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Authors: BRITZ, RALF, and KOTTELAT, MAURICE

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Descriptive Osteology of the Family Chaudhuriidae (Teleostei, Synbranchiformes, Mastacembeloidei), with a Discussion of Its Relationships

RALF BRITZ[1] AND MAURICE KOTTELAT[2]

ABSTRACT

The little known earthworm eel family Chaudhuriidae consists of nine small to minute species of Asian freshwater fishes. In this paper, the osteology of seven representatives of the family is described in detail for the first time. We propose a list of 21 synapomorphies to support chaudhuriid monophyly. Reductive characters are: loss of basisphenoid, pterosphenoid, endopterygoid, dermopalatine, pars autopalatina, posttemporal, gill rakers, toothplate on pharyngobranchial two, distal pectoral radials, lateral line canals, dorsal- and anal-fin spines and their supporting pterygiophores, epurals, uroneurals, parhypural, and reduction in numbers of epicentrals and hypurals. Progressive characters are: presence of a long membrane bone process on autosphenotic, a boomerang-shaped ectopterygoid with a long preorbital extension, an anterior process of membrane bone of the metapterygoid, a unique arrangement of dorsal gill arch elements, separate foramina for the three trigeminal branches, and a ventromedian keel on the first vertebra. The new information is used to critically reevaluate previous hypotheses of chaudhuriid relationships. Finally, the issue of miniaturization in chaudhuriid fishes is addressed and discussed.

[1] Lehrstuhl für Spezielle Zoologie, Universität Tübingen, Auf der Morgenstelle 28, 72076 Tübingen, Germany; and Research Associate, Department of Ichthyology, American Museum of Natural History. Present address: Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington, DC, 20560. e-mail: britz.ralf@nmnh.si.edu

[2] Case postale 57, 2952 Cornol, Switzerland. e-mail: mkottelat@dplanet.ch

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INTRODUCTION

Chaudhuriidae, or earthworm eels, comprise small to minute, eel-like freshwater fishes (fig. 1) distributed in Southeast Asia. They usually live among dense vegetation in standing or slowly flowing waters (Kottelat and Lim, 1994; Kerle et al., 2000). Currently, the family consists of the following nine species in six genera: *Chaudhuria caudata* Annandale, 1918; *Chaudhuria fusipinnis* Kottelat and Britz in Kottelat, 2000; *Pillaia indica* Yazdani, 1972 (fig. 1); *Pillaia kachinica* Kullander, Britz, and Fang, 2000; *Garo khajuriai* Talwar, Yazdani, and Kundu, 1977; *Nagaichthys filipes* Kottelat and Lim in Kottelat, 1991; *Chendol keelini* Kottelat and Lim, 1994; *Chendol lubricus* Kottelat and Lim, 1994; *Bihunichthys monopteroides* Kottelat and Lim, 1994.

The family Chaudhuriidae was erected by Annandale (1918) for the small eel-like fish, *Chaudhuria caudata*, from Lake Inle, Burma. He classified it along with the true eels in the order Apodes, as did Whitehouse (1918). Soon thereafter, Regan (1919) hypothesized a close relationship between the families Chaudhuriidae and Mastacembelidae (spiny eels), a view further supported by Annandale and Hora (1923).

More than 50 years passed until a second species of chaudhuriid was described, *Pillaia indica* (Yazdani, 1972), which was subsequently placed in a separate new family Pillaiidae (Yazdani, 1976). Talwar et al. (1977) described a second species of *Pillaia*, *P. khajuriai*, transferred four years later to a new genus *Garo* by Yazdani and Talwar (1981). Annandale (1918), Whitehouse (1918), and Annandale and Hora (1923) provided more cursory remarks regarding osteology, but Travers (1984a, 1984b) published the first comprehensive osteological description of Chaudhuriidae and Pillaiidae and reviewed their phylogenetic relationships with Mastacembelidae. Travers (1984a, 1984b) considered the differences between *Chaudhuria*, *Pillaia*, and *Garo* insufficient to keep them in different genera and families and therefore united the three species in *Chaudhuria*, family Chaudhuriidae. Strangely, Yazdani (1990) did not discuss or even cite Travers' (1984a, 1984b) two papers and, as in his earlier publications, without justification placed the three genera in two families, Chaudhuriidae and Pillaiidae, the latter containing *Garo* and *Pillaia*. Travers' (1984b) synonymization of the three chaudhuriid genera was criticized by Kottelat and Lim (1994) who retained *Pillaia* as a valid genus. Subsequently, Kullander et al. (2000) presented evidence for the validity of *Garo*.

Travers (1984b) concluded that the three chaudhuriid species known at that time formed a monophyletic lineage with the mastacembelid *Sinobdella* (as *Rhynchobdella*) *sinensis* and transferred the latter taxon from Mastacembelidae to Chaudhuriidae. Travers' (1984b) changes were criticized by Kottelat (1991) and Kottelat and Lim (1994). Johnson and Patterson (1993) reported problems with Travers' (1984b) characterization of the Chaudhuriidae, and Britz (1996), reinvestigating Travers' (1984b) hypothesis of a monophyletic Chaudhuriidae including *Sinobdella*, demonstrated that the latter genus is a plesiomorphic mastacembelid rather than a chaudhuriid.

Travers' (1984a, 1984b) osteological studies were based only on two, and Britz' (1996) account only on one, of the nine chaudhuriid species because additional material of the remaining taxa was not available, and some of the species were not described at that time. Recent extensive collections of well-preserved specimens of chaudhuriids from different areas in Southeast Asia yielded the opportunity to study the osteology of representatives of this poorly known family. Our investigation has several objectives. First, we provide a detailed description of the skeleton of seven of the nine species of Chaudhuriidae as a reference work for future studies. We then utilize this new information to critically reevaluate and discuss the characters that Travers (1984b) listed as synapomorphies for Chaudhuriidae and Mastacembeloidei. Finally, we address the issue of miniaturization in chaudhuriid fishes, when compared to their closest relatives, the mastacembelids and synbranchids. A phylogenetic analysis of chaudhuriids is beyond the scope of this paper and will be dealt with in a forthcoming publication.

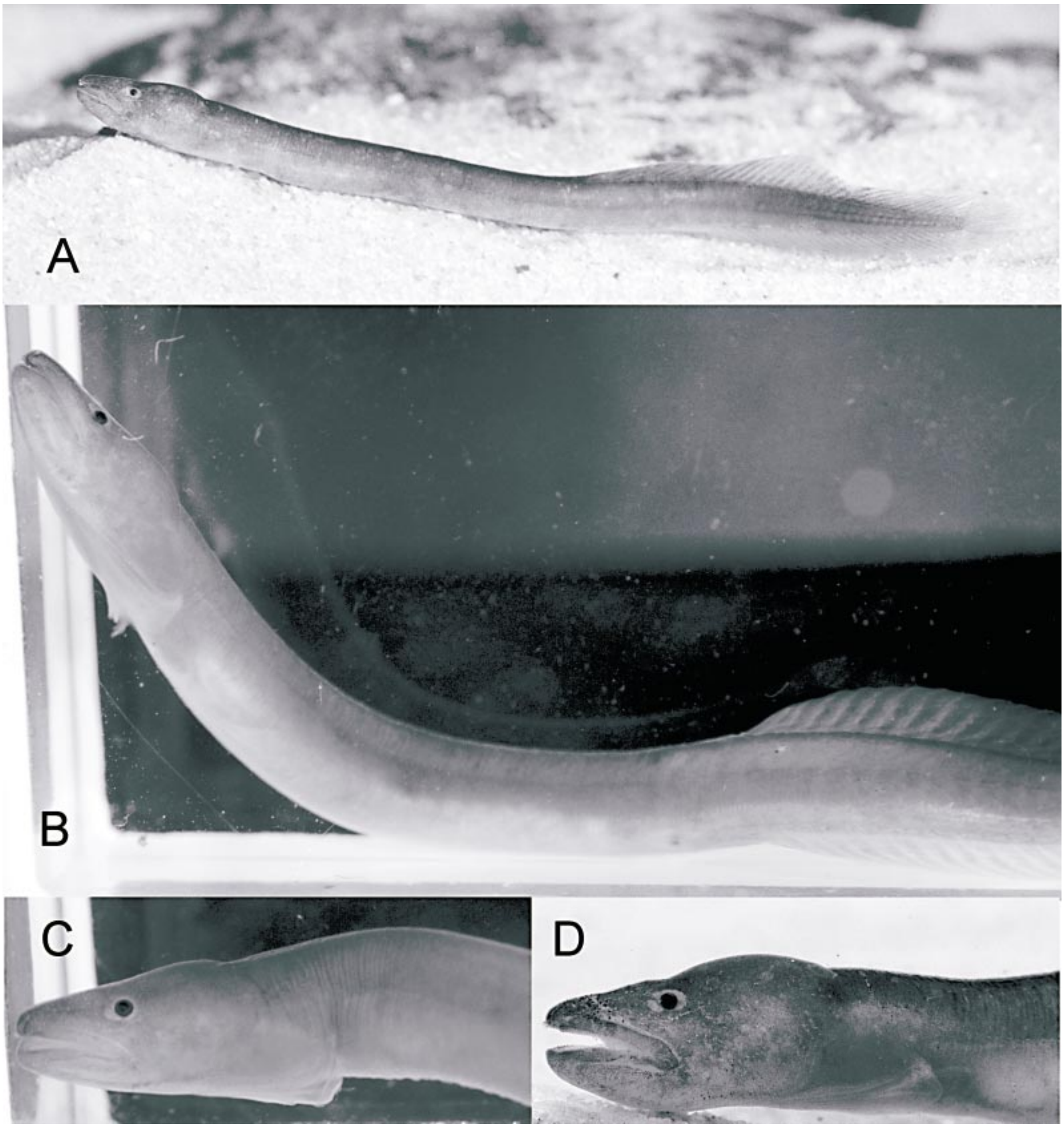

Fig. 1. *Pillaia indica*, live individuals. **A.** Adult male, ca. 80 mm. **B.** Subadult male, ca. 65 mm. **C.** Close-up of head of same specimen. **D.** Close-up of adult male, ca. 85 mm. Note absence of rostral tentacle.

MATERIALS AND METHODS

Our study is based on the following cleared and double-stained (C&S) material, provided length is standard length (SL): *Bihunichthys monopteroides*: AMNH 217765 (1, 42 mm), CMK 7947 (2, paratypes, 31–36 mm), ZRC 16835–847 (2, disarticulated); *Chaudhuria caudata*: AMNH 217415 (1, 40 mm), CMK 7934 (1, 52 mm), CMK 8241 (6, 34–38 mm), CMK 5510 (1, disarticulated), CMK 15965 (6, 26.5–42.7 mm); *C. fusipinnis*: CMK 15967 (6, paratypes, 29.7–36.5 mm); *Chendol keelini*: AMNH 217795 (10, 7.5–65 mm), CMK 7949 (1, paratype, 44.2 mm), ZRC 17779 (1, ca. 49 mm); *C. lubricus*: CMK 10638 (2, paratypes, 38.2–50 mm); *Nagaichthys filipes*: CMK 6660 (1, paratype, 30.8 mm), CMK 9601 (1, 27 mm), CMK 10870 (2, 25–28 mm), CMK 11387 (1, 28.5 mm); *Pillaia indica*: USNM 372577 (1, 85.8 mm), USNM 372577 (1, 61 mm). Fin ray counts reported in table 6 for *Nagaichthys filipes* are based on additional alcohol specimens: CMK 11267 (6, 20.7–27.6 mm), CMK 10870 (2, 25.5–26.4 mm), CMK 9601 (1, 29.4 mm), CMK 10623 (1, 26.0 mm), CMK 16683 (2, 16.6–20.6 mm), CMK 16705 (3, 27.3–29.0 mm), CMK 16723 (1, 31.2 mm), CMK 16718 (3, 25.3–27.4 mm).

Cleared-and-stained representatives of mastacembelid and synbranchid taxa used as comparative material: *Macrognathus pancalus*: AMNH 217414 (8, 4.5–36 mm); *Mastacembelus erythrotaenia*: AMNH 42129 (1, 277 mm); *M.* sp. (incorrectly labeled as *Macrognathus aculeatus*): AMNH 097654 (1, 158 mm). *Macrotrema caligans*: MCZ 47107 (2, 172–178 mm); *Monopterus albus*: AMNH 41579 (1, 167 mm); *Ophisternon aenigmaticum*: AMNH 31573 (1, 72 mm); *Synbranchus marmoratus*: AMNH 30213 (1, 142 mm), MCZ 52376 (3, 65–140 mm; 1, disarticulated).

We were able to include in our study representatives of seven of the nine described chaudhuriid species. Because of scarcity of material we could not investigate specimens of *Garo khajuriai* and *Pillaia kachinica*. Some additional remarks on the material are pertinent. We cannot be certain that all our material from different areas in Southeast Asia listed as *Chaudhuria caudata* is conspecific with *C. caudata* from Inle Lake, Burma. Although we tried hard, we were not successful in obtaining material of this taxon from the type locality, Lake Inle, from our own collecting there or loans from the Zoological Survey in India.

For his osteological study of the three species known at his time, Travers (1984a, 1984b) had specimens of *Pillaia indica* and *Chaudhuria caudata*, but not of *Garo khajuriai*. Concerning *Chaudhuria caudata*, he studied three specimens, two from BM(NH) that he listed as types (Travers, 1984a: 8) and that were stained with alizarin only and one from MCZ that was double stained. It is unlikely that the three specimens from BM(NH) are actually types because Annandale (1918) mentioned only four specimens in the type series. The BM(NH) material rather seems to have come from additional specimens of *Chaudhuria caudata* that Annandale and Hora collected during a second trip to Lake Inle in 1922 and that were used in part for Annandale and Hora (1923). This interpretation is in accordance with the information provided in the online catalog of the British Museum. There, only one specimen (BMNH 1920.1.20.1) is listed as paratype of *C. caudata*, and those specimens cited by Travers as types (BMNH 1923.3.10.1–4) have no such status. It is unfortunate that Travers (1984a) did not specify if the three C&S specimens agreed in all the characters that he described for *C. caudata* because it is still unclear if the Thai and Burmese populations are conspecific. However, because he did not mention any differences among the specimens, it may be assumed that no major differences existed. Travers' (1984a) MCZ specimen (MCZ 47058) was collected in Thailand. We could not compare Travers' (1984a) description with this specimen to clarify discrepancies we encountered between his description of *C. caudata* and our own material, because it now lacks its head.

We are also not certain if our specimens of *Pillaia* (fig. 1) actually belong to the species *P. indica*. They came from a local ornamental fish exporter in Coochbehar in Western Bengal and were purportedly collected not far from this locality. The locality for the holotype and three of the paratypes of *P. indica* is Sumer stream of the Khasi and Jaintia Hills 22 km north of Shillong (at 1068 m altitude), and the fourth paratype came from a stream at Umshing 13 km north of Shillong (at 1524 m altitude). Both these localities are about 240 km from the area of Coochbehar, the source of our specimens. The specimens of *Pillaia* at our disposal, however, can be clearly assigned to this genus on the basis of a single element in the upper jaw (fused maxilla and premaxilla?). They also do not differ substantially in the characters provided in the original description of *P. indica* (Yazdani, 1972), and we therefore consider them to be conspecific with that species. However, we are unable to explain significant differences between the osteological features we observed in our specimens and those described by Travers (1984a). These differences will be addressed below. Of the two specimens of *P. indica* that Travers (1984a: 43) had on loan from the Zoological Survey of India, the larger specimen (68 mm) was ‘‘poorly preserved and stained (alizarin only).’’ Thus it is most likely, although not stated clearly by Travers (1984a: 43), that his description was based mainly on the smaller specimen (44.5 mm) that ‘‘has responded well to both stains (alizarin & alcian blue).’’

The only other chaudhuriid species described from northern India is *Garo khajuriai*. The holotype was collected from rice paddies at Rongrengiri, Garo Hills, Meghalaya, the paratype from Baguri (Kaziranga Wildlife Sanctuary) Sibsagar district, Upper Assam. No osteological information is available for this species, and all other information provided in the original description (Talwar et al., 1977) is scarce and unsatisfactory. However, a recently collected specimen from Assam assigned to the genus *Garo* (Kullander et al., 2000) shows that its upper jaw consists of the usual two paired bones, maxilla and premaxilla. Therefore, it seems we can exclude the possibility that we could explain the differences between our specimens and Travers’ (1984a) account of *P. indica* by assuming ours were actually a *Garo* species. One unlikely explanation for the observed differences is that our specimens from Coochbehar represent an additional yet undescribed species of *Pillaia*. These taxonomic uncertainties can only be resolved once comparative material of the different species involved from the poorly collected area of northeastern India becomes available.

ABBREVIATIONS

ACh	anterior ceratohyal
An	angular
Ana	anguloarticular
Asph	autosphenotic
Bb	basibranchial
BbC	basibranchial cartilage
Bh	basihyal
Boc	basioccipital
BR	branchiostegal ray
Cb	ceratobranchial
ChC	ceratohyal cartilage
Cl	cleithrum
Cm	coronomeckelian
Co	coracoid
CoC	coracoid cartilage
CR	caudal-fin ray
De	dentary
DHh	dorsal hypohyal
DR	distal radial of pterygiophore
Eb	epibranchial
Ecpt	ectopterygoid
Epo	epiotic
EthPl	ethmoid plate
Exoc	exoccipital
Fe	fenestration of neural arches
Fr	frontal
$FV_{1,2,3}$	foramen of first, second, or third branch of trigeminal nerve
FVII	foramen of facial nerve
FX	foramen of vagal nerve
H	hypural
Hb	hypobranchial
HS	hemal spine
HsyC	hyosymplectic cartilage
Hy	hyomandibular
Ih	interhyal
IhC	interhyal cartilage
Iop	interopercle
LC	lateral commissure
LE	lateral ethmoid
LO	lamina orbitonasalis
MC	Meckel’s cartilage
Me	mesethmoid
Mpt	metapterygoid
Mx	maxilla
Na	nasal
NS	neural spine
Op	opercle
Pap	parapophysis
Pb	pharyngobranchial
PCh	posterior ceratohyal
Pcl	postcleithrum
PMpt	pars metapterygoidea of palatoquadrate
P-MR	proximal-middle radial of pterygiophore
Pmx	premaxilla
Pop	preopercle
Poza	postzygapophysis
PQ	pars quadrata of palatoquadrate
PR?	pectoral radial?
Pro	prootic
PRPl	pectoral radial plate
Prza	prezygapophysis
Psph	parasphenoid
Pto	pterotic
PU	preural centrum
Q	quadrate
R	fin soft ray
Ra	retroarticular
RC	rostral cartilage
Ri	rib
Sc	scapula

ScC	scapular cartilage
SccoC	scapulocoracoid cartilage
Scl	supracleithrum
Soc	supraoccipital
Sop	subopercle
SP	spinelike projection on neural arch in front of neural spine
Sy	symplectic
TH	trabecular horn
TrC	trabecula communis
TS	tectum synoticum
U	ural centrum
UP4	fourth upper pharyngeal toothplate
V1, 2, . . .	first, second, . . . vertebra
VHh	ventral hypohyal
VHhC	ventral hypohyal cartilage
VK	ventral keel on first centrum
Vo	vomer

RESULTS

For the purpose of description, the skeleton of chaudhuriids is divided into the following major parts: neurocranium; hyopalatine arch and opercular apparatus; hyoid, urohyal, and branchial arches; shoulder girdle with pectoral fin; vertebral column with dorsal, anal, and caudal fins; and scales, if applicable.

OSTEOLOGY OF *CHENDOL KEELINI*

Chendol keelini reaches a size of at least 57 mm at the type locality in Malaysia (Kerle et al., 2000), but specimens from the population in Jambi, Sumatra, grow to 81.3 mm (ZRC 41666, Tan, personal commun.). It is thus the second largest species studied here. *C. keelini* is the only chaudhuriid with scales. They are confined to the posterior third of the body (Kottelat and Lim, 1994; personal obs.).

NEUROCRANIUM (fig. 2): The neurocranium is a solidly ossified case with the widest part in the occipital region from where it tapers to the snout.

The ethmoid region consists of four bones. The elongate nasal covers the olfactory organ dorsally. It is sutured to the lateral ethmoid, which forms the caudal and dorsolateral wall of the nasal capsule. The lateral ethmoid has developed an anterior dorsal lamina of membrane bone, which, along with the nasal, forms a rigid cover for the nasal organ (fig. 2). Where the lateral ethmoids meet in the midline, an elongate block of cartilage, a remnant of the trabecula communis, extends back into the orbit (fig. 2B). The ventral corner of the lateral wing of the lateral ethmoid bears an articular facet for the lacrimal, the only bone of the circumorbital series developed in chaudhuriids. The lacrimal forms the lateral wall of the nasal capsule (fig. 2B). Its posteriormost part has an ascending process that contacts the posterior part of the dorsal anterior lamina of the lateral ethmoid. Slightly anterior to this, the lacrimal has an incisure that represents the ventral rim of the posterior nasal opening. The anterior dorsal lamina of the lateral ethmoid forms its dorsal rim. In front of the posterior nasal opening the lacrimal contacts the anterior lamina of the lateral ethmoid and the nasal bone, so that the orifice is completely surrounded by bone. In specimens smaller than the one figured, the respective bones may leave narrow gaps between each other.

Medially the nasals are separated by the unpaired mesethmoid, a thin, vertical, bladelike bone whose anterior end is fused to the vomer (fig. 2B). The mesethmoid is connected ventrally by a short cartilaginous rod to the area where the lateral ethmoids meet in the midline. This cartilage is a remnant of the narrow nasal septum found in other chaudhuriids and in mastacembelids (see Britz, 1996). A conspicuous rodlike rostral cartilage articulates with the anteriormost dorsal part of the mesethmoid (fig. 2A, B). The proximal part of the cartilage, which lies anterior to the tip of the vomer and between the heads of the maxillae, may ossify in larger specimens. The vomer underlies the ethmoid region as a thin splint of bone. Posteriorly the vomer tapers to a needle-thin process located in a groove of the parasphenoid and extends along half the length of that bone (fig. 2C). The anterior end of the vomer, which is indistinguishably fused to the mesethmoid, is enlarged and bears two articular facets for the maxillary bones.

The orbital region, as the area between the otic and the ethmoid part, is dominated in dorsal aspect by the large frontal, which extends from the anterior end of the otic region to the anterior part of the orbit (fig. 2A, B). The paired frontals are sutured to each other along most of their length and taper toward their anterior end where they contact the na-

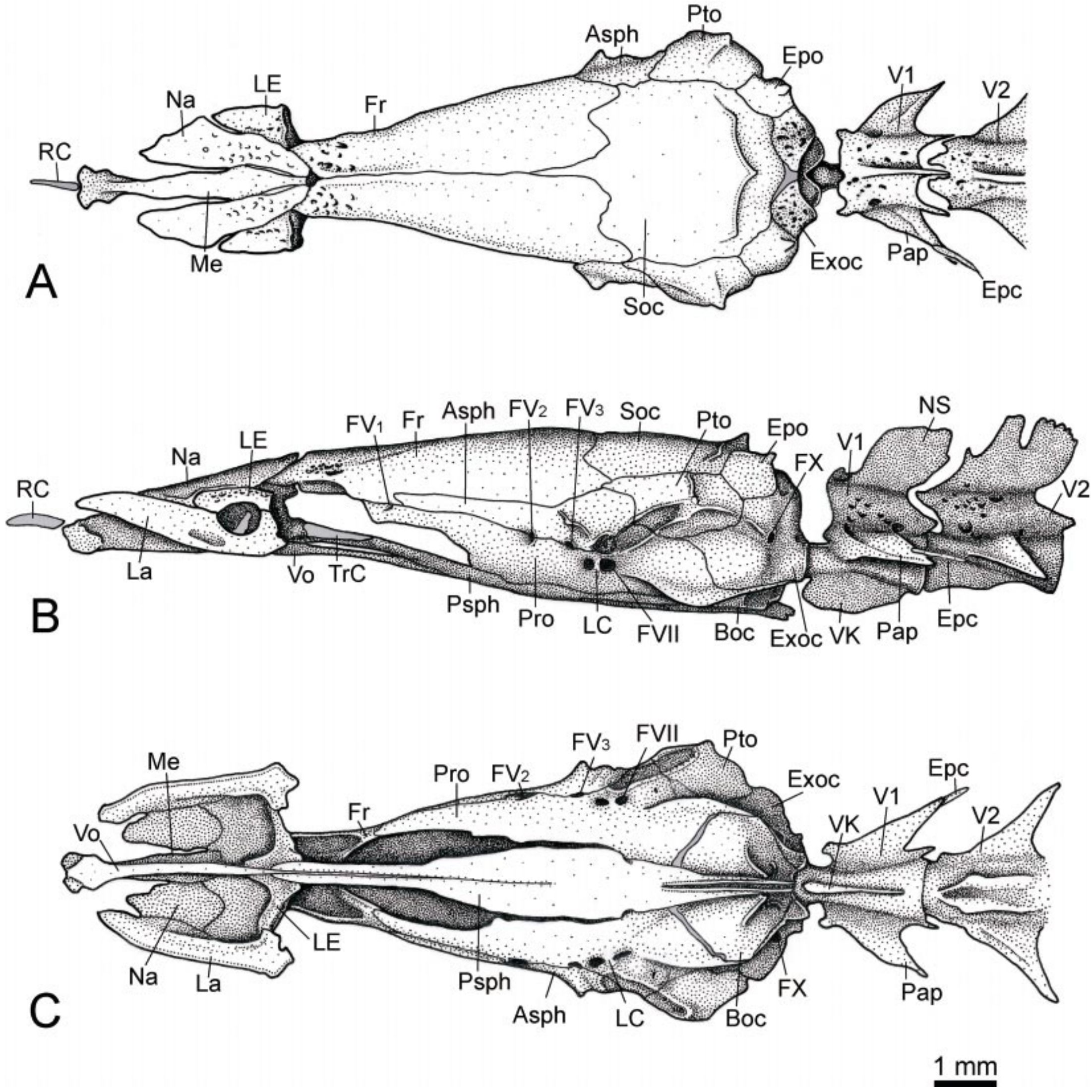

Fig. 2. *Chendol keelini*, AMNH 217795, 65 mm, neurocranium and anterior vertebrae, cartilage in gray. **A.** Dorsal view, second vertebra only shown in part. **B.** Lateral view. **C.** Ventral view, second vertebra only shown in part.

sals. There is no trace of a cephalic sensory canal within these bones. The frontal is bordered ventrally over most of its length by the autosphenotic, and it contacts the prootic anteriorly and pterotic posteriorly (fig. 2B). Caudally the frontal reaches the large supraoccipital. The autosphenotic is an elongate bone tapering toward its anterior end. Its posterior part contributes to the anterior articulation for the hyomandibular and in larger specimens it has a ridge from which the levator arcus palatini originates. There is no pterosphenoid or basisphenoid developed.

The prootic is the dominant bone in the lateral wall of the cranium (fig. 2B, C). It is sutured dorsally to the autosphenotic over most of its length, and only its most anterior tip contacts the frontal. Ventrally at the posterior two-thirds it is bordered by the parasphenoid. It encloses or contributes to the foramina for the cranial nerves $V_{1,2,3}$ and VII, all of them exiting through separate foramina. The prootic also contributes to the anterior articulation of the hyomandibular and to the articulatory groove that extends to the pterotic. It also forms a canal for the jugular vein bridged laterally by a narrow ring of bone, the lateral commissure, situated ventrolateral to the anterior articulation of the hyomandibular with the ear capsule. This lateral commissure represents the anterior border of the foramen for the hyomandibular branch of the facialis nerve. The prootic also houses the anterior part of the auditory bulla.

The parasphenoid spans from the orbital to the occipital region (fig. 2B, C). It is narrow in the orbital region, broadest at the level of the anterior articulation of the hyomandibular, then tapers again and splits into two long, thin arms that extend to the articulation of the occipital region with the first vertebra. Anteriorly it has a shallow ventral groove for reception of the vomer, which extends over half of its length. In the area of the trabecula communis in the orbital region, the parasphenoid slightly curves dorsally, becoming detached from the underlying vomer. Thus a narrow gap forms between the two bones.

The pterotic is situated at the widest part of the cranium and forms the posterior part of the articulatory groove and articulation for the hyomandibular (fig. 2B, C). The epiotic is a small cap of bone at the posterodorsal corner of the otic capsule. It may possess a posteriorly directed process in larger specimens to which attach tendons of the trunk musculature.

The broad supraoccipital forms the roof of the posterior part of the cranium (fig. 2A, B). In this large specimen it has a prominent transverse ridge along its posterior margin for insertion of the trunk musculature. There are no parietals. They are not fused to the supraoccipital, but are rather lost, as evidenced by our ontogenetic series of *C. keelini*.

The exoccipital forms the posterodorsal part of the otic bulla, the dorsal part of the ball and socket articulation with the first vertebra, and the lateral and dorsolateral wall of the foramen magnum (fig. 2). The paired exoccipitals are separated from each other in the dorsal midline by a cartilaginous area. In a dorsal view they may have some small depressions in the bone, which may or may not traverse the bone. Similar depressions are also present in the rostral part of the frontals, on the dorsal face of the nasals and the membranous wings of the lateral ethmoid (fig. 2A). The intercalar is absent. The posteroventral part of the otic bulla and the ventral part of the ball-and-socket articulation with the first vertebra are formed by the basioccipital.

HYPOPALATINE ARCH AND OPERCULAR APPARATUS (fig. 3): The hyopalatine arch consists of hyomandibular, symplectic, quadrate, metapterygoid, and ectopterygoid. There is no endopterygoid or palatine (neither dermo- nor autopalatine) developed. The hyomandibular has three articular heads. The anterior head articulates with the autosphenotic/prootic, the posterior head with the pterotic, and the opercular head with the opercle. The crest between the anterior and the posterior head rests in a groove on the prootic and pterotic to which it is attached by connective tissue. The lateral side of the hyomandibular possesses a vertical crest that is bound to the preopercle by connective tissue (fig. 3A). The hyomandibular is pierced by a foramen of the hyomandibular trunk of the facial nerve. An anterior lamina of membrane bone extends toward, but does not contact, the metapterygoid and ventrally contacts the symplectic. The symplectic is long and rodlike and its anterior end fits into a groove in the quadrate (fig. 3B). The latter has a strong posteroventral process of membrane bone tightly bound to the preopercle by connective tissue.

A small zone of cartilage separates the quadrate and metapterygoid (fig. 3). An anterior process of membrane bone from the metapterygoid bridges the gap between this bone and the quadrate. The ectopterygoid is long and narrow and curved like an asymmetrical boomerang. Its posterior end articulates with the medial part of the quadrate. The area of the ectopterygoid that turns from an anterodorsal to a more horizontal plane is tightly bound to the lateral ethmoid. The anteriormost tip of the ectopterygoid is directed toward the midline and there is firmly attached to the vomer.

The four bones of the opercular apparatus are thin and in some areas only weakly ossified (fig. 3A, C). The large opercle articu-

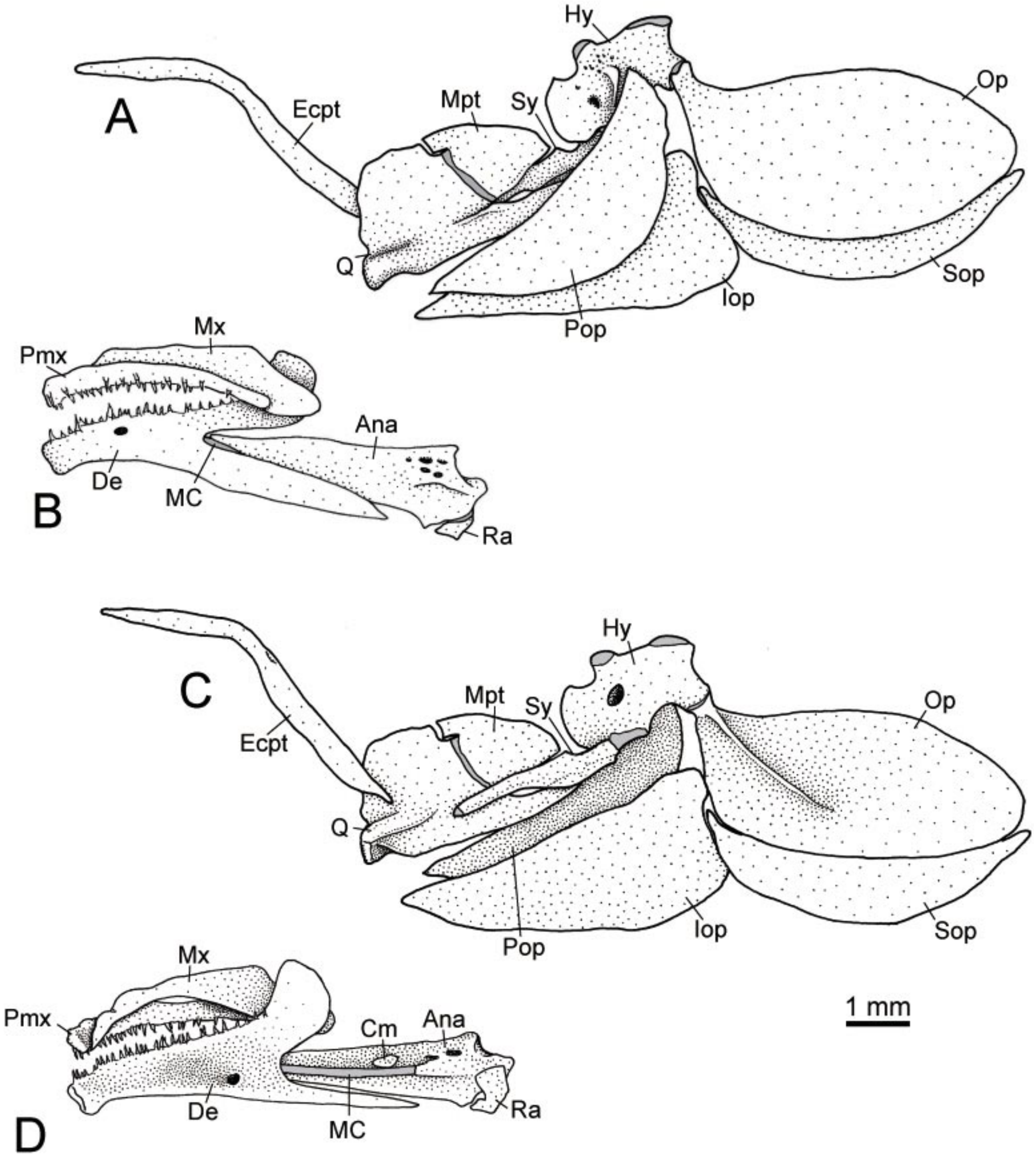

Fig. 3. *Chendol keelini*, AMNH 217795, 65 mm, cartilage in gray. **A.** Hyopalatine arch, lateral view. **B.** Upper and lower jaws, lateral view. **C.** Hyopalatine arch, medial view. **D.** Upper and lower jaws, medial view.

lates with the opercular head of the hyomandibular. It has a prominent ridge on its inner side that extends from the articulation with the hyomandibular caudoventrally (fig. 3C). The subopercle is a thin, weakly ossified plate ventral to the opercle. The preopercle is well ossified in its anterodorsal part, which is connected to the hyomandibular, the symplectic, and the posteroventral process of the quadrate. Ossification is weaker in its posterior area. The interopercle is located medial and ventral to the preopercle; it is wide in the posterior part and attenuates rostrally to a tip (fig. 3C) from which the interoperculo-retroarticular ligament originates. The anterodorsal area of this bone is better ossified than the caudoventral area.

The upper jaw comprises the maxilla and premaxilla, which are tightly bound together (fig. 3B, D). The premaxilla bears teeth along its ventral margin. The maxilla is toothless with a wide posterior part that tapers anteriorly. Its anterior head articulates with the ventrolateral face of the rostral tip of the fused mesethmoid/vomer. The dentary opposes the premaxilla and bears teeth along its dorsal margin. Its posterior end bifurcates into a winglike dorsal coronoid process that is ligamentously attached to the medial side of the posterior end of the maxilla, and a long posteroventral process that runs along the anguloarticular (fig. 3D). The latter bone articulates posteriorly with the quadrate. From its widest part it tapers anteriorly and ends at the base of the bifurcation of the dentary. The posteroventral corner of the anguloarticular is capped by the small retroarticular, to which the ligament from the interopercle is attached. Meckel's cartilage is still well developed and visible in a medial view of the lower jaw. Dorsal to its posterior end lies the small round coronomeckelian bone.

HYOID, UROHYAL, AND BRANCHIAL ARCHES (fig. 4): The interhyal is relatively large (fig. 4A, B). Its upper tip articulates with the hyopalatine arch at the cartilaginous area between hyomandibular and symplectic and its lower tip with the posterior end of the posterior ceratohyal. The latter bone is separated from the anterior ceratohyal by a cartilaginous strip. This strip is bridged on the medial side by a strong caudally directed dorsal process of the anterior ceratohyal that fits into a groove of the posterior ceratohyal (fig. 4B). The anterior ceratohyal has a wide hind part that tapers at about half its length. The dorsal and ventral hypohyals are small ossifications capping the rostral end of the anterior ceratohyal (fig. 4A, B). The ventral hypohyal also serves as point of attachment for the ligament from the urohyal. The dorsal hypohyal articulates with the basihyal and extends posteriorly beyond the posterior tip of the ventral hypohyal. The basihyal is a stout and elongate bone with a cartilaginous tip (fig. 4D).

There are six well-developed long branchiostegal rays, four articulating with the anterior and two with the posterior ceratohyal (fig. 4A, B). The four posterior rays articulate with the lateral face and the anterior ones with the medial face of the ceratohyals. If the branchiostegal membrane is folded, the two anterior rays come to lie medial to the ceratohyals along their whole length and thus are separated from the posterior four rays.

The urohyal (fig. 4C) is bladelike with a vertical lamina of bone and two anterior processes that attach to the ventral hypohyals by ligaments.

There are three ossified basibranchials (fig. 4D), with the first being shorter than the second and third. The latter ends between the third hypobranchials. There are three hypobranchials of different shape. The first hypobranchial is a short rodlike bone. It articulates with the anterior third of the second basibranchial. The second hypobranchial bears a ventrally directed, cartilaginously tipped process at its anterior end. It articulates with the anterior third of the third basibranchial. The third hypobranchial bears several teeth on its dorsal surface. Its anterior end also has a ventrally directed anterior process. The posteriomedial part of hypobranchial 3 is produced into a short broad caudal process with a cartilaginous tip. This articulates with the fourth basibranchial, a small nodule of cartilage that articulates posteriorly with the cartilaginous anterior tip of ceratobranchial 4 (fig. 4D). All ceratobranchials are elongate rodlike bones. Ceratobranchial 5 bears numerous conical teeth on its dorsal surface.

There are four epibranchials whose lateral ends articulate with the respective ceratobranchials (fig. 4D). Epibranchials 1 and 2 are short, thin, and rodlike. The medial end of epibranchial 1 articulates with the anterior end of pharyngobranchial 2; the medial end of epibranchial 2 articulates with the posterior end of the same pharyngobranchial and the anterior end of pharyngobranchial 3. Epibranchial 3 is also rodlike but bears a dorsally directed uncinate process that articulates with a similar process on epibranchial 4. The latter has a club-shaped medial tip for

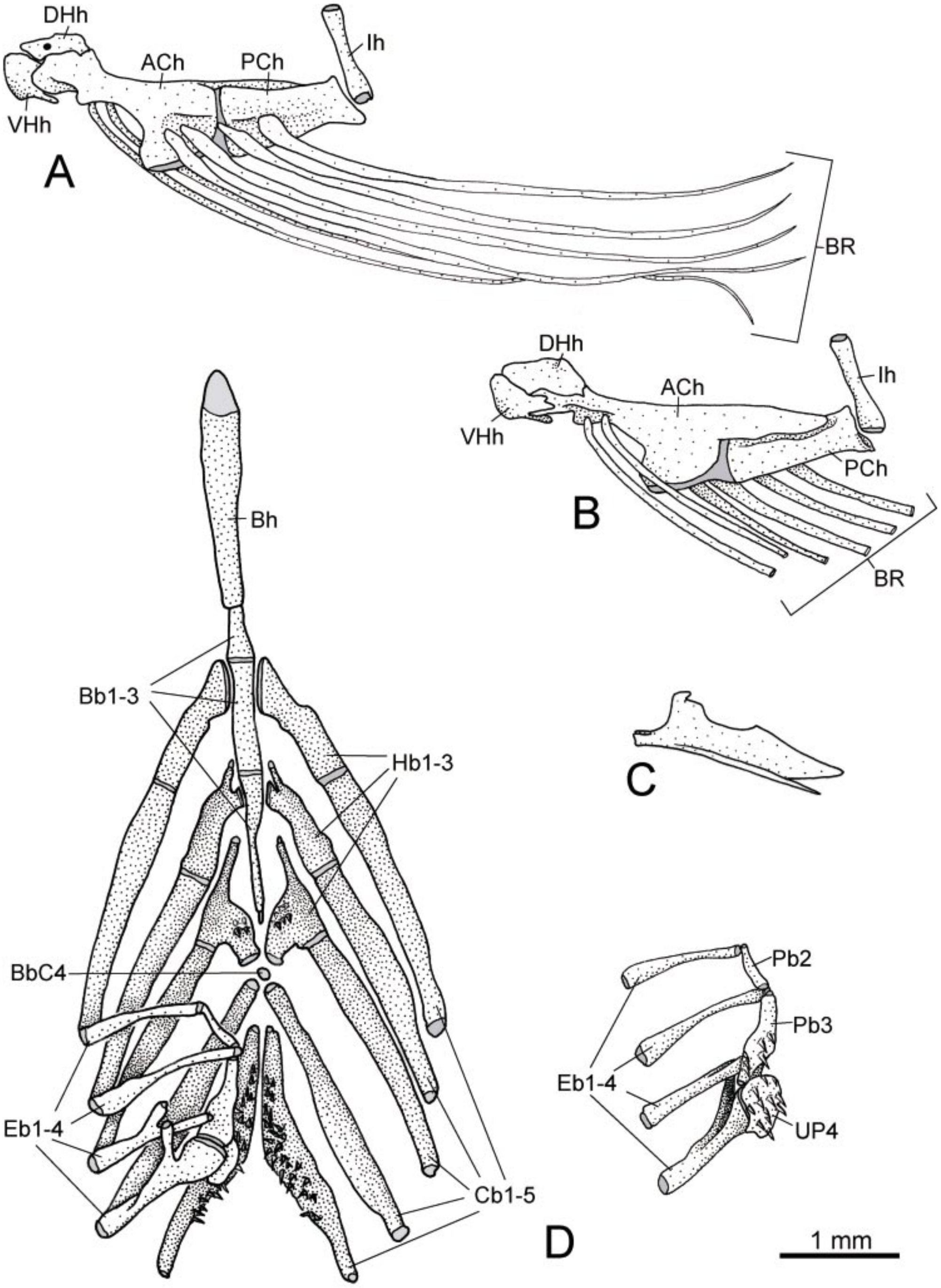

Fig. 4. *Chendol keelini*, AMNH 217795, 65 mm, cartilage in gray. **A.** Hyoid, lateral view. **B.** Hyoid, medial view. **C.** Urohyal, lateral view. **D.** Branchial arches, dorsal view, dorsal gill arches of right side removed and shown in ventral view.

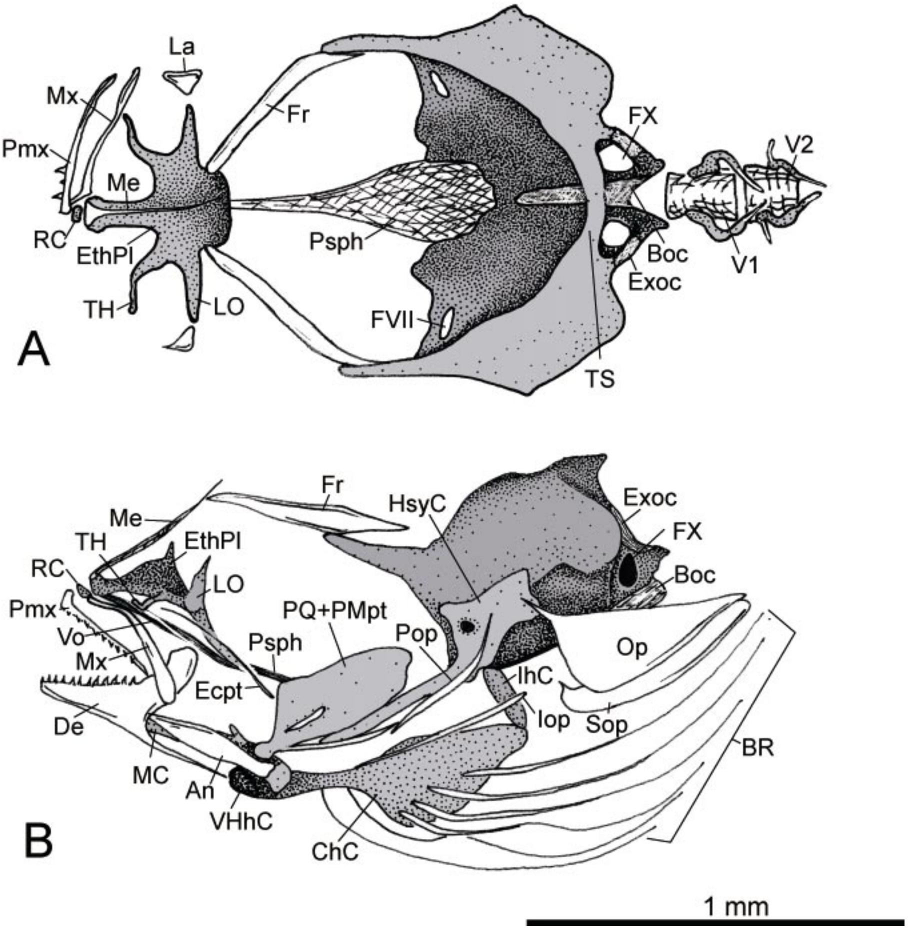

Fig. 5. *Chendol keelini*, AMNH 217795, 7.5 mm, cartilage in gray. **A.** Neurocranium and anterior vertebrae, dorsal view. **B.** Skull and anterior vertebrae, lateral view.

the articulation with the third pharyngobranchial and the fourth upper pharyngeal toothplate (sensu Johnson, 1992). There are only two pharyngobranchials. Pharyngobranchial 2 is the small elongate element whose tips articulate with epibranchials 1 and 2, respectively, and is the anteriormost pharyngobranchial. Its posterior tip is also in contact with the anterior tip of pharyngobranchial 3. The latter is also an elongate bone with a few teeth on the ventral side, indicating its fusion with the respective toothplate. The fourth upper pharyngeal toothplate is roundish in dorsal view with teeth on its ventral side. A pharyngobranchial 4 cartilage is not developed.

REMARKS ON AN EARLY DEVELOPMENTAL STAGE OF THE CRANIUM: The cranium of our 7.5-mm larva (fig. 5), the smallest available specimen, is not described in detail but some unusual characters are pointed out. There is a small autogenous cartilage in front of the tip of the ethmoid block, the rostral cartilage, which is still round and knoblike as in other larval and adult percomorphs. The chondrocranium consists of two separate units unconnected by cartilage, the ethmoidal and the otico-occipital units (fig. 5A). The ethmoidal plate has two prominent pairs of processes, long anterior trabecular horns, and laminae orbitonasales at whose lateral tips the lacrimals articulate. The mesethmoid is a long membranous, posterodorsally directed splint of bone on the dorsal aspect of the anterior

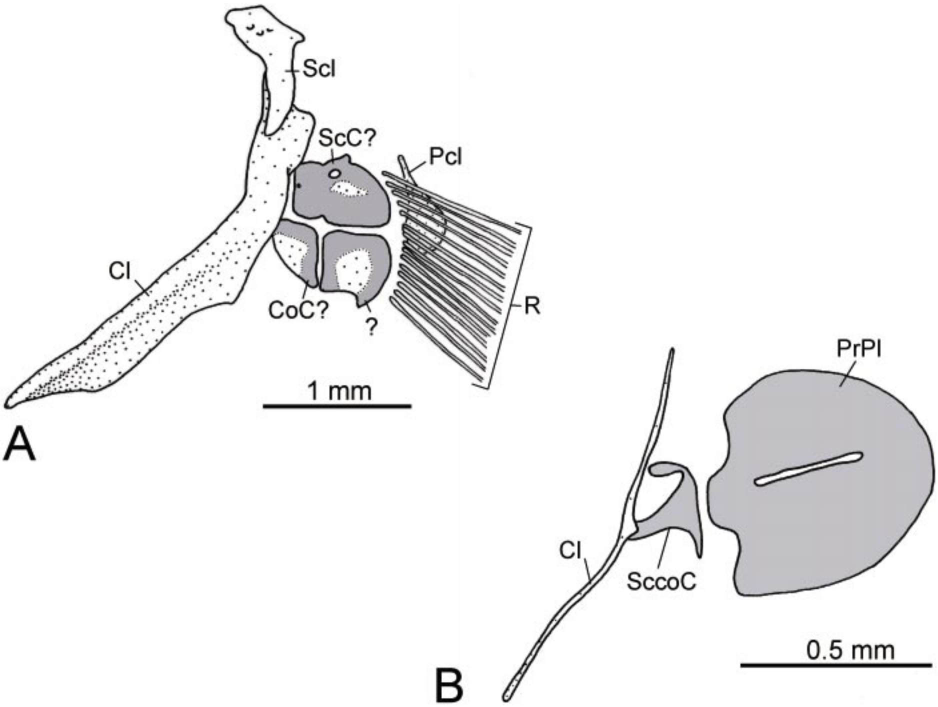

Fig. 6. *Chendol keelini*, AMNH 217795, shoulder girdle, lateral view, cartilage in grey. **A.** 65 mm. **B.** 7.5 mm.

tip of the nasal septum (fig. 5B). The two large otic capsules are in contact dorsally through the relatively narrow tectum synoticum. The occipital area has a large foramen for the vagal nerve.

The hyosymplectic cartilage is not ossified yet (fig. 5B). The palatoquadrate has no pars autopalatina, and not even the cartilage bar that connects it to pars quadrata et metapterygoidea is developed, as it would be in early stages of many teleosts. Pars quadrata contains an elongate opening. The quadrate's posteroventral process of membrane bone is present. The ectopterygoid is an extremely narrow, needlelike ossification extending from the anterior face of the quadrate to the trabecular horn, and at this stage it does not have the long preorbital extension as in the adult. Meckel's cartilage bears a small anterodorsal process at a position where in many other adult teleosts an ascending process of the anguloarticular is developed. Additional bones present at this stage are: vomer, parasphenoid, frontal, maxilla, praemaxilla, angular, dentary, opercle, preopercle, subopercle, and interopercle. There are no teeth on hypobranchial three in this 7.5-mm specimen, but they are present in our 11.2-mm juvenile.

SHOULDER GIRDLE AND PECTORAL FIN (fig. 6A): The cleithrum is the dominant element of the shoulder girdle. It is a stout bone extending from the upper third of the body downward to the midline, where it meets its counterpart in a ligamentous connection. Its dorsal end articulates with the supracleithrum, a small curved bone lateral to it. The cleithrum articulates with two cartilaginous discs that are part of the endoskeletal shoulder girdle but can hardly be referred to as the scapula and coracoid of other fishes. The upper element is the largest and bears a foramen in its dorsal part. There is a weakly developed ossification in its posterior area and an indentation at the upper and lower edge suggesting an incomplete separation into two elements. On the right shoulder girdle this upper element is separated into two plates of cartilage. In other specimens, some variation can be observed regarding the separation of the upper element into two plates. The lower plate is smaller, triangular in shape, and also shows a weak ossification. Its caudal border and the ventral border of the upper element both contact a third mainly cartilaginous element whose middle part is only weakly ossified. The rays of the pectoral fin articulate without intervening distal radials with the caudal edge of the upper element (or, if separate, with the posterior upper plate), and with the lower posterior element that we interpret as possibly a pectoral radial. A postcleithrum is also developed as a thin plate of bone posterior to the cleithrum.

REMARKS ON THE DEVELOPMENT OF THE SHOULDER GIRDLE (fig. 6B): In our 7.5-mm specimen only the cleithrum is developed as a thin splint of bone. The endoskeletal part of the shoulder girdle is represented by the irregularly shaped curved scapulocoracoid cartilage. The pectoral-fin fold is supported by a broad and thin plate of cartilage, the pectoral radial plate (sensu Johnson and Brothers, 1993), with a central, transverse fissure, which is typical of the developing pectoral fin of many teleosts (see e.g. Potthoff et al., 1984, 1987, 1988; Potthoff and Tellock, 1993; Grandel and Schulte-Merker, 1998; Britz and Johnson, 2002). The pectoral radial plate is still present in a juvenile of 22 mm. In our 37-mm specimen the typical four-part fin skeleton is developed and the fin rays have ossified. The supracleithrum is ossified in a larva of 11.3 mm, and the postcleithrum is present at 22 mm.

VERTEBRAL COLUMN, DORSAL, ANAL, AND CAUDAL FINS (figs. 2, 7): Our figured specimen has 68 vertebrae, the first three vertebrae without ribs (figs. 2, 7A). An epicentral bone (= epineural of Patterson and Johnson, 1995) is attached to the tip of the first transverse process of the left side only (fig. 2), but other specimens have epicentrals on both sides of the first vertebra (see table 1). There are 37 rib-bearing vertebrae starting with the fourth (fig. 7A). There are 28 vertebrae with hemal arches and spines starting with vertebra 40. The first three vertebrae possess prominent lateral parapophyses, which are in a more or less horizontal position (figs. 2, 7A). Towards the more posterior rib-bearing vertebrae, parapophyses are longer and directed ventrally (fig. 7A, B). The first vertebra has a ball-like articular head that fits into a socket on the occipital region of the skull formed by the exoccipitals and the basioccipital (fig. 2). In the ventral midline, the first vertebra has a prominent vertical keel that is connected tightly to the posterior skull base, predominantly to the posterior processes of the parasphenoid (fig. 2). The first six anterior vertebrae bear laterally expanded neural spines (figs. 2, 7A). In lateral view, there is a smaller anterior spinelike projection in front of the expanded neural spine. In more posterior vertebrae this anterior projection gradually becomes less conspicuous and eventually disappears (fig. 7A–C), with vertebra 27 being the last vertebra that still has the anterior projection and the neural spine present. The anterior vertebrae have well-developed pre- and postzygapophyses (fig. 7A–C) that are less prominent toward the tail (fig. 7D) and are eventually absent from the posteriormost vertebrae (fig. 7E). There is also a change in the shape of the vertebrae from the head to the tail region, with the centra becoming much narrower and more elongate with much shorter neural and hemal spines (compare fig. 7A–C with D, E). Another modification along the vertebral column concerns the development of paired fenestrations in the neural arches at the base of the neural spine from about vertebra 5 and posteriorly (fig. 7A, B). These fenestrae become larger in more caudal vertebra so that only a narrow bony bridge connects the prezygapohyses and the anterior spinelike projection dorsally with the neural spine (fig. 7B). Eventually from about vertebra 28 and posteriorly, this bridge is lacking so that the prezygapophses have no dorsal connection to the neural spine

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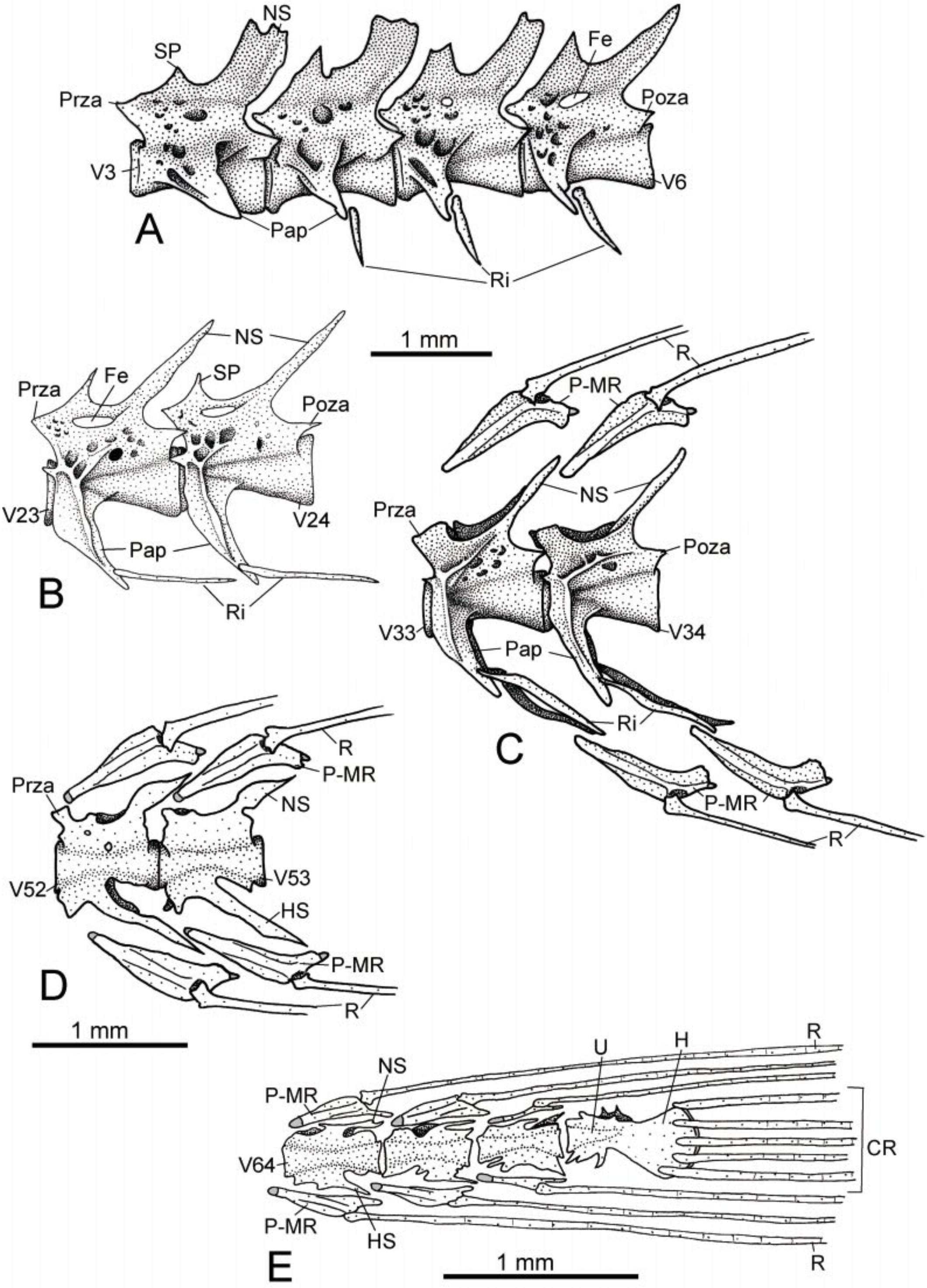
Fig. 7. *Chendol keelini*, AMNH 217795, 65 mm, lateral view, cartilage in gray. **A.** Vertebrae 3–6. **B.** Vertebrae 23 and 24. **C.** Vertebrae 33 and 34 and associated dorsal- and anal-fin pterygiophores and rays. D. Vertebrae 52 and 53 and associated dorsal- and anal-fin pterygiophores and rays. E. Caudal fin supporting skeleton and preural vertebrae 3–5 with associated dorsal- and anal-fin pterygiophores.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(fig. 7C–E). The skeletal support of the caudal fin consists of a single hypural fused to the last centrum (fig. 7E). The caudal fin bears 5 fin rays and is confluent with the dorsal and anal fins.

The dorsal fin has 44 fin rays and 45 pterygiophores, with the first one being somewhat rudimentary and the last one without a serially associated ray. The series of dorsal pterygiophores starts behind the neural spine of vertebra 23. The proximal-middle radials of the pterygiophores show the common upside-down L-shape, the ventral and caudal tips being cartilaginous (fig. 7C–E). In the anterior region of the dorsal series of pterygiophores, they form an angle of about 45° with the vertebral column (fig. 7C), with this angle becoming gradually smaller toward the caudal fin (fig. 7D), so that the last few pterygiophores have an almost parallel orientation to the vertebral column (fig. 7E). There is a small kidney-shaped distal radial intervening between each proximal-middle radial and the bases of each fin ray. It is completely covered by the fin-ray base and cannot be seen in lateral view.

The anal fin has 42 rays and 43 pterygiophores, with the first being rudimentary and the last lacking a serially associated ray. There are 17 pterygiophores in front of the first hemal spine, so that the body cavity reaches much farther posteriorly into the area of the anal fin when compared to other chaudhuriids. Each pterygiophore consists of an L-shaped proximal-middle radial and a tiny kidney-shaped distal radial as in the dorsal fin, except the last one consisting only of the proximal-middle radial. From anterior to posterior, pterygiophores show the same changes in shape and position as described for those of the dorsal fin (see fig. 7C–E).

Information on the intraspecific ranges of several meristic parameters is provided in table 1.

REMARKS ON ONTOGENY OF VERTEBRAL COLUMN, FINS, AND FIN SUPPORTS (fig. 8): The smallest specimen available, 7.5 mm, has 42 ossified centra (fig. 8A). Cartilaginous neural arches are present on vertebrae 1–33. Left and right halves are separated in the midline by a gap. There are neural spines of membrane bone on the neural arches of vertebrae 1–10. They also fail to meet in the dorsal midline. The first five vertebrae already possess bony parapophyses; they originate at the base of the neural arches in vertebrae 1–4 and on the centrum in vertebra 5. There are seven dorsal-fin pterygiophores developed, with the first situated between neural spines of vertebrae 23 and 24 (fig. 8A). Judging from the position in relation to the vertebrae, the first pterygiophore correlates with the anteriormost pterygiophore in the adult fish so that dorsal-fin pterygiophores apparently develop rostrocaudally. The single hypural of the caudal fin is already chondrified and articulates with a single caudal-fin ray, although the ural centrum has not ossified yet (fig. 8A). There is still a large gap between the hypural and the posteriormost ossified centra.

In the 11.9-mm specimen (fig. 8B), 68 vertebrae are ossified. Vertebrae 1 to about 40 have ossified neural arches, spines, and parapophyses. Posterior to about vertebra 43, neural arches are still in cartilage, as are the hemal arches. Cartilaginous ribs are present on vertebrae 13–37 with the nine posterior ribs being longer than the anterior ones (fig. 8B). Ribs thus seem to develop caudorostrally (they are absent also in an 11.3-mm larva and developed up to vertebra 5 in a 14.5-mm specimen). The caudal fin has no ossified centrum yet; only the cartilaginous hypural, which bears four fin rays, is present. The dorsal fin has 36 cartilaginous proximal radials of which numbers 1–17 possess serially associated distal radials too and numbers 1–29 possess serially associated ossified fin rays (fig. 8B). The anal fin shows a similar condition. There are 36 cartilaginous proximal radials—numbers 1–19 have serially associated distal radials and numbers 1–28 have serially associated ossified fin rays.

The dorsal bony bridges that connect the prezygapophyses with the neural spines on vertebrae 5–27 in the adult specimens are not present yet in our small specimens up to 22 mm. At that stage the neural arches show no fenestration but resemble those of the posterior caudal region of the adult fish. The bony bridges develop later in ontogeny and occur up to vertebra 18 in our 31-mm specimen.

SCALES: Numerous thin cycloid scales (fig. 9) are confined to the posterior part of the

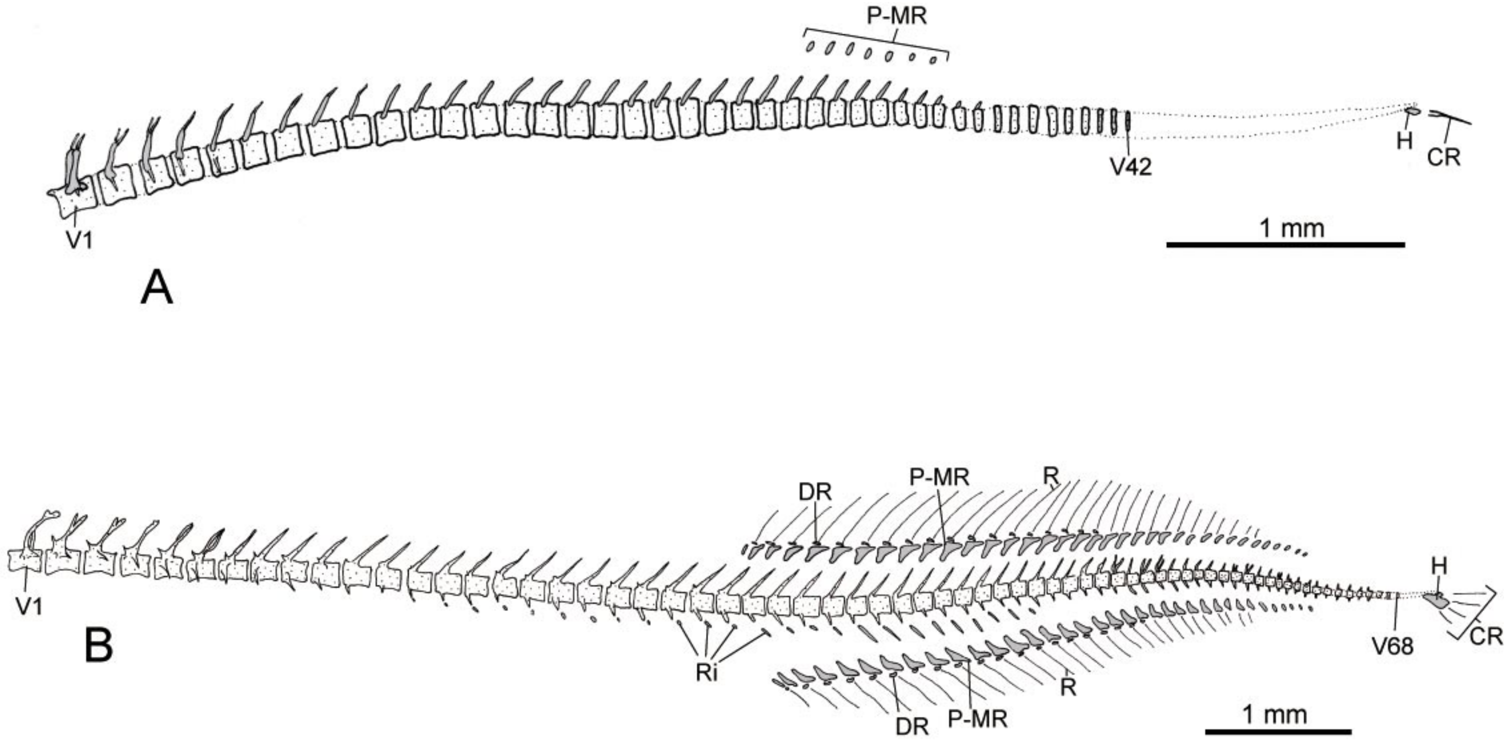

Fig. 8. *Chendol keelini*, AMNH 217795, ontogenetic stages of vertebral column, dorsal, anal, and caudal fins, cartilage gray. **A.** 7.5 mm, neural arches, hypural, and proximal-middle radials of dorsal fin cartilaginous. **B.** 11.9 mm, posterior neural and hemal arches (from about 43 on), ribs, hypural, and proximal-middle and distal radials of dorsal and anal fin cartilaginous.

Fig. 9. *Chendol keelini*, AMNH 217795, scales of anterior part of caudal body area.

body. They are weakly ossified and tiny, measuring 0.3–0.35 mm in diameter. They bear up to six radii in their anterior field and up to 12 concentric circuli on the body of the scale.

OSTEOLOGY OF *CHENDOL LUBRICUS*

Two C&S specimens of *C. lubricus*, 38.2 mm and 50 mm, were available for study. Only those aspects that differ markedly from the condition described in *C. keelini* are mentioned here.

NEUROCRANIUM (fig. 10): The shape of the neurocranium in dorsal view differs between the two specimens studied (compare fig. 10A and B). That of the 50-mm specimen has a more elongate shape, tapering continuously from the otic region (the widest part of the cranium) to the ethmoid region (fig. 10B). The 38.2-mm specimen instead shows a slighter attenuation from the otic to the orbital region but then becomes much narrower in the latter part (fig. 10A).

The ethmoidal region consists of the same bones as in *C. keelini* and differs from that species only in the shape of the different elements. The nasal is smaller and less ossified so that its boundaries are more difficult to discern (fig. 10). It seems to be narrower than in *C. keelini* and does not reach the mesethmoid in the midline. The lateral ethmoid shows the same anterior dorsal lamina of membrane bone that along with the nasal forms a dorsal wall for the olfactory organ. In the 38.2-mm specimen the nasal and this lamina are fused (fig. 10A, C), but both are clearly separate in the 50-mm specimen (fig. 10B). Contrary to the situation in *C. keelini*, the lacrimal does not contact the anterior dorsal lamina of the lateral ethmoid or the nasal bone in front of the posterior nasal opening (fig. 10C). The ascending process at the caudal end of the lacrimal is present but does not reach as far dorsally as in *C. keelini*. There is also a cartilaginous rod, part of the narrow elongate nasal septum, in the midline in front of the lateral ethmoids, which reaches anteriorly to the mesethmoid ossification (fig. 10C), but it appears longer than in *C. keelini* (fig. 2B).

The vomer extends posteriorly to slightly more than half the length of the neurocranium (fig. 10D). At the border of ethmoidal and orbital region the vomer is separated from the dorsally curving parasphenoid (fig. 10C). This is also present in *C. keelini*, but is less conspicuous (fig. 2B). The anterior tips of the frontals leave a gap between each other in which the posterior tip of the mesethmoid is located (fig. 10A, B). This gap is wider and more prominent than in *C. keelini*. The ventral lamina of the frontal in this area

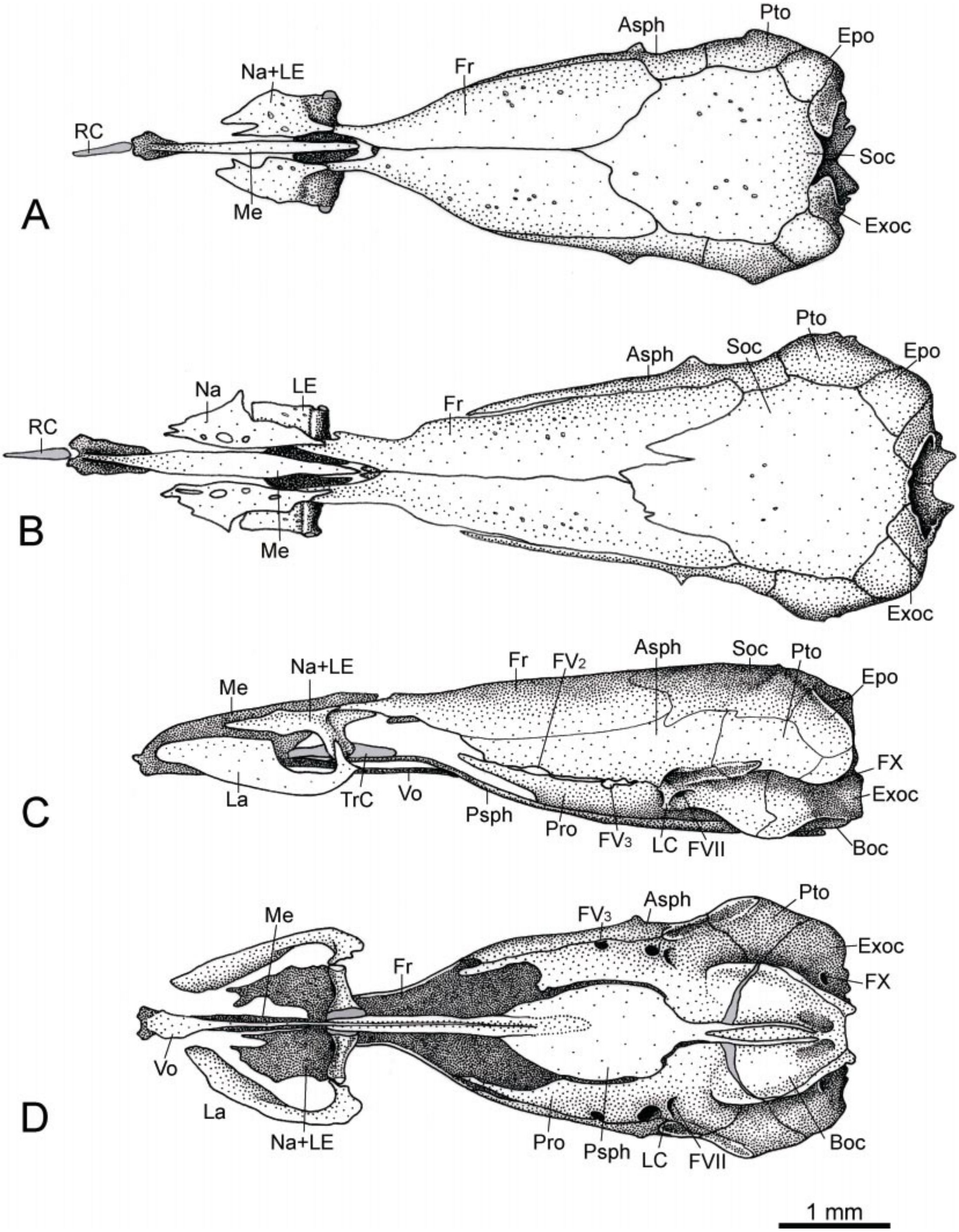

Fig. 10. *Chendol lubricus*, CMK 10638, neurocranium, cartilage in gray. **A.** 38.2 mm, dorsal view. **B.** 50 mm, dorsal view. **C.** 38.2 mm, lateral view. **D.** 38.2 mm, ventral view.

is less conspicuous than in *C. keelini*. Unlike *C. keelini*, the anterior tip of the large prootic fails to contact the frontal but rather ends freely in the orbital region (fig. 10C, D). Cranial nerves $V_{2,3}$ and VII have their openings in the suture between the autosphenotic and prootic (fig. 10C, D). Both bones do not reach anteriorly far enough to enclose the exit of V_1 from the braincase. Parietals are lacking (fig. 10A, B) as in *C. keelini*. The parasphenoid has a different shape than in *C. keelini*. Its anterior part is narrower and widens suddenly at the level of the anterior tips of prootic and autosphenotic but narrows again abruptly at the level of the anterior articulation of the hyomandibular (fig. 10D). Its caudal end bifurcates but does not extend beyond the basioccipital. The other bones of the occipital region are similar to the condition described for *C. keelini* except that the exoccipitals are clearly separated by the supraoccipital (fig. 10A, B).

HYOPALATINE ARCH AND OPERCULAR APPARATUS (fig. 11): The principal arrangement and shape of the different bones that comprise the hyopalatine arch and lower jaw are similar to those in *C. keelini*. There are a few differences between the two specimens of *C. lubricus*, however. In the 38.2-mm specimen there is no dorsal lamina of membrane bone of the metapterygoid bridging the cartilaginous strip between this bone and the quadrate (fig. 11 A, B), but there is a short lamina present in the 50-mm specimen (not illustrated). The basal part of the ectopterygoid in both specimens is comparatively broader than in *C. keelini*. The bones of the opercular apparatus are less stained than in *C. keelini*. Their distal parts in particular picked up almost no stain and their precise shape and extension had to be studied by transferring them to ethanol and observing them in front of a black background.

HYOID, UROHYAL, AND BRANCHIAL ARCHES (fig. 12): There are no striking differences in the arrangement of the bones of the hyoid.

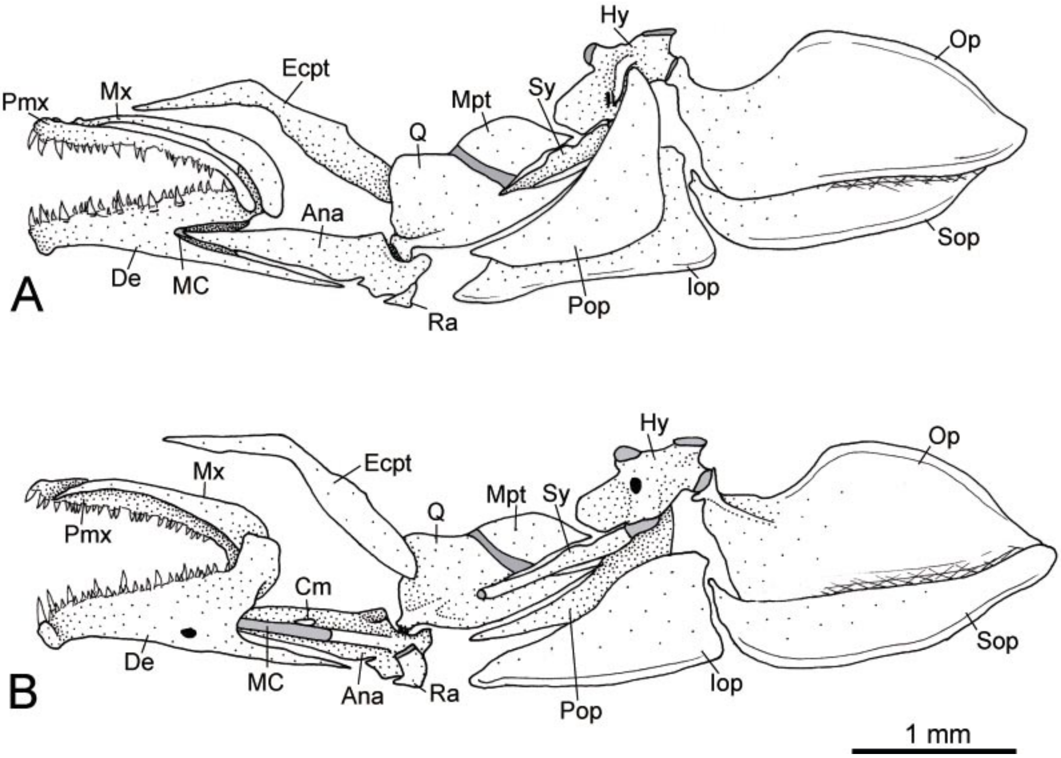

Fig. 11. *Chendol lubricus*, CMK 10638, 38.2 mm, hyopalatine arch, upper, and lower jaws, cartilage in gray. **A.** Lateral view. **B.** Medial view. Unstippled areas of opercular bones not well stained.

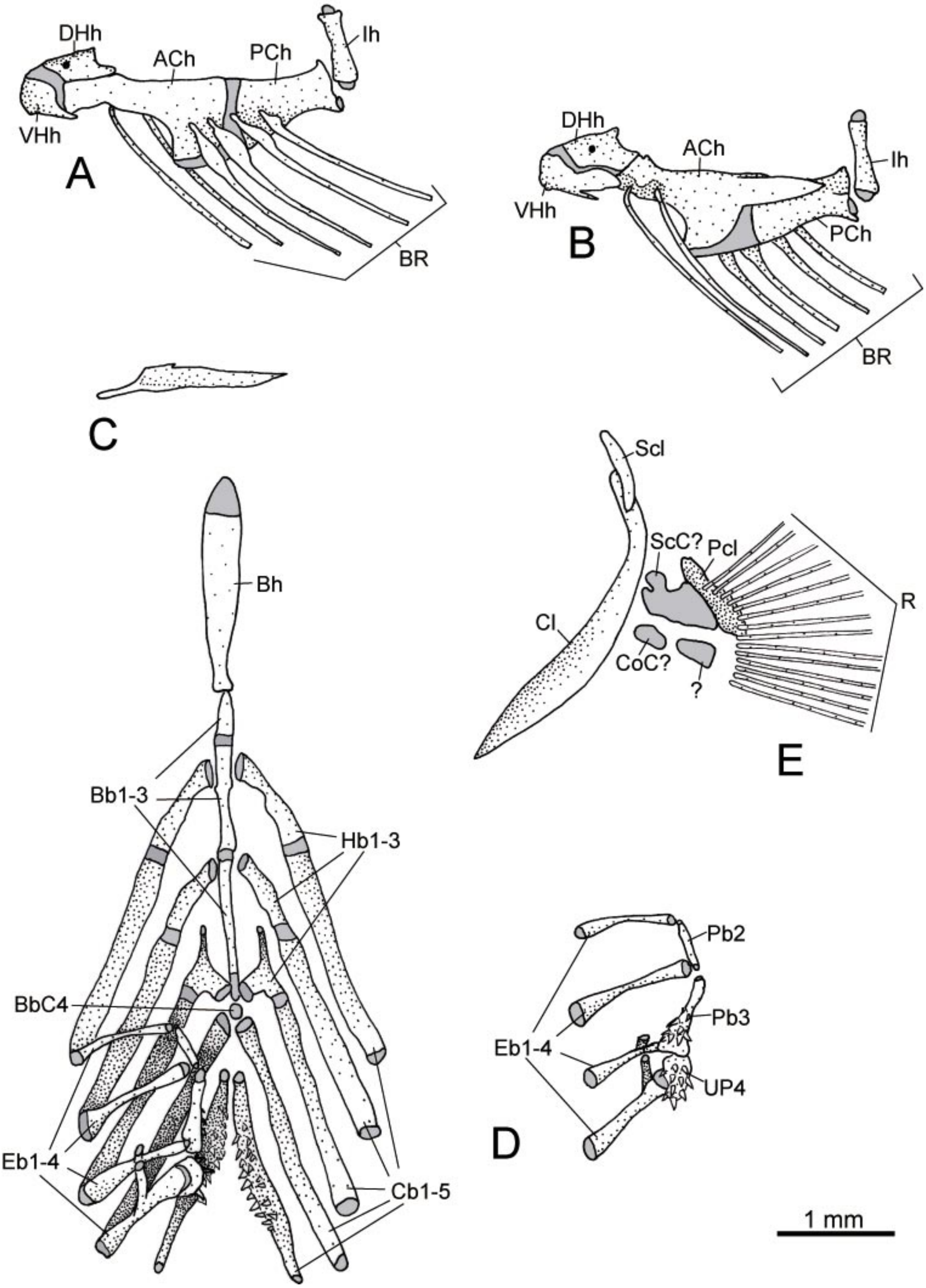

Fig. 12. *Chendol lubricus*, CMK 10638, 38.2 mm, cartilage in gray. **A.** Hyoid, lateral view. **B.** Hyoid, medial view. **C.** Urohyal, lateral view. **D.** Gill arches, dorsal view, dorsal gill arches of right side removed and shown in ventral view. **E.** Shoulder girdle.

The branchiostegal rays show the same pattern of articulation with the ceratohyals as in *C. keelini*, that is, the anterior two articulate on the medial face of the anterior ceratohyal, the posterior four on the lateral face of both anterior and posterior ceratohyal (fig. 12A, B). The urohyal is much shallower (fig. 12C), lacking the vertical lamina that characterizes the urohyal of *C. keelini*.

The most obvious difference between *C. lubricus* and *C. keelini* in the branchial arches is the lack of teeth on hypobranchial 3 in both specimens of the former (fig. 12D). The prominent anteroventral process on hypobranchial 2 in *C. keelini* is lacking in *C. lubricus*.

SHOULDER GIRDLE AND PECTORAL FIN (fig. 12E): This character complex is less developed and ossified compared to *C. keelini*. Both dermal bones, the cleithrum and the supracleithrum are narrower. There is also a postcleithrum present but it is weakly stained. The endoskeletal support of the pectoral fin is represented by only three separate pieces of cartilage, a larger upper one and two smaller ones below it (fig. 12E). They probably correspond to the three elements reported in *C. keelini*. No ossification of these elements could be detected in the 38.2-mm specimen (fig. 12E), but a slight pinkish stain in the 50-mm specimen may be evidence of light ossification. There may also have been some slight decalcification of thin bony tissue during the alcian blue staining step because both specimens are double stained.

VERTEBRAL COLUMN, DORSAL, ANAL, AND CAUDAL FINS (fig. 13): The vertebral column of *C. lubricus* consists of 69 vertebrae. Ribs are developed on 30 or 31 vertebrae, starting with no. 4 or 5, respectively. They are much shorter and smaller compared to those of *C. keelini* and hardly reach the length of the parapophyses with which they articulate (fig. 13B, C). They are least developed in the middle part between about vertebrae 15 and 30 (fig. 13B) and seem to be missing on some of these vertebrae in contrast to the situation in *C. keelini*. There are no epicentral bones in the two available specimens (fig. 13A). As in *C. keelini*, the anterior tip of the first vertebra is modified into a ball-like process for articulation with the socket in the occipital region of the skull (fig. 13A). In the ventral midline it also has a keel-like process (fig. 13A), which is less prominent than in *C. keelini*. The neural spines of the anterior three (small specimen, fig. 13A) to five (large specimen) vertebrae are expanded. The anterior additional neural spinelike projections of the first few vertebrae in *C. keelini* are lacking altogether in *C. lubricus* (fig. 13A). Compared to *C. keelini*, the characteristic fenestrae at the base of the neural spines are much smaller and less conspicuous in *C. lubricus* (fig. 13B). They are developed on vertebrae 5–29 in the 50-mm specimen (fig. 13B), but only on vertebrae 4–9 in the 38.2-mm specimen. All subsequent vertebrae lack the dorsomedian bony bridge between the parapophyses and the neural spine (fig. 13C). Hemal spines are present on 35 vertebrae starting with vertebra 35. The dorsal fin of the 50-mm specimen consists of 38 pterygiophores, of which the first 37 are serially associated with fin rays, and the last one is not. In the 38.2-mm specimen there are 36 pterygiophores and fin rays, with the first pterygiophore bearing a supernumerary ray in addition to its serially associated ray and the last one lacking a serially associated ray. The dorsal fin starts between vertebrae 31 and 32 (50-mm specimen) or 32 and 33 (38.2-mm specimen) respectively. There are 38 anal fin pterygiophores in the 50-mm specimen, with the first 37 being serially associated with fin rays and the last one lacking a serially associated ray. The 38.2-mm specimen has 37 anal-fin pterygiophores, with the first 36 being serially associated with rays and the last lacking a serially associated ray. The first proximal-middle radial in both specimens is rudimentary. Distal radials occur on all ray-bearing pterygiophores of the dorsal and anal fins. The caudal fin consists of six rays and is confluent with the anal and dorsal fins (fig. 13D). Its rays are supported by a single hypural. In both specimens, the last anal fin ray and distal radial, being serially associated with the penultimate proximal middle radial, are very short and closely approach the terminal centrum with the hypural plate (fig. 13D). This may have caused Kottelat and Lim's (1994: 187) erroneous description of *C. lubricus* as having seven caudal-fin rays. Meristic data for the two specimens of *C. lubricus* are summarized in table 2.

There are no scales.

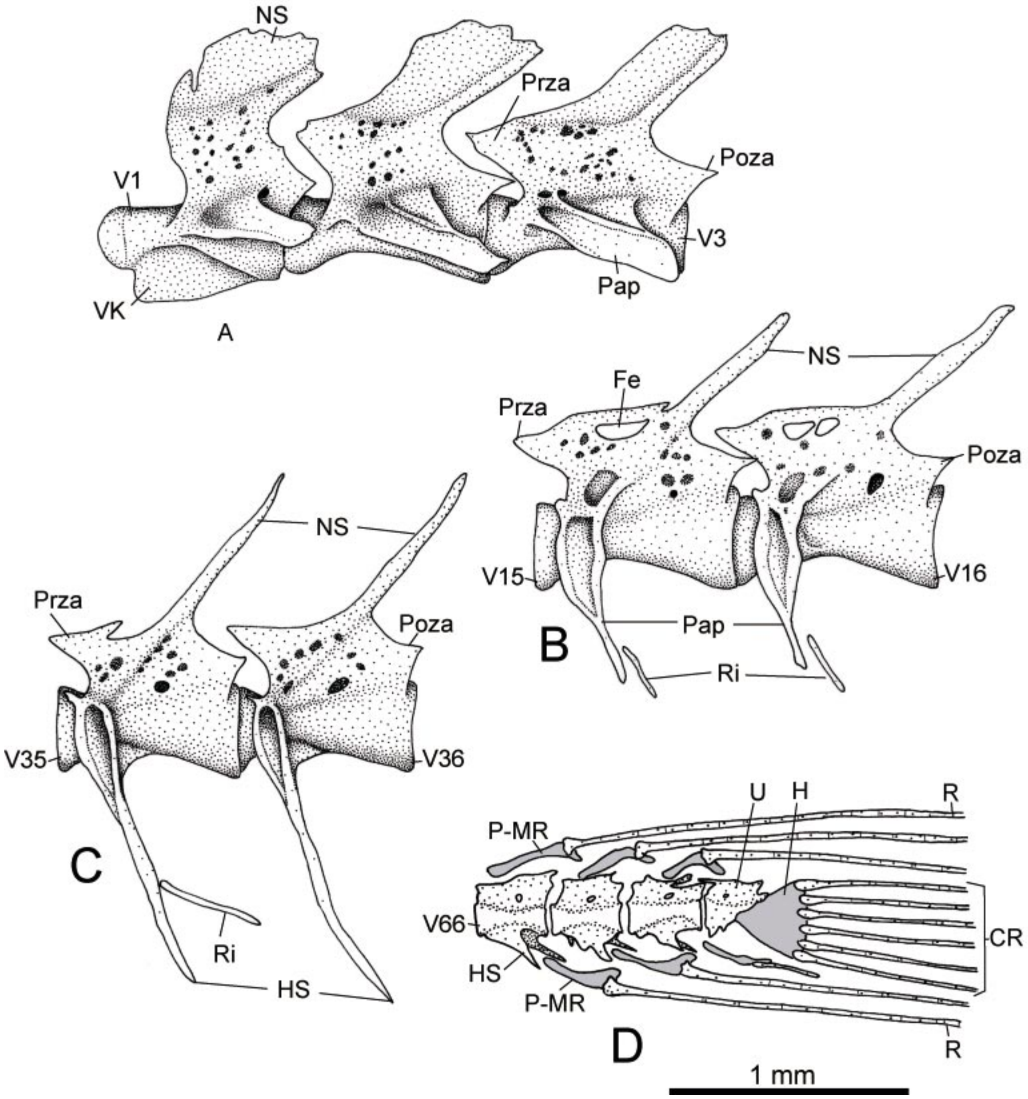

Fig. 13. *Chendol lubricus*, CMK 10638, lateral view, cartilage in gray. Parts A–C are 50 mm. **A.** Vertebrae 1–3. **B.** Vertebrae 15 and 16. **C.** Vertebrae 35 and 36. **D.** Caudal fin supporting structures, preural vertebrae 2–4, and associated dorsal- and anal-fin pterygiophores and rays, 38.2 mm.

Osteology of *Pillaia indica*

Two C&S specimens were available for study, a male 85.8 mm SL and a female 61 mm SL. Our specimens most likely belong to *Pillaia indica* (see remarks in Materials and Methods). This species and *C. keelini* are the largest chaudhuriids with the fewest modifications (i.e., reductions related to small size). There are numerous neuromasts present on the head and there is a lateral line along the body, not mentioned in the original description (Yazdani, 1972).

Neurocranium (fig. 14): The shape of the neurocranium in the larger male *P. indica* is conspicuously more elongate than in *C. keelini*, especially in the orbital region but also in the ethmoid region (fig. 14A). This is due to a stronger attenuation of the whole preotic area of the skull. The frontals are apparently fused in the dorsal midline in the larger spec-

TABLE 1

Selected Meristic Data of C&S Specimens of *Chendol keelini*

Compound ural centrum counted as one vertebra.

	Vertebrae total, without/with hemal spines	With ribs, starting with no. 4	Epicentral bone on V1	Dorsal-fin pterygiophores starting between vertebrae (*x*/*y*); dorsal-fin rays	Anal-fin pterygiophores (in front/behind first hemal spine); anal-fin rays	Pectoral-fin rays right + left
ZRC 17779						
50 mm	67, 41/26	38 (39)	both sides	46 (22/23); 45[a]	45 (21/24); 44[a]	16 + 16
CMK 7949						
44 mm	67, 40/27	37	right side only	45 (23/24); 44[a]	42 (17/25); 41[a]	15 + 15
AMNH 217795						
65 mm	68, 40/28	37	left side only	45 (23/24); 44[a]	43 (17/25); 42[a]	15 + 15
60 mm	67, 40/27	37	lacking	44 (22/23); 43[a]	44 (18/25); 43a	16 + 17
44 mm	67, 39/28	36	both sides	45 (22/23); 44[a]	44 (17/25); 43[a]	15 + 15
43 mm	68, 42/26	39	both sides	46 (22/23); 45[a]	44 (20/24); 43[a]	15 + 14
37 mm	68, 41/27	38	right side only	44 (23/24); 44[b]	42 (18/24); 42[b]	not developed
22 mm	66, 41/25	38	right side only	46 (22/23); 45[a]	43 (20/23); 42[a]	not developed

[a] All pterygiophores, except last, are serially associated with fin rays.

[b] As footnote a, but first pterygiophore with supernumerary ray.

TABLE 2

Selected Meristic Data of C&S Specimens of *Chendol lubricus*

	Vertebrae total, without/with hemal spines	With ribs	Dorsal-fin pterygiophores starting between vertebrae (*x*/*y*); dorsal-fin rays	Anal-fin pterygiophores (in front/behind first hemal spine); anal-fin rays	Pectoral-fin rays right + left
CMK 10638					
50 mm	69, 34/35	31 starting with no. 4 on right and no. 5 on left side	38 (31/32); 37[a]	38 (4/34); 37[a]	13 + 12
CMK 10638					
38.2 mm	69, 34/35	30 starting with no. 5 on both sides	36 (32/33); 36[b]	37 (4/33); 36[a]	13 + 14

[a, b] For explanation, see table 1.

TABLE 3

Selected Meristic Data of C&S Specimens of *Pillaia indica*

	Vertebrae total, without/with hemal spines	With ribs, starting with no. 4	Epicentral bone on VI	Dorsal-fin pterygiophores starting between vertebrae (*x/y*); dorsal-fin rays	Anal-fin pterygiophores (in front/behind first hemal spine); anal-fin rays	Pectoral-fin rays right + left
USNM 372577						
85.8 mm	67, 29/38	24	long, both sides	39 (27/28); 39[b]	39 (3/36); 38[a]	9+9
61 mm	64, 28/36	23	long, both sides	35 (27/28); 35[b]	36 (2/34); 36[b]	6+6

[a, b] For explanation, see table 1.

imen (fig. 14A), but traces of a suture are visible in the smaller one. As in the two species of *Chendol*, the lateral ethmoid possesses an anterior dorsal lamina of membrane bone that roofs the posterior part of the olfactory chamber (fig. 14A, B). In ventral view, the lateral ethmoid bears long anterior processes that reach alongside the vomer and mesethmoid to about half of their preorbital length (fig. 14C). The nasal is broad, well developed, and posteriorly overlaps the anterior tip of the fused frontals (fig. 14A). Parietals are lacking. The large supraoccipital bears a pair of curved longitudinal ridges that extend to the posteriormost part of the occiput where they are continued by the epiotic and exoccipital (fig. 14A, B). The supraoccipital separates the exoccipitals in the dorsal midline. The autosphenotic forms most of the lateral wall of the orbital region (fig. 14B). It has a strong lateral process for the origin of the levator arcus palatini. The prootic bears only a short anterior process (fig. 14B, C) and thus differs substantially from the condition in other chaudhuriids except *Nagaichthys*. The parasphenoid is broad over most of its orbital part and tapers less anteriorly (fig. 14C).

HYOPALATINE ARCH AND OPERCULAR APPARATUS (fig. 15): The most obvious difference from all other chaudhuriids, except *Nagaichthys* (see fig. 23), in the hyopalatine arch is the presence of only one element in the upper jaw, which has been interpreted in the past as a fused maxilla and premaxilla by Yazdani (1978) and Travers (1984a). The element is a strong, curved bone with numerous teeth on its ventral face. As there are no data on its ontogeny, its identity cannot be resolved at the moment. The lower jaw is also quite massive, and especially in the large male it curves out laterally in its middle part (fig. 15). The ectopterygoid is comparatively weakly developed. As in the two *Chendol* species, the metapterygoid has a dorsal membranous anterior process that bridges the cartilage strip between this bone and the quadrate. All remaining bones of the hyopalatine arch differ very little from the condition in *Chendol*.

HYOID, UROHYAL, AND BRANCHIAL ARCHES (fig. 16): The hyoid closely resembles those of other chaudhuriids except that the strong

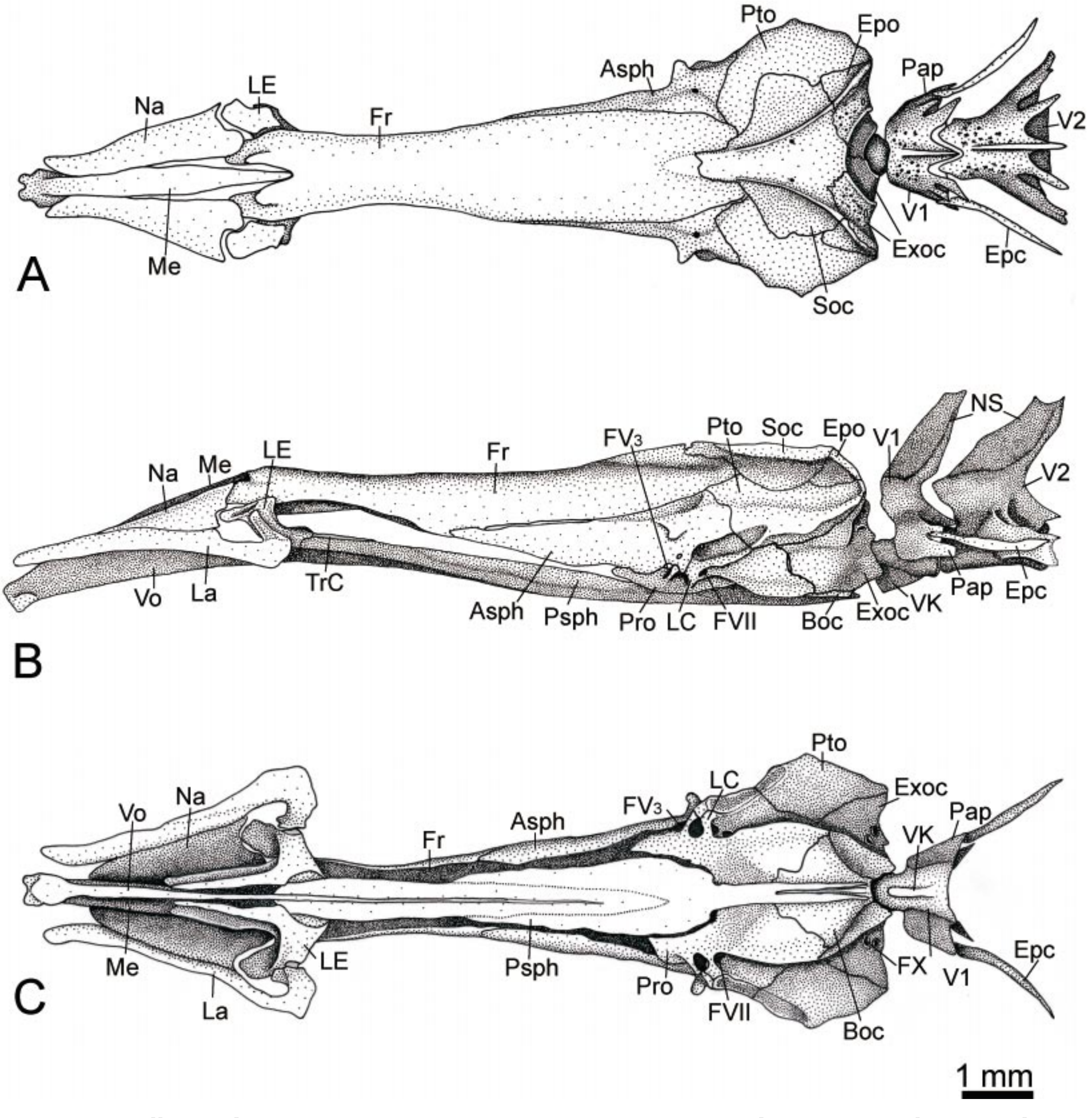

Fig. 14. *Pillaia indica*, USNM 372577, 85.8 mm, neurocranium and anterior vertebrae, cartilage in gray. **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view, only first vertebra shown.

dorsal posterior process of the anterior ceratohyal also covers the dorsolateral face of the posterior ceratohyal and thus can be seen in a lateral view (fig. 16A, B). The urohyal is elongate and its dorsal lamina is comparatively low (fig. 16C).

The overall arrangement of the branchial arches of *P. indica* shows a close resemblance to that of *Chendol*. The following differences, however, can be noted. Basibranchial 3 reaches posteriorly between the anterior tips of ceratobranchials 4 in the larger specimen (fig. 16D), but only to the level of the third hypobranchials in the smaller one. There are no teeth on hypobranchial 3, as in *Chendol lubricus*. Pharyngobranchial 2 is a short stout bone (fig. 16D) and not as elongate as in the other species.

SHOULDER GIRDLE AND PECTORAL FIN (fig. 16E): The dermal part of the shoulder girdle does not differ in any essential features from that of *Chendol*. Its endoskeletal part, how-

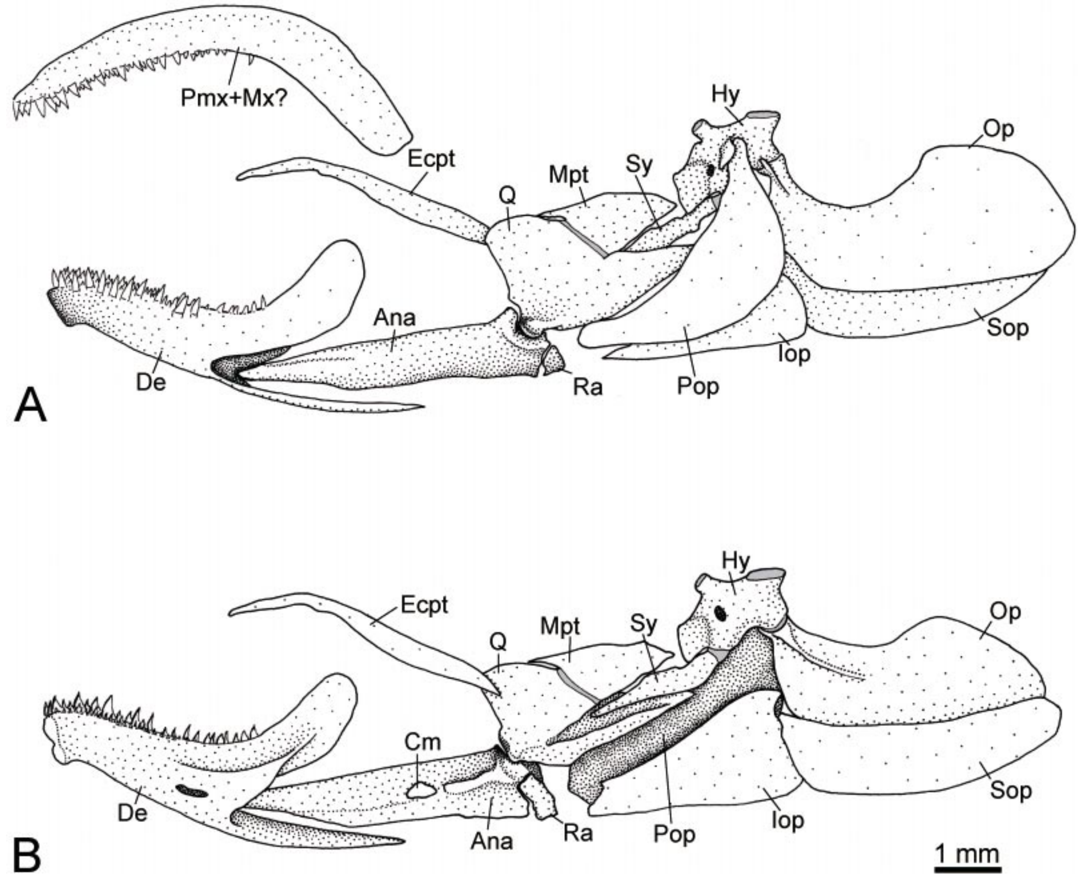

Fig. 15. *Pillaia indica*, USNM 372577, 85.8 mm, hyopalatine arch, upper and lower jaws, cartilage in gray. **A.** Lateral view. **B.** Medial view, upper jaw not shown.

ever, consists only of two ovoid cartilages. Only the upper one shows some ossification and is connected to the cleithrum. Nine pectoral-fin rays are developed in the larger specimen (fig. 16E), but only six in the smaller specimen.

VERTEBRAL COLUMN, DORSAL, ANAL, AND CAUDAL FIN (fig. 17): The two specimens differ slightly in their number of vertebrae. The 85.8-mm male has 67 vertebrae, the 61-mm female 64. The anteriormost vertebra shows the typical ball-and-socket articulation with exoccipitals and basioccipital (fig. 14). It also bears a ventromedian keel of bone. The parapophysis of the first vertebra is strong and its tip articulates with an epicentral bone (fig. 14). The first three vertebrae have an expanded neural spine (figs. 14, 17A). The additional anterior neural-spinelike process found in *C. keelini* is not developed in *P. indica*. Only vertebrae 4–9 show an inconspicuous additional anterior extension (fig. 17A) resembling the anterior spine in *C. keelini*. There are 24 (23 in the female) rib-bearing vertebrae starting with vertebra 4 (fig. 17A). The parapophyses of the 11 anterior vertebrae end in a wide vertical flange. Ribs of these vertebrae are attached to the upper corner of these flanges (fig. 17A). In more posterior rib-bearing vertebrae, in which parapophyses end in a ventrolaterally directed tip, ribs are attached toward the end of these tips (fig. 17B). In more posterior abdominal vertebrae the parapophyses become longer and are directed more ventrally; the last abdominal vertebra of the 85.8-mm specimen, which is vertebra 28, has very long parapophyses, not developed in the 61-mm speci-

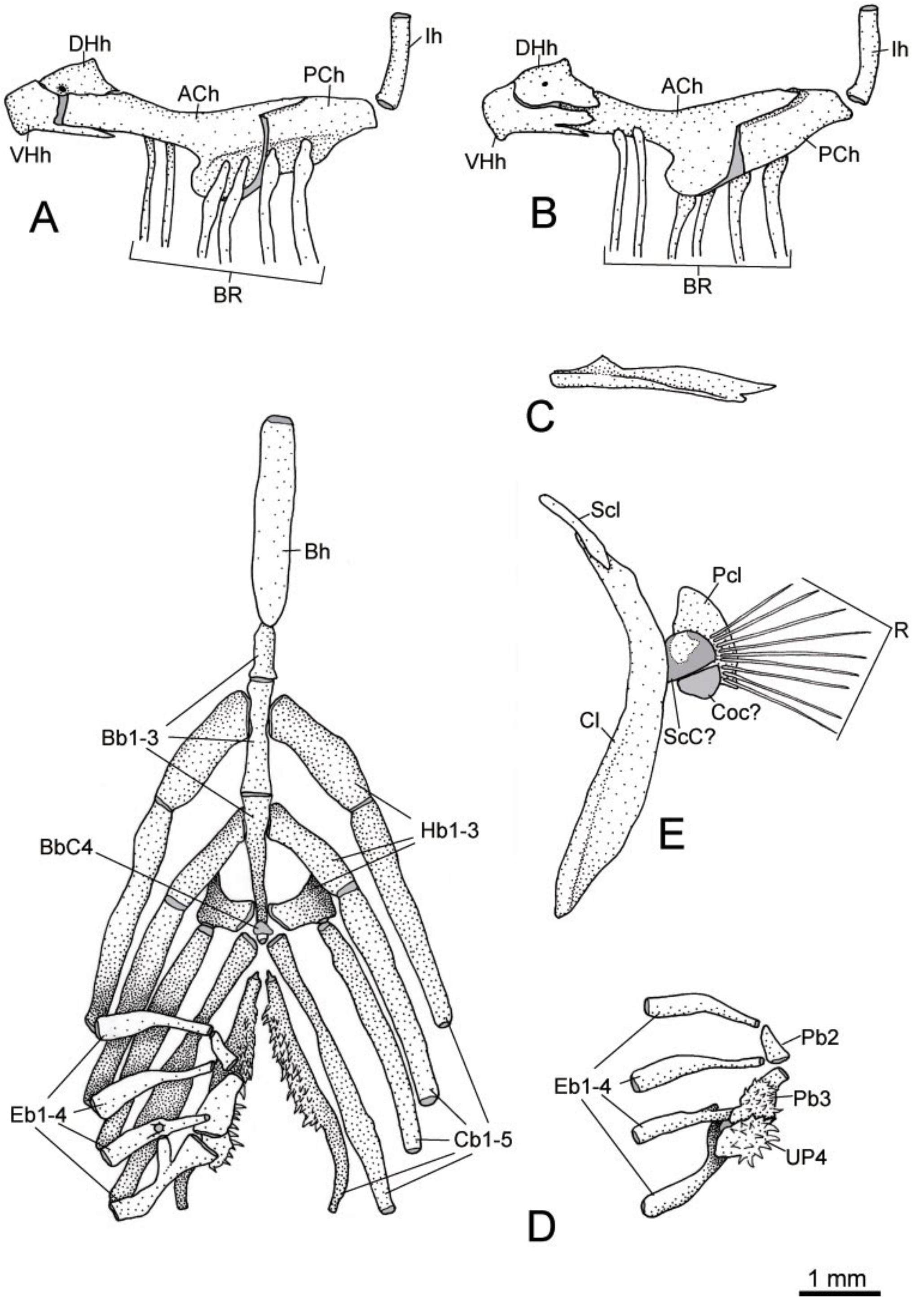

Fig. 16. *Pillaia indica*, USNM 372577, 85.8 mm, cartilage in gray. **A.** Hyoid, lateral view. **B.** Hyoid, medial view. **C.** Urohyal, lateral view. **D.** Gill arches, dorsal view, dorsal gill arches of right side removed and shown in ventral view. **E.** Shoulder girdle, lateral view.

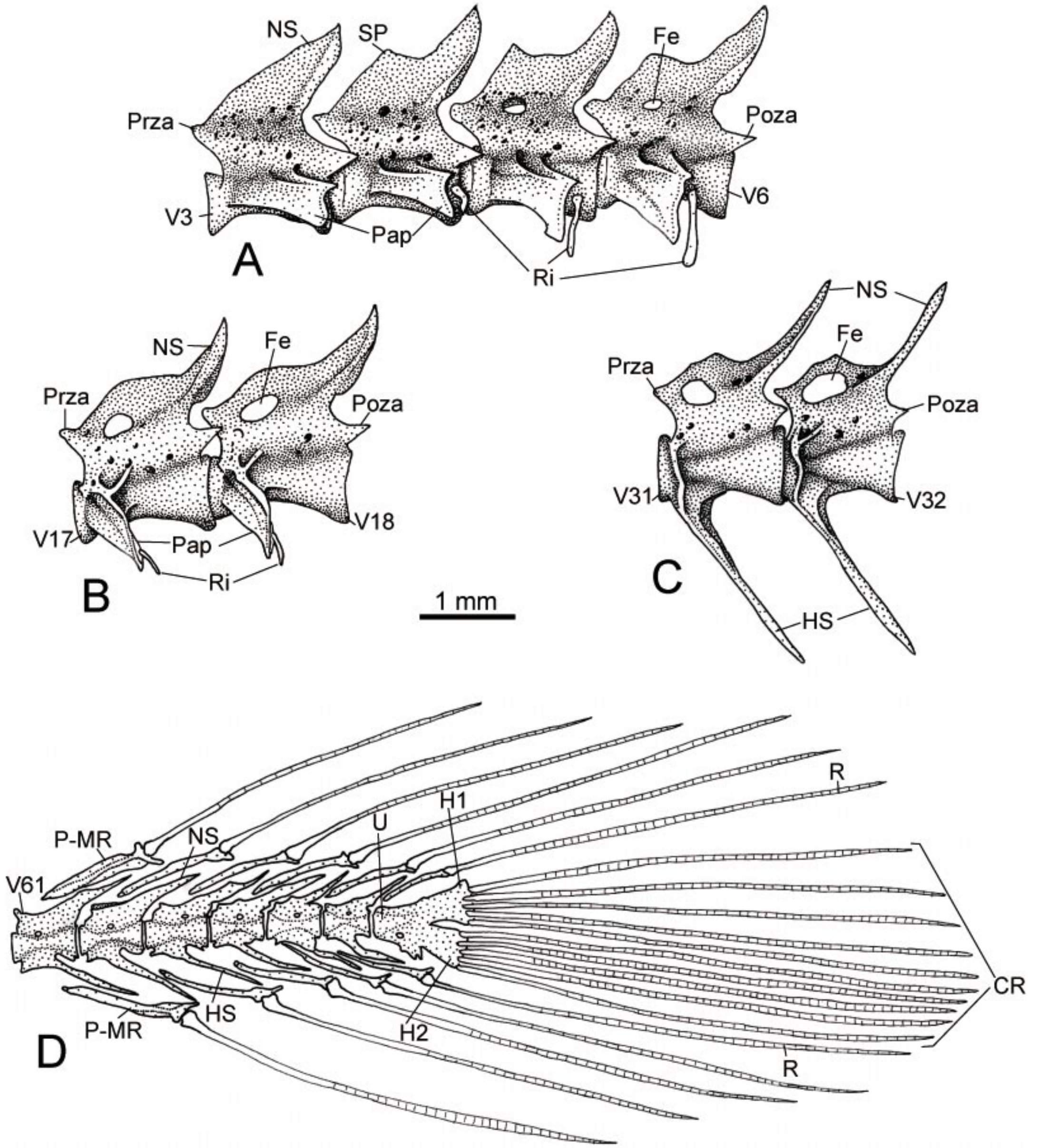

Fig. 17. *Pillaia indica*, USNM 372577, 85.8 mm, lateral view. **A.** Vertebrae 3–6. **B.** Vertebrae 17 and 18. **C.** Vertebrae 31 and 32. **D.** Caudal fin supporting structures, preural vertebrae 2–7, and associated dorsal- and anal-fin pterygiophores and rays.

men. In both specimens, this vertebra bears no ribs. The first caudal vertebra that is the first vertebra with the hemal arches connected in the ventral midline is vertebra 29 in the 85.8-mm specimen and 28 in the 61-mm specimen.

From vertebra five on, the fenestration of the neural arch is developed at the base of the neural spine (fig. 17A). These fenestrae become comparatively larger toward more posterior vertebrae (fig. 17B, C), so that the narrow bony bridge, already described above in the two *Chendol* species, is present in the dorsal midline between the neural arch and the prezygapophyses of the respective vertebrae. Eventually, this bony bridge is absent from all vertebrae posterior to vertebra 39 in the 85.8-mm specimen and vertebra 41 in the 61-mm specimen so that their prezygapophyses and the neural spine are no longer connected dorsally (fig. 17D).

In the 85.8-mm specimen the dorsal fin has 39 pterygiophores and fin rays, with the first pterygiophore bearing a supernumerary ray and the last one without a serially associated ray. The 61-mm specimen has 35 pterygiophores and rays; the first pterygiophore has a supernumerary ray and the last is without a serially associated ray. The dorsal fin starts in both specimens between vertebrae 27 and 28. In the 85.8-mm specimen there are 39 pterygiophores in the anal fin, of which the anterior 38 support serially associated rays and the last lacks a serially associated ray. The 61-mm specimen has 36 pterygiophores and fin rays, with the first pterygiophore supporting a supernumerary ray and the last lacking a serially associated ray. There are three pterygiophores in front of the first hemal spine in the 85.8-mm specimen and two in the 61-mm specimen; the anteriormost pterygiophore of the larger specimen is rudimentary. The last dorsal pterygiophore is situated posterior to the neural spine of the first preural vertebra in the 85.8-mm specimen, but anterior to the neural spine of the second preural vertebra in the other. The last anal pterygiophore sits anterior to the hemal spine of the first preural vertebra in both specimens (fig. 17D). Thus, the dorsal and anal fins are confluent with the caudal. The two hypurals are fused to the ural centrum and each supports five caudal-fin rays (fig. 17D). Meristic data for the two specimens of *P. indica* are summarized in table 3.

There are no scales.

OSTEOLOGY OF *CHAUDHURIA CAUDATA*

Specimens of *Chaudhuria caudata* from several different localities were available for investigation. The one used for the description and the figures is CMK 7934, a specimen from Thailand (Sakhon Nakhon Province: Nong Han). Differences among specimens from the different localities are provided at the end of this section. The specific status and the conspecificity of the specimens studied herein with *C. caudata* from Lake Inle are still uncertain (see Materials and Methods). The wide distribution of the specimens of our sample and the reported smaller differences between specimens from the different localities suggest that there is more than one species involved. In fact, one sample has been described recently as a distinct species, *C. fusipinnis* (Kottelat and Britz in Kottelat, 2000).

Descriptions of the skeleton of *C. caudata* or parts thereof have already been provided by Annandale (1918), Whitehouse (1918), Regan (1919), Annandale and Hora (1923), Travers (1984a), and Britz (1996). Most of the older papers suffered from problems associated with the poor preservation of the material investigated and the minuteness of the objects studied, so that some bones have been overlooked and others misinterpreted.

NEUROCRANIUM (fig. 18): The overall shape of the neurocranium resembles roughly that of the two species of *Chendol*. The following differences are noted. The nasal and lacrimal are poorly ossified at their anterior tips. The lacrimal is much less developed and narrower. Its posterior tip articulates with a prominent cartilaginous knob that arises from the ventral part of the wings of the lateral ethmoid (fig. 18B, C). The lacrimal has no ascending process at its posterior end and thus fails to contact the lateral ethmoid. The latter bone is only a small ossification building the caudal wall of the nasal capsule but lacks an anterior dorsal lamina and any contact with the frontal. The foramen for V_3 of the trigeminal nerve is located exclusively in the prootic bone (fig. 18B, C) and not in the sutural line between prootic and autosphenotic. The most obvious difference to the *Chendol* species and *P. indica* is the presence of a parietal in the skull roof (fig. 18A, B). It is an ovoid bone overlying the lateral part of the supraoccipital, the caudal part of the frontal, the anterior part of the epiotic, and the medial area of the pterotic. Both exoccipitals meet in the dorsal midline and thus keep the supraoccipital from bordering the foramen magnum (fig. 18A).

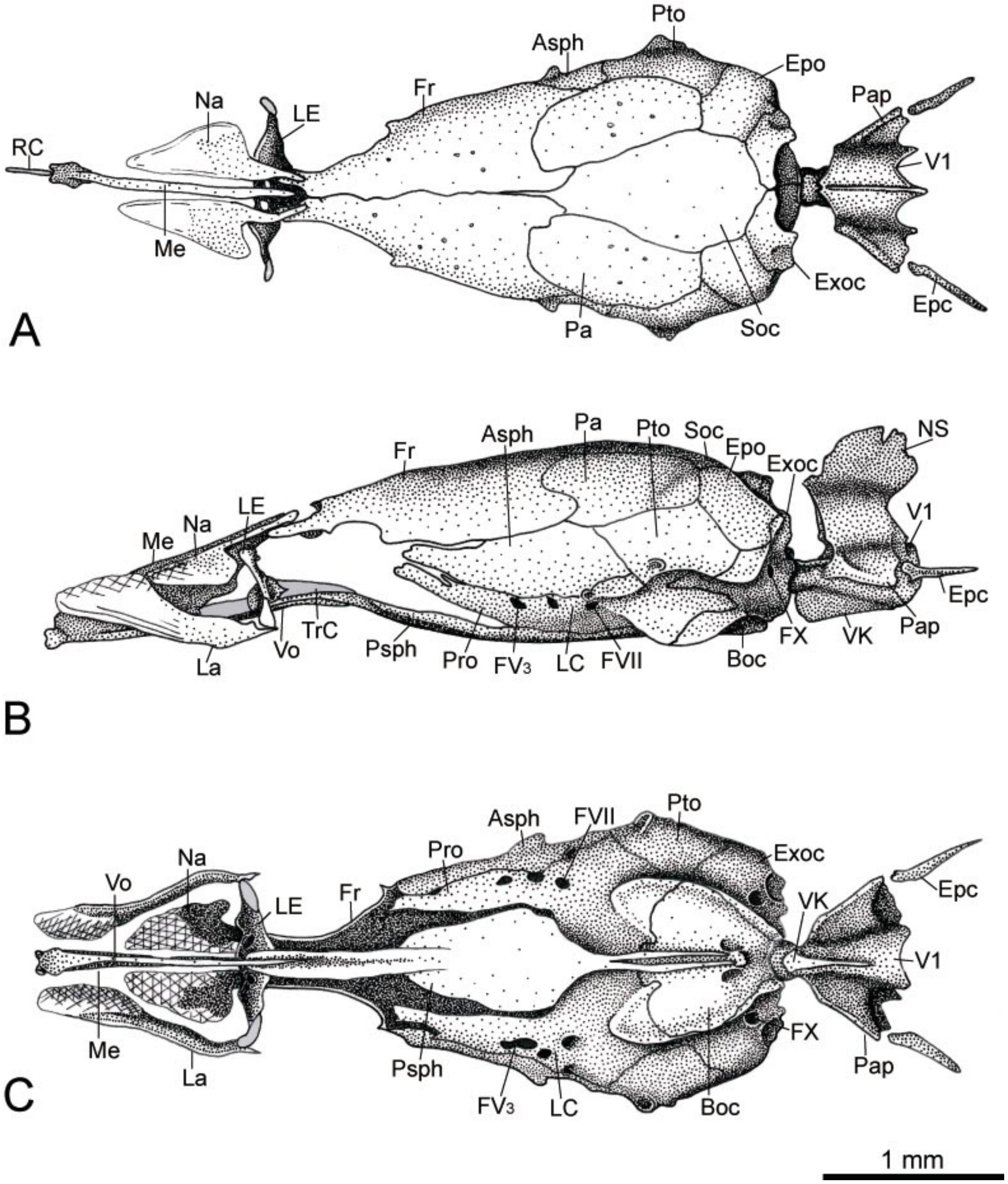

Fig. 18. *Chaudhuria caudata*, CMK 7934, 52 mm, neurocranium and first anterior vertebra, cartilage in gray. **A.** Dorsal view. **B.** Lateral view, rostral cartilage not shown. **C.** Ventral view, rostral cartilage not shown. Unstippled areas of nasal and lacrimal not well stained.

HYOPALATINE ARCH AND OPERCULAR APPARATUS (fig. 19): This complex shows principally the same arrangement as in the two species of *Chendol*. There is a prominent anterior dorsal process on the metapterygoid that bridges the cartilaginous strip between this bone and the quadrate. The ectopterygoid has a much wider proximal portion articulating with the medial face of the quadrate (fig. 19B). This part of the ectopterygoid also shows a short but prominent projection at its posterior face. Another difference is the

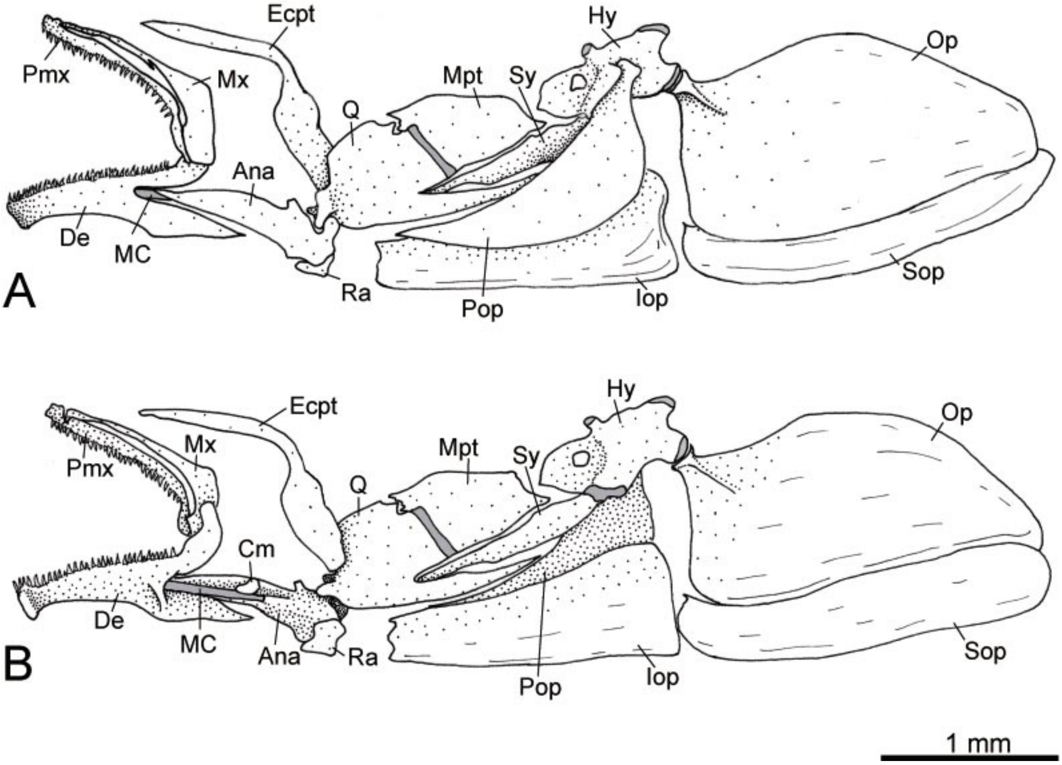

Fig. 19. *Chaudhuria caudata*, CMK 7934, 52 mm, hyopalatine arch and upper and lower jaws. **A.** Lateral view. **B.** Medial view. Unstippled areas of opercular bones not well stained.

presence of a short distinct process on the posterior part of the anguloarticular from which a strong ligament originates extending to the posterior arm of the maxilla.

HYOID, UROHYAL, AND BRANCHIAL ARCHES (fig. 20): These elements are not significantly different in shape or arrangement from the condition in *Chendol* or *Pillaia*. The urohyal (fig. 20C) has a shallower vertical lamina than *C. keelini*, but a comparatively deeper one than in *C. lubricus* or *P. indica*.

The branchial arches (fig. 20D) show a similar structure as in the *Chendol* species and *P. indica*. There are several teeth on hypobranchial 3 as in *C. keelini*, but unlike *P. indica*. A difference, however, is the relative size of pharyngobranchial three with its fused toothplate to the fourth upper toothplate behind it. In *Chendol* species and in *P. indica*, pharyngobranchial 3 is smaller than the fourth toothplate (figs. 4D, 12D, 16D), but in *C. caudata* the former is larger, almost double the size of the latter (fig. 20D). Hypobranchial 2 has an anteroventrally directed process, as in *C. keelini*.

SHOULDER GIRDLE AND PECTORAL FIN (fig. 20E): The three exoskeletal parts of the shoulder girdle, the cleithrum, supracleithrum, and postcleithrum, show a similar structure as in *Chendol* and *Pillaia*. There are, however, differences in the endoskeletal part. There is only an undivided block of cartilage present with two weak ossifications (fig. 20E)—one at the dorsal area and one at the ventral area separated by a broad zone of cartilage. The upper ossification is pierced by a foramen. This condition is difficult to compare with either the adult condition of *C. keelini* in which three or four pieces are present (fig. 6A), that in *C. lubricus* with its three unossified parts (fig. 12E), or that in *P. indica*, which has two cartilages (fig. 16E).

VERTEBRAL COLUMN, DORSAL, ANAL, AND CAUDAL FINS (fig. 21): The figured *Chaudhuria caudata* has 73 vertebrae, more than any of the *Chendol* species or *P. indica*, although

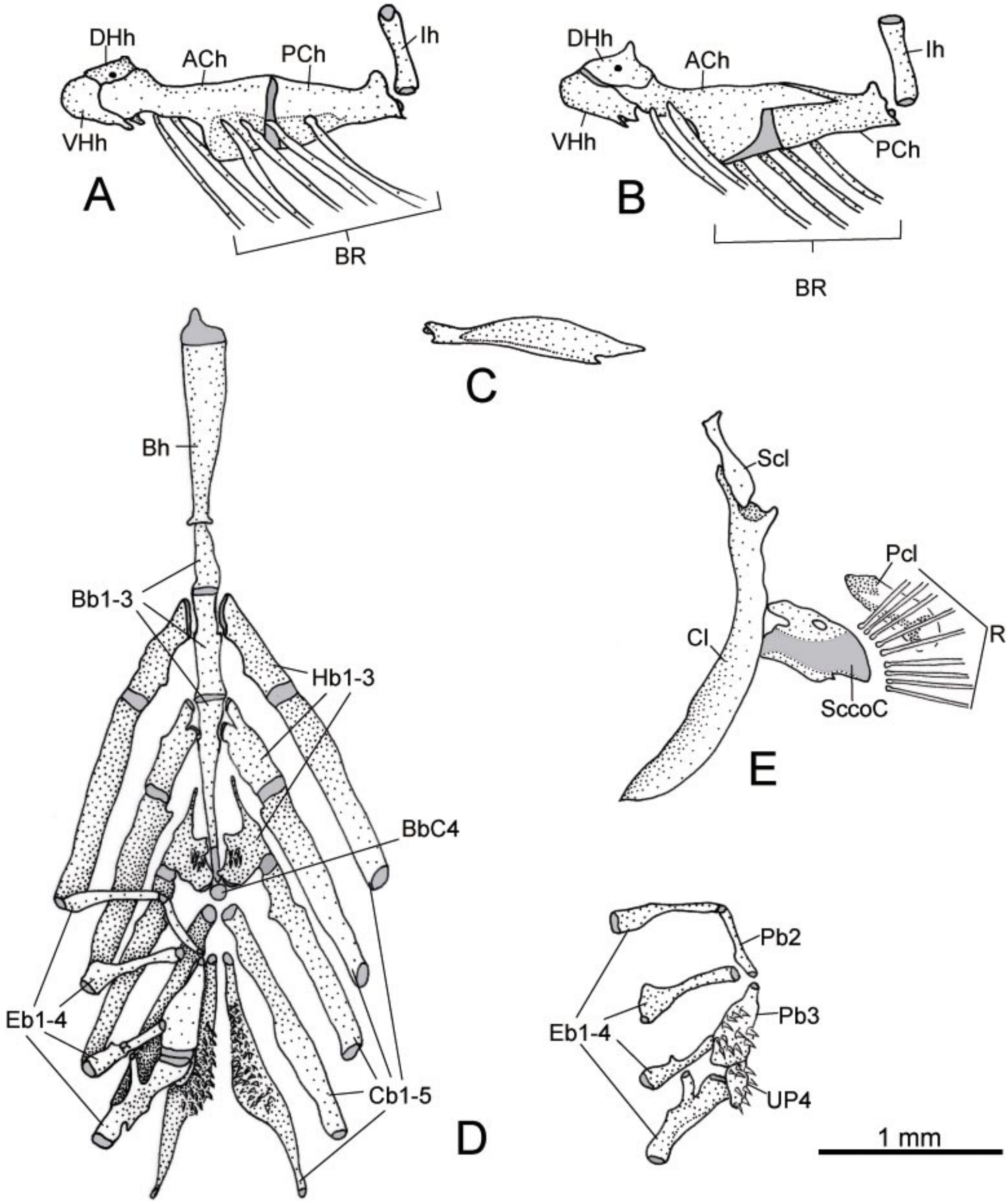

Fig. 20. *Chaudhuria caudata*, CMK 7934, 52 mm, cartilage in grey. **A.** Hyoid, lateral view. **B.** Hyoid, medial view. **C.** Urohyal, lateral view. **D.** Gill arches, dorsal view, with dorsal gill arches of right side removed and shown in ventral view. **E.** Shoulder girdle, lateral view.

their number varies according to the sample (see table 4). The first vertebra bears a strong medioventral keel (fig. 18B), as in other chaudhuriids, and its parapophysis supports a stout epicentral bone (fig. 18). The first four vertebrae possess an expanded neural spine (figs. 18B, 21A). From vertebra four on, there is an anterior spinelike projection in front of the actual neural spine (fig. 21A). This projection becomes comparatively shorter toward posterior vertebrae (fig. 21B, C) and is eventually lacking on vertebrae of

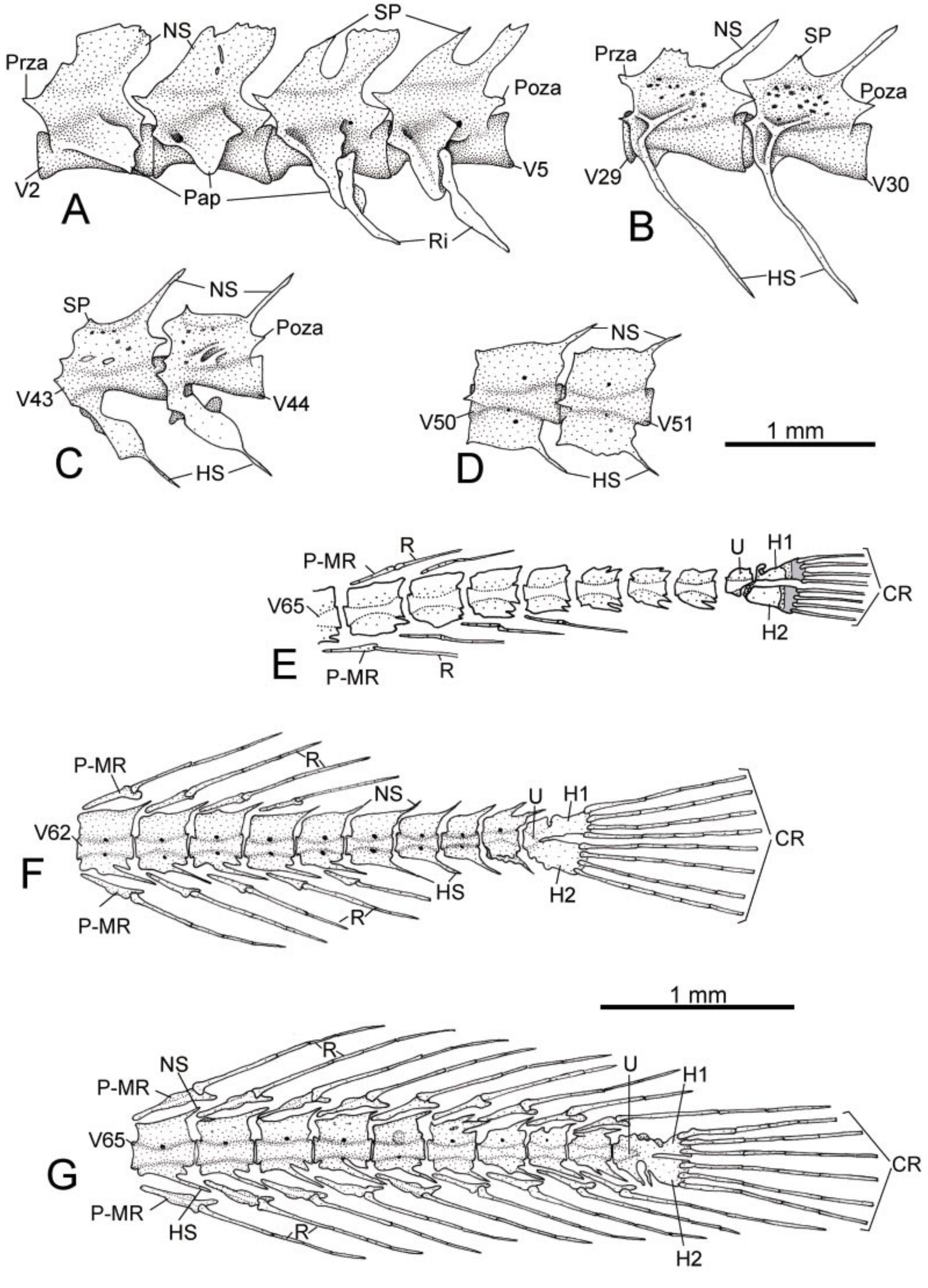

Fig. 21. **A–E.** *Chaudhuria caudata*, CMK 7934, 52 mm, lateral view. **A.** Vertebrae 2–5. **B.** Vertebrae 29 and 30. **C.** Vertebrae 43 and 44. **D.** Vertebrae 50 and 51. **E.** Caudal fin supporting structures, preural vertebrae 2– and associated dorsal- and anal-fin pterygiophores and rays. **F.** *C. caudata*, CMK 15965,

the posterior caudal region (fig. 21D, E). The characteristic fenestration of the neural arches of anterior vertebrae, present in *Chendol* and *Pillaia*, is lacking in this specimen of *Chaudhuria* (fig. 21A–E, but see below for *Chaudhuria* from other localities). There are 24 vertebrae bearing well-developed ribs starting with vertebra 4 (fig. 21A). The first vertebra with a hemal spine that is also the first one without a rib is vertebra 28. There are in total 46 vertebrae with hemal spines. From vertebra 48 on, hemal arches develop wide lateral expansions distally (fig. 21C), which in more posterior vertebrae (from no. 49 on) contact and fuse to a lamina of bone that extends from the lower face of the centrum ventrally, resulting in a cylindrical hemal arch with a very broad base in lateral view (fig. 21D). Toward the caudal fin the neural and hemal spines become shorter so that the last 10 vertebrae appear to lack them completely (fig. 21E). The dorsal fin has 43 pterygiophores and 42 rays starting between vertebrae nos. 26 and 27. The first 42 pterygiophores are serially associated with rays, but the last one lacks a serially associated ray. The anal fin consists of 44 pterygiophores, with three in front of the first hemal spine and 41 behind it. The first pterygiophore bears a supernumerary ray and the last one lacks a serially associated ray. In contrast to the two *Chendol* species and *P. indica*, the caudal fin is separated from the dorsal and anal fin by a gap of four vertebrae. Two hypurals support eight caudal-fin rays (fig. 21E).

DIFFERENCES AMONG *CHAUDHURIA* FROM DIFFERENT LOCALITIES (for meristic differences refer to table 4): *Chaudhuria caudata* from Malaysia, Terengganu (CMK 8241): All six specimens from this lot stained poorly with alizarin. However, a few characters could still be noted. The exoccipitals are separate in four specimens and almost meet in two. In four specimens there is an epicentral bone on both sides, but in two specimens it is developed on the right side only. There are no fenestrations on the neural arches in any of the specimens, as in CMK 7934. Unusually, the hemal spines of the first 12–18 vertebrae posterior to the last rib-bearing vertebra fail to meet in the ventral midline.

Chaudhuria caudata from Viet Nam, Phu Quoc (AMNH 217415): The shape of the postorbital skull appears to be shorter and wider than in CMK 7934. Exoccipitals meet in the dorsal midline. There is no fenestration of the neural arches. Vertebra 43 is the first vertebra with an expanded hemal arch, and vertebra 49 is the first with this expansion being continuous with the ventrolateral face of its centrum. Neural and hemal spines of the caudal vertebrae become smaller toward the caudal fin but are still discernible. The caudal fin bears seven rays, four articulating with the upper and three with the lower hypural.

Chaudhuria caudata from Laos, Vientiane Province (CMK 15965): There are no epicentral bones in any of the six specimens. Exoccipitals approach each other closely in the dorsal midline in five and actually contact each other in one specimen. Contrary to *C. caudata* from Thailand and Viet Nam, in most specimens the neural arches of the posterior abdominal and anterior caudal region possess paired fenestrae in the neural arches. On the more caudal vertebrae there are no lateral extensions of the middle part of hemal arches, as those found in CMK 7934 or AMNH 217415. Rather, the bases of the hemal arches are in broad contact with the centra. The first preural centra bear well-developed neural and hemal arches (fig. 21F) and do not have the cylindrical shape as those of CMK 7934 (fig. 21E).

REMARKS ON THE OSTEOLOGY OF *CHAUDHURIA FUSIPINNIS* (CMK 15967): This species has been described only recently (Kottelat and Britz in Kottelat, 2000). Apart from the characters provided in the original description and listed below, there are no significant differences from *C. caudata* (CMK 7934) in the overall shape or arrangement of the skeletal

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34.9 mm, caudal fin supporting structures, preural vertebrae 2–10, and associated dorsal- and anal-fin pterygiophores and rays. **G.** *C. fusipinnis*, CMK 15967, 35 mm, caudal fin supporting structures, preural vertebrae 2–10, and associated dorsal- and anal-fin pterygiophores and rays.

osteology that would warrant a more detailed osteological account of this species.

Chaudhuria fusipinnis differs from *C. caudata* in having the dorsal and anal fins confluent with the caudal fin (fig. 21G), so that the posteriormost pterygiophores of the dorsal and anal fin are located in front of the neural and hemal spines of PU2, respectively (in other *Chaudhuria*, in front of PU5, 6, or 7). This results in a comparatively higher number of dorsal and anal-fin rays. The species is further distinguished by the lack of teeth on hypobranchial three and by only 3+3 caudal-fin rays (fig. 21G). In our six specimens, the anterior five to seven neural spines are expanded. There are no epicentral bones on the first vertebra. In contrast to *C. caudata* from Thailand or Viet Nam, *C. fusipinnis* possesses the paired fenestrae in the neural arch found in other chaudhuriids. Depending on the specimen, fenestration starts already on anterior abdominal vertebrae or is restricted to caudal vertebrae. Additional meristic information is provided in table 4.

OSTEOLOGY OF *NAGAICHTHYS FILIPES*

The description of the skeleton of *Nagaichthys filipes* is based primarily on the C&S paratype. Additional specimens from localities other than the type locality were also available but they may not be conspecific with *N. filipes*, as they differ in several characters (see tables 5, 6).

NEUROCRANIUM (fig. 22): The overall shape of the neurocranium resembles that of *Chendol* and *Chaudhuria* with the exception that in *Nagaichthys* the skull does not taper anteriorly to the same extent as in the other two genera. This makes the frontals almost rectangular in dorsal view (fig. 22A). A further difference is the prootic's anterior extension of membrane bone, which is very short and hardly reaches half the length of the autosphenotic (fig. 22B, C). This condition resembles that in *P. indica* (fig. 14B, C). Thus it encloses the foramina for the hyomandibular trunk of VII and the mandibular branch of V (fig. 22B, C), but not its maxillary and ophthalmic branches. A third major difference is the well-developed supraoccipital crest in *Nagaichthys*, which is lacking in the other taxa. The supraoccipital clearly separates the exoccipitals in the dorsal midline (fig. 22A). As in *Chaudhuria* and *Bihunichthys*, *Nagaichthys* has a parietal, which is lacking in *Chendol* and *Pillaia*.

HYOPALATINE ARCH AND OPERCULAR APPARATUS (fig. 23): The hyopalatine arch also differs in several aspects from that of the other species described above. The ectopterygoid is reduced in size (fig. 23), even more so than in *P. indica* (fig. 15). The anterior arm that runs parallel to the vomer is especially short and thin. It ends just anterior to the lateral ethmoid and unlike in *Chendol*, *Pillaia*, or *Chaudhuria*, does not reach farther anteriorly. Contrary to what was reported in the original description (Kottelat and Lim in Kottelat, 1991), the C&S paratype of *Nagaichthys filipes* has the maxilla and premaxilla fused over most of their length (fig. 23), although the original shape of the bones is still discernible. The anterior process of the metapterygoid is present, though rudimentary, and does not bridge the cartilaginous strip between metapterygoid and quadrate.

HYOID, UROHYAL, AND BRANCHIAL ARCHES (fig. 24): The urohyal is relatively small and has a comparatively high vertical lamina (fig. 24C), but the rest of the hyoid arch is similar to that of the described species. The branchial arches have several reductive characters (fig. 24D): there are no teeth on hypobranchial 3, and the anteroventral process on hypobranchial 2 is lacking. Pharyngobranchial 3 and the fourth upper pharyngeal toothplate have a similar size.

SHOULDER GIRDLE AND PECTORAL FIN (fig. 24E): Other reductive differences distinguishing *N. filipes* from *Chendol*, *Pillaia*, and *Chaudhuria* concern the shoulder girdle and pectoral fin. The supracleithrum is tiny (fig. 24E). The endoskeletal part of the pectoral-fin support consists of a single cartilaginous piece bifurcating proximally at its articulation with the cleithrum. There are three zones slightly stained, which represent weakly ossified areas. There is typically only a single segmented pectoral-fin ray articulating with that piece of cartilage (but see tables 5, 6 for variation). The postcleithrum seems to be absent, although there is a possibility that it is only poorly ossified and did not stain with alizarin.

VERTEBRAL COLUMN, DORSAL, ANAL, AND

TABLE 4

Selected Meristic Data of C&S Specimens of *Pillaia indica* from Different Localities, and *C. Fusipinnis*

	Vertebrae total, without/with hemal spines	With ribs, starting with no. 4	Epicentral bone on V1	Dorsal-fin pterygiophores starting between vertebrae (*x*/*y*); dorsal-fin rays	Anal-fin pterygiophores (in front/behind first hemal spine); anal fin rays	Caudal-fin rays	Pectoral-fin rays right + left
Chaudhuria caudata							
CMK 7934							
52 mm	73, 27/46	24	both sides	43 (26/27); 42[a]	44 (3/41); 44[b]	4 + 4	9 + 9
AMNH 217415							
40 mm	73, 27/46	24	left side	41 (26/27); 40[a]	43 (3/40); 42[a]	3 + 4	7 + 10
CMK 8241							
38 mm	69, 26/43	23	right side	38 (25/26); 38[b]	40 (2/38); 40[b]	4 + 4	6 + 6
32 mm	73, 28/45	25	right side	38 (28/29); 38[b]	39 (3/36); 39[b]	3 + 3	7 + 7
35.5 mm	69, 26/43	23	both sides	37 (26/27); 37[b]	39 (3/36); 39[b]	4 + 4	7 + 6
36 mm	70, 29/41	26	both sides	38 (27/28); 38[b]	39 (3/36); 39[b]	4 + 4	5 + 6
35 mm	72, 26/46	23	both sides	40 (26/27); 40[b]	40 (2/38); 40[b]	4 + 3	7 + 6
34 mm	caudal area damaged	24	both sides	—	—		6 + 6
CMK 15965							
26.5 mm	67, 25/42	23	—	37 (25/26); 36[a]	39 (3/36); 39[b]	4 + 4	6 + 6
31 mm	70, 27/43	24	—	37 (27/28); 37[b]	38 (2/36); 38[b]	4 + 4	8 + 7
33.6 mm	71, 28/43	24	—	39 (27/28); 38[b]	40 (3/37); 40[b]	4 + 4	8 + 6
34.9 mm	71, 28/43	25	—	37 (28/29); 37[b]	40 (3/37); 40[b]	4 + 4	7 + 7
41.8 mm	70, 27/43	24	—	40 (26/27); 39[a]	38 (3/35); 38[b]	4 + 4	9 + 8
42.7 mm	70, 27/43	23	—	38 (23/24); 38[b]	39 (2/37); 39[b]	4 + 4	9 + 9
Chaudhuria fusipinnis							
CMK 15967							
29.7 mm	74, 27/47	24	—	47 (26/27); 47[b]	47 (3/44); 47[b]	3 + 3	7 + 6
33.8 mm	72, 27/45	24	—	46 (25/26); 46[b]	46 (3/43); 46[b]	3 + 3	9 + 8
35.3 mm	73, 28/45	25	—	46 (25/26); 46[b]	46 (4/42); 46[b]	3 + 3	9 + 9
34.6 mm	71, 28/43	25	—	44 (25/26); 44[b]	45 (5/40); 44[a]	3 + 3	9 + 10
35 mm	74, 29/45	26	—	47 (26/27); 46[a]	46 (3/43); 46[b]	3 + 3	9 + 9
36.5 mm	74, 29/45	26	—	48 (26/27); 47[a]	46 (4/42); 45[a]	—	8 + 8

[a, b] For explanation, see table 1.

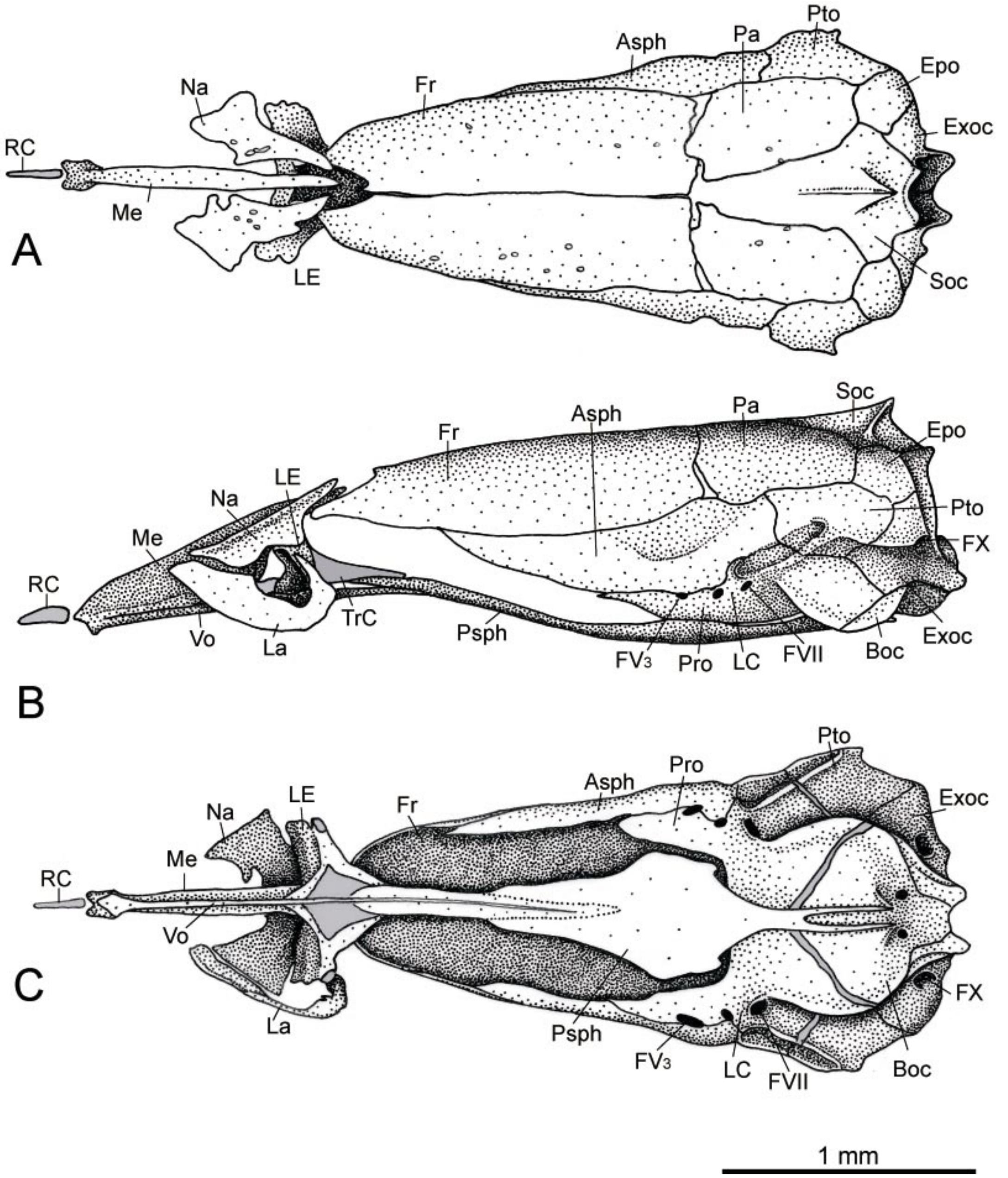


Fig. 22. *Nagaichthys filipes*, CMK 6660, 30.8 mm, neurocranium, cartilage in gray. **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view.

CAUDAL FINS (fig. 25): The C&S paratype of *N. filipes* shows a formerly damaged (bitten off?) and later regenerated caudal fin, as already remarked by Kottelat and Lim (in Kottelat, 1991). The total 54 vertebrae may be slightly low for this species, due to the regenerated caudal region. No epicentral bones are developed. The neural spines of the first two vertebrae are expanded (fig. 25A). There are 23 rib-bearing vertebrae starting with no. 4. Ribs are comparatively short and thin (fig. 25A, B), only one-fourth to one-third the

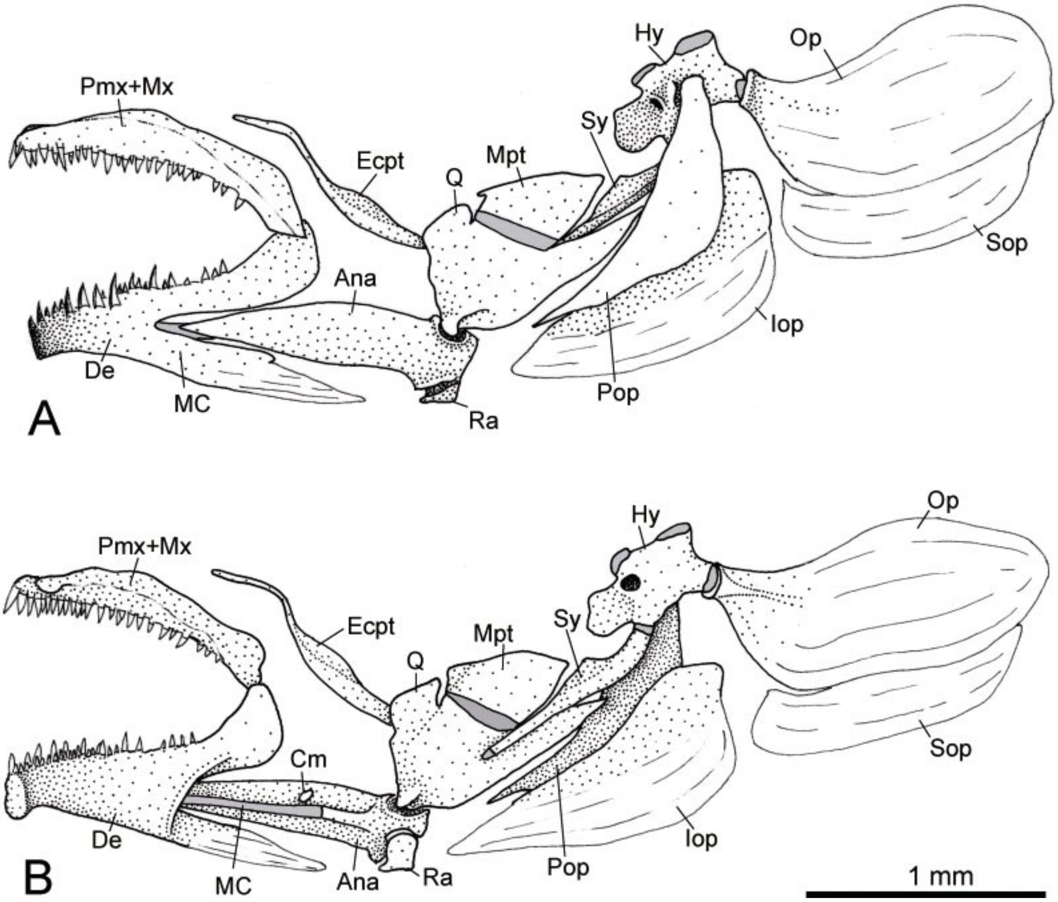


Fig. 23. *Nagaichthys filipes*, CMK 6660, 30.8 mm, hyopalatine arch, upper and lower jaws, cartilage in gray. **A.** Lateral view. **B.** Medial view. Unstippled areas of opercular bones not well stained.

length of the supporting parapophyses, resembling the condition in *C. lubricus* (fig. 13B, C). All 26 abdominal vertebrae show some fenestration of their neural arches (fig. 25A, B). It consists of numerous small foramina on the first seven, but of a large paired foramen on subsequent vertebrae up to 26. As in *Chendol* species, *P. indica*, and some *Chaudhuria*, a bony bridge that extends between the prezygapophyses and the neural spine forms the dorsal border of the foramen (fig. 25B). This bony bridge is absent from all 27 vertebrae with hemal spines (fig. 25C).

The dorsal fin has 29 fin rays and pterygiophores and starts between vertebrae 25 and 26. The anal fin also has 29 fin rays and pterygiophores, with the anterior 28 pterygiophores being serially associated with fin rays and the first pterygiophore supporting a supernumerary ray. There are two pterygiophores in front of the first hemal spine, and 27 behind it. Due to the regenerated caudal area of our specimen of *N. filipes*, this number of dorsal- and anal-fin pterygiophores and rays may be too low (see tables 5, 6 for variation among samples). Nothing definite can be said about the caudal fin of this specimen of *N. filipes*. The last vertebra, no. 54, does not articulate with any fin rays. Caudal to it are several cartilages, modified pterygiophores of the dorsal and anal fin that support seven fin rays thus forming a ‘‘new’’, functional caudal fin.

There are, however, an additional four C&S specimens of *Nagaichthys* available for

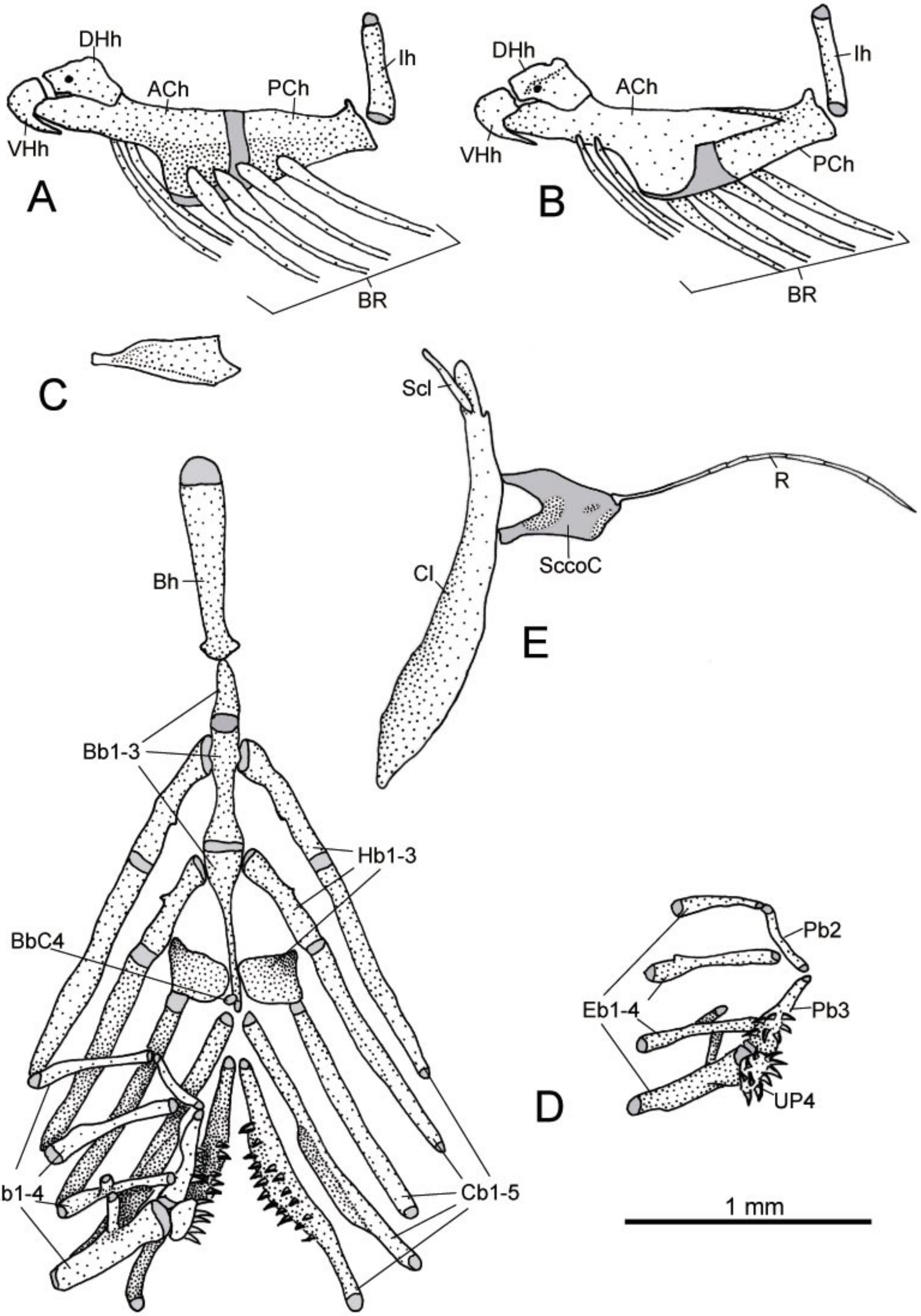


Fig. 24. *Nagaichthys filipes*, CMK 6660, 30.8 mm, cartilage in gray. **A.** Hyoid, lateral view. **B.** Hyoid, medial view. **C.** Urohyal, lateral view. **D.** Gill arches, dorsal view, with dorsal gill arches of right side removed and shown in ventral view. **E.** Shoulder girdle, lateral view.

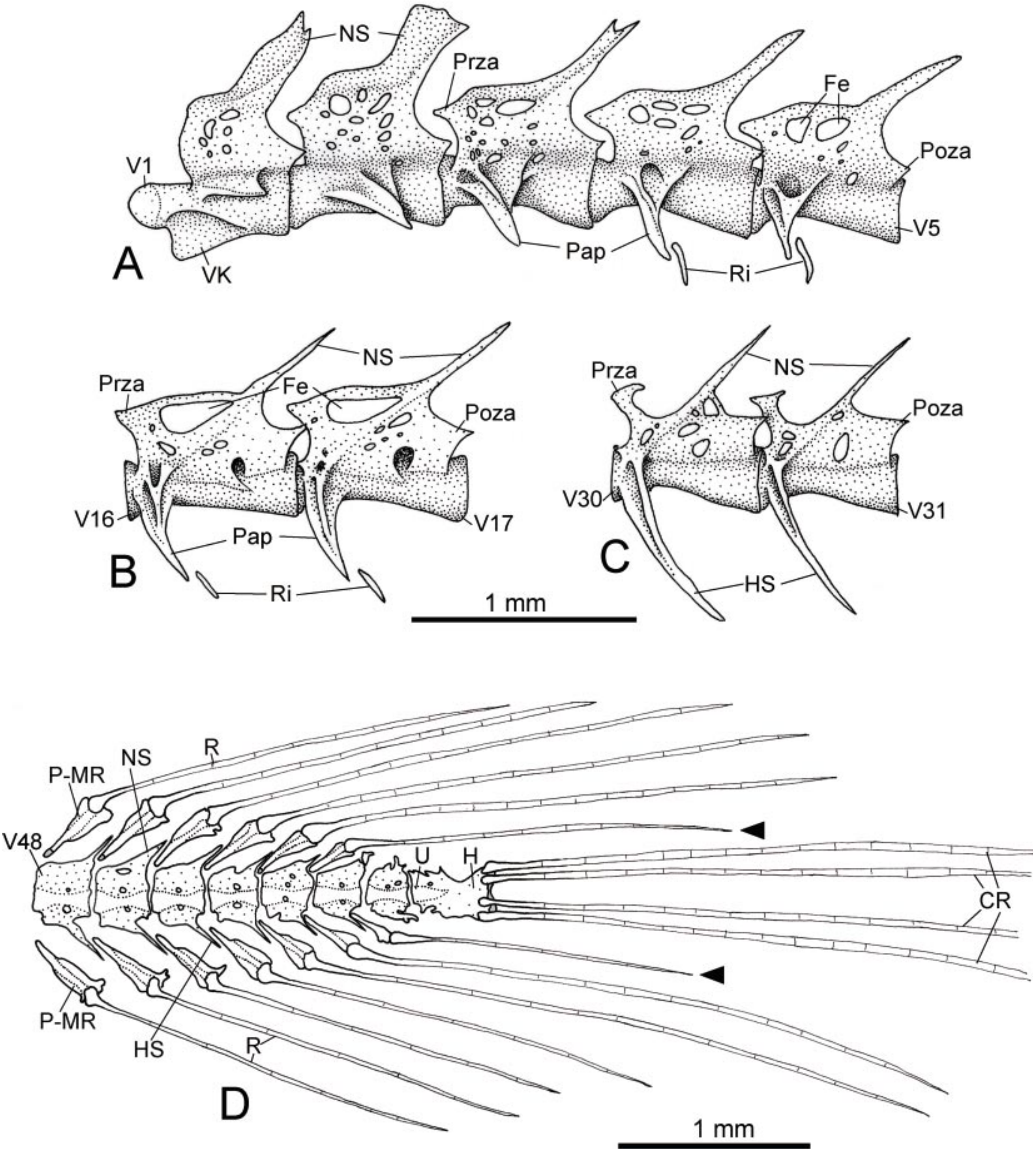


Fig. 25. **A–C.** *Nagaichthys filipes,* CMK 6660, 30.8 mm, lateral view. **A.** Vertebrae 1–5. **B.** Vertebrae 16 and 17. **C.** Vertebrae 30 and 31. D. *Nagaichthys filipes*, CMK 10870, 28 mm, caudal fin supporting structures, preural vertebrae 2–8, and dorsal- and anal-fin pterygiophores and rays, lateral view, cartilage in gray, full length of caudal fin rays not shown; arrows point to shorter last dorsal and anal fin rays, respectively.

study from localities other than the type locality. They agree in all essential details with the description provided above, but, because their caudal fins are undamaged, they provide information on its precise structure. We describe here the caudal fin of the 28-mm specimen of CMK 10870 (from Sarawak, fig. 25D). Dorsal, anal, and caudal fins are confluent. The latter consists of a single hypural fused to the ural centrum and four caudal-fin rays articulating with it. The caudal-fin area is peculiar in that the last dorsal- and anal-fin rays are much shorter than either the penultimate fin ray of dorsal or anal, or the dorsal- or ventralmost caudal-fin ray, resulting in a frayed appearance (fig. 25D, arrowheads). This special arrangement of the caudal-, dorsal-, and anal-fin rays was found in all additional specimens of *N. filipes*.

Differences among the samples of *N. filipes* from various localities in the number of vertebrae and fin rays are provided below in tables 5 and 6. All the alcohol specimens we studied had a number of free neuromasts on the head, although their presence was not specifically mentioned in the original description of *N. filipes* (Kottelat and Lim in Kottelat, 1991).

OSTEOLOGY OF *BIHUNICHTHYS MONOPTEROIDES*

Bihunichthys monopteroides is the smallest chaudhuriid species. Description and figures are based mainly on AMNH 217765, with additional information from CMK 7947.

NEUROCRANIUM (fig. 26): In dorsal view the shape of the neurocranium does not have the strongly attenuated orbital area of *Chendol* (figs. 2, 10), *Pillaia* (fig. 14), and *Chaudhuria* (fig. 18), but is rather fairly rectangular (fig. 26A), resembling more the condition in *Nagaichthys* (fig. 22). *Bihunichthys* differs from *Chendol* species and *P. indica* in the lack of an anterior dorsal lamina on the lateral ethmoid and the presence of a parietal (fig. 26A, B). It differs from all other chaudhuriids in that the anterior membrane bone extensions of the autosphenotic and prootic are narrow, needlelike, and free from each other and from the frontal (fig. 26B). This condition of the two bones, however, is characteristic of smaller juvenile specimens of *Chendol keelini*. Only the foramina for the mandibular branch of the trigeminal nerve and for the facial nerve are present at the suture between prootic and autosphenotic (fig. 26B, C). The exits for the other two branches of the trigeminal nerve, V_2 and V_3 from the brain cavity, are located farther anteriorly and are thus not enclosed by bone. In the occipital region, the exoccipitals are

TABLE 5

Selected Meristic Data of C&S Specimens of *Nagaichthys filipes* from Different Localities

	Vertebrae total, without/with hemal spines	With ribs, starting with no. 4	Dorsal-fin pterygiophores starting between vertebrae (x/y); dorsal-fin rays	Anal-fin pterygiophores (in front/behind first hemal spine); anal fin rays	Caudal-fin rays	Pectoral-fin rays right + left
CMK 6660, paratype 30.8 mm	54, 26/28	23	29 (25/26); 29[b]	29 (2/27); 29[b]	caudal fin regenerated	1 + 1
CMK 10870 28 mm	56, 25/31	22	31 (25/26); 30[a]	32 (2/30); 32[b]	4	3 + 2
CMK 10870 25 mm	55, 25/30	22	29 (25/26); 29[b]	31 (2/29); 31[b]	4	2 + 2
CMK 9601 27 mm	58, 27/31	24	31 (26/27); 30[a]	32 (3/29); 31[a]	4	1 + 1
CMK 11387 28.5 mm	59, 27/32	24	33 (26/27); 32[a]	33 (3/30); 32[a]	4	1 + 1

[a], [b] For explanation, see table 1.

TABLE 6

Selected Meristic Data of Alcohol Specimens of *Nagaichthys filipes* from Different Localities

	Dorsal-fin rays	Anal-fin rays	Caudal-fin rays	Pectoral-fin rays right + left
CMK 11267				
27.6 mm	30	30	4	1 + 1
25.9 mm	29	31	4	1 + 1
24.6 mm	30	31	4	1 + 1
25.9 mm	29	30	4	1 + 0
21.5 mm	29	31	4	1 + 1
20.7 mm	30	31	4	1 + 1
CMK 10870				
25.5 mm	31	32	4	2 + 3
26.4 mm	32	33	4	2 + 4
CMK 9601				
29.4 mm	29	31	4	1 + 1
CMK 10623				
26.0 mm	33	33	4	1 + 1
CMK 16683				
20.6 mm	31	31	4	1 + 1
16.6 mm	28	29	4	1 + 1
CMK 16705				
29.0 mm	30	32	4	0
27.3 mm	28	30	4	0
27.4 mm	31	29	4	0
CMK 16723				
31.2 mm	28	29	4	1+1
CMK 16718				
25.4 mm	29	29	4	1+1
25.3 mm	29	29	4	1+1
27.4 mm	30	30	4	1+1

widely separated in the dorsal midline by the supraoccipital (fig. 26A), as in small specimens of *Chendol keelini* and in adults of *C. lubricus*, *P. indica*, and *N. filipes*.

HYOPALATINE ARCH AND OPERCULAR APPARATUS (fig. 27): Except for its smaller size, no major differences in the hyopalatine arch and opercular apparatus from other chaudhuriids could be observed. The anterior membrane bone process of the metapterygoid is well developed. The ethmoid part of the ectopterygoid is more slender and the whole bone comparatively small, but not as reduced as in *N. filipes* (fig. 23).

HYOID, UROHYAL, AND BRANCHIAL ARCHES (fig. 28): The overall arrangement of the bones is similar to that of other chaudhuriids. Hypobranchials 2 and 3 possess anterior processes (fig. 28D). Hypobranchial 3 bears only few teeth in the 42-mm specimen of AMNH 217765, but is toothless in the 30-mm specimen of CMK 7947. As in *C. caudata* (fig. 20D), the fourth upper pharyngeal toothplate of *B. monopteroides* (fig. 28D) is comparatively smaller than in the other chaudhuriids (figs. 4D, 12D, 16D, 24D).

SHOULDER GIRDLE AND PECTORAL FIN (fig. 28E, F): The main difference from all other chaudhuriids, except some specimens of *Nagaichthys*, is the presence of only one pectoral-fin ray. It articulates with a roughly rectangular cartilaginous plate of the endoskeletal shoulder girdle that, depending on the specimen, shows some ossification proximally. The remaining part of the endoskeletal shoulder girdle also shows some variation among specimens. In AMNH 217765 (fig. 28E), it consists of two separate plates

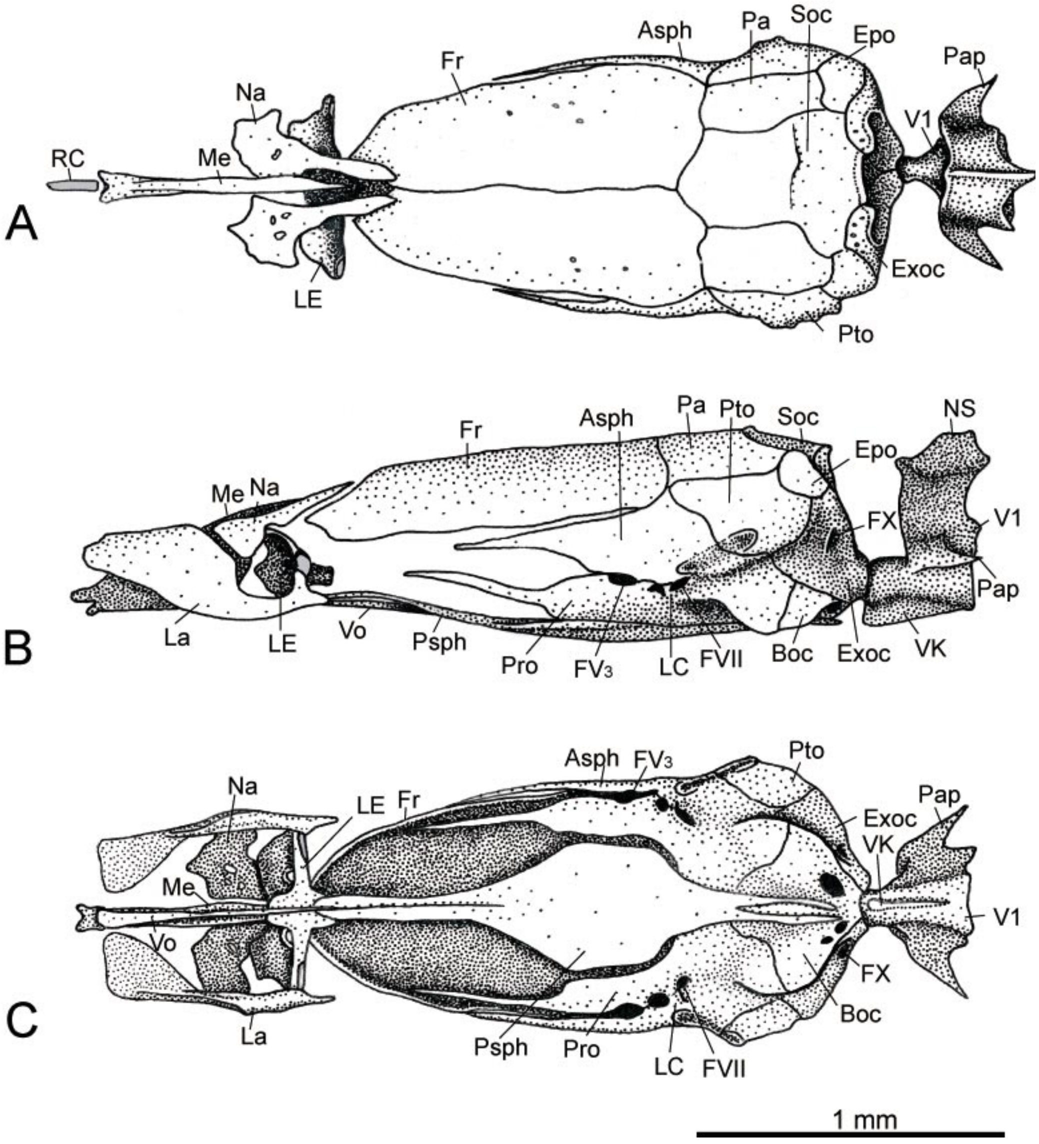


Fig. 26. *Bihunichthys monopteroides*, AMNH 217765, 42 mm, neurocranium, cartilage in gray. **A.** Dorsal view. **B.** Lateral view, rostral cartilage not shown. **C.** Ventral view, rostral cartilage not shown.

of cartilage (scapula and coracoid cartilages?), with the upper element being pierced by a foramen. The 36-mm specimen of CMK 7947 (fig. 28F) has only one larger piece of cartilage whose distal two-thirds are ossified and which bears a foramen. In this specimen the supracleithrum is also better developed. As in *N. filipes*, but unlike other chaudhuriids, the postcleithrum seems to be lacking in all our specimens of *B. monopteroides*, unless it is too poorly ossified to stain with alizarin.

VERTEBRAL COLUMN, DORSAL, ANAL, AND CAUDAL FINS (fig. 29): The specimen of *B. monopteroides* figured herein has 74 vertebrae, and together with *C. fusipinnis* (table 4) has the highest number among chaudhuriids (see also table 7 for variation among *B. monopteroides*). Only the three anterior vertebrae have expanded neural spines (fig.

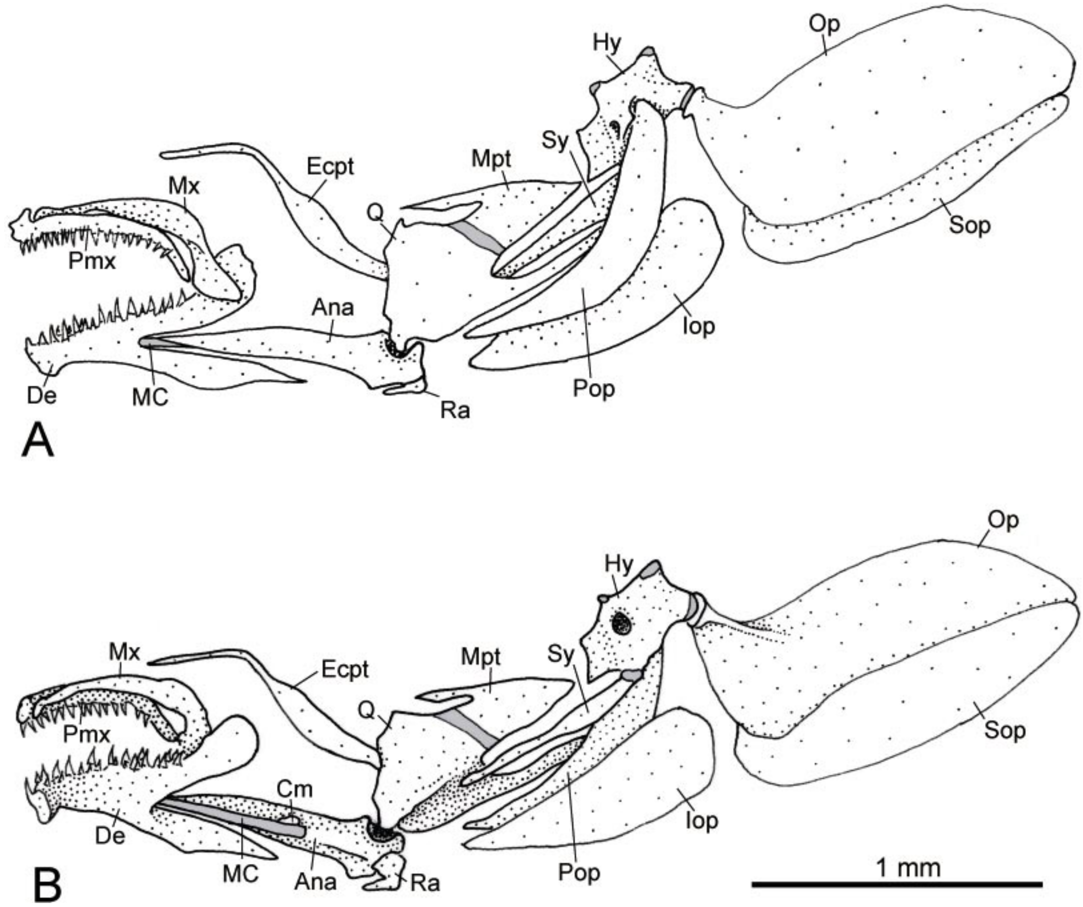
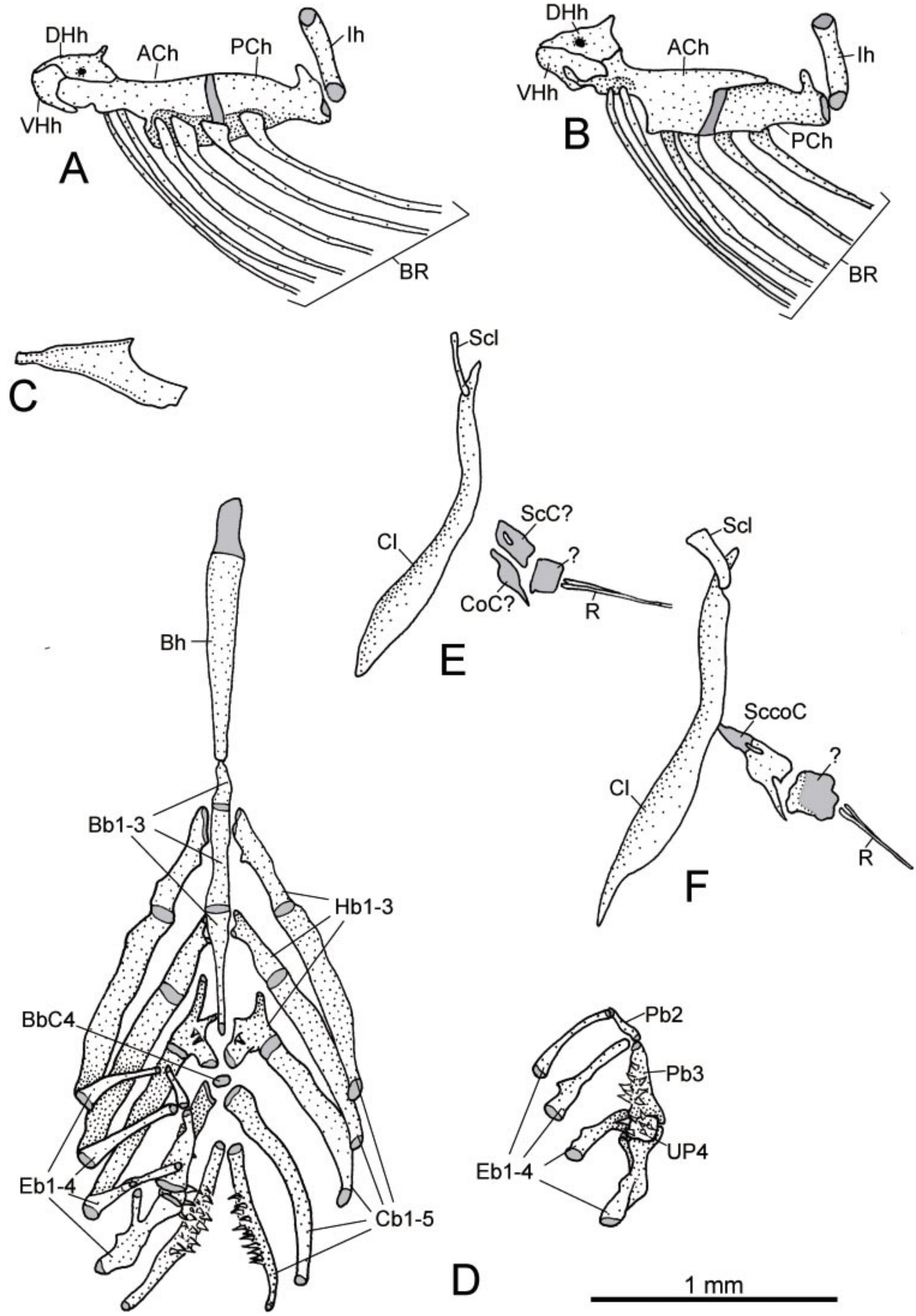


Fig. 27. *Bihunichthys monopteroides*, AMNH 217765, 42 mm, hyopalatine arch, upper and lower jaws, cartilage in gray. **A.** Lateral view. **B.** Medial view.

26B). They also possess a complete roof above the neural canal without fenestration. On subsequent vertebrae the fenestration of the neural arches with the typical bony bridge dorsal to the paired fenestrae, as described in most other chaudhuriids, is not present, except on one or two individual vertebra (e.g., fig. 29A, vertebra 7; also vertebra 3 of 30-mm specimen of CMK 7947). The vertebrae rather resemble posterior caudal vertebrae of other chaudhuriids or earlier developmental stages of anterior vertebrae in *C. keelini*, in both of which the dorsal bridge has not formed. Thus, the vertebrae of *B. monopteroides*, except the most anterior ones, bear a deep incisure in the bony lamella between the prezygapophysis and the neural spine. In the 36-mm specimen of CMK 7947 this type of vertebra starts only at vertebra 18. All preceding vertebrae have a more or less complete bony roof above the neural canal. In the same specimen, the anterior 28 vertebrae possess an anterior neural spinelike process on the centrum, whereas this is only present on vertebrae 3–12 in the figured specimen (fig. 29A) or 4–13 in the 30-mm specimen of CMK 7947. The posteriormost 9–10 caudal vertebrae in all three specimens are long bony cylinders without any neural or hemal spines (fig. 29D). In the specimen figured, short, small ribs are developed on vertebrae 4 through 7 or 8, depending on the side (fig. 29A). Hemal spines are present from vertebra 35 on. There are 40 dorsal-fin pterygiophores starting between vertebrae 23 and 24, with the anterior 39 being serially


DHh
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E
Scl
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?
Cl
R
F
Bh
Bb1-3
Hb1-3
BbC4
Eb1-4
Cb1-5
D
Pb2
Pb3
UP4
Eb1-4
1 mm

associated with fin rays and the last lacking a serially associated ray. The anteriormost pterygiophore is rudimentary. The anal fin has 41 pterygiophores with 11 in front of the first hemal spine. The anterior 40 are serially associated with fin rays, the anteriormost pterygiophore bears a supernumerary ray, and the last lacks a serially associated ray. The caudal fin of *Bihunichthys* (fig. 29D) is peculiar in possessing only a single long caudal-fin ray that articulates with the tip of a single hypural fused to the elongate terminal centrum. Meristic data for the three studied specimens of *B. monopteroides* are summarized in table 7.

DISCUSSION

When we started this project in 1996, information on chaudhuriid osteology was very limited, and other than the cursory remarks on selected osteological features by Annandale (1918), Regan (1919), Annandale and Hora (1923), Yazdani (1972, 1976, 1978), Yazdani and Talwar (1981), Kottelat and Lim in Kottelat (1991), and Kottelat and Lim (1994), the only comprehensive treatment was that of Travers (1984a, 1984b).

Different authors had subsequently found problems with Travers' phylogenetic conclusions concerning chaudhuriids (Kottelat and Lim, 1994; Johnson and Patterson, 1993; Britz, 1996), and we will address this issue here in more detail.

Travers (1984b) concluded that the families Synbranchidae, Mastacembelidae, and Chaudhuriidae form a monophyletic group, Synbranchiformes, based on six synapomorphies. Johnson and Patterson (1993) added additional evidence for monophyly of synbranchiforms. When Britz (1996) reviewed Travers' (1984b) six characters, he discarded two because they are not valid at the level Travers (1984b) had proposed. We do not comment further on the monophyly of the Synbranchiformes, but conclude that there is still convincing evidence that the Synbranchidae and Mastacembeloidei form a monophyletic group.

Travers (1984b) also defined the Mastacembeloidei consisting of the two families Mastacembelidae and Chaudhuriidae on the basis of 18 synapomorphies. We will comment on some of these.

COMMENTS ON TRAVERS' (1984A) SYNAPOMORPHIES OF MASTACEMBELOIDS

1. *Concomitant elongation of the supraethmoid, vomer and 1st infraorbital bone, accompanied by a long nasal with a broad dorsal surface:* A similar elongation of the preorbital region, and especially of the mesethmoid (= Travers' supraethmoid), occurs also in synbranchids (see Rosen and Greenwood, 1976: figs. 57–59; Britz, 1996: fig. 9) and thus may rather be a synbranchiform synapomorphy. There is even a much closer resemblance between the preorbital regions of mastacembelids and synbranchids when the latter are compared to earlier developmental stages of the former before the preorbital region of mastacembelids starts to elongate considerably (compare fig. 4 with fig. 9C in Britz, 1996). In representatives of all three families the mesethmoid is strongly displaced anteriorly so that it has no contact with the lateral ethmoid, except through the posterior lamina of membrane bone that develops in ontogeny.

2. *Tubular lateral ethmoids:* The lateral ethmoids are not tubular in chaudhuriids (figs. 2, 10, 14, 18, 22, 26) and therefore this character is not a valid synapomorphy at this level. Synbranchids also lack tubular lateral ethmoids (Rosen and Greenwood, 1976; personal obs.). This character is most likely a synapomorphy of mastacembelids.

3. *Wide anterolateral face of the pterosphenoid and its ventro-medial connection to its opposite member; a feature associated with a very compressed basisphenoid:* The

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Fig. 28. **A–E.** *Bihunichthys monopteroides*, AMNH 217765, 42 mm, cartilage in grey. **A.** Hyoid, lateral view. **B.** Hyoid, medial view. **C.** Urohyal, lateral view. **D.** Gill arches, dorsal view, with dorsal gill arches of right side removed and shown in ventral view. **E.** Shoulder girdle, lateral view. **F.** *B. monopteroides*, CMK 7947, 36 mm, shoulder girdle, lateral view, cartilage in gray.

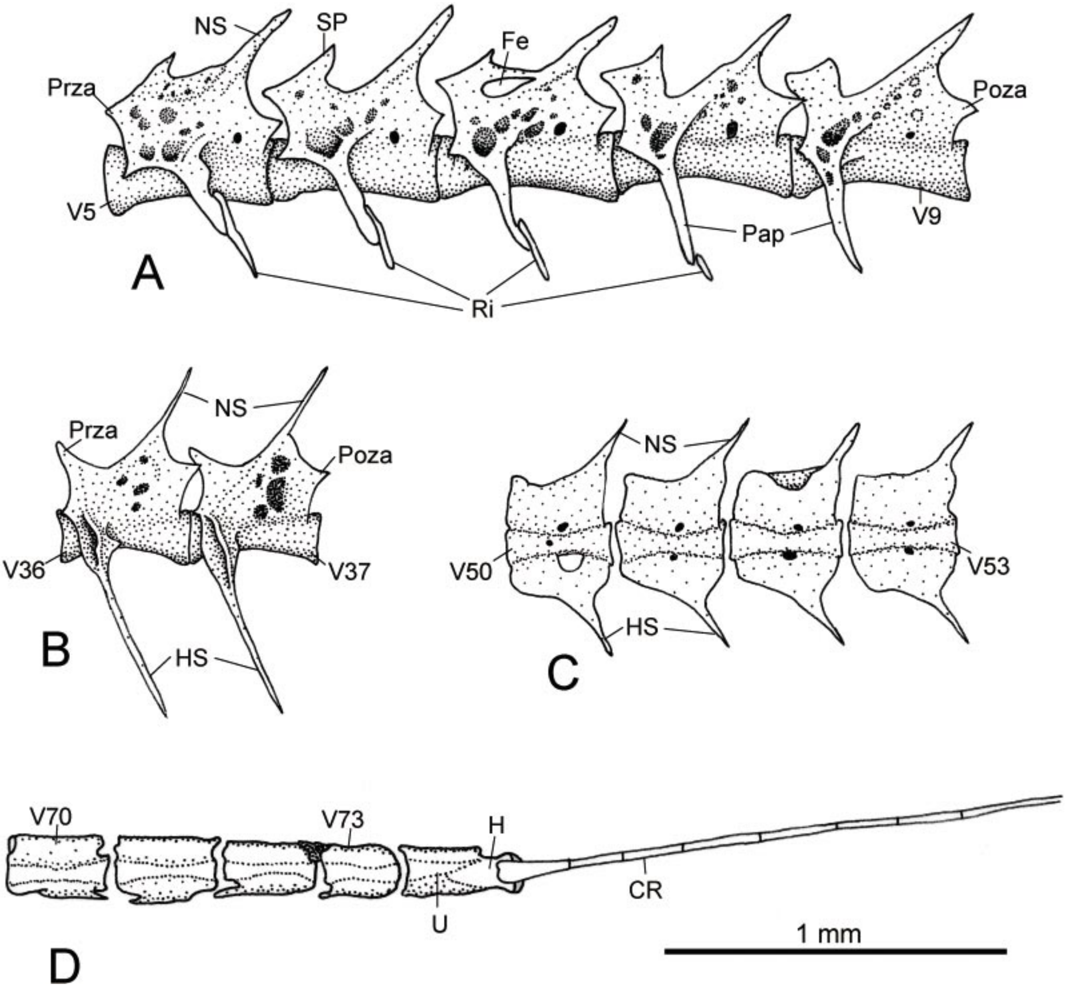

Fig. 29. *Bihunichthys monopteroides*, AMNH 217765, 42 mm, lateral view, cartilage in gray. **A.** Vertebrae 5–9. **B.** Vertebrae 36 and 37. **C.** Vertebrae 50–53. **D.** Caudal fin supporting structures, and preural vertebrae 2–5.

pterosphenoid and basisphenoid are absent in chaudhuriids (figs. 2, 10, 14, 18, 22, 26). This character is therefore not applicable to this taxon and is consequently of uncertain significance. A compressed basisphenoid may also be present in synbranchids. Pterosphenoids meeting in the ventral midline may thus rather be a synapomorphy of mastacembelids.

4. *Preorbital spine formed by the enlarged 1st infraorbital bone:* There is no preorbital spine on the lacrimal in chaudhuriids (figs. 2, 10, 14, 18, 22, 26), as Travers (1984a: 55) noted himself. Also, synbranchids lack a preorbital spine. This character is thus a synapomorphy of mastacembelids.

5. *Long anterior process on the prootic that passes across the anterolateral (precommissural) wall of the braincase and into the orbital cavity:* Such a process, although with different relations to surrounding bones, is present in chaudhuriids (figs. 2B, 10B, 14B, 18B, 22B, 26B) and is very long, except in *P. indica* (fig. 14B) and *N. filipes* (fig. 22B). It develops as membrane bone, as our ontogenetic series of *C. keelini* demonstrates. The prootic of synbranchids does not possess such a long anterior process. We agree with

TABLE 7
Selected Meristic Data of C&S Specimens of *Bihunichthys monopteroides*

	Vertebrae total, without/with hemal spines	Vertebrae (v), with ribs	Dorsal-fin pterygiophores starting between vertebrae (*x*/*y*); dorsal-fin rays	Anal-fin pterygiophores (in front/behind first hemal spine); anal fin rays	Pectoral fin rays right + left
CMK 7947					
38 mm	74, 33/41	v 4–7	41 (25/26); 41[b]	44 (10/34); 43[a]	1 + 1
31 mm	74, 33/41[c]	right, v 4–6 left, v 4–7	44 (22/23); 43[a]	45 (9/36); 44[a]	1 + 1
AMNH 217765					
42 mm	74, 35/39	right, v 4–7 left, v 4–8	40 (23/24); 39[a]	41 (11/30); 41[b]	1 + 1

[a], [b] For explanation, see table 1.

[c] Vertebra 41 with double neural and hemal spine.

Travers (1984a, 1984b) that this character is a synapomorphy of mastacembeloids.

6. *Wide anterolateral flange on the sphenotic associated with the posterior position of the postorbital process:* Travers (1984b) noted that the anterior part of the autosphenotic that lies in front of the lateral commissure is elongated in mastacembeloids compared to other teleosts, including synbranchids (see Rosen and Greenwood, 1976). Although we think this interpretation may be correct, we nevertheless have difficulties describing this character unambiguously. Anterior elongation of the autosphenotic is greatly pronounced and immediately obvious in chaudhuriids (figs. 2B, 10B, 14B, 18B, 22B, 26B) because this bone extends up to about two-thirds of the length of the frontal. Elongation, however, is less developed in mastacembelids and not so clearly different from the typical teleost condition. We therefore are reluctant to consider this character a meaningful synapomorphy of mastacembeloids.

7. *Small saccular bulla housed entirely within the prootic:* In chaudhuriids, the saccular bulla is housed in the prootic, exoccipital, and basioccipital (figs. 2, 10, 14, 18, 22, 26). This is the plesiomorphic condition (also present in synbranchids; see Rosen and Greenwood, 1976: figs. 58–59). This character is therefore a synapomorphy of mastacembelids.

8. *Large coronomeckelian, lying dorsally across the anterolateral face of the suspensorium:* In chaudhuriids the coronomeckelian is in the usual teleostean position at the dorsal surface of the posterior part of Meckel's cartilage (figs. 3, 11, 15, 19, 23, 27). This is thus the plesiomorphic condition because it is also present in Synbranchidae and almost all other teleosts, except in the gasterosteoid *Indostomus* (Banister, 1970; Britz and Johnson, 2002), in which the bone has also shifted dorsally. A coronomeckelian ossifying dorsal to Meckel's cartilage in the tendon of the A3 portion of the adductor mandibulae is thus a synapomorphy of mastacembelids (see discussion in Britz, 1996).

9. *Ventral processes on basibranchial 2:* In chaudhuriids (figs. 4D, 12D, 16D, 20D, 24D, 28D) and synbranchids (Rosen and Greenwood, 1976; personal obs.) these processes are not developed. This is the plesiomorphic condition, and development of these processes is a synapomorphy of all mastacembelids, except *Sinobdella*, which also lacks them.

10. *Long dorsal (and anal) fin composed of isolated short, stout spines unconnected by membrane, anterior to a long series of soft branched rays:* In chaudhuriids there are no dorsal- or anal-fin spines. This character is therefore not applicable. Isolated dorsal-fin spines also occur in many gasterosteiforms, and along with their specific structure they have been interpreted as a synapomorphy of

that taxon by Johnson and Patterson (1993: 579, character 6). More information is needed, but this character may turn out to be a synapomorphy of Gasterosteiformes plus Synbranchiformes and thus a plesiomorphy at the level of Mastacembelidae.

11. *The presence of a ‘‘musculus intraoperculi’’:* In addition to several mastacembeloids, Travers’ (1984a: 87) figured this muscle for *Pillaia*. We checked this character with our material of *P. indica* and *C. keelini*, but were not able to corroborate Travers’ (1984a) finding. There is no musculus intraoperculi in *P. indica* or *C. keelini*. In the area where Travers’ (1984a) figured the musculus intraoperculi in *Pillaia*, we find in *Chendol* a portion of the musculus hyohyoideus that extends between the uppermost branchiostegal ray and the prominent bony ridge on the medial side of the opercle. We think that Travers (1984) probably misidentified this muscle with the musculus intraoperculi in *Pillaia*. Based on these observations, we think that the presence of a musculus intraoperculi in chaudhuriids is an erroneous observation and not a valid synapomorphy for mastacembeloids. We confirmed the presence of a musculus intraoperculi in one mastacembelid species, *Mastacembelus unicolor*, and therefore consider the presence of such a muscle a synapomorphy of mastacembelids.

12. *Anterior tendinous insertion of the obliquus superioris muscle on the posteroventral edge of the exoccipital:* In his section titled ‘‘comparative myology of the Mastacembeloidei’’, Travers (1984a: 122) noted that ‘‘this comparison only includes the most superficial muscles in specimens of *Chaudhuria* and *Pillaia*, partly because of their small adult size and partly because none could be serially sectioned.’’ In figure 87, he depicts a lateral view of the ‘‘superficial muscles after removal of the skin’’ of *P. indica*. Based on these remarks we doubt that Travers (1984a) actually dissected any chaudhuriid specimen to check this character in this family. Our material of *Chendol keelini* did not show a tendinous insertion of the obliquus superioris muscle, as claimed by Travers (1984a). A distinctive muscle spans from the transverse process of the first vertebra to the exoccipital part of the otic bulla, but it is not tendinous. Another bundle of musculature originating from the ventral surface of the first vertebra runs below the transverse process of that vertebra, dividing into two distinct bundles that insert on the basioccipital part of the otic bulla on both sides of the skull. On the basioccipital this muscle inserts along a prominent bony ridge (compare fig. 2 and 3), and in the slight depression posterior to this ridge. Based on this information, we consider Travers’ (1984b) character not a valid synapomorphy of mastacembeloids. We did not check this character for mastacembelids and therefore cannot comment on its significance for this taxon.

13. *Baudelot’s ligament forked posteriorly, connected to the supracleithrum and cleithrum, lying between the obliquus superioris and expaxialis [sic] muscles:* Travers (1984b: 122) described Baudelot’s ligament as ‘‘small . . . closely associated with the prominent anterior tendon of the obliquus superioris, and . . . discernible only after careful dissection.’’ This ligament was figured by Travers (1984a: fig. 83) for the mastacembelid *Mastacembelus mastacembelus*, and a few pages further on he (Travers, 1984a: 128) claimed that it is present in all taxa. We have some doubt if Travers (1984a) was actually able to check this character in his chaudhuriid material because, as he states himself (Travers 1984a: 122), its demonstration needed a careful dissection, but he could dissect only the most superficial muscles in chaudhuriids. We did not encounter Baudelot’s ligament as described by Travers (1984a) in our C&S specimens of chaudhuriids. Even transferring some of them into ethanol did not reveal Baudelot’s ligament, but rather a strong ligament extending between the shoulder girdle and the tip of the transverse process of the third vertebra. We therefore consider this character not a valid synapomorphy of mastacembeloids.

14. *Anterior nasal openings at the end of long tubular epidermal extensions of the olfactory sac lying on either side of a central rostral tentacle:* Chaudhuriids do have tubular anterior nostrils but do not possess the central rostral tentacle. There is only a slight skin projection (see further discussion below). A rostral appendage with a central rostral tentacle is a synapomorphy of mastacembelids.

15. *Massive nervus olfactorius connecting telencephalon with the olfactory organ:* It is unclear to us what this character means. In every vertebrate the olfactory organ is connected to the telencephalon via a nervus olfactorius, so that the only apomorphic state might be the massiveness of the nerve, but we have been unable to quantify this in an objective way.

16. *Loss of lateral and medial extrascapular bones, associated with incorporation of the supratemporal branch of the cephalic sensory canal system into the parietal:* Chaudhuriids have lost their sensory lateral line canals in the skull bones (figs. 2, 10, 14, 18, 22, 26). It is therefore not clear if chaudhuriids, before the loss of the canals, possessed the mastacembelid state with the supratemporal branch incorporated into the parietal or if they had the plesiomorphic state still present in synbranchids, in which the extrascapulars are present and carry the supratemporal branch. This character is therefore not applicable as a synapomorphy of mastacembeloids.

17. *Round toothplate fused to the dorsal surface of hypobranchial 3:* All chaudhuriids except *Chendol lubricus* (fig. 12D), *Pillaia indica* (fig. 16D; Travers, 1984a: fig. 20), *Chaudhuria fusipinnis* (Kottelat and Britz in Kottelat, 2001), and *Nagaichthys filipes* (fig. 24D) possess a toothplate fused to hypobranchial 3. A similar fused toothplate occurs in most mastacembelids and is a possible synapomorphy of the mastacembeloids. Such a toothplate fused to hypobranchial 3 is also present in different species of the genera *Nandus*, *Badis*, and *Channa* (Nelson, 1969), where it apparently was developed independently from that of mastacembeloids, as the latter do not seem to be more closely related to the former.

18. *Development of the tripartite occipital facet into a concave socket, the anterior face of the centrum into a hemispherical condyle and their articulation as a ‘‘ball and socket’’ joint:* Johnson and Patterson (1993) pointed out that synbranchids possess a similar ‘‘ball and socket’’ joint between the occiput and the first centrum and used this character as additional evidence for a monophyletic Synbranchiformes comprising synbranchids, chaudhuriids, and mastacembelids. It is thus not a synapomorphy at the level of mastacembeloids. We note here, however, that there is a difference of this articulation in synbranchids and mastacembeloids. In the former the ball-like articulatory head of the first vertebra articulates only with the basioccipital, but in the latter it articulates with the basi- and exoccipitals. The ball-like articular head of the first vertebra is a putative synapomorphy of Synbranchiformes, but we are as yet unable to decide which of the two conditions of the occipital part of the articulation is the plesiomorphic state for synbranchiforms.

We can thus summarize that from Travers list of 18 synapomorphies for Mastacembeloidei only 2 (5, 17) remain valid. We therefore provide an emended and supplemented list of characters that we consider valid synapomorphies of Mastacembeloidei:

(1) Presence of an elongate rostral cartilage that has lost its function during jaw protrusion but instead rests on the anterodorsal tip of the vomer and projects into a median skin fold at the tip of the snout. This skin fold is progressively developed into the central rostral tentacle in mastacembelids and is supported there by a long rodlike rostral cartilage.

(2) Anterior nostrils at the tip of tubelike extensions, or, in other words, the presence of nasal tentacles. Although the nasal organ of synbranchids shares some apomorphic similarities with that of mastacembeloids, synbranchids do not possess nasal tentacles (see Rosen and Greenwood, 1976). Their anterior nostrils sit at the tip of the upper lips.

(3) Toothplate fused to hypobranchial 3.

(4) Long anterior process of membrane bone on the prootic that extends anteriorly into the orbital cavity.

(5) Loss of interarcual cartilage. An interarcual cartilage is a synapomorphy of Percomorpha sensu Johnson and Patterson (1993) and is widespread among representatives of this taxon (see Travers, 1981). All chaudhuriids and mastacembelids lack an interarcual cartilage, whereas synbranchids have an interarcual bone that arises from a cartilaginous precursor (personal obs. on juveniles of *Monopterus* sp., USNM 339154). Loss of the interarcual cartilage is thus a synapomorphy of Mastacembeloidei.

SYNAPOMORPHIES OF CHAUDHURIIDAE

Travers (1984b) included the genus *Sinobdella* in the family Chaudhuriidae based on 10 shared synapomorphies. Kottelat (1991) and Kottelat and Lim (1994) expressed their doubt about Travers' (1984b) phylogenetic placement of *Sinobdella*. Johnson and Patterson (1993) and Britz (1996) already commented critically on Travers' (1984b) character list for Chaudhuriidae, and Britz (1996) concluded that only 1 of the 10 characters provided by Travers (1984b) actually remains as a potential synapomorphy for Chaudhuriidae with the inclusion of *Sinobdella*, that is, loss of the endopterygoid. On the presence of two uniquely derived complex characters that *Sinobdella* shares with the Mastacembelidae, this taxon was included in the latter family (Britz, 1996). These characters are (1) a special articulation of the ectopterygoid with the lateral ethmoid via a cartilaginous meniscus (a remnant of pars autopalatina), and (2) the peculiar elongate and dorsally shifted coronomeckelian bone.

After having studied additional chaudhuriids not available to Johnson and Patterson (1993) or Britz (1996), we can state that their interpretations still remain valid. We can add here an additional character complex with two characters to the list of synapomorphies that *Sinobdella* shares with mastacembelids: the presence of a rostral appendage, consisting of a central rostral tentacle supported by a long rostral cartilage, and the presence of tubular nostrils that are shifted anteriorly along the sides of the tentacle. Although *Pillaia* has been credited with a rostral appendage, this is not true. Yazdani (1972: 134) called the rostral appendage in *Pillaia* ''rather indistinct'', whereas Yazdani (1976: 167, 1978: 283, 1990: 27) considered it ''very indistinct''. However, in our specimens of *Pillaia* (fig. 1) and all other chaudhuriid taxa we studied there is no rostral appendage. Their short and roughly triangular rostral cartilage supports a short and blunt skin projection between the nasal tubes. This situation differs significantly from the mastacembelid rostral tentacle. We are thus unable to explain why Travers (1984a: fig. 87) even figured *Pillaia* with a typical mastacembelid-type rostral appendage. As a consequence, Travers (1984b: 133) ''loss of a rostral appendage'' as a defining character for *Chaudhuria* is not valid. A rostral appendage is primitively absent in chaudhuriids.

We encountered several additional inconsistencies between Travers' (1984a) anatomical description of *Pillaia indica* and *Chaudhuria caudata* and our own specimens of these two species. Travers (1984a) described *P. indica* as possessing parietal bones. For the description of *P. indica*, two specimens were available to him, and from his introductory remarks it seems clear that he most likely used exclusively the smaller specimen because the larger was ''poorly preserved and stained'' (Travers, 1984a: 43). Our two specimens of *P. indica* clearly lack parietals (fig. 14). We think that his description was erroneous in this regard, but unfortunately we did not have access to Travers' (1984a) material to check it, because all efforts to borrow this material from the Zoological Survey in Calcutta failed.

Travers (1984a: 36, fig. 16a) noted and figured a dentary with a bifurcating posterior end. He later (1984b: 133) used this character ''Ventral edge of dentary divided'' among others to define the genus *Chaudhuria*, which he (1984: 114) described as ''the ventral edge of the dentary is forked giving rise to a distinct pair of posteroventral processes.'' We did not find a ventrally forked dentary in any of our specimens of *Chaudhuria* (fig. 19). There is usually a medially projecting corner at the position where Travers (1984a, 1984b) claimed a separate process. This corner is strong and well ossified and may create the impression of a separate process when the surrounding bone is poorly stained due to decalcification. We think that this is the reason for Travers' (1984a) erroneous account. Our view receives support from Travers' (1984a) own description of *Chaudhuria*. He (Travers, 1984a: 36) noted that the ''ventral arm of the dentary extends posteriorly as a long pointed process lying below the margin of the anguloarticular. From the ventral edge of this process a further short posteromedially directed process may develop. The region between these processes may be bridged by partly ossified tissue.'' We interpret this latter remark as evidence that Travers (1984a) worked with partly decalcified specimens so that he was unaware that the separate process he described was actually just a projecting corner from the main body of the dentary.

In *P. indica*, Travers (1984a: 45) described and figured (1984a: figs. 15biii, 16b, 18b, 21bi) ‘‘short branches of the cephalic sensory canal system . . . in the preoperculum, dentary, frontal, 1st infraorbital and nasal bones . . . ’’. We were unable to verify this statement in our specimens of *Pillaia* and think that he mistook differences in the structural appearance of the bone for lateral line canals. In *C. caudata*, he (Travers, 1984a: 36) noted that there ‘‘is no sign of the cephalic lateral line system in any neurocranial bones’’, but that the ‘‘somatic component passes through the tip of the supracleithrum.’’ As in the case of *Pillaia*, we were unable to verify this latter statement with any of our numerous *Chaudhuria* specimens. We therefore consider Travers’ (1984a) report of lateral line canals in bones of the skull or shoulder girdle of chaudhuriids erroneous.

Travers (1984a) claimed that there is no postcleithrum in these two taxa but we found a single postcleithrum in all specimens of all chaudhuriid species we studied, except in the smallest juveniles of *C. keelini*, in which it was not yet ossified, and in the two smallest chaudhuriid species, *B. monopteroides* and *N. filipes*, in which it is either absent or poorly ossified so that it did not stain with alizarin. We think that Travers (1984a) was dealing with decalcified specimens of *Pillaia* and *Chaudhuria* and overlooked the postcleithrum because it did not stain with alizarin. In some of our specimens, the postcleithrum stained only faintly and this was probably also due to decalcification. Faint staining or failure to stain due to decalcification occurs frequently in small species in which calcification of bones may not be so strong (see e.g. Johnson and Brothers, 1993; Britz and Kottelat, 1999).

Travers (1984a) credited *Chaudhuria* and *Pillaia* with one epural and one uroneural. We did not find an epural or uroneural in any of our chaudhuriid specimens and therefore think that his observation was erroneous. Travers (1984a: fig. 23) labeled a parhypural in the caudal fin of *Chaudhuria* and *Pillaia* and described it as ‘‘fused along the ventral edge of the hypaxial hypural’’ for *Chaudhuria* and as ‘‘sutured along the ventral edge of the hypaxial hypural’’ for *Pillaia*. We did not find a parhypural sutured along the ventral edge of the hypaxial hypural in our two specimens of *Pillaia*. Travers (1984a) also did not present any evidence for his assumption of a fusion of the parhypural to the lower hypural in *Chaudhuria*. We did not find a parhypural in any of the chaudhuriids we studied. Our ontogenetic series of *Chendol keelini*, a species with only a single hypural, demonstrates that only a single hypural cartilage forms during ontogeny. We therefore think that Travers’ (1984a) report of a parhypural in chaudhuriids is erroneous.

Given the exclusion of *Sinobdella* from chaudhuriids (Britz, 1996), Travers’ (1984: 132) list of 14 synapomorphies of *Chaudhuria* and *Pillaia* may be considered as a list of synapomorphies for Chaudhuriidae. We will comment on that list in light of the data we gathered from the chaudhuriids we studied.

1. *Posterior end of vomerine shaft ventrally depressed.* Travers (1984b) cited Travers (1984a: 43, fig. 15ai, bi) as support for this character. However, having read his account and looked at his figures, we are unable to determine what he actually meant by this character. The vomer in chaudhuriids is a narrow bone with a needlelike posterior end that is housed in a shallow longitudinal depression of the parasphenoid (figs. 2C, 10C, 14C, 18C, 22C, 26C). An almost identical situation is found in mastacembelids (see Travers, 1984a: figs. 1, 24–30, 35–40) and even in synbranchids (Rosen and Greenwood, 1976: figs. 58, 59). Consequently this is not a valid synapomorphy of *Chaudhuria* and *Pillaia* or of chaudhuriids.

2. *Loss of pterosphenoid.* A pterosphenoid is lacking in all chaudhuriids. This is a valid synapomorphy of the family.

3. *Loss of basisphenoid.* A basisphenoid is lacking in all chaudhuriids. This is another valid synapomorphy of the family.

4. *Single foramen in pars jugularis.* Travers (1984b) claimed that ‘‘*Chaudhuria* (fig. 5ai), *Pillaia* (fig. 15bi) and *Mastacembelus crassus* (fig. 39a) lack separate trigeminal and facial foramina, and have a single foramen in the trigeminofacialis chamber.’’ We

found that in all chaudhuriids there are two foramina from the trigeminofacialis chamber that are separated by a narrow bony bridge, the lateral commissure (figs. 2C, 10C, 14C, 18C, 22C, 26C). This bony bridge is figured for *Chaudhuria* and *Pillaia* by Travers (1984a: figs. 15, 16) himself. We also found additional foramina anterior to those of the trigeminofacialis chamber. In *Chendol keelini*, in which we checked the nerves and vessels going through the different foramina, the hyomandibular branch of the facialis and the jugular vein exit through the foramen posterior to the lateral commissure. The foramen directly anterior to the commissure serves as entrance for the jugular vein, and no nerve exits there. The three branches of the trigeminal nerve exit through three additional openings, all anterior to the above foramina (see fig. 2B, C). We found a similar arrangement of foramina in the other chaudhuriids and conclude that the courses of the nerves are similar to that in *C. keelini*. Thus, chaudhuriids have no trigeminofacialis chamber in its true sense. In some species, such as *P. indica*, *B. monopteroides*, or *N. filipes*, the prootic does not reach so far anteriorly as in *C. keelini* so that the exit of the first and/or second branch of the trigeminal nerve is not enclosed in bone. Travers' (1984a) observation that chaudhuriids lack separate foramina for the facialis and trigeminus nerves is incorrect.

5. *Large saccular bulla lying within the prootic, exoccipital and basioccipital.* This is the plesiomorphic condition for mastacembeloids and not a synapomorphy for chaudhuriids (see above discussion of character 7 of mastacembeloid synapomorphies).

6. *Loss of frontal descending lamina.* In mastacembelids, synbranchids, and many other teleosts, the frontal has a descending lamina that contacts the pterosphenoid (and/or the orbitosphenoid if this is still present). The pterosphenoid is lacking in chaudhuriids but there is a small descending lamina at the anterior third or fourth of the frontal in our specimens of *P. indica* and in the *Chendol* species. Reduction of the lamina thus occurs within Chaudhuriidae.

7. *Cephalic sensory canal system reduced or lost.* Travers' (1984a) account of cranial lateral line canals is erroneous for reasons discussed above. We therefore consider the loss of lateral line canals in the bones of the skull and the shoulder girdle a synapomorphy of Chaudhuriidae.

8. *Coronomeckelian a small ossicle on medial face of anguloarticular*. Britz (1996: 16) already commented on this character, and it is further discussed above. The presence of a small coronomeckelian on the medial face of the anguloarticular is the plesiomorphic condition shared with synbranchids and most teleosts, and the elongate coronomeckelian remote from the lower jaw found in mastacembelids is a synapomorphy for this family, including *Sinobdella* (Britz, 1996).

9. *Loss of palatine.* There is no palatine in any chaudhuriid we studied, and this is thus a valid synapomorphy of chaudhuriids. Mastacembelids have lost the autopalatine and only the dermopalatine is developed (Britz, 1996). So the correct description of this character is ''loss of dermopalatine''. Strangely, Travers (1984a: 45–46) suggested that the palatine ''may be incorporated into the anterior arm of the ectopterygoid, possibly by fusion, during ontogeny.'' There is no evidence for this scenario and our developmental stages of *Chendol keelini* clearly show that the preorbital part of the ectopterygoid develops in ontogeny from the ectopterygoid. There is no additional bone involved in its formation.

10. *Ectopterygoid articulation with lateral ethmoid absent, its long anterodorsal arm contacting the vomerine shaft.* A direct articulation of the ectopterygoid with the lateral ethmoid was considered a synbranchiform synapomorphy by Travers (1984b: 109, character 21). Britz (1996) studied the articulations of the ectopterygoid in the three synbranchiform families in detail and demonstrated that they differ considerably among the three taxa. Juvenile synbranchids still retain the primitive condition in which the palatine, not the ectopterygoid, articulates with the lateral ethmoid. Mastacembelids have a cartilaginous meniscus between the ectopterygoid and the lateral ethmoid, and in *Chaudhuria*, the only chaudhuriid available to Britz (1996), the ectopterygoid articulates on its lateral side with an elongate cartilaginous projection that arises from the lateral ethmoid. In other chaudhuriids, such a promi-

nent cartilaginous projection is not developed and the ectopterygoid is attached ligamentously to the ventral face of the lateral ethmoid. Therefore, this character of Travers (1984b) is not a valid synapomorphy, stated as it is, because it incorrectly assumes that the mastacembelid condition is primitive for Mastacembeloidei.

11. *Loss of pharyngobranchial 2 toothplate.* There are no teeth on pharyngobranchial 2 in any chaudhuriid we studied. This is therefore a valid synapomorphy of the family.

12. *Loss of dorsal and anal spines.* All fin rays in chaudhuriids are segmented soft rays. The loss of dorsal- and anal-fin spines, present in mastacembelids, is thus a valid synapomorphy of Chaudhuriidae.

13. *Scaleless.* Although we confirmed that *Chaudhuria* and *Pillaia* have no scales, one of the chaudhuriid species, *Chendol keelini*, has numerous well-developed cycloid scales on the posterior part of the body (fig. 9; Kottelat and Lim, 1994). If *C. keelini* turns out to be the basal member of chaudhuriids, reduction of scales would occur within chaudhuriids and would not be a synapomorphy of the family.

14. *Extremely small adult size.* The largest chaudhuriids reach up to at least 85.8 mm SL and thus are about half the size of the smallest mastacembelid species, as, for example, *Sinobdella sinensis* (190 mm according to Nichols, 1943) or *Macrognathus pancalus* (180 mm, in some areas only 9 cm according to Talwar and Jhingran, 1992) or the smallest synbranchid species, the basal *Macrotrema caligans* (not more than 200 mm according to Rosen and Greenwood, 1976). An extremely small body size is a feature of such genera as *Bihunichthys* or *Nagaichthys*, and thus occurs within the chaudhuriids.

In summary, of the 14 characters listed by Travers (1984b) as synapomorphies of Chaudhuriidae, with the exclusion of *Sinobdella*, only five characters remain valid after our critical evaluation (nos. 2, 3, 9, 11, 12)

We have compiled a list of 22 synapomorphies of chaudhuriids, adding 16 to the 5 valid characters identified by Travers (1984b). Although we were not able to study all nine species currently included in Chaudhuriidae, the character descriptions seem to apply to the family as a whole and we do not expect any major alterations once specimens of the two species not included in this paper, *Garo khajuriai* and *Pillaia kachinica*, become available for closer study. The character states provided are derived compared to mastacembelids. We have listed and discuss reductive characters, some of which are probably correlated with minute size, separately from progressive characters.

Reductive characters of Chaudhuriidae:

(1) Loss of basisphenoid (Travers, 1984b: 132, character 39). A basisphenoid is present in mastacembelids (Travers, 1984a) and synbranchids (Rosen and Greenwood, 1976).

(2) Loss of pterosphenoid (Travers, 1984b: 132, character 38). Mastacembelids (Travers, 1984a) and synbranchids (Rosen and Greenwood, 1976) have a well-developed pterosphenoid.

(3) Loss of endopterygoid (Travers, 1984b: 132, character 29). Most mastacembelids have an endopterygoid and it is only lacking in *Sinobdella sinensis* (Travers, 1984: fig. 47). The tooth-bearing pterygoid in synbranchids was interpreted as an ectopterygoid by Rastogi (1964), Rosen and Greenwood (1976), Gosline (1983), and Britz (1996), but as an endopterygoid by Lauder and Liem (1983). Additional studies will have to resolve these conflicting interpretations.

(4) Loss of the pars autopalatina and dermopalatine. Both structures are present in mastacembelids (see Britz, 1996). Loss of an autopalatine is shared with mastacembelids, in which the pars autopalatina develops but fails to ossify (Britz, 1996). The autopalatine and dermopalatine are present in synbranchids (personal obs.).

(5) Loss of circumorbital bones except the lacrimal. Mastacembelids may have a complete infraorbital series consisting of up to five bony tubes in addition to the lacrimal. In some species the number is reduced but there is at least one element present in addition to the lacrimal. Synbranchids have retained only the lacrimal.

(6) Loss of lateral-line canals on all bones of the skull and shoulder girdle. All chaudhuriids we studied have lost their lateral-

line canals on the cranial bones and the shoulder girdle, contrary to Travers' (1984a) description (see discussion above). Mastacembelids and synbranchids have lateral-line canals on the skull bones and the shoulder girdle, which represents the plesiomorphic condition.

(7) Loss of gill rakers. Toothed gill rakers occur in a number of mastacembelid species, but from Travers' account (1984a) distribution of this character is not clear. He figured gill rakers for *M. mastacembelus*, *M. zebrinus*, *M. cunningtoni*, and *M. tanganicae*, but according to his drawings they seem to be absent in *M. maculatus*, *M. flavomarginatus*, and *M. liberiensis*. Our specimens of *M.* sp. (AMNH 09765), *M. erythrotaenia* (AMNH 42129), and *Macrognathus pancalus* (AMNH 217414) clearly have gill rakers. Gill rakers are also present in the synbranchids, *Macrotrema caligans* (MCZ 47107), *Ophisternon aenigmaticum* (AMNH 31573), and *Synbranchus marmoratus* (MCZ 52376).

(8) Loss of posttemporal. In mastacembelids the posttemporal is present as a row of lateral-line tubes between the occiput and the supracleithrum (Travers, 1984a: figs. 11, 67–72). All synbranchids have a posttemporal (Rosen and Greenwood, 1976). It connects the shoulder girdle to the skull in basal members of the family (Rosen and Greenwood, 1976; personal obs. on *Macrotrema caligans*). It is remote from the shoulder girdle, but still attached to the skull in the two *Synbranchus* species, in *Monopterus boueti* and in *M. cuchia* (Rosen and Greenwood, 1976).

(9) Loss of distal pectoral radials. Although not figured in Travers (1984a), distal pectoral radials are clearly present in mastacembelids between the pectoral radials and the fin rays, as our specimens of *Mastacembelus erythrotaenia* (AMNH 42129) and *Macrognathus pancalus* (AMNH 217414) demonstrate. Synbranchids completely lack the endoskeletal support and the pectoral fin as adults and therefore cannot be scored for this character. They possess a larval pectoral fin, in which no fin rays are developed and the fin-fold is supported by the cartilage of the pectoral radial plate.

(10) Reduction of number of epicentrals (= epineurals of Johnson and Patterson, 1993, 2001, and Patterson and Johnson, 1995) to one attached to the transverse process of the first vertebra or completely absent. Mastacembelids have a series of up to four (Travers, 1984a) or five (personal obs.) epicentral bones attached to the parapophyses of the anterior vertebrae. In synbranchids there is a long series of epicentrals running almost along the whole vertebral column and articulating with the tip of the laterally directed parapophyses.

(11) Loss of dorsal and anal-fin spines and supporting pterygiophores (Travers, 1984b: 132, character 48). Possession of dorsal- and anal-fin spines is a synapomorphy of Acanthomorpha (Johnson and Patterson, 1993), and their presence in mastacembelids is thus the primitive condition. Synbranchids lack dorsal and anal fins altogether so they are not comparable in this character.

(12) Loss of epurals. Although Travers (1984a: fig. 23) reported one epural in *Chaudhuria* and in *Pillaia*, we were unable to confirm this observation. In none of our chaudhuriid material, including numerous *Chaudhuria* and two specimens of *Pillaia*, are any epurals present. Mastacembelids have up to three epurals (Travers, 1984a), a number that is also commonly present among other acanthomorph fishes (see Monod, 1968; Fujita, 1990). All synbranchids have completely lost the caudal fin, except *Macrotrema caligans* (Rosen and Greenwood, 1976: fig. 2). The elements of its caudal fin, however, are difficult to identify and thus it is unclear if an epural is present. The same problem applies also to the following two synapomorphies.

(13) Loss of uroneurals. Although some elements of the caudal fin may be incorrectly identified by Travers (1984a), mastacembelids have at least one uroneural, and in acanthomorphs there are up to two uroneurals developed (Fujita, 1990).

(14) Loss of parhypural. Mastacembelids have a well developed parhypural that may fuse in some species to hypural 1 (Travers, 1984a: figs. 14, 75–78). Rosen and Greenwood (1976: 48) mentioned a ''parhypural-like'' element in the caudal fin of the synbranchid *Macrotrema caligans*. A parhypural is commonly present among acanthomorphs (Fujita, 1990).

(15) Reduction of number of hypurals to two (further reduced to one within chaudhu-

riids). Mastacembelids have a various number of hypural elements, the composition of which is not always clear. Travers (1984a: figs. 14, 75, 76, 78) interpreted some of the larger elements as being composed of fused hypurals without providing ontogenetic evidence for this, and he therefore reported the total number of hypurals in various mastacembelids as six. In two species, *Mastacembelus ellipsifer* and *M. aviceps*, he found only a single hypural plate, which he labeled as such. Even though there is no developmental information demonstrating the presence of six hypurals in mastacembelids, our developmental material of *Macrognathus pancalus* (AMNH 217414) shows three separate hypural cartilages in the 12.8-mm specimen and three hypurals in the 36-mm specimen, of which the lowermost two have fused at their distal third. At least four separate elements are figured for *M. erythrotaenia*, and we confirmed this number for our specimen (AMNH 42129) of this species. So, primitively there are at least four hypurals present in mastacembelids. Rosen and Greenwood (1976: 48 and fig. 2) depicted the caudal skeleton of the basal synbranchid *Macrotrema caligans* and described ''five cartilaginous hypural-like'' elements. The primitive number for acanthomorphs is six separate hypurals, as in *Polymixia* (Fujita, 1990: fig. 185). This number is variously reduced through loss or fusion in the different acanthomorph subgroups.

Progressive characters of Chaudhuriidae:

(16) Presence of a long anterior process of membrane bone on the autosphenotic running along the ventrolateral border of the frontal. In mastacembelids, a descending lamina of the frontal sutures the pterosphenoid's dorsal edge, thereby excluding the autosphenotic from the orbital region (Travers, 1984a: figs. 1, 24–40). In synbranchids the autosphenotic has no anterior extension and is excluded from the orbit by the pterosphenoid, which sits in front of it and sutures dorsally with the frontal (Rosen and Greenwood, 1976; personal obs.).

(17) Presence of a modified boomerang-shaped ectopterygoid with a long preorbital extension that runs alongside the vomer. In mastacembelids and synbranchids the ectopterygoid stops at about the level of the lateral ethmoid and has no extension that reaches beyond the orbital region (see Britz, 1996). This is probably true for all other teleosts.

(18) Separate foramina for the different branches of the trigeminal nerve (see discussion above). In all chaudhuriids, the trigeminal branches do not exit from the trigeminofacialis chamber, but leave the brain from more anterior openings, which are not always enclosed by bone. In synbranchids and mastacembelids (personal obs. *Synbranchus* USNM 128514, *Mastacembelus* AMNH 097654; for *M. armatus*, see Bhargava, 1958), the three trigeminal branches exit together from a large foramen anterior to the lateral commissure and the facialis foramen. This foramen is figured but not labeled in Rosen and Greenwood (1976: figs. 57–59) for one mastacembelid and two synbranchid species. Except for the unusually large size and anterior position of the trigeminal foramen, this condition with the three trigeminus branches exiting from one foramen resembles that found commonly among percomorphs (see Patterson, 1964, 1975; Greenwood, 1986) and represents the primitive state for synbranchiforms.

(19) Presence of an anterior process of membrane bone on the dorsal face of the metapterygoid bridging the cartilaginous strip that separates this bone from the quadrate. In mastacembelids and synbranchids, the metapterygoid and quadrate are connected by a cartilaginous strip, as in chaudhuriids, but the metapterygoid never develops an anterior membrane process on its dorsal face that extends beyond this cartilaginous strip (Rosen and Greenwood, 1976; Travers, 1984a; Britz, 1996).

(20) Special arrangement of dorsal gill arches. Chaudhuriids are unique among synbranchiforms in having pharyngobranchial 2 in line with and entirely anterior to pharyngobranchial 3 and the anterior tip of pharyngobranchial 3 articulating with the posterior tip of pharyngobranchial 2 and with the distal tip of EB2 (see figs. 4D, 12D, 16D, 12D, 26D). In mastacembelids (Travers, 1984a; personal obs.), and synbranchids (Rosen and Greenwood, 1976; personal obs.), and generally in acanthomorphs (see Rosen,

1973; Rosen and Patterson, 1990) the major portion of pharyngobranchial 2 lies lateral to pharyngobranchial 3, and if pharyngobranchial 3 articulates with pharyngobranchial 2, it is with its anterior end. Mastacembelids share with chaudhuriids the loss of an interarcual cartilage (Travers, 1984a, 1984b; Johnson and Patterson, 1993), whereas synbranchids possess an interarcual bone between the proximal part of epibranchial 1 and the small pharyngobranchial 2 (Rosen and Greenwood, 1976: figs. 27–41). The presence of a rodlike interarcual cartilage between the uncinate process of epibranchial 1 and pharyngobranchial 2 was considered one of the synapomorphies for percomorphs (sensu Johnson and Patterson, 1993, i.e., including atherinomorphs), and the lack of both, the interarcual cartilage and the uncinate process on epibranchial 1, as well as the loss of pharyngobranchial 1 are certainly derived, though not unique, states for mastacembeloids.

(21) Presence of a ventromedian keel on the first vertebra. This prominent keel is present in all chaudhuriid taxa we studied, but was not been mentioned or illustrated by Travers (1984a: fig. 21aii, bii). The anterior tip of the keel is tightly connected to the skull by strong connective tissue. Such a keel is not present in mastacembelids (Travers, 1984a; fig. 12; personal obs.) or synbranchids (Rosen and Greenwood, 1976; personal obs.).

DISTRIBUTION AND EVOLUTION OF REDUCTIVE CHARACTERS AMONG CHAUDHURIIDAE

Many of the above synapomorphic reductions can be aligned as a series of further reduction within chaudhuriids. Most of these concern the number of fin rays and their supports.

The number of pectoral-fin rays is highest in *Chendol keelini*, ranging from 14 to16 (Kottelat and Lim, 1994); there are 13–15 pectoral-fin rays in *C. lubricus*; 13 in Kullander et al.'s (2000) specimen of *Garo*; 10–11 in *Pillaia kachinica* (Kullander et al., 2000); 7–9 in *P. indica* (Yazdani, 1972) (Travers [1984b: 48] claimed ‘‘fin rays do not appear to have differentiated in the specimens I examined, but Yazdani (1978) records 6 rays in the pectoral fin’’; having checked Yazdani [1978: 285] we find that this author gave 7–9 rays for *P. indica*), but 6–9 in our specimens of *P. indica*; 6 in *Chaudhuria caudata* according to Yazdani (1976) (no fin ray count provided in Annandale [1918], 7 fin rays drawn in fig. 3 of Annandale and Hora [1923: 330], fin rays considered ‘‘indistinct in the specimens examined’’ by Travers [1984a]), but 9 in our figured *C. caudata* (CMK 7934) and it may range from 5 to 10 (see Table 4); 6–10 in *Chaudhuria fusipinnis* (see table 4); the number of pectoral-fin rays was reported to be 2 in *Bihunichthys monopteroides* (Kottelat and Lim, 1994), but in our five specimens there is only 1; there is also a single ray in the two type specimens of *Nagaichthys filipes* (Kottelat and Lim, 1994), but the number may range from 0 to 4 in specimens from other localities (see table 6). The high number of 19–20 pectoral-fin rays reported by Talwar et al. (1977) in the original description of *Garo khajuriai* was questioned by Kullander et al. (2000) based on the fact that pectoral-fin rays in chaudhuriids are hard to count, unless the specimens are cleared and stained. We have encountered similar difficulties and concur with Kullander et al.'s (2000) conclusion. The wide range of variation in the number of pectoral-fin rays within a single species demonstrates that this feature has not stabilized during evolution and indicates that it is only of limited significance in phylogenetic studies.

Pillaia kachinica (Kullander et al., 2000) appears to have the highest number of caudal-fin rays, with 10–12. Talwar et al. (1981) reported 12 caudal-fin rays for *Garo khajuriai*, but material of this species was not available to us. The specimen assigned to the genus *Garo* by Kullander et al. (2000) has 10 caudal-fin rays. *Pillaia indica* has 8–10 caudal-fin rays according to Yazdani (1972, 1976, 1978, 1990) and 10 in our own material; there are 7 in *Chaudhuria caudata* according to Whitehouse (1918), and 7 are figured by Annandale (1918), but our figured specimen of *C. caudata* (CMK 7934) has 8; we usually encountered 8 caudal-fin rays in *Chaudhuria* from other localities, but their number is occasionally 6 or 7 (see table); there are 6 in *C. fusipinnis* (Kottelat and

Britz in Kottelat, 2000); 4–6 in *Chendol keelini* (Kottelat and Lim, 1994; personal obs.); 7 in *Chendol lubricus* according to Kottelat and Lim (1994), but we counted only 6 rays in both specimens of CMK 7780; there are 4 in *Nagaichthys filipes* according to Kottelat and Lim (1994), and also 4 in the other material of *Nagaichthys* we studied; there is only 1 caudal-fin ray in *Bihunichthys monopteroides* (Kottelat and Lim, 1994; personal obs.).

With the reduction in the number of caudal-fin rays, the number of hypurals is reduced from two in *Pillaia indica* (Yazdani, 1976, 1978; Travers, 1984a), *P. kachinica* (Kullander et al., 2000), *Garo* sp. (Kullander et al., 2000), *Chaudhuria caudata* (Annandale, 1918; Whitehouse, 1918; Travers, 1984a; personal obs.), and *C. fusipinnis* (Kottelat and Britz in Kottelat, 2000) to a single hypural in the remaining species.

The number of epicentral bones is reduced from one in *Pillaia indica* (Travers, 1984a; fig. 14), *Chendol keelini* (fig. 2), *Chaudhuria caudata* (Travers, 1984a; fig. 18) to none in *Chendol lubricus* (fig. 13), some samples of *Chaudhuria caudata* (see table 4), *Chaudhuria fusipinnis* (Table 4), *Nagaichthys filipes* (fig. 25), and *Bihunichthys monopteroides* (fig. 26).

Unexpectedly, we noted that the largest chaudhuriid taxa, the two species of *Chendol* and our specimens of *Pillaia indica*, which otherwise have retained a number of plesiomorphies, have lost the parietal. The parietal, however, is present in all other species including the smallest taxa *N. filipes* and *B. monopteroides*.

CHAUDHURIIDS AS MINIATURIZED, DEVELOPMENTALLY TRUNCATED MASTACEMBELIDS?

Weitzman and Vari (1988) reviewed the phenomenon of miniaturization in South American freshwater fishes and listed the following characters as associated with small size: reduction of the laterosensory system of the head and body, reductions in the number of fin rays and body scales, and a diminution of the sculpturing on the surface bones of the head. The first two of these certainly apply to chaudhuriids. Based on habitat data for the different species, Weitzman and Vari (1988) further concluded that miniature fishes are associated predominantly with still or slow-flowing waters. Those chaudhuriid species for which habitat information is available seem to agree with this habitat type.

Weitzman and Vari (1988) used an arbitrary upper size limit of 26 mm standard length for what they called miniature fishes. The authors noted, however, that in some elongate fishes, a better parameter may be head length, because although these fishes have a greater standard length, they may possess head sizes comparable to those of miniature fishes below 26 mm. All chaudhuriid species are longer than 26 mm as adults, but have eel-like body forms. Therefore at least the smaller taxa, such as *Bihunichthys*, and *Nagaichthys* may be considered miniaturized.

Miniaturization may have different consequences whose extremes may be described as follows: (1) the miniaturized species may be just a dwarfed but otherwise identical image of its larger relatives, or (2) the miniaturized species may closely resemble an early developmental stage of the larger relatives. The latter case can be regarded as effected by developmental truncation, a form of heterochrony. Striking examples for developmentally truncated, larval-like teleosts are the gobioid genus *Schindleria* (Johnson and Brothers, 1993) and the clupeoid genus *Sundasalanx* (Siebert, 1997; Britz and Kottelat, 1999). In these taxa, large parts of the skeleton remain cartilaginous and a number of bones never ossify. In *Schindleria*, Johnson and Brothers (1993) listed 16 cartilage bones that fail to ossify from their cartilaginous precursors, another 5 that show only weak perichondral but no endochondral ossification, and another 11 bones (the ectopterygoid, a dermal bone, was erroneously cited by them as cartilage bone) whose cartilaginous precursors do not even form. Sixteen dermal bones never develop in *Schindleria*, and an additional four bones exhibit an ontogenetically truncated configuration. Based on this impressive list, Johnson and Brothers (1993: 469) concluded that *Schindleria* ‘‘is the most radically developmentally truncated fish’’.

The numerous reductions in the skeleton

of chaudhuriids at first glance seem to be related to their dwarfism and may possibly result from developmental truncation. A similar list as that of Johnson and Brothers (1993) for *Schindleria* can be compiled for chaudhuriids. Only the bones present in their sister group, the mastacembelids, and absent in chaudhuriids are listed. Contrary to the situation in *Schindleria*, not a single cartilage bone in chaudhuriids remains in the developmental state of its cartilaginous precursor but rather has disappeared completely. The skull of adult chaudhuriids thus has no additional cartilaginous components that would not be present in mastacembelids.

The following cartilage bones never ossify and their cartilaginous precursors fail to develop: pterosphenoid, basisphenoid, pterygiophores of spinous dorsal and anal fin, hypurals 3–5, and epurals. The following endoskeletal membrane bones never form: uroneurals. The following dermal bones never ossify: endopterygoid, dermopalatine, circumorbital bones except lacrimal, toothplate on pharyngobranchial 2, gill rakers, and posttemporal. The following cartilages never form: pars autopalatina and distal pectoral radials.

It is interesting that all of these major structural modifications also occur in the larger species, like *Pillaia indica* and *Chendol keelini*, which are apparently the family's basal taxa, having retained more plesiomorphic features than the other taxa. Turning to the smaller species, however, all additional reductions concern only the number of fin rays in the dorsal, anal, caudal, and pectoral fins, but no additional losses of skull bones or other elements. The skull in all species is solidly ossified, presumably associated with their burrowing behavior. Although a comprehensive comparison is still lacking, Chaudhuriidae seem to have no obvious characters that would resemble character states of earlier ontogenetic stages of their closest relatives the Mastacembelidae. We thus can conclude that miniaturization has certainly occurred in chaudhuriids, but the loss of a number of bones did not go along with any striking developmental truncations, as reported for *Schindleria* (Johnson and Brothers, 1993) or *Sundasalanx* (Roberts, 1984; Siebert, 1997).

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