

## Osteology of the Quillfish, *Ptilichthys goodei* (Perciformes: Zoarcoidei: Ptilichthyidae)

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The Quillfish, *Ptilichthys goodei*, is a slender, elongate fish distributed along the coastline of the North Pacific from Oregon to the Sea of Japan. It is the sole member of the monotypic family Ptilichthyidae, which is classified among the Zoarcoidei (eelpouts and their allies). Little is known of its osteology and there is much conflicting information in the literature regarding its morphology. In this paper we describe the skeleton of *Ptilichthys* based on newly collected and prepared specimens. Because of the small number and size range of our specimens, the emphasis of our study is on the juvenile skeleton, although the adult skeleton is also described as far as our material allows. We conclude by briefly discussing the phenomenon of axial elongation in *Ptilichthys*.

TARLETON H. Bean (1881) described a small, “serpentine” fish based on two specimens collected at Port Levasheff (now Captains Bay; Mecklenburg, 2003a), Unalaska (Aleutian Islands), under the name *Ptilichthys goodei*. A third specimen, from a dredging at 85 fathoms in Unalaska Harbor, was described by Gilbert (1896). At the time of its original description, Bean suggested tentatively that this species should be placed in the family Mastacembelidae. Jordan and Gilbert (1883) further proposed the monotypic subfamily Ptilichthyinae within Mastacembelidae. Gill (1885) soon suggested that *Ptilichthys* should be placed in its own family, Ptilichthyidae, “among the Blennioid series” (e.g., Jordan and Evermann, 1898: 2452), or the so-called “northern blennys” (e.g., Makushok, 1958; see Springer, 1993 for comments on the “unfortunate” use of this common name, as these fishes do not share a close relationship with Blennioidei). *Ptilichthys goodei* has remained the sole representative of the family Ptilichthyidae, which is now considered to be in the suborder Zoarcoidei (e.g., Springer and Anderson, 1997; Eschmeyer, 1998; Mecklenburg, 2003a). Zoarcoidei also includes the ronquils (Bathymasteridae), eelpouts (Zoarcoidei), pricklebacks (Stichaeidae), wrymouths (Cryptacanthodidae), gunnels (Pholidae), wolf-fishes (Anarhichadidae), the prowlfish (Zaproridae), and the graveldiver (Scytalinidae). Anderson (1994) included cryptacanthodids within Stichaeidae.

*Ptilichthys* inhabits the northern Pacific Ocean, ranging from Oregon north through the Bering Sea and west to the Sea of Okhotsk and the Sea of Japan (e.g., Kobayashi, 1961; Hart, 1973; Dokolovskaya and Sokolovskiy, 1995). Little is known of its natural history, but it is believed to be a near shore inhabitant,

spending the day burrowed in the sand and mud and then feeding near the surface at night; most specimens are taken at night near an attractant light (e.g., Clemens and Wilby, 1961; Hart, 1973; Mecklenburg, 2003a).

*Ptilichthys* is an extremely slender fish (Fig. 1; see also Lamb and Edgell, 1986: photo 70, for a photograph of a living specimen). The maximum recorded size is 390 mm SL, for a specimen recovered from the stomach contents of a gadid (Mecklenburg et al., 2002), although an incomplete specimen that we examined (USNM 119436) is estimated to have been 450 mm SL (it measures 410 mm with an incomplete tail). The lower jaw of *Ptilichthys* supports a large fleshy protuberance at the junction between the left and right rami of the lower jaw (Fig. 2A), giving the appearance of a greatly protruding lower jaw (in fact, the skeleton of the lower jaw only protrudes slightly; Fig. 2B). This protuberance, which begins to develop around 86.5 mm TL (Kobayashi, 1961), has been variously called a “mental barbel” (Regan, 1912:274) or a “fleshy tip” (Clemens and Wilby, 1961:367), but its function is unknown. The single naris on each side of the head is extended away from the head by a well-developed tube. The left and right opercular flaps join each other in the ventral midline, and insert dorsally onto the body at about the level of the middle part of the pectoral fin. The elongate dorsal and anal fins are continuous with the caudal fin. Clemens and Wilby (1961) mistakenly reported the caudal fin absent. The posterior tip of the tail supports an elongate post-ural caudal filament (Fig. 2C). *Ptilichthys* transforms from larva to juvenile at around 114 mm SL (Matarese et al., 1984). Data on its ontogeny are limited (e.g., Kobayashi, 1961; Richardson and DeHart, 1975), and much

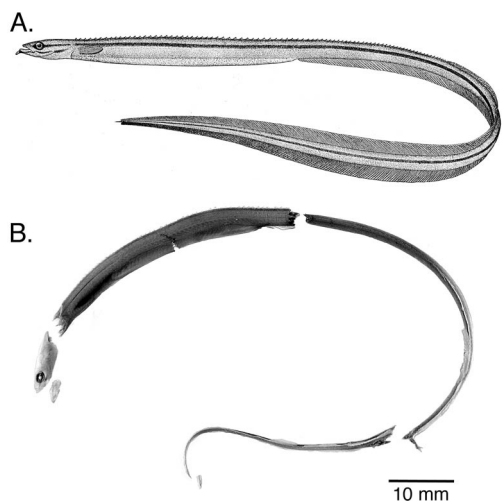


Fig. 1. *Ptilichthys goodei* Bean, 1881. (A) Illustration of holotype from Goode and Bean (1896:Fig. 304). (B) Photograph of holotype (USNM 26619, est. 155 mm SL).

of what is known was summarized by Matarese et al. (1984; see also Matarese et al., 1989).

*Ptilichthys* is poorly represented in collections, and it is therefore not surprising that little is known of its osteology. One of us (NJK) obtained a small juvenile specimen of *Ptilichthys* (FMNH 113542; 124 mm SL) while night lighting at Friday Harbor Laboratories (University of Washington, San Juan Island). This specimen was caught in mid-July, 2001 and kept in captivity in a sea table until mid-August, at which time it was preserved in formalin and cleared-and-stained. The most complete description of the skeleton of *Ptilichthys* was given by Makushok (1958), although many aspects of its osteology are omitted from his account and there is much conflicting information in the literature (e.g., Mecklenburg, 2003a). Because of the small number and size range of the specimens available, our study emphasizes the skeletal anatomy of small juvenile specimens that have just undergone metamorphosis and is based largely on two specimens (FMNH 112919 and FMNH 113542). Many of the other specimens that we prepared became partially disarticulated during the process of clearing and staining, particularly the bones of the skull (the musculature appears to have become extremely friable while in alcohol and responded poorly to enzyme treatment). We also had access to two adult cleared-and-stained specimens, although these specimens also became partially disarticulated during preparation or were found as such in collections. Many aspects of its osteology, partic-

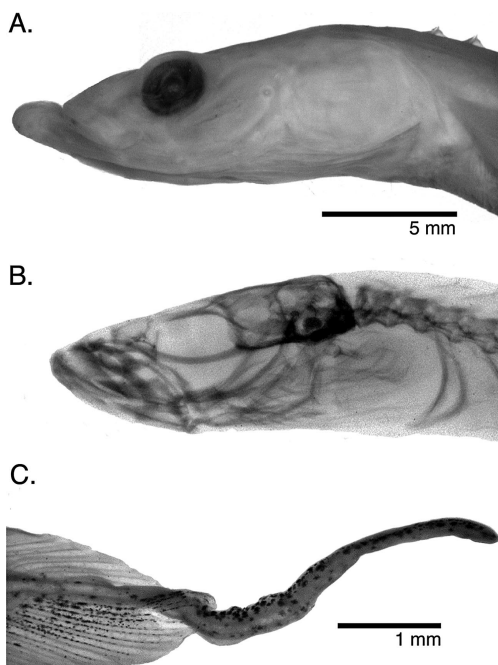


Fig. 2. *Ptilichthys goodei*. (A) Head of adult alcohol specimen (UW 027210, 294 mm SL) in lateral view, showing prominent fleshy protuberance of lower jaw. (B) X-ray of specimen shown in A. (C) Caudal filament of a juvenile alcohol specimen (FMNH 80675, 136 mm SL) in lateral view. Anterior facing left in all.

ularly of the adult skeleton, remain unknown. The paucity of osteological data available for *Ptilichthys*, however, prompts us to add our observations here.

#### MATERIALS AND METHODS

Specimens were cleared and double stained for bone (alizarin red-S) and cartilage (alcian blue 8-GX) following the method of Dingerkus and Uhler (1977), as modified by Hanken and Wassersug (1981). Specimens were examined with either a Wild M5 binocular microscope with a camera lucida attachment or a Wild Photomakroskop M400 binocular dissecting microscope and photographed digitally with a Nikon COOLPIX camera mounted onto the microscope. Line illustrations were drawn electronically using Adobe Illustrator software from digital images and camera lucida sketches.

We examined five cleared-and-stained (CS) specimens of *Ptilichthys* that represent a range of post-larval ontogenetic stages (see Material Examined). Additionally, several alcohol-stored specimens were measured and meristic data were collected. Some alcohol specimens were also x-rayed, and the radiographs were used to

determine vertebral and fin ray counts. Institutional abbreviations follow Leviton et al. (1985) with the addition of AB (Auke Bay Laboratory, National Marine Fisheries Service, Juneau, AK).

#### RESULTS

*Morphometrics.*—Head length (4.2–5.8% SL), pre-pectoral fin length (4.8–6.1% SL), and pre-dorsal fin length (4.4–5.5% SL) of *Ptilichthys* are all very similar in terms of percent standard length, averaging 5.2% SL ( $n = 11$ ), 5.7% SL ( $n = 10$ ), and 5.2% SL ( $n = 11$ ), respectively. The pre-orbital length (1.3–1.7% SL) averages 1.5% SL (29% of head length;  $n = 10$ ). The anal fin is set back on the body, with pre-anal fin length (27.9–30.6% SL) averaging 29.2% SL ( $n = 11$ ).

*Skull roof and neurocranium.*—The skull roof and neurocranium of adult *Ptilichthys* were described and illustrated by Makushok (1958:Fig. 82; see our Fig. 3). The skull roof is dominated by the paired frontals (Fig. 3), which comprise over half the total length of the skull roof. In our small juvenile specimens (Fig. 4), the anterior halves of the frontals meet in the midline, yet the posterior portions are widely separated and show irregular medial margins; in the adults the left and right frontals meet in the midline along most of their length (pers. obs., also Makushok, 1958; Fig. 3). Laterally, the frontals carry the supraorbital sensory canal (Fig. 4). Contrary to Makushok (1958), pterosphenoids are absent. What were labeled as pterosphenoids in his illustration (see Fig. 3) are ventral laminae from the lateral margin of the frontals. These laminae are deceptively similar to pterosphenoids in their position, although they were found to be continuous with the frontals even in small specimens (e.g., UW 027009). They are particularly well-developed in the adult (e.g., UW 16753) and broadly contact the parasphenoid ventrally. The paired nasals of our juvenile specimens are slender elements that are little more than ossified tubes surrounding the anteriormost extent of the supraorbital sensory canal; the preservation of our adult specimens does not allow us to determine the shape of the nasals, and they were not illustrated by Makushok (1958; Fig. 3). Between the left and right nasals is the mesethmoid, which ossifies in the ethmoid cartilage and extends posteriorly between the anterior tips of the left and right frontals. The paired lateral ethmoids also develop in the cartilage of the ethmoid region and form the posterior walls of the nasal capsules.

The paired autosphenotics and parietals and

the median supraoccipital contact the posterior margins of the frontals. The supraoccipital is an elongate bone, and its anterior portion is partially overlapped by the posterior portion of the frontals (Figs. 3A, 4A). The parietals are relatively small, squarish elements that contact the supraoccipital medially, the frontals anteriorly, the autosphenotics and pterotics laterally, and the epioccipitals posteriorly. Together with the prootics, the autosphenotics form the anterior articulatory surfaces for the hyomandibulae; the posterior articulatory surfaces for the hyomandibulae are completely within the ventral surface of the pterotics. The exoccipitals are large and form a complete arch over the foramen magnum. Posteriorly, they form the dorsolateral components of the occipital condyle. Ventrally, the exoccipitals are greatly expanded and contact the basioccipital. The basioccipital is centrum-like posteriorly, where it articulates with the first vertebral centrum. Anteriorly, it has a sharp median process that interdigitates with the posterior processes of the parasphenoid. The prootics are the largest bones on the ventral surface of the braincase, making contact with the parasphenoid, autosphenotics, and pterotics in the juvenile specimens (Fig. 4), but also the exoccipitals and basioccipital in the adult (Fig. 3B).

We were unable to identify an intercalar in our specimens of *Ptilichthys* (e.g., Fig. 4A–D), although Makushok (1958) illustrated one in his specimen (Fig. 3). In many zoarcoids, the intercalar is reduced in size, and this reduction is often coincident with a reduction in the size of the pectoral girdle (Gosztanyi, 1988). Because the posttemporal of *Ptilichthys* is very slender and completely lacks an anteroventral limb, the absence of an intercalar is not surprising but should be confirmed with additional specimens.

The dermal bones of the ventral surface of the neurocranium and ethmoid region of *Ptilichthys* include two median bones: the vomer and parasphenoid. The edentulous vomer is broadest anteriorly and tapers posteriorly to a sharp point. The parasphenoid is extremely long, running most of the length of the skull. It is broadest in its middle section, between the anterior ascending processes and the more posterior prootic processes. The posterior end of the parasphenoid is forked and embraces the median anterior process of the basioccipital.

*Infraorbital bones and sclerotic ring.*—The only infraorbital bone present in *Ptilichthys* is the lacrimal, which lies ventral to the lateral ethmoid and lateral to the suspensorium (Fig. 5). Although it is broad, this bone is very thin in our

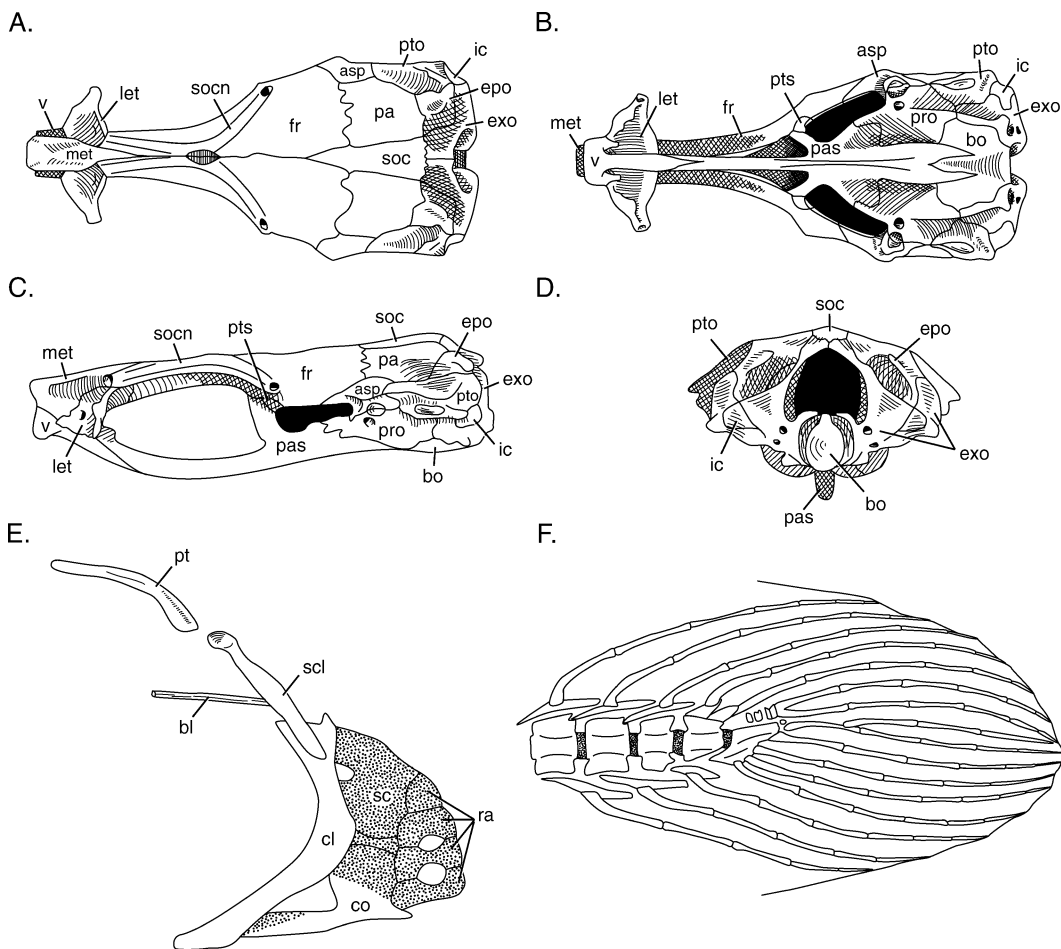


Fig. 3. Illustrations of the adult osteology of *Ptilichthys goodei*, redrawn, relabeled, and rearranged from Makushok (1958). (A) Dorsal, (B) ventral, (C) lateral, and (D) posterior views of skull roof and braincase. (E) Lateral view of pectoral girdle. (F) Lateral view of caudal skeleton and fin. Stipple indicates unossified portions. No lengths for the specimen(s) were provided by Makushok (1958), although he did indicate that the length of the skull was 11 mm (although likely, it is unclear if the illustrations of the other portions of the skeleton were drawn from the same individual). A, B, C, and D from Makushok (1958:Fig. 82); E from Makushok (1958: Fig. 81); F from Makushok (1958:Fig. 80). Note that we did not find an intercalar or a pterosphenoid in our specimens. Abbreviations: asp = autosphenotic, bl = Baudelot's ligament, bo = basioccipital, cl = cleithrum, co = coracoid, epo = epioccipital, exo = exoccipital, fr = frontal, ic = intercalar, let = lateral ethmoid, met = mesethmoid, pa = parietal, pas = parasphenoid, pro = prootic, pt = posttemporal, pto = pterotic, pts = pterosphenoid, ra = radial, sc = scapula, scl = supracleithrum, soc = supraoccipital, socn = supraorbital sensory canal, v = vomer.

juvenile specimens; it is more heavily ossified in our adult specimens. The lacrimal is most heavily ossified at the point at which it forms a facet for articulation with the lateral ethmoid. There is no trace of association with the lateral line system, but because the infraorbital lateral line in *Ptilichthys* is reduced overall, this is not surprising (other portions of the sensory canal system are "completely reduced"; e.g., Makushok, 1961). Other zoarcoids (e.g., stichaeids; pers. obs.) have a similar articulation with the lac-

rimal and the lateral ethmoid. Sclerotic cartilages and bones are absent in *Ptilichthys*.

*Jaws, suspensorium, and opercular series.*—The oral jaws of adult *Ptilichthys* were described and illustrated by Makushok (1958:Fig. 77); the suspensorium has not been illustrated until now (Fig. 5). The upper jaws of *Ptilichthys* consist of paired maxillae and premaxillae. The edentulous maxilla has a hooked posteroventral margin. Dorsally, there are two prominent articulatory pro-

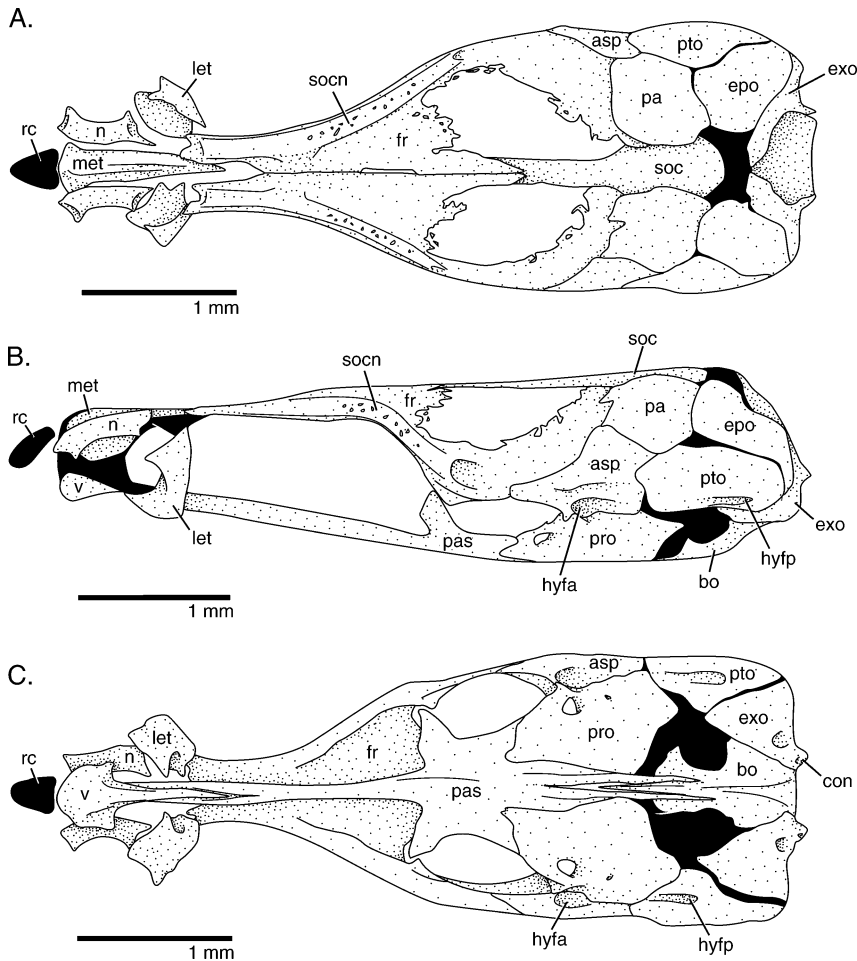


Fig. 4. Skull roof and neurocranium of a juvenile specimen of *Ptilichthys goodei*, FMNH 112919 (119 mm SL). (A) Dorsal, (B) lateral, and (C) ventral views; anterior facing left. Cartilages shown in black. Cartilages of ethmoid region based on FMNH 113542 and, except for the rostral cartilage, are shown only in lateral view. Abbreviations: asp = autosphenotic, bo = basioccipital, con = exoccipital portion of the occipital condyle, epo = epioccipital, exo = exoccipital, fr = frontal, hyfa = anterior articular surface of the hyomandibular, hyfp = posterior articular surface of the hyomandibular, let = lateral ethmoid, met = mesethmoid, n = nasal, pa = parietal, pas = parasphenoid, pro = prootic, pto = pterotic, rc = rostral cartilage, soc = supraoccipital, socn = supraorbital sensory canal, v = vomer.

cesses of the maxilla: a posterior process that is directed dorsally and slightly medioposteriorly and articulates with the rostral cartilage; and an anterior process that is directed anteriorly and articulates with the premaxilla. There is also a distinct extension lateral to the posterior process of the maxilla that serves as the attachment site of a ligament. The premaxilla has a prominent ascending process that is not in contact with its antimere. Dorsoposteriorly, the ascending processes curve laterally slightly on either side of the ethmoid cartilage. In FMNH 112919 and FMNH 113542 the premaxilla supports 18

to 24 teeth, the largest of which are positioned most anteriorly.

The lower jaw of *Ptilichthys* consists of Meckel's cartilage and four bony elements: the dentary; the anguloarticular; the retroarticular; and the coronomeckelian. The dentary is the largest of the bony elements of the lower jaw and bears a single series of strongly developed teeth along its dorsal margin (20–22 teeth in FMNH 112919 and FMNH 113542). The tips of the dentary teeth are distinctly hooked, particularly those more posterior in the series. The posterior margin of the dentary is strongly forked and sepa-

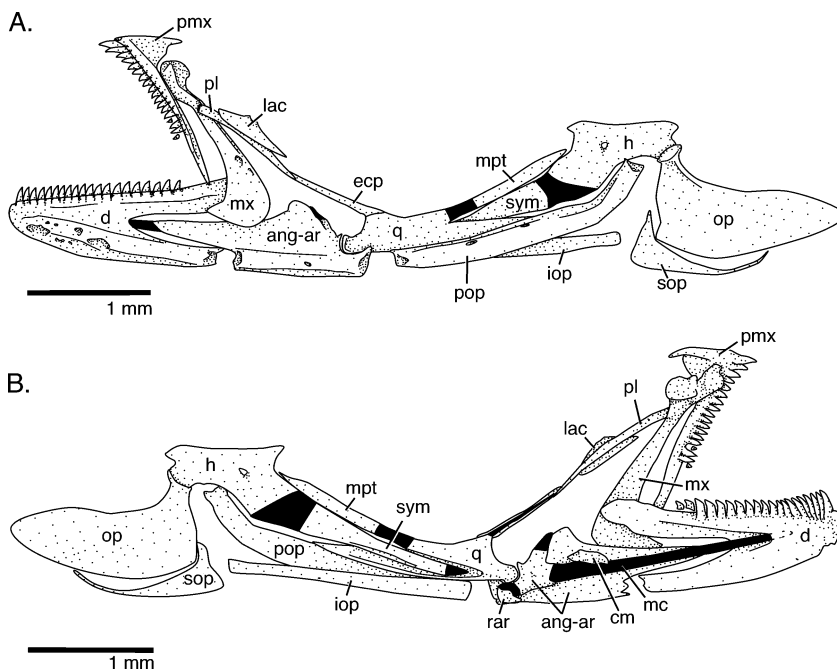


Fig. 5. Left suspensorium of a juvenile specimen of *Ptilichthys goodei*, FMNH 112919 (119 mm SL). (A) Lateral (anterior facing left), and (B) medial (anterior facing right) views. Note that the palatine in this specimen is displaced ventrally. Abbreviations: ang-ar = anguloarticular, cm = coronomeckelian, d = dentary, ecp = ectopterygoid, h = hyomandibular, iop = interopercular, lac = lacrimal, mc = Meckel's cartilage, mpt = metapterygoid, mx = maxilla, op = opercle, pl = palatine, pmx = premaxilla, pop = preopercular, q = quadrate, rar = retroarticular, sop = subopercle, sym = symplectic.

rated from the more posterior anguloarticular; this separation persists in the adult and is bridged by Meckel's cartilage (Fig. 5). The ventral portion of the dentary supports the anterior portion of the mandibular sensory canal.

The anguloarticular is the largest bone of the posterior portion of the lower jaw and comprises the dermal angular and the chondral articular. The angular portion of this bone supports the posterior portion of the mandibular sensory canal. There is an anterior elongation of the anguloarticular that fits into the forked posterior margin of the dentary (Fig. 5A). The articular portion of the anguloarticular forms the facet for articulation with the quadrate. The retroarticular is a small, separate ossification of Meckel's cartilage; this bone is separate even in adults. The coronomeckelian is a small, irregularly shaped bone that is positioned along the dorsal surface of Meckel's cartilage just anterior to the articular portion of the anguloarticular.

The hyomandibula has a broad dorsal articulatory head where it meets the neurocranium. The opercular articulatory head is angled posteroventrally. The main axis of the hyomandibula is oriented obliquely, contributing to the overall elongation of the suspensorium. In the

center of the hyomandibula there is a prominent foramen for the hyomandibular trunk of the facial nerve. The symplectic is also oriented obliquely and is more elongate than the hyomandibula. The anterior half of this bone rests in a deep concavity on the medial surface of the quadrate.

The palatoquadrate cartilage of *Ptilichthys* is persistent in our juvenile specimens and links the palatine, quadrate, and metapterygoid. The metapterygoid is the posteriormost bone of the palatoquadrate and lies anterodorsal to the hyomandibula and symplectic. The quadrate lies nearly parallel to the long axis of the skull and is closely associated with the symplectic. The posteroventral process of the quadrate is joined to the main body of the quadrate by a thin lamina of bone; this part of the quadrate forms the concavity that articulates with the symplectic. The dermal ectopterygoid contacts the anterodorsal part of the quadrate and lies lateral to the cartilaginous bridge between the quadrate and palatine. The palatine is an elongate bone that contacts the maxilla lateral to its posterior head. There is a slight curve to the anterior part of the palatine at the level of the lateral ethmoid. The anteriormost tip of the palatine is

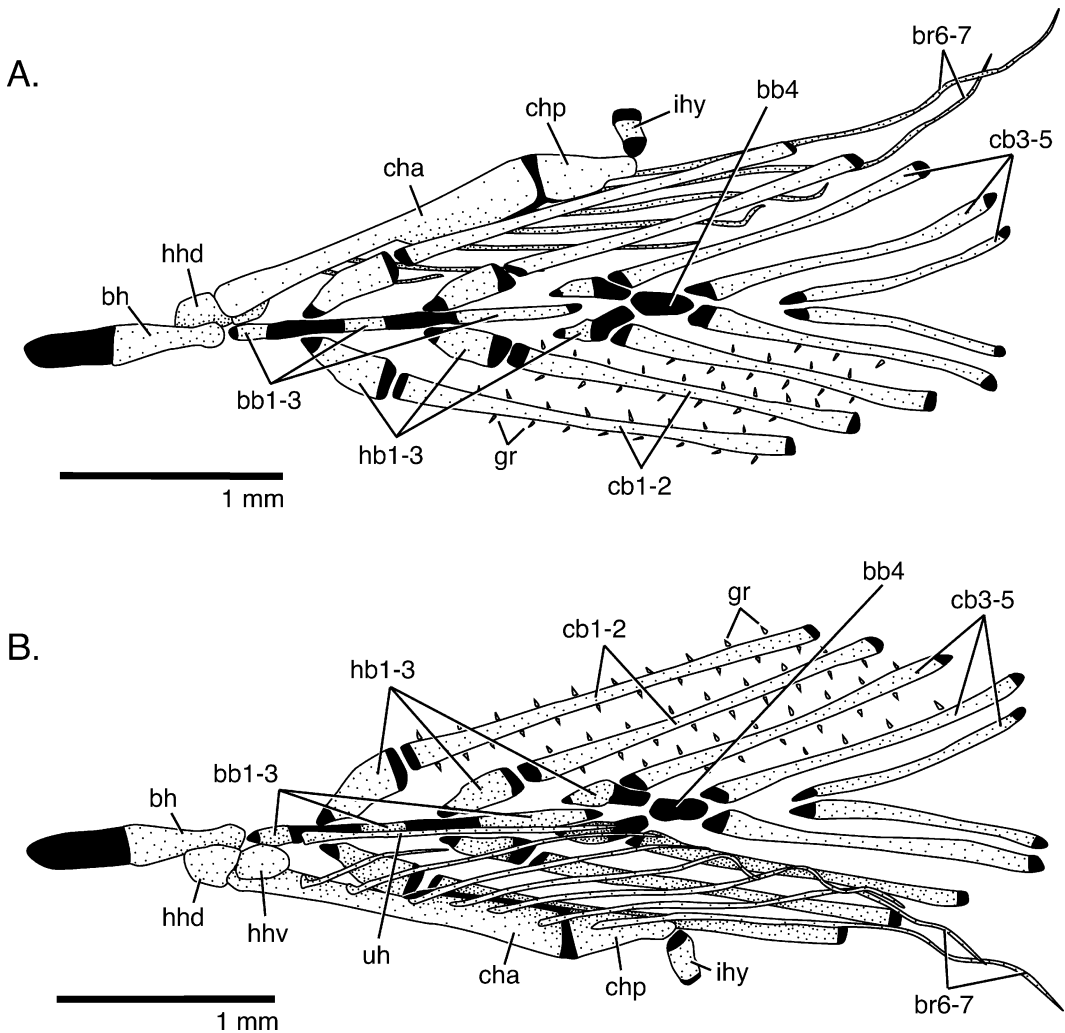


Fig. 6. Ventral gill arches and right ventral hyoid arch of a juvenile specimen of *Ptilichthys goodei*, FMNH 112919 (119 mm SL). (A) Dorsal (= oral) and (B) ventral views; anterior facing left. Abbreviations: bb = basibranchial, bh = basihyal, br = branchiostegal, cb = ceratobranchial, cha = anterior ceratohyal, chp = posterior ceratohyal, gr = gill rakers, hb = hypobranchial, hhd = dorsal hypohyal, hhv = ventral hypohyal, ihy = interhyal, uh = urohyal.

cartilaginous. The endopterygoid is absent in *Ptilichthys*, as was reported by Makushok (1958).

The opercular bones of *Ptilichthys* have not been illustrated previously. The preopercle is little more than an ossified tube surrounding the preopercular sensory canal. The opercle is slightly falcate in shape in our juvenile specimens, but the dorsal margin is straighter in our adult specimens. The subopercle is a sickle-shaped element. The interopercle is a thin strip of bone that lies on the medial surface of the preopercle, although its posterior half is visible in lateral view as well (Fig. 5A). The branchiostegals are extremely elongate and thread-like, particularly the more posterior ones (Fig. 6).

There are seven branchiostegals on each side of the two specimens for which they could be counted reliably; the anterior ceratohyals support five each, and the posterior ceratohyals support two each. Makushok (1958) reported only three in his specimens, although this is likely in error (he noted that his material was poorly preserved; Makushok, 1958:114, p. 97 of English translation).

*Ventral portion of the hyoid arch and the gill arches.*—The ventral hyoid arch and the gill arches of *Ptilichthys* have not been illustrated until now (Figs. 6, 7). The ventral hyoid arch consists of a median basihyal, paired dorsal and ventral hy-

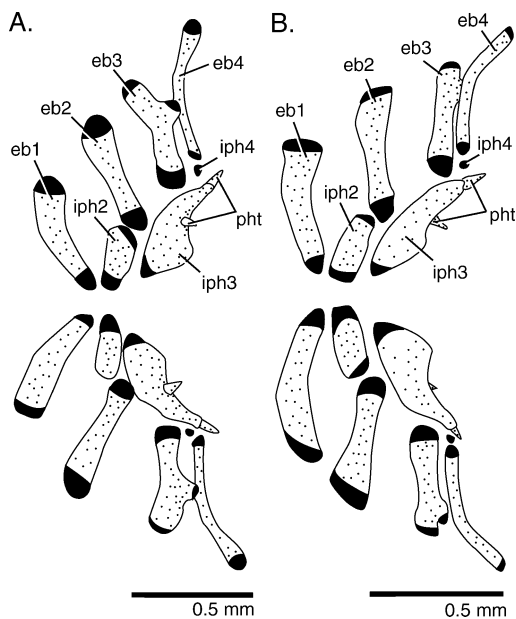


Fig. 7. Dorsal gill arches of a juvenile specimen of *Ptilichthys goodei*, FMNH 112919 (119 mm SL) in (A) ventral (= oral), and (B) dorsal views; anterior facing left. Abbreviations: eb = epibranchial, iph = infrapharyngobranchial, pht = pharyngeal teeth.

pohyals, anterior and posterior ceratohyals, and interhyals; all of these elements are ossified. The anterior ceratohyal is the largest element of the ventral hyoid arch and is hatchet-shaped in lateral view, with a deep posterior portion and a narrow anterior portion. The posterior ceratohyal is roughly triangular in shape and articulates with the interhyal. Both the anterior and posterior ceratohyals support the branchiostegals, which are described above.

The urohyal is extremely elongate and lies ventral to the anterior basibranchial copula. The anterior portion of the urohyal is well-separated from the basihyal and hypohyal elements.

The ventral portion of the gill arches consists of a median basibranchial skeleton and paired series of hypobranchials and ceratobranchials (Fig. 6). The basibranchial skeleton of the gill arches consists of two copulae (e.g., Nelson, 1969:480). In FMNH 112919, the anterior basi-

branchial copula supports three distinct basibranchial ossifications (= bb1–3), although the presence of bb1 could not be confirmed in other specimens (e.g., FMNH 113542). The posterior basibranchial copula (= bb4) is not ossified. The ceratobranchials are highly elongate bars that support the gill rakers.

The dorsal portion of the gill arches comprises four pairs of epibranchials and three pairs of infrapharyngobranchials (Fig. 7). The four epibranchials are simple bars of bone; eb1 is the shortest, and eb4 is the longest. Infrapharyngobranchial 3 is the largest element of the dorsal branchial arches, and bears two teeth. The posterior tooth is oriented posterolaterally and is in line with the long axis of iph3. The anterior tooth is directed ventromedially and is positioned along the medial margin of iph3 at about its midpoint. Infrapharyngobranchial 4 is represented by a small nodule of cartilage that is intercalated between iph3 and eb4 (Fig. 7). We only found iph4 in FMNH 112919; FMNH 113542 was not dissected to examine this character.

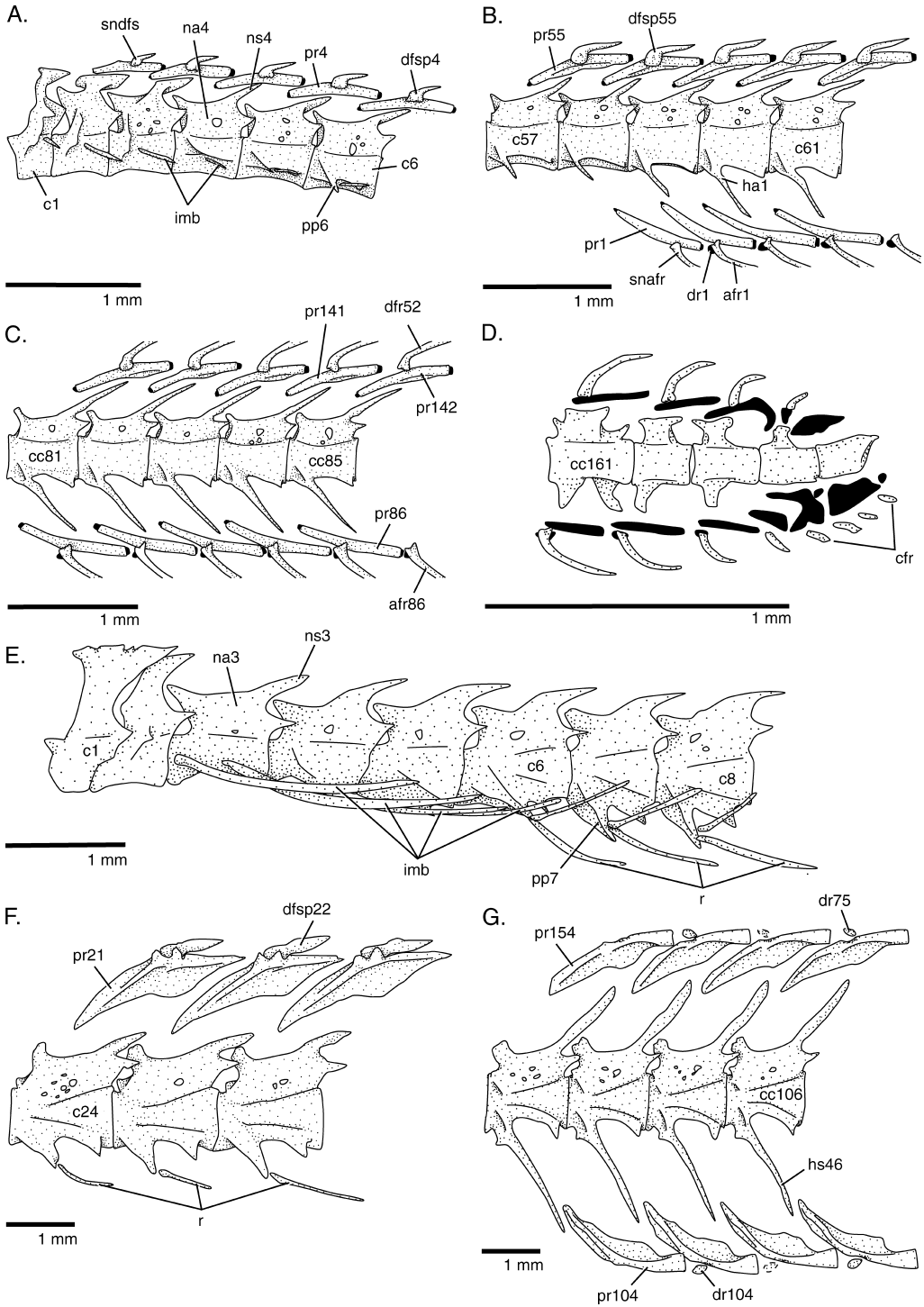
The gill rakers of *Ptilichthys* are simple in form and are widely spaced along the anterior and posterior margins of each gill arch (Fig. 6). Gill rakers are restricted to the ventral portions of the gill arches.

*Vertebral column.*—Matarese et al. (1984:table 147; see also Mecklenburg, 2003a), citing data from Makushok (1958), give the range of total vertebrae of *Ptilichthys goodei* as 227–240, with 53–59 abdominal vertebrae and 170–181 caudal vertebrae. For our two complete cleared-and-stained specimens (FMNH 112919 and FMNH 113542), vertebral counts were 57 + 166 = 223 and 55 + 167 = 222, respectively (25–26% abdominal). The large alcohol specimen that was x-rayed (UW 027010) has 53 + 170 = 223 total (24% abdominal). A small segment of the abdominal vertebral column was illustrated by Makushok (1958:Fig. 79), although his figure is very diagrammatic, and no details are provided. The vertebrae of *Ptilichthys* are shown in Figure 8.

The centra of *Ptilichthys* are elongate, spool-shaped elements that have an anterior constriction around the notochord, as was noted by

Fig. 8. Post-cranial axial skeleton of *Ptilichthys goodei*. (A) Anterior vertebrae and dorsal fin elements of a juvenile specimen. (B) Abdominal and caudal vertebrae, and dorsal and anal fin elements of a juvenile specimen. (C) Caudal vertebrae and dorsal and anal fin elements of a juvenile specimen. (D) Terminal caudal vertebrae of a juvenile specimen. (E) Anterior vertebrae of an adult specimen showing elongate anterior intermuscular bones (first is associated with c2; first ribs associated with c6). (F) Abdominal vertebrae and





dorsal fin supports of an adult specimen. (G) Caudal vertebrae and dorsal and anal fin supports of an adult specimen. All are shown in lateral view with anterior facing left. A–D, FMNH 112919 (119 mm SL); E–G, UW 16753 (204 mm SL). Abbreviations: afr = anal fin ray, c = abdominal centrum, cc = caudal centrum, cfr = caudal fin ray, dfr = dorsal fin ray, dfsp = dorsal fin spine, dr = distal radial, ha = haemal arch, hs = haemal spine, imb = intermuscular bone, na = neural arch, ns = neural spine, pp = parapophyses, pr = proximal radial, r = rib, snafr = supernumerary anal fin ray, sndfs = supernumerary dorsal fin spine.

Makushok (1958) and Yatsu (1986). The neural arches, parapophyses, and haemal arches are fused to the centra. Each neural arch is the length of its associated centrum. The lateral surfaces of the neural arches are marked by a variable number of foramina. The neural arches bear short anterior and posterior zygapophyses, which articulate with those of adjacent vertebrae. The neural spines, which incline posteriorly from the posterior edges of the neural arches, are relatively short anteriorly on the body, but gradually elongate at about the abdominal-caudal boundary. The parapophyses are moderately elongate and extend ventrolaterally from the anteriormost portion of the centrum. Makushok (1958) noted that the parapophyses begin on the fifth centrum in *Ptilichthys*. There are, however, ridges more dorsally on c1–4 that are likely small rudimentary parapophyses (Fig. 8A). The parapophyses are continuous with a wing-like bony lamina that extends ventrolaterally from the posterior portion of the centrum. These posterior laminae continue along most of the length of the body (continuous with the haemal arch in caudal vertebrae). The haemal arches are restricted to the anterior portion of the centra and are very narrow compared to the neural arches. The haemal spines are elongate along most of the length of the caudal region. The neural and haemal arches and spines become irregular near the posterior end of the caudal region (e.g., Fig. 8D).

In *Ptilichthys*, there is a series of short, slender ribs. The ribs begin relatively far back on the axial skeleton (on c6 in the specimen illustrated in Fig. 8E) and were only found in our two largest cleared-and-stained specimens (AB 69–50 and UW 16753). Makushok (1958) found ribs beginning on c5 in his specimens of *Ptilichthys*. These bones are associated with the tips of the parapophyses proximally and are oriented obliquely posteroventrally.

There is a series of intermuscular bones present in *Ptilichthys*. The proximal ends of some of these bones (= epineurals of Patterson and Johnson, 1995, Johnson and Patterson, 2001; = epicentrals of Gemballa and Britz, 1998) contact the proximal tips of the ribs (Fig. 8E). The series begins far forward on the axial skeleton (c1 on the specimen in Fig. 8A; c2 on the specimen in Fig. 8E). Anteriorly, the intermuscular bones are relatively high on the centra and are oriented posteroventrally (e.g., Fig. 8A). More posteriorly, however, the proximal tips of the intermuscular bones “migrate” ventrally, to near the parapophyses. Consequently, intermuscular bones posterior to vertebrae five or six are oriented more posterodorsally (e.g., Fig. 8E). In

the adult specimens the anterior intermuscular bones are elongate (Fig. 8E). These are in a similar position to the “epicentrals” of *Melanostigma* illustrated by Yarberry (1965:Fig. 7).

*Caudal fin and supports.*—The caudal fin and skeleton of *Ptilichthys* were described and illustrated by Makushok (1958:Fig. 80; see Fig. 3F). The caudal filament (Fig. 2C), which is supported by a post-ural extension of the notochord (e.g., USNM 306358), was reported to begin to form at 108 mm TL (Dokolovskaya and Sokolovskiy, 1995) and is well-developed by 144.6 mm TL (Kobayashi, 1961). It is present and well-developed in some of our specimens (e.g., Fig. 2C). Unfortunately, most available specimens are damaged or incomplete at their caudal tip, thereby limiting our description.

Only our two small cleared-and-stained specimens (e.g., FMNH 112919, Fig. 8D) are sufficiently complete to allow description of the internal caudal skeleton (differences in ontogenetic stages likely are responsible for at least some of the differences between Makushok’s 1958 illustration of the adult condition and that presented here; cf. Fig. 3F and Fig. 8D). The terminal vertebral centrum is slightly upturned and its concave posterior surface reflects the spool-like shape of the centrum. In FMNH 112919, there are no neural or haemal arches associated with this centrum (Fig. 8D). In contrast, in FMNH 113542 there is a small neural arch at the anterior end of the terminal centrum, and an irregularly shaped rod of cartilage lies partially inside the posterior concavity of this centrum. It is probable that the terminal centrum of FMNH 113542 represents a fusion of the last two centra found in FMNH 112919 (Fig. 8D). This hypothesis is supported by the presence of irregularly shaped cartilages, which are perhaps the parhypural and hypurals, that lie ventral to the last two centra in FMNH 112919; these are ventral to only the last centrum of FMNH 113542 (in which the posteriormost element is partially ossified). We were unable to describe the caudal skeleton of our adult specimens. Although complete posteriorly, the hypurals were too faint to be interpreted on our x-ray of the large adult alcohol specimen (UW 027010).

*Dorsal and anal fin and supports.*—The pterygiophores of the dorsal and anal fin in *Ptilichthys* consist of a series of elongate, ossified proximal radial elements (= fused proximal + middle radials) and a series of small, spherical distal radial elements (Fig. 8) that ossify in adults (e.g., UW 16753); distal radials are restricted to the

soft portion of the fins. Earlier ontogenetic stages of *Ptilichthys* are needed to determine if the proximal elements represent a true ontogenetic fusion of independent radials. The anteriormost proximal radial lies between the neural spines of c1 and c2 (between c3 and c4 according to Makushok, 1958). The median distal radials of the dorsal fin are restricted to the pterygiophores that support the soft fin rays and are absent from all pterygiophores supporting spines (the support of the posteriormost fin spine also was found to have a small distal radial in FMNH 113542). The proximal radials that support the dorsal fin spines are slightly curved centrally. This curve becomes filled in by a bony lamina in the adult (Fig. 8F, G). The fin spines and soft rays articulate with both the distal radial of its pterygiophore (soft fin rays only) and the middle portion of the proximal radial of the next posterior pterygiophore (i.e., they are in supernumerary association with the proximal radials; see Britz and Johnson, 2002:25–26). Makushok (1958) noted that a ligamentous connection between the posteriormost spine-bearing radial and the first soft fin ray in the dorsal fin (present in most “stichaeoids”) is absent in *Ptilichthys*.

In *Ptilichthys*, there are 70–90 dorsal fin spines and 115–148 dorsal fin rays (Mecklenberg, 2003a); in our sample the number of dorsal fin spines ranged from 84–90 (mean = 87; n = 9) and dorsal fin rays ranged from 130–143 (mean = 136; n = 7). In our two best-preserved and prepared cleared-and-stained specimens, FMNH 112919 and FMNH 113542, there are 89 and 87 fin spines, respectively, and both have 130 soft fin rays; all of the fin rays are unsegmented. There is a single supernumerary dorsal fin spine (Patterson, 1992) in FMNH 112919; in FMNH 113542 there is a small, rudimentary proximal radial anterior to the first full proximal radial and therefore there is no supernumerary spine in this specimen. We were unable to determine the number of supernumerary spines in our other cleared-and-stained specimens.

The anal fin of *Ptilichthys* comprises only soft fin rays (unique among Makushok’s “stichaeoids”). Mecklenburg (2003a) reported 166–196 anal fin rays, but counts from USNM 104368 and USNM 130266 extend the lower end of the range to 153. There is a single supernumerary anal fin ray in some specimens (e.g., Fig. 8B). An x-ray of UW 022359 indicates that the anteriormost anal fin ray is associated with a small, irregularly rod-shaped radial. This radial, which is absent in some specimens (e.g., FMNH 113542) has a different shape than the

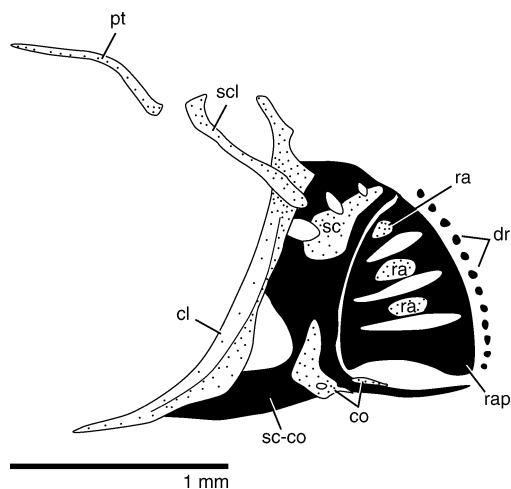


Fig. 9. Left pectoral girdle and fin supports of a juvenile specimen of *Ptilichthys goodei*, FMNH 113542 (124 mm SL) in lateral view. Note that the pectoral fin rays have been omitted. Anterior facing left. Abbreviations: cl = cleithrum, co = coracoid, dr = distal radial, pt = posttemporal, ra = radial, rap = radial plate, sc = scapula, scl = supracleithrum, sc-co = scapulocoracoid cartilage.

following proximal radials, which are as shown in Fig. 8G. Makushok (1958) noted that *Ptilichthys* lacks a ligament between the proximal radial and the next posterior fin ray.

*Pectoral girdle, fin, and supports.*—Makushok (1958:Fig. 81) illustrated the pectoral girdle of an adult *Ptilichthys*. There are 13 pectoral fin rays in *Ptilichthys* (Makushok, 1958; pers. obs.). The pectoral fin inserts onto the body at an oblique angle, with the dorsal insertion notably anterior to the ventral insertion.

The dermal bones of the pectoral girdle of *Ptilichthys* include a posttemporal, supracleithrum, and cleithrum (Fig. 9) and neither the posttemporal nor the supracleithrum carry a sensory canal. The posttemporal has a simple shape and does not contact either the skull or the more ventral elements of the girdle, but rather floats in soft tissue. The supracleithrum and cleithrum also have very simple shapes and only loosely articulate with each other. The cleithra are the largest dermal elements of the pectoral girdle, are gently curved throughout their length, and bear a prominent medial flange. The left and right cleithra are separated ventrally, or make only weak contact. Postcleithra are absent.

The endochondral portion of the pectoral girdle includes the scapula and coracoid. In juvenile specimens, the ventral portion of this car-

tilage bears an elongate posteroventral process (Fig. 9; not illustrated by Makushok, 1958, see Fig. 3, but this is likely due to different ontogenetic stages of the illustrated specimens, as this is a common structure in early ontogenetic stages of percomorphs). Directly supporting the pectoral fin are four radials (= actinosts) and 12 distal radials, one per fin ray except for the dorsalmost. Makushok (1958) and Anderson (1984) reported in error that the radials (actinosts) do not ossify in *Ptilichthys*. In the specimen illustrated in Figure 9, the independent radials of the adult have not completely differentiated from the radial plate and only three have begun to ossify.

*Pelvic girdles, fins, and supports.*—These elements are entirely absent in *Ptilichthys*.

*Scales.*—We found no trace of scales in *Ptilichthys*, although it is possible that scales are deeply embedded in the skin, and this should be checked in new material. Bean (1881:157) originally described the body of *Ptilichthys* to be “covered with very thin scattered scales.” Goode and Bean (1896:302), in their description of the family Ptilichthyidae, which they regarded as monotypic, reported that scales are absent. However in their account for the genus *Ptilichthys*, they reported that the body is “apparently covered with very thin, scattered scales.” Regan (1912) concluded that *Ptilichthys* lacks scales completely. Makushok (1958:Fig. 78) illustrated a small patch of scales posterior to the pectoral fin, although these illustrations are not very detailed and no description was provided in the text.

#### DISCUSSION

*Limitations of this study.*—During the course of this study, we discovered that specimens of *Ptilichthys* are rare in museum collections and that many of these specimens were not easily prepared as quality cleared-and-stained specimens. Indeed, it was those specimens that were collected, preserved, and cleared-and-stained all within a relatively short time that yielded the best results (FMNH 112919 and FMNH 113542). Future studies should be made of additional newly collected specimens to confirm or expand upon our descriptions. For example, we did not find an intercalar in our specimens, even in the two largest specimens (AB 69–50, UW 16753). This needs to be confirmed in better preserved and prepared adult material, as our study was based largely on juvenile specimens.

Mecklenburg (2003a) suggested that there may be significant clinal variation or undescribed taxonomic variation of *Ptilichthys* across its range, citing the broad ranges for meristic variation in dorsal fin spines, soft dorsal and anal fin rays, and vertebral counts. Because our few specimens are from only the coast of North America, we could not address these issues.

*Comments on interrelationships.*—Nelson (1994:388) noted that “no known diagnostic character or simple combination of characters... distinguish [Zoarcoidei] from the other blennylike perciforms. The monophyly of this taxon and most of its families is uncertain.” Anderson (1994), however, listed three synapomorphies of Zoarcoidei, including *Ptilichthys*: 1) loss of basisphenoid; 2) loss of posterior nares; and 3) medial portion of A2, 3 division of adductor mandibulae is posterior to the levator arcus palatini. Anderson (1984:Fig. 1) suggested that *Ptilichthys* is the sister group of the group (Zaproridae (Anarhichadidae (Stichaeidae (Pholidae, Scytaliniidae))) based on a single synapomorphy: the presence of 15 or more dorsal fin spines; he also listed a number of autapomorphies for the genus. The reductive nature of the skeleton of *Ptilichthys* (e.g., absence of the pelvic girdle and fins, loss of a bony articulation between the pectoral girdle and skull, an incomplete cephalic lateral line sensory canal system, absence of the intercalar and pterospheoid, a very simple caudal skeleton, etc.) will make difficult the search for morphological characters useful for systematic analyses.

*Axial elongation in Ptilichthys.*—One of the most striking features of *Ptilichthys* is its extremely slender and elongate “serpentine” body (Bean, 1881). Axial elongation in *Ptilichthys* appears to have evolved through an increase in vertebral number. Although the exact magnitude of this increase cannot be determined because the phylogenetic interrelationships within Zoarcoidei remain poorly understood (e.g., see Anderson, 1984, 1994), the extraordinarily high number of vertebrae in *Ptilichthys* (222–240) clearly represents a derived condition. With the exception of *Anarrhichthys*, which has a similar number of vertebrae to that of *Ptilichthys* (221–251; Mecklenburg, 2003b), all other species currently recognized within Zoarcoidei have fewer than 150 vertebrae, and many have fewer than 100 (e.g., Mecklenburg, 2003a–g; Anderson and Federov, 2004; Mecklenburg and Sheiko, 2004). Moreover, vertebral counts in Bathymasteridae, generally considered to be the sister group to all other zoarcoids (e.g., Anderson, 1984; a view

also supported by Imamura and Yabe, 2002), range only between 46 and 55 (Matarese et al., 1984; Mecklenburg, 2003a).

In *Ptilichthys*, the number of abdominal vertebrae is known to range between 53 and 59, whereas most other zoarcoids have fewer than 40 abdominal vertebrae (Makushok, 1958; Matarese et al., 1984; Anderson, 1994), indicating an increase in the absolute number of abdominal vertebrae in *Ptilichthys*. However, as a percent of the total number of vertebral segments, *Ptilichthys* has a much smaller abdominal region (24–26% abdominals in our specimens) than other zoarcoids (e.g., see Makushok, 1958:app. 2) and a much longer caudal region (i.e., approximately 75% of total vertebrae are caudals). At the other extreme, pholids are unique among zoarcoids in that there are roughly 50% abdominals and 50% caudals (Makushok, 1958; pers. obs.), possibly due to the development of haemonephrapophyses in the abdominal vertebrae (e.g., Yatsu, 1981, 1986). Therefore the number of caudal vertebrae has increased dramatically in *Ptilichthys* and elongation of its axial skeleton occurs primarily as a result of an increase in the number of caudal vertebrae, a pattern also characteristic of zoarcids (e.g., Asano, 1977) and nearly all other elongate acanthomorph fishes.

When considered in the broader context of teleostean fishes in general, the high vertebral counts exhibited by *Ptilichthys* appear even more striking. Although some elopomorphs have more than 240 vertebrae (e.g., Notacanthidae, Ophichthidae, Nemichthyidae, Nettastomidae, Saccopharyngidae; Nelson, 1994), with an excess of 500 vertebrae in some nemichthyids (e.g., Beebe and Crane, 1937), such high vertebral counts are extraordinarily rare. In fact, the only acanthomorphs that we are aware of that have more than 220 vertebrae are the zoarcoids *Anarrhichthys ocellatus* (e.g., Mecklenburg, 2003b) and *Ptilichthys*.

#### MATERIAL EXAMINED

The following specimens of *Ptilichthys* were examined and are indicated as alcohol stored specimens (a) or cleared-and-stained skeletons (CS); standard lengths (SL) are provided: AB 69–50 (1 CS; est. 200 mm SL; specimen is 192 mm but tail is incomplete); AB 91–17 (1 CS; SL unknown; a disarticulated transforming juvenile); FMNH 80675 (2 a; 136–150 mm SL; x-rayed); FMNH 112919 (1 CS; 119 mm SL); FMNH 113542 (1 CS; 124 mm SL); USNM 104368 (4 a; 112–132 mm SL); USNM 026619 (1 a; est. 155 mm SL; holotype); USNM 130266

(1 a; 237 mm SL); USNM 60910 (1 a; 333 mm SL); USNM 119436 (1 a; est. 450 mm SL; 410 mm preserved but tail is incomplete); UW 027009 (1 CS; est. 135 mm SL, specimen is 126 mm but tail is incomplete); UW 16753 (1 CS; 204 mm SL); UW 022359 (1 a; 346 mm SL); UW 027010 (1 a; 294 mm SL; x-rayed).

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