Osteology and relationships of *Pseudotrichonotus altivelis* (Teleostei: Aulopiformes: Pseudotrichonotidae)

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Abstract   The osteology of the rare Japanese fish *Pseudotrichonotus altivelis* is described based on several specimens collected off the Izu Peninsula. Relationships of *Pseudotrichonotus* are discussed based on osteological comparisons with other neoteleosts. The placement of *Pseudotrichonotus* among iniomous fishes has been questioned because of its lower numbers of caudal-fin, pelvic-fin, and branchiostegal rays. Our investigation supports an iniomous affinity for *Pseudotrichonotus,* specifically as a member of the Aulopiformes. Within that group, *Pseudotrichonotus* belongs in a new suborder diagnosed herein, the Synodontoidei, which also includes the Aulopidae *(Aulopus),* Synodontidae *(Synodus* and *Trachinocephalus),* and Harpadontidae *(Harpadon* and *Saurida).* A synodontoid affinity for *Aulopus* has never been suggested, but numerous osteological features support the monophyly of this clade. Synodontoids have a peculiar proximal segmentation of most principal caudal-fin rays, expanded neural and haemal spines on posterior vertebrae, cartilage extending along the ventral margin of the anterior ceratohyal, ventral displacement of the first one to three epineurals, supraneurals with large laminar expansions and six or more branchiostegals on the posterior ceratohyal. They lack median caudal cartilages. Among synodontoids, *Pseudotrichonotus* is the sister group of the Synodontidae plus Harpadontidae, with which it shares paired peritoneal pigment spots, an abrupt transition between the epipleurals in and beneath the horizontal septum, and absence of the fourth pharyngobranchial toothplate. Our study does not support a previously proposed relationship between *Bathysaurus* and synodontids.

Key words. — Pseudotrichonotus; Aulopiformes; lizardfishes; osteology; phylogeny.

P*seudotrichonotus altivelis* Yoshino & Araga (Fig. 1) is a small bottom-dwelling fish known from one locality off Izu Oceanic Park, Izu Peninsula, Japan, where it occurs on sand bottom at 30 to 50 meters in an area of strong tidal currents. The status of a second species, from the Indian Ocean, *P. xanthotaenia* Parin, 1992, remains uncertain (Parin, pers. comm.). As the generic name implies, *Pseudotrichonotus*

bears a superficial resemblance to the perciform genus *Trichonotus* and shares with it the habit of diving rapidly into the sand when threatened. Yoshino and Araga (in Masuda et al., 1975) described *P. altivelis* in a monotypic family, Pseudotrichonotidae, which they placed among the Myctophiformes (s.l.), stating that the reasons for this alignment would be forthcoming. R. K. Johnson (1982) noted that several charac-
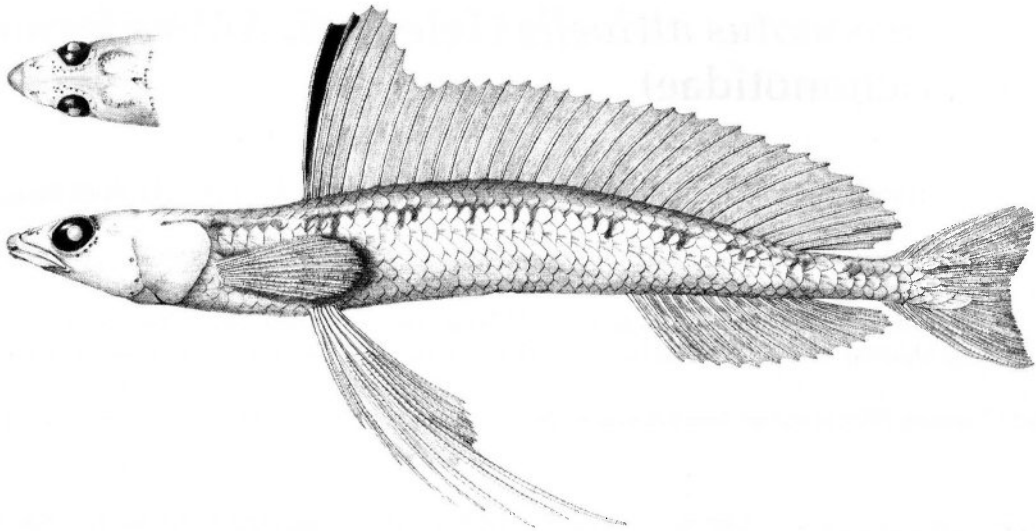
Fig. *1.* *Pseudotrichonotus altivelis, USNM* 280366, 81.5 *mm* **SL.**

ters reported in the original description (specifi-
cally, low numbers of caudal-fin rays, pelvic-fin
rays and branchiostegal rays) strongly suggested
that the authors' alignment of this species with
myctophiforms was incorrect. Masuda et al.
(1984) retained *Pseudotrichonotus* in the Myc-
tophiformes without discussion. The purpose of
this paper is to describe the osteology and cer-
tain other aspects of the anatomy of *Pseudotri-
chonotus altivelis* and, based on this information,
to formulate a hypothesis about its phylogenetic
relationships.

Materials and Methods

Terminology of the laterosensory system of
the head follows Weitzman (1962). Terminology
of the bony condyles and ligaments of the upper
jaw follows Stiassny (1986). Other osteological
terms are those in general use. Abbreviations
used in illustrations of osteological features are
given in Table 1. Illustrations depict left side
of specimen unless otherwise indicated. Char-
acters were polarized following the outgroup
comparison algorithm of Maddison et al. (1984).
Outgroups for the Aulopiformes are (1) Cteno-
squarnates (myctophiforms+acanthomorphs) and
(2) stomiiforms (Johnson, 1992). Outgroups for
polarization of characters within aulopiform

clades are (1) other aulopiforms and (2) cteno-
squamates.

The description of the osteology of *Pseudotri-
chonotus altivelis* herein is based on examination
of three cleared and stained specimens: USNM
280366 (1, 80.0 mm SL); ZUMT 55678 (1,
58.0 mm SL); and ZUMT 59882 (1, 72.0 mm
SL). Comparative, cleared and stained aulopi-
form and outgroup material examined in this
study is listed below. Institutional abbreviations
follow Leviton et al. (1985). *Ahliesaurus berryi*:
USNM 240505 (1 specimen). *Alepisaurus* sp.:
MCZ 60345 (1). *Anotopterus pharao:* USNM
140825 (1); USNM 221035 (1). *Anotopterus* sp.:
SIO 62-775 (1). *Aulopus jilamentosus:* USNM
292105 (1). *Aulopus japonicus:* AMNH
28635SW (1). *Aulopus* sp.: AMNH 28635 (1).
Bathymicrops regis: BMNH 1989.7.25.56.61 (2).
Bathypterois pectinatus: FMNH 88982 (1). *Ba-
thysaurus mollis*: *VIMS* 6107 (1). *Bathysaurop-
sis gigas*: AMS I. 22822001 (1). *Benthalbella
dentata:* SIO 63-379 *(1). Chlorophthalmus agas-
sizi: AMNH* 40829SW *(1);* USNM 159385 (1).
Coccorella atlanticum: USNM 235199 (1).
Diplophos taenia: MCZ 55469 (1); USNM
206614 (1). *Evermannella indica:* U.H. 71-3-9
(1). *Gigantura vorax:* AMNH 55345SW (1).
Harpadon nehereus: AMNH 17563 (1); FMNH
179018 (2). *Harpadon squamosus:* FMNH
80823 (3). *Ipnops agassizi*: USNM 54618 (1,

gill arches only). *Lestidiops* sp.: USNM 307290 (1). *Lestidium atlanticum:* USNM 201183 (1).

Lestidium sp.: USNM uncat. (1). *Macroparalepis affine:* USNM 302410 (1); 201184 (1).

Table 1. Abbreviations for Figures

Aa	Anguloarticular		MMP	Maxillary Median Process
AC	Anterior Ceratohyal		Mx	Maxilla
AHF	Anterior Hyomandibular Fossa		NS	Neural Spine
Ba	Basipterygium		O	Opercle
BB_n	nth Basibranchial		P	Palatine
BH	Basihyal		Pa	Parietal
BHTP	Basihyal Tooth Plate		Para	Parasphenoid
BL	Baudelot's Ligament		PBn	Pharyngobranchial
Bo	Basioccipital		PC	Posterior Ceratohyal
Br	Branchiostegal		PeFR	Pelvic-fin Ray
CB_n	Ceratobranchial		PeR	Pelvic-fin Radial
CC	Cranial Condyle of Maxilla		PFR	Pectoral-fin Ray
Cl	Cleithrum		Ph	Parhypural
Co	Coracoid		PIR	Pleural Rib
D	Dentary		Pmx	Premaxilla
DH	Dorsal Hypohyal		Po	Preopercle
DHe	Dorsal Hemitrich		PP	Posterior Process
DP	Dorsal Pterygiophore		PR	Pectoral-fin Radial
DPcl	Dorsal Postcleithrum		Princ	Principal Caudal Ray
E	Epural		Pro	Prootic
EB_n	Epibranchial		Proc	Procurrent Caudal Ray
EC	Ethmoid Cartilage		Pt	Posttemporal
Ecp	Ectopterygoid		Pte	Pterotic
En	Epineural		Pts	Pterosphenoid
Enp	Endopterygoid		PU_n	Preural Vertebra
Ep	Epipleural		Q	Quadrate
EP	Ethmoid Process		Ra	Retroarticular
Epo	Epioccipital		S	Sphenotic
Es	Extrascapula		SC	Supracleithrum
Ex	Exoccipital		SDR	Supernumerary Dorsal Ray
F	Frontal		Smx	Supramaxilla
H_n	Hypural		Sn	Supraneural
HB_n	Hypobranchial		So	Subopercle
HS	Haemal Spine		Sob	Supraorbital
Hy	Hyomandibula		Soc	Supraoccipital
Ic	Intercalar		Sph	Sphenotic
Ih	Interhyal		Sy	Symplectic
IL	Interoperculomandibular Ligament		TP	Trisegmental Pterygiophore
			U_n	Ural Vertebra
Io	Interopercle		UN_n	Uroneural
Io_n	Infraorbital		UP5	5th Upper Pharyngeal Toothplate
La	Lacrimal		V	Vomer
LE	Lateral Ethmoid		VC	Vertebral Centrum
LO	Lamina Orbitonasalis		VH	Ventral Hypohyal
Me	Mesethmoid		VHe	Ventral Hemitrich
Mep	Metapterygoid		VPcl	Ventral Postcleithrum

Macroparalepis sp.: FMNH 49988 (1). Mycto-phum *obtusirostris*: AMNH 29140SW (1). Neo-scopelus *macrolepidotus*: USNM 188056 (2); 317160 (1). Notolepis rissoi rissoi: USNM 283485 (1). Notoscopelus resplendens: AMNH 25928SW (1). Odontostomops normalops: USNM 235029 (1). Paralepis brevirostris: USNM 196109 (1). Paralepis coregonoides: USNM 290253 (1). Parasudis truculentus: FMNH 67150 (1); USNM 159407 (1); 159850 (1). Saurida brasiliensis: USNM 185852 (2); 187994 (3). Saurida gracilis: USNM 256409 (1). Saurida *normani*: USNM uncat. (1). Saurida *parri*: USNM 193763 (2). Saurida undosqua-mous: USNM 325180 (10). Scopelarchus *analis*: USNM 234988 (1). Scopelarchus nicholsi: USNM 201154 (2). Scopelarchoides *signifer*: USNM 274385 (1). Scopelosaurus *hoedti*: USNM 264256 (2). Scopelosaurus sp.: MCZ uncat., RHB 2902 (2). Synodontidae: USNM 309851 (5). *Synodus* jenkensi: USNM 321745 (1). *Synodus synodus*: USNM 318960 (1). Syn-odus variegatus: USNM 140825 (2); 315318 (1). Trachinocephalus *myops*: FMNH 45392 (1); USNM 185861 (1).

Osteology

Neurocranium (Figs. 2–4)

The anteriormost element of the neurocra-nium is the vomer, the anterior face of which is rectangular in shape and convex. The anteroven-tral margin bears a convex band of small, conical teeth. Approximately midway between the dorsal and ventral margins of the anterior face, the vomer gives rise to a thin, horizontal, tongue-like shelf that extends posteriorly to the anterior margin of the orbit.

Posterior to the vomer, two ethmoid ossifi-cations form the anterodorsal surface of the neu-rocranium. Both are rounded anteriorly, but the left one extends further posteriorly than the right one. Near the center of each bone, an antrorse prong arises (herein referred to as the "ethmoid process") which is the site of attachment of the ethmo-maxillary ligament (see "Ligaments of the Upper Jaw" below). A second pair of ossifi-

cations in the ethmoid region, the lateral eth-moids, provides the anterior structure of the orbit. In dorsal view, the lateral ethmoids are v-shaped bones: a medial branch flanks (and is partially covered by) the anterior frontal and rep-resents the only lateral ossification of the neuro-cranium anterior to the orbit; a lateral branch projects outward and forms the anterior margin of the orbit. The supraorbital bone (see "Circum-orbital Bones" below) lies above the posterodor-sal corner of the lateral ethmoid.

The area of the neurocranium between the ethmoids and the lateral ethmoids is occupied by the ethmoid cartilage, which continues posteri-orly beyond the lateral ethmoids as the lamina orbitonasalis (see de Beer, 1937), in this case a median wall of cartilage that extends into the anterior third of the orbit. An elliptical fossa, oriented anteroventrally to posterodorsally is present in the anterior portion of the lamina, pre-sumably for the passage of the profundus nerve from the orbit into the nasal cavity (de Beer, 1937).

Most of the floor of the neurocranium is formed by the large, median parasphenoid. Ante-riorly, the posterior process of the vomer is tightly bound to the ventral surface of the paras-phenoid. The anterior portion of the parasphe-noid is dorso-ventrally flattened, and the anterior margin is round. The bone has more vertical re-lief in the orbital region, where it has steep, ven-trally curved sides. The parasphenoid flattens out again posteriorly and ends slightly bifurcated be-neath the basioccipital.

A large portion of the roof of the neurocra-nium is occupied by the paired frontals. They are bordered anteriorly by the paired mesethmoids and extend posteriorly, covering the posterior corners of the lateral ethmoids, the orbital region and part of the otic region. They articulate with the paired parietals posteriorly. The frontals are narrow bones anteriorly, where they frame the dorsal portion of the orbit, but they widen poste-riorly, forming part of the posterior border of the orbit. Ventral flanges of bone, one from the ven-tral surface of each frontal in the dorsalmost re-gion of the orbit, join and form a median orbital septum. The septum bifurcates posteriorly as the frontals turn downward to form the posterodor-
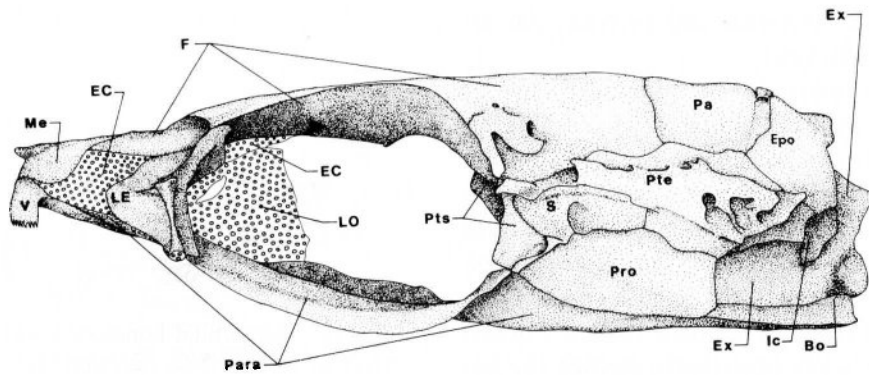
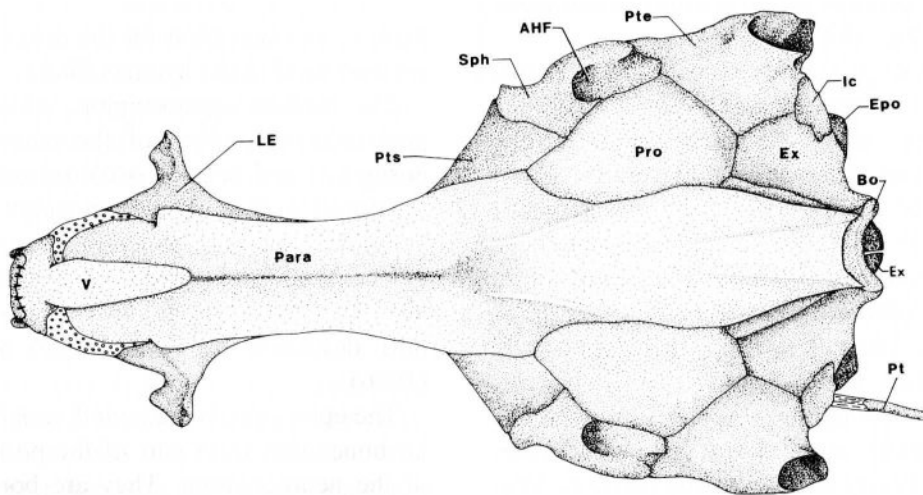**Fig. 2.** Neurocranium of *Pseudotrichonotus altivelis* (ZUMT 59882, 72.0 mm SL), lateral view.

Fig. 3. Neurocranium of *Pseudotrichonotus altivelis* (ZUMT 59882, 72.0 mm SL), ventral view.
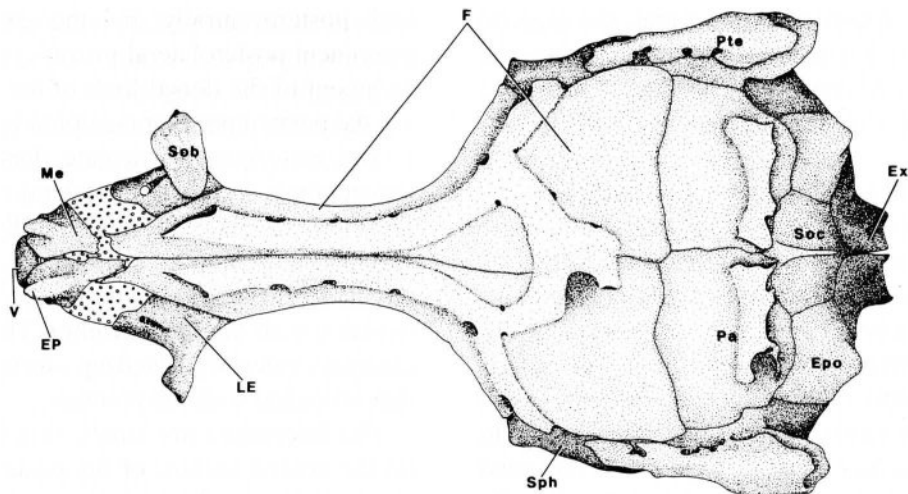

Fig. 4. Neurocranium of *Pseudotrichonotus altivelis* (ZUMT 59882, 72.0 mm SL), dorsal view.

sal orbit, and the two branches articulate ventrally with a flange of bone from each pterosphe-

noid. Between the articulations with the parietals and pterosphenoids, the frontals are bordered

ventrally by the sphenotic and pterotic. An or-
bitosphenoid is lacking.

The frontals house the supraorbital branch of
the laterosensory head canal. From an anterior
opening, where the lateral line is received from
the nasal, the canal follows the edge of the orbit
and then divides. The posterior branch curves
medially and connects with its opposite member,
terminating and opening to the surface via a sin-
gle canal posteriorly. The main branch extends
ventrally and slightly posteriorly, passing the lat-
eral line to the pterotic canal. There are about
five lateral openings in the portion of the canal
that borders the orbit.

The parietals, which are rectangular in shape,
also bear a cephalic lateral-line canal, the
supratemporal canal. The canal runs along the
posterior border of the parietal, covering most of
its width, and connects with the extrascapular
canal (see "Pectoral-fin Girdle"). The parietals
meet in the midline, separating the frontals from
the supraoccipital ("medioparietal" type skull of
Rojo, 1991). The parietals are flanked laterally
by the pterotics, which form most of the lateral
border of the otic region.

A horizontally oriented sensory canal covers
most of the lateral surface of the pterotic. Ven-
tral to the canal, there is a shallow groove for the
articulation of the dorsal head of the hy-
omandibula. Posterior to the canal, the pterotic
terminates in a posteriorly directed, wing-like
process that is concave ventrally, providing a
large surface area for attachment of the levator
operculi.

In addition to the frontals and parietals, the
pterotics articulate with the sphenotics (anteroven-
trally), prootics and exoccipitals (ventrally), in-
tercalars (posteroventrally), and epioccipitals
(posterodorsally). The sphenotics form the an-
terolateral portion of the otic region, just poste-
rior to the orbit. They articulate anteriorly with
the pterosphenoids, which extend medially to
form the posterior border of the orbit. As noted
above, the pterosphenoids articulate dorsally
with the frontals.

The prootics lie between the sphenoticl
pterotic and the parasphenoid and form the
major part of the floor of the otic region. At the
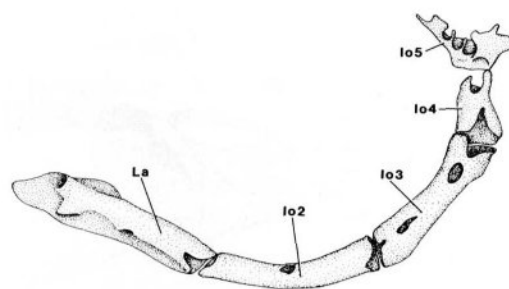junction of the sphenotic, pterotic and prootic,

there is an excavation for the articulation of the
anterior head of the hyomandibula.

The median supraoccipital, which forms the
posterodorsal portion of the neurocranium, is
hexagonal and bears a small raised ridge along
the dorsal midline. The supraoccipital articulates
anteriorly with the parietals, laterally with the
epioccipitals, and posteriorly with the exoccipi-
tals. The supraoccipital lacks the spina occipi-
talis described by Allis (1909) and Stiassny
(1986).

The epioccipitals are paired, roughly rectangu-
lar bones that form part of the posterior border
of the neurocranium. They are bordered medi-
ally by the supraoccipital, anteriorly by the pari-
etal~ ,ventrally by the pterotics and intercalars,
and posteroventrally by the exoccipitals. A
prominent posterolateral process is the site of at-
tachment of the dorsal limb of the posttemporal,
via the posttemporal-epioccipital ligament.

The exoccipitals articulate dorsally with the
epioccipitals and form the lateral margins of the
foramen magnum. Posteroventrally, each exoc-
cipital gives rise to a facet that sits on one of the
dorsolateral corners of the basioccipital and ar-
ticulates with the first vertebra. The exoccipitals
continue anteriorly as deep, rectangular bones
that articulate with the prootics.

The intercalars are small, thin bones that lie
on the ventral surface of the posterior neurocra-
nium, partly on the pterotics and partly on the
exoccipitals. They do not extend anterior to the
prootics. The ventral limb of the posttemporal is
ligamentously attached to the posterior edge of
the intercalar.
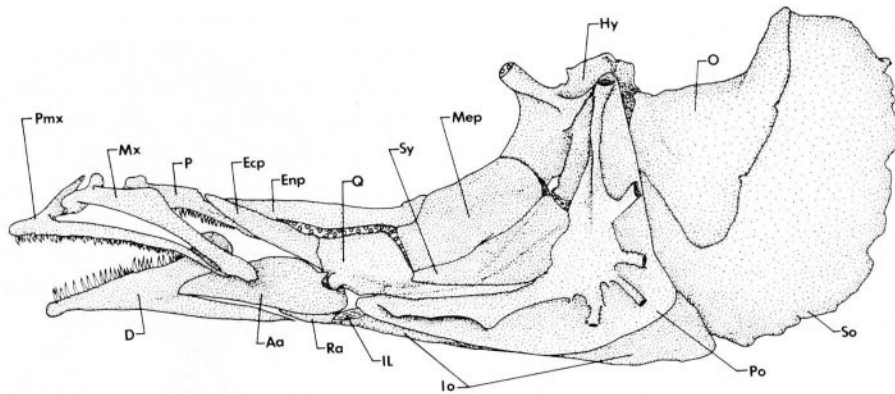
The anterior portion of the basioccipital is a

Fig. *6.*   Suspensorium of *Pseudotrichonotus altivelis* (ZUMT 59882, 72.0 mm SL).

thin flange of bone lying ventral to the exoccipital. It deepens posteriorly and ultimately forms a condyle for the articulation of the first vertebral centrum.

Circumorbital bones (Figs. 4, 5)

This series comprises six paired bones. A thin, plate-like bone that lacks sensory canals, the supraorbital, forms the anterodorsal border of the orbit. An antorbital is lacking. The lacrimal is a straight, elongate bone that covers a portion of the maxilla anteriorly and articulates with the second infraorbital posteriorly. The second and third infraorbitals are elongate and slightly curved, forming the ventral and posteroventral margins of the orbit, respectively. The fourth and fifth infraorbitals are much shorter, although the fifth has an anterodorsally directed process that forms part of the posterodorsal margin of the orbit. All infraorbitals have a bony canal that extends from one end of the bone to the other and accommodates the infraorbital branch of the cephalic laterosensory system. There are one to several small pores in the canal of each infraorbital.

Nasals (not illustrated)

The nasals are paired, elongate, tube-shaped bones. Anteriorly, they lie above the ethmoid processes; posteriorly, they curve dorsally, ending near the anterior terminus of the frontals, to which they conduct a branch of the cephalic lat-

eral line. A single opening is present at both ends of each nasal.

Upper jaw (Fig. 6)

The premaxillae are the tooth-bearing bones of the upper jaw. From the symphysis, where the two bones are bound tightly together with connective tissue, the slender, main body of each premaxilla (alveolar ramus) extends posteroventrally, decreasing gradually in width as it descends. Rows of small conical teeth cover the ventral surface of the anterior three-quarters of the bone; teeth in the outer row are the largest and are directed ventrally, whereas the innermost are smaller and curve inward, projecting almost medially. Teeth are depressible, exhibiting the Type 4 tooth attachment of Fink (1981). The ascending process is long, reaching to the posterior extent of the cranial condyle of the maxilla when the mouth is closed. The well-developed ascending processes as well as the configuration of buccal ligaments (see next section) allow for moderate protrusion of the upper jaw. The articular process of the premaxilla is well developed.

The edentulous maxilla is excluded from the gape by the premaxilla. The maxilla originates anteriorly in a slender, slightly pointed maxillary median process that articulates with the ventral surface of the articular process of the premaxilla. Just distal to that process, a well developed cranial condyle projects posteriorly, nearly at a 90° angle to the median process. The remainder of the maxilla is slender except for a slight widen-
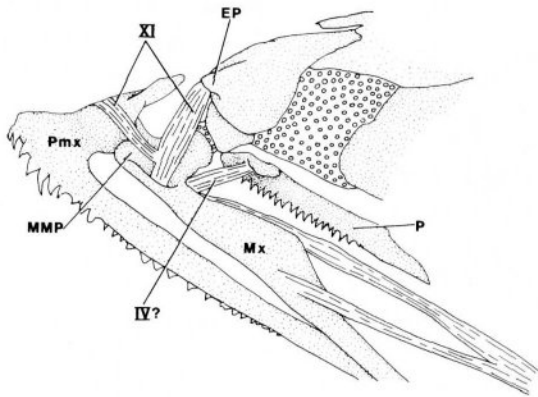
Fig. 7. Ligaments of the upper jaw of Pseudotri-chonotus altivelis (ZUMT 59882, 72.0 mm SL), lateral view. IV—median palato-maxillary ligament; *XI*—ethmo-maxillary ligament.
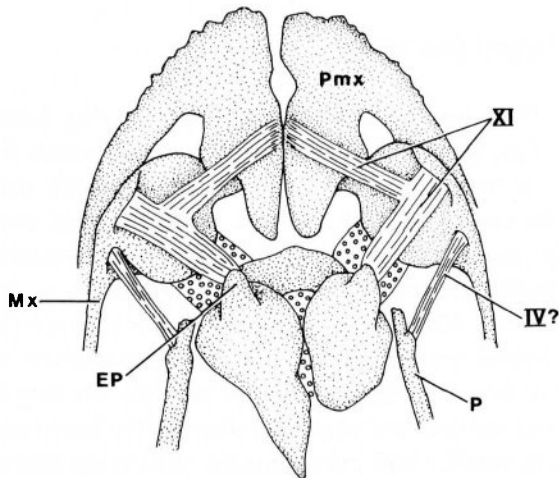

Fig. 8. Ligaments of the upper jaw of Pseudotri-chonotus altivelis (ZUMT 59882, 72.0 mm SL), dorsal view. IV—median palato-maxillary ligament; XI—ethmo-maxillary ligament.

Fig. 9. Ligaments of the upper jaw of Pseudotri-chonotus altivelis (ZUMT 59882, 72.0 mm SL), ventral view. I—interpremaxillary ligament; *IV*—median palato-maxillary ligament; V—anterior palato-vomer-ine ligament.

ing just anterior to the center of the bone. The maxilla is only slightly wider than the premaxilla. There is no supramaxilla.

Ligaments of the upper jaw (Figs. 7–9)

The upper jaw is moderately protrusible, an unusual feature among non-acanthomorph teleosts and one necessitating modifications of the buccal ligaments. Where the homology is clear, we have designated buccal ligaments of *Pseudotrichonotus* using Stiassny's (1986) sys-
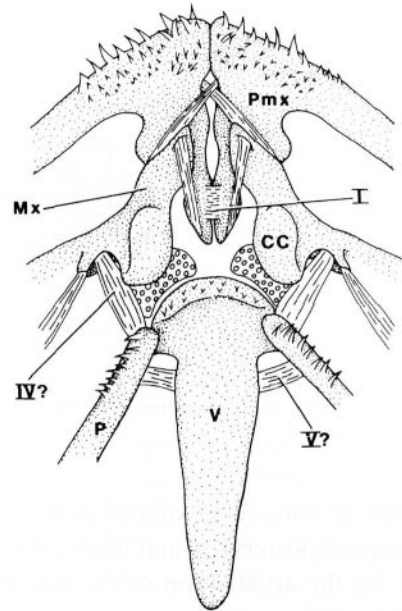
tem of enumeration.

The proximal area of the maxilla is the site of insertion for several ligaments. A well-developed ethmo-maxillary ligament (XI) originates on the ethmoid process and attaches to the lateral surface of the maxilla just posterior to the median process. Just above its attachment on the maxilla, it gives rise to a medial branch that attaches to the ascending process of the premaxilla. A single palato-maxillary ligament originates on the ventrolateral aspect of the palatine and inserts onto a small bony process just posterior to the insertion of the ethmo-maxillary ligament. Stiassny (1986) described anterior (IX), median (IV) and posterior palato-maxillary ligaments among teleosts, but noted that the anterior ligament is present only in some "higher percoids," and the posterior ligament is a synapomorphy of stomiiforms. Although the palato-maxillary ligament in *Pseudotrichonotus* is thus most likely the homolog of the median palato-maxillary ligament of other teleosts, it inserts onto the maxilla much further anterodorsally than does the median palato-maxillary

ligament in other aulopiforms (see Stiassny, 1986: fig. 6); it attaches to the maxilla in the area of the "maxillary saddle" (Stiassny, 1986), which is the site of articulation of the palatine prong of other aulopiforms and acanthomorphs (as noted below, the palatine prong is lacking in Pseudotrichonotus). A single ligament connects the palatine and vomer anteriorly, and it is uncertain if this represents the anterior- or posterior palato-vomerine ligament (V or VI) of Stiassny (1986).

Two pairs of ligaments connect the premaxillae and maxillae, neither of which we can homologize with ligaments described by Stiassny (1986). One originates on the ventral surface of the anterior tip of the maxillary median process and extends posterodorsally to insert on the posterior tip of the ascending process of the premaxilla. The other originates on the dorsal surface of the maxillary median process and extends ventromedially across the midline to insert on the medial edge of the contralateral premaxilla. A strong interpremaxillary ligament (I) binds the ascending processes to one another near their posterior tips.

Lower jaw (Fig. 6)

The dentary is slender anteriorly and widens considerably posteriorly. The posterior margin is deeply indented, and the anterior, pointed portion of the anguloarticular fits into this indentation, the very tip lying against the medial surface of the dentary just anterior to the point where the dentary bifurcates. Several rows of depressible, conical teeth are present on the dorsal surface of the dentary, from the symphysis to near the terminus of the bone posteriorly.

The anguloarticular gradually widens posteriorly, but it does not give rise to a prominent coronoid process dorsally. Posterodorsally it bears a well developed socket for articulation with the quadrate. The retroarticular is a small bone that is tightly bound to the posteroventral margin of the anguloarticular. Meckel's cartilage remains as a cylindrical rod that runs horizontally along most of the midlateral, medial surface of the anguloarticular and then continues for a short distance along the medial surface of

the dentary.

Suspensorium (Fig. 6)

The suspensorium articulates with the lower jaw via the quadrate, the anteroventral corner of which has a ball-like articular facet for the anguloarticular. The quadrate is not triangular as in most teleosts because the posteroventral portion (the preopercular process or quadratojugal — see Patterson, 1973; Rojo, 1991) is very long and extends much further posteriorly than the remainder of the bone. The main body of the quadrate is not fan-shaped, but has three distinct sides for articulation with other bones of the suspensorium. Anteriorly, the quadrate articulates with the ectopterygoid via connective tissue at a nearly vertical joint. Dorsally, the margin of the quadrate is roughly horizontal, and it has a synchondral joint with the endopterygoid. Posteriorly, the main body of the quadrate articulates with the anterior border of the metapterygoid via cartilage.

The ectopterygoid and endopterygoid are joined synchondrally, at least along the posterior portion of the former. The ectopterygoid overlaps and is bound by connective tissue to the palatine, which has numerous (e.g., ca. 30 in one specimen), small, slightly recurved, conical teeth on its ventral border. The anterior tip of the palatine is cartilaginous, but lacks the articular process or prong that typically articulates with the maxilla. A short ligament connects the two bones (see "Ligaments of the Upper Jaw").

The endopterygoid is a long, relatively slender bone. Posterior to its articulation with the dorsal margins of the ectopterygoid and quadrate, it articulates with and terminates over the anterior one-third of the metapterygoid. The metapterygoid is a large, rectangular bone, the posterodorsal corner of which overlies the anteroventral flange of the hyomandibula. At its posterior tip, the metapterygoid bears a small pad of cartilage for articulation with the hyomandibula and symplectic. The metapterygoid is bordered posteroventrally by the symplectic. The symplectic is a long bone bound by connective tissue ventrally to the posterior process of the quadrate. Its anterior extremity is a slender, cartilage-tipped
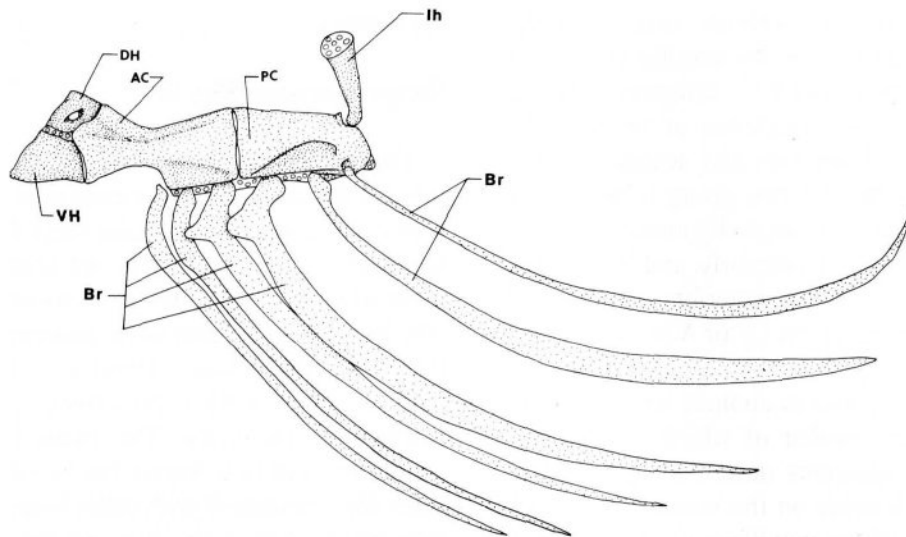
Fig. 10. Hyoid arch, ventral portion, of *Pseudotrichonotus altivelis* (ZUMT *59882*, 72.0 mm SL).

projection that lies medial to the posterior portion of the main body of the quadrate.

The suspensorium is anchored to the neurocranium via the hyomandibula, which is roughly square in shape due, in part, to the presence of a large anteroventral flange. It bears three articular surfaces dorsally (an anterior and central one for the neurocranium and a posterior one for the opercle). Ventrally, the main shaft of the hyomandibula articulates with the symplectic via a synchondral joint, and the ventral tip of the anteroventral flange is overlain by the metapterygoid. Part of the posterior portion of the hyomandibula is covered laterally by the preopercle.

Opercular series (Fig. 6)

The preopercle is a large, posteriorly curved bone that borders the suspensorium posteriorly. The horizontal limb of the preopercle is tightly adhered to the posterior process of the quadrate, and the vertical limb is bound to the lateral surface of the hyomandibula. A large sensory canal runs along the inner margin of the preopercle (i.e., along the anterior margin of the vertical limb and dorsal margin of the horizontal limb) and has an opening at both ends of the bone. Additionally, four finger-like branches of the canal

extend outward from the main canal onto the lateral surface of the preopercle, each with an opening at its terminus. There may be one or two other perforation(s) of the main canal that are not at the end of a branch.

The ventral border of the opercular membrane is formed by the interopercle, which is ligamentously attached anteriorly to the retroarticular (interoperculomandibular ligament) and more posteriorly to the ventral hyoid arch (interoperculohyoid ligament). The interopercle is partially covered by the preopercle, and it is attached posteriorly to the ventro-lateral aspect of the subopercle. The subopercle is a very large bone that is closely bound to the opercle; it extends along the entire posterior margin of the opercle, around the v-shaped ventral projection and part way up the anterior border. The lateral surface of the subopercle has numerous small, low ridges radiating outward. The dorsal margin of the opercle is concave, and the facet for articulation with the hyomandibula is at the anterodorsal corner of the bone.

Ventral portion of the hyoid arch (Figs. 10, 11)

The ventral portion of the hyoid arch is bound to the suspensorium by a small, rod-shaped in-
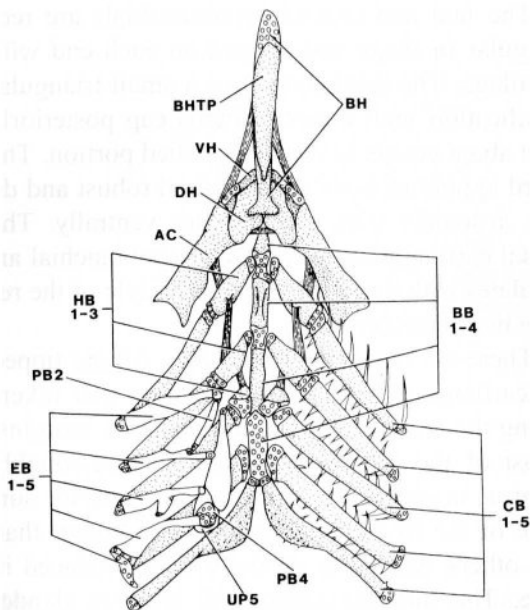
Fig. 11. Branchial apparatus of *Pseudotrichonotus altivelis* (ZUMT 59882, 72.0 mm SL), dorsal view; dorsal elements of right side removed; dorsal bony elements of left side unstippled.

Fig. 12. Posterior basibranchials and associated elements of *Pseudotrichonotus altivelis* (ZUMT 59882, 72.0 mm SL), ventral view.

terhyal. The interhyal articulates synchondrally with the suspensorium on the medial surface of the joint between the hyomandibula and symplectic. It is joined by connective tissue to the posterior ceratohyal at a fossa on its posterodorsal corner, which is also the site of insertion of the interoperculohyoid ligament. The posterior ceratohyal is rectangular in shape and separated from the anterior ceratohyal by a thin, vertical strip of cartilage. A band of cartilage extends along the ventral border of the posterior ceratohyal and continues uninterrupted along the posterior portion of the anterior ceratohyal. This cartilage is continuous with the small strip of cartilage that lies between the anterior and posterior ceratohyals.

Anterior to this cartilage, the anterior ceratohyal abruptly narrows and then widens again forming a convex anterior border that articulates with the dorsal and ventral hypohyals. The hypohyals are bound to one another synchondrally and to the posteroventral surface of the basihyal by connective tissue.

The basihyal is a large, elongate bone that is tipped in cartilage anteriorly. Most of the dorsal
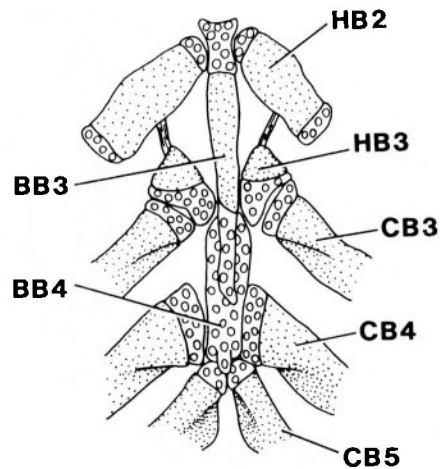
surface of the bone is covered by an edentulous toothplate.

The ventral hyoid supports six branchiostegal rays, three on each ceratohyal and most articulating with the ventral cartilage. The third and fourth have a prominent anteriorly directed process proximally that is poorly developed or lacking in the others.

Gill arches (Figs. 11–14)

Four unpaired basibranchials form the median base of the branchial skeleton. The first three are incomplete ossifications of a single cartilage. The ossified portions are thus separated from one another by blocks of cartilage, but there are no joints between them. The anterior three basibranchials are separate from the fourth, cartilaginous basibranchial. The first basibranchial is a small triangular perichondral ossification attached by connective tissue to the dorsal hypohyals. A small, rectangular cartilage follows the first basibranchial; its concave, lateral borders are the sites of articulation of the first hypobranchials. The second basibranchial is an elongate, rectangular ossification followed by another small, rectangular cartilage that supports the second hypobranchials. The third basibranchial is the last ossified element in the series; it is elongate, rectangular, and terminates as a cartilagi-
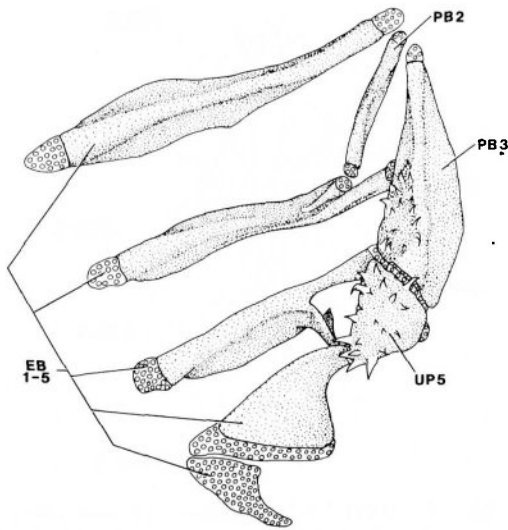
Fig. 13. Dorsal portion of branchial apparatus of *Pseudotrichonotus altivelis* (ZUMT 59882, 72.0 mm SL), right side, ventral view.
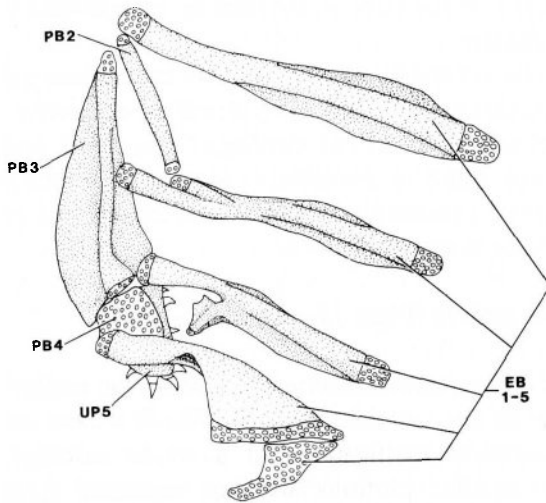
Fig. 14. Dorsal portion of branchial apparatus of *Pseudotrichonotus altivelis* (ZUMT 59882, 72.0 mm SL), right side, dorsal view.

nous "tail" ventral to the elongate, cartilaginous, fourth basibranchial (Fig. 12). The third hypobranchials flank the third basibranchial just anterior to its passage beneath the fourth basibranchial, but they articulate synchondrally with the anterior margin of the fourth basibranchial. The fourth and fifth ceratobranchials also articulate with the fourth basibranchial near (fourth) or on (fifth) its posterior border. A fifth basibranchial is lacking.

The first and second hypobranchials are rectangular in shape and capped on each end with cartilage. The third comprises a small triangular ossification with a cartilaginous cap posteriorly that about equals in size the ossified portion. The third hypobranchials are short and robust and do not articulate with one another ventrally. The distal cartilaginous tip of each hypobranchial articulates with the cartilaginous condyle of the respective ceratobranchial.

There are five ceratobranchials. All are tipped in cartilage at both ends, and have gill rakers along the anterior margin and posterior margins. Most of the gill rakers are small and roughly conical in shape, but those on the anterior surface of the first ceratobranchial are longer than the others, and those on the fifth are reduced in size. The fifth ceratobranchial is more slender distally than the others but widens proximally where it bears an approximately elliptical tooth patch on the posterodorsal margin near its proximal base.

There are five epibranchials, the first four ossified, the fifth cartilaginous. The first three epibranchials are long and rod-like, and the main ramus of each is flanked by small bony laminae (the third epibranchial lacks a bony lamina anteriorly). They are tipped at both ends in cartilage and articulate with the first through third ceratobranchials diarthrodially. The first epibranchial lacks an uncinate process. The second epibranchial has a long, medially directed uncinate process with a cartilaginous head that fits into a small depression on the lateral side of the dorsal surface of the third infrapharyngobranchial, approximately midway down the length of the bone. The third epibranchial articulates at the junction between the third and fourth infrapharyngobranchials. Near its center, the third epibranchial gives rise to a slender, cartilage-tipped, dorsolaterally directed uncinate process.

The fourth epibranchial is thin distally, where its cartilaginous cap articulates with the dorsal surface of the fourth pharyngobranchial cartilage near the posteromedial margin. The fourth epibranchial widens greatly towards its proximal end, which is capped by a large band of cartilage. Between this fourth epibranchial cap and the cartilage-tipped distal end of the fourth cera-
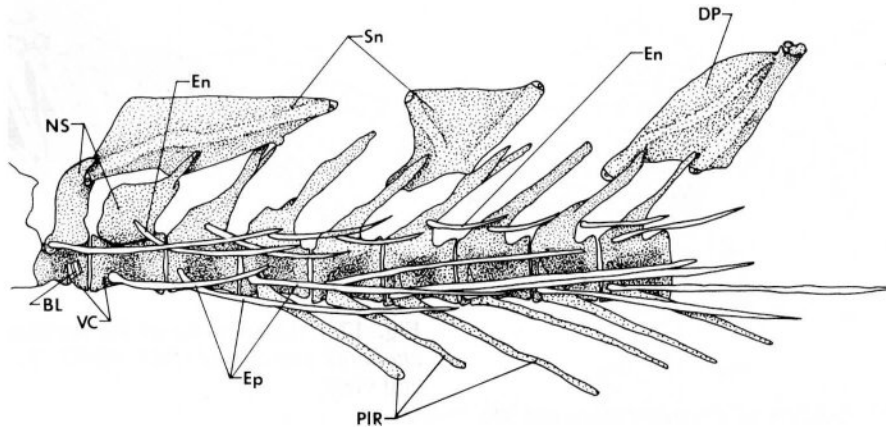
Fig. 15. Anterior vertebral column of *Pseudotrichonotus altivelis* (ZUMT 59882, 72.0 mm SL), lateral view.

tobranchial, there is a large, separate cartilaginous structure. As noted by Nelson (1967), this cartilage, which is present in many lower teleosts, was demonstrated to be the fifth epibranchial in a developmental study of Hepsetus by Bertmar (1959). There is no uncinate process on the fourth epibranchial, and all epibranchials lack toothplates.

The first infrapharyngobranchial is absent. The second infrapharyngobranchial is an elongate, edentulous rod. The anterior tip is bound to the distal end of the first epibranchial and anterior end of the third infrapharyngobranchial by connective tissue. From this association anteriorly, the second infrapharyngobranchial extends posterolaterally and articulates with the main ramus of the second epibranchial. The third infrapharyngobranchial is a long, robust bone oriented in an anterior-posterior direction; its anterior tip reaches a point near the distal ends of the first epibranchial and second infrapharyngobranchial and is bound by connective tissue to them. The second and third infrapharyngobranchials are tipped in cartilage at both ends, but they lack other cartilaginous condyles. Ventrally, the third infrapharyngobranchial bears a patch of teeth on the lateral and middle portions of the posterior end. A well developed round fourth infrapharyngobranchial cartilage is located at the posterior base of the third infrapharyngobranchial. The toothplate associated with the fourth infrapharyngobranchial cartilage

(the fifth toothplate—see Johnson, 1992) covers the entire ventral surface and extends laterally, medially and posteriorly beyond the margin of the cartilage.

Postcranial axial skeleton (Fig. 15)

The three specimens each have 50 vertebrae, comprising 24 abdominal and 26 caudal vertebrae, and 48 preural and two ural centra ($PU_1 +$ U, and U,). As discussed below (see "Median Fins"), neural spines of several anterior vertebrae are intimately associated with two supraneural bones and the anterior dorsal-fin pterygiophores. Left and right halves of neural spines are not fused to one another anteriorly, but become fused at approximately vertebra 14. The first and second neural arches are autogenous, the remainder fused to the centra.

In addition to pleural ribs, the vertebral column supports three series of intermusculars, two in bone and one in ligament. For details concerning the intermuscular series of *Pseudotrichonotus*, see Patterson and Johnson (1995: table 4). Epineural bones originate on neural arches or spines of vertebrae 1 through 26, but in one specimen (USNM 280366) epineurals are missing on vertebra 3 and in another (ZUMT 59882) there are no epineurals on vertebrae 3–6 on the right side. Epineurals on the first through third vertebrae are directed more ventrally than are subsequent epineurals. Epipleural bones occur
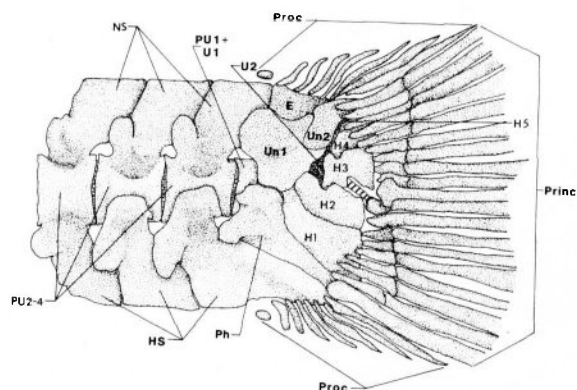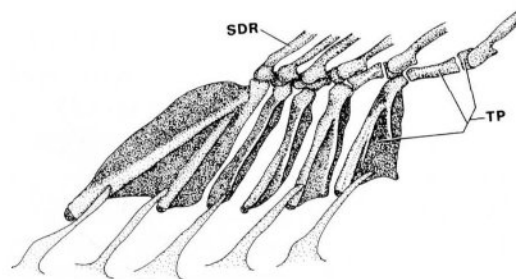
Fig. 16. Caudal skeleton of *Pseudotrichonotus altivelis* (ZUMT 59882, 72.0 mm SL).

Fig. 17. Anterior dorsal-fin skeleton of *Pseudotrichonotus altivelis* (ZUMT 59882, 72.0 mm SL), lateral view.

on vertebrae 2 through 31 or 32; posteriorly, the point of attachment of epipleurals changes progressively from the centrum to the parapophysis to the haemal arch or spine. Between those two series of intermuscular bones is a series of poorly defined epicentral ligaments (not shown in the illustration). The epicentral series is discontinuous, the first ligament occurring on the occiput, the second on vertebra 16. The series then continues to about vertebra 29, attaching to parapophyses or, more posteriorly, centra. Baudelot's ligament attaches to the first centrum. Ossified ribs begin on vertebra 4 and end on vertebra 23; they do not form in cartilage.

Caudal skeleton (Fig. 16)

The neural and haemal spines of the five posteriormost preural vertebrae are greatly expanded (spatulate) and articulate with one another anteriorly and posteriorly. The anteriormost portions of the neural and haemal arches of those caudal vertebrae embrace the expanded neural and haemal spines, respectively, of the preceding vertebra. The posterior axial skeleton is thus relatively rigid. Haemal spines of PU_2 and PU, are autogenous. A compound centrum comprising $PU,+U_1$ supports an autogenous parhypural and hypurals one and two. The terminal centrum, U_2, bears the third through fifth hypurals. A sixth hypural is lacking. A large anterior uroneural pair (UN,) and smaller poste-

rior uroneural pair (UN_2) lie above the ural centra. Like the neural arches of the preceding five vertebrae, the left and right halves of the anterior uroneural embrace the posteroventral corner of the expanded neural spine of PU, as well as the ventral margin of the single epural located above UN,. Likewise, the anterodorsal portion of the parhypural embraces the posterodorsal margin of the expanded haemal spine of PU_2.

Nineteen principal caudal-fin rays (10+9) are supported by the parhypural, hypurals and the posterior uroneural. All principal rays are segmented distally, and most also have a joint proximally that separates a small proximal segment from the remainder of the ray. This joint is well separated from the normal segmentation that begins more distally. In two specimens, all principal rays except the two medialmost rays and the outermost ray of the dorsal and ventral lobes have this joint (in one of those specimens, only the right half of the outermost principal ray of the dorsal lobe has it). In the third specimen, the ventral lobe is as described above, but all principal rays except the medialmost element of the dorsal lobe have the joint.

There are sixteen procurrent caudal-fin rays; eight in the dorsal lobe are supported by the single epural and posterior uroneurals, and the remaining eight in the ventral lobe by the haemal spine of PU_2. The anteriormost procurrent element in both the dorsal and ventral series is a small nodule of bone, not a slender, elongate element like the other rays.
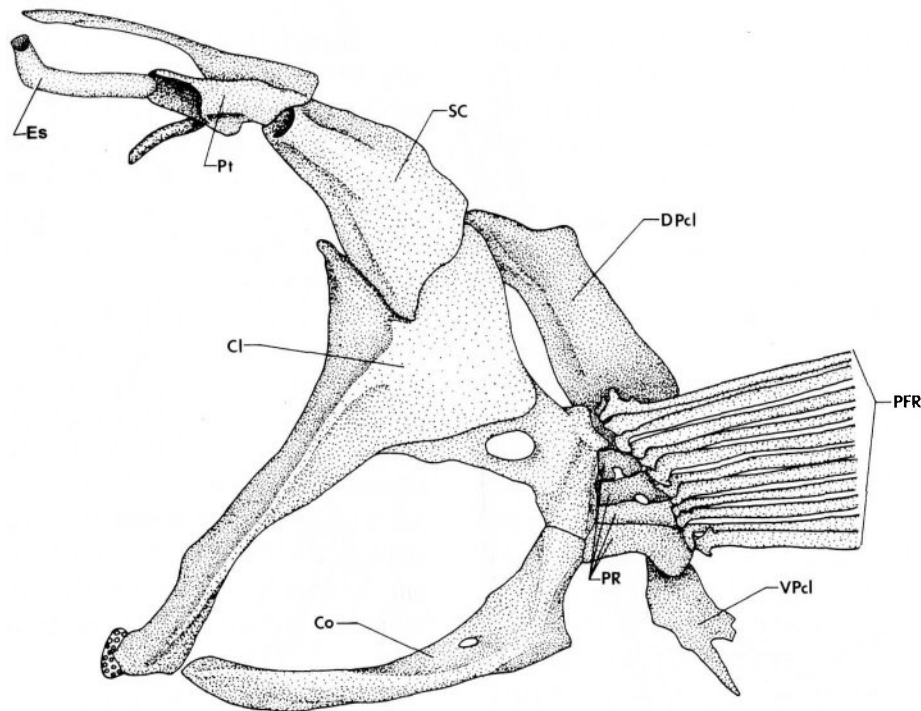
Fig. 18.   Pectoral-fin girdle of *Pseudotrichonotus altivelis* (ZUMT *59882, 72.0* mm SL).

Median fins (Figs. 15, 17)

Two large, posteriorly inclined supraneurals precede the dorsal fin. The first extends from the first to near the fourth neural spines, the other from the fifth to sixth neural spines. Neural spines of one or more vertebrae embrace the ventral margin of each supraneural. The anteroventral and posterodorsal corners of each supraneural are tipped in cartilage.

The anteriormost portion of the first dorsal-fin pterygiophore inserts into the seventh interneural space (counting the space between the first and second neural spines as the first). There are 34 dorsal-fin rays (33 in one specimen) supported by 33 (32) pterygiophores. The first pterygiophore supports two rays, one in supernumerary association and one serially. All other dorsal-fin pterygiophores serially support a single ray. The unfused left and right halves of neural spines embrace the ventral portions of many of the anteriormost dorsal-fin pterygiophores.

Thirteen trisegmental anal-fin pterygiophores (14 in one specimen) support 14 (15) rays. The

ray in supernumerary association with the first pterygiophore in both the dorsal and anal fins embraces a free distal radial. A bony stay is present at the posterior base of the dorsal and anal fin.

Pectoral-fin girdle (Fig. 18)

There is a single tube-like extrascapular bone. It accepts a branch of the lateral-line canal from the lateral opening of the parietal canal, then bends almost 90° posteriorly near its center, passing the branch to a canal that overlies the ventral limb of the posttemporal. The dorsal limb of the posttemporal is flat and slender, and is ligamentously connected to the epioccipital; the ventral limb is slender, rod shaped and attached by ligament to the intercalar. The posttemporal terminates posteroventrally in a blunt projection that overlies the rounded dorsal tip of the supracleithrum to which it is bound by a short, broad ligament. Where the two bones overlap, a lateral-line canal passes from the medial aspect of the posttemporal to the lateral aspect of the supracleithrum. The canal continues
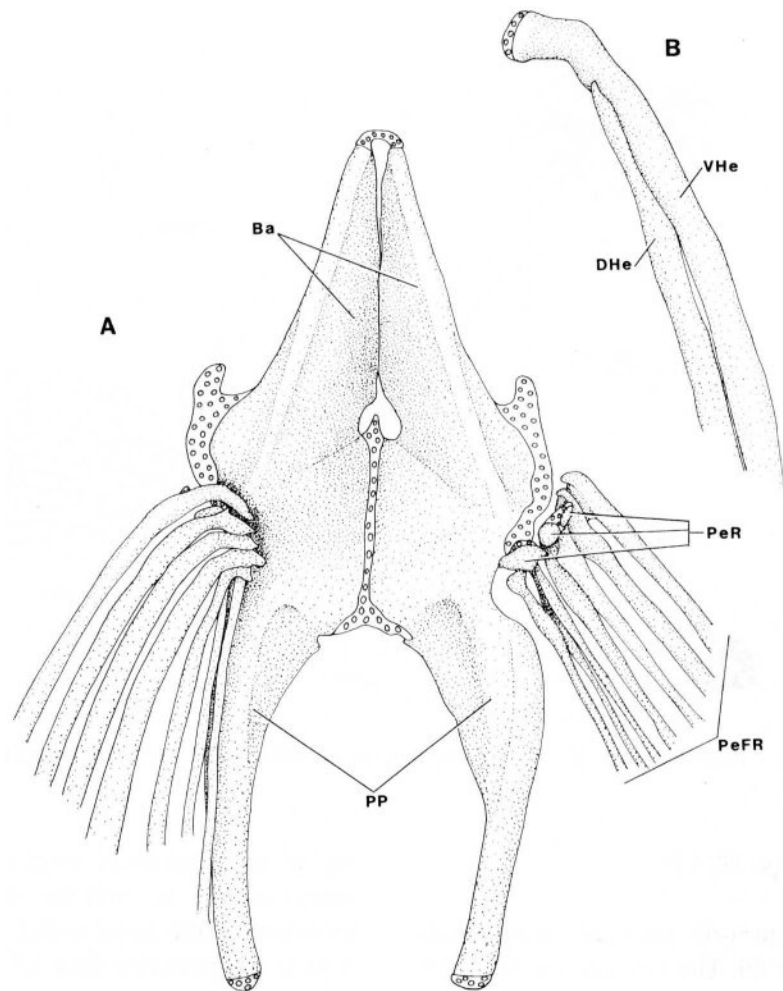
Fig. 19. **A)** Pelvic-fin girdle of *Pseudotrichonotus altivelis* (ZUMT 59882, 72.0 mm SL), ventral view, dorsal hemitrichs of rays of right side removed; B) proximal end of medialmost pelvic-fin ray, left side, in dorsal view.

posteroventrally on the supracleithrum, passing to the trunk via a medial opening approximately half way to the posteroventral extremity of the bone. The supracleithrum broadens posteroventrally, and Baudelot's ligament attaches to its medial surface near the ventralmost end.

The supracleithrum partially overlaps the dorsal, v-shaped portion of the cleithrum and the dorsal tip of the dorsal postcleithrum. The main body of the cleithrum covers the anterior part of the scapula. Just above the scapular foramen, the posterior margin of the cleithrum curves anteriorly, and the bone extends anteroventrally as a slender column. A small pad of cartilage is bound to the anterior tip of this limb. The pos-

teroventral tip is bound by a very short ligament to the anterior extent of the coracoid. A very conspicuous laterally elevated ridge extends the length of this narrow cleithral limb.

The scapula is roughly rectangular. It has a curved articular surface posterodorsally that supports the first two pectoral-fin rays, and, more ventrally, it supports four columnar pectoral-fin radials. The scapula ends posteroventrally in a flat, horizontal surface that articulates synchondrally with the posterodorsal surface of the coracoid.

The coracoid approximates the width of the anteroventral limb of the cleithrum. From its articulation with the scapula, it curves anteroven-

trally toward the ventral tip of the cleithrum.

There are two postcleithra. The dorsal one originates near the posteriormost point of the supracleithrum and terminates at a point medial to the proximal bases of the central pectoral-fin rays; at its terminus, the dorsal postcleithrum covers the dorsal portion of the ventral postcleithrum, which continues only a short distance beyond the ventral margin of the pectoral fin.

The scapula and four autogenous proximal pectoral-fin radials support 11 fin rays in each specimen. Lateral and medial halves of all rays except the dorsalmost embrace a tiny ossified distal radial proximally. A ventrally directed process is present on the proximal base of the medial branch of each ray except the one adjacent to the dorsalmost ray; in the latter the process is considerably larger than in the other rays.

Pelvic-fin girdle (Fig. 19)

The pelvic girdle comprises the paired basipterygia, which are associated with one another in three ways: by a small bridge of cartilage that extends from the anterior tip of one half to the anterior tip of the other; by simple abutment along the internal wings (see Stiassny and Moore, 1992); and by cartilage that joins the median sections (in the region of fin articulation, between the internal wings and posterior processes) of the bones. The girdle continues posteriorly as two widely separated, laterally curved posterior processes that are tipped in cartilage. The surface for articulation of the pelvic-fin rays is covered laterally with a band of cartilage. Each pelvic fin comprises seven rays supported primarily by four ossified pelvic radials. The medialmost radial is tipped anteriorly in cartilage and is fused to the ventral half of the medialmost ray (see Johnson, 1992). The two lateral radials are autogenous and associated with a single cartilage that covers them anteriorly.

Relationships

Yoshino and Araga (in Masuda et al., 1975)

erected the family Pseudotrichonotidae for *Pseudotrichonotus altivelis*, and placed it in the Myctophiformes (s.l.), noting that it differs from the members of that group in numbers of branchiostegal rays, pelvic- and caudal-fin rays and absence of an adipose fin. They based the name *Pseudotrichonotus* on the external resemblance of *P. altivelis* to fishes of the perciform family Trichonotidae, but pointed out that the two are readily distinguishable by the placement of, and number of rays in, the pelvic fin.

In his analysis of iniome relationships, R. K. Johnson (1982) briefly commented on the possible affinities of Pseudotrichonotus, stating that "A number of characters reported for this species (which I have not had the opportunity to examine) strongly suggest that the authors incorrectly allied it with iniomous fishes..." He went on to list the number of principle caudal-fin rays (17 in *Pseudotrichonotus* vs. 19 in all inioms); branchiostegal rays (six vs. usually seven or more); and pelvic-fin rays (seven vs.' usually eight or more). One implication of Johnson's (1982) comments is that *Pseudotrichonotus* is advanced relative to myctophiforms and thus more closely related to acanthomorphs.

Because the ordinal placement of *Pseudotrichonotus* has been questioned, our initial goal is to identify the major group of neoteleosts to which it belongs. Several recent studies (Rosen, 1985; Stiassny, 1986; Johnson, 1992; Johnson and Patterson, 1993) have reviewed and progressively clarified the evidence for monophyly of the higher euteleostean clades (Neoteleostei, Eurypterygii, Ctenosquamata, Acanthomorpha) and identified additional synapomorphies for each. We will briefly review the diagnostic characters for each major clade with respect to *Pseudotrichonotus*.

Pseudotrichonotus is not an acanthomorph. It is primitive with respect to acanthomorphs in lacking dorsal- and anal-fin spines; separate anterior and medial infracarinales muscles in the pelvic-fin girdle; a tight, immobile connection of the dorsal limb of the posttemporal to the epioccipital (relatively loose, ligamentous connection in *Pseudotrichonotus*); complete ossification of the posterior pelvic processes (tips cartilaginous in *Pseudotrichonotus*); and distinct facets on an-

terior surface of the first centrum for articulation with the exoccipital condyles (Rosen, 1985; Stiassny, 1986, 1993; Johnson and Patterson, 1993; this study). Pseudotrichonotus also lacks a maxillo-rostroid ligament (VII), the absence of which is presumably correlated with absence of a median rostral cartilage (Figs. 7 and 8). Both the maxillo-rostroid ligament and a median rostral cartilage have been hypothesized to be acanthomorph synapomorphies (Hartel and Stiassny, 1986; Stiassny, 1986; Johnson and Patterson, 1993). Other acanthomorph specializations of the buccal region include presence of a distinct anterior palato-vomerine ligament (VI) and absence of the median palato-maxillary ligament (IV). As described above, Pseudotrichonotus has a single palato-vomerine ligament and a single palato-maxillary ligament, but we lack information to homologize them with respect to ligaments described by Stiassny (1986). *Pseudo-trichonotus*, along with aulopids, synodontids and harpadontids, exhibits one reductive acanthomorph specialization, absence of the median caudal cartilages. This loss is most parsimoniously interpreted as convergent and, as discussed below, we consider it a synapomorphy of our Synodontoidei.

Pseudotrichonotus is a neoteleost. It has all four apomorphies considered diagnostic of the Neoteleostei by Johnson (1992), a retractor dorsalis muscle, insertion of the third internal levator on the fifth upper pharyngeal toothplate, a y-shaped suture joining the posteriorly exposed exoccipitals and basioccipital, and Type 4 tooth attachment.

Pseudotrichonotus is a eurypterygian. It has an interoperculohyoid ligament and the ventral hemitrich of the medial pelvic ray fused to the medial pelvic radial (Fig. 16), two of the three apomorphies considered diagnostic of the Eurypterygii by Johnson (1992). It lacks the most variable of the three, a toothplate fused to the third epibranchial.

Pseudotrichonotus is not a ctenosquamate. It lacks the gill-arch specialization considered by Johnson (1992) to uniquely characterize the Ctenosquamata, absence of the fifth upper pharyngeal toothplate and the associated third internal levator. Pseudotrichonotus has both

structures (Fig. 10).

Pseudotrichonotus is thus a non-ctenosquamate eurypterygian. We adopt the scheme proposed by Rosen (1973) in which non-ctenosquamate eurypterygians (Alepisauridae, Anotopteridae, Aulopidae, Bathypteroidae, Bathysauridae, Chlorophthalmidae, Evermanellidae, Giganturidae, Harpadontidae, Ipnopidae, Omosudidae, Paralepididae, Scopelarchidae, Scopelosauridae, and Synodontidae) comprise a monophyletic Aulopiformes. Although the monophyly of Rosen's (1973) Aulopiformes was challenged by R. K. Johnson (1982), Rosen (1985) and Stiassny (1986), it was supported by Johnson (1992) and further corroborated by Patterson and Johnson (1995). Rosen (1973: fig. 1) diagnosed his aulopiforms on the basis of an elongation of the uncinate process of the second epibranchial, a feature also characteristic of Pseudotrichonotus (Figs. 13 and 14). Following Johnson (1992), we accept this as a diagnostic character of the Aulopiformes, and conclude that Pseudotrichonotus is an aulopiform.[1]

A more comprehensive analysis of aulopiform monophyly and interrelationships by the first two authors is presented in a separate paper (Baldwin and Johnson, in press). Our purpose here is to describe the characters that bear directly on the relationships of Pseudotrichonotus and support the following scheme: (Aulopidae (Pseudotrichonotidae (Synodontidae, Harpadontidae))). We follow Sulak (1977) in recognizing a close relationship between Saurida and *Harpadon* (Harpadontidae herein) and between *Synodus* and the monotypic Trachinocephalus (Synodontidae herein). Sulak (1977) included those genera and *Bathysaurus* in a single family,

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[1] The concerns raised by Yoshino and Araga (in Masuda et al., 1975) and R. K. Johnson (1982) about the placement of *Pseudotrichonotus* among inioms despite its possession of more advanced teleostean numbers of principal caudal-fin rays, pelvic-fin rays and branchiostegals are ameliorated by the fact that *Pseudotrichonotus* has 19 principal caudal-fin rays, not 17 as reported in the original description. This discrepancy was first noted by Parin (1992) for *P. xanthotaenia*, and 19 principal caudal rays are also characteristic of the three cleared and stained specimens of *P. altivelis* examined in this study. The low numbers of pelvic-fin rays and branchiostegals in *Pseudotrichonotus* are best interpreted as having evolved independently of those of more advanced teleosts.

Synodontidae, but as discussed below (see "Comments on Bathysaurus"), our study rejects a synodontoid affinity for Bathysaurus.

Beginning with Rosen (1973), we briefly review our reasons for disagreeing with previous authors who have placed aulopids distant from synodontoids. Rosen (1973) separated his Aulopiformes into two purportedly monophyletic groups, Aulopoidei and Alepisauroidei. He placed the Aulopidae together with the Chlorophthalmidae, Bathysauridae, Scopelosauridae, Bathypteroidae and Ipnopidae in his Aulopoidei, for which he somewhat cryptically (pp. 435–346) cited three specializations. The first, presence of a toothplate fused to the third epibranchial (EB3), is invalid because it is a synapomorphy of neoteleosts (Fink and Weitzman, 1982; Johnson, 1992) and occurs in some of Rosen's (1973) alepisauroids (e.g., harpadontids, some paralepidids and all scopelarchids). The second, reorientation of the fifth upper pharyngeal toothplate (UP5) so that it lies along the shaft of the fourth epibranchial (EB4), is invalid because it also is found in some alepisauroids where Rosen incorrectly believed UP5 was absent or fused with the fourth upper pharyngeal toothplate (UP4—see Johnson, 1992). The third, reduction in length and expansion of the neural spine on the second preural centrum, shows no consistent, quantifiable pattern in either group (compare illustrations of each in Rosen, 1973: fig. 43–53).

Evidence for monophyly of Rosen's (1973) Alepisauroidei, in which he placed the synodontoids (Synodontidae and Harpadontidae) together with the Omosudidae, Alepisauridae, Anotopteridae, Scopelarchidae, and Evermanellidae, is equally ambiguous. In the dorsal gill arches, he cited absence of toothplates on the second pharyngobranchial (PB2) and EB3 and complete absence of UP5 as alepisauroid specializations. Some of Rosen's aulopoids (e.g., most ipnopids) lack a toothplate on PB2, and most synodontoids have one. As noted, many of Rosen's alepisauroids also have a toothplate on EB3. As for the upper pharyngeal toothplates, both UP4 and UP5 are present in all alepisauroids except synodontoids and anotopterids, which lack UP4, not UP5 (Johnson, 1992).
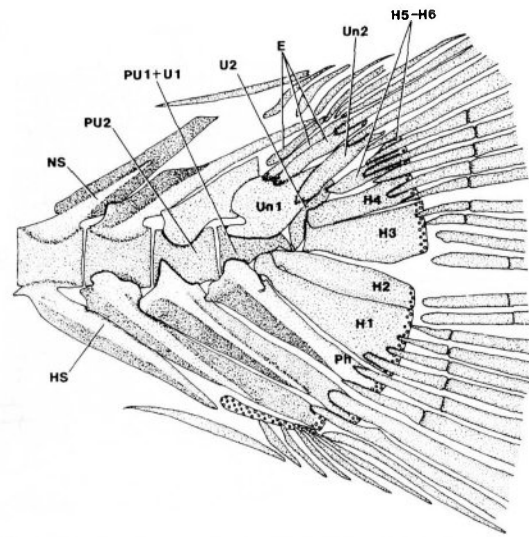

Fig. 20. Caudal skeleton of *Aulopus* japonicus (AMNH 28635SW, **ca.** 98 mm SL).
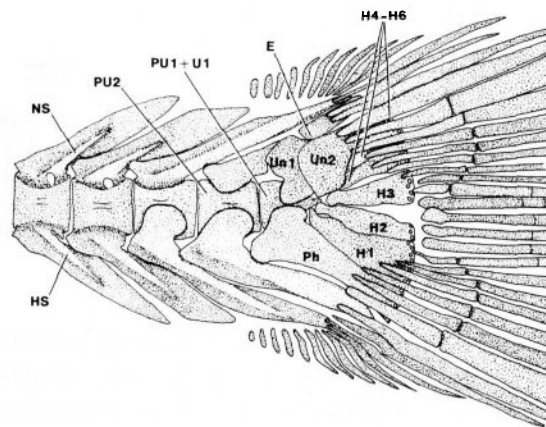

Fig. 21. Caudal skeleton of *Synodus* variegatus (USNM 315318, 77.0 mm SL).

Rosen suggested that jaw musculature and caudal skeletons also provide support for his alepisauroids, but, as with the aulopoids, his descriptions (p. 436, 438) and illustrations (figs. 43–53, 59–64) indicate no consistent diagnostic features in either complex.

Two subsequent hypotheses (Rosen, 1985; Stiassny, 1986) placed aulopids even more remote from synodontoids, but both would reject the monophyly of Rosen's (1973) Aulopiformes, which we believe is well supported (Johnson, 1992; Patterson and Johnson, 1995). Johnson (1992) discussed the shortcomings of Rosen's (1985) analysis and his reasons for disagreeing
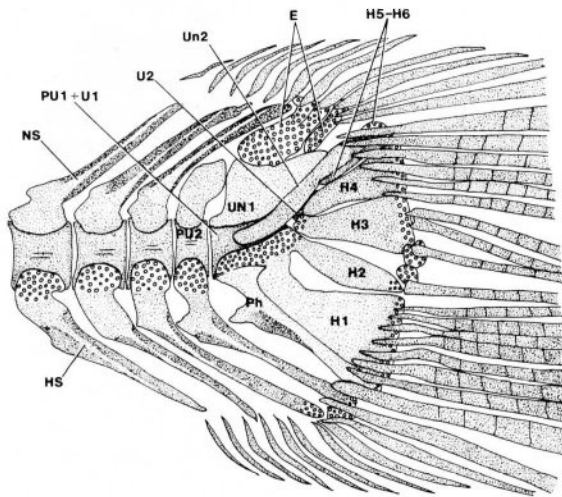
Fig. 22. Caudal skeleton of Parasudis truculentus (USNM 159850, 84.5 mm SL).
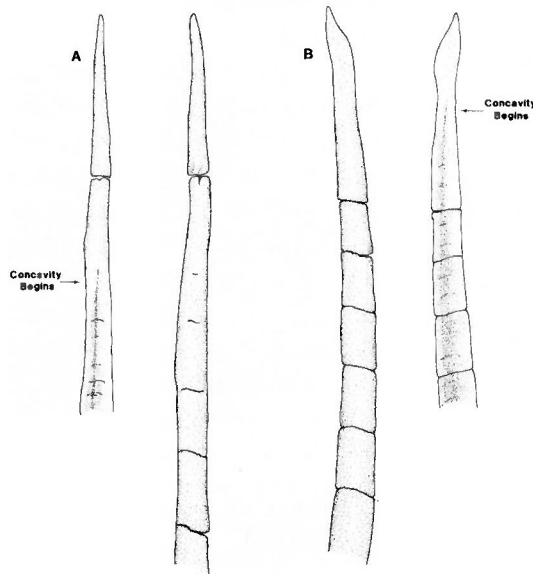

Fig. 23. A) Medial (left) and lateral (right) views of proximal end of right hemitrich of eighth principal ray of ventral lobe of caudal fin of *Synodus variegatus* (USNM 315318, 77.0 mm SL); B) lateral (left) and medial (right) views of right hemitrich of eighth principal ray of ventral lobe of caudal fin of Parasudis truculentus (USNM 159850, 84.5 mm SL). Note that in medial views, the concave nature of the hemtrich begins well anterior to first joint in Parasudis, but posterior to the first joint in *Synodus* (top of drawing is anterior).

with **Stiassny's** proposal that Aulopus is more closely related to ctenosquamates than to most aulopiforms.

Below, we list and discuss characters that defend our hypotheses of synodontoid relationships.

Synodontoidei

(Aulopidae + Pseudotrichonotidae Synodontidae + Harpadontidae)

Modified proximal segmentation of *caudal-fin* rays (Figs. 16, 20–23). — Pseudotrichonotus (Fig. 16) shares with Aulopus (Fig. 20), *Synodus* (Fig. 21), Trachinocephalus, *Harpadon* and *Saurida* (Sulak, 1977: fig. 4A) a peculiar segmentation of most principal caudal rays in which a small proximal section is separated from the remainder of the ray by a distinctive joint. This joint differs from the normal segmentation of caudal rays in that it is located near the proximal end of each ray, some distance from the beginning of normal segmentation, and the ends of the ray that meet at the joint are round (e.g., as in *Synodus*, Fig. 23A). Posterior to this joint, each hemitrich becomes laterally compressed and curved (concave in medial view, as in *Synodus*, Fig. 23A). The normal segmentation involves simple abutment of the compressed, curved ends of each segment. We have not observed the modified, proximal segmentation in any other fishes, although in some aulopiforms (e.g., Chlorophthalmus [Sulak, 1977: fig. 8], Parasudis [Figs. 22 and 23B], Bathysauropsis, No-*tolepis*, Macroparalepis and Evermannella), the normal segmentation extends to near the proximal end of the ray. In those fishes, the compressed, curved nature of the hemitrichs begins considerably more anteriorly than in synodontoids, and the first joint is not modified (Fig. 23B). The two conditions are distinct.

Absence of median caudal cartilages (Figs. 16, 20–22). — Pseudotrichonotus (Fig. 16), Aulopus (Fig. 20), *Synodus* (Fig. 21), *Saurida, Harpadon* and Trachinocephalus lack the free median caudal cartilages (cmc's of Fujita, 1990) at the distal tips of the second and third hypurals that characterize other aulopiforms (e.g., Parasudis, Fig. 22) as well as myctophiforms and most stomiiforms. Median caudal cartilages also are absent in acanthomorphs (Johnson and Patter-

son, 1993), but it is most parsimonious to interpret the loss in synodontoids as unique.

Expanded neural and haemal spines on posterior vertebrae (Figs. 16, 20–22). — The neural and haemal spines of the last three to six preural vertebrae are broadened by laminar expansions that extend anteriorly and posteriorly along the entire length of each spine in Pseudotrichonotus (Fig. 16), Aulopus (Fig. 20), *Synodus* (Fig. 21), Saurida and Trachinocephalus. The anterior portions of the neural and haemal arches of each of those vertebrae typically embrace the neural and haemal spines, respectively, of the preceding vertebra. Flanges are strongly developed on posterior neural and haemal spines in *Pseudotri-chonotus* and synodontids, where they form a nearly solid plate of bone. This effective stiffening of the caudal region may be advantageous for burrowing in sand and/or making quick lunges for food (see Anderson et al., 1966, for discussion of synodontoid behavior). Flanges are less prominent but nonetheless well developed in the posterior vertebral column of Aulopus and Saurida. They are essentially absent in the secondarily pelagic Harpadon.

The synodontoid condition is unique among aulopiforms, although a few other genera (e.g., Bathysauropsis, Bathypterois, Chlorophthalmus, Parasudis) have small flanges associated with the posterior neural and haemal spines (e.g., Parasudis, Fig. 22) or larger flanges that are confined to the proximal portion of the spine. In other aulopiforms, stomiiforms and myctophiforms examined, posterior neural and haemal spines are not modified.

Ventral ceratohyal cartilage (Figs. 10, 24). — In Pseudotrichonotus, like other synodontoids, the cartilage that separates the anterior and posterior ceratohyals continues anteriorly and posteriorly along the ventral margins. This cartilage extends only part way along the anterior ceratohyal, but often extends the entire length of the posterior ceratohyal to become continuous with the cartilage that typically caps its posterior end. Where present, the ventral ceratohyal cartilage serves as the site for articulation of the branchiostegal rays. In other aulopiforms (e.g., *Para-sudis*, Fig. 24C) and the outgroups, there usually is no cartilage along the ventral margin of the
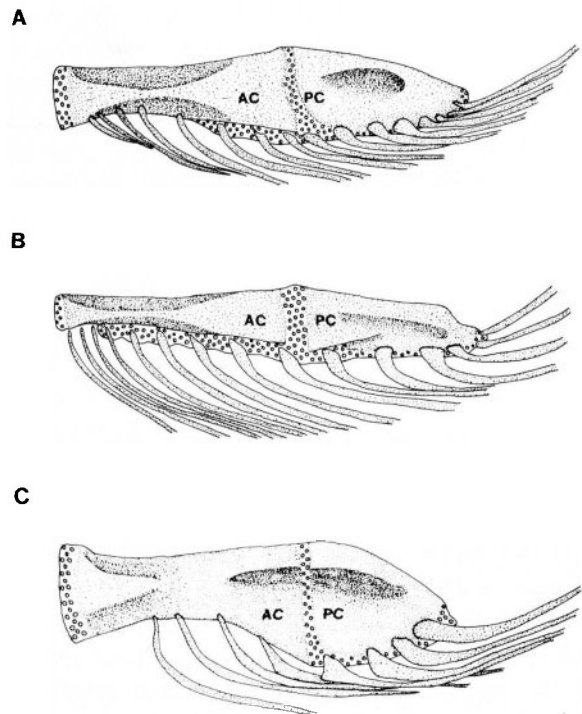
Fig. 24. Anterior and posterior ceratohyals of *A)* Aulopus filamentosus (USNM 292105, ca. 115 mm SL); B) *Synodus variegatus* (USNM 31518, 77.0 mm SL); C) *Parasudis truculentus* (USNM 159850, 84.5 mm SL).

anterior ceratohyal. In some myctophiforms, the ventral margin of the anterior ceratohyal is sometimes unossified, a condition superficially similar but not homologous to that of synodontoids, in which the ventral ceratohyal cartilage is autogenous.

Ventral displacement of the *first* one to three epineurals. — In Aulopus, synodontids, Pseudotrichonotus and most Saurida, the distal part of the first one to three epineurals is displaced ventrally to a position in or near the horizontal septum (Patterson and Johnson, 1995). Absence of this condition in myctophiforms and stomiiforms suggests it is derived within aulopiforms, where it occurs elsewhere (presumably independently) only in Chlorophthalmus. The anterior epineurals are secondarily unmodified in Harpadon.

Supraneurals expanded. — In aulopids, Pseudotrichonotus (Fig. 15), synodontids and Saurida, the slender central shaft of each supraneural is flanked by large laminar flanges, these being
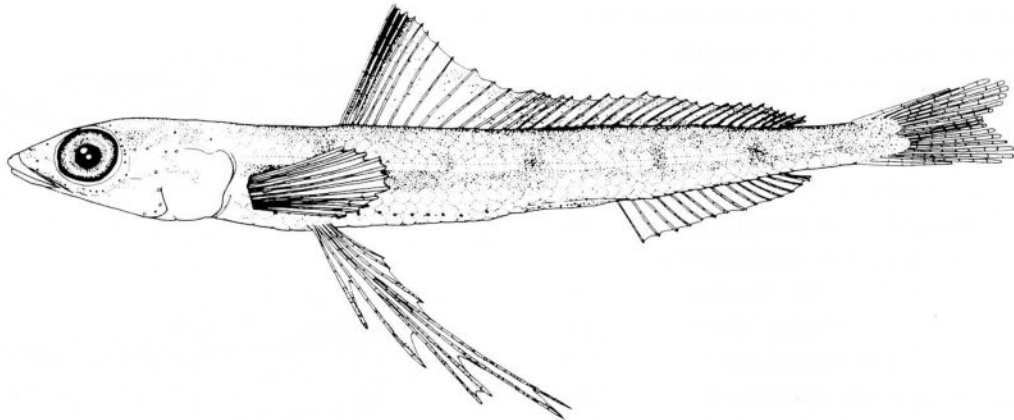
Fig. 25.   Juvenile specimen of *Pseudotrichonotus altivelis* **(***ZUMT* **59506, 24.6 mm SL).**

best developed on the first supraneural. Supraneurals of *Harpadon* are usually not expanded, although the anteriormost usually has a flange anterodorsally. In all synodontoids, at least some of the supraneurals are elongate and oriented more horizontally than vertically. They overlie (and sometimes articulate with) neural spines of three or more vertebrae. Although neither the presence of long, slender supraneurals nor their angle of orientation can be considered unequivocally synapomorphic for synodontoids (also present in some other aulopiforms, e.g., Omosudis, Ahliesaurus, Scopelosaurus), supraneurals with those features and with large flanges of bone are restricted to Aulopus, Pseudotrichonotus, *Synodus*, Trachinocephalus, and Saurida, and may be further evidence of the monophyly of the Synodontoidei.

Six or more branchiostegals on posterior *ceratohyal.* — Aulopids, synodontids and harpadontids have six or more (6–8 in Aulopus, *Synodus*, Saurida, Trachinocephalus; 13 in Harpadon) branchiostegals on the posterior ceratohyal. All outgroups and other aulopiforms have five or fewer, usually two or four. R. K. Johnson (1982) considered the high number of branchiostegals on the posterior ceratohyal in synodontoids as primitive for inioms, and hypothesized independent reductions of branchiostegals in his alepisauroid and chlorophthalmoid+myctophoid lineages. However, the presence of four or fewer branchiostegals on the posterior ceratohyal in stomiiforms (including

Diplophos) and all myctophiforms suggests that this is the primitive condition for aulopiforms and that the higher number in synodontoids is derived. Resolution of relationships among aulopiforms is needed to test this hypothesis. The presence of only two branchiostegals on the posterior ceratohyal in Pseudotrichonotus is a reversal.

Pseudotrichonotidae + Synodontidae + Harpadontidae

Absence of fourth phayngobranchial toothplate. — Johnson (1992) discussed the homology of the fourth and fifth upper pharyngeal toothplates among neoteleosts, and argued that loss of UP5 is a synapomorphy of ctenosquamates. Many nonctenosquamates, including most aulopiforms, have both UP4 and UP5 (e.g., Aulopus, see Rosen, 1973: fig. 4), but *Pseudotri*chonotus (Fig. 13), *Synodus*, Trachinocephalus (see Johnson, 1992: fig. 7), Saurida and *Harpa*don have only UP5. Because UP4 is also lacking in stomiiforms, strict polarity of this character for the Aulopiformes is equivocal. Nonetheless, the presence of UP4 in all other aulopiforms (except Anotopterus and Bathymicrops) and all ctenosquamates suggests that UP4 has been lost independently in stomiiforms and within the Synodontoidei.

Peritoneal pigment. — There is considerable diversity among aulopiform larvae in patterns of peritoneal pigmentation and the fate of that pig-

ment ontogenetically (Gibbs, 1959; Okiyama, 1974, 1984; Moser and Ahlstrom, 1974; R. K. Johnson, 1974, 1982, 1984a, 1984b; Cressey, 1981; Ahlstrom et al., 1984; Kawaguchi and Moser, 1984; Moser et al., 1984; Hartel and Stiassny, 1986). Synodontids and harpadontids have pairs of peritoneal pigment spots (two to about 12, the number increasing ontogenetically, at least in Saurida—Okiyama, 1974) that are retained in adults as tiny, dense discs of pigment (Gibbs, 1959; Cressey, 1981). Larvae of Pseudotrichonotus are unknown, but in a 24.6-mm SL juvenile specimen (ZUMT 59506) 12 small but distinct pairs of peritoneal pigment spots are visible through the translucent body wall (Fig. 25). In adults, tiny pigment discs like those of synodontids and harpadontids are present on the inner wall of the abdominal cavity. The unique presence of paired peritoneal pigment spots in larvae and adults is a synapomorphy of Pseudotrichonotus, synodontids and harpadontids.

Abrupt transition between epipleurals in and beneath the horizontal septum (see Patterson and Johnson, 1995). — In Pseudotrichonotus, *Synodus*, and Trachinocephalus, the point where the anterior epipleurals leave their dorsally displaced position in the horizontal septum is marked by an abrupt transition. The posteriormost epipleural in the horizontal septum is stout, directed posterolaterally, and closely associated with the epicentral ligament of the same vertebra. The next (posterior) epipleural is slender, directed ventrolaterally, and not associated with the free epicentral ligament lying above it. Many other aulopiforms (including *Harpadon* and *Saurida*) have anterior epipleurals displaced dorsally into the horizontal septum, but in those taxa, the transition between epipleurals in and beneath the horizontal septum is gradual. We interpret the condition in harpadontids as a reversal.

Sixth hypural usually lacking. — Six hypurals are present in the outgroups and most aulopiforms, including Aulopus, but Pseudotrichonotus, Harpadon, Trachinocephalus, and some species of *Synodus* have only five. Saurida has six. We agree with R. K. Johnson (1982) that it is the small, sixth hypural that is missing in syn-

odontoids. The sixth hypural is also lacking in Anotopterus, Omosudis and Alepisaurus, and a parsimony analysis is necessary to test the homology of the loss in synodontoids. Five hypurals also are present in some paralepidids, but in those taxa, the reduction appears to be the result of fusion of the first and second hypural (R. K. Johnson, 1982).

Synodontidae + Harpadontidae

Modified suspensorium, including quadrate with produced anterior limb and two distinct cartilaginous condyles. — In Aulopus (Sulak, 1977: fig. 3A) and most aulopiforms, the quadrate is fan-shaped and articulates with the metapterygoid and endopterygoid through a large cartilage that borders the dorsal and anterodorsal margins (anterior to the symplectic incisure). Additionally, the metapterygoid typically overlies the quadrate and does not extend anteriorly over the ectopterygoid. The endopterygoid overlies the ectopterygoid and terminates posteriorly on the medial surface of the anterior portion of the metapterygoid, directly above the quadrate (as in Bathysaurus, Fig. 29).

In Saurida (Fig. 26), *Harpadon* (Fig. 27), Synodus (Fig. 28) and Trachinocephalus, the anterior portion of the quadrate is produced into a long, slender limb with a small cartilaginous cap for articulation with the metapterygoid and endopterygoid (synchondrally) and ectopterygoid (by connective tissue). This limb is illustrated in *Synodus* by Sulak (1977: fig. 5B) and also in Saurida and *Harpadon* (Sulak, 1977: fig. 3B,C), although in the harpadontids it is incorrectly labelled the ectopterygoid (suspensorium of harpadontids is discussed in more detail below). On the posterior side of the main body of the quadrate (anterior to the symplectic incisure), the quadrate has another discrete, cartilage-tipped condyle—for articulation with a similar condyle on the posteroventral corner of the metapterygoid in harpadontids (Figs. 26 and 27), and with the tip of the ventral limb of the hyomandibula in synodontids (Fig. 28).

In both harpadontids and synodontids, then, the shape of the quadrate is modified by the presence of a produced anterior limb. Other
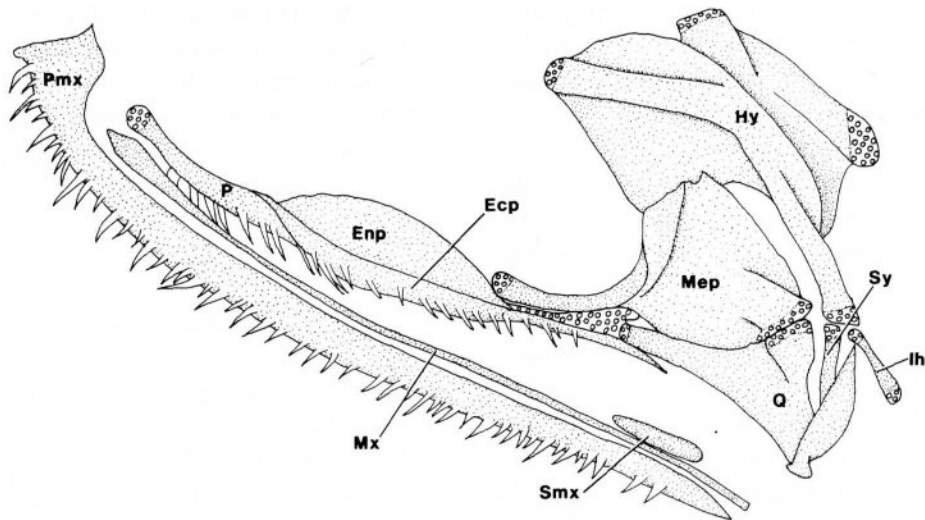
Fig. 26. Jaws and suspensorium of *Saurida undosquamous* (USNM 325180, 45.0 mm SL).
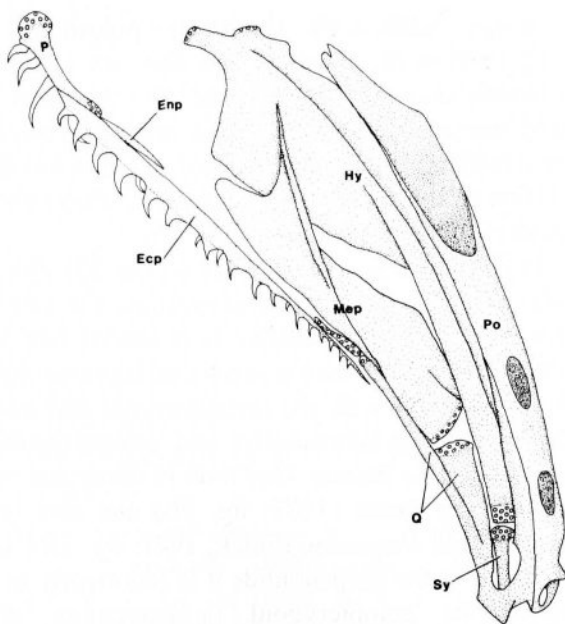

Fig. 27. Suspensorium of *Harpadon nehereus* (FMNH 179018, 96.0 mm SL).

modifications of synodontid and harpadontid suspensoria include having the metapterygoid produced anteriorly, well over the posterior part of the ectopterygoid (Figs. 26–28). The endopterygoid is thus displaced anteriorly, so that no part of it overlies the quadrate.

Synodus and *Trachinocephalus* are uniquely modified in having a large concavity in the dor-

sal margin of the quadrate between the anterior and posterior cartilaginous condyles (Fig. 28). The posterior condyle articulates with the hyomandibula, the ventral cartilaginous head of the latter thus serving as the site of articulation of three bones (interhyal, symplectic and quadrate) rather than two (interhyal and symplectic).

Separation of the quadrate cartilage into two discrete cartilaginous condyles occurs elsewhere among aulopiforms and the outgroups examined only in *Ahliesaurus* and *Scopelosaurus*. However, in those taxa, the quadrate is still fan-shaped because it lacks the produced anterior limb that characterizes synodontids and harpadontids. Furthermore, as in other aulopiforms, the metapterygoid is not produced anteriorly, and the ectopterygoid overlies a portion of the quadrate.

The unique complex of suspensorial modifications in synodontids and harpadontids is evidence of their close relationship. Relationships of *Ahliesaurus* and *Scopelosaurus* within the Aulopiforms are uncertain, and will be addressed in another paper (Baldwin and Johnson, in press).

Maxilla reduced. — In most aulopiforms and the outgroups, the maxilla is a long bone that originates near the proximal portion of the premaxilla, parallels that bone for its entire length, and terminates slightly (aulopiforms and
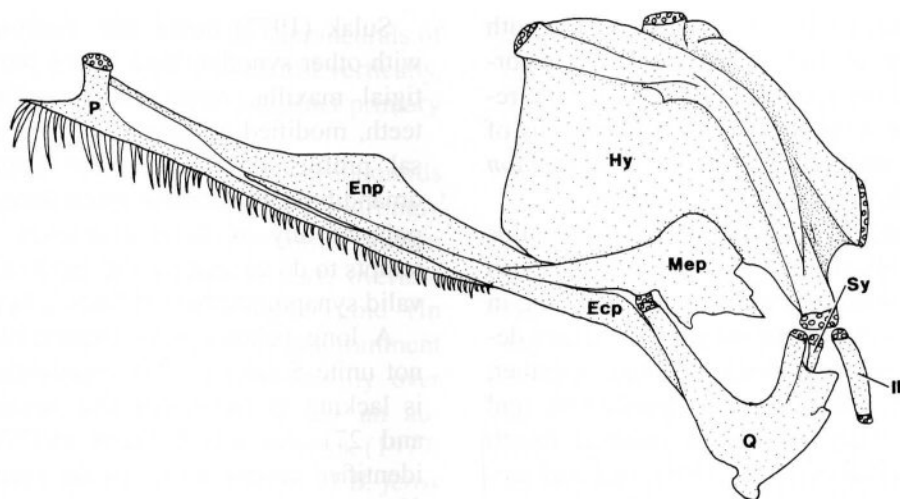
Fig. 28. Suspensorium of *Synodus* variegatus (USNM 315318, 77.0 mm SL).
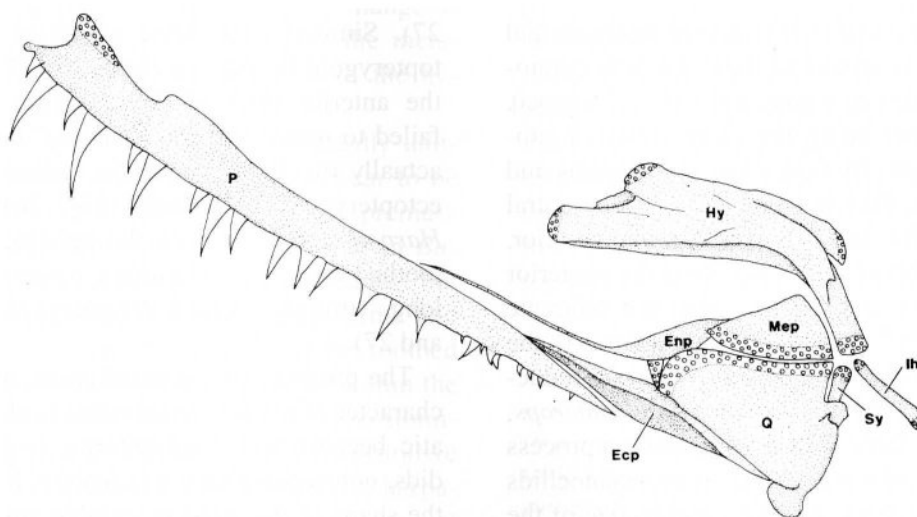

Fig. 29. Suspensorium of *Bathysaurus mollis* (VIMS 6107, 190 mm SL).

ctenosquamates) or greatly (stomiiforms) beyond its distal tip; the maxilla is usually deepest posteriorly (e.g., Sulak, 1977; Fink and Weitzman, 1982). The maxilla is not modified in *Aulopus* or Pseudotrichonotus, but it is reduced in all other synodontoids. In *Synodus* (see Sulak, 1977: fig. 5B) and Trachinocephalus, the maxilla extends along the entire length of the premaxilla, but it is very slender and does not deepen posteriorly. Sulak (1977: fig. 3) described and illustrated a unique separation of the maxilla into anterior and posterior portions in Saurida and Harpadon. However, in all specimens of Saurida we examined (including larvae, juveniles and adults, e.g., Fig. 26), the maxilla is extremely slender (and thus often damaged in cleared and stained material), but it remains intact from its origin near the proximal end of the premaxilla to its terminus, just posterior to the distal extreme of the premaxilla.

In Harpadon, the maxilla is reduced to a tiny vestige, labelled "posterior maxilla" by Sulak (1977:fig. 3). The remaining portion of the maxilla is absent, and the bone labelled "anterior maxilla" by Sulak (1977) is the palatine (Fig. 27), as evidenced by the presence of teeth (lacking on the maxilla in adults of all other aulopiforms), cartilage at both ends of the bone (the

maxilla is a dermal bone), and articulation with the ectopterygoid (which Sulak, 1977, incorrectly labelled the palatine). We consider the reduction in size of the maxilla a synapomorphy of harpadontids and synodontids, with *Harpadon* representing the most derived condition.

Modifications of gill arches. — Harpadontids and synodontids share a number of features in the branchial skeleton that are usually lacking in other aulopiforms and the outgroups. All are derived within the Synodontoidei and, together, suggest a common origin for synodontids and harpadontids. They include: a reduced fourth pharyngobranchial cartilage (PB4); first and second hypobranchials (HB1 and HB2) with ventrally directed processes; fourth ceratobranchial (CB4) bearing a process directed toward the third ceratobranchial (CB3); fourth basibranchial cartilage (BB4) separated from the fifth ceratobranchials (CB5) by a gap; and CB5 "v" shaped, the medial limb being the more robust, toothbearing segment. In most other aulopiforms and the outgroups, PB4 is large; HB2 lacks ventral processes; CB4 lacks processes; the anterior, cartilaginous tip of each CB5 abuts the posterior margin of BB4; and CB5 is either not bifurcate or, if "v" or "y" shaped, the lateral limb is the more substantial. Homoplasies include a reduction or loss of PB4 in *Ipnops* and *Bathymicrops*, respectively; a large PB4 in Harpadon; a process on CB4 directed toward CB3 in evermannellids and Macroparalepis; and the variable size of the gap between BB4 and CB5 in synodontids and harpadontids, usually being much larger in the latter.

Comments on *Bathysaurus*

Sulak's (1977) interpretation of aulopiform suspensoria, in part led him to hypothesize a close relationship between Bathysaurus, *Synodus*, *Trachinocephalus*, *Harpadon* and Saurida (his Synodontidae). He cited numerous osteological differences between Bathysaurus and his other synodontids, but concluded, based primarily on features of the jaws and suspensorium, that Bathysaurus is "a very basal and rather distinct entity within the Synodontidae."

Sulak (1977) noted that Bathysaurus shares with other synodontids a strong premaxilla, vestigial maxilla, long palatine with depressible teeth, modified gillrakers, pointed snout in dorsal profile, three large supraneurals and hyomandibula with anteroventral flange. He did not polarize any of those characters, and our attempts to do so suggest that most of them are not valid synapomorphies of Sulak's Synodontidae.

A long palatine with depressible teeth does not unite Sulak's (1977) synodontids because it is lacking in *Harpadon* and Saurida (Figs. 26 and 27). As noted, Sulak (1977) incorrectly identified several bones of the suspensorium of Harpadon: his anterior maxilla, palatine and ectopterygoid are the palatine, ectopterygoid and anterior limb of the quadrate, respectively (Fig. 27). Similarly, the bone identified as the ectopterygoid in Saurida (Sulak, 1977: fig. 3B) is the anterior limb of the quadrate, and Sulak failed to notice that the "palatine" of Saurida is actually two bones, a palatine anteriorly and an ectopterygoid posteriorly (Fig. 26). Thus, in *Harpadon* and Saurida, the palatine is a short, toothed bone that articulates posteriorly with a long, strongly toothed ectopterygoid (Figs. 26 and 27).

The presence of a pointed snout as a unifying character of Sulak's synodontids is also problematic because many aulopiforms (e.g., paralepidids, notosudids) have this feature. Furthermore, the shape of the snout is variable among species of *Synodus*, and in *Trachinocephalus* it is distinctly round.

The presence of three supraneurals is not a synapomorphy of Sulak's synodontids because it is characteristic of *Aulopus*, at least some other aulopiforms (e.g., scopelarchids), and is the primitive ctenosquamate condition (present in myctophids). Sulak (1977) described the supraneurals of his synodontids as "large," but the configuration of the supraneurals of the Synodontoidei is distinct from that of most other aulopiforms, including Bathysaurus. In synodontoids, each supraneural has a narrow primary shaft with broad laminar expansions on one or both sides. Most of them are long, almost horizontally oriented bones that extend over several vertebrae (e.g., the first supraneural of

Pseudotrichonotus, Fig. 15). The supraneurals of Bathysaurus are short, oriented almost vertically, and have a wide body without a distinct primary shaft.

Harpadontids (Figs. 26 and 27), synodontids and Pseudotrichonotus (Fig. 6) have a strongly developed flange on the anteroventral portion of the hyomandibula that is, in part, overlain by the dorsal portion of the metapterygoid. (In *Harpadon* and Saurida, there is a prominent metapterygoid strut that extends dorsally over the hyomandibular flange, presumably an autapomorphy of the Harpadontidae.) Sulak (1977: fig. 5A) illustrated the suspensorium of B. ferox with a prominent anteroventral hyomandibular flange that is overlain ventrally by the metapterygoid; however, a hyomandibular flange is completely lacking in B. *mollis*, and the metapterygoid does not overlap any part of the hyomandibula (Fig. 29).

Three of Sulak's characters purportedly uniting Bathysaurus and synodontoids appear to be derived within the Aulopiformes. The premaxilla is strongly fortified with large teeth in *Bathysaurus*, synodontids and harpadontids, but more weakly toothed in other aulopiforms and myctophiforms. However, a strongly toothed premaxilla has arisen numerous times within the Eurypterygii and is characteristic of some stomiiforms, including the cladistically primitive *Diplophos*. Bathysaurus, synodontids and harpadontids also share gill rakers in the form of clusters of small teeth, but reduction or loss of gill rakers is common among aulopiforms, small patches of teeth similar to those of Sulak's synodontids occurring in scopelarchids, evermannellids, paralepidids, alepisaurids, and omosudids. Sulak's third character, presence of a vestigial maxilla, occurs among aulopiforms only in *Harpadon* and Bathysaurus. However, in Harpadon, the anterior part of the maxilla has been lost, whereas the posterior portion is missing in Bathysaurus, and as noted above, all synodontids and harpadontids have a reduced maxilla.

Patterson and Johnson (1995) proposed a close relationship between Bathysaurus and Gigantura based on evidence from the intermuscular elements, and this is corroborated by similarities in the jaws and suspensorium. The homology of the

vestigial maxilla, strongly toothed premaxilla and reduced gill rakers of Bathysaurus and at least some synodontoids are examined in the context of other characters in a more comprehensive analysis of aulopiform phylogeny (Baldwin and Johnson, in press). For now, we note that in addition to sharing only questionably homologous features with some synodontoids, Bathysaurus lacks all diagnostic characters of the Synodontoidei and the clade comprising Pseudotrichonotidae + Synodontidae + Harpadontidae described in the preceding sections: the peculiar proximal segmentation of principal caudal-fin rays, expanded neural and haemal spines on posterior vertebrae, cartilage on the ventral surface of the anterior ceratohyal, ventrally displaced anterior epineurals, six or more branchiostegals on the posterior ceratohyal, paired peritoneal pigment spots in larvae and an abrupt transition between epipleurals in and beneath the horizontal septum. Unlike synodontoids, Bathysaurus has free median caudal cartilages and UP4. We conclude that the affinities of Bathysaurus lie outside of the Synodontoidei.

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