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Comparative Morphology and Development of Bony Elements in the Head Region in Three Species of Japanese Catfishes (*Silurus*: Siluridae; Siluriformes)

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Abstract The shape and development of bony elements of the neurocranium and suspensorium were studied in three species of Japanese catfish (*Silurus*) from the viewpoint of comparative morphology. In *S. asotus* and *S. biwaensis* the order of appearance of the bony elements was similar, but the ossification of most elements was delayed in *S. lithophilus*. The neurocranium and suspensorium of adult *S. lithophilus* retain juvenile features compared with the other two species. On the other hand, in the skull of *S. biwaensis* the sagittal crest of the supraoccipital, the ridge of the pterotic, and the hyomandibular process are more developed than in the other two species.

Of the three species of silurid catfish inhabiting the Japanese islands, *Silurus asotus* is widely distributed throughout East Asia (Nikolsky, 1961), but the other two species, *S. lithophilus* and *S. biwaensis*, are endemic to the water basin of Lake Biwa (Tomoda, 1961). These species are so similar in appearance that they had been considered to be a single species before Tomoda (1961) separated them on the basis of morphological and ecological characteristics. Until now the osteology of these species has not been studied, although it is important and useful for determining their phylogenetic relationships.

Many authors have described various catfish skulls (Regan, 1911; Gregory, 1933; Alexander, 1965; Tilak, 1965) but have concentrated on the adult skull or only part of the skull. Chen (1977) compared the skulls of *S. asotus* with several other Chinese silurid fishes, but his observations were restricted to the dorsum of adult skulls. Only a few researchers have considered the development of the entire skull (Bamford, 1948; Srinivasachar, 1958).

In this study the morphological differences between the skull of the three Japanese silurids and the mode of development of the skull elements are described. In addition, the time and order of appearance of each skull element is clarified.

Materials and methods

Catfishes were collected from Lake Biwa during their spawning season in May and June in 1974, 1975, 1978, and 1982. Five adult specimens of both sexes, of estimated age three or four years, were examined in each species.

The specimens were fixed with 10% neutral formalin, and after removal of the skin and flesh, the skulls were stained with alizarin red S. For the topological arrangement of bony elements, four measurements were taken: skull width at the level of the lateral ethmoids (W1), width at the level of the projections of the sphenotics (W2), width at the level of the postero-lateral projections of the pterotics (W 3), and length between the anterior margin of the mesethmoid and the posterior end of the supraoccipital (L).

Other adult specimens of each species were captured during their spawning seasons in 1978, 1979, and 1982 to obtain eggs, and the females injected with gonadotropin (10 I.U./1 g BW). From 18 to 20 hours after injection, the eggs were squeezed out and fertilized artificially in a sperm suspension prepared from dissected and homogenized testes of the conspecific males. Larvae and juveniles were fed on *Daphnia pulex*, *Tubifex* sp., larval *Cylonomus plumosus* and the fry of cyprinid fish. They were sampled at intervals and fixed with 10% neutral formalin.

The division of prelarval stages established by the degree of morphogenesis, based mainly on the fins, was used to compare the development of bony elements with other morphological features. After the standard lengths (SL) were measured, the 20 larvae

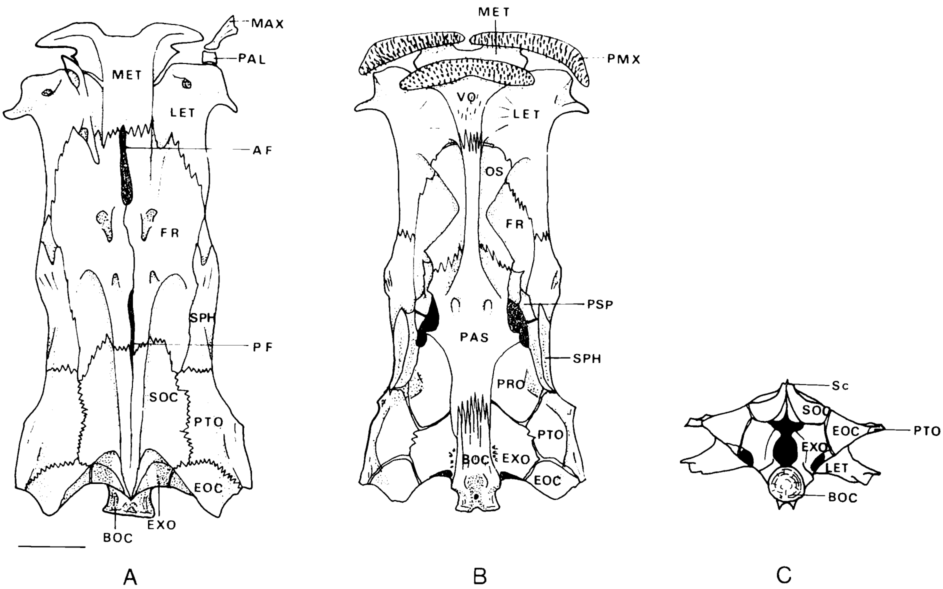

Fig. 1. Skull of *Silurus asotus*. A: dorsal view; B: ventral view; C: posterior view. AF, anterior fontanel; BOC, basioccipital; EOC, epioccipital; EXO, exoccipital; FR, frontal; LET, lateral ethmoid; MAX, maxilla; MET, mesethmoid; OS, orbitosphenoid; PAL, palatine; PAS, parasphenoid; PF, posterior fontanel; PMX, premaxilla; PTO, pterotic; SOC, supraoccipital; SPH, sphenotic; PRO, prootic; PSP, pterosphenoid; Sc, sagittal crest; VO, vomer. Scale bar indicates 1 cm.

and juveniles of each stage were stained with alizarin red S, and later transferred to pure glycerin through a H_2O-glycerin series. When the specimens had become translucent, the skin and flesh were removed under a binocular dissecting microscope. The skull bone elements were then measured as in the adult specimens. The time of appearance of bony elements was recorded as days after insemination. The beginning of ossification was taken as the onset of visible alizarin staining viewable by binocular microscope.

Identification of each element was made from the distribution pattern of the lateral line canal in the head region (Lundberg, 1975). Nomenclatures of Patterson (1975), Howes (1983), and Howes and Teugels (1989) were adopted for the skull bone elements and the suspensorial bones.

Results

In all adult specimens of the three species the bony elements of the neurocranium observed in dorsal view are: the premaxillae, maxillae, palatines, mesethmoid, lateral ethmoids, frontals, sphenotics, pterotics, supraoccipital, epioccipitals, exoccipitals, and nasals. The elements observed in the ventral view are the premaxillae, maxillae, mesethmoid, vomer, palatines, lateral ethmoids, orbitosphenoids, frontals, pterosphenoids, sphenotics, prootics, pterotics, basioccipital, epioccipitals, and exoccipitals. In the suspensorium the hyomandibular, quadrate, metapterygoid, and entopterygoid are observed.

Adult skull morphology. Sexual dimorphism in the arrangement of the bony elements of the skulls is not observed in any of the three species.

The arrangement of the skull elements is generally similar in the three species in both dorsal and ventral views (Figs. 1, 2 and 3). However, the pterosphenoids and the pair of large foramina through which pass cranial nerves V and VII are invisible in ventral view in *S. biwaensis* (Fig. 3), since the foramina open laterally in this species and can be seen only in lateral view.

In posterior view, the sagittal crest, which provides the attachment surface for the epaxial portion of the lateral muscle, is clearly seen in all species. The development of the crest is most remarkable in *S. biwaensis*; the outer ridge of pterotics rises upwards much more distinctly (Fig. 3C) than in *S. asotus* (Fig. 1C) and *S. lithophilus* (Fig. 2C). Fur-

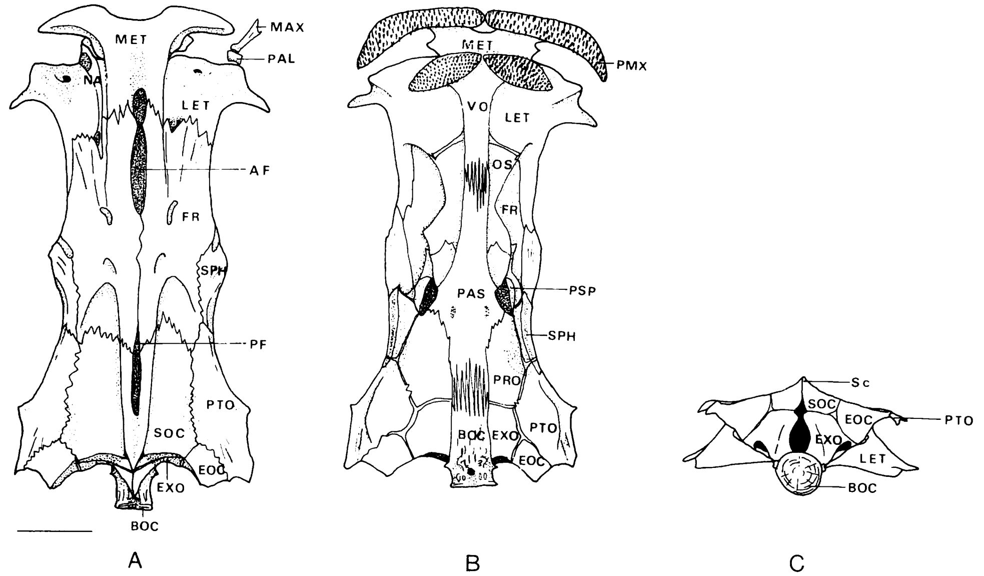

Fig. 2. Skull of *Silurus lithophilus.* A: dorsal view; B: ventral view; C: posterior view. See Fig. 1 for abbreviations. Scale bar indicates 1 cm.

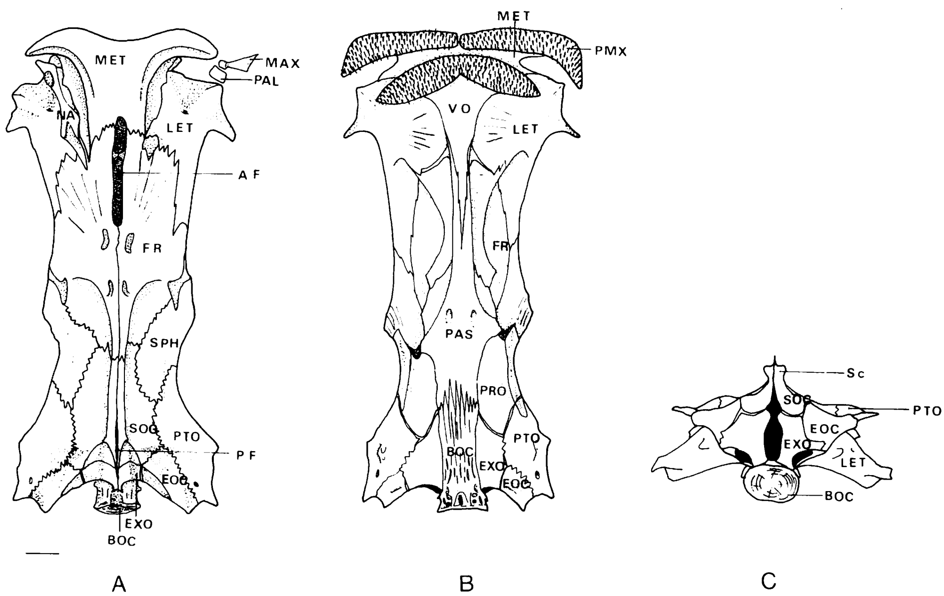

Fig. 3. Skull of *Silurus biwaensis.* A: dorsal view; B: ventral view; C: posterior view. See Fig. 1 for abbreviations. Scale bar indicates 1 cm.

thermore, in *S. biwaensis* the sagittal crest is fully developed even in a young specimen (20.5 cm SL), whereas such development is not evident even in larger specimens of *S. asotus* (30.2 cm SL) or *S. lithophilus* (22.5 cm SL).

The ratio of skull width to length (W/L) is shown in Table 1. *S. asotus* and *S. lithophilus* have nearly the same W2/L ratios, somewhat larger than that of *S. biwaensis* (Table 1).

In juveniles, in which all the skull bony elements have begun to ossify, W1/L and W2/L are larger than those of conspecific adults. W3/L of adult *S.*

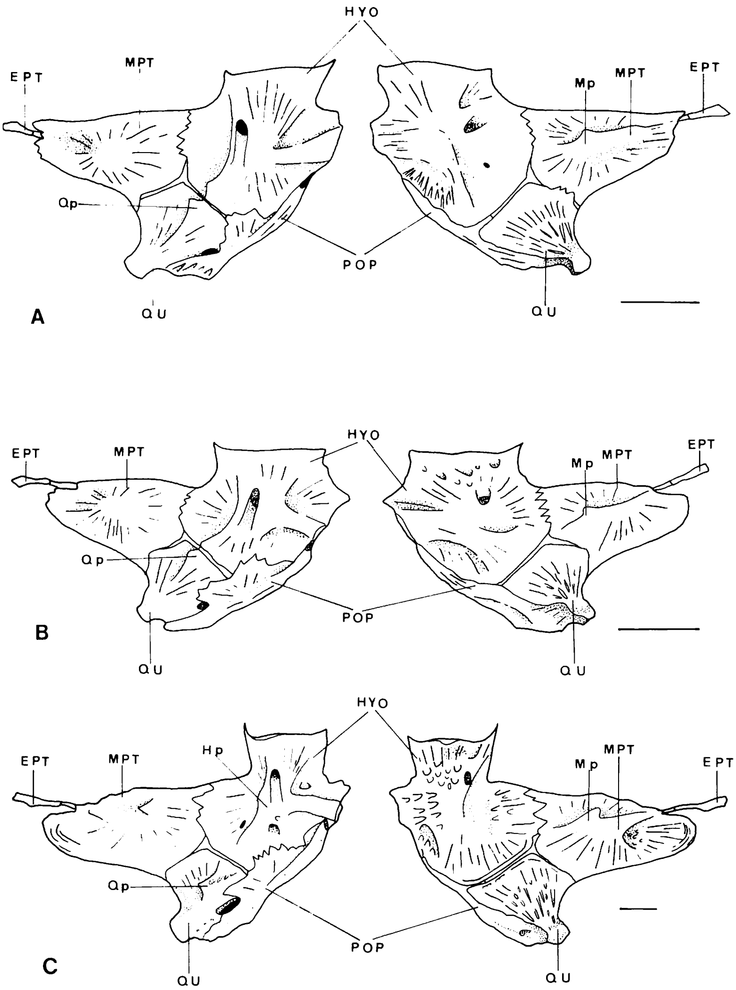

Fig. 4. Suspensorium of the three Japanese silurids. A: *Silurus asotus*; B: *S. lithophilus*; C: *Silurus biwaensis.* Left row shows outer view, and right row inner view. EPT, entopterygoid; Hp, hyomandibular process; HYO, hyomandibular; Mp, metapterygoid process; MPT, metapterygoid; POP, preopercular; Qp, quadrate process; QU, quadrate. Scale bars indicate 1 cm.

Table 1. Mean ratio of width to length of the skull in three species of Japanese catfishes.

Species	Juvenile				Adult			
	N	W1/L	W2/L	W3/L	N	W1/L	W2/L	W3/L
Silurus asotus	4	0.59	0.58	0.56	10	0.59	0.42	0.57
Silurus lithophilus	4	0.58	0.56	0.56	10	0.60	0.40	0.54
Silurus biwaensis	5	0.59	0.59	0.53	5	0.55	0.35	0.48

L: skull length between anterior margin of mesethmoid and posterior end of supraoccipital.
W1: width at lateral process of lateral ethmoid.
W2: width at lateral process of sphenotic.
W3: width at postero-lateral process of pterotic.

biwaensis is especially small compared with the other two species, and it is also smaller in juvenile stages ($P<0.05$, ANOVA and T-test).

In the suspensorium the hyomandibular process, from which a part of the adductor mandibulae muscle originates, and quadrate process, which provides the attachment area for a part of the levator arcus palatini muscle, are well-developed in adult *S. biwaensis*, whereas the processes are poorly developed in adult *S. asotus* and *S. lithophilus* (Fig. 4). Moreover, in the adults the hyomandibular/sphenotic attachment area is narrower in *S. biwaensis* than other two species. The suspensorial bones of the juveniles are not clearly different between the species.

Development of skull elements. The main criteria for the classification of larval stages are:

Stage 1: Unpaired fin still membranous; no pelvic fins; sometimes with membranous pectoral fins; no air bladder; yolk invariably found; melanophores found in eye region, but rare on body surface; notochord straight.

Stage 2: Primordia of tail and anal fin rays present; spherical air bladder attached to dorsal wall of coelom; end of notochord sometimes bent slightly upward; yolk still present; melanophores distributed all over body surface, making body completely black.

Stage 3: Anterior caudal fin rays formed; pectoral fin rays also formed from proximal part of fins; primordium of dorsal fin developed in membrane fin; posterior end of notochord completely bent upward; yolk disappeared.

Stage 4: Pectoral fin rays completely formed; anal fin rays present; dorsal fin extended from membrane fin; pelvic fins present but still membranous; air bladder divided into right and left chambers.

Stage 5: Caudal and dorsal fin rays completely formed; pelvic fin rays present in membrane fin.

Stage 6: Anal and pelvic fin rays completely formed; membrane fin beginning to be absorbed.

Stage 7: Rays of fins completely formed and can be stained with alizarin red S; membrane fin fold and hind barbels of lower jaw entirely absorbed.

The mean standard length of each stage is shown in Table 2.

During Stages 1 through 3 none of these species shows ossified, i.e. alizarin-stained, elements in the head region. The ossification begins at Stage 4 and all the skull elements have begun to ossify by Stage 7, the juvenile stage.

The ossified parts of the skull elements are shown in Figs. 5 and 6. The stages in which each element appears are the same in *S. asotus* and *S. biwaensis*, but different in *S. lithophilus* (Fig. 7). Orders of the development of bony elements in the skull and suspensorium based on the developmental stage and days from insemination are shown in Figs. 7 and 8,

Table 2. Standard length at each developmental stage of larval and juvenile Japanese silurids.

Species	Stage	No	Mean (mm)	Range (mm)
Silurus asotus	1	31	5.67±0.74	4.46–7.53
	2	22	6.75±0.77	5.23–7.10
	3	17	8.57±0.60	7.38–9.90
	4	17	13.27±1.83	10.50–17.10
	5	10	16.60±2.21	12.30–20.00
	6	34	31.92±9.54	19.10–51.30
	7	11	69.55±20.00	50.00–118.80
Silurus lithophilus	1	26	5.79±0.30	4.94–6.18
	2	31	7.29±0.52	6.58–8.50
	3	56	10.16±1.19	7.71–12.60
	4	37	13.89±1.29	11.70–17.60
	5	22	16.94±1.34	15.00–19.40
	6	59	27.64±5.54	18.80–42.60
	7	74	44.86±8.01	31.40–70.40
Silurus biwaensis	1	15	5.68±0.61	4.45–6.35
	2	22	6.92±0.59	6.01–8.37
	3	26	9.71±1.02	8.25–11.60
	4	18	13.08±1.48	11.10–15.80
	5	26	17.80±3.10	13.80–25.40
	6	36	34.56±9.86	19.00–58.90
	7	13	52.80±7.88	38.60–66.40

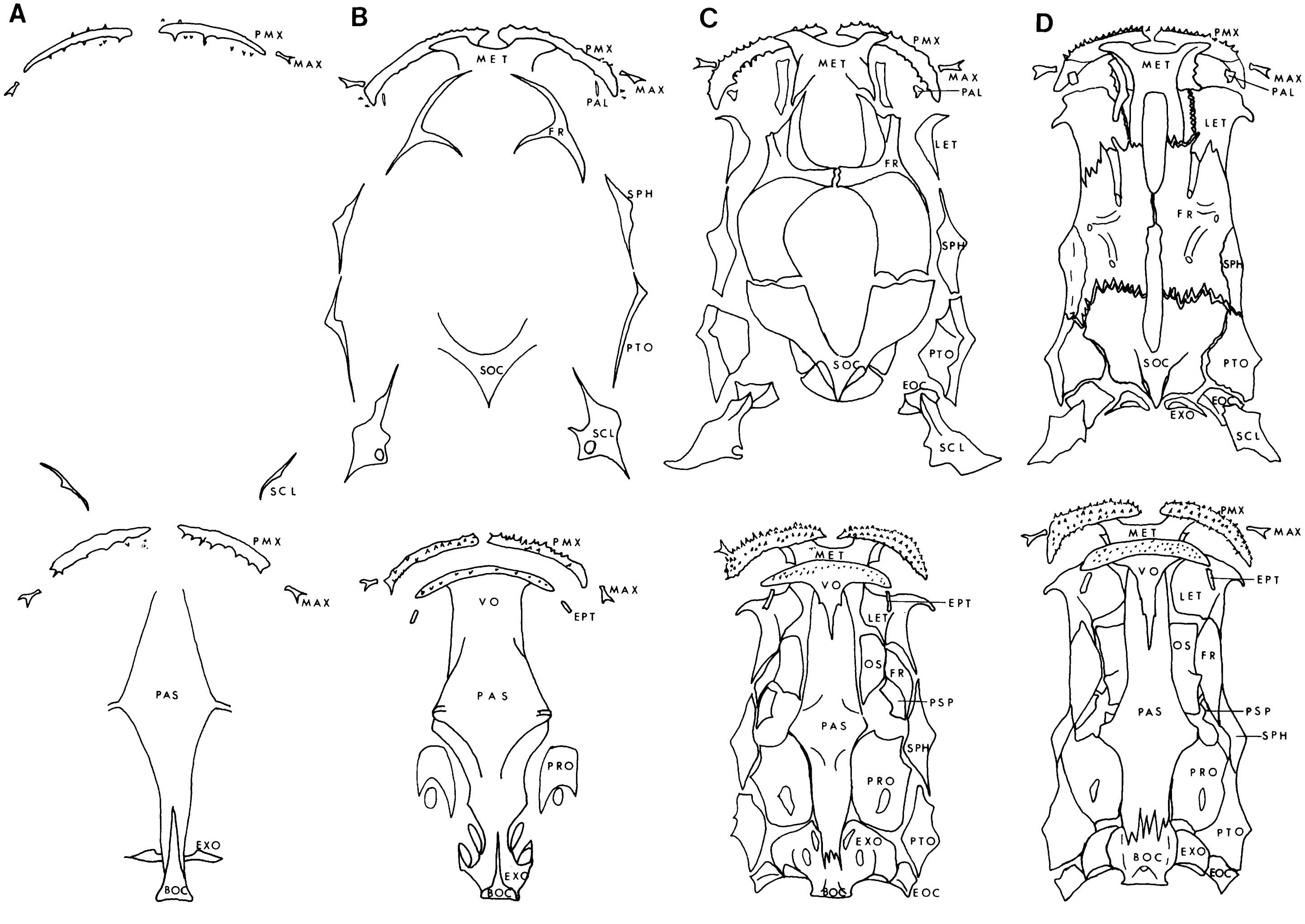

Fig. 5. Development of the skull of *Silurus biwaensis*. A: stage 4; B: stage 5; C: stage 6; D: stage 7. Upper row shows dorsal view and lower row shows ventral view. See Fig. 1 for abbreviations. Scale bars indicate 1 mm.

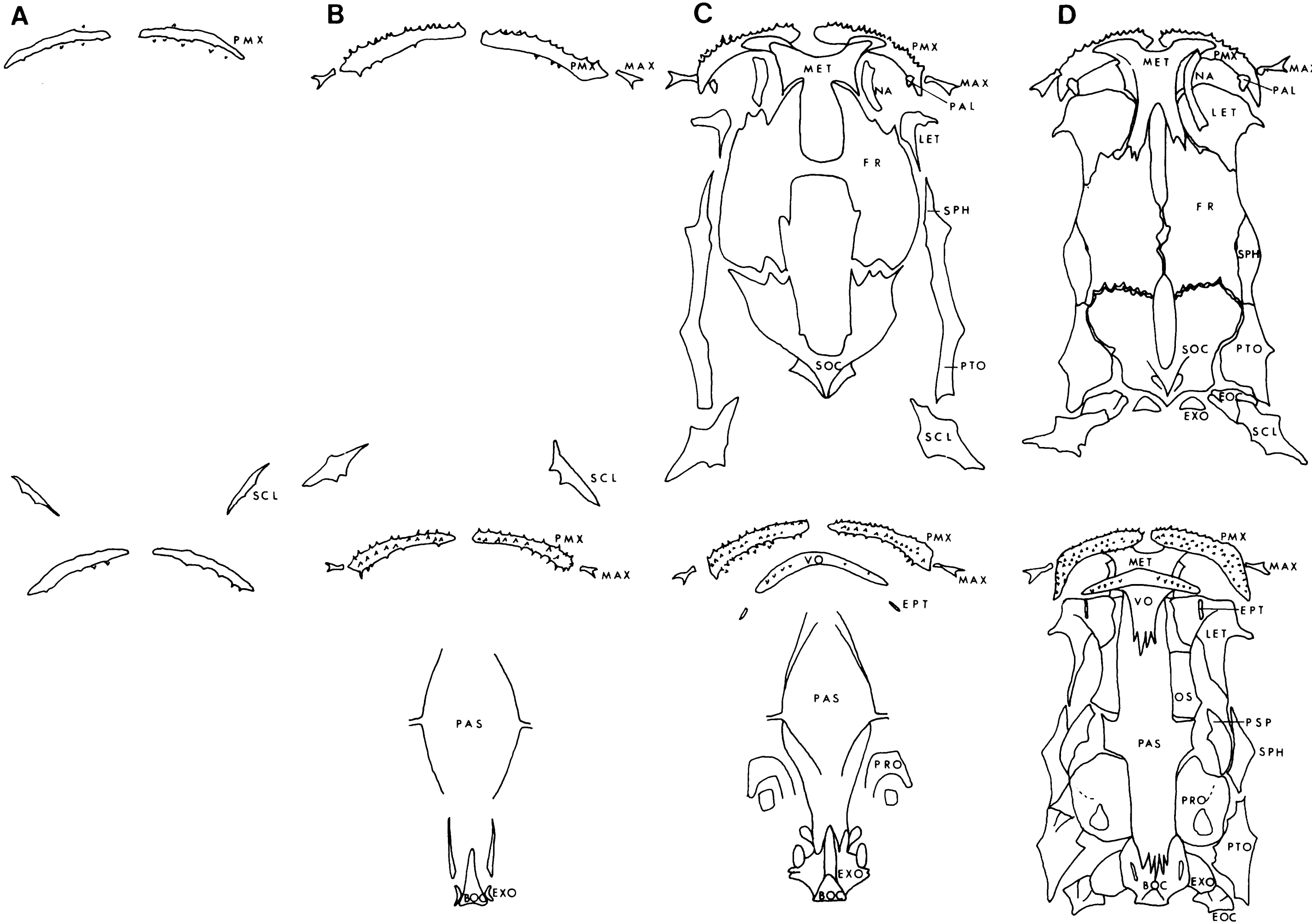

Fig. 6. Development of the skull of *Silurus lithophilus.* A: stage 4; B: stage 5; C: stage 6; D: stage 7. Upper row shows dorsal view and lower row shows ventral view. See Fig. 1 for abbreviations. Scale bars indicate 1 mm.

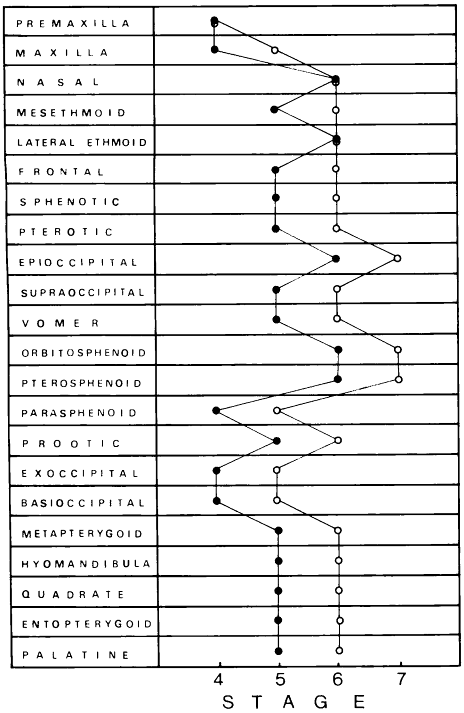

Fig. 7. Order of appearance of the bony elements in the skull and suspensorium based on the developmental stage in the three Japanese silurids. Solid circles: *Silurus asotus* and *Silurus biwaensis*; open circles: *Silurus lithophilus.*

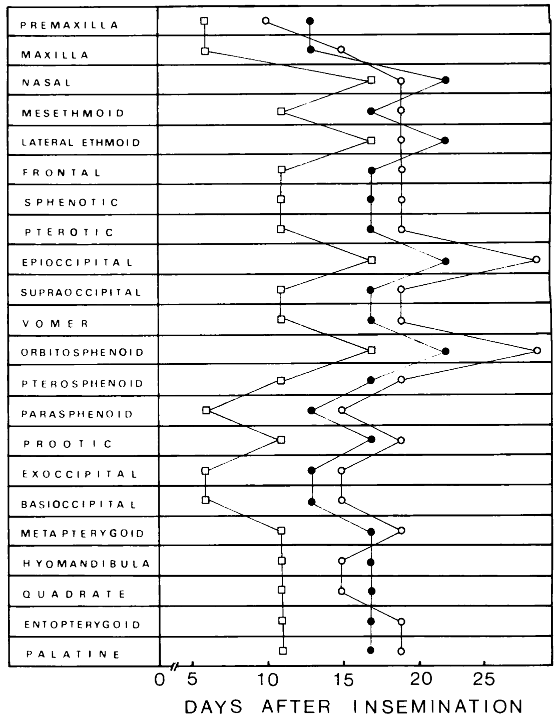

Fig. 8. Order of appearance of the bony elements in the skull and suspensorium based on the days after insemination of the three Japanese silurids. Solid circles, *Silurus asotus*; open circles, *Silurus lithophilus*; squares, *Silurus biwaensis.*

respectively. The development of each element is as follows:

Premaxillae: Ossification of each of these paired bones begins from their proximal parts and expands distally. When the ossification begins, these bones already have a few tooth rows.

Maxillae: Ossification of the paired maxillae begins from their proximal parts and spreads fanwise to the distal edge, which forms the basis of the barbel.

Palatines: In the massive bones forming a complex with the maxilla for moving the maxillary barbel, ossification begins in the postero-lateral part of the cartilaginous palatine and expands antero-medially.

Nasals: The nasals are canal bones that lie on the suture of the lateral ethmoid and mesethmoid. They are rod-shaped at Stage 6, subsequently showing a gradual increase in length and thickness gradually.

Mesethmoid: The unpaired mesethmoid is located at the anterior end of the skull and has a characteristic lateral process where ossification begins. Although at Stage 5 the posterior border is not clear, i.e. posterior part has not ossified, ossification proceeds posteriorly, until final suturing of the element with the frontal by Stage 7.

Lateral ethmoid: These paired bones have massive lateral processes in which ossification begins, to subsequently expand medially.

Frontals: These are the largest paired elements of the skull roof. One ossification center appears in each element, and the ossification spreads from the center in three directions, anteriorly, posteriorly, and medially, to sheathe the orbital cartilage. As the ossificated region expands, the orbital cartilage becomes entirely covered by the frontals. They form the posterior margin of the anterior fontanel and the anterior margin of the posterior fontanel. The right and left processes which are located on the epiphysial bar grow proximally to be sutured with each other.

Sphenotics: Ossification begins in the lateral canal regions and expands proximally to form a suture with the frontals.

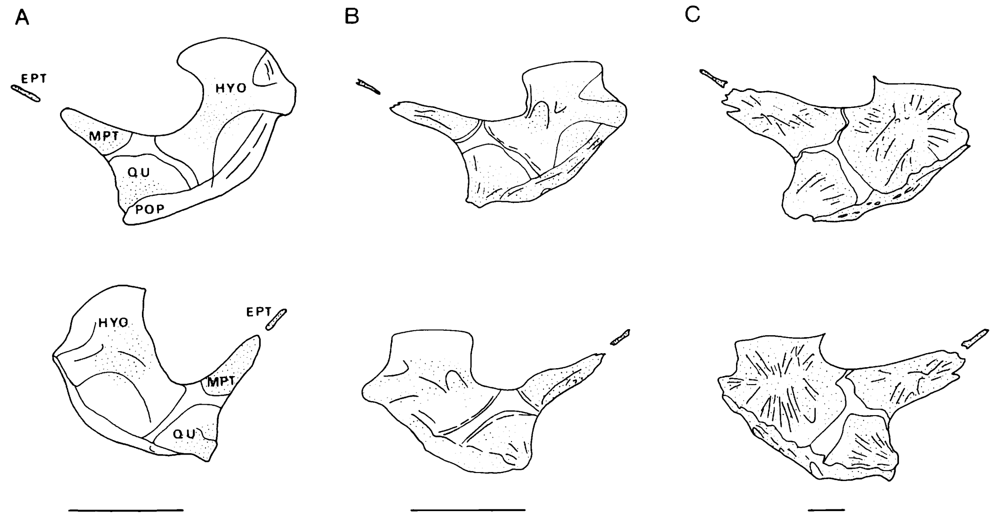

Fig. 9. Development of the suspensorial bones of *Silurus biwaensis*. A: stage 5; B: stage 6; C: stage 7. Upper row shows outer view, and lower row shows inner view. Dotted area represents ossified parts. See Fig. 4 for abbreviations.

Epioccipitals: Ossification begins in the postero-lateral part of the paired elements. It expands anteriorly, but the suture with the pterotics and supraoccipital is not completed until at the end of the juvenile stage.

Pterotics: Ossification begins in the lateral canal region, and expands proximally to form a suture with the supraoccipital. The suture between these bones, supraoccipital and epioccipitals is not completed until well after the sphenotic/frontal sutures have formed.

Supraoccipital: Ossification begins at the border of the posterior fontanel covering the tectum synocticum, and then expands antero-laterally. Even after the suture with the frontals is formed, a gap between this bone, pterotics and exoccipitals is observed. When the suture with the pterotic and epioccipital is formed at Stage 7, a bump surrounding the posterior border of the posterior fontanel has already formed.

Vomer: Ossification begins in the region of the tooth bands and expands posteriorly. The posterior end of this bone forms a complicated suture with the parasphenoid.

Orbitosphenoids: In each of these paired bones ossification begins in the posterior part and forms the margin of a large foramen for nerve II. The anterior end forms a synchondrosis with the lateral ethmoids, and the peripheral cartilage persists to the adult stage.

Pterosphenoids: In these paired elements ossification begins at the margin of the foramen for nerves V and VII.

Parasphenoid: Ossification of this unpaired bone begins in a thin diamond-shaped sheet lying on the ventral surface of the anterior end of the notochord. The anterior border, however, is not distinct at this stage, although the suture with the basioccipital is clearly seen. As ossification expands, the lateral ridges where the adductor arcus palatini muscles originate becomes more evident.

Prootics: Ossification, which begins anterior to the lapillus, subsequently expands and completely surrounds its ventral surface.

Exoccipitals: At first these paired bones look like lateral processes of the basioccipital. As ossification advances, they completely surround the ventral circumference of two small otoliths, the sagitta and asteriscus.

Basioccipital: Ossification of this unpaired bone begins around the anterior end of the notochord.

Development of suspensorial elements. The ossification of bony elements in the suspensorium begins at Stage 5 for *S. asotus* and *S. biwaensis* (Fig. 9), but at Stage 6 for *S. lithophilus* (Fig. 10).

Hyomandibular: Ossification begins in the center of the cartilaginous hyomandibular.

Quadrate: Ossification begins at the joint with the articular, and it expands medially. The synchondrosis between this bone and the hyomandibular is re-

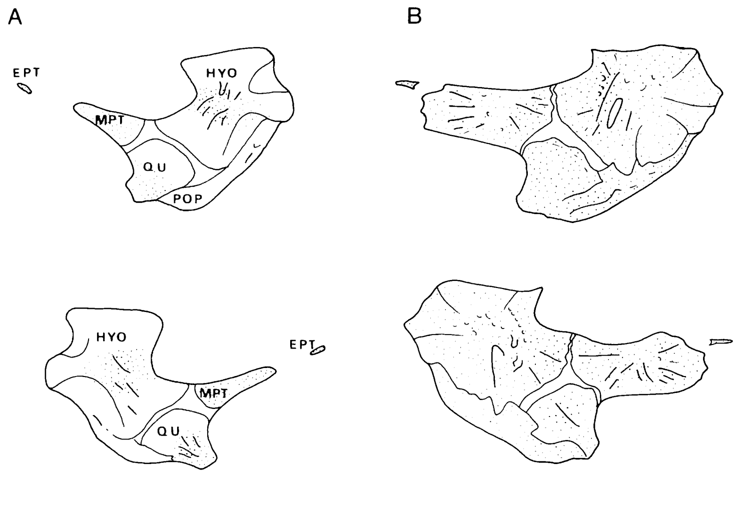

Fig. 10. Development of the suspensorial bones of *Silurus lithophilus*. A: stage 6; B: stage 7. Upper row shows outer view, and lower row shows inner view. Dotted area represents ossified parts. See Fig. 4 for abbreviations.

tained even in the adult.

Metapterygoid: Ossification of this bone begins throughout the cartilaginous metapterygoid.

Entopterygoid: This bone appears as a small, rod-shaped bone connected by ligaments with the metapterygoid posteriorly and the ventral surface of the lateral ethmoid anteriorly.

The number of days from insemination to the appearance of each bony element is fewest in *S. biwaensis* (Fig. 8), though each element appears at the same stage in *S. asotus* (Fig. 7).

Discussion

Morphological differences in adult skulls of the three Japanese silurids are found in the ratio of width to length, *S. biwaensis* having a relatively narrower skull than other two species. This difference is due to the well developed sagittal crest and the shape of the pterotics, which curve distinctly upward. The narrow skull of *S. biwaensis* is also the result of morphological peculiarities in the elements in the posterior half of the skull; the anterior part of the supraoccipital and the adjacent part of the frontals are narrow relative to their length. The epaxial portion of the lateral muscle originates from the posterior half of the skull, and the rise of the supraoccipital on the median line of the skull, i.e. the sagittal crest, provides an essential surface for attachment of the lateral muscles. Although in *S. biwaensis* the posterior part of the skull is relatively narrow and the horizontal area for the attachment of muscles very small, the strongly developed sagittal crest provides a large vertical area for muscle attachment (Fig. 1). Further compensation for the small horizontal muscle attachment surface is seen wherein the outer ridges of the pterotics rise upward and a depression for the origin of the epaxial muscles is developed in the posterior part of the skull along the sagittal crest.

In all these species, the value of W2/L decreases during development, i.e. the value in juveniles is clearly smaller than that of the adult. In the juvenile stage the skulls of Japanese silurids are flat without any concavity or crest, but these later appear and develop in the adult stage (Fig. 11). The change in values of W2/L and W3/L during development from juvenile to adult are largest in *S. biwaensis*, owing to the well developed sagittal crest and bending of the sphenotics in adults.

In suspensorium, the nomenclature of the bones has been discussed by many authors (Bamford, 1948; Fink and Fink, 1981; Howes, 1983; Howes and Tuegels, 1989). In Japanese *Silurus* the number of bones observed in the adult is rather small for a catfish: the hyomandibular, quadrate, metapterygoid, and entopterygoid. The entopterygoid has ligaments on both its anterior and posterior sides from the onset of ossification. There is only a single ossification center in the pterygoid region at least when this bone can be detected as an alizarin stained area.

In the suspensorium the hyomandibular process provides the attachment area for a part of the adductor mandibulae (A3) muscle and the quadrate process for a part of the levator arcus palatini. The remarkably developed processes in *S. biwaensis* may indicate that these muscles are well developed in this species.

The relationships between ossification, developmental stage (i.e. development of other morphological features) and body size vary between the three species. *S. biwaensis* and *S. asotus* are similar in the stages at which the skull elements ossify, but are different from *S. lithophilus*. In *S. lithophilus* many bony skull elements ossify one stage later than those in the other two species. From Stage 1 through Stage 4 *S. lithophilus* has the largest standard length at each stage. However, from Stage 5 the standard length of this species becomes smaller than that of the other two species at comparable stages (Table 2). In *S. lithophilus* ossification begins at Stage 4 as in the other two species, but from Stage 5 the ossification in *S. lithophilus* begins to be retarded.

In all species the premaxillae, maxillae, parasphenoid, exoccipitals, and basioccipital develop earlier than all other cranial elements observed. The mesethmoid, frontals, sphenotics, supraoccipital, vomer, prootics, metapterygoids, hyomandibulars, quadrates, entopterygoids, and palatines develop subsequently, with the nasals, lateral ethmoids, epioccipitals, orbitosphenoids, pterosphenoids being last to appear. Ossification of bony skull elements begins during the short period of the postlarval stage, and expands from the feeding apparatus and median part of the skull, as has been observed also in the red sea bream (Matsuoka, 1985).

In *S. biwaensis* all the elements begin to ossify earlier than in the other two species relative to number of days from insemination. However, in terms of external morphology, on which the developmental stages were based, the appearance of bony elements coincides completely in *S. asotus* and *S. biwaensis*, being earlier than in *S. lithophilus*. It is, therefore, considered that the order of ossification of the skull bone elements is similar, though slightly different in the three Japanese silurids. The time of ossification of each bony skull element is species-specific, and it is earlier in *S. biwaensis* which develops more rapidly than the other two species during the skull elements ossify.

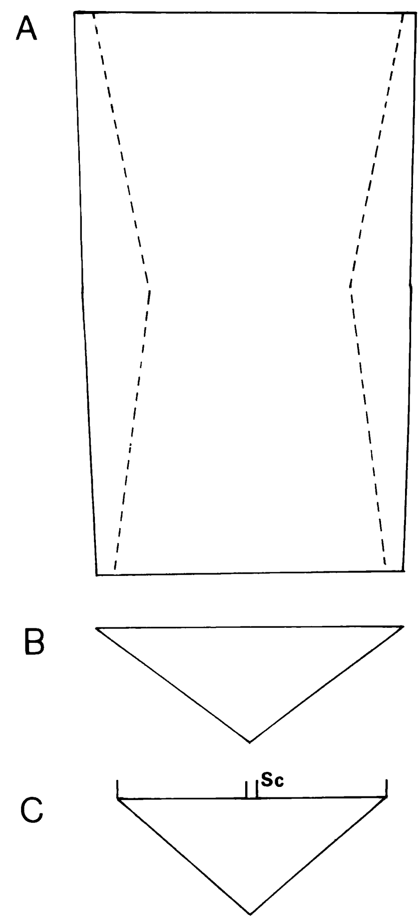

Fig. 11. Schematic skull development. A: solid line shows dorsal view of juvenile skull and dotted line adult; B: posterior view of juvenile skull; C: posterior view of adult skull. Sc, sagittal crest of supraoccipital. As the sagittal crest and bending of the outer edge of the pterotic are well developed in *S. biwaensis*, the width of the skull becomes narrower than the other two species.

In all species the ratio of head width to length at the level of the sphenotic process decreases remarkably as the juveniles develop into the adult stage (Table 1). A wide skull can therefore be regarded as a juvenile feature, and a narrower skull as a derived adult condition. Similarly, the prominent sagittal crest and hyomandibular process can be regarded as more hypermorphic features. These adult features are developed strongly in *S. biwaensis*, moderately in *S. asotus*, and weakly in *S. lithophilus*. In addition, these characteristics become obvious at different stages during the development of each species. *S. biwaensis* has a narrower skull even in the juvenile stage, with the sagittal crest developing at a young stage unlike the other two species. These facts suggest the occurrence of heterochronic development in the skulls of the three Japanese silurids.

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日本産ナマズ属魚類 3 種の頭部骨格の比較とその発生

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日本産のナマズ 3 種，ナマズ (*Silurus asotus*)，イワトコナマズ (*S. lithophilus*)，ビワコオオナマズ (*S. biwaensis*) の成体の頭蓋と懸垂骨を比較し，それらの発生を記載した．稚魚期の成長の速いビワコオオナマズでは，他 2 種に比べ化骨の時期が早く，上後頭骨の矢状隆起の発達の度合いや，翼耳骨の側上方への反り返りが大きく，懸垂骨にみられる筋付着突起の発達も著しかった．

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