CTT CTG CTT CAA
E. newberryi ATT CTC TCC ACC TGG CAA AAG CTT GCA CCC TTC GCA CTC CTT CTT CAA
G. seta ATT CTC TCT ACA TGA CAG AAG TTA GCC CCC TTT GCC CTC CTC ATC CAA
R. giurinus ATT CTC TCC ACC TGA CAA AAA CTA GCC CCC TTT ATA CTG CTC CTT CAA
A. flaviman CTC CTC TCA ACA TGA CAA AAA CTT GCC CCA TTC TTA ATC CTT ACT CAA
A. lactipes CTC CTC TCA ACA TGA CAA AAA CTT GCC CCA TTC TTA ATC CTT ACT CAA

480

G. breunigii ATT CCT GCA TCC GGA CAA GAA CTC CTC ATG ?TT CTA GGT ATA ACT TCT
G. castaneus ATT CCT GCA TCC GGA CAA GAA CTC CTC ATT TTT TGG GTT A?A GCT TCT
G. heptacant CTA CCC GCA GCC AAT CAA GAA CTC CTC ATC TTT TTA GGA CTT ACA TCT
G. isaza ATT CCT GCT GCC AAC CAA GAA CTT CTG GTC TTT TTA GGC CTT ACC TCA
G. petschili ATT CCT GTT GCC AAC CAA GAA CTR CTG ATC TTT TTA GGC CTT ACM TCC
G. opperiens ATT CCT GCA GCT AAC CAG GAA CTA CTT GTC TTT TTA GGA CTT ACA TCT
G. urotaenia ATT CCT GCT GCC AAC CAA GAA CTA CTG ATC TTT TTA GGC CTT ACC TCC
C. annularis ATT CCT ACT GCT AAC CAA GAA CTG ATT GTT TTA CTA GGT ATT ACA TCT
E. newberryi GTT CCC GCT GCG AAT CAA GAG CTA CTT GCC CTA CTT GGT CTT ACC TCC
G. seta AT? CCT AGT GTC TAC AAA AAA CTG CTT GTC ?TC CTA GGG CTC AAC TTC
R. giurinus ATC CCT TGT CAC GAC CAA GAA CTT TTA ATT CTC CTA GGA CTA ACT TCA
A. flaviman ATT CCC CTT AAT GAT A?T AGT TTG CTT ATT TTT TTA GGG TTA ACA TCC
A. lactipes ATT CCC CTT AAT GAT AAT AGT TTG CTT ATT TTW TTA GGG TTA ACA TCC

528

G. breunigii ACC CTA TGT GGG GGC TGA GGG GGT CTA AAT CGA GAC CAG CTT CGG AAA
G. castaneus ACC CTT GTT GGG GGC TGA GGG GGC CTA AAT C?A GAC CAG CTG CGC AAG
G. heptacant ACA CTT GTT GGG GGA TGA GGC GGT TTA AAC CAA ACG CAA CTT CGT AAG
G. isaza ACT CTC GTT GGC GGG TGA GGC GGG CTC AAC CAA ACA CAG CTT CGT AAA
G. petschili ACT CTT GTC GGT GGG TGA GGT GGM CTC AAC CAG ACA CAA CTT CGT AAG
G. opperiens ACT CTT GTA GAA GAT GGG GGG GAC TTA TAC CAA ACG CAA CTT CG? AAA
G. urotaenia ACT CTT GTT GGA GGG TGA GGC GGA CTC AAC CAA ACA CAA CTT CGT AAA
C. annularis ACC CTT GTT GGG GGC TGA GGA GGC CTA AAT CAA ACA CAA ATG CGC AAA
E. newberryi ACA CTT GTC GGG GGG TGG GGA GGG CTA AAC CAG ACC CAG CTT CGT AAA
G. seta AAC CTT ATT GGA GGA TGG GGG GGG TTA AT? CAA CAC CAC TTC GCT AAA
R. giurinus ACC CTT GTT GGG GGC TGA GGA GGC CTA AAC CAA ACG CAG CTA CGC AAA
A. flaviman ACT CTA GTC GGA GGC TGA GGA GGA CTA AAC CAG ACC CAG CTC CGC AAA
A. lactipes ACT CTA GTC GGA GGC TGA GGA GGA CTA AAC CAG ACC CAA CTT CGA AAA

576

G. breunigii ATC CAT G?? TA? TCA TC? ATT GCC ?AT CTA GGT TGG AT? GTG ATT GTT
G. castaneus ATC CTT GCA TAC TCA TCC ATT GCC CAC CTA GGY TGG ATG TTG ATT GTT
G. heptacant ATC CTT GCA TAC TCT TCT ATT GCC ?AC CTA GGC TGA ATG CTA ATT ATT
G. isaza ATC T?? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
G. petschili GTA CTT GCA TAC TCA TCA ATT GCC CAT CTT GGC TGA ATA TTA ATT ATC
G. opperiens ?TA CTT GCA TAC TCA TCT ATT GCC CAT CTT GGC TGA ATA CAT TAT TAT
G. urotaenia GTA CTT GCA TAT TCA TCA ATT GCC CAT CTT GGC TGG ATA CTA ATT ATC
C. annularis ATC CTT GCT TAC TCA TCA ATT GCT CAT CTT GGA TGA ATG CTT ATT ATC
E. newberryi ATC CTT GCT TAC TCC TCT ATT GCC CAC CTT GGA TGA ATA ATT ATT ATC
G. seta ATC CTA GC? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
R. giurinus ATT CTA GCC TAC TCT TCT ATT GCC CAC CTC GGC TGA ATG ATC ATT ATT
A. flaviman ATC ATG GCC TAC TCA TCC ACA GCC CAC CTT GGA TGA ATG ATC CTC GTT
A. lactipes ATT ATA GCC TAT TCA ACA GCA CAC CTA GGC TGA ATG GTC CTG ATT

624

G. breunigii TTA CAA TGT GCA CCT TCC CTA ACA CTG ?T? GCC CTT ATA ACA TAT CTT
G. castaneus TTA CAA TTT GCA CCT TCC CTA ACA CTG CTT GCC CTT ATA ACA TAT CTT
G. heptacant TTA CAA TTT ACC CCC TCA TTG ACA CTC CTG GCC CTC ATT ACA TAT CTT
G. isaza ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
G. petschili CTT CAA TTT GCA CCA TCC TTG ACA CTC TTG CGC TCT CTG ACG TAC CTT
G. opperiens TTT CAA TTT GCA CCA TCC CTA ACA CTC TTG CAC T?T CTA ATG TAC CTT
G. urotaenia CTT CAA TTT GCA CCA TCC TTG ACA CTC CTT GCA CTC CTG ACG TAC CTT
C. annularis TTG CAA TTT GCC CCC TCA CTG ACA CTG CTA GCC CTA ACT ACT TAT CTT
E. newberryi ATC CAA TTT GCC C?T TCC TTA AC? CTT GTC GCC ATA GTC GCC TAC CTT
G. seta ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
R. giurinus ATC CAG TTT GCC CCC TCC CTT ACA CTC CTG GCC CTT GTA ACC TAT CTA
A. flaviman GTA AAA TAT GCC CCC GCC CTA ACC CTG TTT ACC CTA ATG GTT TAC TGG
A. lactipes GTA AAA TAT GCC CCA ACT TTG ACC ATC CTA GCT TTA GTA ACC TAC TGA

672

G. breunigii ATT ATG ACT TCC TCC ATA TTT CTC CTA CTA AAC TTT AAT AAT GCC ACC
G. castaneus ATT ATG ACT TCC TCC ATA TTT CTC CTA CTA AAC TTT AAT AAT GCC ACC
G. heptacant GTT ATG ACT TCT TCC ATG TTC CTC ATA CTA AAC TTT AAC AAT GCC ACT
G. isaza ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
G. petschili ATT ATA ACC TCT TCA GCA TTC CTT ACC CTT GAC TTT AAT GGT GCT ACT
G. opperiens ATT ATA ACT TCT TCA GCA TTT CTT ACT CTT AAC TTC AAT TGT GCT ACA
G. urotaenia ATT ATA ACC TCT TCA GCA TTC CTT ACC CTT AAC TTT AAT GGT GCT ACT
C. annularis ATC ATG ACT TCC TCA GTG TTT CTT ACC CTT AAC TTT AAT AAT GCC ACC
E. newberryi GTT ATA ACA TCA TCA GAT TTT AGT ACC CTA AAC GGT AAT ART GCA GAG
G. seta ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
R. giurinus CTT ATG ACA TCT TCA GCC TTC TTA ACC CTA AAG TTT AAC GAC ACA ACT
A. flaviman GTC ATA ACA TCC TCA GCA TTC CTT ACA TTC AAA TTC AAT AAG GCC TAT
A. lactipes GTC ATG ACA TCA TCA GCA TTC CTT ATG TTT AAG TTT AAC AAA ACT TTC

720

G. breunigii AAT ATT AAC TCG CTC TCA ACA GAC TGG GCA AAA GCC CCT ATT ATT ACG
G. castaneus AAT ATT AAC TCG CTC TCA ACA GAC TGG GCA AAA GCC CCT ATT ATT ACG
G. heptacant AGT ATT AAC TCA TTA GCA ACA ACC TGA ACG AAA GCC CCT CTT GCC ACG
G. isaza ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
G. petschili AAT ATT AAT TCT CTG GCA ACA ACT TGG ATG AAA GCA CCT CTG GTT ACA
G. opperiens AAT ATT AAT TCT ?TA GCA ACA ACT TGA GCT AAA GCA CCT CTA ATT ACA
G. urotaenia ACT ATT AAC TCT CTG GCA ACG ACT TGA ATA AAA GCA CCT CTA GTT ATA
C. annularis AAC ATG AAT TCT CTG GCA ACA ACC TGA GCA AAG GCA CCT TTA CTA GCT
E. newberryi CAC ATA CGT CC? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
G. seta ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
R. giurinus AAC ATT AAT TCT CTA GCA ATA GCC TGG ACA AAA TCT CCC TTA ATT GTA
A. flaviman ACA ATT AAT GCT CTA GGA CTA TCA TGA GCA GAC TCA CCC CTA ATA ACA
A. lactipes ACA ATC AAT GCT YTA GGR CTC TCA TGA ACA GGC TCC CCC ATG ATA ACA

768

G. breunigii G?C CTC ACC CCC CTT CTT CTT TCT CTG GGG GGT CTT CCC CCT ATA
G. castaneus GCC CTC ACC CCC CTT CTT CTT TCT CTG GGG GGT CTT CCC CCT ATA
G. heptacant ACC CTG GCC CCC CTC CTC CTC CTC TCC CTC GGG GGC CTT CCT CCC ATG
G. isaza ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
G. petschili GCT TTA ACC CCC TTA CTT CTC CTT TCA TTA GGG GGC CTT CCC CCA ATA
G. opperiens GCT TTA GCC CCC CTC CTC CTC CTT TCA CTG GGG GGC CTT CCC CCT ATA
G. urotaenia GCT TTA ACC CC? TTA CTT CTC CTT TCA TTA GGG GG? CTT CCC CCA ATA
C. annularis GCC CTT ACT CCA CTA CTT TTG CTC TCC CTA GGG GGA CTC CCC CCC ATG
E. newberryi ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
G. seta ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
R. giurinus GCC TCC GCA CCT TTA CTG CTC TCA CTT GGA GGA CTG CCC CCC ATA
A. flaviman AGC ATA GTA CCA CTC ATT CTT TTT TCA CTA GCT GGA CTC CCT CCT ATA
A. lactipes GCC CTT CTA CCC CTC GTT TTG TTC TCG ATG GGC GGC CTA CCC CCC ATA

816

G. breunigii ACG GGC TTC ATA CCC AAG TGA ?TC ATT CTT CAG GAA CTA ACC AAG CGA
G. castaneus ACG GGC TTC ATA CCC AAG TGA CTC ATT CTT CAG GAA CTA ACC AAG CAA
G. heptacant ACA GGC TTT ATG CCA AAA TGG CTA ATT CTA CAA GAG CTT ACT AAA CAG
G. isaza ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
G. petschili ACA GGA TTC TTG CCA AAA TGA CTC ATC CTC CAA GAA CTT ACT AAG CAA
G. opperiens ACA GGC TTT ATA CCC AAG TGG CTG ATT CTG CAG GAA CTC ACT AAG CAG
G. urotaenia ACA GG? ATC ATA CC? AAA TGG TTR ATC CTC CAG GAA CT? ACT AAG CAR
C. annularis ACG GGG TTT ATA CCC AAG TGA CTT ATT CTT CAA GAA CTC ACT AAG CAA
E. newberryi ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
G. seta ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
R. giurinus ACA GGC TTT CTT CCA AAA TGG CTT ATC TTA CAA GAG CTT ACA AAA CAA
A. flaviman ACA GGA TTT GCC CCC AAA ?TA CTT ATT CTC CAG GAG CTT ACT AAG CAA
A. lactipes ACA GGA TTT GCA CCA AAG ATA CTT ATT CTC CAG GAG CTT ACT AAA CAA

864

G. breunigii CAG CTC CCT ATG ACA GCT ACT TTT GCA GCC TTA ACA GCC TTA CTC AGG
G. castaneus CAG CTC CCT ATG ACA GCT ACT TTT GCA GCC TTA ACA GCC TTA CTC AGT
G. heptacant GGA CTT CCA ATG ACA GCC ACT TTC GCA GCT TTA ACT GCT TTA CTG AGC
G. isaza ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
G. petschili CAA CTA CCT ATA ACT GCA ACT CTT GCA GCC TTG ACT GCT CTT TTA AGT
G. opperiens CAG CTA CCT CTA ACT GCT ACT CTT GCA GCC TTG ACT GCT CTT TTA AGT
G. urotaenia CAA TTA CCT ATA ACT GG? ACT CTT GCA GCC TTG ACT GGT CTT TTA AGT
C. annularis GGC CTA CCC CTG ACC GCC ACA CTT GCA GCC TTG ACT GCT CTT TTA AGC
E. newberryi ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
G. seta ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
R. giurinus CAA CTC CCC CTT ACT GCC ACA ATT GCA GCC CTT ACC GCC CTT CTG AGC
A. flaviman GAA CTA GGA CTG ACA G?? ACT ATT CGT GCT CTA ATG GCC T?? ??? ???
A. lactipes GGC CTA GGA CTA ACC GCC CTC TTA GTC TCC CTT ACT GCC CTA AGC

912

G. breunigii CGG TAC TTT TAT CTT CGA GTC TCC TAT GCT GTT ACC CTA ACC ATA GCC
G. castaneus TTG TAC TTT TAT CTT CGA GTC TCC TAT GCT GTT ACC CTA ACC ATA GCC
G. heptacant TTG TAC TTT TAT CTT CGA GTT TCA TAC GCC ATT ACT TTA ACT ATT TCT
G. isaza ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
G. petschili CTA TAC TTT TAC CTT CGA GTC TCT TAT GCT ATT ACT TTA ACC ATT GCC
G. opperiens CTA TAC TTT TAT CTT CGA GTC TCT TAT GCT CTT AAC CTG ACT ATT GCC
G. urotaenia CTA TAC TTY AAT CTT CGA GTC TC? TAT GCT AT? AAY TTA AC? ATA GCC
C. annularis TTA TAT TTT TAC CTT CGA ATA TCG TAT GCA ATT TCG TTG ACT ATT GCC
E. newberryi ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
G. seta ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
R. giurinus CTT TAC TTC TAC CTA CGA CTA TCC TAC GCA ATA ACC CTT ACT ATT TCC
A. flaviman ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
A. lactipes TTA TAC TTT TAC CTA CGA CTC TCT CAC GCA ATA ACT CTA ACC CTT TAC

923

G. breunigii CCC AAC AAC TC
G. castaneus CCC AAC AAC TC
G. heptacant CCT AAC AAC TC
G. isaza ??? ??? ??? ??
G. petschili CCT AAT AAT TT
G. opperiens CCA AAT AAT TT
G. urotaenia ??? ??? ??? ??
C. annularis CCT AAC AAT TT
E. newberryi ??? ??? ??? ??
G. seta ??? ??? ??? ??
R. giurinus CCA AAC AAC CT
A. flaviman ??? ??? ??? ??
A. lactipes CCA AAT AAC AT

VITA

Duane E. Stevenson was born in Lewisburg, Pennsylvania, on 8 December 1970. He spent his childhood in central and western Pennsylvania, and graduated from Southwestern Central High School in Jamestown, New York. He received a Bachelor of Arts degree in Biology from Washington and Jefferson College in 1993 and a Master of Science degree in Marine Biology from the University of Charleston, South Carolina in 1996. In 2002 he earned a Doctor of Philosophy degree at the University of Washington in Aquatic and Fishery Sciences. He is currently employed by the National Marine Fisheries Service as a Fishery Research Biologist at the Alaska Fisheries Science Center in Seattle, Washington.