Ontogeny of the Ethmoidal Region and Hyopalatine Arch in *Macrognathus pancalus* (Percomorpha, Mastacembeloidei), with Critical Remarks on Mastacembeloid Inter- and Intrarelationships

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ABSTRACT

Ontogenetic changes in head shape and structure during development of *Macrognathus pancalus* Hamilton, 1822, were investigated. The ontogeny of the skeleton in the ethmoidal and hyopalatine complex is described. The following notable features were discovered: pars autopalatina chondrifies autogenously and lacks a maxillary process at all developmental stages; the unusually situated palatine bone develops without a cartilaginous precursor and is considered a dermopalatine; the autopalatine is apparently lacking; the

cartilaginous meniscus, which forms the articulation of the ecto- and entopterygoid with the lateral ethmoid in juvenile and adult specimens, develops ontogenetically from the anterior tip of the pars autopalatina.

Hypotheses about inter- and intrarelationships of mastacembeloids are reviewed and tested using ontogenetic data. The phylogenetic position of *Sinobdella* among mastacembeloids is reinvestigated, and the genus is excluded from the Chaudhuriidae and reassigned to the Mastacembelidae.

INTRODUCTION

The percomorph suborder Mastacembeloidei consists of the families Mastacembelidae and Chaudhuriidae (Travers, 1984b). The mastacembeloids currently comprise about 67 species that are restricted to the freshwaters of Africa, the Middle East, and Asia (Nelson, 1994). Earlier authors considered them to be closely related to true eels, but Günther (1861, 1880) demonstrated their affinities with acanthopterygian fishes. Nev-

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ertheless, their relationships within Acanthopterygii have remained obscure. Gosline (1983) hypothesized that mastacembeloids are the closest relatives of the swamp-eel family Synbranchidae, and this view subsequently was supported by Travers (1984a, 1984b) and Johnson and Patterson (1993).

Mastacembelids possess a peculiar snout, a feature noted by early ichthyologists (e.g., Bloch, 1786). It consists of an unpaired median trunklike tentacle flanked by a pair of prominent tubular nostrils. The skeleton of the ethmoidal region, also remarkable in structure and shape, has been described by Regan (1912), Sufi (1956), Bhargava (1963), Roberts (1980), Gosline (1983), and Travers (1984a, 1984b). Although these authors commented on the unusual shape and position of the mastacembelid palatine bone, no studies have been conducted to reveal its development. Bhargava's (1958) ontogenetic investigation of the cranium of *Mastacembelus mastacembelus* was restricted to the cartilaginous skull only.

This paper provides a detailed account of the ontogeny of the hyopalatine arch and ethmoidal region in *Macrognathus pancalus,* an Asian representative of the family Mastacembelidae. This ontogenetic information is then used to evaluate the homology of the palatine bone in mastacembelids. Since the study of ontogeny can also provide new insights into the phylogenetic relationships between taxa, Travers's (1984b) hypotheses about the intra- and interrelationships of Mastacembeloidei then were tested with these new developmental data.

MATERIAL, METHODS, AND TERMINOLOGY

I follow Patterson (1977: 79) in the definition of dermal bone, cartilage bone, and membrane bone, and the terminology I use for the different parts of the chondrocranium is that of Gaupp (1906) and de Beer (1937).

Pars autopalatina, pars quadrata, and pars metapterygoidea refer to parts of the cartilaginous palatoquadrate, but the terms autopalatine, quadrate, and metapterygoid are restricted to the cartilage bones of the palatoquadrate, as they are in Arratia and Schultze (1991). Autopalatine and dermopalatine refer to a cartilage bone and a dermal bone, respectively. The term palatine is used when dermo- and autopalatine have fused during ontogeny or when a distinction between the two components cannot be made.

Seven wild-caught specimens of *Macrognathus pancalus* Hamilton, 1822, were obtained from an aquarium fish importer in Frankfurt, Germany. They were kept and bred in a 40-liter tank and fed mainly on aquatic insect larvae. When spawning first began—usually in May or June—the eggs were removed, and the hatched larvae were reared in another tank. In the first few days after the beginning of external feeding, larvae fed mainly on *Artemia* nauplii. Their diet was later changed to *Cyclops, Daphnia,* and the larvae of ephemeropterans, plecopterans, and dipterans in accordance with their size.

Specimens were fixed in buffered formalin at regular intervals. All measurements refer to total length.

Five fixed specimens of *M. pancalus* (AMNH 217413: 8, 12, 17.8, 33, and 107 mm) were chosen for investigation of the gross ontogenetic changes associated with head shape. They were stained for 10 to 40 seconds in a concentrated solution of methylene blue, then excess stain was removed by rinsing in

water for one to two minutes. In the study of skeletal development, 49 specimens of *M. pancalus* between 3.3 mm (newly hatched) and 36 mm (~3 months) were cleared and stained for cartilage and bone. In addition, eight specimens ranging from 5.7 to 26 mm were stained with alizarin only. Clearing and staining followed the procedure outlined by Dingerkus and Uhler (1977), including the modifications for larval material described by Taylor and vanDyke (1985). The eight double-stained specimens of *M. pancalus* figured in this paper were deposited under AMNH 217414.

For comparison, the following cleared and double-stained material also was studied: MASTACEMBELOIDEI: *Chaudhuria* sp., 42 mm (AMNH 217415); *Macrognathus maculatus,* 22, 32 mm (AMNH 217416); *Macrognathus circumcinctus,* 19 mm (AMNH 217412); *Sinobdella sinensis,* 53 mm (AMNH 10259) and 113, 114, 117 mm (all AMNH 11078, caudal fins missing); "*Mastacembelus pancalus,*" 15 mm head length (AMNH 3447); *Mastacembelus armatus,* 111, 130 mm (both AMNH 10274, caudal fins missing); *Afromastacembelus congicus,* 53, 62 mm (AMNH 6157). SYNBRANCHOIDEI: *Ophisternon aenigmaticum,* 72 mm (AMNH 31573); *Synbranchus marmoratus,* 47 mm (AMNH 74541), 184 mm (AMNH 215280); *Monopterus albus,* 41 mm (AMNH 41579), 164 mm (AMNH 41579).

All drawings were made with the aid of a camera lucida attached to a stereomicroscope (Zeiss SV8). One 9-mm specimen of *Macrognathus pancalus* was prepared for scanning electron microscopy (SEM) according to the procedure described by Britz et al. (1995).

ABBREVIATIONS

artmen	articulatory meniscus
cartpr	cartilaginous process on lateral ethmoid
dp	dermopalatine
ectp	ectopterygoid
entp	entopterygoid
ethpl	ethmoidal plate
f	frontal
hy	hyomandibula
hys	hyosymplectic cartilage
leth	lateral ethmoid
lo	lamina orbitonasalis
meth	mesethmoid
mtp	metapterygoid
ns	nasal septum
pap	pars autopalatina
pmt+pq	pars metapterygoidea and pars quadrata
ppq	posterior process of quadrate
ps	parasphenoid
q	quadrate
sy	symplectic
tmarg	taenia marginalis
tr	trabecula
trcom	trabecula communis
trh	trabecular horn
v	vomer

RESULTS

DEVELOPMENT OF HEAD SHAPE IN *MACROGNATHUS PANCALUS*

With the exception of Job's (1941) account and some incidental remarks by Polder (1963), the development of the highly peculiar snout structure of the mastacembelids has received little attention, and no detailed information is available.

The snout of the newly hatched embryo of *Macrognathus pancalus* is rounded and much different from that of the adult. Figure 1A shows the head of a larva of 8 mm in which the snout is still rounded and the anterior and posterior openings of the nasal cavity are small apertures in the skin. The lipfolds of the upper and lower jaw are well developed.

At 12 mm, the snout region is slightly elongated (fig. 1B). The anterior nasal openings are now located at the end of ventrally directed tubes.

At 17.8 mm, the snout region has elongated still further (fig. 1C). Its anterior end projects as a median proboscis-like fleshy appendage with paired anterior nasal tubes on either side. At this stage the postorbital region of the head also has undergone significant elongation.

At 33 mm (fig. 1D), the snout region closely resembles that of the adult. The entire ethmoidal region has continued to elongate and now projects in the long fleshy appendage typical of mastacembelids. The lipfolds of the upper jaw are less conspicuous than in earlier stages, and the anterior nostrils open at the end of long nasal tubes. The rim of each tube exhibits two flaps. Medial to the tubes lies the tapering central nasal tentacle.
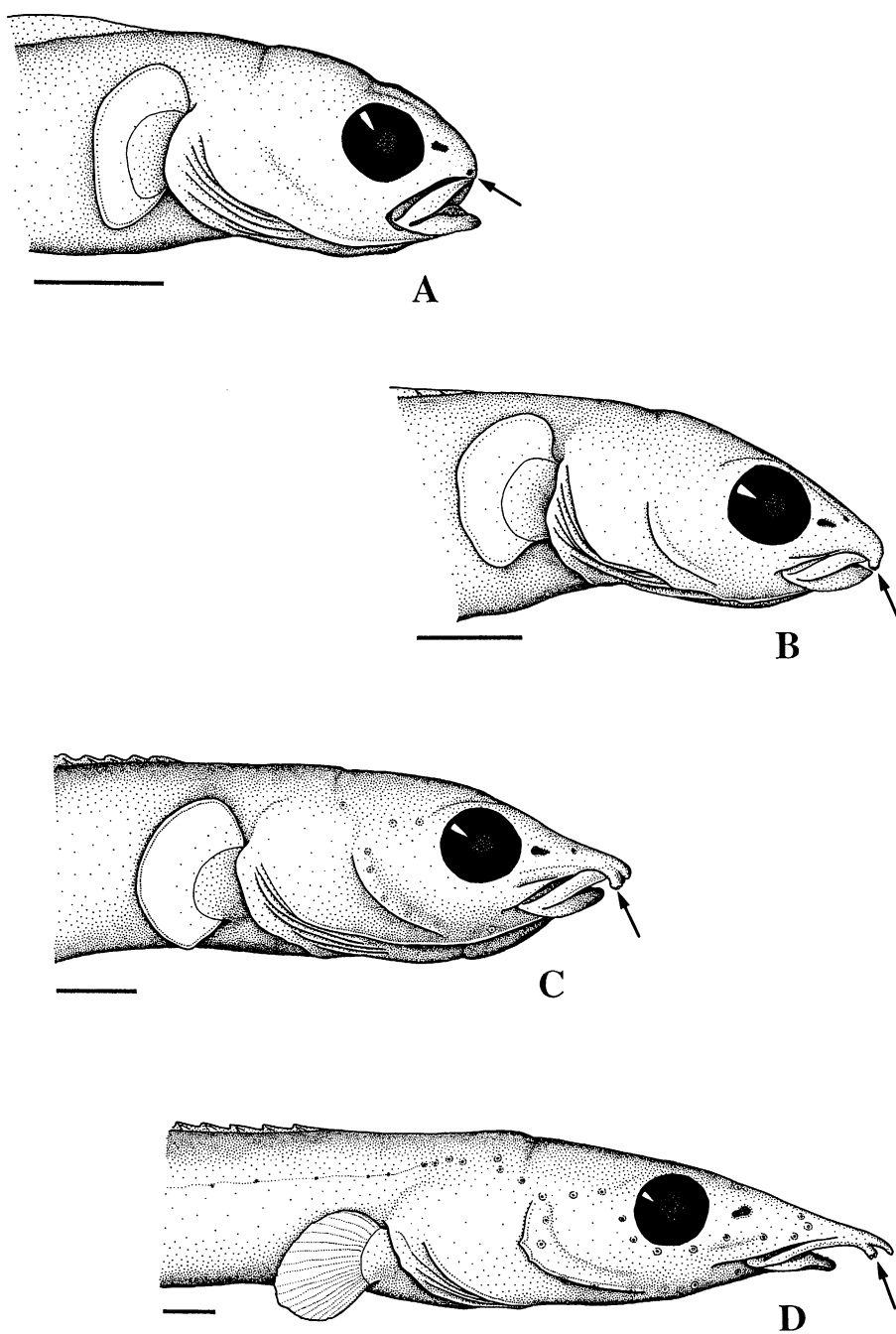
The snout region of adult *M. pancalus* was

Fig. 1. *Macrognathus pancalus*. Ontogeny of the snout region in lateral view. Arrow points to the anterior nasal opening. **A,** 8 mm; **B,** 12 mm; **C,** 17.8 mm; **D,** 33 mm. Scale bar 1 mm.

figured by Travers (1984b: fig. 13b). The main difference from the 33-mm stage is that in the adult the terminal rim of the anterior nasal tubes consists of six flaps of skin instead of two. The 107-mm specimen I examined confirms this observation, but details of the transition from two to six flaps could not be determined.

DEVELOPMENT OF THE HYOPALATINE ARCH AND ETHMOID REGION OF *MACROGNATHUS PANCALUS*

A radical skeletal transformation accompanies the developmental changes in head shape. When the larvae hatch, no traces of the cartilaginous skeleton can be found.

Although the cartilaginous paired trabeculae are separate from each other in the 4.25-mm larva, their rostral parts have already started to fuse along the midline by 4.75 mm (fig. 7A). Their anterior tips are slightly curved outward to form trabecular horns. The symplectic process of the hyosymplectic cartilage approaches the palatoquadrate closely (fig. 2A), and the palatoquadrate consists only of the pars metapterygoidea and pars quadrata; the pars autopalatina has not yet formed.

By 5.6 mm, the anterior parts of the trabeculae have completely fused along the midline, forming the ethmoidal plate. This solid block of cartilage bears five processes (figs. 2B, 7B): originating in the midline is the nasal septum; anteriorly, the trabecular horns are pronounced and form a pair of lateral processes; and posterior to them and directed dorsolaterally are the paired developing rudiments of the laminae orbitonasales. The hyosymplectic cartilage has changed only in size. The pars autopalatina has chondrified as a bar of cartilage, separate from pars metapterygoidea and pars quadrata, with its anterior end projecting toward the orbitonasal lamina of the ethmoidal plate.

By 5.9 mm, the pars autopalatina and pars quadrata have fused (fig. 2C), and the trabeculae have separated from the basal plate. The postorbital process projects rostrally from the auditory capsule. A dorsally directed process has formed on the lamina orbitonasalis, and the nasal septum has become larger.

At the 6.1-mm stage, ossification of the hyopalatine arch has begun. The hyomandibula is a perichondral bone with a small anteriorly directed membranous lamina (fig. 3A). The symplectic forms as a thin perichondral ossification around the symplectic process. In the palatoquadrate, only the quadrate is present, bearing a posteroventral process that consists only of membrane bone, a synapomorphy for teleosts (Arratia and Schultze, 1991). The pars autopalatina approaches the ventrolateral part of the lamina orbitonasalis (figs. 3A, 7B). There is no trace of a maxillary process on the pars autopalatina. In the space between the orbitonasal lamina and the trabecular horn, there is a small, thin splint of bone without any contact to cartilage (fig. 3A); this is the developing dermopalatine (see discussion below). When seen in ventral view (fig. 7B), the dermopalatine is situated in direct anterior prolongation of the tip of pars autopalatina. The nasal septum and the trabecular horns are pronounced. The narrow vomer underlies the broad ethmoidal plate. The postorbital process of the auditory capsule has fused with the lamina orbitonasalis, thus forming a complete taenia marginalis or orbital cartilage (fig. 3A).

By 7.4 mm, the ossifications of the hyopalatine arch cover large parts of the cartilage (fig. 3B). The metapterygoid has formed as a perichondral ossification around the posterodorsal part of the palatoquadrate, but its most distal tip remains cartilaginous. The pars autopalatina is a narrow strip of cartilage still continuous with the pars quadrata, and its anterior tip now articulates with the ventral part of the lamina orbitonasalis. Above and below the pars autopalatina, the entopterygoid and the ectopterygoid, respectively, have formed (fig. 3B). Both are narrow, splintlike dermal bones that ossify without cartilaginous precursors. The dermopalatine is situated in a gap between the orbitonasal lamina and the trabecular horn, which is now only a small cartilaginous nodule lying lateral to the cartilage of the ethmoidal plate but without any connection to it (fig. 3B). Part of the orbital cartilage has been resorbed. The taenia marginalis is thus separated into an anterior and a posterior part, producing a condition that resembles the 6-mm stage (cf. figs. 2C and 3B). The enlarged nasal septum has fused with the orbitonasal lamina to form the olfactory foramen, the passage of the olfac-
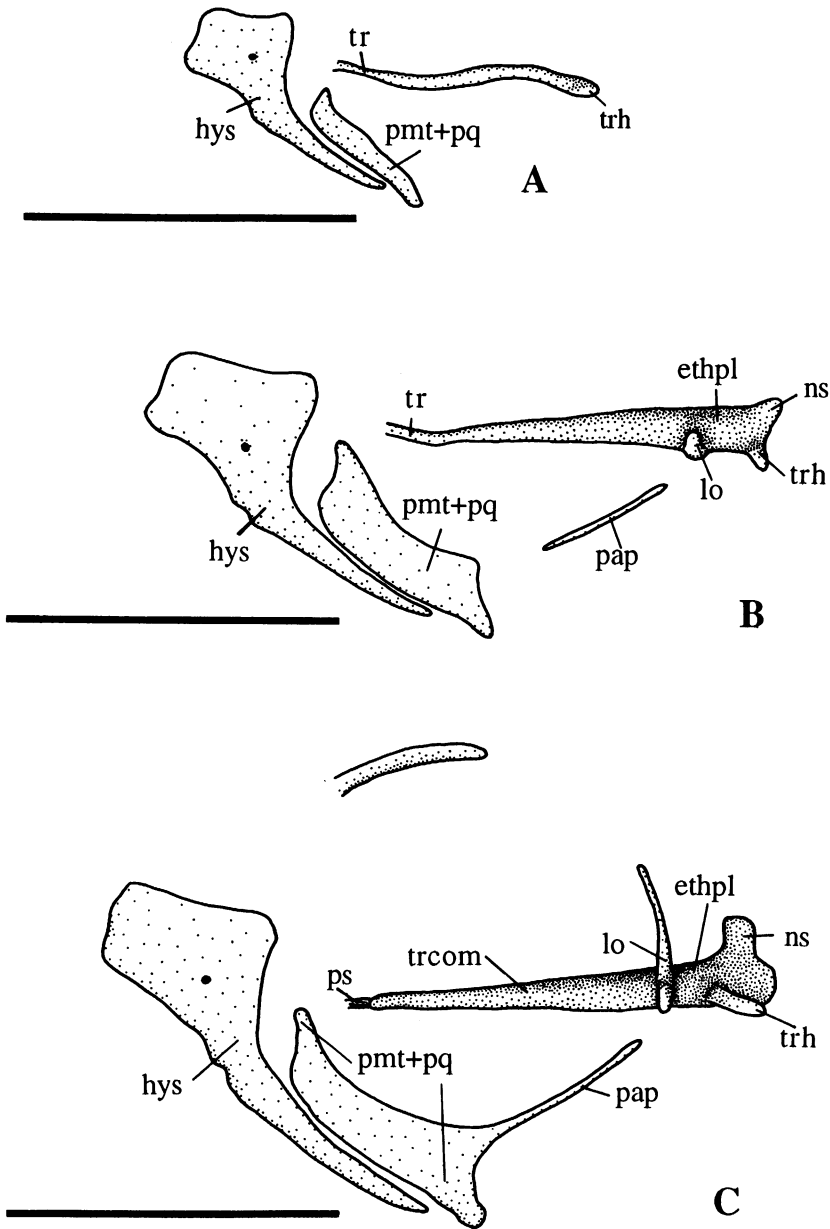
Fig. 2. *Macrognathus pancalus*. Ontogeny of the hyopalatine arch and ethmoidal complex in lateral view. Rostral cartilage not shown; lacrimal and nasal removed where developed; cartilage stippled. **A,** 4.75 mm; **B,** 5.6 mm; **C,** 5.9 mm. Scale bar 0.5 mm.

tory nerve. The most anterior tip of the nasal septum is surrounded by the perichondral ossification of the mesethmoid. It is still separated from the vomer and has already developed a long, pointed posterodorsal process of membrane bone.

By 9 mm, the hyopalatine arch is similar to that of the preceding stage, but the cartilage bones have encroached on larger areas of cartilage (fig. 4). The ecto- and entopterygoid still consist of narrow splints of bone, but the former has broadened its ventrocaudal part.
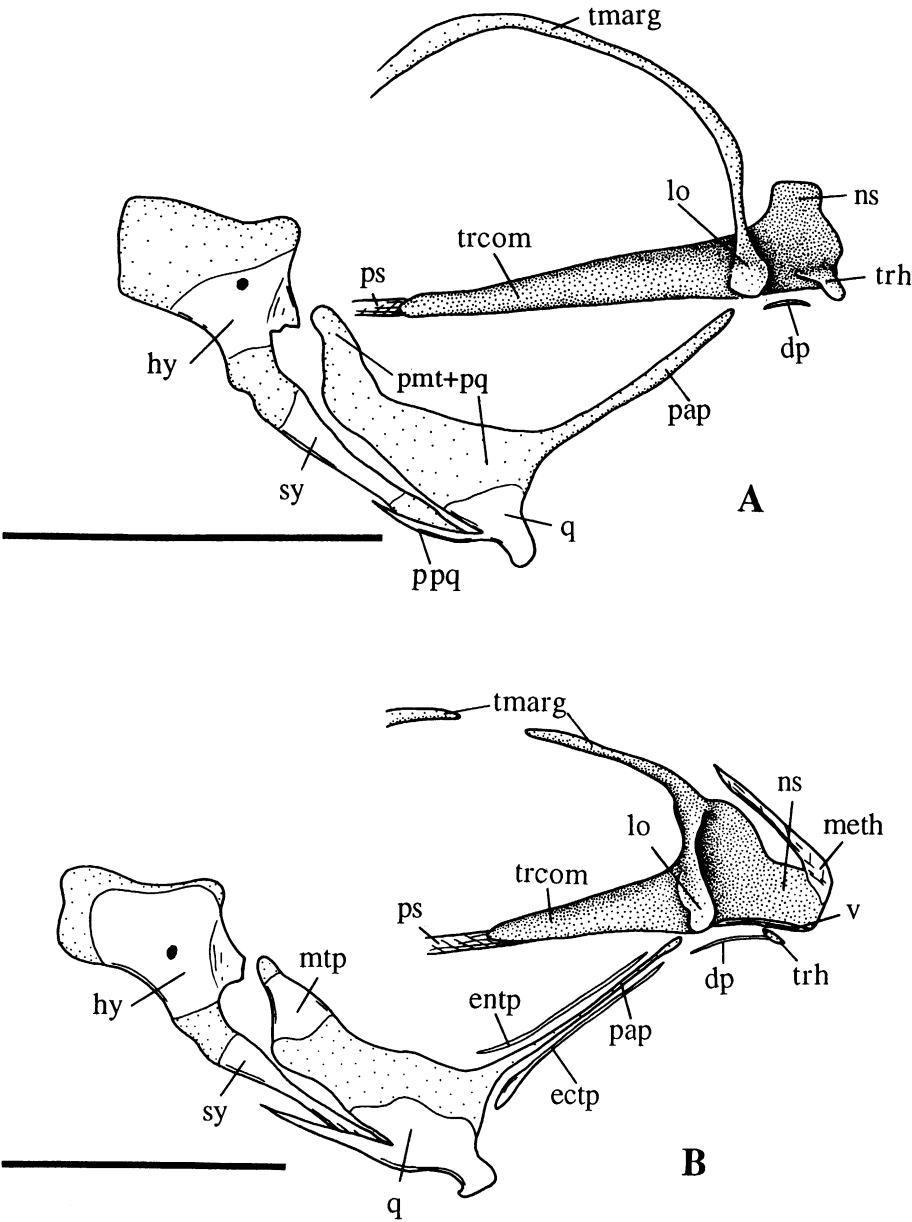
Fig. 3. *Macrognathus pancalus.* Ontogeny of the hyopalatine arch and ethmoidal complex, continued. A, 6.1 mm; B, 7.4 mm. Scale bar 0.5 mm.

The dermopalatine bone is stronger, has shifted closer to the midline, and now exhibits a number of conspicuous fanglike teeth on its ventral surface (figs. 4, 7C, 8). The rudiment of the trabecular horn is fully resorbed. A well-developed frontal bone overlies the anterior part of the taenia marginalis, and the lamina orbitonasalis is covered laterally by the perichondral ossification of the lateral ethmoid (fig. 4). The mesethmoid fully surrounds the dorsal and lateral sides of the anterior part of the ethmoidal plate, and its dorsocaudally directed membranous process lies between the anterior tips of the frontals. The
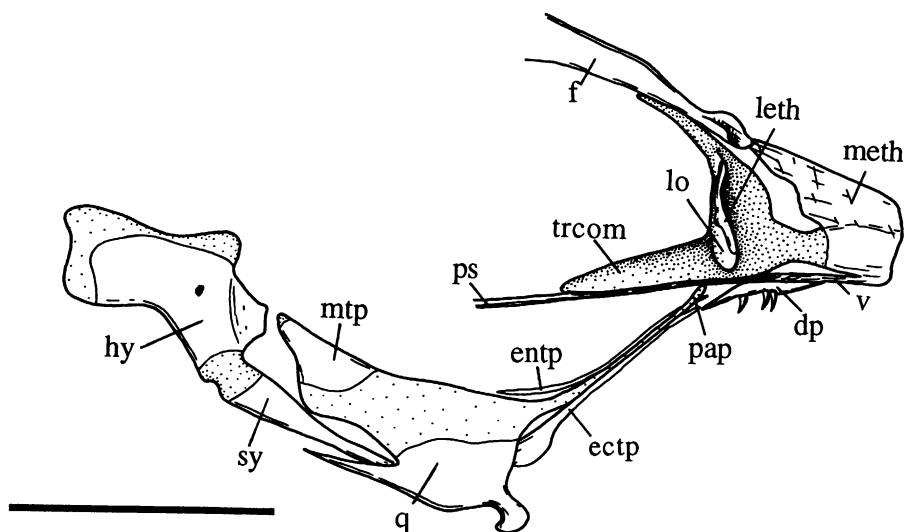
Fig. 4. *Macrognathus pancalus*. Ontogeny of the hyopalatine arch and ethmoidal complex, continued. 9 mm. Scale bar 0.5 mm.

anterior tips of the mesethmoid and vomer have fused.

By 12.8 mm, the cartilaginous connection between the pars quadrata and pars autopalatina (figs. 2C, 3A,B, 4) has been resorbed (fig. 5). Only a small anterodorsally directed process is present on the cartilage of the pars quadrata, but the pars autopalatina persists as an elongate nodule of cartilage (fig. 5, pap) between the anterior tips of ecto- and entop-

terygoid, still articulating with the ventral part of the lamina orbitonasalis. The entopterygoid and, especially, the ectopterygoid are well developed. The dermopalatine still bears a number of teeth. The ossification of the lateral ethmoid covers more of the lamina orbitonasalis, and the mesethmoid has elongated considerably.

The most advanced stage investigated in this study measured 36 mm. All of the car-
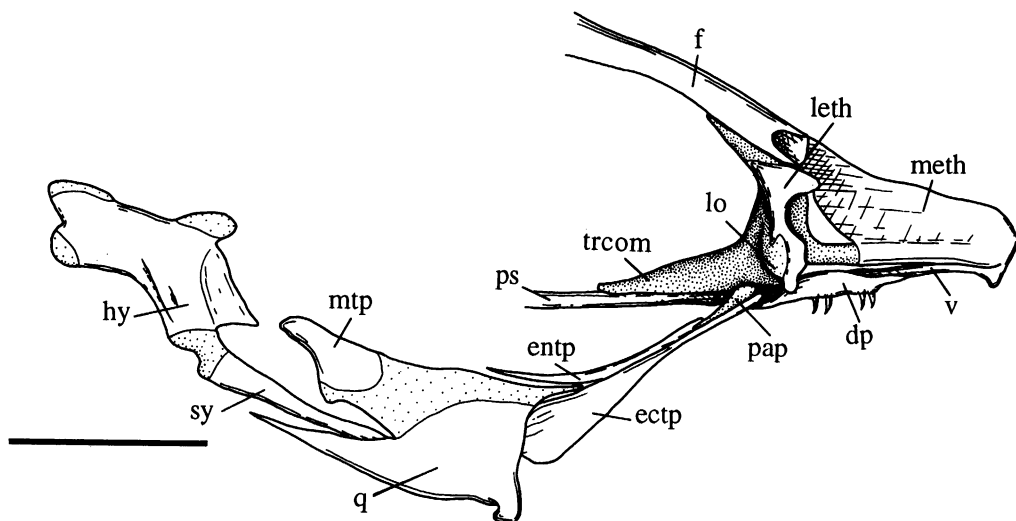

Fig. 5. *Macrognathus pancalus*. Ontogeny of the hyopalatine arch and ethmoidal complex, continued. 12.8 mm. Scale bar 0.5 mm.
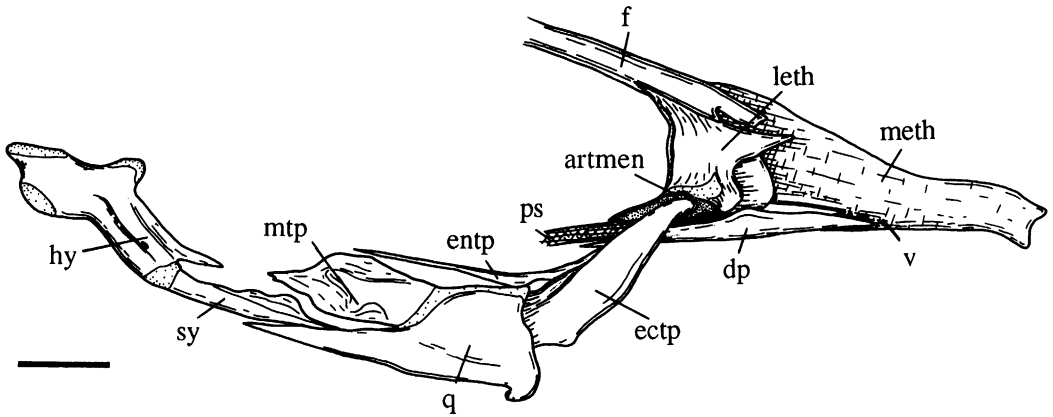
Fig. 6. *Macrognathus pancalus*. Ontogeny of the hyopalatine arch and ethmoidal complex, continued. 36 mm. Scale bar 0.5 mm.

tilage bones in the palatoquadrate have developed considerable amounts of membrane bone (fig. 6). Cartilage in the palatoquadrate is restricted to the articulations of the hyomandibula, small strips between hyomandibula and symplectic and between metapterygoid and quadrate, and a small nodule of cartilage that forms the articulatory meniscus (fig. 6, artmen) of the hyopalatine arch with the ethmoidal region. The complete ethmoidal region has further elongated, especially the mesethmoid and dermopalatine (figs. 6, 7D). The latter has lost all of its teeth and is attached to the vomer very closely for most of its length (fig. 7D).

THE HYOPALATINE ARCH AND ETHMOIDAL SKULL IN *CHAUDHURIA*

The skeleton of a specimen of *Chaudhuria caudata* was described by Travers (1984a). As he pointed out, the Chaudhuriidae lack an entopterygoid as well as a palatine bone (also Kottelat, personal commun.). However, further details are needed before meaningful comparisons can be made between the Chaudhuriidae and the Mastacembelidae.

In *Chaudhuria* sp. (AMNH 217415), the ectopterygoid extends rostrally from the quadrate to the anterior third of the mesethmoid (fig. 9B). It articulates syndesmotically with the medial side of the quadrate, from which it is dorsally directed toward the lateral ethmoid. From here, its anterior body is inclined toward the posterior at an angle, giving

the ectopterygoid a boomerang-like shape (fig. 9B). Anteriorly the ectopterygoid approaches the vomer very closely, running parallel to it, thus occupying the same position as the palatine in mastacembelids. An articulation between the hyopalatine arch and the lateral ethmoid via a cartilaginous meniscus, seen in mastacembelids, is not present in *Chaudhuria*. The large mesethmoid projects as a bony septum between the olfactory organs. Its pointed posterior part separates the two frontals. Its anterior tip is fused to the vomer. The mesethmoid and lateral ethmoid are connected by cartilage that is a rudiment of the nasal septum of the chondrocranium. The lateral ethmoid ossification is small compared to that of *M. pancalus*. Its dorsal part is firmly bound to the nasal, and it has a laterally directed ridge. A long cartilaginous process projects from the ventral part of the lateral ethmoid ventrolaterally (fig. 9B, cartpr). The medial side of this cartilaginous process articulates with the lateral side of the ectopterygoid, and the lateral tip of the cartilage is tightly bound to the posterior end of the lacrimal by connective tissue.

DISCUSSION

THE HOMOLOGY OF THE PALATINE BONE IN MASTACEMBELIDS

Regan (1912: 219) first reported on the peculiar shape and position of the palatine bone in the spiny eels. He described it as "an elongate narrow lamina which is firmly united to
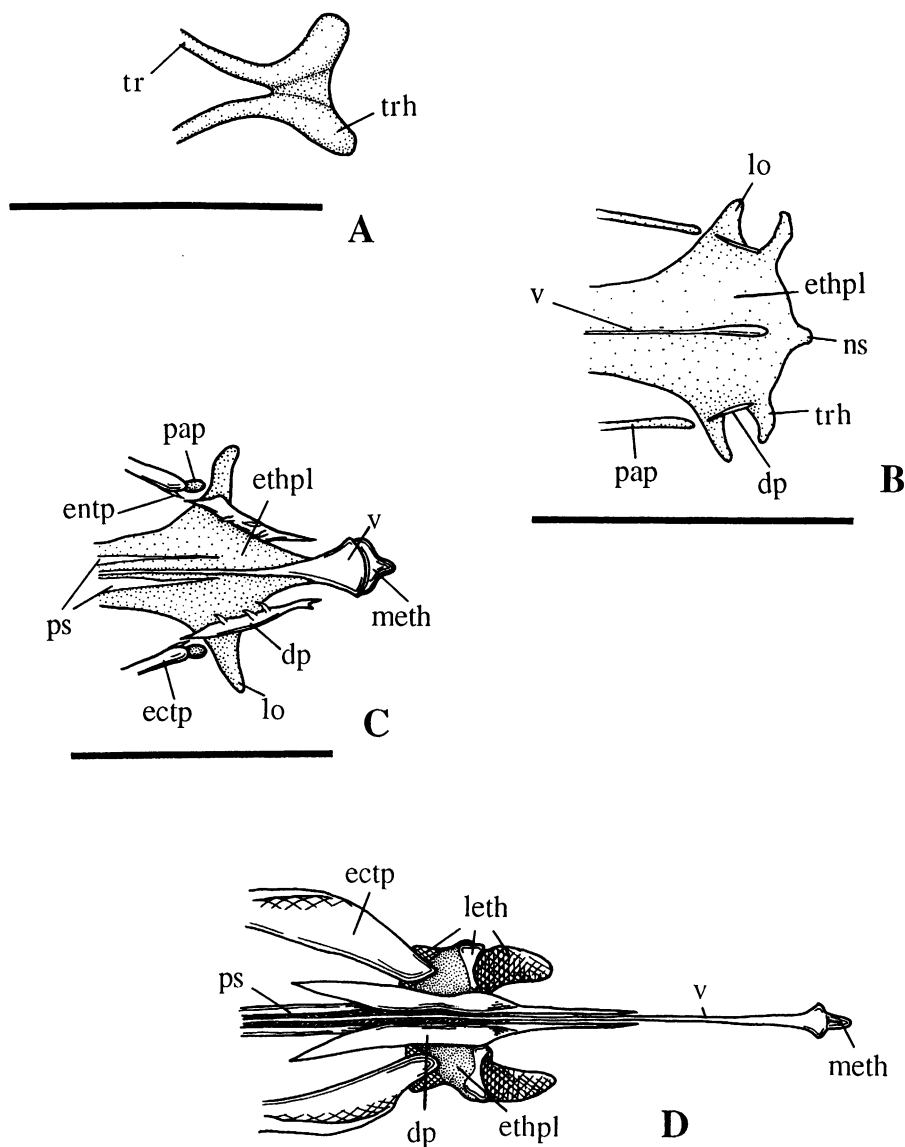
Fig. 7. *Macrognathus pancalus*. Ontogeny of the anterior hyopalatine arch and ethmoidal complex in ventral view. Same specimens as in figures 2A, 3A, 4, 6. Cartilage stippled. **A,** 4.75 mm; **B,** 6.1 mm; **C,** 9 mm; **D,** 36 mm. Scale bar 0.5 mm.

the lower surface of the vomer and also to the mesethmoid, lateral ethmoid, and parasphenoid." However, the exact nature of the palatine in mastacembelids has remained unknown for lack of developmental information. According to Travers (1984a: 21), "dermal and endochondral components cannot be distinguished" in *Mastacembelus mastacembelus*.

The present study of the ontogeny of the hyopalatine arch in *Macrognathus pancalus* reveals that the palatine ossifies without a cartilaginous precursor, and at no time during ontogeny does it have any connection with the cartilage of the palatoquadrate. Even in later development, it never fuses to or is closely connected with any bone of the palatoquadrate. This can be taken as unequiv-

ocal evidence of an exclusively dermal origin of the palatine in *M. pancalus*. Accordingly, this bone is a dermopalatine with no autopalatine component. Given the homogeneity of palatine morphology in all mastacembelids so far studied, it seems reasonable to consider this interpretation valid for all representatives of the family. Moreover, this study has demonstrated that the dermopalatine does not achieve its peculiar position close to the vomer until late in development, gradually shifting from its original lateral position to the final medial position (cf. fig. 7B,C,D).

Another remarkable and unexpected feature of this Asian mastacembelid is the presence of teeth on the palatine of *M. pancalus* during some ontogenetic stages. According to Sufi (1956: 95), the palatines of mastacembelids are "narrow flakes of bone immovably united to mesethmoid, vomer, and parasphenoid, bearing teeth in some African species, toothless in other African and all Asiatic species." This observation was confirmed by Travers (1984a: 84): "All Asian, and the majority of African species lack a palatine, tooth bearing, alveolar surface (dermopalatine)."

In contrast, my observations demonstrate that the palatine of *M. pancalus* bears teeth during a significant phase of development. The times of first appearance and disappearance of palatine teeth in *M. pancalus* are variable. In juveniles of 6.5 mm, teeth on the palatine can be present; these teeth can persist in specimens up to 23.5 mm in length, yet they can be lost in specimens 22 mm long. The fact that palatine teeth cannot be found in specimens of *M. pancalus* larger than 24 mm demonstrates that they are lost during ontogeny, and this is certainly the main reason for the notion that Asian mastacembelids lack palatine teeth. When present in the smaller juveniles of *M. pancalus*, palatine teeth are always fanglike (figs. 4, 5, 8) and probably serve to grasp and hold prey. Observations of larvae and juveniles feeding in captivity show that they are able to engulf prey very much larger in relation to their body size than are adults. Thus, the presence of palatine teeth in earlier ontogenetic stages in *M. pancalus* may be correlated with a different feeding mode of these larvae and juveniles—a hypothesis easily testable in the field
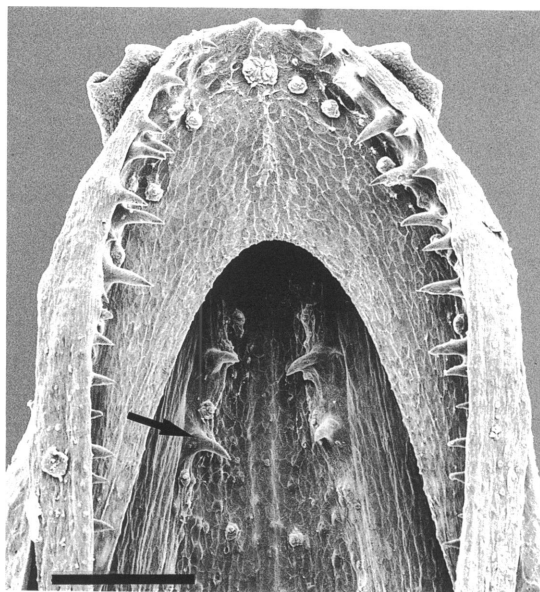

Fig. 8. *Macrognathus pancalus*. 9-mm larva. SEM photograph of the roof of the mouth showing palatal dentition. Arrow points to a tooth on the right palatine. Scale bar 0.1 mm.

by a comparative analysis of the food spectrum at different ontogenetic stages.

The presence of teeth on the palatine of Asian mastacembeloids was confirmed in three additional species. In one of three adult specimens of *Sinobdella sinensis* (AMNH 11078), two teeth are present at the anterior tip of the left palatine. In a smaller specimen of 53 mm, the left palatine bears six teeth and the right bears two (fig. 9A). A 22-mm specimen of *Macrognathus maculatus* (AMNH 217416) showed one tooth on the left palatine, whereas both palatines of a 32-mm specimen (AMNH 217416) of the same species were toothless. Furthermore, a 19-mm specimen of *Macrognathus circumcinctus* (AMNH 217412) had one tooth on each palatine, although this bone is toothless in adults (Sufi, 1956). These three examples can be taken as additional evidence for a change of the palatal dentition during ontogeny and a probable concomitant change in feeding mode in at least some Asian mastacembelids. Further studies must test whether this assumption holds for all Asian spiny eels.
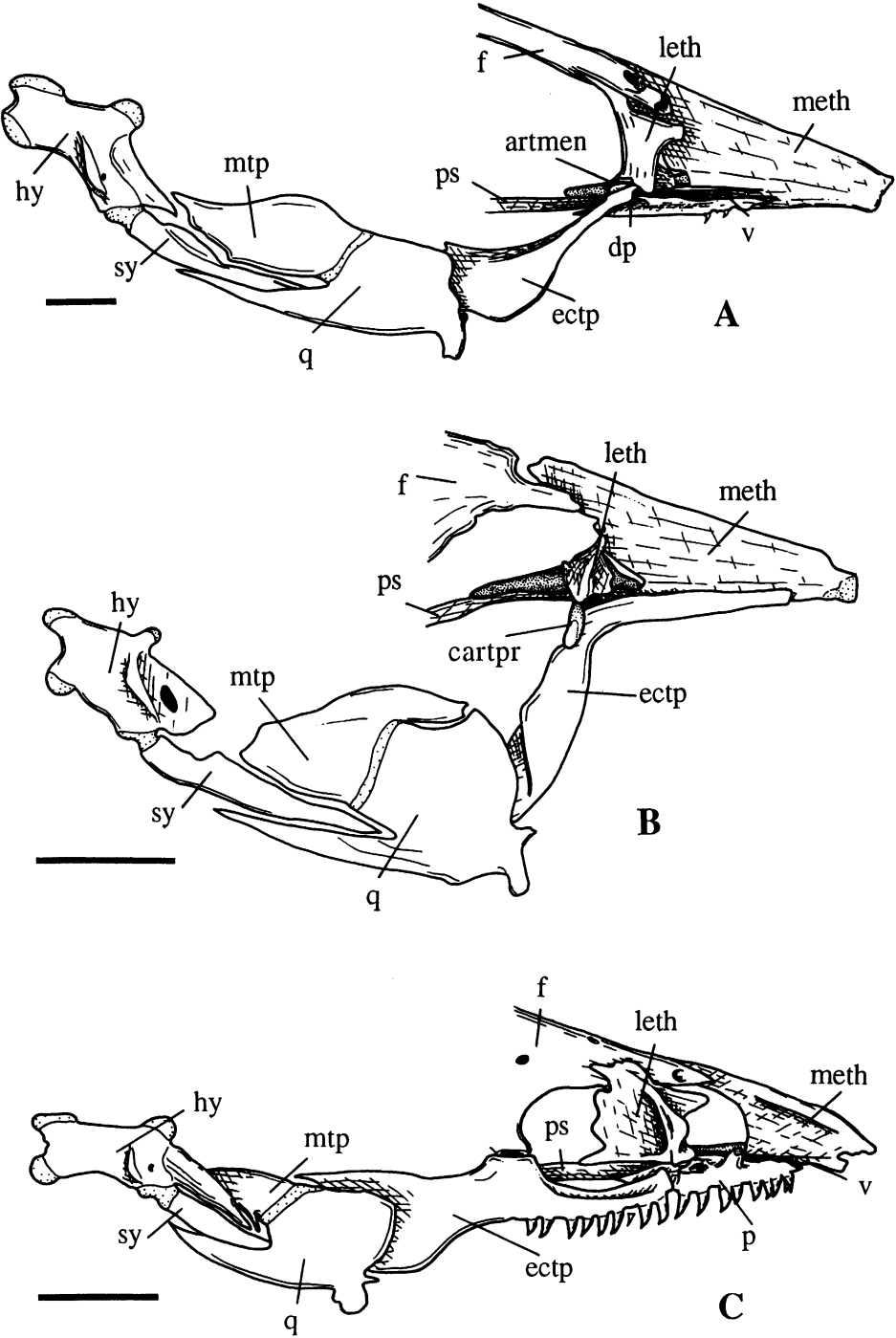
Fig. 9. Hyopalatine arch and ethmoidal complex in ventral view. Rostral cartilage not shown; lacrimal and nasal removed; cartilage stippled. **A,** *Sinobdella sinensis,* 53 mm; **B,** *Chaudhuria* sp., 42 mm; **C,** *Synbranchus marmoratus,* 47 mm. Scale bar 0.5 mm.

FURTHER UNUSUAL FEATURES IN THE ONTOGENY OF THE HYOPALATINE ARCH IN *MACROGNATHUS PANCALUS*

As described above, the pars autopalatina of *M. pancalus* develops as a chondrification separate from all other parts of the palatoquadrate (fig. 2A). In later developmental stages, the pars autopalatina fuses with pars quadrata and metapterygoidea (fig. 2C), establishing a condition that is found in most other teleosts from the beginning (e.g., Swinnerton, 1902; de Beer, 1937; Daget, 1964; Arratia and Schultze, 1991). The separate chondrification and later fusion were described and illustrated by Bhargava (1958) for *Mastacembelus armatus*. Among percomorphs, this seems to be an unusual character, but comparative data are lacking at the moment. In teleosts, a separately chondrifying pars autopalatina has been reported for some clupeids (Wells, 1923; Shardo, 1995), siluroids (Kindred, 1919; Arratia, 1990; Arratia and Schultze, 1991), and syngnathids (Kindred, 1921; Kadam, 1961). All these groups are distantly related to mastacembelids.

A second unusual feature in the skeletal ontogeny of *Macrognathus pancalus* is the lack of a maxillary process of the pars autopalatina (cf. figs. 2C, 3–6). *Mastacembelus armatus* also lacks a maxillary process (Bhargava, 1958: figs. 11, 12, 17, 18). Unlike the situation in most other teleosts, in these mastacembelids, the anterior end of the pars autopalatina stops at the level of the lamina orbitonasalis. Separate chondrification of the autopalatine, as well as lack of a maxillary process, can be hypothesized as synapomorphies for mastacembelids or even mastacembeloids. However, ontogenetic data on chaudhuriids and synbranchids are needed to confirm the hypotheses.

REMARKS ON THE HOMOLOGY OF THE PALATINE IN TELEOSTS

The palatine in teleosts primitively consists of two different bones: the autopalatine, which forms around the anterior tip of the palatoquadrate, and the dermopalatine, which ossifies ventral to the autopalatine without a cartilaginous precursor and bears teeth (Gaupp, 1906; Arratia and Schultze, 1991).

The two bones develop from separate ossification centers and remain separate in lower teleosts but are considered to be fused in Clupeocephala (Arratia and Schultze, 1991), although being separate in *Alepocephalus* (Gosline, 1969) and some osmerids (Johnson, personal commun.). The ontogenetic fusion seems to have been demonstrated in only two clupeocephalans: *Salmo* (de Beer, 1937) and *Plecoglossus* (Howes and Sanford, 1987). The dermopalatine is lost in several teleostean lineages, e.g., the Ostariophysi (according to Fink and Fink, 1981). Teeth on the palatine occur in a wide range of teleosts. Usually the possession of palatal teeth in the adult is taken as evidence for the presence of a dermopalatine. However, detailed studies of the ontogeny of this region that incorporate a well-graded series of developmental stages are lacking for representatives of percomorphs with palatine teeth.

As my ontogenetic studies have revealed, palatine teeth can also be lost during ontogeny, a fact hitherto reported only rarely (Howes and Sanford, 1987, for *Plecoglossus*) and one that must influence the evaluation of the homology of the palatine bone in teleosts. Lack of palatine teeth in adult teleosts cannot be taken as evidence that a dermopalatine is lacking in these fish, as, for example, Travers (1984a) has done. On the other hand, the existence of teeth on the palatine does not necessarily indicate that a dermo- and autopalatine are present, inasmuch as in mastacembelids, only the dermopalatine may be developed. This demonstrates that ontogenetic studies are imperative in order to evaluate the homology of the palatine if this feature is to be used in discussions of phylogeny.

INTERRELATIONSHIPS OF MASTACEMBELOIDEI

The hypothesis of Gosline (1983) that mastacembeloids and synbranchids are closely related was substantiated by Travers (1984b), who cited six derived characters shared by both groups:

1. Loss or reduction in size of the posttemporal bone, accompanied by loss of the connection to the pectoral girdle.
2. Extension of the dentary posteroventrally

along the ventral edge of the angulo-articular.
3. Wide anterolateral face of the ectopterygoid and its direct articulation with the lateral ethmoid.
4. Palatine sutured along the posterolateral face of the vomerine shaft.
5. Insertion of the levator operculi muscle on the dorsolateral face of the operculum.
6. Dorsolateral expansion of the hyohyoidei adductores muscle, sealing the operculum to the body wall and causing a restricted opercular opening.

Doubts concerning the validity of some of these characters as synapomorphies of synbranchids and mastacembeloids arose during this study.

Loss or reduction in size of the posttemporal bone, accompanied by a loss of connection to the pectoral girdle (character 1): The ambiguity of this character as a synapomorphy of synbranchids and mastacembelids can be seen by Travers's (1984b: 96) own remarks: "A well developed, forked, posttemporal connecting the basicranium to the pectoral girdle . . . occurs in *Monopterus albus* and *Ophisternon*. . . ." Thus, disconnection of shoulder girdle and skull and reduction in size of the posttemporal have occurred only in some synbranchids and cannot be used as a synapomorphy to align synbranchids with mastacembelids. To do so is to assume reversal in those genera of synbranchids in which a connection exists between the shoulder girdle and the skull. According to the present hypothesis of the intrarelationships of synbranchids (Rosen and Greenwood, 1976: figs. 66, 67), this is a less parsimonious assumption.

Wide anterolateral face of the ectopterygoid and its direct articulation with the lateral ethmoid (character 3): As Travers (1984a) correctly pointed out and as has been confirmed in this study, a small cartilaginous meniscus situated at the anterior ends of the ecto- and entopterygoid bones forms the articulatory surface between the hyopalatine arch and the ethmoidal region in adult mastacembelids (and in *Sinobdella sinensis*; see below and fig. 9A, artmen). This meniscus is a rudiment of the anterior tip of the cartilaginous palatoquadrate, the pars autopalatina (figs. 2–6).

Strictly speaking, there is no direct articulation between the ectopterygoid and the lateral ethmoid in mastacembelids.

An articulatory cartilage is apparently missing in synbranchids, but there are no detailed data available concerning the ontogeny of the head skeleton of synbranchids. According to my own observations on juvenile *Ophisternon, Synbranchus,* and *Monopterus,* both the ectopterygoid and the palatine contribute to the articulation with the lateral ethmoid (fig. 9C).

The whole picture is further complicated when we consider the condition in chaudhuriids. As previously indicated there is no articulatory cartilage between the ectopterygoid and lateral ethmoid in *Chaudhuria.* The ethmoidal articulation of the ectopterygoid in this taxon is significantly different from that in mastacembelids (cf. fig. 5A and B). Unfortunately, there are no ontogenetic data for any chaudhuriid. It may well be that the chaudhuriid condition evolved from the mastacembelid condition and that, accordingly, an articulatory cartilage was present in the last common ancestor of Chaudhuriidae and Mastacembelidae. On the other hand, it is at least as likely that the meniscus is a synapomorphy of the Mastacembelidae. Additional evidence is needed before a choice can be made between the two hypotheses. However, the question of possible similarities between synbranchids and mastacembeloids in the articulation in the hyopalatine arch with the lateral ethmoid still remains. Despite the weakness of some of Travers's (1984b) characters, the hypothesized sister-group relationship of synbranchids and mastacembeloids still seems to be convincing considering the additional synapomorphies cited by Johnson and Patterson (1993).

REMARKS ON THE PHYLOGENETIC
POSITION OF *SINOBDELLA SINENSIS*

The spiny eel *Sinobdella* (= *Rhynchobdella* in Travers, 1984a, 1984b) *sinensis* was considered to be a member of the family Mastacembelidae until Travers (1984b: 132) included it in the family Chaudhuriidae, as the sister group of all other chaudhuriids, on the basis of shared similarities between *Sinob-*

della, Chaudhuria, and *Pillaia.* These similarities are:

1. Long, narrow posterior parasphenoid processes.
2. Dorsomedial processes of the exoccipital separated by the supraoccipital.
3. Dorsal surface of the exoccipital perforated.
4. One or two inner rows of premaxillary teeth.
5. Loss of entopterygoid.
6. Ectopterygoid with narrow lateral face and very long anterodorsal process.
7. Palatine reduced in size.
8. Interdigitating processes of anterior and posterior ceratohyals reduced or lost.
9. Loss of ventral processes on basibranchial 2.
10. Loss of epipleural ribs and three or fewer epicentral ribs.

Kottelat (1991) disagreed with Travers's (1984b) taxonomic changes and, in addition, Johnson and Patterson (1993: 586) found "problems with Travers's characterization of the Chaudhuriidae." The latter authors pointed out that at least some of the above-cited similarities (nos. 1, 2, 4, 9) may be plesiomorphies and others (nos. 8, 10) may not exist. Recently, Kottelat and Lim (1994) re-expressed their doubt about the phylogenetic placement of *Sinobdella sinensis.* Some of the characters thought by Travers (1984b) to align *Sinobdella* with Chaudhuriidae will be discussed by Kottelat in a forthcoming paper on the osteology of chaudhuriids and will not be addressed in this work. In addition to the criticisms by Johnson and Patterson (1993) and Kottelat (personal commun.), results of my studies further weaken Travers's (1984b) hypothesis of a close relationship between *Sinobdella* and the chaudhuriids. These points will be discussed here in detail.

Dorsomedial processes of the exoccipitals separated by the supraoccipital (similarity 2; cited by Johnson and Patterson [1993: 586] as "presence of a spina occipitalis"): My investigation of four specimens of *Sinobdella sinensis* revealed that in only three of them did the supraoccipital separate the exoccipitals. The specimen of *Chaudhuria* sp. has

the exoccipitals meeting in the midline and not separated by the supraoccipital. In addition, two specimens of *Mastacembelus armatus* (AMNH 10274) showed exoccipitals separated by the supraoccipital. These observations are limited, but clearly demonstrate variation in this character and thus its ambiguity as a synapomorphy for *Sinobdella* and chaudhuriids.

Dorsal surface of the exoccipital perforated (similarity 3): In the four specimens of *Sinobdella* investigated in this study, I was unable to recognize the "dense perforations" that Travers (1984b: 112) described. No striking differences could be discerned between the perforations of the exoccipital in *Sinobdella, Chaudhuria,* and the investigated mastacembelids. Furthermore, there seems to be large intraspecific variation that may have been overlooked by Travers (1984a, 1984b), who, according to his list of study material (1984a: table 3), investigated only one cleared-and-stained specimen of *Sinobdella.*

Loss of entopterygoid; ectopterygoid with narrow lateral face and very long anterodorsal process; and palatine reduced in size (similarities 5, 6, and 7): Inasmuch as these three characters seem to be correlated, they are treated together in this paragraph. In *Sinobdella, Chaudhuria,* and *Pillaia* (Travers, 1984a, 1984b), as well as in other chaudhuriids (Kottelat, personal commun.), an entopterygoid is lacking. However, the articulations of the ectopterygoid with the lateral ethmoid in *Sinobdella* and *Chaudhuria* are quite different from each other. The articulation in *Sinobdella* more closely resembles the condition in all other mastacembelids: the ectopterygoid articulates with the lateral ethmoid via a cartilaginous meniscus (fig. 9A). This meniscus is absent in *Chaudhuria* (fig. 9B). Furthermore, the shape of the ectopterygoid in *Sinobdella* is not significantly different from the shape of the ectopterygoid in other mastacembelids, especially if we consider developmental stages, and is not specifically similar to that in *Chaudhuria* (cf. fig. 9A with figs. 5, 6 and fig. 9B). The dermopalatine of *Sinobdella* cannot be considered reduced in size, inasmuch as it is not different in shape from the dermopalatines in other

mastacembelids and even bears teeth in earlier developmental stages (fig. 9A).

Loss of epipleural ribs and three or fewer epicentral ribs (similarity 10): As already noted by Johnson and Patterson (1993), Travers (1984b) confused intermuscular bones with pleural ribs. Johnson and Patterson (1993) found four intermuscular bones (their epineurals) in *Sinobdella,* not three as reported by Travers (1984a, 1984b), and these originate on the first four centra. Their observation was confirmed by the four specimens of *S. sinensis* examined in the present study. Two of them had four intermuscular bones on both sides one five on the left and four on the right side, and one five on both sides. Pleural ribs are present on all abdominal vertebrae, from the third or fourth toward the rear. The number of intermuscular bones varies among chaudhuriids between zero and two (Kottelat, personal commun). These remarks invalidate the above-cited character as a synapomorphy at this level because *Sinobdella* does not differ in these characters from other mastacembelids like *M. mastacembelus* (see Travers, 1984a: fig. 12).

According to the information presently available, there are no significant similarities between *Sinobdella* and Chaudhuriidae, except for the lost entopterygoid, that would support the inclusion of *S. sinensis* in this family. On the contrary, there are at least two characters shared only by *Sinobdella* and mastacembelids that could be interpreted as synapomorphies for that group.

Sinobdella shares with mastacembelids the special articulation of the ectopterygoid with the lateral ethmoid via a cartilaginous meniscus (a remnant of pars autopalatina; see above) in juveniles and adults. This specific articulation has not been found in chaudhuriids or synbranchids or any other teleost.

Sinobdella shares with mastacembelids the peculiar elongated shape and dorsally shifted position of the coronomeckelian bone that does not occur in chaudhuriids or synbranchids or any other teleost. Travers (1984b: 115) was aware that chaudhuriids lack an especially elongated coronomeckelian, and that it more "resembles the plesiomorphic condition seen in other groups as the percoids," but he interpreted the chaudhuriid condition as "secondarily reduced." This interpretation rests on the hypothesis that *Sinobdella* and the chaudhuriids are sister groups, an assumption that lacks support at present.

Based on these shared characters between *Sinobdella* and the mastacembelids, and on the weakness of a number of Travers's (1984b) similarities, I concur with the recommendation of Kottelat and Lim (1994) that *Sinobdella* should be retained in the family Mastacembelidae, in which it may form the sister group of all remaining mastacembelids.

The present study has demonstrated that investigations of skeletal ontogeny can be of outstanding importance in anatomical and phylogenetic studies. It yields new sources of characters with phylogenetic significance and is a powerful tool in evaluating the homology of osteological characters. A limitation to the utilization of these characters in phylogenetic discussions at the moment seems to be a lack of such ontogenetic data in the majority of teleostean groups—a gap in our knowledge that hopefully will be filled in the future.

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