SCHINDLERIA: A PAEDOMORPHIC GOBY (TELEOSTEI: GOBIOIDEI)

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ABSTRACT

The evolutionary affinities of the tiny, putatively paedomorphic marine fishes of the genus *Schindleria* have remained obscure since 1932, when the two currently recognized species were described as larval hemiramphids. Most subsequent classifications relegated schindler-iids to a separate suborder within the Perciformes, usually placing them near the blennioids or ammodytoids. We present evidence from otolith microstructure, egg surface morphology, male reproductive tract and, in particular, various aspects of the osteology, that we believe demonstrates unequivocally that *Schindleria* is a member of the suborder Gobioidei. Many of the osteological differences between *Schindleria* and other gobioids are the result of developmental truncations in the former. *Schindleria* represents the most extreme example of progenetic developmental truncation known among fishes.

Since its original description (Schindler, 1932), the tiny marine fish genus *Schindleria* has remained an enigma. Most ichthyologists who have examined its anatomy in an attempt to understand its phylogenetic relationships have come away with inconclusive hypotheses, and several have suggested that the correct answer was unlikely ever to be known due to the apparently paedomorphic expression of most characters. Despite the obvious developmental truncation, there has never been an attempt to compare the osteology of *Schindleria* with that of early developmental stages of other groups. We do so in this paper and conclude that *Schindleria* is a gobioid. Its precise relationships within the Gobioidei remain unresolved.

In 1928 Dr. Victor Pietschmann brought to Vienna a collection of larval fishes from the Leeward Islands of Hawaii. Among these were about 100 specimens thought to be larval hemiramphids, which Pietschmann gave to Dr. Otto Schindler for identification. Schindler soon recognized that these specimens, ranging from 11.5 to 22.5 mm in total length, differed in many respects from the Hawaiian *Hemiramphus brasiliensis*, and found that they represented two distinct forms based on meristic and other characters (Fig. 1). Furthermore, Schindler found specimens of both forms with either well-developed eggs or long urogenital papillae and testes filled with ripe spermatozoa. He concluded that these seemingly larval specimens were, in fact, sexually mature individuals, and described them as two new species of what he called "sexually mature larval hemiramphids," *Hemiramphus praematurus* and *H. pietschmanni* (Schindler, 1930, 1931, 1932). In addition to the external features of the two species, Schindler (1932) described in some detail the gross anatomy and histology of selected aspects of the soft anatomy. His primary purpose in doing so was to demonstrate that these specimens were clearly sexually mature while at the same time exhibiting certain features characteristic of a larval stage of development in other fishes. The latter features include placement of the atrium posterior to, rather than dorsal to, the ventricle, restriction of pigment to the dorsal surface of the swim bladder with none on the body surface, and what Schindler thought to be an incompletely developed portion of the vertebral column preceding the caudal skeleton (see Schindler, pls. 1, 4).

Curiously, Schindler never questioned that these fishes were hemiramphids and thus presented no evidence supporting that surmise, discussing instead how they differed from *Hemiramphus brasiliensis*. Soon after the publication of Schindler's
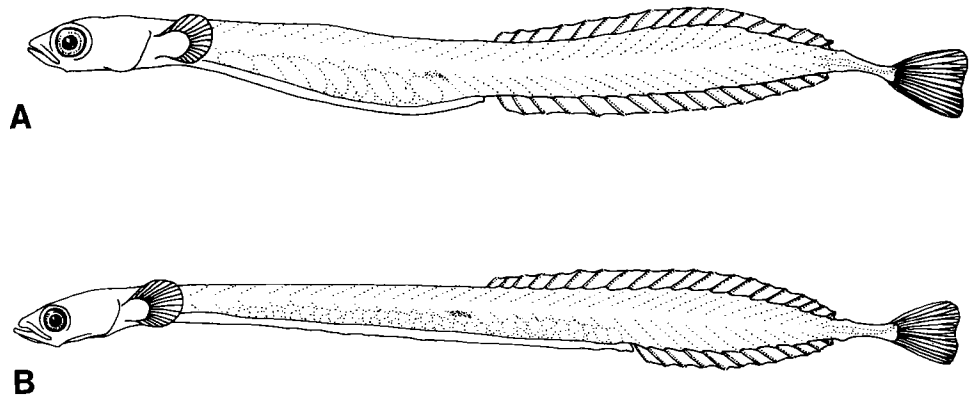
Figure 1.   A. *Schindleria pietschmanni*, adult female, 15.1 mm SL. B. *Schindleria praematura*, adult female, 20.1 mm SL (from Watson et al., 1984).

(1932) paper, Dr. Louis Giltay, of the Royal Museum of Natural History of Belgium, found a single specimen of *H. praematurus* among plankton collections taken by the S. A. R. PRINCE LEOPOLD off New Guinea and made the comparisons that Schindler had failed to make. Giltay (1934) compared his specimen to Delsman's (1924) description of larval *Hemiramphus* and noted that it lacked several features that are prominent in those larvae of equivalent or substantially smaller sizes, including pelvic fins and a notably elongate lower jaw and elongate lower caudal-fin lobe. He also illustrated the caudal skeleton of *Schindleria* and correctly observed that the upturned "cartilaginous rod" that Schindler interpreted as an undeveloped portion of the vertebral column, is actually an exceptionally elongate urostyle. Giltay (1934) argued convincingly that there was no evidence to suggest a close relationship between what he called "Schindler's larvae" and hemiramphids, or any other family of synentognath. He emphasized that they did not exhibit many of the features considered diagnostic of the order Synentognathi by Weber and de Beaufort (1922), including fusion of the lower pharyngeals, presence of supramaxillae, and insertion of the pectoral fins high on the body. Accordingly, Giltay erected a new genus, *Schindleria*, for Schindler's two new species and recommended that it be treated as a distinct family, Schindleriidae. He proposed that schindleriids are percomorphs, possibly related to the Blennioidei (sensu Regan, 1912), with which they share a one-to-one correspondence between dorsal- and anal-fin pterygiophores and neural and haemal spines. Although Schindler (1934) apparently was not convinced by Giltay's (1934) arguments, *Schindleria* has not been placed within or near the Hemiramphidae since then.

Anton Bruun made large collections of *Schindleria* in the South Pacific during the DANA-Expedition around the world in 1928–1930, mostly with night light and dip net. Bruun (1940) described this material, with a major emphasis on distinction and distribution of the two species. He also included a discussion of the extremely small size of *Schindleria*, arguing that although the goby *Pandaka pygmaea* might be the shortest living vertebrate, the lightest is the somewhat longer, but extremely slender *Schindleria praematura*. Bruun offered no new insight on anatomy or relationships, although he once again illustrated the caudal skeleton.

Gosline (1959) was the first to describe and illustrate several aspects of the head skeleton of *Schindleria*. He did not have the advantage of alcian blue cartilage staining, and some of his interpretations of suspensorial and jaw bones are in-

correct (see below). He believed that the bony structures of *Schindleria* were precociously calcified larval features that "bear little comparison with normal adult fishes and are only incompletely comparable with any larval stage." Gosline's (1959) interpretation of the elongate urostyle (similar to that of Schindler's) was also erroneus; he suggested that this "precaudal rod" ". . . represents the posterior portion of the notochord which has been replaced by cartilage and/or bone without dividing into discrete vertebral segments." As for relationships, Gosline (1959) was pessimistic about any further resolution: "The members of the genus are neotenic fishes, apparently without close relatives, which have lost the adult characteristics that would presumably indicate their relationships." Nonetheless, he basically agreed with Giltay (1934) that *Schindleria* is a perciform whose affinities lie somewhere "in the neighborhood of the blennioid fishes," although pointing out that a one-to-one relationship between dorsal and anal fin rays and vertebrae also occurs in trachinoids, ammodytoids and many gobioids. Rather than place *Schindleria* within the Blennioidei, Gosline (1959) erected a new suborder, Schindleroidei, which he felt was warranted by the unique "precaudal rod."

In a paper on the osteology and systematic position of *Hypoptychus* (then considered an ammodytoid, subsequently shown by Ida, 1976, to be a gasterosteoid), Gosline (1963) speculated "If the terminal vertebrae of *Hypotychus* is not merely the result of fusion in an abberant specimen, then a progressive evolution along many of the lines already apparent in that fish might end in a neotenic form very like *Schindleria*." Although Gosline (1963) presented no evidence in support of this relationship, subsequent classifications (Greenwood et al., 1966; Nelson, 1976, 1984) have placed the Schindleroidei near the Ammodytoidei. In reality, no meaningful progress toward understanding the relationships of *Schindleria* has been made since Giltay's (1934) demonstration that it is not a synentognath. Consider the closing statement from the most recent review of the problem (Watson et al., 1984): "Knowledge of spawning and early development might aid in ascertaining schindleriid relationships although at present this group seems destined to remain an enigma."

Our investigation originated with the casual observation that there is a general resemblance between *Schindleria* and some of the more elongate larval gobioids (e.g., microdesmids). In particular, we were struck by the relatively large, conspicuous gas bladder, capped with pigment dorsally, that characterizes both groups. There has been frequent reference to gobioids in previous papers on *Schindleria* (Schindler, 1932; Bruun, 1940; Gosline, 1959), but only as examples of a group in which paedomorphic forms also have evolved. The possibility that *Schindleria* is another paedomorphic goby never has been proposed, and thus no anatomical comparisons with gobioids have been made. Ironically, among major percomorph assemblages, the Gobioidei is one of the most distinctive anatomically, exhibiting a plethora of diagnostic characters. The list of gobioid synapomorphies (Springer, 1983, 1988) continues to grow (Hoese and Gill, 1993; Winterbottom, 1993), and thus the recognition of a given taxon as a gobioid should be relatively straightforward. Why then have the gobioid affinities of *Schindleria* gone so long unrecognized? The answer is now clear. The extreme reductive nature of the paedomorphic *Schindleria* obscures much of the usually obvious evidence, and because the question, "Is *Schindleria* a goby?" has never been asked, the more specific, detailed, comparative investigation that would identify this relationship has not been done.

We recognized that if we were to test the hypothesis that *Schindleria* is a gobioid, the most informative diagnostic characters of gobioids would be those that are identifiable earliest in ontogeny, such as the larval gas bladder that provided an

initial clue. Fortunately, Brothers (1984) had identified a synapomorphy in the configuration of the primordium of the otolith of gobies, a feature that forms in the very early embryo, well prior to hatching but that can be recognized in adult otoliths by grinding back to the core. All gobioids examined to date (including genera from all families of Hoese, 1984, except Xenisthmidae) have an elongate primordium in the sagittae and lapilli, usually with a slight central constriction (Fig. 2C, D). The primordium of other fishes is usually more or less spherical (Fig. 2A, B), and the distinctive gobioid configuration has not been seen in any other group. We suspected, then, that if *Schindleria* were a gobioid, there would be evidence in the otolith primordium. Unfortunately, the otoliths were dissolved in all formalin-fixed specimens we examined initially, and several years passed before we were able to obtain ethanol-fixed specimens with otoliths intact from the larval fish collections at the Australian Museum. Examination of those otoliths revealed that the primordium of *Schindleria* (Fig. 2E, F) has the elongate form unique to the Gobioidei. We also observed additional putative similarities in egg morphology and testicular structure (described below). In light of this evidence we then undertook a detailed systematic comparison of the osteology of *Schindleria* and gobioids, with particular emphasis on early developmental stages of the latter. The results lead unequivocally to the conclusion that *Schindleria* is a member of the suborder Gobioidei.

METHODS AND MATERIALS

We follow the gobioid family classification of Hoese (1984), modified to include the family Odontobutidae of Hoese and Gill (1993). The latter authors recognize the Odontobutidae (comprising the genera *Micropercops, Perccottus,* and *Odontobutis*) as the sister group of all other gobioids except *Rhyacichthys*.

Otoliths (sagittae and lapilli) were dissected from 95% ethanol fixed and preserved specimens. Slide mounts were prepared by immersion of the otoliths in mineral oil. The specimens were examined with video-enhanced compound light microscopy at a magnification of 2,650×.

Eggs were dissected from mature females. The chorion and associated cells were teased from the enclosed yolk before staining in aqueous solutions of eosin and hematoxylin. The stained egg membranes were examined and photographed with light microscopy. For SEM observations, whole eggs and egg membrane preparations were dehydrated with Pel-Dri (reg. trademark; Ted Pella Co., Redding, CA) before sputter-coating with gold-palladium. Male reproductive organs were observed in situ after dissection.

Most osteological specimens were cleared and stained for bone and cartilage by the method of Dingerkus and Uhler (1977), although some specimens (earlier preparations) were stained only for bone. Institutional abbreviations are those of Leviton et al. (1985). For comparative purposes, we examined cleared and stained specimens housed in the USNM collections from a broad range of perciform families. Among the osteological material were adult specimens representing all perciform suborders and all but a few percoid familes, as well as larval specimens from many of these groups. Because the comparative material is extensive, we list below only the gobioid specimens examined, including *Schindleria*. Unless otherwise noted, specimens are cleared and stained. Size ranges (in standard length, SL) are given only for larvae and small juveniles.

Rhyacichthyidae:
   Rhyacichthys aspro, AMNH 48695
Odontobutidae:
   Micropercops swinhonis, AMS I.27275-001
   Odontobutis obscura, AMS I.27277-001
Eleotrididae:
   Butis amboinensis, USNM 224964
   Eleotris amblyopsis, USNM 226200
   Gobiomorus dormitor, USNM 79070
   Hypseleotris sp., AMS uncat., 10 (10–24 mm SL)
   Microphilypnus sp., AMS uncat.
Xenisthmidae:
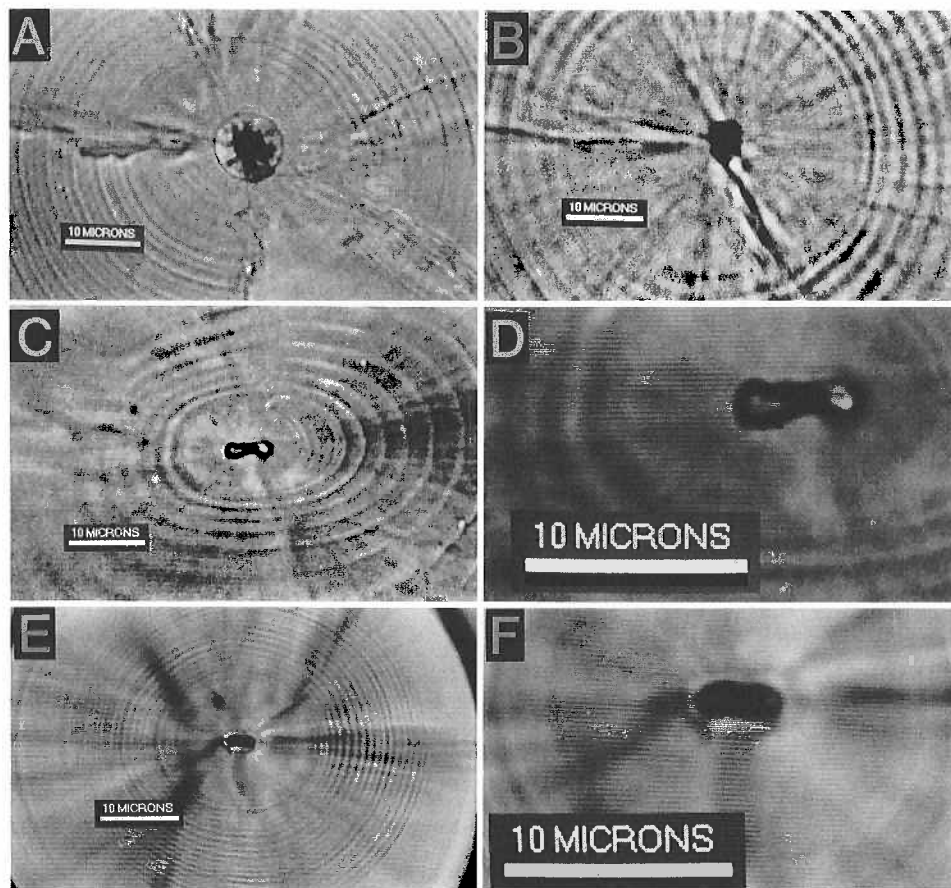   *Allomicrodesmus* sp., AMS I.30608-001 (6.3 mm SL)

Figure 2. Light micrographs (video image) of primordium and core region of the sagittae of: A. *Anchoa* sp. (Engraulidae); B. *Emblemariopsis signifera* (Chaenopsidae); C, D. *Gnatholepis thompsoni* (Gobiidae); E, F. *Schindleria praematura*. Note elongate primordium in C–F.

> *Tyson belos,* USNM 229985 (18.5 mm SL)
> *Xenisthmus clarus,* USNM 235710
> *Xenisthmus* sp., AMS I.30534-001 (7.5 mm SL)

Gobiidae:
> Gobiidae—USNM 322797, 8 (5.9–11.0 mm SL); USNM 322794, 3 (5.2–8.0 mm SL)
> *Fusigobius neophytus,* USNM 287169
> *Gobioides peruanus,* USNM 288656, 5 (33.0–35.9 mm)
> *Gobionellus boleosoma,* USNM 322793, 9 (8.0–13.4 mm SL)
> *Gobionellus shufeldti,* USNM 322790, 1 (22.5 mm SL)
> *Gobionellus* sp.—USNM 322795, 1 (9.0 mm SL)
> *Gobiosoma bosci*—USNM 322792, 12 (7.8–9.2 mm SL); USNM 322791, 58 (6.0–10.3)

Microdesmidae:
> *Microdesmus retropinnis,* USNM 205071, 2 (23.8–51.5 mm SL)
> *Gunnelichthys curiosa,* AMS I.23566-015, 2 (4.9–5.2 mm SL).

Kraemeriidae:
> *Kraemeria bryani*—USNM 143153.

Schindleriidae:
> *Schindleria praematura*—AMS I.23115-004, 13 (2.9–16.0 mm SL); AMS I.23116-001 4 (9.8–12.4 mm SL) in alcohol; AMS I.90160009, 12 (4.1–14.1 mm SL) in alcohol; OTEC Cruise Sta. 5 Tow 1, 1 (18.6 mm SL); Kahe Transects, Sta. VM-20, 1 (17.5 mm SL) in alcohol.

S. pietschmanni—OTEC Cruise Sta. 5, Tow 1, 1 (10.0 mm SL); Kahe Transects, Sta. VM-20, 1 (18.5 mm SL) in alcohol.

Abbreviations

Aa—Anguloarticular, Ba—Basioccipital, Bb—Basibranchial, Bh—Basihyal, Br—Branchiostegals, BC—Basibranchial cartilage, Cb—Ceratobranchial, Cl—Cleithrum, Ch—Ceratohyal, CsC—Coracoscapular cartilage, D—Dentary, E—Ethmoid plate, Eb—Epibranchial, EB—Epiphyseal bar, Ec—Ectopterygoid, F—Frontal fontanel, Hb—Hypobranchial, H-S—Hyomandibulosymplectic, HPU 2–3—Haemal spines of second and third preural centra, Ih—Interhyal, Io—Interopercle, Hh—Hypohyal, M—Maxillo-vomerine meniscus, Ms—Mesopterygoid, Mt—Metapterygoid, Mx—Maxilla, N—Neurocranium, NPU 2-3—Neural spines of second and third preural centra, O—Opercle, Pt—Posttemporal, P—Parasphenoid, Pa—Palatine, Pb—Pharyngobranchial, Pmx—Premaxilla, PR—Pectoral radial, PRP—Pectoral radial plate, PU2—Second preural centrum, Q—Quadrate, R—Ribs, Ra—Retroarticular, RC—Rostral cartilage, S—Saggita, Scl—Supracleithrum, So—Subopercle, TC—Trabecular communis, TM—Taenia marginalis, U—Urostyle, V 1—First vertebrae and VIC—Ventral intercleithral cartilage.

OTOLITHS
Figure 2

The sagittae of *Schindleria* have a distinctly elongate primordium (1 μm × 2–3 μm) like that described by Brothers (1984) as characteristic of and unique to members of the Gobioidei. The primordium of the lapillus appears similar, however its small size made observation difficult. A regular pattern of incremental growth surrounds the saggital core with increment widths 1 μm or less, most probably below the resolving limit for light microscopy. These increments are structurally comparable to the daily growth layers observed in the otoliths of many fishes (Campana and Neilson, 1985).

REPRODUCTIVE ORGANS AND EGGS
Figure 3

Urogenital Papillae.—Mature individuals of *Schindleria* possess well-developed sexually-dimorphic urogenital papillae similar to those seen in gobioids. Schindler (1932), Bruun (1940) and Gosline (1959) all refer to the elongate urogenital papilla of mature males, and females have a blunt, bilobed papilla. We have seen urogenital papillae of this general form in gobioids representing several families, and comparable structures are lacking in most percomorphs. Comparison of the condition in *Schindleria* with Egami's (1960) illustrations of urogenital papillae in a broad range of gobioid taxa with illustrations of those in *Schindleria* (Bruun, 1940: fig. 2; Sardou, 1974: figs. 4, 8) confirms the similarity in configuration.

Sperm Duct Glands.—Schindler (1932: pls. 4B, 8, 9) provided extensive gross anatomical and histological descriptions of the male reproductive system. He noted "... a paired appendage organ, of apparently glandular character, which extends jointly with the *vas deferens* right into the urogenital papilla." Within the Gobiidae, and probably all gobioids, males have a distinctive pair of accessory secretory structures associated with the two testicular lobes (Egami, 1960; Arai, 1964; Miller, 1984, 1986, 1992; Cole, 1990). These structures have been referred to as seminal vesicles, sperm duct glands, and accessory secretory glands. We adopt "sperm duct gland" for the appendage organs described by Schindler and the various accessory structures noted for many goby species (Breder and Rosen, 1966). Such structures are uncommon among fishes. Although the males of some other groups (e.g., blenniids and embiotocids) have accessory glands associated
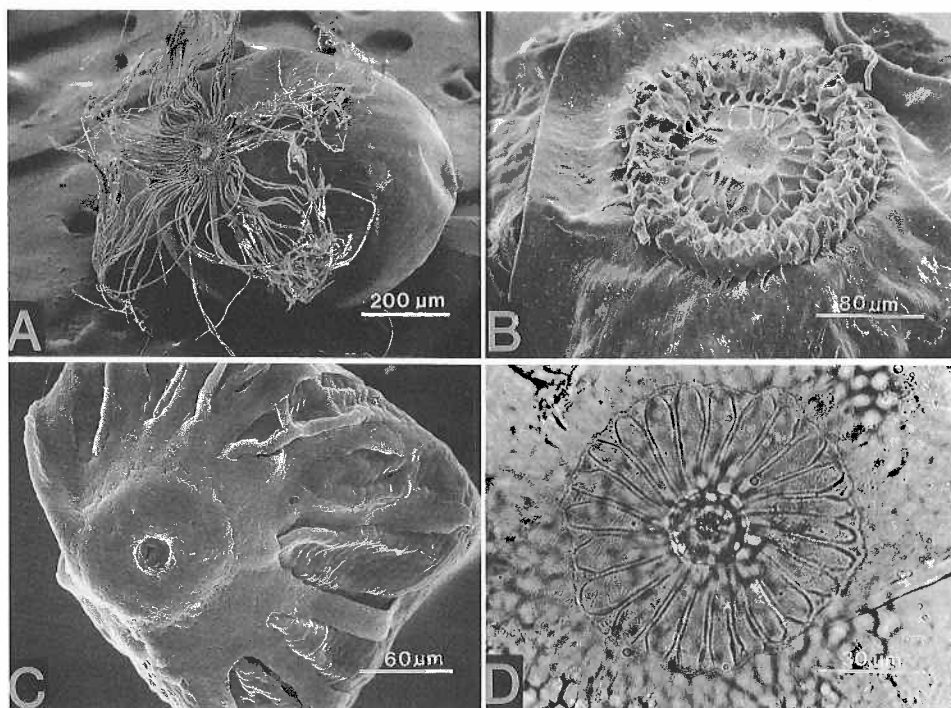
Figure 3. A. SEM micrograph of water hardened ripe ovarian egg of *Clevelandia ios* (Gobiidae)—filaments broken away from vegetal pole and surround the micropylar region; B. SEM micrograph of *Clevelandia ios* egg—filaments pulled away to reveal sculpturing around micropyle; C. SEM micrograph of egg removed from ovary of alcohol-fixed *Schindleria praematura*—note broad filaments surrounding micropyle; D. Light micrograph of micropylar region of egg removed from alcohol-fixed *Schindleria praematura*—whole mount of chorion.

with the genital papillae, they do not have the distinctive association of those structures with the testicular lobes that characterizes *Schindleria* and other gobioids. Miller (1992) described the gross morphology and histology of the male genetalia in *Rhyacichthys aspro* and concluded "that the sperm duct gland is a synapomorphy for the suborder Gobioidei, not merely for the Gobiidae, and that, in the form found among gobioids, this may well qualify as an autapomorphy for the group at least among acanthopterygians." Presumably he meant by the latter part of that statement that the gobioid sperm duct gland is unique among acanthopterygians.

Egg Morphology (Fig. 3).—Schindler (1932) noted the ellipsoid form of mature ovarian eggs of *Schindleria* and ". . . peculiar, stellate, dendritic, branched figures . . ." that appear in the yolk. Bruun (1940: fig. 3) also illustrated an egg with dendritic figures at one pole, along with two broad flaps or filaments originating near the presumptive micropyle region. Elongate or ellipsoidal eggs are characteristic of gobioids (Breder and Rosen, 1966; Leis and Rennis, 1983; Leis and Trnski, 1989). Fertilized goby eggs also have attachment filaments originating around the micropyle. Although this latter feature is not unique among fishes (Boehlert, 1984; Mooi, 1990), there may be a characteristic arrangement of filaments and nutritive and/or supporting cells in the micropylar region of the zone radiata. This is the pattern to which Schindler and Bruun referred. Figure 3
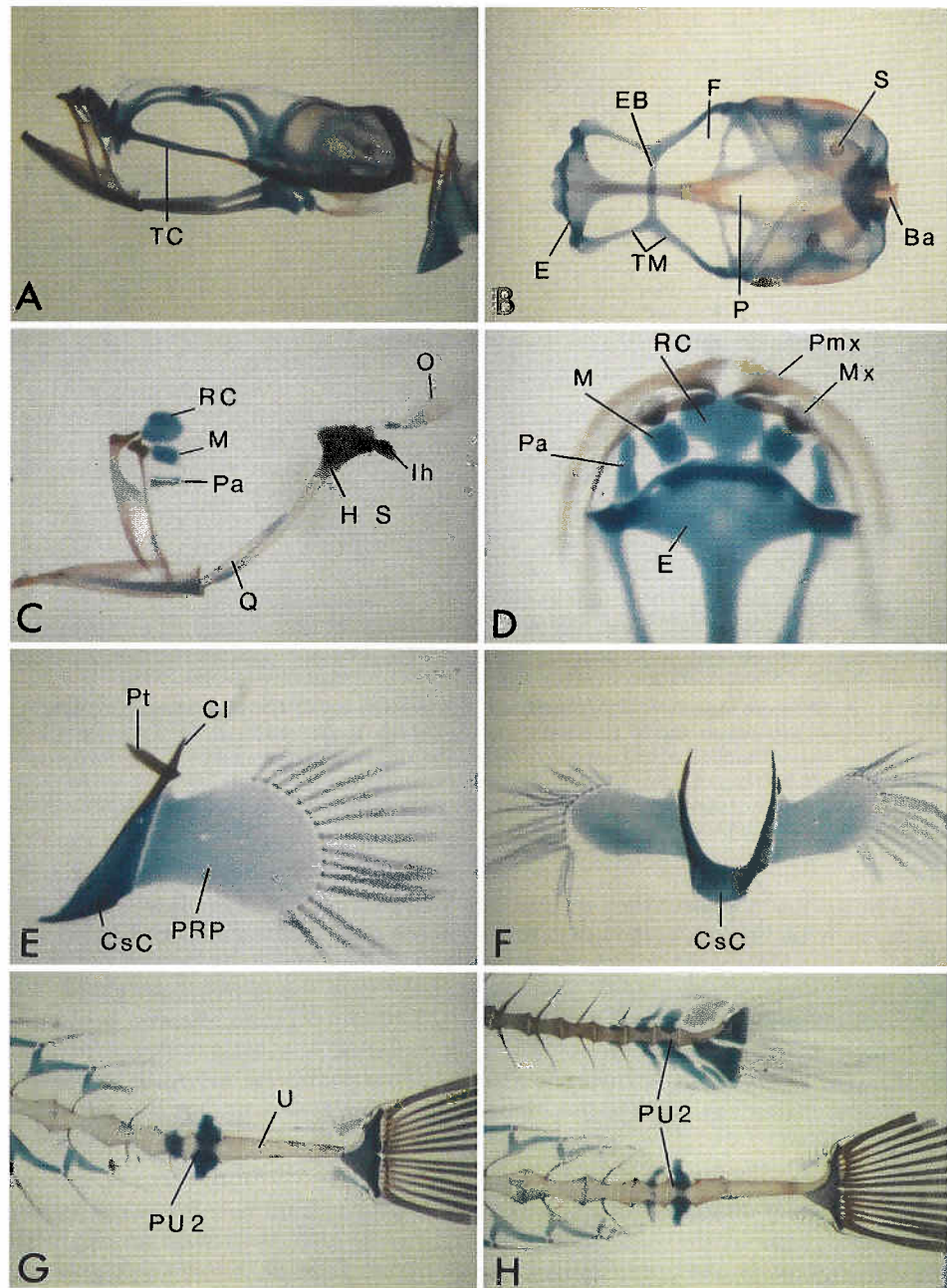
Figure 4. Various aspects of cleared and stained skeleton of adult *Schindleria praematura*, left lateral view, unless otherwise indicated: A. Skull, gill and hyoid arches removed; B. Neurocranium, dorsal view; C. Suspensorium and jaws, with opercle; D. Rostral area, dorsal view; E. Pectoral girdle; F. Pectoral girdles of both sides, frontal view; G. Caudal skelton; H. Caudal skeleton of *Gobiosoma bosci* (6.2 mm SL), upper, and *S. praematura* (urostyle broken), lower.
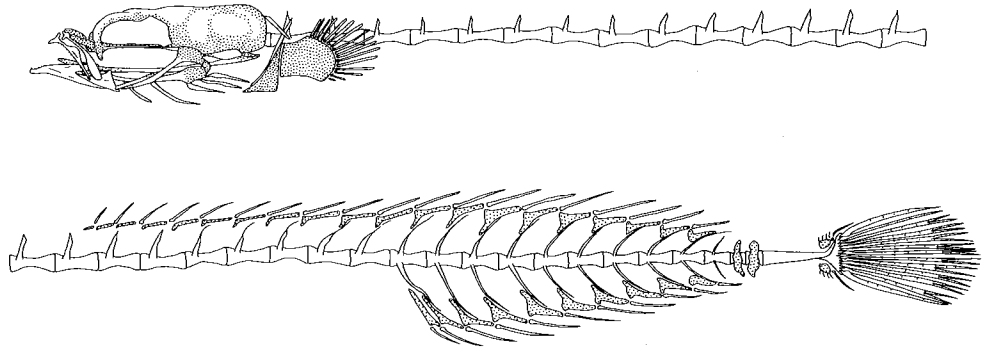
Figure 5. Skeleton of *Schindleria praematura,* AMS I.23115-004, 15.8 mm SL. Distal radials of dorsal- and anal-fin pterygiophores not shown.

illustrates the egg surface morphology of the goby *Clevelandia ios* and *Schindleria.* The *C. ios* eggs were stripped from a ripe female and water hardened but not fertilized, whereas the late stage *Schindleria* eggs were removed from the ovaries of an ethanol fixed female. Both SEM and light microscopy reveal a general similarity in the pattern of attachment of the filaments to the egg. In the SEM example of *Schindleria,* a cap of cells obscures details of this arrangement, but the broad filaments can be seen clearly. We cannot determine whether this is the final form of the filaments or whether they will be further modified before or after release.

OSTEOLOGY OF *SCHINDLERIA*
Figure 4–12

The following description is based on *S. praematura,* unless otherwise indicated. Aside from meristic features we found no substantive osteological differences between the two species.

Neurocranium (Figs. 4A, B, 5).—The neurocranium is largely cartilaginous, with weak ossification in some areas. The cartilaginous ethmoid plate is continuous dorsolaterally on each side with a cartilaginous arch, the taenia marginalis, extending posteriorly over each orbit. A large frontal fontanel, in which there is no ossification, is divided into anterior and posterior portions by a transverse bridge of cartilage, the epiphyseal bar, that joins the taeniae marginales near their mid-length. Ventrally, the ethmoid cartilage extends posteriorly as a median bar, the trabecular communis. A narrow, laminar parasphenoid ossification extends from near the anterior margin of the ethmoid plate along the ventral surface of the trabecula communis, expanding posteriorly to form a major portion of the floor of the cranial vault and joining a relatively well-ossified basioccipital. Although the other cranial bones are not discretely formed, weak ossification is evident in the regions of the prootics, sphenotics, pterotics, epioccipitals, and at the edges of the exoccipitals surrounding the foramen magnum.

Suspensorium (Figs. 4C, D, 5, 6C, 7B).—The suspensorium comprises the hyomandibular, symplectic, quadrate, and a fully detached palatine; the meta-, meso- and ecto-pterygoids are absent. The hyomandibular is an irregular plate of cartilage with evidence of incipient ossification in some specimens. At its anteroventral corner the hyomandibular cartilage is continuous with that of the long, strut-like symplectic, which is ossified perichondrally along most of its length. Because the
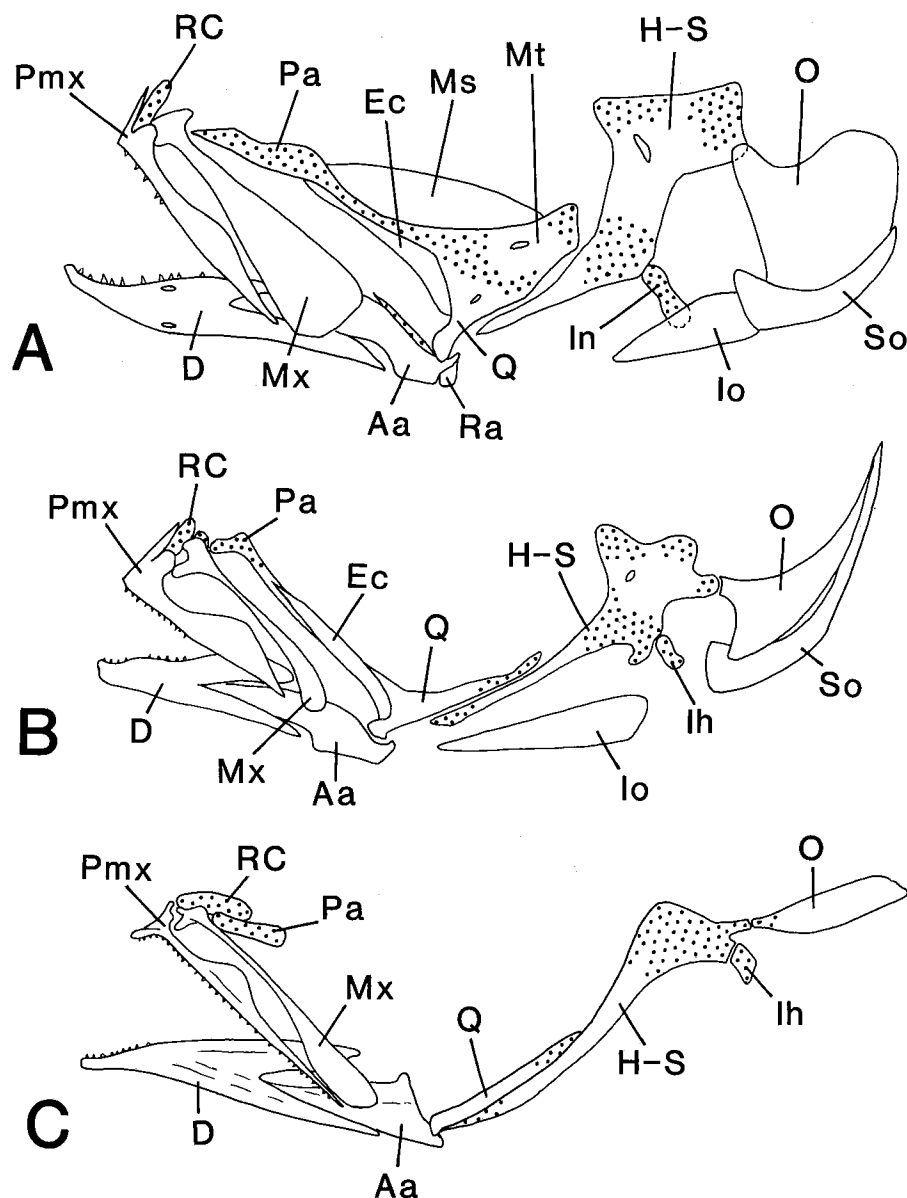
Figure 6. Suspensoria and jaws, left side in lateral view, of: A. *Morone americana*, USNM 322796, 10.0 mm SL; B. Gobiidae USNM 322794, 8.0 mm SL; C. *Schindleria praematura*, AMS I.23115-004, adult. Preopercle removed in A and B.

hyomandibular is unossified, the precise demarcation between it and the sym-plectic is not definite, but it is clear that the hyomandibular is basically an irregular plate without the anteroventral arm that most frequently characterizes the shape of this bone. The quadrate is a simple, posteriorly tapered rod lying along the anterior two-thirds of the dorsal margin of the symplectic; it is weakly ossified along most of its length and slightly expanded at its anterior tip where it articulates with the anguloarticular. The palatine has no association with the remainder of
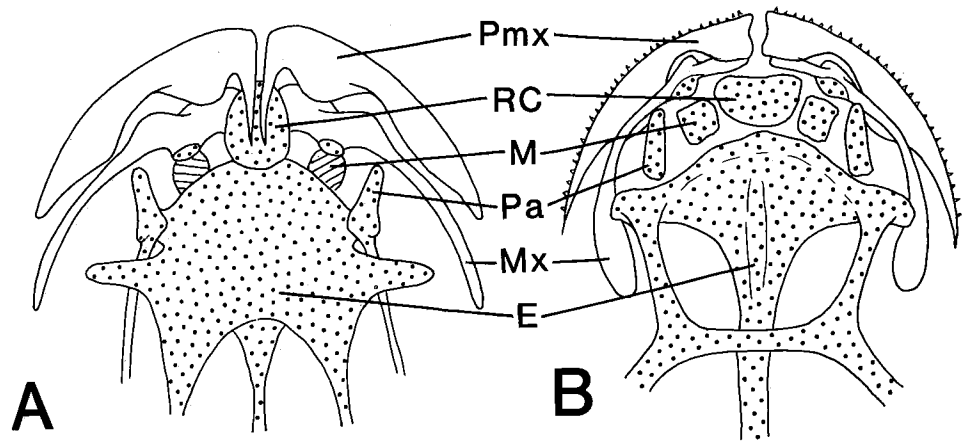
Figure 7. Rostral area and upper jaws in dorsal view of: A. Gobiidae, USNM 322794, 7.8 mm SL; B. *Schindleria praematura*, AMS I.23115-004, adult.

the suspensorium; it is a short rod of cartilage extending from the anterior surface of the cartilaginous ethmoid plate to the maxilla.

Jaws (Figs. 4C, D, 5, 6C, 7B).—The lower jaw comprises a fully ossified dentary and anguloarticular, the latter articulating with the rod-like quadrate; there is no autogenous retroarticular. Tiny teeth are borne along the anterior third of the dorsal margin of the dentary. In the upper jaw the maxilla and premaxilla are fully ossified. The premaxilla bears tiny teeth along the entire length of its ventral margin. There is a broad postmaxillary elevation midway along the alveolar ramus of the premaxilla and a well-developed articular expansion anteriorly at the premaxillary symphysis, but there is no distinct ascending process. The concave posterodorsal margin of the premaxillary articular expansion loosely embraces the anterior margin of the rostral cartilage, a broad, flat, roughly heart-shaped structure that articulates at its posterior tip with the midline of the ethmoid plate. The maxilla is long and thin with some expansion distally. Anteriorly, there is a distinct rounded maxillary head capped posteriorly with cartilage. The maxilla continues anteriomedially beyond the head as a relatively long spatulate process that passes posterior to the articular expansion of the premaxilla and ventral to the anterior margin of the rostral cartilage. A large cylindrical block of cartilage, the maxillovomerine meniscus, lies between the rostral cartilage and the palatine, articulating posteriorly with the anterior surface of the cartilaginous ethmoid plate and anteriorly with the cartilaginous posterior surface of the maxillary head.

Infraorbitals.—There are no infraorbital bones.

Nasals.—There are no nasal bones.

Extrascapulae.—There are no extrascapulae.

Opercular Series (Figs. 4C, 6C).—Only the opercle is present. It is a small, oblong, laminar ossification that articulates anteriorly with a short posterior process of the cartilaginous hyomandibular.

Hyoid Apparatus (Fig. 8B).—The ceratohyal is a single rod-like structure, weakly ossified perichondrally along its midlength, with the cartilaginous posterior end somewhat expanded. There are five branchiostegals, the larger anterior two ar-
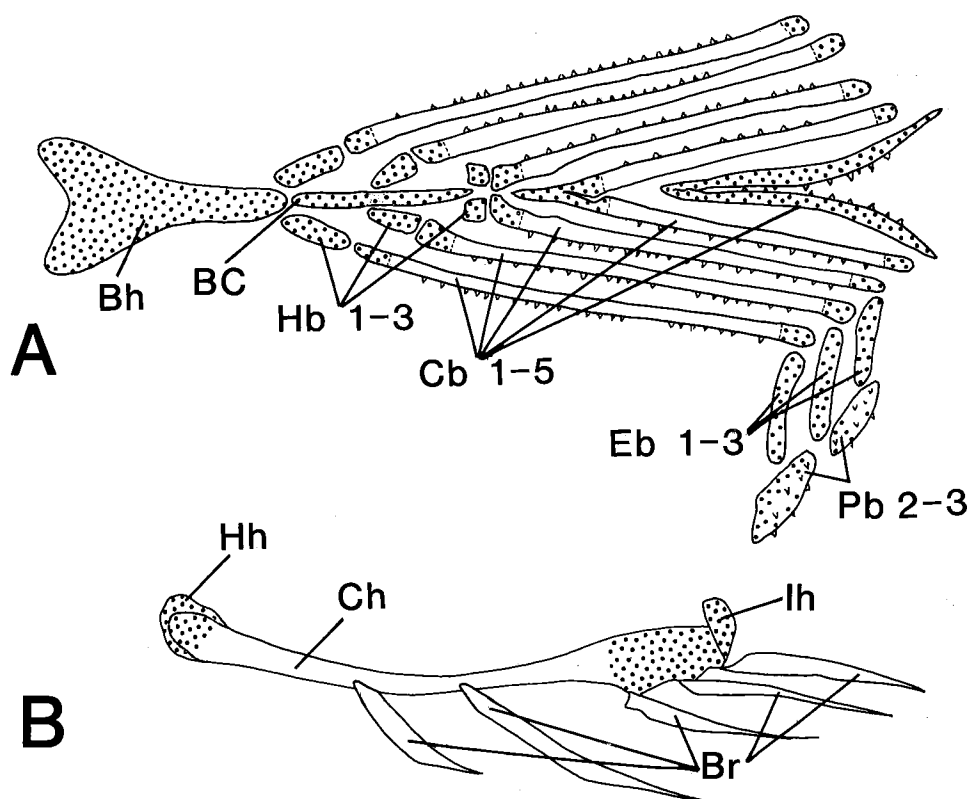
Figure 8. *Schindleria praematura,* AMS I.23115-004, adult. A. Gill arches in dorsal view, dorsal elements of left side folded back, those of right side removed; B. Hyoid apparatus, left side in lateral view.

ticulating along the lateral surface of the ossified midlength of the ceratohyal, the smaller posterior three articulating with processes (the anteriormost process notably the largest) on the ventral margin of the expanded posterior cartilaginous area. There is a single lens-shaped cartilaginous hypohyal on the medial side of the anterior tip of the ceratohyal, articulating medially with the basihyal. At the posterior tip of the ceratohyal a short cartilaginous interhyal extends from the lateral side of the tip to the posteroventral corner of the hyomandibular, well posterior to the presumed hyomandibular-symplectic junction. There is no urohyal.

Gill Arches (Fig. 8A).—All elements of the gill arches except toothplates and ceratobranchials are cartilaginous. The relatively large spatulate basihyal is broadly bifurcate anteriorly with a narrow rod-like posterior portion. The first basibranchial is absent, and the second and third are represented by a continuous rod of cartilage articulating anteriorly with the basihyal. The cartilage that appears to represent the fourth basibranchial is continuous posteriorly with the cartilaginous anterior tips of the fourth ceratobranchials. Hypobranchials 1–3 are present and cartilaginous. Ceratobranchials 1–4 are rod-like bones, weakly ossified perichondrally along most of their length, each with a single row of tiny triangular teeth fused to the dorsolateral margin. The fifth ceratobranchials are slightly curved

cartilaginous rods each with an ossified toothplate attached along the dorsomedial margin. The ceratobranchial toothplates bear several slightly larger teeth and in some specimens the plates may be fragmented rather than continuous. Dorsally there are three rod-like cartilaginous epibranchials (1–3) and two plate-like cartilaginous pharyngobranchials (2–3). The fourth epibranchial is absent as are the interarcual cartilage, first and fourth pharyngobranchials, and fourth upper pharyngeal toothplate. The second pharyngobranchial lies directly anterior to, and is slightly larger than, the third. Each cartilaginous pharyngobranchial bears a toothplate along the ventromedial surface with teeth equivalent in size to those on the fifth ceratobranchials. The epibranchials articulate as follows: first at about midlength of second pharyngobranchial, second at junction between second and third pharyngobranchials, and third at posterolateral corner of third pharyngobranchial.

Vertebral Column (Figs. 5, 9).—There are 31–44 total vertebrae (12–24 precaudal + 13–21 caudal) (Watson, 1989, range includes both species). All centra but the urostyle are hour-glass shaped, and all but the second and third preural centra (described below with caudal skeleton) are elongate, being substantially longer than deep. The longest centra are the most anterior ones, and the first is equal in length to the succeeding several; there is a very gradual decrease in length posteriorly. The centra bear no parapophyses, ribs, or intermuscular bones. Ossified, closed neural arches are borne on every centrum anterior to the third preural. The first neural arch is more robust than the succeeding ones and is fused to the first centrum near the central constriction of the latter; all succeeding neural arches are borne (fused) on the anterior halves of their respective centra. The closed tips of the neural arches become gradually longer, so that near the beginning of the dorsal fin, well-defined, styliform neural spines are evident, becoming increasingly attenuate and inclined posteriorly. Haemal arches and spines appear abruptly on the first caudal vertebrae, and are essentially mirror images of their neural counterparts.

Caudal Skeleton (Figs. 4G, 5, 10C).—The second and third preural centra are abruptly shorter than the preceding centra, and each is encircled by a thick band of cartilage that extends dorsally and ventrally to form thick, short, unossified neural and haemal "spines." The urostylar centrum is an elongate cone with upturned tip, approximately equal in length to the preceding four centra. A single triangular hypural plate is fused to the ventral margin of the upturned tip of the urostyle. The hypural plate is well ossified except along its posterior margin, where the principal caudal-fin rays articulate. A slight notch at about mid-length demarcates the dorsal and ventral halves of the hypural plate. Seven principal rays articulate with the dorsal half, six with the ventral half. The dorsalmost and ventralmost principal rays are notably robust, being about twice as thick as the others. There are 5–7 procurrent caudal-fin rays both dorsally and ventrally. The posteriormost procurrent ray in each series articulates with a small ovoid radial cartilage lying just anterior to the dorsal and ventral tips of the hypural plate. Although we think it unlikely, we cannot discount the possibility that these ovoid cartilages represent distal vestiges of an epural and parhypural, respectively, which are otherwise absent. The remaining rays in each series articulate with an oblong or triangular radial cartilage extending anteriorly from the smaller cartilage. There are no uroneurals.

Dorsal Fin (Fig. 5).—There are 15–22 bilaterally paired dorsal-fin soft rays (Watson, 1989, includes both species), all unbranched and unsegmented, and no spines. All dorsal-fin rays are supported by cartilaginous pterygiophores, each of which
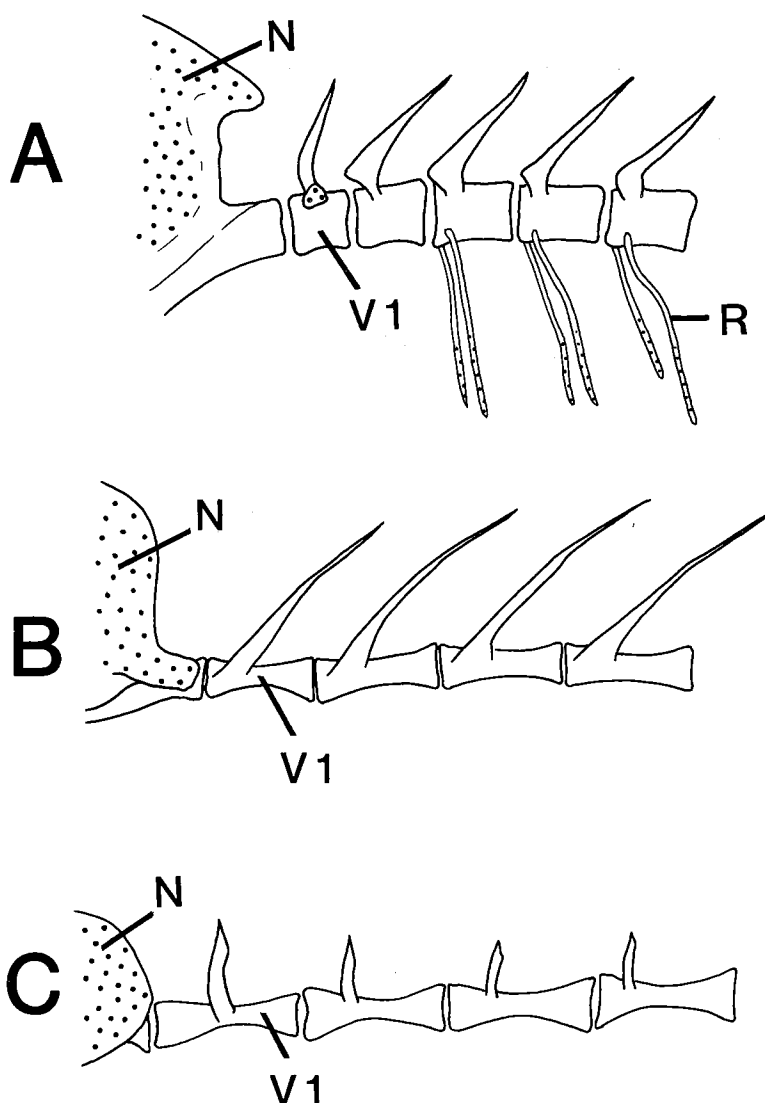
Figure 9. First several vertebrae, left side in lateral view, of: A. *Morone americana,* USNM 322796, 13.0 mm SL; B. *Gobionellus* sp., USNM 322795, 9.0 mm SL; C. *Schindleria praematura,* AMS I.23115-004, adult.

comprises a large proximal-middle radial and a small spherical distal radial (the latter obscured by fin-ray bases in Fig. 5). Each pair of hemitrichs embraces the distal radial of its serial pterygiophore proximally and (with the exception of the last ray) rests on the anterodorsal corner of the succeeding proximal-middle radial; there are no supernumerary rays. The anteriormost pterygiophores and rays of the dorsal fin are weakly developed. In our specimens (all *S. praematura*) the anteriormost three pterygiophores interdigitate between the neural spines of vertebrae 16–17 or 15–16. The next one or two interneural spaces may accommodate more than one pterygiophore, and all succeeding dorsal pterygiophores have one-to-one correspondence with the neural spines. Anteriorly the proximal-middle
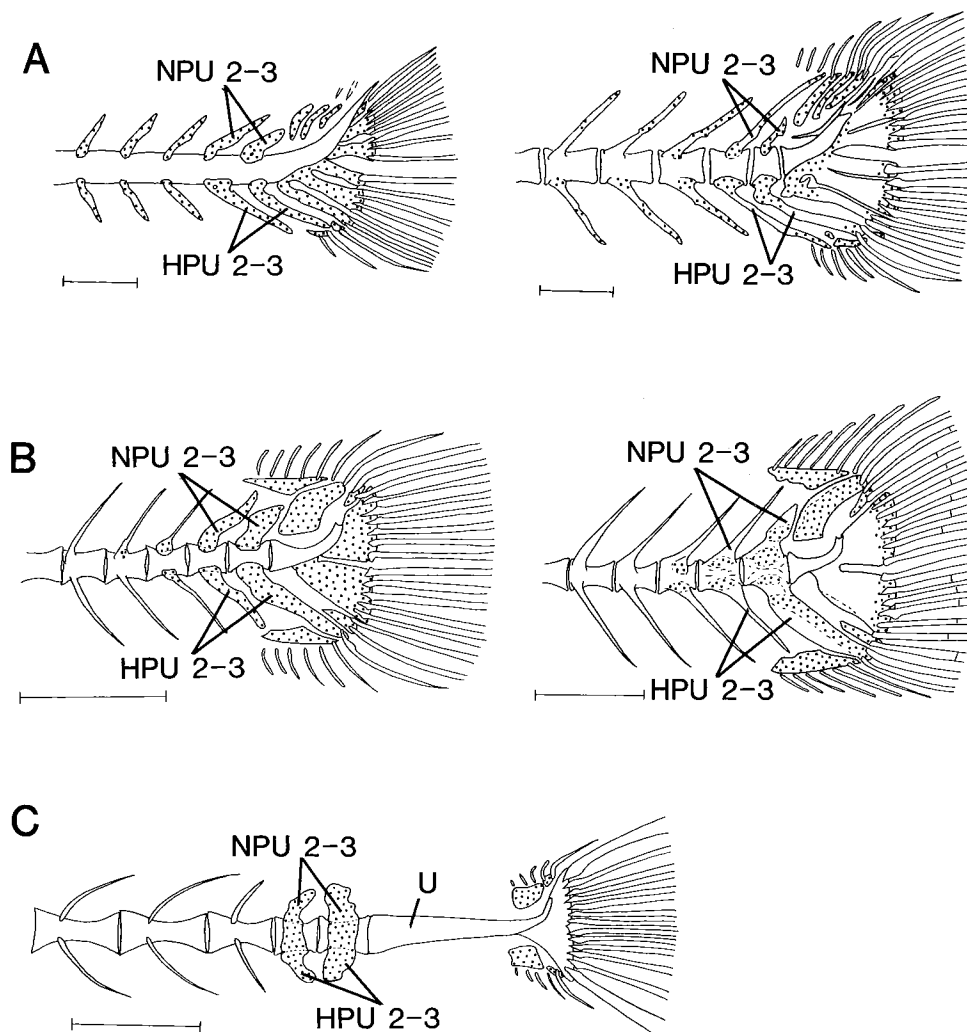
Figure 10. Caudal skeleton and preural vertebrae, left side in lateral view, of: A. *Morone americana*, USNM 322796, left 10.0 mm SL, right 13.0 mm SL; B. *Gobiosoma bosci*, USNM 322792, left 6.6 mm SL, right 9.0 mm SL; C. *Schindleria praematura*, AMS I.23115-004, adult.

radials are simple rods lying almost parallel to the body axis, slightly expanded dorsally and ventrally at their anterior ends in some specimens. Posteriorly, they become more obliquely oriented, more robust, and take on an asymmetrical "y" shape, with the lower arm articulating along the anterior margin of each neural spine.

Supraneurals. — There are no supraneurals.

Anal Fin (Fig. 5, 11C). — There are 10–18 bilaterally paired anal-fin rays (Watson, 1989, includes both species), all unbranched and unsegmented. Although all have been reported previously as soft rays, the first element is a single median structure and thus a true spine. All anal-fin pterygiophores are cartilaginous and all but the first resemble their opposing dorsal counterparts in configuration, support of fin
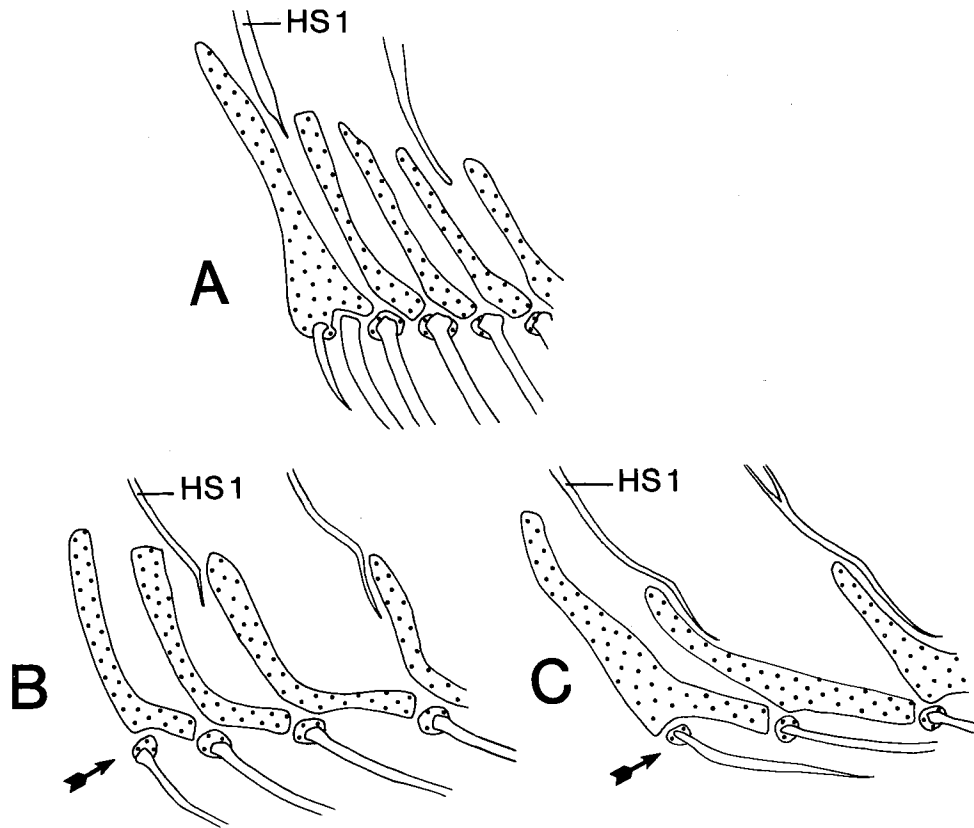
Figure 11.   First several anal-fin pterygiophores, left side in lateral view, of: A. *Morone americana*, USNM 322796, 12.1 mm SL; B. *Gobionellus* sp., USNM 322795, 9.0 mm SL; C. *Schindleria praematura*, AMS I.23115-004, adult. Arrow points to supernumerary distal radial associated with anal spine.

rays, and in articulation of the proximal-middle radials along the anterior margin of succeeding haemal spines. The proximal-middle radial of the second pterygiophore rests along the anterior margin of the first haemal spine. That of the first pterygiophore lies in close proximity to the anterior margin of the second and is basically a simple, distally notched rod supporting two distal radials, one serial and one supernumerary, the latter borne in the distal notch. The first anal soft ray (second element in the fin) is associated with the serial radial. The single anal spine (first element in the fin) is associated with the supernumerary radial. (Distal radials are obscured in Fig. 5, but visible in Fig. 11C.)

Pectoral Girdle (Fig. 4E, F, 5, 12C).—There are 11–18 pectoral-fin rays (Watson, 1989, includes both species) borne along the rounded posterior margin of a large, paddle-like plate of cartilage, which may have two or three small foramina. In most specimens each pectoral ray, all of which are unbranched, embraces a small, spherical distal radial; however, distal radials are not evident in some specimens. The cartilage plate, in which the four actinosts of most teleosts would typically ossify, articulates anteriorly along the posterior margin of the coracoscapular cartilage. Aside from the pectoral rays, there are only two ossified structures in
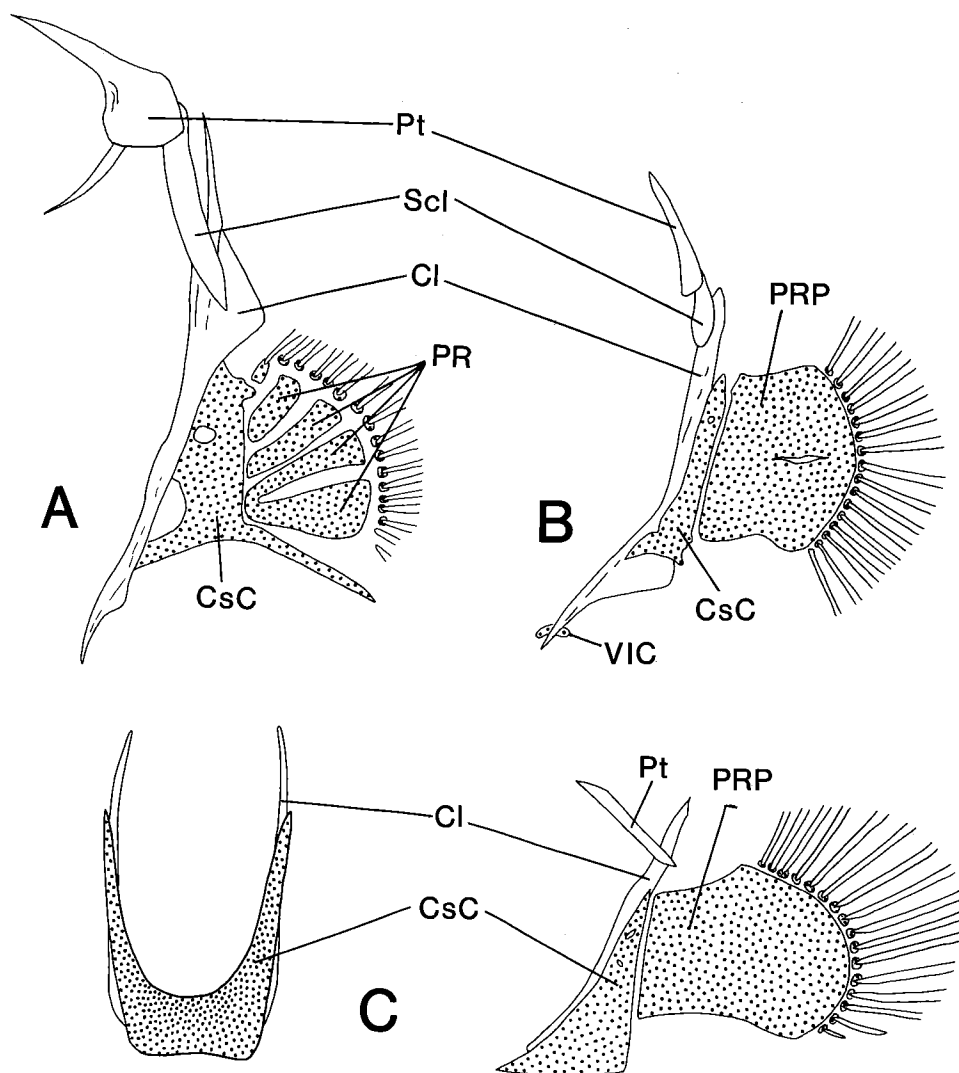
Figure 12. Pectoral girdle, left side in lateral view, of: A. *Morone americana,* USNM 322796, 13.0 mm SL; B. *Gobionellus* sp., USNM 322795, 9.0 mm SL; C. *Schindleria praematura,* AMS I.23115-004, adult, frontal view shown to left of lateral view.

the pectoral girdle. The posttemporal is a small, obliquely oriented blade articulating anteriorly with the neurocranium and posteriorly with the cleithrum; there is no supracleithrum, and Baudelot's ligament is absent. The cleithrum is a simple splint-like bone with the ventral two-thirds of its length tightly adhered to the anterior margin of the coracoscapular cartilage; the cleithra do not meet at the ventral midline. The triangular coraco-scapular cartilage broadens ventrally and is fully continuous across the ventral midline with its contralateral member. There is no ventral intercleithral cartilage.

Pelvic girdle. — There is no pelvic girdle.

COMPARATIVE OSTEOLOGY
Figures 4G–H, 6–12

As we demonstrate in this paper, *Schindleria* represents the most extreme example of apparent paedomorphic reduction known in fishes. Because of this, we have taken a conservative approach in evaluating the evidence supporting its relationships. Winterbottom (1993) reviewed 22 putative apomorphies of adult gobioids. We view all but six of these as potentially uninformative with respect to the possible gobioid affinities of *Schindleria* for the following reasons: 1) Shared absence of certain bones (e.g., infraorbitals, parietals, basisphenoid) could be attributable in *Schindleria* to developmental truncation rather than common ancestry with gobioids; 2) Absence in *Schindleria* of apomorphic features diagnostic of gobioids (cleithral notch, ventral intercleithral cartilage, sensory papillae) may be the result of developmental truncation and thus does not refute the hypothesis of common ancestry; 3) Certain apomorphic configurations diagnostic of gobioids (e.g., gap between symplectic and preopercle, relative sizes of symplectic and metapterygoid, ligament between interhyal and preopercle, pelvic girdle with intercleithral cartilage, first basibranchial cartilaginous) are not identifiable in *Schindleria,* because the bone (or one of the bones) involved never develops.

The problem posed by paedomorphism can be circumvented in part by comparison of *Schindleria* with earlier developmental stages of gobioids and other groups in an attempt to identify shared derived features that characterize early development but later may become obscured. In the section that follows, similarities between the skeleton of *Schindleria* and the developing and/or adult skeleton of gobioids are described. For the developmental comparisons, larvae of the Gobiidae were emphasized, but representatives of the Eleotrididae, Xenisthmidae and Microdesmidae were also examined; larvae of the primitive Rhyacichthyidae and Odontobutidae were not available. Similarities between *Schindleria* and gobioids are contrasted with skeletal and developmental features common to most other perciforms, which are represented in the comparative illustrations by *Morone. Morone* is not to be construed as a precise outgroup (i.e., sister group) for gobioids. Rather, for the features being compared with gobioids, *Morone* exhibits skeletal configurations and developmental patterns that typify most perciforms. As will be clear from the descriptions, some features shared by *Schindleria* and gobiids remain evident in adults of the latter, others can be seen exclusively in the larvae.

Suspensorium (Fig. 7).—Winterbottom (1993) described four putative apomorphies of the gobioid suspensorium. Three of these are inapplicable to *Schindleria,* because they involve relationships with the preopercle or metapterygoid, both of which are absent in *Schindleria.* The fourth, first described by Springer (1983), involves the failure of the interhyal to form a joint with the symplectic. In most teleosts, the interhyal articulates at the synchondral junction of the symplectic with the tip of the strut-like ventral arm of the hyomandibular. In *Rhyacichthys* the ventral arm of the hyomandibular is short and robust, and the interhyal is ligamentously attached to the hyomandibular-symplectic junction. In all other gobioids the hyomandibular is an irregular plate with no distinct ventral arm, and the interhyal articulates at the posteroventral corner of the broadened ventral margin of the hyomandibular, well posterior to its synchondral junction with the relatively long symplectic. In *Schindleria* the hyomandibular never ossifies, but its delineation as an irregular plate with no distinct ventral arm is evident, because the symplectic is ossified. The cartilaginous interhyal of *Schindleria* articulates at

the posteroventral corner of the hyomandibular, well posterior to the hyomandibular-symplectic junction, exactly as in most gobioids.

The mesopterygoid is absent in many gobioids (most gobiids), and the metapterygoid frequently is reduced. Early in its development, the gobiid suspensorium comprises a hyomandibulosymplectic cartilage, a rod-like quadrate cartilage lying along the anterodorsal margin of the latter, and a thin splint of ectopterygoid bone connecting the quadrate with the largely cartilaginous palatine. The symplectic and quadrate begin to ossify soon after their initial appearance, the hyomandibular somewhat later. *Schindleria* lacks all pterygoids, and the hyomandibulosymplectic/quadrate configuration closely resembles that of a developing gobiid prior to ossification of the hyomandibular.

Gobiids have a distinctive T-shaped palatine configuration, wherein a well-developed process extends medially from the head of the palatine, passing anterior to the lateral ethmoid to articulate with the median ethmoid or the medial portion of the lateral ethmoid (Hoese, 1984). This "ethmoid process" together with the head of the palatine appears initially as a thick rod of cartilage extending from the ethmoid cartilage to the shaft of the maxilla and is connected along its ventrolateral margin to the splint-like dermal portion of the palatine. We conclude that the lateralmost rod of cartilage in the snout region of *Schindleria* represents the ethmoid process and head of the palatine of gobiids at an early stage in its development. There is no connection between this palatine cartilage and the remainder of the suspensorium, because the dermal portion of the palatine and the ectopterygoid never develop. The shorter, more robust cylinder of cartilage, lying just medial to the palatine between the ethmoid cartilage and the head of the maxilla, appears to be a hypertrophied maxillovomerine meniscus; however it has the typical appearance of hyaline cartilage and stains deeply with alcian blue. This structure is a common feature of acanthomorph fishes, but typically is in the form of a biconcave disc of fibrocartilage that does not stain or stains only faintly with alcian blue.

Gill Arches (Fig. 8A).—Takagi (1950) noted that a broad spatulate fan-shaped basihyal, frequently with a concave or forked anterior margin, characterizes more derived gobioids, such as the gobiids. Among other perciforms, the basihyal is usually rod like, and, if expanded, does not have a forked or concave anterior margin. Although this character needs to be surveyed more thoroughly, it suffices that the basihyal of *Schindleria*, like that of many gobiids, is large and fan-shaped with a concave anterior margin.

In addition to having most of the gill arch elements cartilaginous, *Schindleria* differs from all other gobioids in lacking an interarcual cartilage (absent also in the xenisthmid *Tyson*) and a fourth epibranchial, and in having the second pharyngobranchial subequal to or larger than the third. Of the gobioids examined, the arrangement of the dorsal elements in *Schindleria* resembles most closely that of the microdesmids. In most acanthomorphs and all other gobioids examined (except *Xenisthmus,* in which the second pharyngobranchial is reduced to a small edentate rod, Springer, 1983, fig. 11) the second pharyngobranchial is displaced so that all, or a major portion of it, lies lateral and/or ventral to the third. *Schindleria* and microdesmids are unusual in having the second pharyngobranchial fully anterior to the third, so that the posterior tip of the former articulates with the anterior tip of the latter.

Hyoid (Fig. 8B).—*Rhyacichthys,* odontobutids, xenisthmids, and eleotridids have the primitive gobioid complement of six branchiostegals, the first (anteriormost)

two relatively slender, the last four more bladelike. The first two articulate with the ventral margin of the narrow portion of the anterior ceratohyal, the next three articulate with the lateral surface of the expanded portion of the anterior cera- tohyal, and the last articulates with the lateral surface of the posterior ceratohyal. The remaining (higher) gobioids (gobiids, microdesmids and kraemeriids) have five branchiostegals, one slender one on the ventral margin of the narrow portion of the anterior ceratohyal separated by a distinct gap from the last four which are bladelike and articulate as described above. This arrangement infers that one of the first two branchiostegals in the primitive gobioid complement has been lost in higher gobioids. *Schindleria* shares the derived number of five branchiostegals with the latter group, but their arrangement is somewhat different. The first two articulate with the narrow portion of the undifferentiated ceratohyal and are separated by a slight gap from the more closely spaced posterior three. V. G. Springer (pers. comm.) suggested to us that this arrangement infers that *Schindleria* has lost the posteriormost branchiostegal of other gobioids (which normally ar- ticulates on the posterior ceratohyal), rather than one of the first two, i.e., that the five branchiostegal condition of *Schindleria* is not homologous with that of the higher gobioid clade. Although we cannot unequivocally reject Springer's hypothesis, we believe the evidence is ambiguous, because the configuration of the hyoid in *Schindleria* differs trenchantly from that of all other gobioids. The anteriormost two branchiostegals are not slender as in other gobioids but actually somewhat broader than the posterior three. Furthermore the anterior two artic- ulate with the lateral rather than ventral surface of the ceratohyal, and the posterior three articulate with processes on the ventral margin, rather than with the lateral surface. The ceratohyal is undifferentiated in *Schindleria,* so reference to narrow and deep portions of the anterior ceratohyal for purposes of homologising points of articulation is uncertain. We prefer the more parsimonious conclusion that the five branchiostegal condition of *Schindleria* is homologous with that of higher gobioids, because it is congruent with other evidence (see Synapomorphies) that places *Schindleria* with them.

Dorsal Fin (Fig. 5)—The dorsal fin of most gobioids has a posterior soft-rayed portion and a separate (continuous in a few groups) spinous portion anteriorly. Development proceeds from posterior to anterior, so that the soft-rayed portion is first to form. In a few gobioid genera, e.g., *Tyson, Leucopsarion,* and *Luciogobius,* the anterior spinous portion never develops (Birdsong et al., 1988), and the same is true for *Schindleria;* we have no other evidence to suggest that *Schindleria* is related specifically to one of these genera. Among the limited array of gobioids we have examined, the dorsal- and anal-fin pterygiophores of *Schindleria,* though uniquely configured, seem to resemble most closely those of microdesmids and certain gobiids (e.g., *Gobionellus*) in which there is consistent one-to-one corre- spondence with neural and haemal spines and the middle radials are frequently equal to or longer than the proximal radials, with the orientation between the two approaching a right angle. In *Schindleria,* the pterygiophores never ossify, and thus there is no actual separation between the proximal and middle radials; we assumed, for this comparison, that delineation between the two radials along each proximal-middle cartilage is located, as it is in other gobioids, at the point of contact of the preceeding distal radial. As in some xenisthmids (Springer, 1988) and microdesmids, all dorsal- and anal-fin rays are unbranched in *Schindleria.*

Supraneurals. —The absence of supraneurals in *Schindleria* could be the result of developmental truncation, however these elements normally form in cartilage quite early in ontogeny. All gobioids also lack supraneurals, a reductive special-

ization included by Winterbottom (1993) in his list of gobioid synapomorphies. Winterbottom noted that absence of supraneurals characterizes several of his putative gobioid sister groups, and they are also lacking in other perciforms such as scombroids, blennioids and zoarcoids.

Anal Fin (Fig. 11).—The anal fin of most gobioids and *Schindleria* has a single spine supported in supernumerary association with the first pterygiophore. In a few gobioid groups (e.g., microdesmids) the first element remains a soft ray (i.e., it fails to transform ontogenetically into a spine), but it is supported in the same way as in other gobioids. An uncommon and distinctive specialization shared by gobioids and *Schindleria* is that the single supernumerary fin ray always embraces a well-developed separate distal radial that is usually accommodated in a concavity in the ventral margin of the first anal pterygiophore (Springer, 1983, figs. 17–18, did not illustrate or describe the supernumerary distal radial in *Xenisthmus* or *Tyson,* but it is present in both). In all percoids and almost all other perciforms (trichonotids and creediids are two exceptions), distal radials are never associated with supernumerary fin rays of the dorsal or anal fin. As in many, but not all, gobioids, *Schindleria* has two anal pterygiophores anterior to the first haemal spine, and like all gobioids we have examined the first pterygiophore is approximately equivalent in size to the second. Neither of these conditions is unique among perciforms, but most percoids have a single, enlarged pterygiophore anterior to the first haemal spine.

Vertebrae (Fig. 9).—In most acanthomorphs, neural and haemal arches and spines form initially in cartilage and exhibit a characteristic pattern of ossification which, at one stage, gives the impression of a separate rod of cartilage impaled on an ossified flagellar extension of the ossifying neural or haemal arch (Potthoff, 1975; Fritzsche and Johnson, 1980; Potthoff et al., 1986, 1988: figs. 2–3). Gobioids we have examined do not exhibit this typical mode of development. They are unusual in that all neural and haemal arches and spines, except those of the second and third preural centra (see comparison of caudal skeleton below), do not form in cartilage but instead appear to ossify directly as membrane bone (sensu Patterson, 1977). The arches appear initially as tiny paired slivers of bone that eventually join at the midline and grow distally to form the spines. We cannot rule out the possibility that there is a cartilage component at earliest formation, but if so, it is relatively minor, and the developing neural and haemal elements never exhibit the usual acanthomorph configuration described above. The neural and haemal elements of *Schindleria* develop like those of gobioids, and we have not observed a similar pattern in other percomorphs, although the available comparative data are limited. Emilianov (1939) reported direct ossification of some or all vertebral arches in some representatives of several major teleostean groups, citing *Gobius* as the exceptional example among the acanthopterygians he examined. Faruqi (1935) described direct ossification of neural and haemal arches in *Gadus.*

Gobioids are also unusual in having pleural ribs that develop as membrane bone; they ossify directly (as opposed to the usual formation in cartilage) and thus appear relatively late in development, concomitantly with first appearance of the directly ossifying epipleurals (=epineurals, sensu Johnson and Patterson, 1993). This specialized feature of the pleural ribs, uncommon, but not unique among percomorphs, can be detected even in adults by the presence of pointed bony tips on the ribs, rather than the usual cylindrical cartilaginous tip. The failure of ribs to develop in *Schindleria* may reflect their relatively late ontogenetic appearance in gobioids, but this inference is speculative. Another uncommon, though not unique, feature of the vertebral column shared by *Schindleria* and gobioids is the

elongate first centrum, equal in length to the succeeding centra. In most acantho-morphs the first centrum is notably shorter than the others, and in some groups (e.g., blennioids) the anterior several centra may be relatively short. *Schindleria* and gobioids also share a neural arch that is fused to the centrum at its first appearance. Most percoids and many perciforms have an autogenous first neural arch, although fusion of the first neural arch commonly occurs.

Caudal Skeleton (Figs. 4G, H, 10).—Winterbottom (1993) considered two apo-morphies of the gobioid caudal skeleton and discussed their distribution among possible sister groups. The first, foreshortening of the parhypural so that it does not articulate with the ural centrum, is inapplicable to *Schindleria,* because the parhypural never develops (although this could be considered a further derived state of the gobioid condition). The second combines several specialized features—absence of uroneurals, fusion of hypurals 1 and 2, and fusion of hypurals 3 and 4 to one another and to the urostyle. *Schindleria* lacks uroneurals, but this is a predictable result of developmental truncation, and may or may not reflect com-mon ancestry. *Schindleria* has a further derived condition of the hypurals in which 1–4 are fused to one another and to the urostyle, and 5 is absent. Similar hypural fusion occurs in other gobioids, including xenisthmids, *Kraemeria* and *Trypau-chen.*

The primitive number of principal caudal fin rays in gobioids is 17 (9 + 8), however most gobioids have fewer. *Schindleria* has 13 (7 + 6), a number that characterizes many gobiids and some eleotridids. Procurrent rays in most gobioids and probably all gobiids are distinctively supported by elongate radial cartilages. Exceptions include *Rhyacichthys* and the odontobutids (Hoese and Gill, 1993, fig. 2A), wherein the radial cartilages are small and the anterior procurrent rays are unsupported. The typical gobioid arrangement is shared by *Schindleria.* Full support of procurrent rays by large radial cartilages is uncommon among other perciforms but does occur in several groups (e.g., blennioids, apogonids, ambas-sids).

The remarkably elongate urostyle of *Schindleria* has consistently caught the interest of those working on *Schindleria,* and the caudal skeleton thus has been illustrated numerous times (Giltay, 1934: fig. 3; Bruun, 1940: fig. 4; Gosline, 1959: fig. 6; Jones and Kumaran, 1964: figs. 2–3; Sardou, 1974: fig. 2). As noted pre-viously, Schindler (1932) and Gosline (1959) incorrectly interpreted the long urostyle as a segment of the notochord in which the usual vertebral segmentation had not occurred. There is no evidence to support that hypothesis, and it is, in fact, refuted by demonstration that the elements preceding the urostyle are the second and third preural centra, which develop distinctively in gobioids, as dis-cussed below.

As shown in previous illustrations of the caudal skeleton of *Schindleria,* but not described, the two centra preceding the putative urostyle lack the ossified styliform neural and haemal spines that characterize the other centra. In alcian-stained specimens it can be seen that these two centra bear, instead, thick blocks or plates of cartilage. Ironically, this seemingly very unusual feature provides some of the most convincing evidence of the gobioid affinities of *Schindleria,* but only through its comparison with the developing caudal skeleton of gobioids. As described above, gobioids are unusual in that the neural and haemal arches and spines on all but the last two or three centra (exclusive of urostyle) ossify directly quite early in development. In contrast, those of the second, third, and usually fourth preural centra appear initially as thick rods or blocks of cartilage, which then ossify gradually, so that a cartilaginous component may be evident very late

in development. As a consequence, the terminal region of the axial skeleton of larval gobioids is unique. It is easily recognized among all other larval teleosts we have examined in that there is an abrupt transition between the fourth and third preural centra from fully ossified, relatively styliform, neural and haemal elements to fully cartilaginous robust elements. Because ossification of these last three elements proceeds slowly, this abrupt transition remains apparent well after their ossification has begun. With this ontogenetic perspective, the caudal skeleton of *Schindleria* is no longer enigmatic. Though uniquely modified, particularly with respect to the extremely elongate urostyle, the preural region is clearly that of a larval gobioid. The second and third preural centra have only cartilage associated with them, the neural and haemal spines of the fourth preural centra are imbedded in cartilage (only in some specimens), and all preceeding neural and haemal elements are fully ossifed.

Pectoral Girdle (Fig. 12).—The pectoral girdle of *Schindleria* is unusual in several respects, and is obviously truncated developmentally. The coracoscapular and radial cartilages never ossify and the cleithrum and posttemporal are simple slivers of bone, all conditions characteristic of an early stage of development in acanthomorphs. Another distinctive feature is that all the pectoral-fin rays are supported along the distal margin of a paddle shaped radial cartilage, such that all of them, including the dorsalmost, are some distance posterior to the coracoscapular cartilage.

Winterbottom (1993) described five putative apomorphies of the gobioid pectoral girdle, mostly inapplicable to *Schindleria* because of the extreme developmental truncation. He was apparently unaware, however, of one of the most distinctive apomorphies of the gobioid pectoral girdle and fin, one that offers cogent evidence for the affinities of *Schindleria,* particularly when viewed ontogenetically.

In most teleosts four proximal pectoral radials, or actinosts, articulate proximally along the posterior margins of the scapula and coracoid and distally support all but the dorsalmost pectoral fin ray. The bases of the two halves of each fin ray, except the dorsalmost (and sometimes the ventral several) embrace an approximately spherical cartilaginous distal radial. Typically (though not true of all teleosts), the actinosts decrease in length dorsally, so that the fin rays gradually approach the posterior margin of the scapula, which lies just above the dorsalmost actinost. The dorsalmost (first) ray articulates directly with a condlye on the scapula and is modified accordingly; it is not associated with a separate distal radial and the base of its medial half is expanded laterally to form a complex articular facet. We find that the complexity of this characteristic association of the first pectoral-fin ray can best be appreciated from an ontogenetic perspective. Incipient rays are borne along the posterior margin of a plate-like radial cartilage in which the four actinosts eventually ossify. The margin of this radial cartilage curves forward so that its anterodorsal corner, and thus the first incipient ray, closely approaches the dorsal portion of the coracoscapular cartilage. At its earliest appearance the first ray is indistinguishable from the other rays, the bases of both halves being simple and flat. The two halves of this ray embrace what appears to be a cartilaginous distal radial, distinguishable, however, from the other distal radials in that it is substantially larger and is ovoid rather than spherical. We have been unable to resolve unequivocally the origin of this cartilaginous element, but it appears that rather than being part of the distal radial series it may originate as part of the coracoscapular cartilage. In any case, it soon fuses to the base of the medial half of the first ray, continues to grow laterally and eventually ossifies

to form the articular facet that abuts the scapular condyle. The medial half of this first ray usually serves as the sole site of insertion for the arrector ventralis muscle (Winterbottom, 1974).

Support of the pectoral fin in gobioids is quite different from that described above. In gobioids, the dorsalmost pectoral ray articulates with the posterior margin of the dorsalmost (first) actinost rather than with the scapula. Primitively (i.e., in *Rhyacichthys* and odontobutids), the scapula is relatively large with its posterior margin exposed above the first actinost, and the dorsalmost ray is in close proximity to the scapular margin, though not actually contacting it (see Winterbottom, 1993: fig. 5; Hoese and Gill, 1993: fig. 3A). In the remaining gobioids, however, the scapula is extremely reduced so that its posterior margin is fully occluded by the first actinost, and thus the dorsalmost ray is well removed from it. All gobioids also lack the articular facet at the base of the medial half of the dorsalmost ray, and most apparently lack the arrector ventralis muscle that normally inserts on that ray half, suggesting that the homolog of the first ray may have been lost (Grenholm, 1923; Gosline, 1980). In *Rhyacichthys* and the odontobutids, however, these is an arrector ventralis inserting on the dorsalmost ray, suggesting that the homolog of the first ray is still present, although it does not develop the articular base. Corroborating this surmise is the fact that there is no distal radial associated with this ray, as one would expect there to be if it represents the homolog of the second ray of most other teleosts (which is always associated with a distal radial). If absence of the arrector ventralis is correlated with absence of the first ray, one might predict that in those gobioids that lack this muscle, the dorsalmost (homolog of the second) ray would always be associated with a distal radial. However, our cursory survey indicates that gobioids lacking an arrector ventralis may or may not have a distal radial associated with the dorsalmost ray; a more extensive survey of the distribution of these two features is needed.

We have no ontogenetic information on the primitive gobioids mentioned above, but in those larval gobioids we have examined, the distinctive configuration of the pectoral girdle is recognizable from its earliest appearance. All fin rays are supported along the distal margin of the paddle-like radial cartilage (in which the four actinosts eventually ossify), and all, including the first are well removed from the very narrow scapulocoracoid cartilage. There is no ovoid cartilage associated with the first ray. Although the pectoral girdle of *Schindleria* differs from that of gobioids in lacking a supracleithrum and in having the coracoscapular cartilage continuous across the ventral midline, its configuration is otherwise clearly that of a developing goby.

The unusual condition of median continuity of the contralateral coracoscapular cartilages in *Schindleria* is not known to occur elsewhere among neoteleosts, although it characterizes larval clupeoids (Goodrich, 1922), larval *Elops,* and adults of the putatively neotenic *Sundasalanx* (Roberts, 1984). Based on limited evidence, Roberts (1984) proposed that *Sundasalanx* is related to the galaxioid family Salangidae and presumed (with no empirical evidence) that larval salangids have a continuous coracoscapular cartilage that is lost in adults. He further suggested that this condition is a primitive characteristic of larval teleosts. We conclude that the extremely limited distribution of a continuous coracoscapular cartilage among lower teleosts does not offer strong support for Roberts' suggestion. In any case, our limited survey of gobioid and other acanthomorph larvae indicates that the continuous coracoscapular cartilage of *Schindleria* is an autapomorphy. Functionally, it may offer protection for the heart and other viscera that would normally be provided by ossified cleithra. Among gobioids, larval microdesmids have what appears to be a structural analog in that the cleithra develop spatulate

expansions at their ventral tips that meet and tightly attach at the ventral midline; this bony intercleithral connection is lacking in adult microdesmids.

Synapomorphies

The following features are apomorphies shared by *Schindleria* and the members of the suborder Gobioidei. Some appear to be unique to these taxa; others, which characterize additional perciform families, may be more universally synapomorphic or independently derived for gobioids. They are included in the list, because they corroborate the hypothesis that *Schindleria* is a gobioid. Developmental characters have been documented in only a few gobioid genera including representatives of the Xenisthmidae, Eleotrididae, Gobiidae, and Microdesmidae but not *Rhyacichthys* and the Odontobutidae. Consequently, some specializations listed as synapomorphies of all other gobioids may also be shared by these two taxa and thus be synapomorphic for the Gobioidei. The last four characters are reductive apomorphies of gobioids also shared by *Schindleria,* but we cannot discount the possibility that in the latter they result from developmental truncation. 1) The sagittae and lapilli have elongate primordia (confirmed in *Rhyacichthys,* but unknown for odontobutids). 2) There are well-developed sperm duct glands in the testes. 3) Hypurals one and two are fused to one another, and hypurals three and four are fused to one another and to the urostyle (where ontogeny is known, hypurals 1–2 and 3–4 each develop as a single block of cartilage); *Schindleria,* like some other gobioids, is further derived in having hypurals one through four fused to one another and to the urostyle. 4) The first centrum is elongate and no shorter than the succeeding centra. 5) The first neural arch is fused to the first centrum (at its initial appearance where ontogeny has been examined). 6) The single supernumerary fin ray (usually a spine) on the first anal pterygiophore embraces a separate distal radial. 7) The dorsalmost pectoral ray articulates with the posterior margin of the dorsalmost actinost (or radial cartilage) rather than with the scapula; the medial half of this ray does not have an enlarged articular base and, in early ontogeny (where known), does not embrace an ovoid cartilage lying at the posterodorsal corner of the scapulocoracoid cartilage. 8) The interhyal does not articulate at the junction between the symplectic and the hyomandibular. 9) There are no supraneurals. 10) There are no parietals. 11) There is no basisphenoid. 12) There are never more than two infraorbitals.

Schindleria shares the following apomorphies with gobioids exclusive of the Rhyacichthyidae: 1) The hyomandibular is an irregular plate of bone (or cartilage) with no strut-like anteroventral arm, and, as a consequence, the symplectic is substantially longer than the hyomandibular. 2) The interhyal articulates at the posteroventral corner of the hyomandibular (usually with a cartilaginous process), well posterior to the symplectic-hyomandibular junction.

Schindleria shares the following apomorphies with gobioids exclusive of the Rhyacichthyidae and Odontobutidae (asterisk indicates condition not known for the latter two families): 1) The scapula is extremely reduced, and its posterior margin is fully occluded by the dorsalmost actinost (or dorsal portion of the radial cartilage), so that the dorsalmost pectoral ray is well removed from it. 2) The procurrent caudal-fin rays are supported by elongate radial cartilages. 3) Neural and haemal arches and spines ossify directly, except for those of the second, third, and fourth preural centra.* 4) The neural and haemal arches and spines of the second, third and sometimes fourth preural centra develop initially as robust cartilaginous structures; these structures then ossify gradually, except in *Schindleria* where they remain fully cartilaginous.* 5) In the larvae (retained in adult *Schindleria*) there is a conspicuous ovoid gas bladder near midbody capped with pigment dorsally.*

Schindleria shares the following reductive apomorphies with the Gobiidae, Microdesmidae, and Kraemeriidae, although their presence in *Schindleria* could be the result of developmental truncation. Those marked by an asterisk are also found in a few eleotridids and xenisthmids: 1) There are only five branchiostegals. 2) There is no mesopterygoid.* 3) There is no dorsal postcleithrum.*

Schindleria and gobiids share the following innovative apomorphies: 1) An anterior portion of the palatine articulates with the anterior surface of the mes-ethmoid or lateral ethmoid. In *Schindleria,* this is the only portion that develops. 2) The basihyal is spatulate, with a broad concave anterior margin (does not characterize all gobiids).

Schindleria shares the following putative apomorphy with the Microdesmidae: 1) The second pharyngobranchial lies fully anterior to the third, so that its posterior tip articulates directly with the anterior tip of the third (also true of *Xenisthmus,* where PB2 is highly modified as a long, curved, edentate rod).

The evidence presented above demonstrates conclusively that *Schindleria* is member of the Gobioidei, and suggests that its affinities may lie with the more derived families, the Gobiidae or perhaps the Microdesmidae (which may itself be derived from within the gobiids). Further resolution of the precise relationships of *Schindleria* is constrained by our limited knowledge of gobioid morphology and poor understanding of gobioid intrarelationships at most levels, confounded by extreme developmental truncation in *Schindleria,* which we document explicitly below. Despite its extraordinary paedomorphism, certain features of *Schindleria* are clearly peramorphic with respect to most other gobioids and these features may provide further morphological clues to the identity of its closest gobioid relatives. Although none of these features are known to occur in other gobioids, morphological details of many taxa remain univestigated. Putatively unique per-amorphic apomorphies of *Schindleria* include the following: 1) The urostyle is extremely elongate. This condition could be related to developmental truncation. In larval gobioids, (as well as many other perciforms), the urostyle is relatively longer than it is in adults, but no larval fishes are known to have a urostyle that is two to three times the length of the preceding centra, as it is in *Schindleria.* 2) The dorsalmost and ventralmost principal caudal-fin rays are relatively robust. This condition has not been reported in larval or adult gobioids. 3) The maxil-lovomerine meniscus is enlarged and apparently composed of hyaline cartilage. In most acanthomorphs, including gobioids, the maxillovomerine meniscus is a small biconcave disc of fibrocartilage. The hypertrophied meniscus that charac-terizes *Schindleria* has not been reported in larval or adult gobioids, but a similar structure is found in pegasids, ammodytids, phallostethids, some mugilids, and epigonids (Pietsch, 1984). 4) The second pharyngobranchial is subequal to or slightly larger than the third. In most acanthomorphs, including the larval and adult gobiids we have examined, the second pharyngobranchial is notably smaller than the third. 5) The contralateral coracoscapular cartilages are continuous across the ventral midline. Although this condition characterizes the larvae of a few primitive teleosts (e.g., *Elops,* clupeoids) it has never been reported in larvae or adults of any other acanthomorph, including gobioids. As noted above, in larval microdesmids the cleithra develop spatulate expansions at their ventral tips that meet and tightly attach at the ventral midline. This bony intercleithral connection, lacking in adults, might be viewed as functionally analogous to the continuous coracoscapular cartilage of *Schindleria,* but it is not structurally homologous.

Paedomorphism

The heterochronic phenomenon of paedomorphosis, or the expression in later developmental stages of features that characterize earlier stages ancestrally, may

well have played a more important role in the evolution of teleost fishes than we recognize. Because paedomorphic expression most commonly affects relatively few characters in any given taxon, it is not usually immediately obvious. As with all forms of heterochrony, its documentation requires comparative study of ontogenetic trajectories of individual characters in a phylogenetic context. Although such detailed and methodologically rigorous studies are few to date, one type of paedomorphosis, progensis (Gould, 1977), has been documented numerous times and is phylogenetically widespread among euteleost fishes. In progenesis, accelerated maturation without accelerated growth results in precocious developmental truncation, producing adults that are smaller than those of the ancestors. Because relatively small size in adults suggests the possibility of progenetic characteristics, this type of paedomorphism has been the most commonly proposed in fishes, although it has rarely been investigated rigorously. Extreme examples of progenesis, though rare, are immediately recognizable even in the absence of a phylogeny, because the resultant taxa are not only extraordinarily small, but are so profoundly truncated that they actually resemble larval stages. Winterbottom (1990) demonstrated how less extreme cases of progenesis can be identified within a precise phylogenetic framework, by outgroup comparison of character states in preterminal stages with those of similar sized adults.

Weitzman and Vari (1988) reviewed miniaturization in neotropical freshwater fishes, listing a total of 85 miniature species representing five orders and eleven families. By their criteria, small size and "numerous apparently paedomorphic morphological reductions," miniaturization invokes progenetic processes. However, for most of these species, phylogenetic hypotheses are unavailable, and thus explicit documentation like that of Winterbottom (1990) has not been done. Weitzman and Vari (1988) found the most common reductive features associated with miniaturization to be reductions in the laterosensory canal system of the head, numbers of fin rays and scales, and sculpturing on the head bones. In most cases, the reduction is not extreme, and these species generally resemble miniature adults of larger species.

There is no comparable review of miniaturization in marine fishes, although diminutive species are known in a number of groups. As is apparently the case for freshwater fishes, the degree of developmental truncation associated with extremely small sizes in marine fishes is not generally extensive and in some may be minimal. Reduced ossification and/or reductions in fin rays and scales have been documented in some diminutive marine gobioids (Springer, 1983, 1988; Winterbottom, 1990), but Johnson and Brothers (1989) found little evidence of paedomorphic expression in the smallest known chaenopsid blenny, which matures at less than 12 mm SL. On the one hand, one might expect progenetic miniaturization to elicit more obvious morphological manifestation in marine fishes, because most of them have planktonic larvae, which, unlike larvae of most freshwater fishes, may differ extraordinarily from the adults. However, with few exceptions, diminutive, putatively progenetic marine species do not remain in the plankton, and thus much of the early morphology would presumably be maladapted for the very different adult habitat. Radical progenesis in marine fishes, then, is rare.

Since its original description, the remarkably paedomorphic nature of *Schindleria* has never been questioned, even though its phylogenetic relationships have remained obscure. We believe it represents the most extreme example of progenetic developmental truncation known among fishes. Unlike most other diminutive fishes, *Schindleria* apparently remains in the water column throughout its life and retains numerous features universally characteristic of a larval stage of development.

Although limited evidence suggests that *Schindleria* is related to higher gobioids, we have no hypothesis about its precise generic relationships. Consequently we cannot make size-specific outgroup comparisons of ontogenetic trajectories and are thus unable to document progenetic truncation as rigorously as did Winterbottom (1990). Size comparisons are problematic in any case, because of the relative elongation of *Schindleria*. Size notwithstanding, we can demonstrate that *Schindleria* is paedomorphic in many characters with respect to other gobiids, based on an admittedly limited sample of their ontogenies. Other reductive characters, because they also characterize some gobiids, may be independently truncated in *Schindleria* or may be synapomorphic.

We list below features of *Schindleria* that appear to be the result of truncation of the typical ontogenetic trajectory of gobiids. Skeletal features are categorized by the bone types of Patterson (1977).

I. The following cartilage bones form in cartilage but never ossify: 1) major endoskeletal component of neurocranium, 2) anterior portion of autopalatine, 3) hyomandibular, 4) interhyal, 5) posterior ceratohyal, 6) hypohyal, 7) basihyal, 8) basibranchials 2–4, 9) hypobranchials 1–3, 10) ceratobranchial 5, 11) epibranchials 1–3, 12) pharyngobranchials 2–3, 13) pectoral radial cartilage, 14) scapulocoracoid cartilage, 15) dorsal- and anal-fin pterygiophores and 16) neural and haemal arches and spines of second and third preural centra.

II. The following cartilage bones show weak perichondral ossification, but little or no endochondral ossification: 17) symplectic, 18) quadrate, 19) anterior ceratohyal, 20) ceratobranchials 1–4, 21) hypural plate.

III. The following cartilage bones never develop: 22) metapterygoid, 23) ectopterygoid, 24) basibranchial 1, 25) pharyngobranchial 1, 26) pharyngobranchial 4, 27) interarcual cartilage (unossified in gobioids), 28) epibranchial 4, 29) ventral intercleithral cartilage (unossified in gobioids), 30) pelvic girdle, 31) spinous dorsal pterygiophores, 32) epurals, 33) fifth hypural and 34) parhypural.

IV. The following dermal bones never develop: 35) frontal, 36) vomer, 37) nasal, 38) lacrimal, 39) dermopalatine, 40) urohyal, 41) fourth upper pharyngeal toothplate, 42) subopercle, 43) interopercle, 44) preopercle, 45) supracleithrum, 46) pelvic-fin rays (correlated with absence of girdle), 47) dorsal-fin spines (correlated with absence of pterygiophores), 48) ventral postcleithra (dorsal absent in all gobiids, both absent in some) and 49) scales (not present in all gobiids).

V. The following dermal bones appear but exhibit an ontogenetically truncated configuration: 50) opercle (extremely small), 51) cleithrum (a needle-like splint), 52) posttemporal (a thin blade), 53) dorsal-, anal-, and pectoral-fin rays (unbranched and unsegmented).

VI. The following membrane bones never develop: 54) pleural ribs, 55) epineurals (sensu Johnson and Patterson, 1993) and 56) intercalar limb of posttemporal.

VII. The following are apparent ontogenetic truncations not associated with the skeleton: 57) transparent body largely devoid of pigment, 58) relatively large eyes, 59) sagitta a tiny, simple disc, 60) atrium posterior to ventricle and 61) conspicuous ovoid swimbladder near midbody capped with pigment dorsally.

It is perhaps no surprise that this apogee of progenesis among fishes would occur within the Gobioidei, a group in which numerous diminutive, putatively progenetic, species are known (e.g., *Tyson belos*, Springer, 1983; *Rotuma lewisi*, Springer, 1988) and in which several unrelated species have been proposed as the smallest (shortest) living vertebrates: *Mystichthys luzonensis* (Smith, 1902; Te Winkel, 1935), *Pandaka pygmaea* (Herre, 1929), *Lythrypnus elasson* and *L. elasson* (Smith and Tyler, 1972) and *Trimmatom nanus* (Winterbottom and Emery,

1981). With the knowledge that *Schindleria* is a member of the Gobioiodei, we can add to the "progenetic record book" of gobioids Bruun's (1940) proposal that *Schindleria* is the lightest vertebrate and the present documentation that it is the most radically ontogenetically truncated fish.

LITERATURE CITED

Arai, R. 1964. Sex characters of Japanese gobioid fishes (I). Bull. Nat. Sci. Mus. Tokyo 7: 295–306.

Birdsong, R. S., E. O. Murdy and F. L. Pezold. 1988. A study of the vertebral column and median fin osteology in gobioid fishes with comments on gobioid relationships. Bull. Mar. Sci. 42: 174–214.

Boehlert, G. W. 1984. Scanning electron microscopy. Pages 43–48 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Amer. Soc. Ich. and Herp., Spec. Publ. 1.

Breder, C. M., Jr. and D. E. Rosen. 1966. Modes of reproduction in fishes. Natural History Press, Garden City. 941 pp.

Brothers, E. B. 1984. Otolith studies. Pages 50–57 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Amer. Soc. Ich. and Herp., Spec. Publ. 1.

Bruun, A. F. 1940. A study of a collection of the fish *Schindleria* from south Pacific waters. Dana Rept. Carlsberg Found. 21: 1–12.

Campana, S. E. and J. D. Neilson. 1985. Microstructure of fish otoliths. Can. J. Fish Aquat. Sci. 42: 1014–1032.

Cole, K. S. 1990. Patterns of gonad structure in hermaphroditic gobies (Teleostei: Gobiidae). Environ. Biol. Fish. 28: 125–142.

Delsman, H. C. 1924. Fish eggs and larvae from the Java Sea. 3. A pelagic scombresocid egg. Treubia 5: 408–418.

Dingerkus, G. and L. D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Tech. 52: 229–232.

Egami, N. 1960. Comparative morphology of the sex characters in several species of Japanese gobies. J. Fac. Sci., Univ. Tokyo, Sec. IV, 9: 67–100.

Emilianov, S. V. 1939. Sequence in the ontogenetic appearance of vertebral arches in teleosts and the omission of chondral stages in their development. Compt. Rend. (Dokl.) Acad. Sci. U.S.S.R. 23: 978–981.

Faruqi, A. J. 1935. The development of the vertebral column in the haddock (*Gadus aeglifinus*). Proc. Zool. Soc. Lond., 1935, 2: 313–332.

Fritzsche, R. A. and G. D. Johnson. 1980. Early osteological development of white perch and striped bass with emphasis on identification of their larvae. Trans. Am. Fish. Soc. 109: 387–406.

Giltay, L. 1934. Notes ichthyologiques. VIII. Les larves de Schindler sont-elles des Hemirhamphidae? Mus. Roy. d'Hist. Nat de Belgique, Bull. 10, no. 13: 1–10.

Goodrich, E. S. 1992. On a new type of teleostean cartilaginous pectoral girdle found in young clupeids. J. Linn. Soc. London 34: 505–509.

Gosline, W. A. 1959. Four new species, a new genus, and a new suborder of Hawaiian fishes. Pac. Sci. 13: 67–77.

————. 1963. Notes on the osteology and systematic position of *Hypoptychus dybowskii* Steindachner and other elongate perciform fishes. Pac. Sci. 27: 90–101.

————. 1980. The evolution of some structural systems with reference to the interrelationships of modern lower teleostean fish groups. Jap. J. Ichthyol. 27: 1–28.

Gould, S. J. 1977. Ontogeny and phylogeny. The Belknap Press of Harvard Univ. Press, Cambridge. 501 pp.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman and G. W. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131: 339–456.

Grenholm, A. 1923. Studien uber die Flossenmuskulatur der Teliostier. Uppsala Universitets Ars-skrift, Matematik och Naturvetenskap 2: 1–296.

Herre, A. W. 1929. The smallest living vertebrate. Science 69: 79–80.

Hoese, D. F. 1984. Gobioidei: relationships. Pages 588–591 in H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Amer. Soc. Ich. and Herp., Spec. Publ. 1.

——— and A. C. Gill. 1993. Phylogenetic relationships of eleotridid fishes (Perciformes: Gobioidei). Bull. Mar. Sci. 52: 415–440.

Ida, H. 1976. Removal of the family Hypoptychidae from the suborder Ammodytoidei, order Perciformes, to the suborder Gasterostoidei, order Syngnathiformes. Jap. J. Ichthyol. 23: 33–42.

Johnson, G. D. and E. B. Brothers. 1989. Acanthemblemaria paula, a new diminutive chaenopsid (Pisces: Blennioidei) from Belize, with comments on life history. Proc. Bio. Soc. Wash. 102(4): 1018–1030.

——— and C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. Bull. Mar. Sci. 52: 554–626.

Jones, S. and M. Kumaran. 1964. On the fishes of the genus Schindleria Giltay from the Indian Ocean. J. Mar. Biol. Assoc. India 6(2): 257–264.

Leis, J. M. and D. Rennis. 1983. The larvae of Indo-Pacific coral reef fishes. New South Wales Univ. Press, Sydney, and Univ. Hawaii Press, Honolulu. 269 pp.

——— and T. Trnski. 1989. The larvae of Indo-Pacific shore fishes. New South Wales Univ. Press, Sydney. 371 pp.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal and C. E. Dawson. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resources collections in herpetology and ichthyology. Copeia 1985: 802–832.

Miller, P. J. 1984. The tokology of gobioid fishes. Pages 119–153 in G. W. Potts and R. J. Wooton, eds. Fish reproduction: strategies and tactics. Academic Press, London.

———. 1986. Reproductive biology and systematic problems in gobioid fishes. Pages 640–647 in T. Uyeno, R. Arai, T. Taniuchi and K. Matsuura, eds. Indo-Pacific fish biology. Tokai Univ. Press, Tokyo.

———. 1992. The sperm duct gland: a visceral synapomorphy for gobioid fishes. Copeia 1992: 253–256.

Mooi, R. D. 1990. Egg surface morphology of pseudochromoids (Perciformes: Percoidei), with comments on its phylogenetic implications. Copeia 1990: 455–475.

Nelson, J. S. 1976. Fishes of the world, 1st ed. John Wiley and Sons, New York. 416 pp.

———. 1984. Fishes of the world, 2nd ed. John Wiley and Sons, New York. 523 pp.

Patterson, C. 1977. Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton. Pages 77–121 in S. Mahala Andrews, R. S. Miles and A. D. Walker, eds. Problems in vertebrate evolution. Linn. Soc. Symp. Ser. 4. Academic Press, London.

Pietsch, T. W. 1984. Enlarged cartilages in the protrusible upper jaws of teleost fishes: phylogenetic and functional implications. Copeia 1984: 1011–1015.

Potthoff, T. 1975. Development and structure of the caudal complex, the vertebral column, and the pterygiophores in the blackfin tuna (Thunnus atlanticus, Pisces, Scombridae). Bull. Mar. Sci. 25: 205–231.

———, S. Kelley and J. C. Javech. 1986. Cartilage and bone development in scombroid fishes. Fish. Bull. 84: 647–678.

———, S. Kelley and L. A. Collins. 1988. Osteological development of the red snapper, Lutjanus campechanus (Lutjanidae). Bull. Mar. Sci. 43: 1–40.

Regan, C. T. 1912. The classification of the blennioid fishes. Ann. Mag. Nat. Hist. Ser. 8, 10: 265–280.

Roberts, T. 1984. Skeletal anatomy and classification of the neotenic asian salmoniform superfamily Salangoidea (icefishes or noodlefishes). Proc. Cal. Acad. Sci. 43: 179–220.

Sardou, J. 1974. Contribution a la connaissance de la faune ichthyologique Malgache: decourverte de poissons de la famille des Schindleriidae dans le canal de Mozambique, a Nosy-Be et etude d'une collection de Schindleria. Cah. O.R.S.T.O.M., Oceanog. 12(1): 3–15.

Schindler, O. 1930. Ein neuer Hemiramphus aus dem Pazifischen Ozean. Anz. Akad. Wiss. Wien 67: 79–80.

———. 1931. Ein neuer Hemiramphus aus dem Pazifischen Ozean. Anz. Akad. Wiss. Wien 6: 2.

———. 1932. Sexually mature larval hemirhamphidae from the Hawaiian Islands. Bull. Bernice P. Bishop Mus. 197: 1–28.

———. 1934. Beitrage zur Kenntnis der Niere mariner fischlarven. SitzBer Akad. Wiss. Wien. 143: 265–283.

Smith, C. L. and J. C. Tyler. 1972. Space resource sharing in a coral reef fish community. Pages 125–170 in B. B. Collette and S. A. Earle, eds. Results of the Tektite Program: ecology of coral reef fishes. Nat. Hist. Mus. L.A. County Sci. Bull. 14.

Smith, H. M. 1902. The smallest known vertebrate. Science 15(366): 30–31.

Springer, V. G. 1983. *Tyson belos,* new genus and species of western Pacific fish (Gobiidae, Xenisthminae), with discusions of gobioid classification. Smithson. Contrib. Zool. 390: 1–40.

———. 1988. *Rotuma lewisi,* new genus and species of fish from the southwest Pacific (Gobioidei, Xenisthmidae). Proc. Bio. Soc. Wash. 101(3): 530–539.

Takagi, K. 1950. On the glossohyal bone of the gobioid fishes of Japan, with some phylogenetic considerations. Jap. Jour. Ichthyol. 1: 37–52. (In Japanese, with English summary)

Te Winkel, L. E. 1935. A study of *Mistichthys luzonensis* with special reference to conditions correlated with reduced size. J. Morphol. 58(2): 463–535.

Watson, W. 1989. Schindleriidae—Schindler's fishes. Pages 270–273 *in* J. M. Leis and T. Trnski. The larvae of Indo-Pacific shore fishes. New South Wales University Press, Sydney, and University of Hawaii Press, Honolulu. 371 pp.

———, E. G. Stevens and A. C. Matarese. 1984. Schindleroidei: development and relationships. Pages 552–554 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Amer. Soc. Ich. and Herp., Spec. Publ. 1.

Weber, M. and L. F. de Beaufort. 1922. The fishes of the Indo-Australian Archipelago, Vol. IV, E. J. Brill, Ltd., Leiden: 410 pp.

Weitzman, S. H. and R. P. Vari. 1988. Miniaturization in South American freshwater fishes; an overview and discussion. Proc. Bio. Soc. Wash. 101(2): 444–465.

Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. Proc. Acad. Nat. Sci. Philad. 125: 225–317.

———. 1990. The *Trimmatom nanus* species complex (Actinopterygii; Gobiidae): phylogeny and progenetic heterochrony. Syst. Zool. 39: 253–265.

———. 1993. Search for the gobioid sister group (Actinopterygii: Percomorpha). Bull. Mar. Sci. 52: 395–414.

——— and A. R. Emery. 1981. A new genus and two new species of gobiid fishes (Perciformes) from the Chagos Archipelago, central Indian Ocean. Environ. Biol. Fishes 6:139–149.

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