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The osteology of *Ilyophis blachei* and its contribution to a diagnosis of the Synaphobranchidae (Pisces, Anguilliformes)

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The osteology of *Ilyophis blachei* was described and shown to conform largely with that of its congeners, *I. arx* and *I. brunneus*. In detail, however, *I. blachei* revealed a new combination of features. It bears fused frontals, a rod-like pterygoid inserted on the almost vertical suspensorium, a third pair of posteriorly directed cartilaginous hypobranchials, a single pair of pharyngobranchials and a tube-like preoperculum. The new information was used to augment a preliminary diagnosis of this morphologically variable family with osteological characters.

KEY WORDS:—*Ilyophis blachei* – slope-dwelling eel – osteology – systematics.

CONTENTS

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INTRODUCTION

The systematics of deep-sea eels of the family Synaphobranchidae have been elucidated by several recent studies (Robins & Robins, 1970; Robins, 1971; Castle, 1975; Robins & Robins, 1976). The investigations, however, have been restricted in detail by the material available. Sampling difficulties in the deep sea, combined with the variability in relative abundance of synaphobranchid species and limited opportunities for inter-ocean population studies, together with the anticipated number of species awaiting discovery (Robins & Robins, 1976) and the dearth of knowledge on spawning, early life history and distribution have all been contributory factors.

A recent addition to the list of synaphobranchid eels is *Ilyophis blachei* Saldanha & Merrett, 1982, which was described mainly on the basis of external characters. These characters, nevertheless, confirm the intermediate position of the genus *Ilyophis* within the family and thereby call into question the discreteness of the sub-families Synaphobranchinae and Ilyophinae (formerly Dysomminae; the name Ilyophinae shown to have priority by Robins & Robins, in press), originally discussed by Robins & Robins (1976). In a subsequent paper (Merrett & Saldanha, 1985), external morphology was used again in an attempt to establish a preliminary diagnosis of the Synaphobranchidae, despite tacit acceptance of the considerable variability involved.

In this paper, we seek to complete the description of *Ilyophis blachei* by considering its osteology. We utilize this for intra- and inter-generic comparisons in order to enhance our preliminary family diagnosis (Merrett & Saldanha, 1985).

MATERIAL AND METHODS

The two specimens used in this work, one a paratype from the Museu Bocage (MB), MB T2532 (455 mm TL), and the other a hitherto unreported and uncatalogued Institute of Oceanographic Sciences (IOS) specimen (Stn 50602#2, 550 mm TL), were collected in the Porcupine Seabight area (49–52°N, 11–14°W) of the eastern North Atlantic from 1506 and 1967 m in mid-depth soundings respectively (cf. Saldanha & Merrett, 1982). They were fixed in 10% saline formalin at sea and ashore transferred to 33% isopropanol.

To increase the chances of success in clearing and staining these specimens (broadly following Hollister (1934)) the smaller specimen (455 mm TL) was carefully sliced into four manageable portions; head and anterior trunk, mid-trunk, transition trunk to caudal and posterior caudal. The musculature was digested in 3% potassium hydroxide (KOH) after which the bones were stained in Alizarin Red. Subsequently, the tissues were cleared in five successive changes of KOH and glycerine, of increasing glycerine concentration (20–100%). In the 455 mm TL specimen the results of clearing were good only in the caudal extremity, necessitating dissection in the head region. Hence the ossicles of the lateralis system, hyal and branchial arches, opercular bones and pectoral girdle were dissected from the left side of the head. While most of the visceral skeleton disintegrated in the larger (550 mm TL) specimen, good results were obtained of the cranial morphology after some dissection. Vertebrae were dissected from both specimens. Radiography facilitated the study of the intermuscular bones (smaller specimen), alongside dissection (both specimens) and observation on the cleared portion of the smaller specimen.

Bones separated by dissection and those over-stained with alizarin were briefly washed in hydrogen peroxide (H_2O_2) or sodium hypochlorite until cleaned or sufficiently de-stained, then rinsed in water.

The results presented are not composite but refer to the specimens in which the feature was observed. Abbreviations for the names of bones used are indicated in the figure captions.

RESULTS

Cranium and jaws
(Figs 1, 2, 3A; 550 mm TL specimen)

The skull is streamlined and triangular in dorsal and ventral aspects. Conspicuous lateral projections are formed by the ventrally directed sphenotic bones, while posteriorly an upturned crest is formed from projections from the supraoccipital, parietals, epiotics, pterotics and exoccipitals. The dorsal outline of the posterior cranial region in lateral view is nearly flat with a slight elevation at the level of the parietals. The supraoccipital is prominent. A small sagittal crest extends the length of the frontals and parietals. The anterior half of the skull is formed by the premaxillary–ethmoid complex. The premaxillary section bears depressions for the maxillary articulation laterally and teeth distally. Ventrally, the premaxillary–ethmoid complex articulates with the elongate vomer, the dentition of which is continuous with that of the premaxillary and is the most robust. Anterolaterally, foramena occur on either side of the premaxillary–ethmoid complex. Posterodorsally, this complex articulates with the frontals and posteroventrally, with the parasphenoid. Together with the basisphenoids and the frontals, these bones form the rim of the orbits. The basisphenoids are conspicuously grooved laterally. The frontals are fused medially.

A longitudinal canal carries the cephalic lateralis system through the pterotic bone. Medially, each prootic bears two conspicuous foramena, the posterior of which has a conspicuous thin semi-circular process associated with it.

The hyomandibular musculature is inserted in depressions in the ventral part of the sphenotics and pterotics, on each side of the cranium. The hyomandibular itself articulates with the sphenotic, prootic and pterotic bones. The parasphenoids bear foramena medially.

The cranium in posterior aspect is sub-circular (laterally elongated) with the *foramen magnum* at its centre (Fig. 3A). The posterior wall of the cranium is comprised of the supraoccipital, epiotic, exoccipital, pterotic and basioccipital bones. An upturned crest formed by projections from these bones forms a marginal ridge within which is a roughened depression, where muscle attachments from the trunk are insterted onto the skull. A small foramen, present between the suproccipital and the *foramen magnum*, is encircled by the epiotic bones. The *foramen magnum* itself is flanked by the epiotics, exoccipitals and basioccipital. the basioccipital bears the condyle that articulates with the first vertebra.

The suspensorium is nearly vertical and is formed by a fused hyomandibular

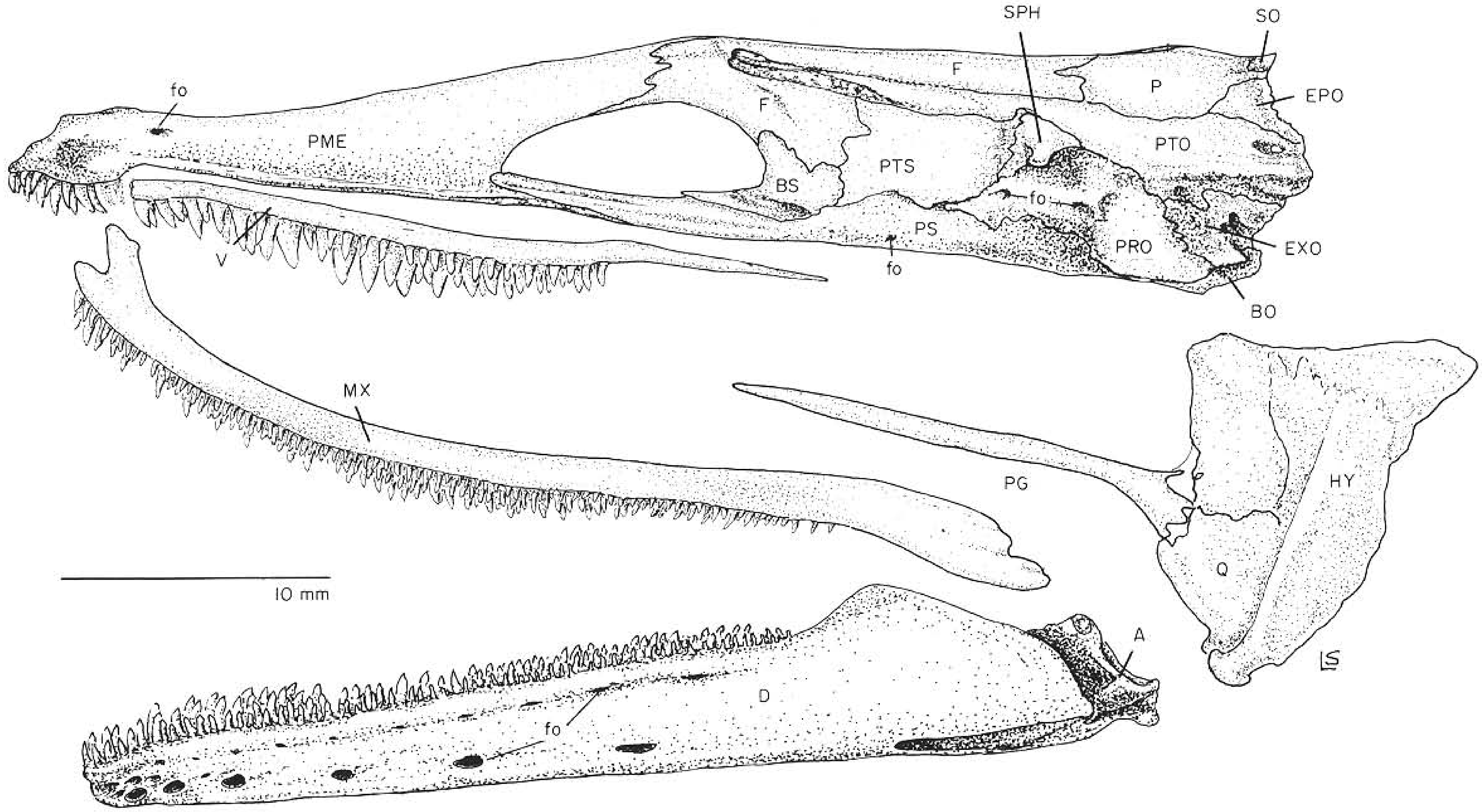

Figure 1. Lateral view of head bones (550 mm specimen). Abbreviations: A—articular; BO—basioccipital; BS—basisphenoid; D—dentary; EPO—epiotic; EXO—exoccipital; F—frontal; FM—*foramen magnum*; FO—*foramen*; HY—hyomandibular; MX—maxillary; P—parietal; PG—pterygoid; PME—premaxillary-ethmoid; PRO—prootic; PS—parasphenoid; PTO—pterotic; PTS—pterosphenoid; Q—quadrate; SO—supraoccipital; SPH—sphenotic; V—vomer.

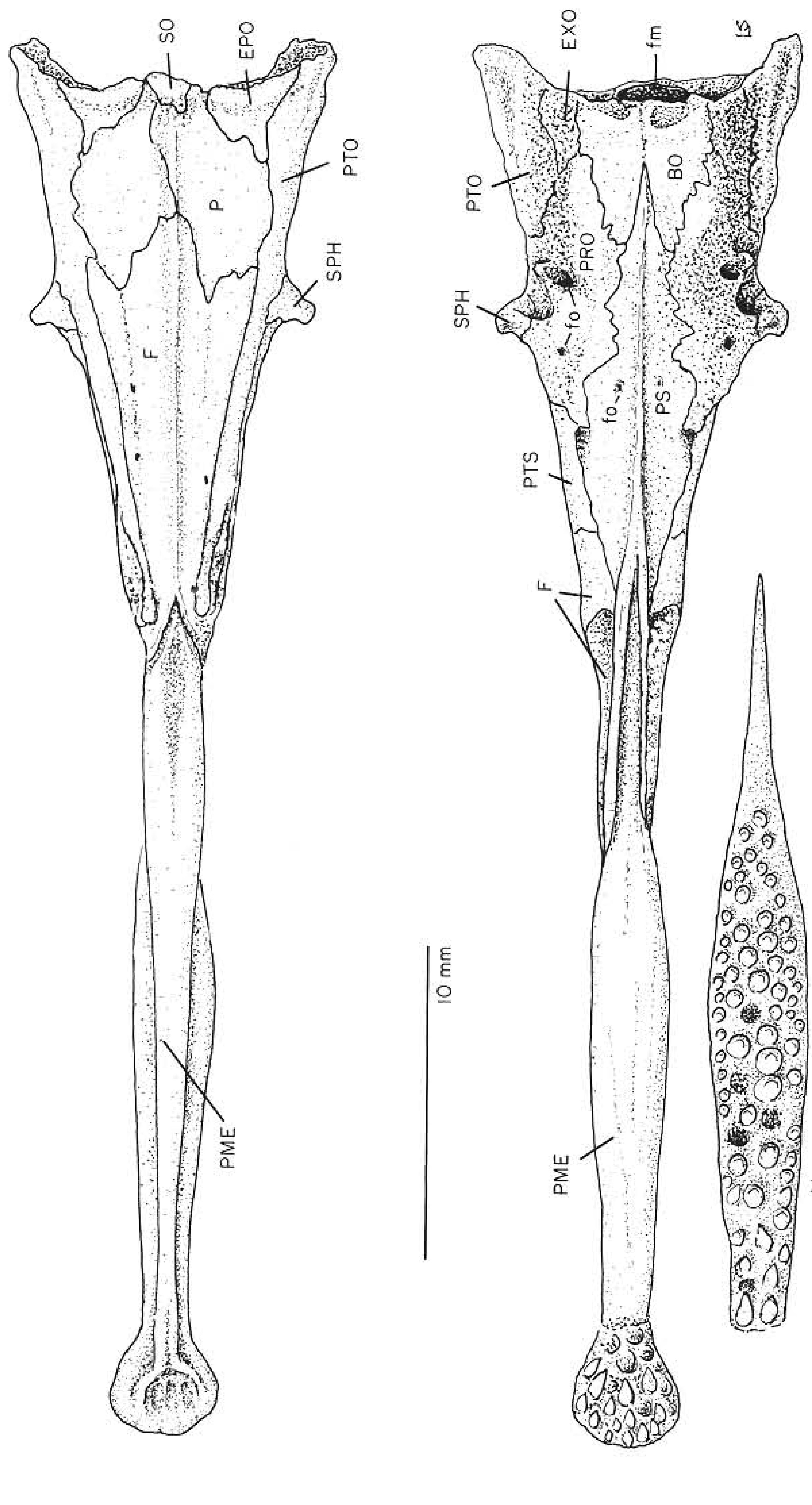

Figure 2. Dorsal and ventral view of cranium (550 mm specimen). Abbreviations as in Fig. 1.

and quadrate. The basal part of the rod-like pterygoid has a close membranous connection with the suspensorium, while it extends forward to mid-orbit level at its tip where there is a membraneous attachment to the latero-inferior surface of the parasphenoid.

The maxillaries are long and slender with the dentition in bands, the inner rows of teeth being the largest. At their anterior ends, nearly vertical processes articulate with the lateral depressions in the premaxillary region of the premaxillary–ethmoid complex.

In lateral view, two bones are visible in the lower jaw; the dentary and the articular. The dentaries are robust with the dentition in bands, also with the largest teeth in the inner rows. A series of foramena are present along the external superior and inferior margins of the dentary bones. The inferior series corresponds with the mandibular lateralis canal which is exposed in the posterior part of the bone where this articulates with the posteroventral part of the articular.

Operculum
(Fig. 3B; 455 mm TL paratype)

The operculum is not expanded, while the suboperculum is scimitar-shaped to accompany the curve of the operculum. The interoperculum is triangular. The preoperculum is semi-cylindrical (carrying the preopercular tube of the cephalic lateralis system) and is superimposed over the other opercular bones.

Gill arches
(Fig. 4A; 455 mm TL paratype)

Basibranchials are not discernible in this preparation due to their probable cartilaginous composition.

There are two ossified pairs of hypobranchial bones and a third cartilaginous pair directed posteriorly, five pairs of ceratobranchials with the fifth supporting the lower pharyngeal tooth-plate and four pairs of epibranchials of which the

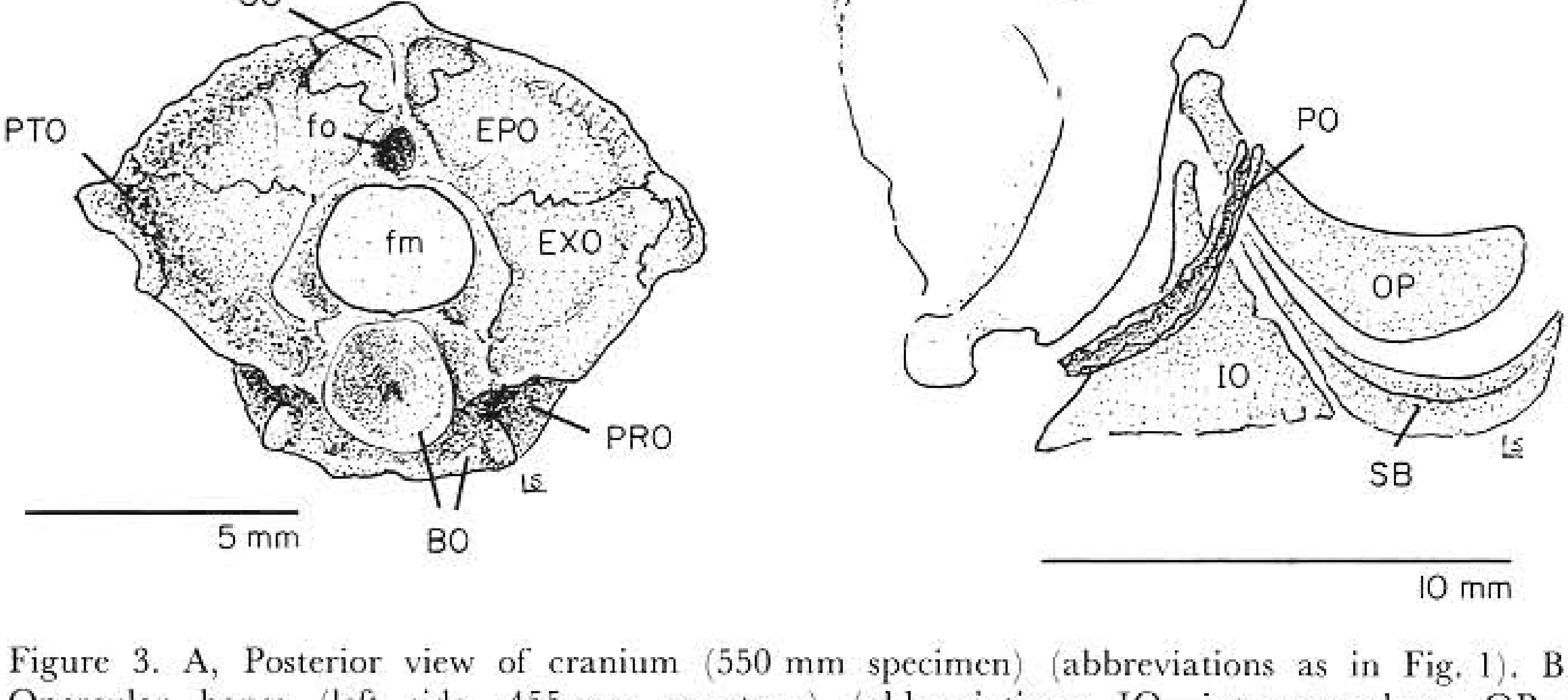

Figure 3. A, Posterior view of cranium (550 mm specimen) (abbreviations as in Fig. 1). B, Opercular bones (left side, 455 mm paratype) (abbreviations: IO—interoperculum; OP—operculum; PO—preoperculum; SB—suboperculum).

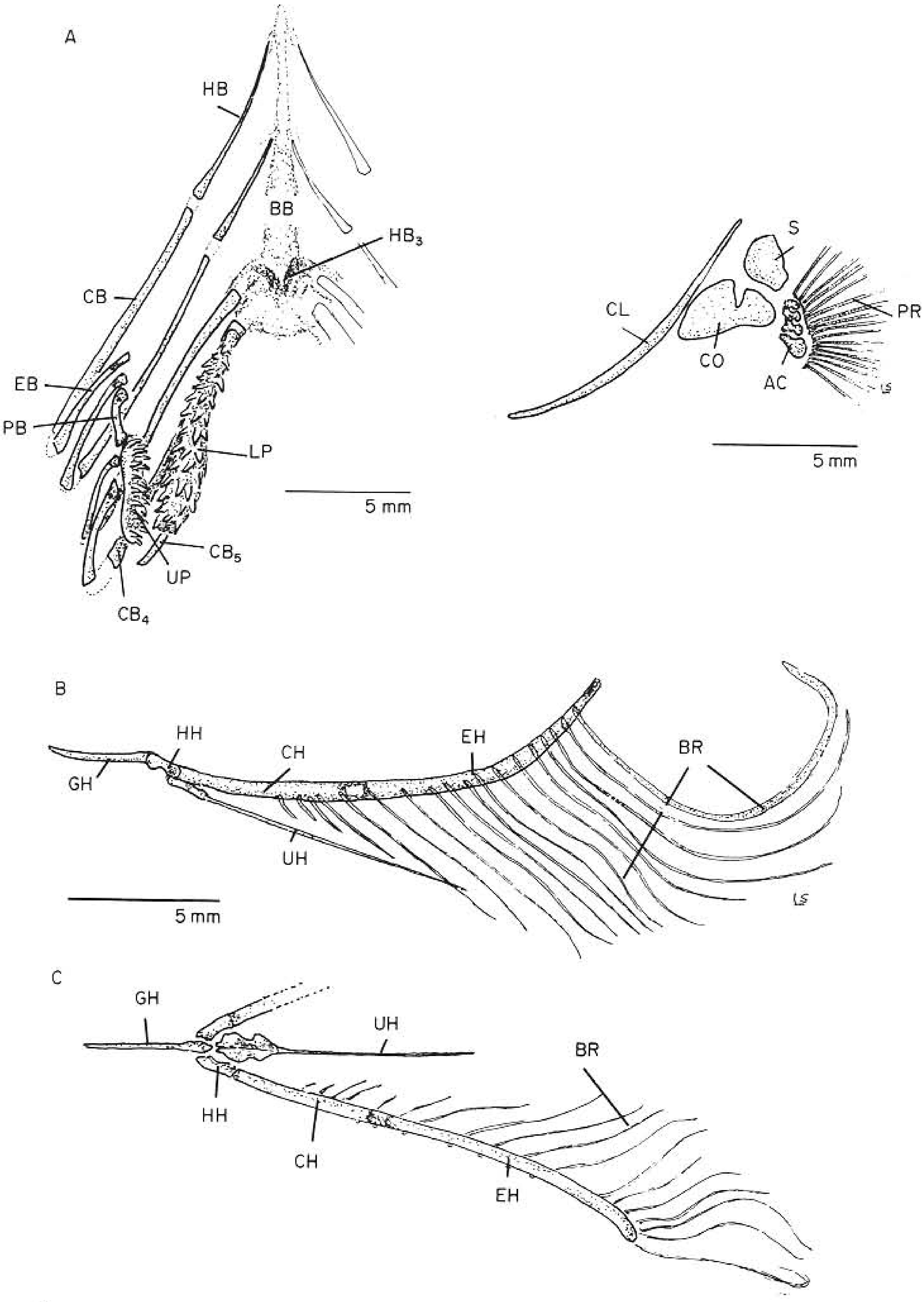

Figure 4. A, Gill arches (455 mm paratype) (abbreviations: BB—basibranchial; CB—ceratobranchial; EB—epibranchial; LP—lower pharyngeal tooth-plate; PB—pharyngobranchial; UP—upper pharyngeal tooth-plate). B, Hyal arch (455 mm paratype) (abbreviations: BR—branchiostegal rays; CH—ceratohyal; EH—epihyal; GH—glossohyal; HH—hypohyal; UH—urohyal). C, Pectoral girdle (455 mm paratype) (abbreviations: AC—actinost (radial); CL—cleithrum; CO—coracoid; PR—pectoral rays; S—scapula).

last connects with the upper pharyngeal tooth-plate. There is only one pair of pharyngobranchials.

Hyal arch
(Fig. 4B; 455 mm TL paratype)

The glossohyal is relatively long and slender. In dorsal view, the anterior part of the urohyal is spatulate and quadrilobate, with a sagittal crest, and then tapers rapidly to a very slender posterior prolongation. The hypohyals are small. In this specimen there are 18 branchiostegal rays on the left side and 17 on the right. On the left side, the ceratohyal bears 5 branchiostegal rays and the epihyal 13. The fifth and sixth rays are inserted near the cartilaginous junction between ceratohyal and epihyal. The posteriormost branchiostegal ray is scimitar-shaped and wider than the others and, together with adjoining rays, concentrically embraces the opercular bones.

Pectoral girdle
(Fig. 4C; 455 mm TL paratype)

The cleithrum is gently curved. Both the scapula and coracoid are small. The radials are massive and closely set. The pectoral fins have 15–17 rays.

Axial skeleton
(Fig. 5; both specimens)

The known vertebral range of *I. blachei* is 179–188 (Saldanha & Merrett, 1982). The neural arch of the first vertebra of the 550 mm specimen (Fig. 5A) is formed by large semi-circular extensions of the neurapophyses which are winged and folded with large posterior projections. The two neurapophyses are juxtaposed, rather than fused, so that the arch is not completely closed. Small haemapophyses are present in this vertebra. In the 35th trunk vertebra (Fig. 5B) the neural arch is well formed with the neurapophyses producing four dorsal expansions. The haemapophyses are also well developed.

In an anterior caudal vertebra (Fig. 5C), selected from the 455 mm paratype, the neural arch bears a long neural spine formed by the union of the dorsal expansions of the neurapophyses at their distal ends. The haemapophyses are elongate and curved, but their extremities do not meet to enclose the haemal arch fully. The same condition prevails closer to the tail, in the 20th vertebra before the caudal skeleton in the same specimen. A single zygapophysis (Fig. 5C—lateral aspect) arises posterolaterally on each side of the centrum, variously developed so that it may equal nearly half the length of the haemapophysis at its longest.

The condition of the cleared material restricted observations of intermuscular bones to those in the extremity of the caudal region of the 455 mm TL specimen (Fig. 6). These epineurals and epipleurals are long and rod-like. More anteriorly, X-radiographs showed these bones to be long, slightly curved and forked.

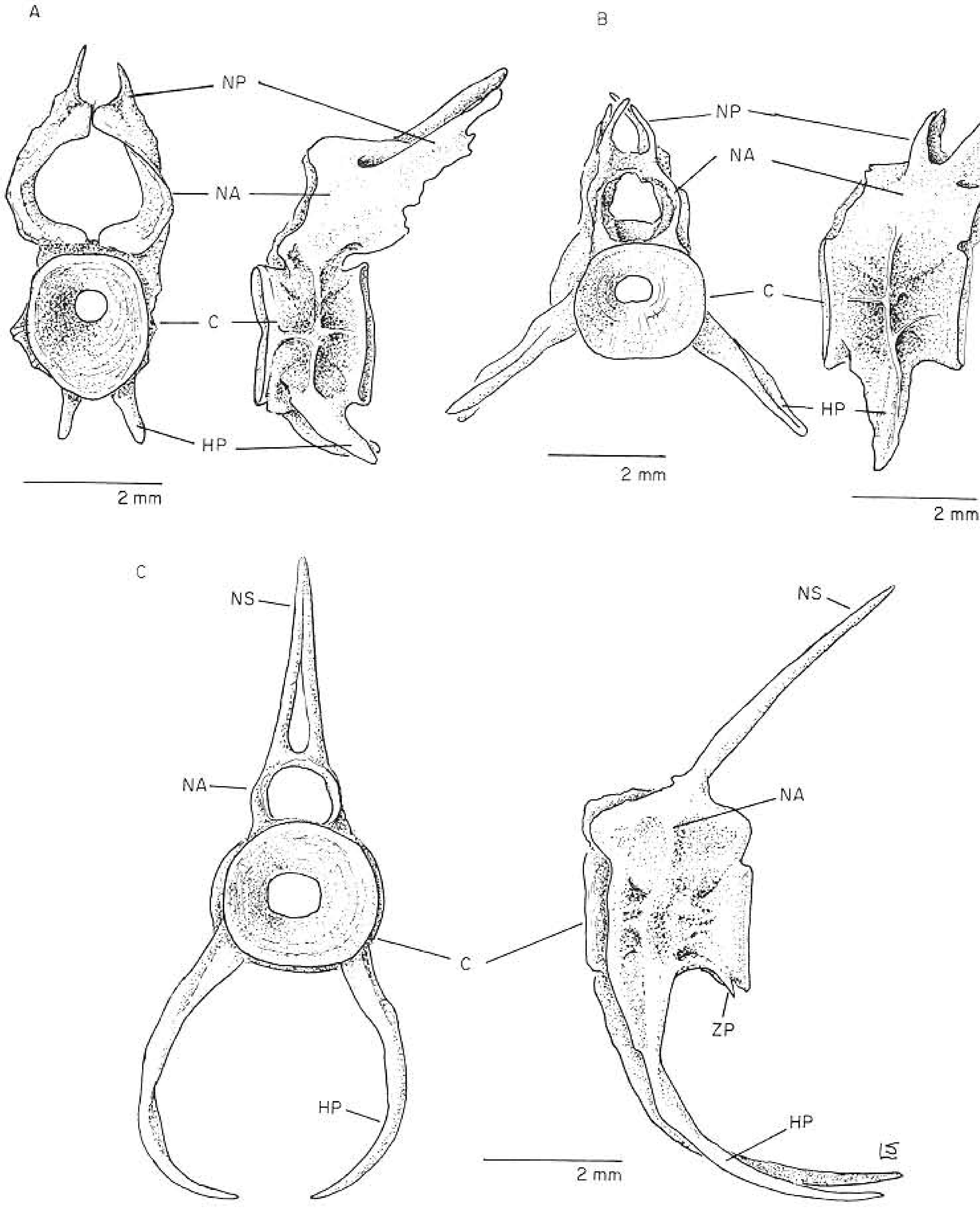

Figure 5. Vertebrae (A and B 550 mm specimen; C 450 mm paratype). A, First vertebra; B, 35th vertebra (trunk); C, caudal vertebra (anterior caudal region). (abbreviations: C—centrum; HP—haemapophysis; NA—neural arch; NP—neurapophysis; NS—neural spine; ZP—zygapophysis).

Caudal skeleton

(Fig. 6; 455 mm TL paratype)

Two hypural plates are present, the upper (H_2) bears eight caudal rays and the lower (H_1) five rays. The preterminal vertebra bears a parhypural supporting two fin rays.

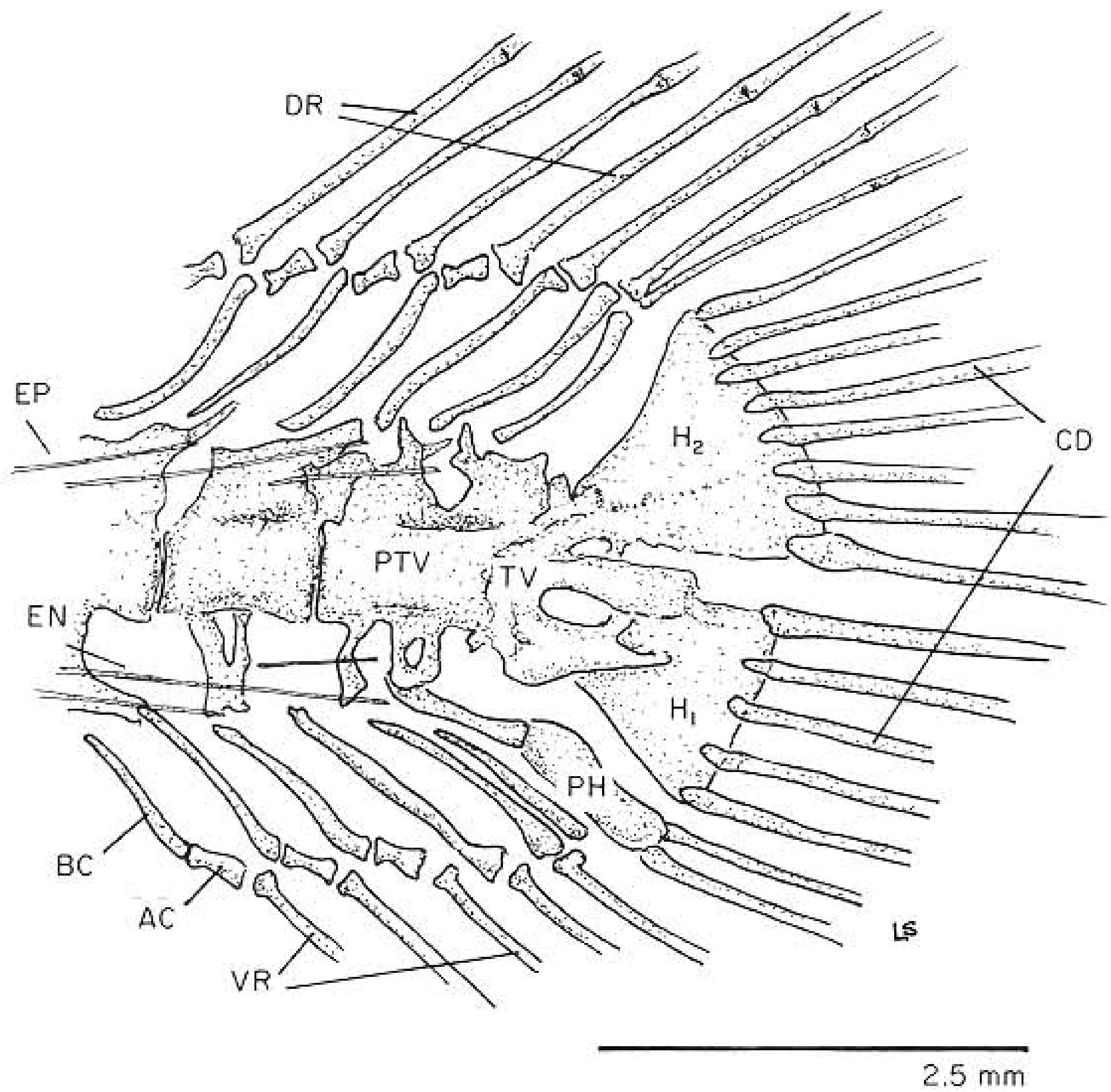

Figure 6. Caudal skeleton (455 mm paratype) (abbreviations: AC—actinost; BC—baseost; CD—caudal rays; DR—dorsal rays; EN—epineural; EP—epipleural; H—hypural; PH—parhypural; PTV—pre-terminal vertebra; TV—terminal vertebra; VR—ventral rays).

Lateralis system
(Fig. 7)

The supraorbital canal of the cephalic lateralis system (Fig. 7A) is supported by a long half-tube extending from the tip of the snout to the level close to the posterior margin of the eye where it interconnects with the pterotic canal. The infraorbital canal is similarly supported by a long tube commencing well posterior to the origin of the supraorbital canal and extending posteriorly to much the same level as the supraorbital. There is a small semi-cylindrical ossicle associated with the small vertical anterior branch of the infraorbital canal, posterior to the anterior nostril. Four similar ossicles support the ascending postorbital branch of this canal which runs close to the posterior edge of the eye to connect with the supraorbital canal. Two digitiform cartilaginous plates arise from the supraorbital and infraorbital bony canals to support the nasal capsule between the anterior and posterior nostrils. The mandibular portion of the preoperculo-mandibular canal is located in the dentary bones and the preopercular portion in the preoperculum, a semi-cylindrical bone.

In *I. blachei* the conspicuous portion of the lateral line extends 87–95% of the standard length along the trunk and caudal region. The lateral line tube is supported by small ossicles, which are sub-circular or sub-rectangular with an irregular contour in plan view in the anterior part of the tube and sub-losangic in the trunk and caudal region (Fig. 7B). An ossicle is located in the interspace between consecutive pores along the lateral line.

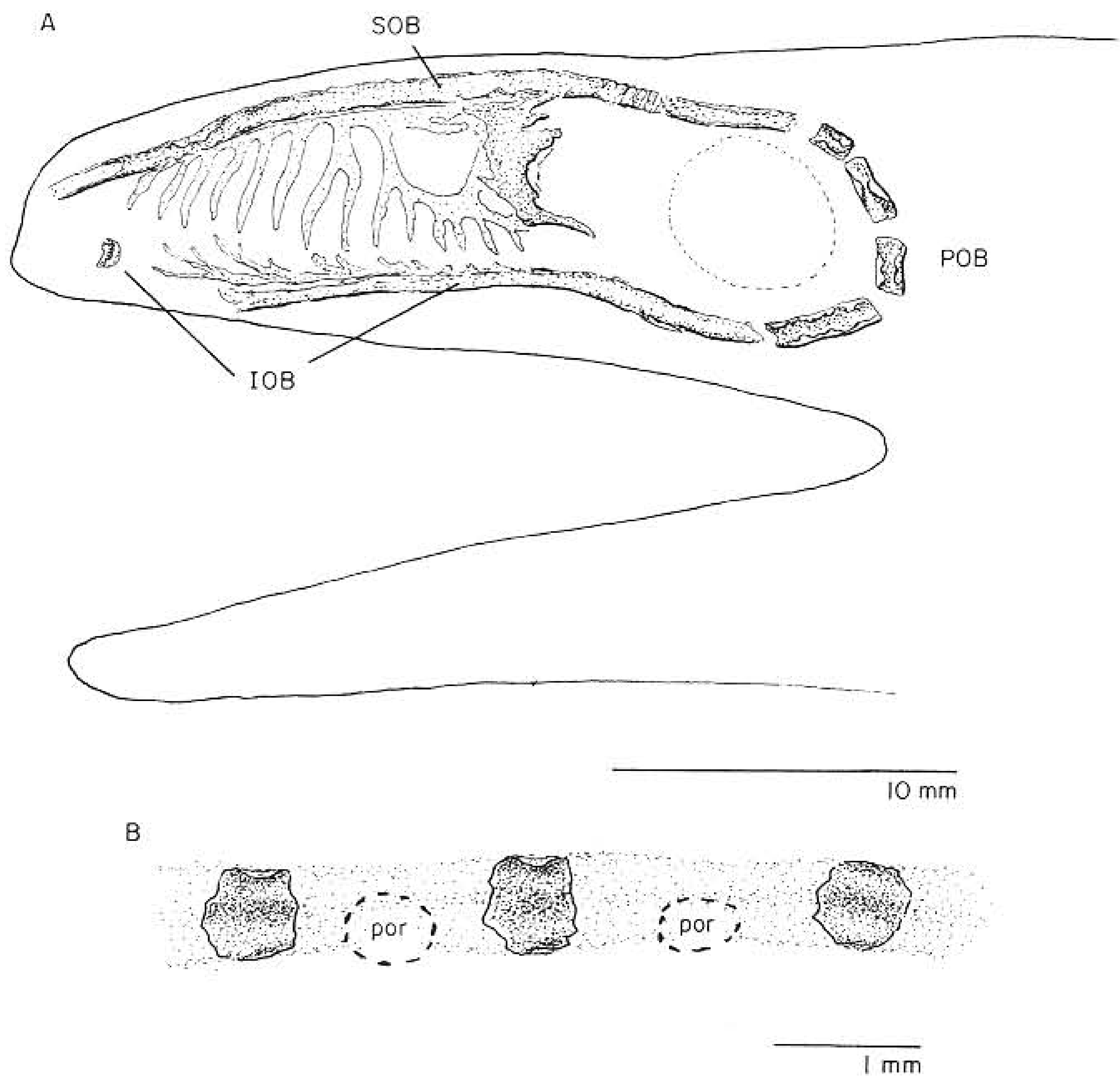

Figure 7. Ossifications of the lateralis system (455 mm paratype). A, Head; B, lateral line (the three anteriormost ossicles—the pores are represented schematically) (abbreviations: IOB—infraorbital; POB—postorbital; SOB—supraorbital).

DISCUSSION

The osteology of *I. blachei* established here may be compared with its congeners and other members of the family Synaphobranchidae on the basis of studies by Robins (1971) and Robins & Robins (1976). The characters examined (Table 1) agree closely with the other species of *Ilyophis*, *I. arx* and *I. brunneus*, and justify the earlier inclusion in the genus of *I. blachei*, which was originally described on the basis of external morphology alone (Saldanha & Merrett, 1982). Noteworthy intergeneric comparisons are the single pair of pharyngobranchial supports to the upper pharyngeal tooth plate which *I. blachei* shares with *Synaphobranchus* species, *Dysomma anguillare* and *D. goslinei*. On the other hand, *I. arx* and *I. brunneus* have two pairs in common with *Dysommina rugosa* and *Atractodenchelys phrix*, while *Simenchelys* possesses three pairs of pharyngobranchials (cf. Jaquet, 1920; Robins & Robins, 1976). *Ilyophis blachei* and *Simenchelys parasitica* share the closely similar morphology of the first vertebra.

To complete the description of *I. blachei*, the possession of one pair of pharyngobranchials and 17–18 branchiostegal rays should be added to the diagnosis given by Saldanha & Merrett (1982). The generic diagnosis may be

Table 1. Interspecific comparison of selected osteological characters

Character	*I. blachei*	*I. arx*	*I. brunneus*
HEAD			
Dorsal profile	Intermediate—parietals domed	Concave—parietals flat	Flat—parietals flat
Size of parietals	Relatively largest	—	—
Premaxillary-ethmoid complex	Long and moderately robust	Short and massive	Long and moderately robust
Posterodorsal suture with frontals	Mid-orbit level		Posterior orbit level
Orbit shape	Sub-oval	tear drop	
Sphenotic & posterior pterotic process protrusions	More developed		Less developed
Development of supraoccipital	Moderately developed		Well developed
Size of prootics	Large	Moderate	
Anterior extent of parasphenoid	Anterior orbit level	Mid-orbit level	—
Suspensorium		Nearly vertical	
Lower jaw		Included by upper jaw	
Lateral aspect of articular	Small	Moderate	
Rudimetary (third) pair of posteriorly directly hypobranchials		Present	
Pharyngobranchials	1 pair	2 pairs	
Number of branchiostegal rays	17/18—last ray width moderate	13—last ray very broad	14—last ray very broad
Relative shape of opercular bones	—	Least similar	—
Preoperculum		Tube-like	
CAUDAL SKELETON		2 hypurals, 1 parhypural	
CEPHALIC LATERALIS SYSTEM			
Number of postorbital pores	3	0	0
Number of postorbital ossicles	3	—	3
Cartilaginous nasal basket	Well developed	—	Well developed

completed with the following osteological characters: suspensorium nearly vertical, pterygoid present, one or two pairs of pharyngobranchials, two hypural plates.

In considering the family Synaphobranchidae to be comprised of the subfamilies Simenchelyinae, Synaphobranchinae and Ilyophinae, Robins & Robins (1976) stressed the gradation of characters observed in the component species. This view was strengthened by the morphological characters found in the novel *I. blachei* by Saldanha & Merrett (1982). The combination of features this species displayed led Saldanha & Merrett (1982, 1985) to propose that the genus *Ilyophis* occupied a transitional position between the Synaphobranchinae and the Ilyophinae, so calling into question the sub-familial distinction. Results from the present study support this view. The box-like sharp-edged cranium, in plan view, of *Ilyophis* with its prominent expansions resembles the synaphobranchine state, for in the Ilyophinae this outline is generally more streamlined. Furthermore, the single pair of pharyngobranchials present in *I. blachei* is shared with some species of *Synaphobranchus* and *Dysomma*, while the two pairs present in *I. arx* and *I. brunneus* are consistent with other ilyophine eels.

A point of distinction between the Synaphobranchinae and the Ilyophinae, however, many possibly exist in the larvae. Known synaphobranchine leptocephali have a simple, unpigmented gut, while the gut in ilyophine leptcephali has irregular loops or thickenings and is conspicuously pigmented (Smith, 1979). Yet, as most synaphobranchid larvae cannot be identified to species, the validity of this distinction remains uncertain (D. G. Smith, personal communication).

Previously, Merrett & Saldanha (1985) proposed a preliminary diagnosis of the Synaphobranchidae based upon external morphological characters and omitting osteological features. They stressed that the representatives displayed such a broad morphological variation, particularly in the head region, that a comprehensive diagnosis was hard to attain. It is not surprising, therefore, that even knowledge of the osteology of *I. blachei* alongside that of other representatives of the family does little to clarify the situation. Nevertheless, common features within the family may be stated as: cranium box-like, sharp angled to streamlined with processes prominent or reduced; premaxillary-ethmoid processes long or short, fusions broad or reduced; orbits large or reduced; frontals fused; basiphenoids discrete or fused with parasphenoid; palato-pterygoid arcade complete (Simenchelyinae) to totally absent (Ilyophinae); suspensorium close to vertical. Pharyngobranchials one to two pairs; hypobranchial two pairs or with a rudimentary cartilaginous third pair directed posteriorly; hypurals two to seven; opercular bones reduced; teeth numerous and small to few and large, sometimes compound (mainly in the vomer); lower jaw included by upper or protruding.

The plasticity of the Synaphobranchidae, as currently recognized, prevents a more rigorous diagnosis. Evidence from larval characters is still largely outstanding as already indicated but, for example, if all leptocephali prove to possess the presumed common feature of telescopic eyes (Castle, 1975; Robins & Robins, 1976), this may well be valuable.

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