DEVELOPMENTAL OSTEOLOGY OF THE LINED SOLE, *ACHIRUS LINEATUS* (PISCES: SOLEIDAE)

Charles R. Futch[1], Robert W. Topp[1], and Edward D. Houde[2]

ABSTRACT

Developmental osteology of the lined sole, *Achirus lineatus*, based on a study of 17 specimens, is described and figured. Chronology of osteological development is documented. Study material, ranging from 2.14 to 93.0 mm SL, included cleared and stained specimens, and disarticulated skeletons.

The adult skull is markedly asymmetrical in the olfactory, orbital, and oromandibular regions, with fusion of ethmoid, lateral ethmoid, and prefrontal components. Although mandibular dentition is restricted to left maxillary and dentary, adult asymmetry is less pronounced in the branchiocranium, as well as the posterior elements of the neurocranium. Branchial arches are typically perciform in composition and arrangement. Otoliths are unsculptured, with no annuli apparent.

Paired neural elements of the atlas are autogenous and do not meet dorsomesially. The second neural spine joins the supraoccipital. Parapophyses first join ventromesially on the fifth trunk vertebra. The three posterior vertebrae are involved in caudal fin support. The hemal spine of the penultimate vertebra is autogenous. The two anteriormost dorsal fin rays are supported by a single pterygiophore. The first five pterygiophores are accommodated by notches in the supraoccipital crest. A right pectoral fin is present, having four to six small rays without bony connection to the cleithrum. A single five-rayed pelvic fin is supported by paired basipterygia.

A. lineatus closely resembles the eastern Atlantic genus *Solea* in most details of its neurocranium, trunk vertebrae and caudal skeleton. *Achirus* differs by absence of a lacrymal, greater symmetry of jaw elements, smaller number of caudal vertebrae, and lack of strong lateral apophyses.

In a series of alizarin-stained larval stages, a cumulative sequence of osteological events is documented: 2.14 mm SL—syncranial elements, neural spines, and cleithral elements present, including large postcleithrum; 2.52 mm SL—appearance of autosphenotic, full branchiostegal complement, distinct arcualia, parapophyses, hemal spines, primordial caudal skeleton, and anterior dorsal lepidotrichs; 3.20 mm SL—proliferation of vertical fin rays; 3.57 mm SL—appearance of bones of olfactory region, full vertebral complement, remaining caudal eleemnts, pelvic girdle and fin, and disappearance of postcleithra; 12 to 14 mm SL—all bony elements present, and in approximate adult configuration.

INTRODUCTION

Most osteological studies on the Pleuronectiformes have dealt with syncranial asymmetry, (e.g., Kyle, 1921; Gregory, 1933; and Chabanaud, 1936). Norman (1934) and Berg (1940) offered general comments on osteology, Ford (1937) discussed the axial skeleton of selected taxa, and Yazdani (1969) compared jaw morphology and function. A brief description and comparison of osteological features of the young of three species of *Paralichthys* (Bothidae) by Woolcott et al. (1968) is the only known descriptive work on the complete flatfish skeleton.

The following description of developmental and adult osteology of *Achirus lineatus* (Linnaeus) was done in conjunction with a study by Houde et al. (1970), who described development of larval stages of *A. lineatus*, and compared morphology of larvae and juveniles from Tampa Bay, Florida, with a series reared in the laboratory.

ACKNOWLEDGMENTS

MATERIALS AND METHODS

Basic nomenclatural synonymy of the skeleton follows Topp and Cole (1968). Articulatory processes of jaw elements follow Yazdani (1969); caudal fin elements follow Monod (1968) and Gosline (1961). Museum prefixes are FSBC (Florida Department of Natural Resources Marine Research Laboratory) and TABL (Tropical Atlantic Biological Laboratory).

Osteology of the adult *Achirus lineatus* was described from three intact cleared and stained skeletons, FSBC 5967, 10.3 mm SL, FSBC 5968, 76.5 mm SL, and FSBC 5969, 14.0 mm SL, from Tampa Bay. Three complete skeletons, FSBC 5969, 10.2 mm SL, Tampa Bay, and FSBC 4362, 92.0 mm SL and 93.0 mm SL, Ponce de Leon Inlet, Volusia County, Florida, were stained with alizarin and disarticulated following the modification of Ossian (1970). Developmental osteology was described from laboratory reared and Tampa Bay larvae. Laboratory material included specimens numbered 26, 3.73 mm SL; 40, 3.31 mm SL; and 42, 5.11 mm SL (uncatalogued. TABL). Tampa Bay material included FSBC 5850L, 3.20 mm SL; FSBC 5868L, 2.14 mm SL; FSBC 5860L, 3.57 mm SL; FSBC 5880L, 2.52 mm SL; FSBC 5883L, 3.35 mm SL; FSBC 5914L, 3.30 mm SL; FSBC 5920L, 3.40 mm SL; and FSBC 5967L, 8.0 mm SL. All skeletons were cleared and stained by the methods of Hollister (1934) and Taylor (1967).

DESCRIPTION

NEUROCRANIUM

Olfactory Region: (Figs. 1A, 1B, 1C, 1D, 2, and 11)

The olfactory region of adult *A. lineatus* is characterized by marked asymmetry and fusion of prefrontal and ethmoid components, forming the right prefrontal complex (rpfc). The right lateral ethmoid (rle) is a small hourglass-shaped bone forming the dorsal, right, and ventral walls of the right olfactory foramen (rof). Ventrally, its base covers part of the prevomer-parasphenoid

suture. A small ventrolateral shelf provides a point of articulation for the right autopalatine. Dorsally, a wide trapezoidal roof fits into a depression in the right prefrontal complex. The latter forms the lateral and anterior walls of the orbit and forms a rostral projection. A boot-shaped element, inseparably fused to the right prefrontal complex, is directed ventrad to the parasphenoid. Its cancellous structure and relative position identify it as the ethmoid component.

The small, tubular autogenous nasals (n), osseous extensions of the supra-orbital laterosensory canal, are imbedded in the snout musculature.

The left prefrontal, left lateral ethmoid, and the ethmoid contribute to the left prefrontal complex (lpfc). The left olfactory foramen (lof) is bounded by eth-moid and left lateral ethmoid components. A large cylindrical shaft of the pre-frontal component joins ventrally with the lateral ethmoid component, forming a median foramen. Posteriorly, the left prefrontal complex is joined by suture to an extension of the left frontal. Laterally, the ventral face of the left prefrontal articulates with the left autopalatine. The base of the left prefrontal is a long triangular element fitting into a deep depression of the parasphenoid.

The median, edentulous prevomer (pv) has a triangular base fitting into a groove in the parasphenoid. Dorsally, it is flexed toward the right side, and pos-teriorly, it joins the left and right prefrontal complexes.

Bones of the olfactory region do not appear until metamorphosis begins. All elements except nasals are present in specimens about 3.3 to 3.5 mm SL (Fig. 10), when the left eye has begun migration. Prefrontal complexes and right lat-eral ethmoid first appear midway between the frontals and parasphenoid. They join to the frontals, then grow ventrad toward the parasphenoid and prevomer. The right nasal appears in larvae at about 5 mm SL, the left shortly thereafter.

Orbital Region (Figs. 1A, 1B, 2, and 11)

Skull asymmetry is pronounced in this region. The right (lower) eye is not enclosed in a bony orbit, but is held in place by muscles, and partially supported by the underlying palatoquadrate arch. The left (upper) eye rests in a large com-posite ring of bone, the orbit. The orbit is atypical in lacking the bony ring of suborbital bones characteristic of most teleosts.

Anteriorly, the broad lateral edge of the left frontal (lf) joins the left pre-frontal complex to comprise the left wall of the orbit. Both left and right prefront-als (lf and rf) contribute to the remainder of the poseterior orbital walls. The right prefrontal complex completes the right wall of the orbit.

The frontals are almost completely separated dorsally by the supraoccipital. The left frontal contributes a mid-dorsal ridge contiguous with the supraoccipital crest.

Each frontal bears a dorsolateral ridge continuous with the corresponding par-ietal ridges. On each frontal, a strongly ossified housing for the laterosensory canal ends in an anterodorsally extended tubule.

The asymmetric pterosphenoids (pts), arising from two centers of ossification, extend from the frontals to the parasphenoid. A triangular projection descends from each frontal from the posterior aspect of the orbit. These curve to mesial symphysis, and extend ventrad to meet ascending trapezoidal members from the

parasphenoid. Dorsal and ventral elements are bordered posteriorly by the auto-sphenotics. The left dorsal element sends a small process dorsad to contact an anteroventral alar process of the autosphenotic. No such connection exists on the right side, although there are vestigial processes on the pterosphenoid and auto-sphenotic.

In 2.14 mm SL larvae, the frontal is the most conspicuous orbital bone. It dom-inates the neurocranium, forming a dorsal hump. Each has an "eyebrow" shaped spinous epidermal ridge, later to become bony coverings for the laterosensory canal system. At about 2 mm SL (Fig. 7), before eye migration, the frontals be-come asymmetric. The anterior portion of the right frontal epidermal ridge lengthens and becomes the interorbital "bony ridge" (Jordan and Evermann, 1898). This asymmetry was ascertained by comparison of measurements of the bony ridges and counts of associated spines of both frontals. At metamorphosis (Fig. 9) both frontals are displaced to the right side. The right epidermal ridge is much longer than its left counterpart. Formation of the orbit by suture of frontals with prefrontal complexes was complete in a specimen 8 mm SL.

Dorsal components of the pterosphenoids appear midway between the para-sphenoid and the posterior aspect of the orbit in larvae between 6 and 8 mm SL. Union of dorsal and ventral components with the frontals and parasphenoid was complete in a 14 mm specimen.

Otic and Basicranial Region: (Figs. 1A, 1B, 1D, 2, 11)

The asymmetric autosphenotics (aso) are ovate bones poterior to the ptero-sphenoids. Each sends a process ventrad. In typical teleosts, this process supports the dermosphenotic, the dorsalmost of the suborbital ossicles. Dorsoposteriorly, the dorsalmost of the suborbital ossicles. Dorsoposteriorly, the autosphenotic joins the autopterotic, and posteroventrally it joins the prootic, with which it shares the hemispherical anterior hyomandibular fossa.

The autopterotic (pto) are roughly hatchet shaped with the "handle" pointed anterodorsad. Posteriorly, they join with each prootic just below the deep poster-ior hyomandibular fossa.

The prootics (pro) are the largest bones of the otic series. They are pierced by anteriorly directed carotid foramina along their junction with the parasphenoid. Anterdorsally, the prootic forms half of the anterior hyomandibular fossa at its junction with the autosphenotic. The left prootic sends an anterior strut mediad to brace the pterosphenoid. A small projection is present on the right prootic but does not touch the pterosphenoid. The prootic contains the trigeminofacialis cham-ber, as discussed by Goodrich (1958). Although location of nerves and blood ves-sels was not examined in detail, the trigeminofacialis chamber of *A. lineatus* presumably conforms in structure to that of most perciform fish, as described and figured by Patterson (1964).

The posterior portion of each prootic contributes to encapsulation of the oto-liths. Each otolith is oval, the margin unsculptured by rostrum or antirostrum. The surface contacting the concave inner surface of the prootic and basioccipital is convex, the inner surface is flat. Sulci are only slightly visible and no annuli are obvious.

The epiotics (epo) form the dorsoposterior corners of the braincase. The two dorsolateral skull ridges extend from the frontals to the parietals and terminate abruptly at the dorsoposterior corners of the skull. The right epiotic is the ultimate dorsoposterior bone on the right side. The dorsal margin of the left epiotic is capped by a projection of the left parietal. Each epiotic presents a posterolateral facet for articulation with the posttemporal.

The opisthotics (opo) are small bony wedges between the autopterotic, exoccipital, and basioccipital. The left opisthotic features a short projection bracing the lower portion of the postemporal.

The exoccipitals (exo) contain the foramen magnum. From rear view, each exoccipital presents a triangular facet which, with the basioccipital, forms the tricondylar articulation with the atlas. One pair of ventrally directed formamina afford passage of the tenth cranial (vagus) nerve. This nerve exits through the exoccipital in all flatfish families examined by Chabanaud (1936).

The supraoccipital (soc) has a low median crest with five serrations articulating with bases of the first five dorsal pterygiophores.

The parietals (p) contact the frontals, supraoccipital, epiotics, and autopterotics. A small finger of the left parietal forms a dorsal cap over the left epiotic.

The small posttemporals (pt) connect the pectoral girdle to the skull. The uppermost portion of each rests on a flat lateroventral surface of the epiotic. The left postemporal is further braced by a projection from the episthotic. Medially, the posttemporal articulates with the supracleithrum on an expanded face.

The anteriormost of the two elements of each lateral extrascapular (les) is a tripartite ossicle serving as the junction of the temporal, supratemporal, and posttemporal sensory canals. The anterior element of the left extrascapular is not as well developed as its right counterpart. The symmetric posterior elements are fused to the posttemporals.

The basioccipital (boc) comprises the posteroventral portion of the cranium, the basal articulation of the atlas to skull, and the posteroventral wall of the auditory capsule. The suture of the basioccipital with the prootic along the parasphenoid is incomplete; a triangular piece of cartilage intervenes.

The parasphenoid (pas) is a large laterally compressed bone, traversing the length of the skull, bridging otic and olfactory regions. Anterior to its suture with the prevomer, a deep groove receives a projection of the left prefrontal complex.

In premetamorphosing larvae (Fig. 7), the parietals, autopterotics, epiotics, and posttemporals are visible. Each parietal bears a small bony ridge with either one or two spines. The autopterotics are small oval bones with a prominent knob on the center of each bone. The epiotics are vaguely discernible in the dorsoposterior aspect of the braincase. The posttemporals are tiny fusiform bones, each bearing a single spine. The basioccipital is a conical projection contiguous with the notochord, overlapping the filiform parasphenoid which extends to the olfactory region.

The autosphenotics first appear in a 2.5 mm SL larva (Fig. 8). The parietals have enlarged, and the bony ridge becomes located farther dorsad. The remaining bones of the otic and basicranial region are essentially the same as those in the 2.14 mm specimen of Fig. 7.
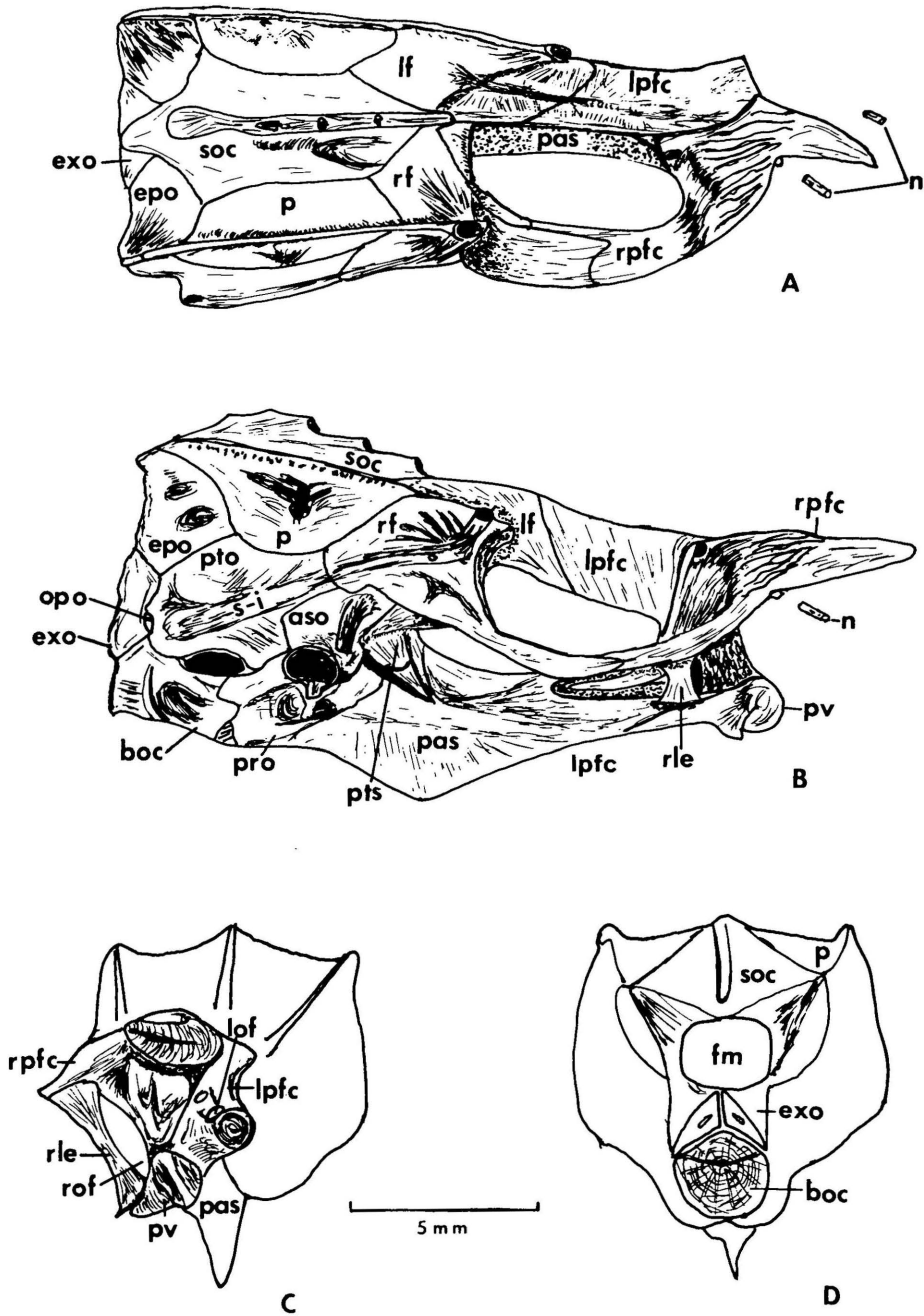
FIG. 1. Neurocranium. A, dorsal view; B, lateral view; C, anterior view; D, posterior view. Drawn from 92 mm SL specimen (FSBC 4362).

At 3.2 mm SL (Fig. 9), when eye migration has begun, all bones of the otic series are more clearly visible. The small knobs of the autopterotics become spinous bony ridges, later forming bony housings over the supratemporal-intertemporal laterosensory system. These elements are here designated the supratemporal-intertemporals, although the homology has not been demonstrated beyond question. The prootics appear posteroventral to the autopterotics. The walls of the basioccipital enclosing the auditory capsule begin to ossify. Throughout development, the parasphenoid lengthens and deepens in the sagittal plane. It becomes curved and deflected toward the right (ocular) side.

In 5 mm SL larvae, all bones of the otic region are easily distinguished, although not all are completely ossified or in obvious contact with neighboring bones. The tenth cranial nerve foramen appears at this stage. The supraoccipital becomes visible in profile as a small sliver of bone above the parietals. Although anterior dorsal pterygiophores are present, supporting serrations of the supraoccipital crest have not developed in larvae of this size.

All bones of the otic and basicranial region except the prootics had attained adult form in a 14 mm juvenile. The prootics continue to ossify anteriad toward, but never reaching, the pterosphenoids, thus forming foramina for the jugular and orbital arteries.

Some comparisons between neurocrania of *A. lineatus* and the genus *Solea* are possible. Chabanaud (1936) figured the orbital and olfactory regions of *Achirus* and *Solea*. Synonymy of Chabanaud's terms with those presented herein are as follows: ME = right prefrontal complex; PEZ = right lateral ethmoid; PEN = left prefrontal complex; FZ = right frontal; FN = left frontal; SPZ = right autosphenotic; SPN = left autosphenotic; SO = supraoccipital; and V = prevomer. *Solea* apparently has fusion of prefrontal and lateral ethmoid elements similar to that of *A. lineatus*, thus indicating that orbits of each genus are composed of the same series of bones. The autosphenotics of *Solea* are larger than their counterparts in *Achirus*, and project anteriad into the orbital region. Paired asymmetric first infraorbitals (= lacrymals) are present in *Solea solea* (Yazdani, 1969) but not in *A. lineatus*.

Otoliths of *A. lineatus* are similar to those of *S. solea*, as described and figured by Schmidt (1968). Schmidt notes an otolith length-width-depth ratio for the otoliths of *S. solea* from three specimens, 180, 300, and 370 mm in length, as 1.00/0.86/0.27. The ratio for an otolith of a 92 mm specimen of *A. lineatus* was 1.00/0.66/0.27.

BRANCHIOCRANIUM

Oromandibular Region (Figs. 2, 3, and 11)

The premaxillaries (pm) are asymmetric. The right is edentulous and short, not excluding the maxillary from the gape. Its medial ascending process (as) is broadened anteriorly, forming a deep posteromedial depression which fits the right anterior surface of a median rostral cartilage. The small articular process (ar) fits a maxillary facet. The left premaxillary, heavily toothed with sharp villiform teeth, completely excludes the maxillary from the gape. The proximal

end of the medial ascending process caps the left anterior surface of the rostral cartilage. The distal end overlies this cartilage. The articular process is received by a shallow fossa in the maxillary. Distally, the premaxillary is broadened, with a small postmaxillary process (pp) near the articulation with the maxillary.

The right maxillary (mx) bears a large proximal cranial condyle (cc) articulating with the dextrally deflected head of the prevomer. A dorsal projection, the maxillary spike (mk) articulates with the right lateral surface of the rostral cartilage. A small lateral process, the "dorsal process" of Yazdani (1969), is directed anteriad toward the premaxillary. Distally, the maxillary curves ventrad to contact the coronoid process of the dentary. The left maxillary has three proximal processes, the dorsal cranial condyle (cc), the ventral premaxillary condyle (py), and the medial maxillary spike (mk). The cranial condyle articulates with the prevomer, the premaxillary condyle receives the articular process of the premaxillary, and the maxillary spike contacts the lateral surface of the rostral cartilage. A small dorsal facet receives the ventral projection of the autopalatine head. Distally, the maxillary has a broadened end which intercedes between the premaxillary and the coronoid process of the dentary and the anterodorsal arm of the angular.

The dentaries (d) meet in mesial symphysis. The right is edentulous. Its coronoid process articulates with the maxillary, and a large lateral knob probably prevents anterior displacement of the maxillary. A medial groove receives the anterior portion of the angular (a). A perforated bony tube houses the right mandibular laterosensory canal. The anterodorsal surface of the left dentary bears sharp villiform teeth. Posteriorly, the coronoid process curves dorsad. The maxillary contacts the coronoid process and the anterodorsal arm of the angular. Ventrally, small bony arches partially enclose the left mandibular laterosensory canal. The anterior portion of the right angular is recessed in the dentary. Posteriorly, a deep fossa receives the quadrate condyle. Ventrally, the mandibular sensory canal is partially enclosed in a bony sheath. The left angular is positioned like that of the right side, but is more heavily ossified. The anterodorsal arm of the angular contributes, with the coronoid process of the dentary, a connection with the premaxillary and maxillary. The mandibular branch of the laterosensory canal is only partially enclosed in a bony housing.

The coronomeckelians (unfigured) are small chip-like bones on medial surfaces of both angulars.

The retroarticulars (rar) cap the ventroposterior corners of the angulars.

The edentulous autopalatines (ap) are the anteriormost bones of the palatoquadrate arch. Posteriorly, they are connected to the ectopterygoids and endopterygoids, contributing to the palate. The right autopalatine curves dorsally beneath a shelf formed by the right lateral ethmoid, and is connected there by cartilage. There is no point of articulation with the maxillary. The left autopalatine sends one condyle anterodorsad, making a cartilaginous connection with the left prefrontal complex. An anteroventral condyle rests in a dorsal depression in the left maxillary.

The ectopterygoids (ecpt) curve dorsoanteriad from the anterior edge of the
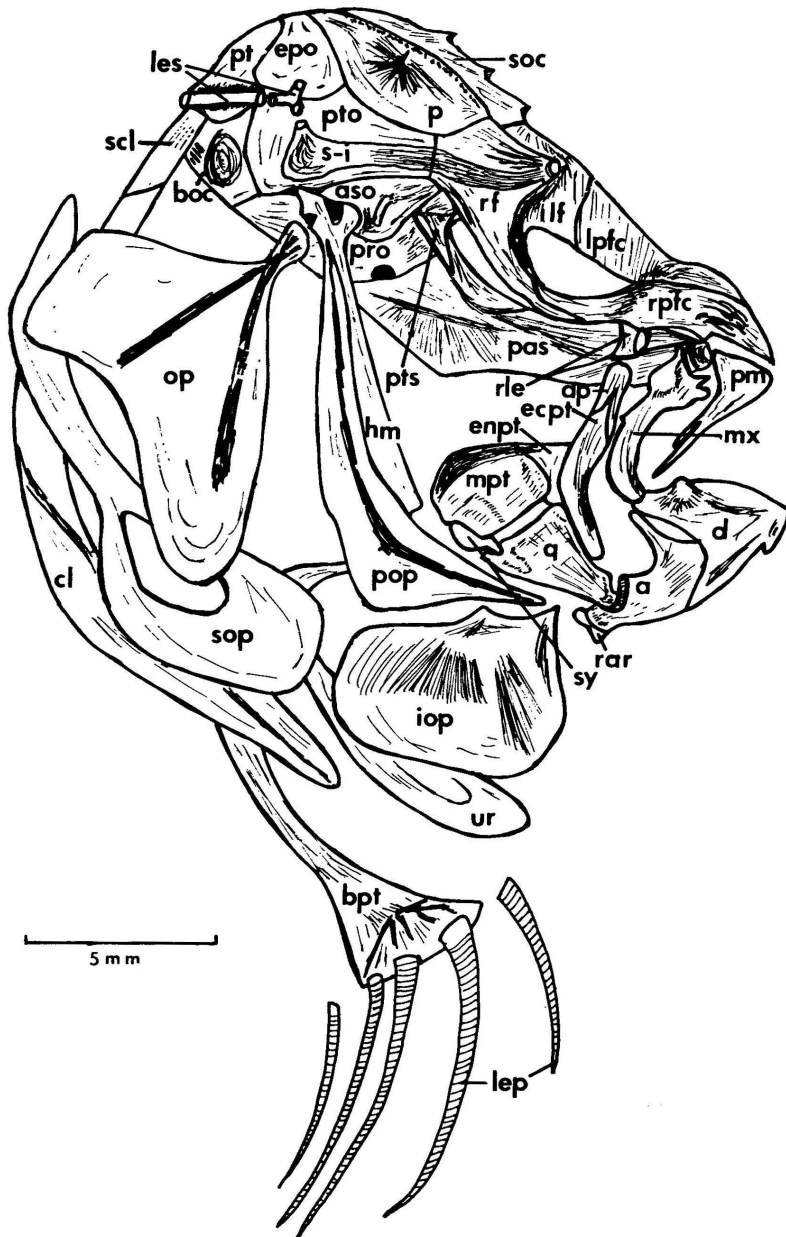
Fig. 2. Syncranium and appendicular skeleton. Drawn from 76.5 mm SL specimen (FSBC 5968).

quadrate to the autopalatines. The left ectopterygoid is longer than its right counterpart.

The endopterygoids (enpt) are roughly triangular. Their anterior margins are curved and sutured to the medial faces of the autopalatines and ectoptery-

goids. The posterior margins broadly join the anteromedial surfaces of the metapterygoids and quadrates. The dorsal margins are directed mediad, contributing to the palate.

The metapterygoids (mpt) overlap the endopterygoids anteriorly, and the symplectics posteriorly, each contributing to the palate.

The quadrates (q) are triangular in profile. The lower vertices broaden into strong transverse condyles articulating with the angulars. A deep medial groove accommodates the lower shaft of each symplectic. The dorsal margins do not contact the metapterygoids but are joined by connective tissue.

The dentaries and angulars are the most conspicuous bones of the oromandibular series in premetamorphosing larvae (Figs. 7 and 8). They appear as lamellae arising from the anteromesially joined rami of Meckel's cartilages. Posteriorly, each angular is curved, forming a fossa to receive the quadrate condyle. Ventrally, each dentary and angular bears several spinous epidermal ridges later to become bony coverings for laterosensory canals. The posterior ends of Meckel's cartilages bend ventrad, ending in the retroarticulars. The maxillaries are small filiform bones extending from the olfactory region to the coronoid processes of the dentaries.

In early metamorphosing larvae (Fig. 10) both premaxillaries are present, and are overlapped by lateral process of the maxillaries. In 5mm SL larvae, the now dentate left premaxillary completely excludes the maxillary from the gape. Jaw structures have attained adult form on fish of about 10 mm SL.

The quadrates are visible in premetamorphosing larvae (Figs. 7 and 8). Although ossification of the neurocranium and hyoid arch is incomplete, and bony neurocranial suspension is not effected, the cartilaginous connection between the quadrate, symplectic, and hyomandibular apparently offers sufficient resistance so that an adductor-abductor muscle system can effectively operate the jaws.

The pterygoid series and autopalatines appear when larvae are about 3 mm SL (Fig. 9). The ectopterygoids and autopalatines first appear as small curved filaments between the quadrates and the olfactory-oromandibular regions. They are always asymmetric; those of the left side are larger than those of the right. These bones, like those of the upper and lower jaws, attain adult form when fish are about 10 mm SL.

Morphology and function of the jaws of *Solea solea* and *Achirus fasciatus* (=*Trinectes maculatus*) were compared by Yazdani (1969). Lower jaws of both species and upper jaws of *S. solea* are capable of independent movement. In both, upper and lower jaws of the blind side are toothed, and are especially adapted to dislodge and consume polychaete worms, the major food item of both species. According to Yazdani (1969), the edentulous upper and lower jaws of the ocular side do not function in feeding, but open and close to allow respiratory current passage.

The jaws of *A. lineatus*, *T. maculatus*, and *S. solea* are similar although the "dorsal process" (actually a lateral process) of the maxillaries overlies the premaxillaries in *S. solea* and *T. maculatus* (Yazdani, 1969), but does not in *A. lineatus*. The lower jaws of *A. lineatus* and *T. maculatus* are similar. The left dentary of *S. solea* is smaller than that of either *A. lineatus* or *T. maculatus*. Thus,
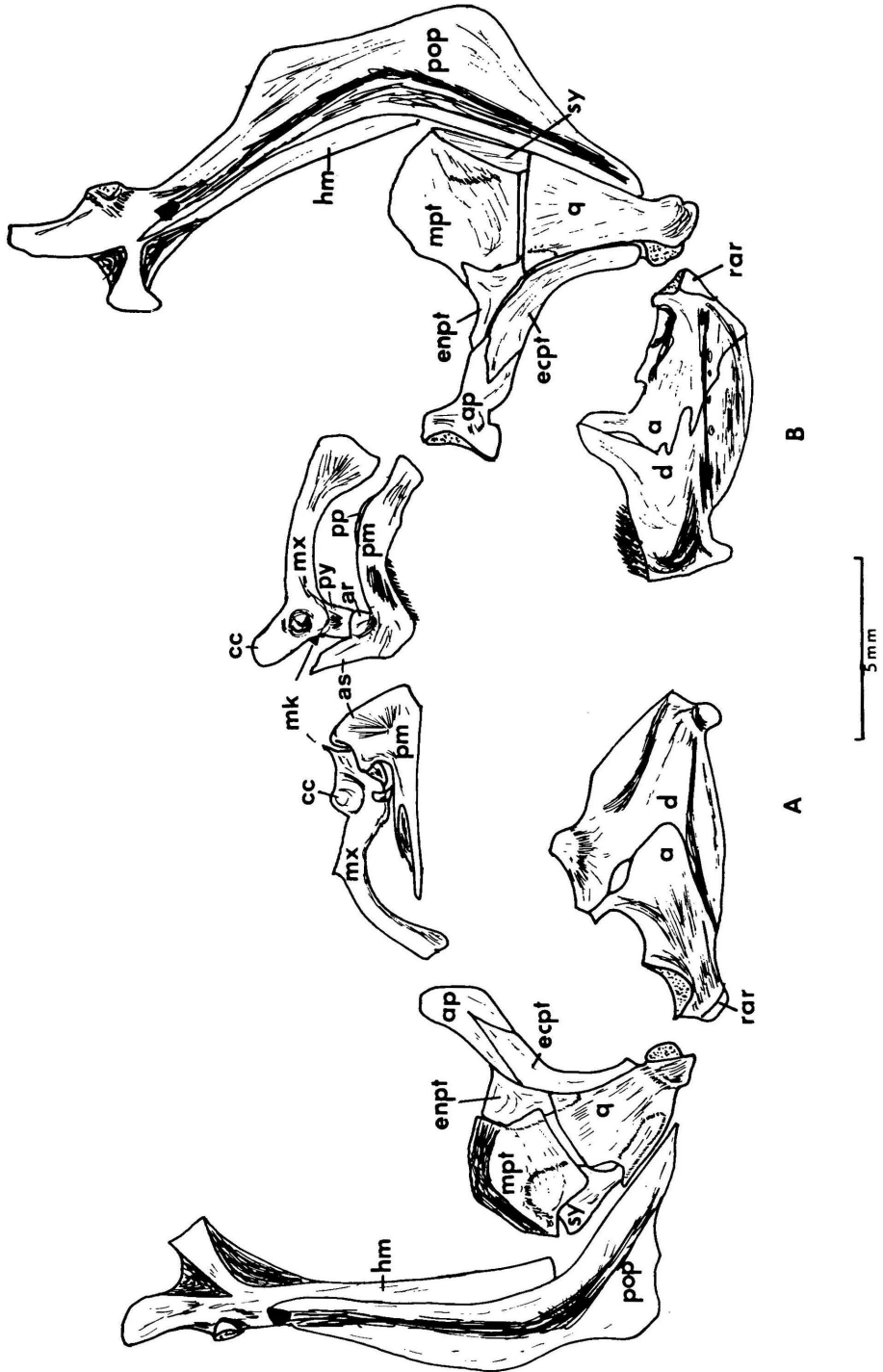
FIG. 3. Jaws and palatoquadrate arches. A, right side; B, left side. Drawn from 92 mm SL specimen (FSBC 4362).

Yazdani considers the jaws of *Trinectes* primitive with respect to the specialized lower jaws of *Solea*.

Hyoid Region (Figs. 2, 3, and 4)

The hyomandibular (hm) is a large cruciform bone forming the main attachment of the branchiocranium to neurocranium. The anterior and dorsal arms of the hyomandibular articulate with the neurocranium. The anterior arm fits into a fossa formed by the prootic and autosphenotic, and the dorsal arm lies in a deep depression on the underside of the autopterotic. The short posteriorly directed arm forms a fossa for articulation with the opercular. The long ventral arm, the symplectic process, extends ventrad to the cartilaginous attachment with the symplectic and interhyal. A depression on the lateroposterior margin of the symplectic process receives the dorsal end of the preopercular. A medial canal directs the hyomandibular branch of the facial nerve ventrad. Laterally, the hyomandibular branch of the laterosensory canal system is encased in a bony sheath.

The symplectics (sy) are two small wedges of bone fitting into a groove on the posteromedial portion of each quadrate. They expand dorsally and are partially overlain by each metapterygoid. The left symplectic has broad contact with the leading edge of the preopercular, but the right symplectic does not contact the right preopercular.

The interhyal (ih) is a small rod-like bone fitting into the cartilaginous connection between the symplectic and the symplectic process of the hyomandibular. Ventrally, it attaches near the posterodorsal border of the epihyal.

The epihyal (eh) is a broad quadrangular bone inseparably joined to the ceratohyal by strong odontoid processes across medial faces of both bones. Because homology of the epihyal is uncertain (McAllister, 1968; Nelson, 1969), we prefer generally accepted terminology, as suggested by McAllister. The epihyal supports three branchiostegals.

The ceratohyal (ch) is a broad semicircular bone with a stout anterior ramus. Above and below this ramus are attached the upper and lower hypohyals. Four branchiostegals are supported by the ceratohyal.

The upper hypopyal (uhh) fits dorsally onto the anterior ramus of the ceratohyal. It has a concave face fitting between the junction of the basibranchial and first hypobranchial. A small medial foramen pierces each upper hypohyal.

The lower hypohyal (lhh) caps the anteromedial end of the ceratohyal.

The basihyal (bh) is a median flattened bone, rounded posteriorly, forming the base of the tongue.

The urohyal (ur) is an intramembranous ossification lying beneath the basibranchial elements. Its anterior end lies in the hypohyal region. Posteriorly, it deepens in the sagittal plane, and curves ventrad. Its posterior margin is adjacent to the anterior margins of the cleithra.

The seven pairs of acinaciform branchiostegals (b) increase in size, proceeding posteriad. Four are attached to the ceratohyal, and three to the epihyal. Occasionally, one side may have only six branchiostegals.

The second through fifth branchiostegals have broad anteriorly directed proc-

esses which overlap adjacent branchiostegals, giving extra support to gill membranes. The first branchiostegal of each side is in mesial contact with its fellow, as in other Soleidae (McAllister, 1968).

The preopercular (pop) is a large crescentic bone following the suspensorial curve. Its leading edge partially covers the symplectic process of the hyomandibular, and ends posterolaterally in a hyomandibular sulcus. The trailing edge is thin, with a prominent bulge at the angle. The laterosensory canal from the temporal to the mandibular region is completely encased within the preopercular.

The opercular (op) is a broad, thin triangular bone. The posteriorly directed fossa of the hyomandibular articulates with the opercular condyle. The opercular condyle is contiguous with two thickened ridges, one directed posteriad, the other ventrad, the latter comprising the opercular leading edge.

The subopercular (sop) is a long thin bone extending from the angle of the preopercular to a point above the opercular. It is ventrally broadened, but narrows abruptly about at its midpoint. The ventral corner of the opercular rests in an elliptical aperture in the subopercular. In older specimens, this aperture becomes completely ossified.

The interopercular (iop) is a heavy quadrangular bone lying below the preopercular and sutured to the epihyal.

The sympectics and hyomandibulars are conspicuous in premetamorphosing larvae (Figs. 7 and 8). The branchiostegals develop as small filiform rods emanating from the epihyal and ceratohyal cartilages. When larvae are about 2.5 to 3.2 mm SL, the full complement of branchiostegals is usually present.

In 3.2 mm SL larvae (Fig. 9), the interhyal is visible between the epihyal and the cartilage intervening between the symplectic and hyomandibular. In juveniles of about 10 mm SL, the hyoid and branchial arches may be dissected from the neurocranium.

At 10 mm SL, the ceratohyal is incompletely sutured to the epihyal and perforated by a large foramen, the "beryciform foramen . . . found in the beryciforms and some of their derivatives" (McAllister, 1968). Accordingly, he proposed that presence of this foramen in some adult members of the order indicates a preperciform origin of Pleuronectiformes. In adult *A. lineatus*, only a small depression is present as a remnant of this foramen.

Opercular elements are present in premetamorphosing larvae (Fig. 7 and 8). The opercular is a small Y-shaped ossification directed posteriad from the posterior arm of the hyomandibular. The preopercular is a small crescentic bone at the angle of the hyomandibular and symplectic. It bears three or four epidermal spines, later to become the bony covering for a laterosensory canal. The interopercular is a tiny oval bone bearing two epidermal spines, located ventral to the preopercular and posterior to the symplectic. During development, the Y-shaped bifurcation of the opercular widens, and ossification occurs between the rami. The preopercular maintains its crescentic configuration and grows dorsad and ventrad. The interopercular broadens ventrally to assume the adult form. Formation of all bones of the opercular series is essentially complete by 14 mm SL.

Branchial Region (Fig. 4)

Following Topp and Cole (1968), "the terms 'proximal' and 'distal' are used with respect to the neurocranium; 'abpharyngeal' and 'adpharyngeal' are used in respect to the pharyngeal cavity."

The ventromesial basibranchials (bb) are located in the floor of the pharynx. The first basibranchial is a triangular bone resting between the upper hypohyals and posterior to the basihyal. The second basibranchial is spatulate; the heavy body of the bone is hourglass-shaped, with the widest part posterior. Laterally, thin lamellae complete the spatulate profile. The third basibranchial is a long bone posterior to the second basibranchial.

The first hypobranchial (hb) is a quadrangular bone articulating distally with the first and second basibranchials, and proximally with the first ceratobranchial. The similar second hypobranchial articulates distally with the second and third basibranchials, and proximally with the second ceratobranchial. The third hypobranchial is square, the anterior vertex bearing a strong ventral process. This element connects distally with the third basibranchial, and proximally with the third ceratobranchial.

The first four ceratobranchials (cb) are similar, but decrease in size posteriorly. Each has a small abpharyngeal groove for conduction of branchial blood vessels. The first four have proximal cartilaginous attachments to their respective epibranchial elements. The first three articulate distally with the three basibranchials. The fourth ceratobranchials have no ossified distal support. The fifth ceratobranchials (lower pharyngeal toothplates of Nelson, 1969) bear sharp villiform, dorsally directed teeth. The fifth ceratobranchials have no circumpharyngeal elements.

The four epibranchials (eb) angle anterodorsad from the cartilaginous connections with their corresponding ceratobranchials, the blood vessels continuing in abpharyngeal grooves. The first are slender rods with truncate projections directed dorsad. The slightly S-shaped second epibranchials are still shorter, each bearing a lateroposterior process involved in the insertion of the external *levatores arcuum branchialum* (Branson, 1966). The third epibranchials bear small proximal tooth plates. The fourth epibranchials are slightly curved.

Confusion exists regarding homology and terminology of pharyngobranchial elements and associated tooth plates (Nelson, 1968, 1969). We, therefore, follow generally accepted terminology (Topp and Cole, 1968).

The first pharyngobranchials (pb) are small rods directed dorsad from proximal ends of the first ceratobranchials. They are apparently involved in suspension of the branchiocranium from the neurocranium. The second pharyngobranchials are ovate, each with a small dorsal projection. Their adpharyngeal surfaces bear tooth plates with curved villiform teeth. The third pharyngobranchials, the largest of the series, are roughly triangular, each with an anterior projection and adpharyngeal tooth plate. The fourth pharyngobranchials are slender dentate bones adjacent to the posterior margin of the third. Nelson (1969) believes this element to be "purely dermal in origin, corresponding to the fourth upper pharyngeal plate . . ."
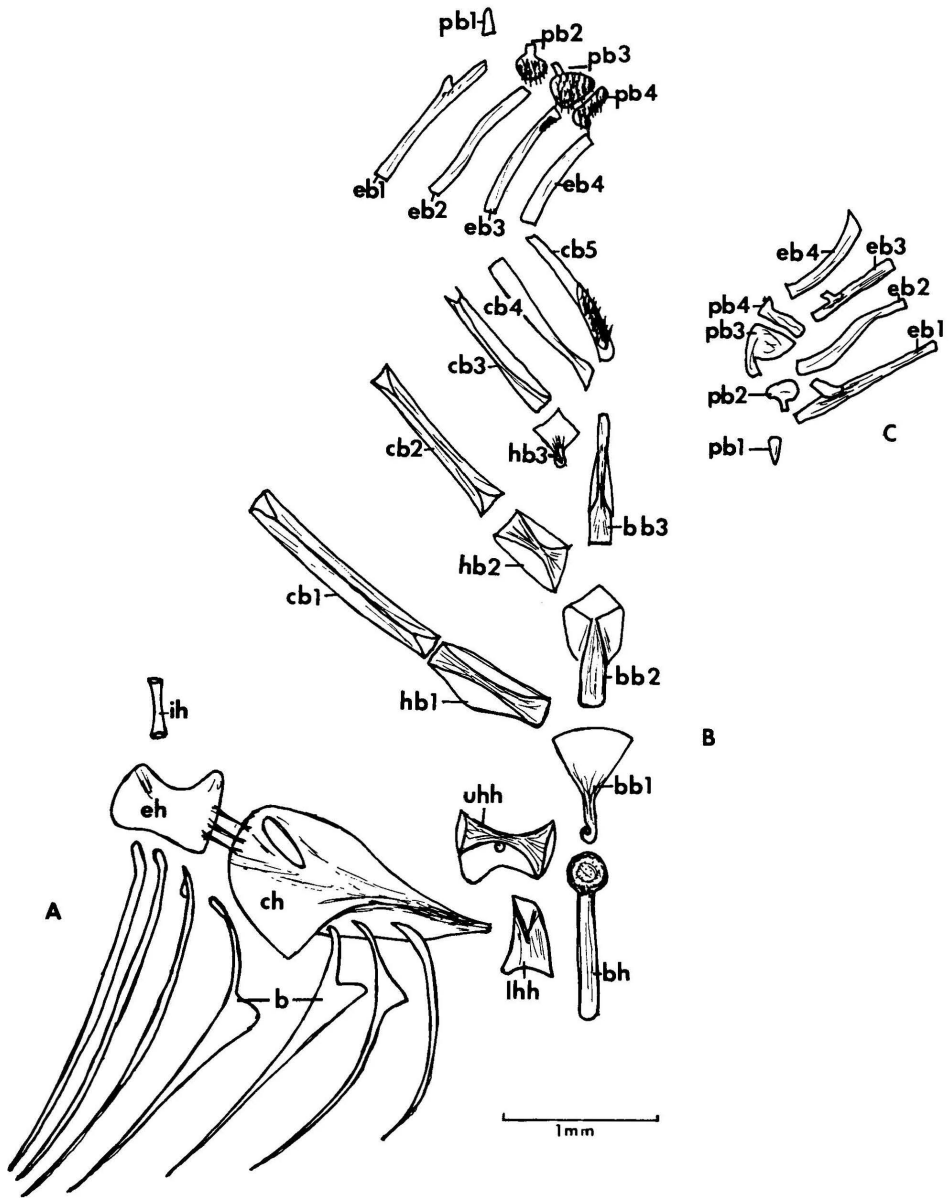
Fig. 4. Hyoid and branchial arches. A, right hyoid arch; B, adpharyngeal view; C, abpharyngeal view of upper elements. Drawn from a 10.2 mm SL specimen (FSBC 5969).

In premetamorphosing larvae, cerato- and epibranchial elements are visible as cartilage, or as very poorly ossified elements. In early metamorphosing larvae about 3.2 mm SL (Fig. 9) these elements, as well as basibranchials and hypohyals, are visible. The upper pharyngeal and fifth ceratobranchial teeth are well developed and, at this stage, probably compensate for poor jaw dentition.

VERTEBRAL COLUMN

The vertebral column (Figs. 5 and 11) consists of 9, sometimes 8 track vertebrae (tv) and 18, or less often 17, caudal vertebrae (cv) including the urostylar vertebra. No ribs are present in *A. lineatus*, nor in other soleids (Norman, 1966). In general, the elements resemble those in perciform fishes.

The first vertebra (atlas) is a short disk-shaped centrum with two anterodorsal condylar surfaces which, with the concave centrum below, form the tricondylar attachment to the skull. The paired elements forming the neural arch are autogenous, each articulating with the centrum by a bipedal facet. The two elements are joined to the second neural arch by connective tissue, but do not meet dorsomesially.

The second vertebra (axis) bears a lateral apophysis located well above the midline of the centrum. This apophysis has a bony laminar connection to a small posterodorsal knob, representing the neural prezygapophysis, which forms a shelf for the lateral facet of the autogenous first neural arch. The wide base of the neural arch expands posteriorly to form a large neural postzygapophysis. The anterior profile of the neural arch is slightly concave to accommodate the first neural elements. The straight portion of the neural spine is joined to the supraoccipital by connective tissue (in Fig. 11 the first and second neural spines are obscured by the posttemporal).

The lateral apophysis of the third centrum is slightly above the axial midline. The small neural prezygapophysis is located almost directly above the lateral apophysis, and articulates with the neural postzygapophysis of the second vertebra. The third neural arch sends back a strong postzygapophysis. The neural spine is strongly curved forward.

The lateral apophysis of the fourth trunk vertebra is directly on the midline of the centrum and is the most developed of any on the entire column. The neural arch and spine incline forward.

The fifth trunk vertebra bears a lateral apophysis below the central midline. The neural prezygapophysis is very prominent. Paired parapophyses meet ventrally to form the first hemal arch. The neural arch and spine are strongly bowed anteriad.

The sixth through ninth trunk vertebrae possess consecutively less prominent lateral apophyses. Caudal vertebral apophyses are represented only by curvatures in central margins. The neural prezygapophyses become increasingly prominent in trunk vertebrae and parapophyses increase in length. The neural arches and spines are angled anteriad.

The first caudal vertebra has an exceedingly large hemal spine, its anterior face deeply grooved to accommodate the first anal pterygiophore.

Proceeding posteriad, caudal vertebrae reduce in size. Neural and hemal components of the first caudal vertebra are approximately vertical, becoming posteriorly directed in successive vertebrae.

The last three vertebrae are modified for caudal fin support.

Development of the vertebral column proceeds posteriad. The first neural elements appear on the trunk vertebrae of premetamorphosing larvae (Figs. 7 and
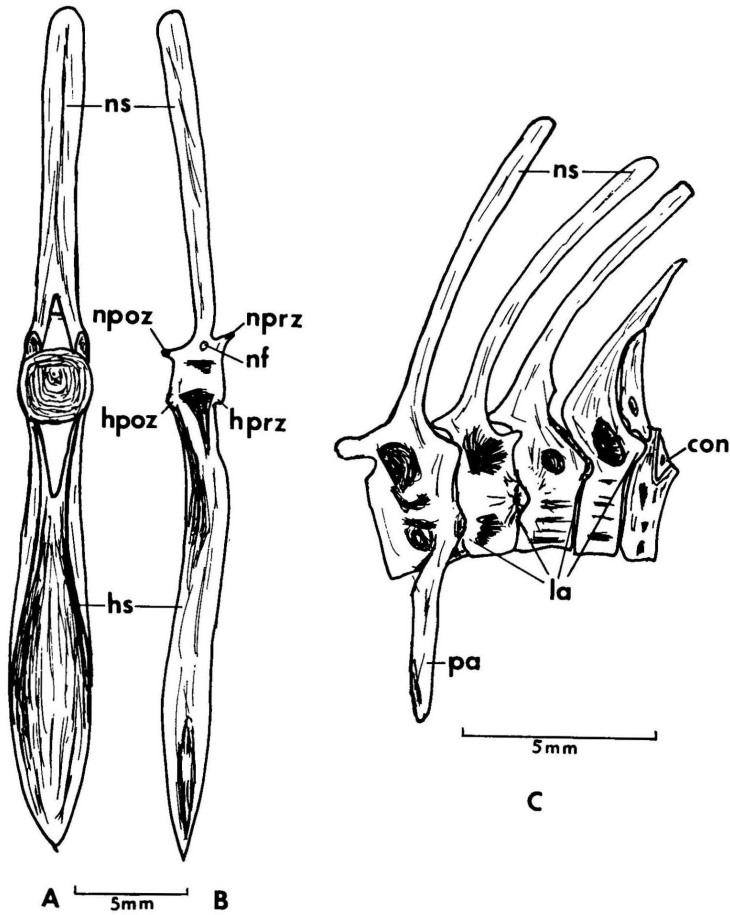
FIG. 5. A, anterior view of first caudal vertebra; B, lateral view of first caudal vertebra; C, first through fifth (right to left) trunk vertebrae. Drawn from 92 mm SL specimen (FSBC 4362).

8) as small filaments of bone arising from lateral surfaces of indistinct arcualia. The remainder of the vertebral column is undifferentiated. The full complement of vertebrae is attained by larvae between 2.5 and 3.0 mm SL (Fig. 9). At this size, the posterior end of the notochord, later to becofe the urostylar vertebra, is flexed dorsad. During antogeny, intervertebral cartilages become much reduced, and vertebrae become more closely approximated.

Although axial skeleton structure of *A. lineatus* is similar to that of *S. solea* as described by Ford (1937), the two differ greatly in numbers of caudal vertebrate; *S. solea* has 40, *A. lineatus* 17 or 18. Trunk vertebrae of the two are almost identical. The first neural spine of *S. solea* is not closed to form a complete arch (Ford, 1937). Further, his photographs show that neural elements of the first vertebra are attached to the second neural arch and that the second neural spine contacts the supraoccipital, as in *A. lineatus*. A similar configuration is present in *S.*

vulgaris (Kyle, 1921). *S. solea* and *A. lineatus* each have five trunk vertebrae with parapophyses meeting ventromesially to form hemal arches. Lateral apophyses are different, however. They extend throughout the vertebral column in *S. solea* but are obvious only on the second through fifth vertebrae of *A. lineatus.*

CAUDAL SKELETON

The caudal skeleton resembles in essential respects that described by Gosline (1961) as primitive among perciform fishes. Gosline established the rationale for numbering hypural elements from ventral to dorsal. For convenience, we advocate numbering caudal lepidotrichs in the same manner.

The hemal spine of the antepenultimate (25th) vertebra is longer and heavier than its preceding counterpart, and supports one or more lepidotrichs. The neural spine does not enter into caudal fin support. The autogenous hemal spine of the penultimate (26th) vertebra is long and deepened in the sagittal plane. It supports the second, and sometimes part of the first lepidotrich.

The proximal ends of hypurals 1–4 originate from the ventral and posterior margins of the urostylar vertebra; the fifth arises above the tip. Hypurapophyses (Nursall, 1963) are absent.

The single parhypural (*sensu* Monod, 1968) is proximally adjacent to the autogenous 26th hemal spine. It typically supports the third, fourth, and part of the fifth lepidotrichs.

The single epural lies adjacent and posterior to the neural spine of the 26th vertebra. It typically supports the 15th and part of the 16th lepidotrichs.

Caudal fin elements appear in larvae about 2.5 mm SL (Fig. 8), although the posterior section of the notochord is undifferentiated and straight. Four cartilaginous elements are located on the posteroventral surface of the notochord. In metamorphosing larvae (Fig. 9), the last three vertebrae are undifferentiated from the dorsally flexed notochord, but neural and hemal spines of the 25th and 26th vertebrae are visible. The parhypural also arises immediately posterior to the 26th hemal spine. Four hypurals arising from the ventral surface of the urostylar vertebra are present.

In more advanced larvae (Fig. 10), the last three vertebrae are distinct. The parhypural is definitely associated with the 26th vertebra. In the adult, it may be located such that it appears to have arisen from the urostylar vertebra, and might mistakenly be considered a hypural. Its true origin from the 26th vertebra is shown during ontogeny.

The fifth hypural develops dorsal to the urostylar vertebral tip in metamorphosing larvae, all caudal elements being present at this stage (Fig. 10). Increased ossification, and some fusion of caudal elements occur in older specimens.

The caudal skeleton of *S. solea*, as described by Monod (1968), is remarkably similar to that of *A. lineatus.*

MEDIAL FINS

Considerable variation exists in dorsal and anal fin ray counts. Jordan and Evermann (1898) list: dorsal, 49–58, and anal, 38–44. Although numbers vary,
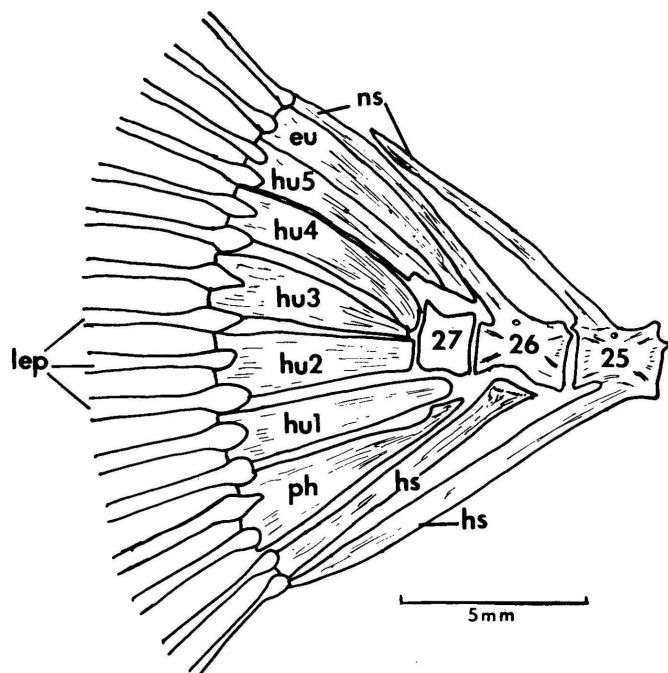
FIG. 6. Caudal fin. Drawn from 76.5 mm SL specimen (FSBC 5968).

basic triserial structure of fins is uniform. Basic median fin structure of the type encountered in *A. lineatus* is adequately discussed by Topp and Cole (1968).

The first and second (anterior) lepidotrichs of the dorsal fin are supported by one pterygiophore whose base rests in the anterior-most notch of the supraoccipital crest. Proximal bases of the next four pterygiophores have similar cranial support. The sixth interdigitates with the cranium and third neural spine. The proximal bases of the posterior three dorsal fin lepidotrichs have no neural connection.

Anal fin morphology is similar to that of the dorsal fin. The first (anterior) anal pterygiophore is a massive shaft of bone curving anteriorly from its proximal base set in the deeply grooved anterior face of the first caudal hemal spine. Ventrally, it presents facets for two lepidotrich attachments. This large bone, the "abdominal rod" of Kyle (1921) and Woolcott et al. (1968), and the "interhemal spine" of Norman (1934), should be properly termed "first anal pterygiophore" because of its obvious homology. Four pterygiophores arise from the grooved ventroposterior surface of the first anal pterygiophore. The posterior four anal pterygiophores occur between but do not interdigitate with, hemal spines of the 23rd and 24th vertebrae.

Development of median fins of *A. lineatus* discussed by Houde et al. (1970) may be summarized. The first median fin structures to develop are the dorsal fin pterygiophores. These appear in larvae between 2.1 and 2.4 mm SL, with anal pterygiophores developing shortly thereafter. Development proceeds posteriad.

The full complement of dorsal and anal rays is attained by individuals about 12 mm SL.

APPENDICULAR SKELETON

Loss and reduction of pectoral elements is characteristic of Soleidae. The right pectoral fin of *A. lineatus* consists of four to six small lepidotrichs without bony connection to the pectoral girdle. The left pectoral fin is absent.

The cleithrum (cl), the largest bone of the girdle, consists of dorsal and ventral limbs of equal length forming an angle of about 100°. The cleithra meet in ventromesial symphysis.

The supracleithrum (scl) fits into a shallow dorsolateral depression on the cleithrum and into a ventromedial facet of the posttemporal, connecting the two.

A postcleithrum (pcl), a tubular structure extending posteroventrad from the angle of the cleithum, occurs only in premetamorphosing and metamorphosing larvae (Figs. 7, 8, and 9) but atrophies during metamorphosis. Postcleithra are absent in adult soles (Norman, 1966).
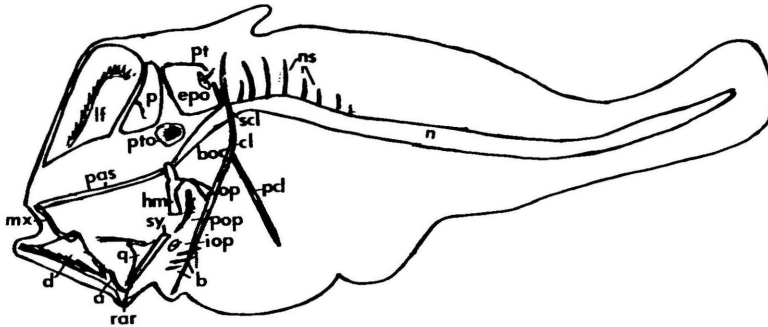

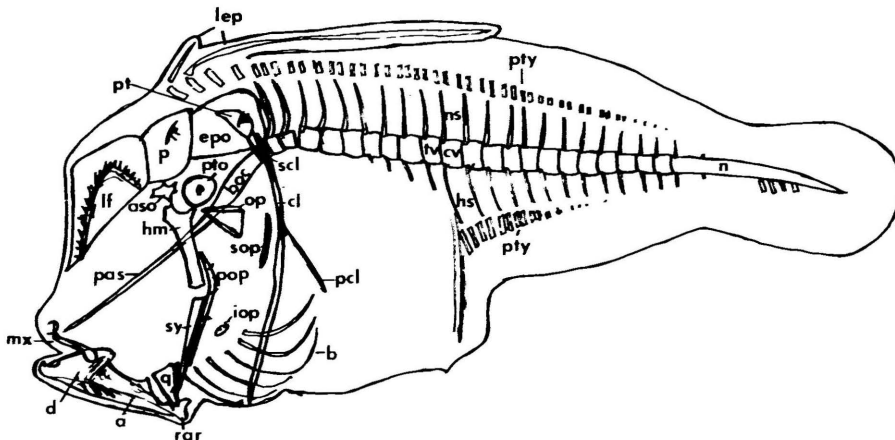Fig. 7. Skeleton. Drawn from 2.14 mm SL specimen (FSBC 5865L).

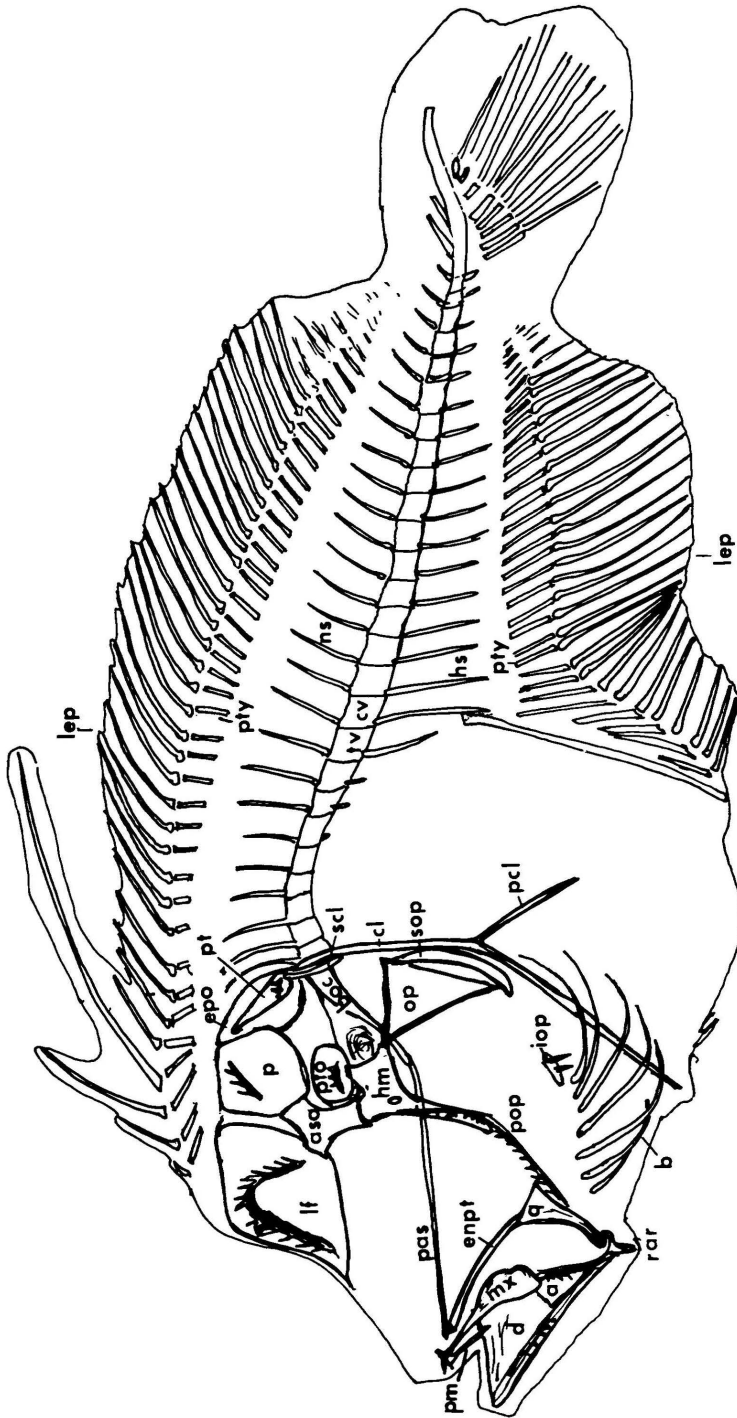Fig. 8. Skeleton. Drawn from 2.52 mm SL specimen (FSBC 5880L).

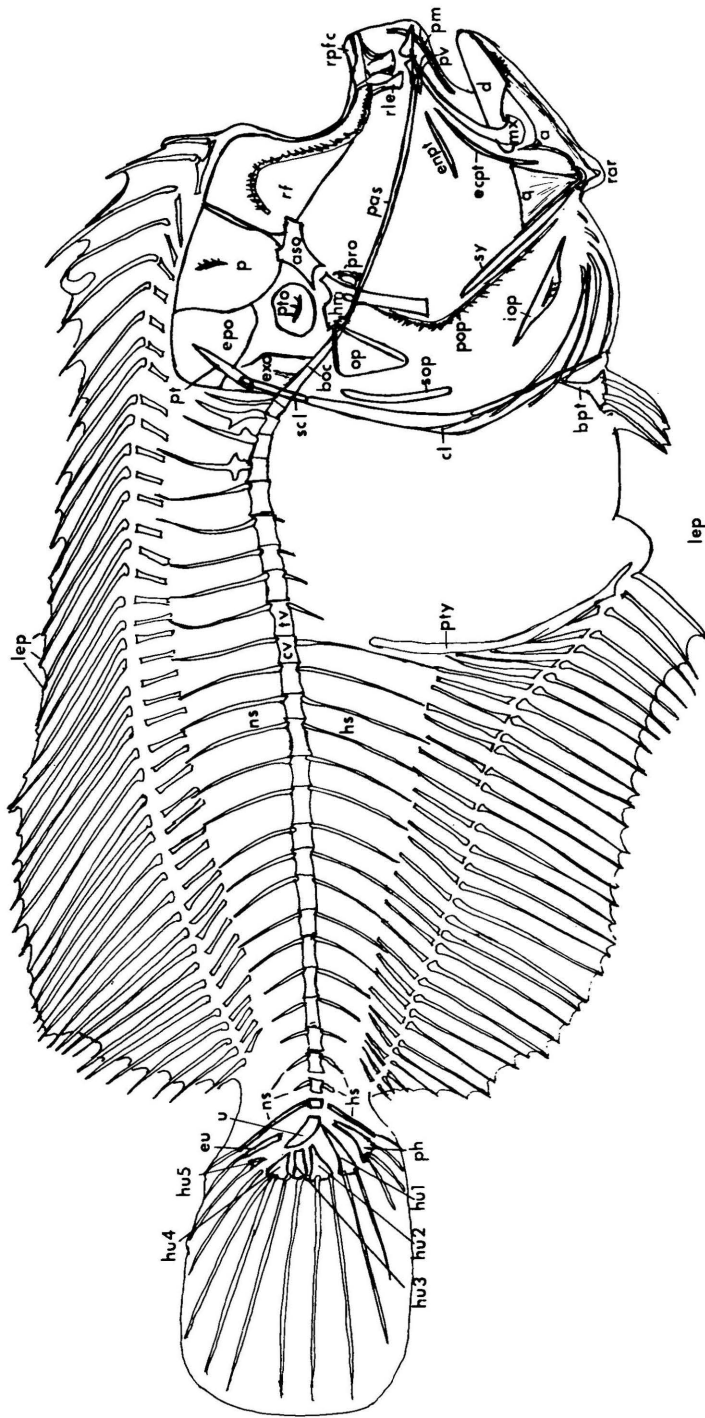Fɪɢ. 9. Skeleton. Drawn from 3.20 mm SL specimen (FSBC 5850L).

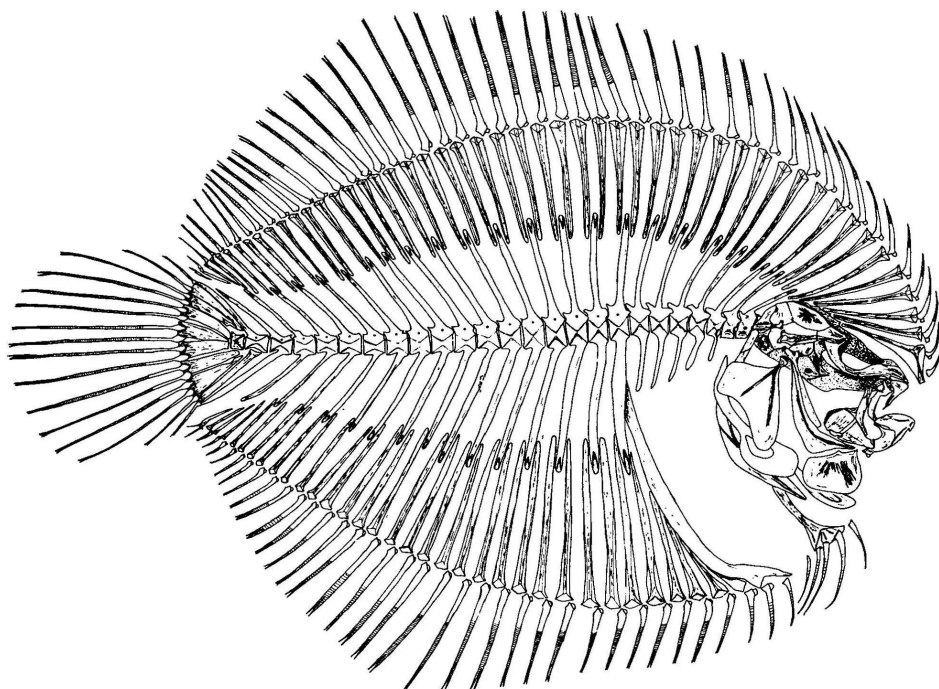FIG. 10. Skeleton. Drawn from 3.57 mm SL specimen (FSBC 5860L).

Fig. 11. Skeleton. Drawn from 76.5 mm SL specimen (FSBC 5968).

The basipterygia (bpt) are thin, sagittally flattened shafts of bone ending ventrally in broad triangular expansion. The proximal ends of the shafts are connected by ligaments to the cleithra near their ventromesial union. The ventral triangular surface supports three lepidotrichs; the first and last are free (Fig. 2).

Development of paired fins discussed by Houde et al. (1970) may be summarized. The pectoral fins of larvae have a cartilaginous base. No rays are present in larvae about 4.5 mm SL. The right pectoral fin assumes adult form by about 8 mm SL. The left pectoral is present in larvae, but atrophies and usually disappears in fish of 5 to 6 mm SL.

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LIST OF ABBREVIATIONS

Neucrocranium

Olfactory Region

lof	left olfactory foramen
lpfc	left prefrontal complex
n	nasal

rle	right lateral ethmoid
rof	right olfactory foramen
rpfc	right prefrontal complex
pv	prevomer

Orbital Region

lf	left frontal
pts	pterosphenoid
rf	right frontal

Otic and Basicranial Region

aso	autosphenotic
boc	basioccipital
epo	epiotic
exo	exoccipital
fm	foramen magnum
les	lateral extrascapular
opo	opisthotic
p	parietal
pas	parasphenoid
pro	prootic
pt	posttemporal
pto	autopterotic
s-i	supratemporal-intertemporal
soc	supraoccipital

Branchiocranium

Oromandibular Region

a	angular
ap	autopalatine
ar	articular process of premaxillary
as	ascending process of premaxillary
d	dentary
ecpt	ectopterygoid
enpt	endopterygoid
mk	maxillary spike
mpt	metapterygoid
mx	maxillary
pm	premaxillary
pp	postmaxillary process of premaxillary
py	premaxillary condyle of maxillary
q	quadrate
rar	retroarticular

Hyoid Region

b	branchiostegal
bh	basihyal
ch	ceratohyal
eh	epihyal
hm	hyomandibular
ih	interhyal
iop	interopercular
lhh	lower hypohyal
op	opercular

pop	preopercular
uhh	upper hypohyal
ur	urohyal
sop	subopercular
sy	symplectic

Branchial Region

bb	basibranchial
cb	ceratobranchial
eb	epibranchial
hb	hypobranchial
pb	pharyngobranchial

Vertebral Column

con	condylar surface
cv	caudal vertebra
hpoz	hemal postzygapophysis
hprz	hemal prezygapophysis
hs	hemal spine
la	lateral apophysis
n	notochord
nf	nerve foramen
npoz	neural postzygapophysis
nprz	neural prezygapophysis
ns	neural spine
pa	parapophysis
tv	trunk vertebra

Median Fins

lep	lepidotrich
pty	pterygiophore

Caudal Skeleton

eu	epural
hu	hypural
lep	lepidotrich
ph	parhypural

Appendicular Skeleton

bpt	basipterygium
cl	cleithrum
lep	lepidotrich
pcl	postcleithrum
scl	supracleithrum