THE OSTEOLOGY OF BREVOORTIA PATRONUS AND BREVOORTIA GUNTERI (PISCES; CLUPEIDAE)

A Thesis

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By

Walter V. Robertson

Approved as to style and content by:

Richard L. Baldauf ....
(Chairman of Committee)

W. B. Davis ....
(Head of Department)

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Five species of menhaden are known from the coasts of the United States; two occur in the Gulf of Mexico and three are found along the Atlantic Coast. Based upon scale size and the shape of the pelvic fins, four of the species comprise two closely-related groups. *Brevoortia patronus* (Goode) from the Gulf and *B. tyrannus* (Latrobe) from the Atlantic have rounded pelvic fins and moderately large scales arranged in regular series on the sides of the body. *B. gunteri* (Hildebrand) from the Gulf and *B. smithi* (Hildebrand) from the Atlantic have pointed pelvic fins and smaller scales in more irregularly arranged rows. One species, *B. brevicaudata* (Goode), is restricted to the region of Noank, Connecticut.

Hildebrand (1948) pointed out the possibility that the ranges of the Atlantic and Gulf groups were continuous at one time and that such continuity was ended when the last passageway for fishes across the Florida peninsula became closed. He gave further evidence indicating that today the Florida peninsula serves to separate many Atlantic and Gulf coast fishes including the menhaden. With this separation, and under the influence of different environments, it appears that the two groups of menhaden became sufficiently differentiated to constitute distinct species.

Goode (1878) described B. patronus from a series of specimens collected at Brazos Santiago, Texas, and for a long time this was the only menhaden known from the northern Gulf of Mexico. While working on the marine fishes of Texas, Gunter (1945) recognized two kinds of Brevoortia on the Texas Coast. He identified one as the Atlantic B. tyrannus and stated that the other one might possibly represent Goode's B. patronus, but that it was rather close to or possibly identical with B. smithi of the Atlantic. Hildebrand (1948) revised the genus and indicated that the species which Gunter regarded as B. tyrannus was actually B. patronus and that the Gulf menhaden which Gunter associated with B. smithi was a new species and named it B. gunteri.

The difference in size of scales and shape of fins, along with certain meristic characteristics used to separate the various species of Brevoortia, are relative and are not always reliable. Except for large specimens, it is extremely difficult to distinguish between the two species of Gulf menhaden and there is some question regarding the validity of B. gunteri as a full species.

Osteological studies have been successfully employed in the past for a better understanding of certain natural relationships of fishes. Although such studies often have greater application at higher taxonomic levels, it was thought that a comparison of the skeletal systems of two similar species, such as the Gulf menhadens, might help to clear up their taxonomic status. Among the most prominent osteological studies of clupeoid fishes are those of Bamford (1941), Chapman (1944, 1948), Phillips (1942), and Ridewood (1904), but these do not treat the genus Brevoortia.

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Materials and Methods

Specimens for this study were collected from the coastal waters of Louisiana and Texas. Some were placed at my disposal by the persons and institutions mentioned above; others were collected by the writer at Rockport, Texas.

Ten specimens of B. patronus (total length, 140-210 mm.) and four specimens of B. gunteri (total length, 150-260 mm.)

were cleared and stained in a manner similar to that described by Hollister (1932). Additional material included mature specimens of B. patronus which were dissected without preliminary clearing. The entire skeleton of B. patronus has been described and illustrated, after which is a comparison with B. gunteri. Illustrations were drawn from specimens measuring approximately 200 mm. in total length. Specimens of equal size, assumed to be approximately the same age, were used for all comparisons.

The nomenclature of skeletal elements follow, for the most part, those used by Phillips (1942).

The Osteocranium of B. patronus

Dorsal and Basal Aspects of the Neurocranium

Bones included here are the ethmoid, the frontals, the supraoccipital, the parietals, the pterotics, the epiotics, the exoccipitals, and the basioccipital.

The ethmoid (ETH, Figs. 1, 3, 4, 10) possesses a pair of ventrolateral projections which connect with the palatines. Dorsally there is a broad median elevation which bears two short posterior processes. The knobbed dorsal ends of the maxillaries meet anteromedially below the ethmoid. The bifurcate posterior border of the ethmoid serves as the anterior border of the median fontanelle. Each posterior branch of the ethmoid is directed laterally and terminates below the frontal.

The frontals (F, Figs. 1, 3, 10) are the largest bones of the cranium and extend about two-thirds of the cranial length. Medially they are joined along an irregular suture. Anteriorly they diverge to form the posterior border of the median fontanelle.

The posterior roof of the cranial vault is formed by the median supraoccipital (SOC, Figs. 1, 2, 4) and the paired parietals (PAR, Figs. 1, 4, 10). An anterior extension of the supraoccipital lies between the frontals. The parietals meet the frontals anteriorly and the supraoccipital medially and posteriorly. The anterolateral margin of the parietal contributes to the roof of the temporal foramen (T.F, Figs. 1, 4, 10); the posterolateral margin serves as a roof for the temporal groove (T.G, Figs. 1, 4). A small foramen pierces the lateral extension of the supraoccipital immediately behind each parietal.

Ventrolaterally each parietal is joined by a pterotic (PTR, Figs. 1, 2, 3, 4). Anteriorly the pterotic is contiguous with the margins of the frontal and sphenotic bones. Dorsomedially the pterotic contributes to the floor of the temporal foramen and the temporal groove. The dorsolateral margin of the pterotic serves as a part of the latero-sensory canal (LS.C, Fig. 4). The roof of the pterotic bulla lies between this canal and the temporal groove. Posteriorly the pterotic ends as a sharp process.

The cone-shaped epiotic (EP, Figs. 1, 2, 3, 4, 10) meets the ventrolateral margin of the supraoccipital. The temporal groove extends onto the anterolateral surface of the epiotic while a part of the posttemporal is contiguous with the posterolateral surface.

Attached to the posterior end of the epiotic, a series of very fine filamentous bones (osseous brush) extends back into the trunk muscles. Ventrolateral to each osseous brush is another small terminally branched bone (filamentiferous rod) which extends under the supratemporal and into the temporal groove anteriorly and into the trunk muscles posteriorly. These structures are illustrated by Phillips (1942) in his description of Sardinops caerulea.

Posteroventrally the supraoccipital and the epiotic are joined by the large exoccipitals (EX, Figs. 1, 2, 3, 4). The exoccipital joins the lower posteromedial part of the pterotic and is a large part of the base of the cranium. The exoccipitals surround the foramen magnum (F.M, Figs. 1, 2). Two small crests of the exoccipitals form the lateral limits of the foramen magnum and extend dorsomedially to enclose a depression above the foramen. Posterolaterally the exoccipital sheaths the surface of the basioccipital. This sheath-like extension of the exoccipital is pierced by two foramina; anterior to these foramina the exoccipital extends to meet the prootic. The anteroventral margin of the exoccipital borders the large auditory fenestra (A.F, Figs. 3, 4), an elongate opening which communicates with the perilymphatic cavity of the ear.

Immediately below the foramen magnum is the median basioccipital (BOC, Figs. 2, 3, 4). The posterior surface of this bone is concave like the centrum of a vertebra; the upper surface bears a condyle which articulates with the first vertebra. A small bony arch (B.A, Figs. 1, 2, 4) lies above the juncture of the basioccipital and the first vertebra. The basioccipital forms the ventromedial margin of the auditory fenestra. Two slender bones are attached to each lateral surface of the basioccipital. These bones are branched posterodorsally and extend into the trunk muscles.

Ventral and Lateral Aspects of the Neurocranium

The bones included here are the vomer, the parasphenoid, the prefrontals, the orbitosphenoid, the alisphenoids, the prootics, the sphenotics, and the opisthotics.

The rounded anterior end of the flat, median vomer (VO, Figs. 3, 4) lies directly beneath the ethmoid. The vomer tapers to a point toward the rear and, for most of its length, lies in a slot in the parasphenoid.

The median parasphenoid (PSP, Figs. 1, 2, 3, 4) is the longest bone of the cranium. Its anterior end possesses a slot to accommodate the vomer which it partially sheaths. The middle portion of the parasphenoid is small and cylindrical, but the posterior end is broadened and bifurcated to form two thin, almost vertical, alae. The alae converge along their ventral margins and diverge dorsally where they are attached to other bones of the cranium. A space, the myodome (MY, Fig. 2), is enclosed by the wings. A small recess near the anterior base of the alae marks the point of attachment of the suspensory pharyngeals. Posteriorly the winged parasphenoid extends beyond the cranium to about the third vertebra.

Dorsal to the parasphenoid and just below the anterior ends of the frontals are the paired prefrontals (PF, Figs. 1, 3, 4). The suture between the prefrontals may be seen through the fontanelle from a dorsal view. A compressed lateral projection of the prefrontal forms a vertical shield which is the anterior limit of the orbit. Posteriorly each prefrontal tapers to a point which meets the orbitosphenoid.

The anterior part of the median orbitosphenoid (OSP, Figs. 3, 4, 10) is narrow and cylindrical while the middle portion is laterally compressed and slightly decurved. Posteriorly it is larger at the juncture with the frontals above and the alisphenoids behind. The posterodorsal surface of the orbitosphenoid is recessed and forms the floor of the passageway for the olfactory tract.

The paired alisphenoids (ALI, Fig. 3) join anteroventrally and form the anterior and lateral borders of the median optic foramen. Lying between the alisphenoids and forming the posterior border of the optic foramen is the median basisphenoid. The optic foramen and the basisphenoid are not illustrated here since they can be seen only from an anterior view or when the parasphenoid is removed.

Posteriorly the alisphenoids join the paired prootic bones (PRO, Figs. 3, 4), but the suture is obscured by the anterior free margin of the prootics which proceed laterally to join a similar extension of the sphenotics. Ventromedially the prootics are joined and enclose a small foramen just posterior to the basisphenoid; the foramen is hidden by the parasphenoid. Centrally located on each prootic is the pronounced auditory bulla (AU.B, Figs. 3, 4) which is a hollow, imperfect sphere with an elongated, vertical opening on the inside surface. Anterior to each bulla is an ovoid foramen while anteroventrally another more elongate foramen pierces the prootic.

Joining each prootic anterodorsally is the sphenotic (SP, Figs. 1, 3, 4, 10). The anteromedial margin of the sphenotic joins the frontal while the posterior end joins the pterotic. A small medially directed foramen pierces the sphenotic-pterotic lateral juncture.

The opisthotic (OPI, Figs. 2, 3, 4) is attached to the posterolateral surface of the cranium and is bounded by the pterotic above, the prootic anteriorly and the exoccipital below. The opisthotic is thin anteriorly, but it tapers to a thickened nodule toward the rear where it extends slightly laterad and is joined by a ligament to a small branch of the posttemporal.

Hyopalatine Series

Bones comprising this series consist of the palatines, the pterygoids, the mesopterygoids, the metapterygoids, the hyomandibulars, the quadrates, and the symplectics. These bones are best observed from a mesial view.

The palatine (PAL, Figs. 5, 6) is the most anterior bone of this series. The knobbed anterior portion extends upward and articulates behind with the lateral extension of the ethmoid and in front with the maxillary. Posteriorly the palatine is broad and thin, and it joins the pterygoid and the metapterygoid.

The pterygoid (PT, Figs. 5, 6) is a thin, flat bone which tapers to a sharp point ventrally and joins the upper anterior margin of the quadrate. The posterodorsal margin of the pterygoid meets the mesopterygoid and a small dorsal projection meets the lateral extension of the prefrontal. A narrow sheet of cartilage bridges between the pterygoid and the metapterygoid.

The mesopterygoid (MSPT, Figs. 5, 6, 10) is a thin rectangular bone which curves medially to contribute to the floor of the orbit. It is bounded posteriorly and ventrally by the metapterygoid which it overlaps slightly. Dorsally it is not in contact with any other bone.

The decurved anterodorsal margin of the metapterygoid (MTPT, Figs. 5, 6) is overlapped by the mesopterygoid. A dorsal finger-like projection extends upward behind the mesopterygoid. The ventral limit is a narrow shank attached to the lower anterior margin of the hyomandibular. A portion of the metapterygoid is curved, along with a part of the mesopterygoid, to contribute to the floor of the orbit. The posterodorsal margin of this bone is overlapped by a thin anterior extension of the hyomandibular; a narrow projection (not shown) extends upward into a deep anterior groove of the hyomandibular. Ventrally the metapterygoid is connected to the quadrate by a thin sheet of cartilage.

The hyomandibular (HY, Figs. 5, 6, 10) is the chief suspensorium for the lower jaw. The upper portion is fan-shaped and bears two rounded condyles on the dorsal margin which articulate with the cranium. The smaller anterior condyle fits into a recess of the sphenotic anterodorsad to the auditory bulla while the posterior condyle fits into a recess of the pterotic posterodorsad to the auditory bulla. The bulla lies in the concavity between the condyles. A small rounded condyle on the posterodorsal margin of the hyomandibular articulates with a socket on the opercle. This is the only firm attachment between the hyomandibular and any opercular bone. The preopercle is loosely attached to the posterolateral edge of the hyomandibular. Ventrally the hyomandibular tapers to a narrow shank and is attached by cartilage to the interhyal, symplectic, and quadrate bones. The anterior margin of the hyomandibular is V-shaped, a condition that is more pronounced on the upper, broad part of the bone.

On the inner surface of the upper part of this bone is an elliptical opening, the hyomandibular embrasure (HY.E, Figs. 5, 6), which marks the beginning of an anteriorly directed recess. A large opening extends from the ventral part of this embrasure to the lateral surface of the hyomandibular and is the passageway for the facial nerve. A thin anterior extension of the hyomandibular overlaps and is contiguous with the posterodorsal margin of the metapterygoid.

In close proximity with the shank of the hyomandibular and the metapterygoid is the posterior arm of the V-shaped quadrate (Q, Figs. 5, 6, 10). The shape of this bone is quite different from that of any other fish genus with which this author is familiar. The main difference concerns the dorsal margin which is greatly decurved, giving the bone its V-shape. Anteroventrally a condyle of the quadrate fits into a recess of the articular to form a movable joint. The anterior arm of the quadrate extends upward to join the posterior margin of the pterygoid.

In junction with the posterior margin of the quadrate is the small symplectic (SYM, Figs. 5, 6). This bone does not reach the upper margin of the quadrate, and in this respect differs from the condition described for many clupeoids.

Opercular Series

Bones comprising this series consist of the opercle, the subopercle, the interopercle, and the preopercle.

Largest of the opercular series and uppermost in position is the opercle (OP, Figs. 5, 6, 10). A condyle on the posterodorsal margin of the hyomandibular fits into a recess of the opercle forming a slightly movable joint. The dorsal margin of the opercle is rounded; the lower margin overlaps obliquely the upper edge of the subopercle. Numerous radiating striations arise from the upper lateral surface of the opercle.

Just below the opercle is the subopercle (SOP, Figs. 5, 6, 10). The subopercle is characterized by a curved lower margin which constitutes the posteroventral limit of the operculum and by a straight upper margin, the hinder part of which is contiguous with the lower margin of the opercle. A small finger of bone arises from the upper margin of the subopercle just anterior to the opercle.

Anterodorsad to the subopercle is the interopercle (IOP, Figs. 5, 6, 10) which is contiguous with the front margin of the subopercle. The crescent-shaped interopercle ends anteriorly below the point of articulation of the lower jaw.

The preopercle (POP, Figs. 5, 6, 10) is long and narrow. Its posterodorsal margin slightly overlaps the anterior margin of the opercle. The anterodorsal margin of the preopercle is contiguous with the posterolateral edge of the hyomandibular while the lower portion extends forward and ends just above the anterior limit of the interopercle. A branch of the latero-sensory canal system extends down the anterolateral surface of the preopercle.

Orbital Series

The eight thin bones of the orbital series extend almost completely around the orbit. The posterior bones of this series are the four suborbitals (SBO, Fig. 10). The uppermost and smallest suborbital is joined loosely to the lateral edge of the sphenoid just anterior to the sphenoid-prootic suture. The next three suborbitals extend anteroventrally. Their orbital margin is evenly decurved and the posterior margin of each is very close to the anterior margin of the preopercle and in some places overlaps it. The second suborbital is about twice the size of the first, while the third is as large as the first and second combined. The fourth suborbital is the largest of the series and is located with its anterior margin vertical to the middle of the orbit. The ventral edge of this bone conceals the major portion of the metapterygoid and the posterior arm of the quadrate when viewed laterally.

Completing the ventral portion of the orbital rim are the two narrow preorbitals (POB, Fig. 10). The posterior preorbital overlaps the anterior edge of the fourth suborbital and the posterior edge of the anterior preorbital. The anterior preorbital extends anterodorsally and terminates just below the anterior limit of the palatine.

Located above the anterior rim of the orbit are two small supraorbitals (SRO, Fig. 10). The shorter anterior supraorbital is attached to the lateral edge of the palatine;

the posterior supraorbital is attached to the lateral edge of the frontal.

Two scleral bones (not shown) lie within the orbit and form an almost complete ring around the eye.

Nasals

The small paired nasal bones (N, Fig. 10) lie above the supraorbitals and are loosely connected to the cranium.

Maxillary Series

This series includes the premaxillaries, the maxillaries, and the supplemental maxillaries.

The small, curved premaxillaries (PMX, Figs. 6, 10) form the anterior limits of the snout. The broadened dorsal ends of the premaxillaries are connected to the ethmoid by cartilage-like material while the midlateral portion is in direct contact with an anterior knob of the maxillaries. The lower end of each premaxillary is connected to the maxillary by cartilage-like material.

Lying behind the premaxillaries are the much larger maxillaries (MX, Figs. 6, 10), the upper ends of which are in contact with the ethmoid and the vomer. A posterior condyle in this same area articulates with the palatine. The free end of the maxillary extends backward to about the center of the orbit when the mouth is closed. Loosely attached to the free end of the maxillary are two smaller supplemental maxillaries (SMX, Figs. 6, 10).

Mandibular Series

The dentaries, the angulars, the splenials, and the articulars are the bones of the mandible.

The dentary (DEN, Figs. 5, 6, 10) constitutes the largest portion of the mandible and meets its counterpart from the other side at the tip of the lower jaw. Behind the dentary is the triangular articular (ART, Figs. 5, 6, 10). The anterior portion of the articular joins the dentary while the posterior portion is recessed for articulation with the quadrate. Just below the articulation point of the lower jaw is the small angular bone (AN, Figs. 5, 10) which is joined to the ventral margin of the articular and to the posterior end of the dentary. The splenial (SPL, Fig. 5) is a small inconspicuous bone located mesiad to and fused with the articular. The splenial is very important as a point of muscular attachment for the lower jaw.

Hyobranchial Apparatus

The hyobranchial apparatus is composed of two units, the hyoid arch and the branchial arches. The hyoid arch consists of the interhyals, the epihyals, the ceratohyals, the basihyals, the glossohyal, and the urohyal. Closely associated with the hyoid arch are the branchiostegal rays. Bones of the branchial arches are the suspensory pharyngeals, the epibranchials, the pharyngobranchials, the upper pharyngeals, the ceratobranchials, the hypobranchials, the basibranchials, and the lower pharyngeals.

The hyoid arch is suspended from the cranium by means of a cartilaginous connection between the shank of the hyomandibular and the uppermost bones of the arch, the small interhyals (IHY, Figs. 5, 6, 8). The lower end of the interhyal is connected by cartilage to the upper posterior margin of the broad epihyal (EHY, Figs. 6, 8). Anterior to each epihyal, and connected to it by cartilage, is a larger ceratohyal (CHY, Figs. 6, 8). The anterior ends of the ceratohyals meet the four basihyals (BHY, Figs. 6, 8), of which there is an upper and a lower element on each side. Each epihyal is pierced by one large and three smaller foramina. Each ceratohyal is pierced by one large foramen.

The small, spatulate glossohyal (GHY, Figs. 8, 9), or tongue bone, is connected to the anterior end of the first basihyal. Attached to the basihyal below and extending backward to the coracoid is the single, trough-shaped urohyal (UHY, Fig. 9).

Seven branchiostegal rays (BRG, Figs. 6, 8, 10) are attached to the lateral surface of the hyoid arch. The knobbed anterior end of each of the first four rays fits into a perforation in the ceratohyal while the expanded anterior end of each of the last three is loosely connected to the ceratohyal and epihyal. The first branchiostegal ray is the smallest of the series; the remaining six are progressively larger.

The branchial apparatus is suspended from the cranium by a pair of small suspensory pharyngeals (S.PH, Figs. 7, 9). The small end of each suspensory pharyngeal is attached to the base of the wing of the parasphenoid. The broader end of the suspensory pharyngeal is attached to the epibranchial (EBR, Figs. 7, 9) of the first gill arch. Anteroventrally the branchial apparatus is attached to the basihyals of the hyoid arch.

There are five pairs of gill arches, the first two of which are composed of four separate bones. The third and fourth arches are supported by three separate bones, and the fifth arch by two bones.

Medially situated in the upper element of the branchial apparatus are the three pairs of pharyngobranchials (PBR, Figs. 7, 9). Each pharyngobranchial connects to a corresponding epibranchial which extends posterolaterally to the upper angle of the arch. This connection is accentuated in the first two arches by a small lateral projection of the pharyngobranchial which approaches a similar medial projection of the epibranchial. Only the medial projection is present in the third arch, where the pharyngobranchial is flat and triangular. The epibranchial of the fourth arch bears a thin osseous flange which is medially concave. A cartilaginous extension of this flange curves medially to form an imperfect hemisphere. Contained within each hemisphere are two rows of delicate gill rakers. This structure is very similar to the "pharyngeal pockets" of _Dorosoma cepedianum_ (Lagler and Kraatz; 1944). Anteriorly this cartilage is connected to a posterodorsal spicule of the third epibranchial; posteriorly it is contiguous with the lower pharyngeal. The remaining upper element of the branchial apparatus is the broad, thin upper pharyngeal (U.PH, Fig. 7). The anteromedial end of the fourth epibranchial is attached to the dorsal surface of the upper pharyngeal.

A ceratobranchial (CBR, Figs. 8, 9) is attached by cartilage to the distal end of each of the first four epibranchials. These ceratobranchials extend ventrally and slightly anteriorly. Each of the ceratobranchials of the first two arches connects to an elongate hypobranchial (HBR, Figs. 8, 9) which in turn extends down to attach to basibranchials (BBR, Figs. 8, 9) one and two, respectively. In arch three the hypobranchial is greatly reduced and is contiguous with the second basibranchial. The lower element of the fifth arch consists of one bone, the lower pharyngeal (L.PH, Fig. 8), which connects anteroventrally to the fourth ceratohyal. The dorsomedial surface of the lower pharyngeal bears a thin, elongate crest.

The inner surface of each gill arch bears one row of ossified filamentous gill rakers (not shown). In arch number one the rakers from the epibranchial extend down and overlap those on the upper half of the ceratobranchial. The uppermost eighteen to twenty rakers on the ceratobranchial of the first arch become progressively shorter toward the angle of the arch. This condition prevails for the other arches but is not so pronounced as in the first. Each raker is composed of an outer long, and an inner shorter, portion. Two rows of minute, spine-like processes occur on the medial surface of the long element of each raker.

The Girdles of B. *patronus*

Pectoral Girdle

The posttemporal (PTM, Figs. 3, 10) is the uppermost bone of the pectoral girdle. Its upper arm is attached to the flattened posterolateral surface of the epiotic. A second arm of the posttemporal extends from a ventromedial position and is attached to the opisthotic.

Anterolateral to the upper part of the posttemporal is the supratemporal (STM, Figs. 3, 10) which separates above the temporal groove; one part is attached to the parietal and the other to the sphenotic. Posteriorly the supratemporal is attached to the anterolateral surface of the posttemporal. The lateral surface of the supratemporal provides a passageway for the latero-sensory canal system.

Ventrally the posttemporal overlaps the dorsal end of the supracleithrum (SCL, Fig. 10). A flattened scale-like extension forms the posterodorsal limit of the supracleithrum. The mesial surface of the narrower ventral portion of the supracleithrum overlaps the cleithrum (CL, Figs. 10, 11, 12, 13).

The pointed distal end of the cleithrum terminates just below the upper part of the supracleithrum. Otherwise, the dorsal extension of the cleithrum is broadened anteriorly and is roughly T-shaped in cross-sectional view. Ventrally the cleithrum broadens into a thin curved structure with a concave, ventrolateral surface. The cleithrum meets its counterpart from the opposite side on the midline. The union of the cleithra is enhanced by small interlocking elements along their dorsomedial margins. A thin, saber-like, dorsal projection arises from each cleithrum just behind this juncture.

The flat, slender postcleithrum (PCL, Fig. 10), with its dorsal end rigidly fixed between the cleithrum and the supracleithrum, extends ventrally behind the pectoral fin and is adherent to an abdominal scute.

The ventromedial margin of the cleithrum joins the thin coracoid (COR, Figs. 10, 11, 12, 13). The paired coracoids meet along the midventral line and lie within the entrenchment formed by the abdominal scutes. Posteriorly each coracoid is lattice-like and ends in an upwardly directed keel.

Arising from a mesial projection formed at the juncture of the coracoid and the scapular is the mesocoracoid (MOC, Fig. 12) which arches over to join the anteromesial margin of the cleithrum. The large scapular foramen is obscured in a mesial view by the mesocoracoid.

The scapula (SCA, Figs. 10, 12, 13) is attached to the posteroventral margin of the cleithrum and to the posterodorsal margin of the coracoid. Its connection with the mesocoracoid was mentioned above. The anterior portion of the scapula is pierced by the scapular foramen. Posteriorly the scapula provides a base for the attachment of small actinosts (ACT, Figs. 12, 13) which support the rays of the pectoral fin (PC.F, Fig. 13).

Pelvic Girdle

The pelvic girdle is attached to the muscles of the body wall and consists of two, thin cuneiform pelvic bones (P.B, Figs. 14, 15) and the small actinosts. The posterior end of each pelvic bone is thickened into an irregular-surfaced nodule to which the four small actinosts are attached. These actinosts support the rays of the pelvic fin (PV.F, Figs. 14, 15). The posteroventral margins of the pelvic bones are separated. Their dorsal margins meet but are not joined except at the posterior end.

The Vertebral Column and Associated Structures of <u>B. patronus</u>

The vertebral column may contain from 42 to 48 vertebrae, but the usual number is between 45 and 47 (Hildebrand; 1948). Specimens illustrated here had 46, including the urostylar segment. Eight of the vertebrae and the urostylar segment are illustrated in figures 18-34. Structures mentioned in the following discussion appear in several illustrations, but reference will be made only to that figure in which the structure is labeled for the first time.

The first haemal arch occurs at the 16th or 17th vertebra. Vertebrae anterior to this level are those of the abdominal or trunk region; the remaining vertebrae are those of the caudal region.

The centrum (C, Fig. 19) of each vertebra is pierced by a median opening which marks the passageway for the remnant of the notochord. A neurapophysis (NP, Fig. 19) arises from the right and left dorsolateral surface of each vertebra. Each neurapophysis extends dorsomedially and joins its counterpart along the middorsal line to form the neural spine (N.S, Fig. 19). The space enclosed by the neural arch (N.A, Fig. 19) is limited by the neurapophyses and the dorsal surface of the centrum. Posterolaterad to each neural spine is a thin intermuscular bone, the epimeral (EM, Fig. 18). The shape and position of the epimerals are variable. A haemal rib (R, Fig. 18) is associated with each of the anterior 25 vertebrae. With the exception of the first rib, these ribs are connected ventromedially to an abdominal scute (A.S, Fig. 20). A filamentous bone, the epicentral (EC, Fig. 19), extends posterolaterally from each of the first 30 vertebrae. A series of variously-shaped hypomerals (HM, Fig. 20) occurs in the lateral muscles of the trunk. Only the anterior two vertebrae are without an associated hypomeral. The small anteriorly-projecting process arising near the base of each neurapophysis is the neural prezygapophysis (N.PZ, Fig. 20); this structure is obscure on the first vertebra. On the anterior 20 vertebrae another small process, the neural roof plate (N.R.P, Fig. 19) extends anteromedially from above the neural prezygapophysis. In the anterior 13 vertebrae the neural roof plates join above the neural arch. A small parapophysis (PAP, Fig. 18) projects down from the anterior ventrolateral surface of the abdominal vertebrae to meet the proximal end of the haemal rib. The parapophyses become progressively longer toward the tail and are termed haemapophyses (HP, Fig. 26) where they join medially to enclose a haemal arch below each vertebra. The haemapophyses form the haemal spines (H.S, Fig. 29) in vertebrae 24-46. A small anterior process, the haemal prezygapophysis (H.PZ, Fig. 28), arises from the haemapophysis in the region of the twenty-fifth vertebra and is present on the remaining haemapophyses. The posterior end of each vertebra gives rise to two pairs of processes. From each dorsolateral surface a neural postzygapophysis (N.PTZ, Fig. 18) extends backward to articulate with a neural prezygapophysis of the succeeding vertebra. The ventrolateral surface of each vertebra gives rise to a haemal postzygapophysis (H.PTZ, Fig. 24). The haemal postzygapophyses serve as articulating mechanisms in the last 20 to 25 vertebrae.

Regional Account of the Vertebrae

The following notations are designed to point out the major changes occurring in the vertebrae and associated structures, starting with the first vertebra and proceeding to the urostylar segment.

Vertebra 1 (Figs. 18, 19): The haemal ribs are ventrally bifurcate and free. The epicentrals are attached to the dorsomedial ends of the rib. The epimerals are branched distally. These branches, plus the osseous brushes and the filamentiferous rods from the cranium, constitute the numerous small bones of the nape. The neural roof plates bridge over the neural arch; neural prezygapophyses are wanting. The neural postzygapophyses are well defined, but the haemal postzygapophyses are minute.

Vertebra 3 (Figs. 20, 21): The haemal rib is long and ventrally associated with an abdominal scute (this is also the case for the second rib). The first hypomeral occurs as a single structure attached dorsomedially to the rib. The epimeral is trichotomous and the neural prezygapophyses are apparent.

Vertebra 7 (Figs. 22, 23): The haemal rib is attached to an abdominal scute and the hypomerals are dorsally bifurcate; the anterior branch is attached to the rib.

Vertebra 14 (Figs. 24, 25): The haemal rib is ventrally contiguous with a highly modified abdominal scute. The parapophyses show a slight ventral curvature and the distal end of the neural spine is forked; however, the latter condition may be affected by the clearing process. The neural roof plates have rotated to the anterior surface of the neurapophyses.

Vertebra 20 (Figs. 26, 27): The hypomerals are dorsally trichotomous and lie free in the trunk muscles. The haemapophyses replace the parapophyses and are bridged medially to enclose the fourth haemal arch. Proximally the haemal ribs adhere to the ventrolateral surfaces of the haemapophyses. Each haemal postzygapophysis is pierced by a small foramen. The epimerals are ventrally bifurcate.

Vertebra 25 (Figs. 28, 29): The haemal ribs are greatly shortened. Their dorsal ends adhere to the haemal spine while the ventromedial ends join the smallest and last abdominal scute. The bifurcate hypomerals are greatly shortened. The third pair of haemal prezygapophyses occur on the haemapophyses. The haemal postzygapophyses are without foramina.

Vertebra 30 (Figs. 30, 31): The haemal ribs are wanting (the last pair are associated with vertebra 26). The hypomerals and epimerals are shortened and have progressively assumed an anteroposterior orientation. The haemal spine is long and the haemal prezygapophyses are close to the centrum.

Vertebra 40 (Figs. 32, 33): The hypomerals and epimerals are unbranched and assume an almost horizontal anteroposterior position. The haemal spine is conspicuously adpressed toward the centrum.

Other Intermuscular Bones

Two other paired series of intermuscular bones are discernible in cleared specimens. Both are composed of slender unbranched bones which lie free in the musculature just below the skin. An upper series of 20 to 30 bones lie on each side of the midline in the vicinity of the dorsal fin. The foremost bone of this series is anterior to the dorsal fin; the last bone is just anterior to the caudal fin. Each bone extends posteroventrally and those near the end of the series lie in a near-horizontal plane.

A lower series consisting of three to four bones lies on each side of the body just above the posterior limit of the anal fin. The bones of this series extend anterodorsally.

Urostylar Segment

The urostylar segment provides a firm but flexible basis for the attachment of the caudal fin rays. Ten individual elements of this structure are discernible. The last vertebra is greatly modified with articulating surfaces below and behind. The posteriorly entrenchant urostyle (URS, Fig. 34), with two laterally associated small bones, provides the basis of attachment for the upper four laterally compressed hypurals. The remaining three hypurals (also laterally compressed) are more closely associated with the vertebra. The haemal spines of the penultimate and antepenultimate vertebrae are elongate and laterally compressed to contribute to the support of the caudal fin. A median keel arises from the lower anterior surface of the urostyle and extends posterodorsally.

The urostylar segment supports the 35 or 36 rays of the caudal fin. Each ray is composed of two elements, with the exception of the most anterior ray, above and below, which is single. Eight to nine rays precede the urostyle and approximately the same number precede the most ventrad hypural. The remaining rays are attached to the lateral surfaces of the flattened hypurals. The pointed proximal end of each ray is unjointed. The distal end of each ray is jointed and, in most instances, branched. The proximal ends of the two rays immediately above and below the fork of the caudal fin are xiphiform.

The Interspinal Bones and Associated Structures of B. patronus

Three series of unpaired interspinal bones occur in the menhaden. One series, the interneural, is associated with the dorsal fin. Another, the interhaemal, is associated with the anal fin. The supraneural series lies in the dorsal muscles between the dorsal fin and the occiput.

Interneural Series

Twenty interneural spines (INR.S, Fig. 16) lie in the muscles immediately below the dorsal fin. The pointed distal end of each of the dagger-shaped anterior interneurals extends between two neural spines. The distal end of the more cylindrical, posterior interneurals is anteriorly directed and two may lie between the same two neural spines. The most anterior interneural possesses a thin anterior keel; succeeding ones are progressively more cylindrical toward the rear. The proximal end of each interneural is enlarged and elongate and is connected to its adjacent fellows. The posterodorsal end of each interneural lies just above the anterodorsal surface of the succeeding one, a condition more pronounced toward the rear, starting with the eighth bone, where the posterior extension is a separate element. The last bone of this series is the narrow, posteriorly directed dorsal fin stay (D.ST, Fig. 16)

Each dorsal fin ray (D.R, Fig. 16) is composed of two parts. Except for the first two rays, a pair of small bones, the pterygophores, lies between the proximal end of each ray and the adjacent interneural. The paired elements of each ray are joined medially except in the region of the pterygophores. Distally the fin rays are jointed and branched.

Interhaemal Series

The interhaemal spines (IHM.S, Fig. 17) lie immediately above the anal fin. Approximately 20 bones comprise this series. The interhaemals are narrow and cylindrical with knobbed, horizontally-elongate ventral ends which are joined to each other with cartilage. The last bone of this series is the bifurcate, horizontal anal fin stay (A.ST, Fig. 17). The last interhaemal spine arises from the anterodorsal surface of the stay. Attached to the ventral surface of each interhaemal (except the first) is a pair of small pterygophores (not shown) which lie between the broadened ends of the two elements of each anal fin ray (A.R, Fig. 17). The two elements of each fin ray join below the pterygophores. Except for the first two, the anal fin rays are jointed distally and all rays succeeding number four are branched distally.

Supraneural Series

The supraneural series (SN.B, Figs. 18, 20, 22) consists of ten spike-shaped bones which lie along the midline between the dorsal fin and the occiput. The dorsal end of each is embedded just below the skin from which point it descends between the muscles of the right and left sides. The most anterior supraneural is the broadest of the series and lies in front of the first neural spine. The succeeding supraneurals are progressively more cylindrical and each lies between two neural spines.

The Scales of <u>B</u>. <u>patronus</u>

The discussion here deals with the scales, the abdominal scutes, and the axillary appendages.

The size and shape of the scales (Figs. 35, 37, 39) vary from one part of the body to another. Their posterior margins are pectinate and the greater portion of each scale is covered by preceding scales. The exposed portion of the scale is generally without circuli.

A series of 29 (28-32; Hildebrand; 1948) bony elements, the abdominal scutes (A.S, Figs. 10, 14, 20-29), extend along the ventral midline from just anterior to the coracoid to the anus. Each scute is V-shaped and possesses an anterior extension which lies in the trough of the preceding scute. All scutes except the anterior seven and the last one bear pointed, dorsolateral projections which extend under the skin and are associated with the haemal ribs. Twelve scutes precede the pelvic fin. The dorsal extension of the thirteenth scute is greatly reduced or absent. The last scute is reduced in size.

The axillary pectoral and axillary pelvic appendages (not illustrated) consist of two or three elongate and posteriorly-pointed scales. They are attached just above the base of the fin in a typical scale-like manner. The length of the longest element of the axillary appendage is usually about half that of the fin.

Osteological Comparison of B. patronus and B. gunteri

Certain differences between B. patronus and B. gunteri given by Hildebrand (1948) pertain to osteological features. These differences concern the scales, the number of vertebrae, the shape of the pelvic fins, and the radiating striae on the opercle. These differences may be summarized as follows:

B. patronus	B. gunteri
Scales: 36-50 oblique series crossing side of body; larger than in gunteri.	Scales: 60-75 oblique series crossing side of body; smaller.
Vertebrae: 42-48, usually 45 to 47.	Vertebrae: 43 or 44, rarely 42.
Pelvic fins: posterior margin convex; little difference in length of fin rays.	Pelvic fins: posterior margin oblique; outermost rays larger than innermost.
Radiating striae on opercle: pronounced.	Radiating striae on opercle: feeble or none.

The osteological features of both B. patronus and B. gunteri show variation with size. It is therefore necessary to compare specimens of approximately equal size. When comparing the scales of the two it is further necessary to compare those from the same part of the body. Observations are misleading if this procedure is not followed.

Based on evidence presented here, Hildebrand's characters are for the most part recognizable with respect to species. The scales of the two species differ in size and number. The major difference is that a greater portion of the scale is exposed on patronus. The pectinations on the scales from gunteri (160 mm. in total length) are more narrow and spaced farther apart than those on the scales of patronus (Figs. 35-40).

The number of vertebrae in specimens examined here was 46 and 47 for patronus and 44 for gunteri. The first haemal arch in gunteri occurs on the fifteenth vertebra. On the basis used above for dividing abdominal and caudal vertebrae, this indicates that the number of abdominal vertebrae in gunteri is less than in patronus. The structures associated with the vertebrae are not noticeably different between the two species.

The pelvic fins of specimens examined for this study agree with the characters presented by Hildebrand (Figs. 41, 42); however, the difference is often difficult to recognize.

The difference in the radiating striae on the opercle is another character which is difficult to evaluate. However, in the large specimen of gunteri examined here, the striae are less pronounced. In two smaller specimens of gunteri the striae are easily discernible and are not noticeably different from those of patronus. The evidence suggests that this character might be more applicable to large specimens (greater than 160 mm. in total length).

Based on evidence from this study, the osteology, other than those features mentioned above, is not appreciably different between patronus and gunteri. Certain features vary with the size of the specimen, but the variation is as great within a species as between two species. Among those features showing variation with size, the following are more prominent.

The orbitosphenoid is decurved more in larger specimens.

The posterior extension of the pterotic is blade-like in large specimens and more cylindrical in smaller ones.

The depth and length of the wings of the parasphenoid are proportionately brooder and shorter in large specimens.

Larger specimens have a greater number of intermuscular bones in the series located to the right and left of the mid-dorsal line.

Certain other variations were observed. Most of these pertain to the margins of some of the thinner bones and to their juncture with other bones. Such variations do not show any general trend.

It should be pointed out that this comparison is based on observation and does not attempt to incorporate meristic data pertaining to size relationships of bones. It should also be noted that the comparison is based on only four specimens of gunteri.

Conclusion

Having examined the osteology of Brevoortia patronus and B. gunteri, the writer is unable to enumerate any osteological features other than those previously recorded which would allow distinction between the two species. How this situation compares with other species within this genus is not known.

This study indicates a close relationship between the two species. However, to say that the two should not be separated at the species level would be to disregard certain morphological differences between them which cannot be explained on the basis of geographic variation. Evidence has been given by Gunter (1945) that there is some ecological difference between the two, with B. gunteri being more common in waters of lower salinity. A thorough study of the ecological relationships between the two should indicate the degree of isolation between them if such exists. Until such information is available the true taxomonic relationship of B. patronus and B. gunteri will likely remain obscure.

The presence of "pharyngeal pockets", a specialized structure associated with the fourth gill arch, indicates a possible close relationship between Brevoortia and Dorosoma.

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Explanation of Figure Abbreviations

ACT - actinosts
A.F - auditory fenestra
ALI - alisphenoid
AN - angular
A.R - anal fin ray
ART - articular
A.S - abdominal scute
A.ST - anal fin stay
AU.B - auditory bulla

B.A - bony arch
BBR - basibranchial
BHY - basihyal
BOC - basioccipital
BRG - branchiostegal

C - centrum
CBR - ceratobranchial
CHY - ceratohyal
CL - cleithrum
COR - coracoid

DEN - dentary
D.R - dorsal fin ray
D.ST - dorsal fin stay

EBR	-	epibranchial
EC	-	epicentral
EHY	-	epihyal
EM	-	epimeral
EP	-	epiotic
ETH	-	ethmoid
EX	-	exoccipital
F	-	frontal
F.M	-	foramen magnum
GHY	-	glossohyal
H.A	-	haemal arch
HBR	-	hypobranchial
HM	-	hypomeral
HP	-	haemapophyses
H.PTZ	-	haemal postzygapophyses
H.PZ	-	haemal prezygapophyses
H.S	-	haemal spine
HY	-	hyomandibular
HY.E	-	hyomandibular embrasure
IHM.S	-	interhaemal spine
IHY	-	interhyal
INR.S	-	interneural spine

IOP - interopercle

L.PH - lower pharyngeals

LS.C - latero-sensory canal

MOC - mesocoracoid

MSPT - mesopterygoid

MTPT - metapterygoid

MX - maxillary

MY - myodome

N - nasal

N.A - neural arch

NP - neurapophyses

N.PTZ - neural postzygapophyses

N.PZ - neural prezygapophyses

N.R.P - neural roof plate

N.S - neural spine

OP - opercle

OPI - opisthotic

OSP - orbitosphenoid

PAL - palatine

PAP - parapophyses

PAR - parietal

P.B	-	pelvic bone
PBR	-	pharyngobranchial
PC.F	-	pectoral fin
PCL	-	postcleithrum
PF	-	prefrontal
PMX	-	premaxillary
POB	-	preorbitals
POP	-	preopercle
PRO	-	prootic
PSP	-	parasphenoid
PT	-	pterygoid
PTM	-	posttemporal
PTR	-	pterotic
PV.F	-	pelvic fin
Q	-	quadrate
R	-	haemal rib
SBO	-	suborbitals
SCA	-	scapula
SCL	-	supracleithrum
SMX	-	supplemental maxillary
SN.B	-	supraneural bone
SOC	-	supraoccipital
SOP	-	subopercle

SP - sphenotic
S.PH - suspensory pharyngeal
SPL - splenial
SRO - supraorbitals
STM - supratemporal
SYM - symplectic

T.F - temporal foramen
T.G - temporal groove

UHY - urohyal
U.PH - upper pharyngeals
URS - urostyle

VO - vomer

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PLATE I

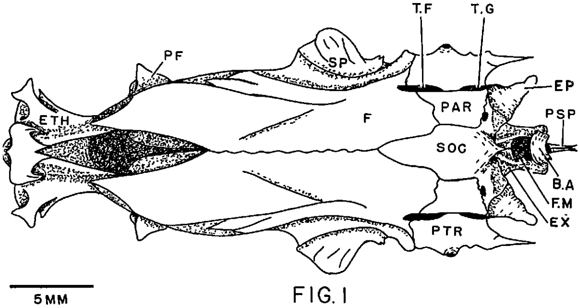


FIG. 1

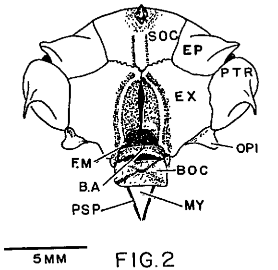


FIG. 2

PLATE II

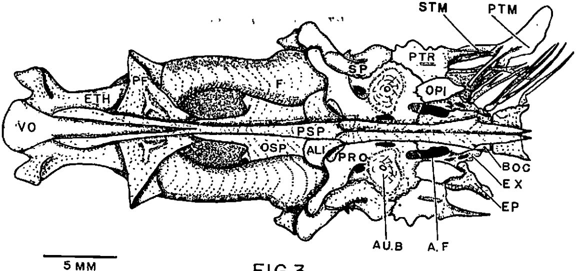


FIG.3

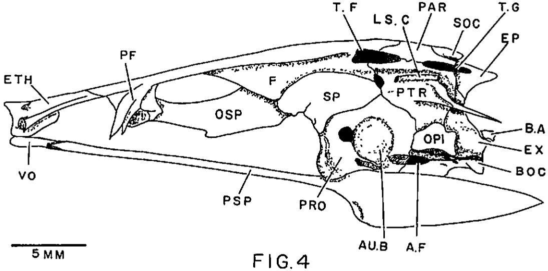


FIG.4

PLATE III

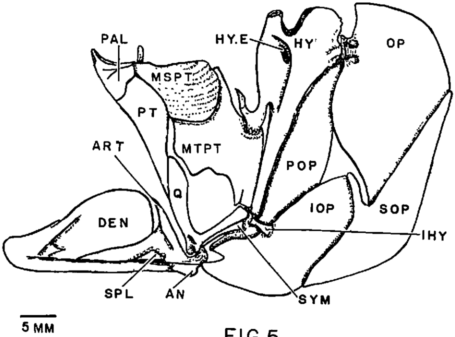


FIG.5

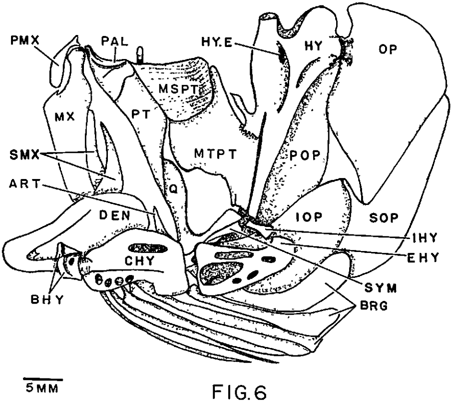


FIG.6

PLATE IV

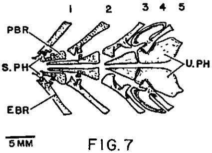


FIG. 7

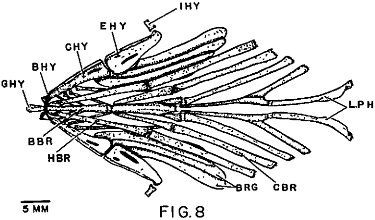


FIG. 8

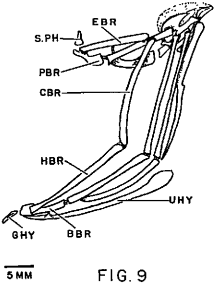


FIG. 9

PLATE V

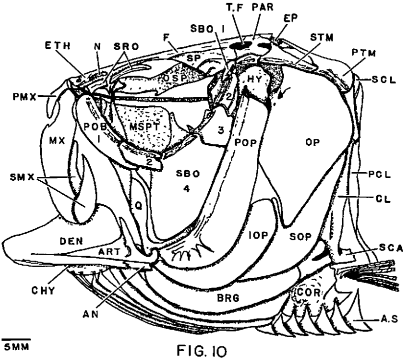


FIG. 10

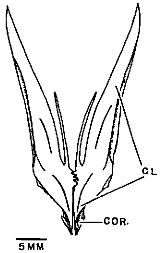


FIG. 11

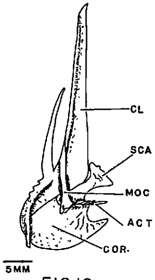


FIG. 12

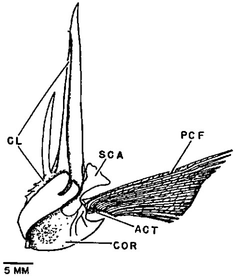


FIG. 13

PLATE VI

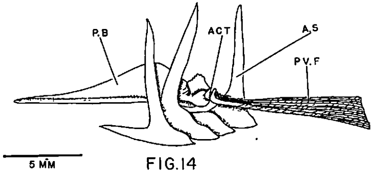


FIG.14

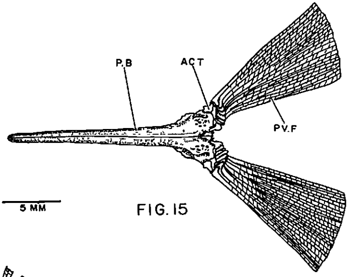


FIG. 15

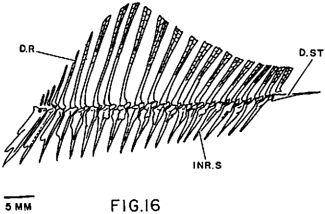


FIG.16

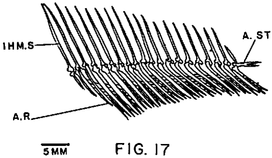


FIG. 17

PLATE VII

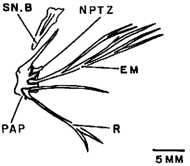


FIG. 18

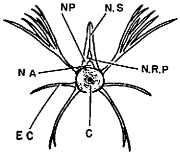


FIG. 19

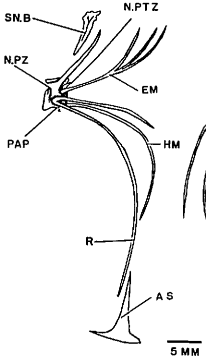


FIG. 20

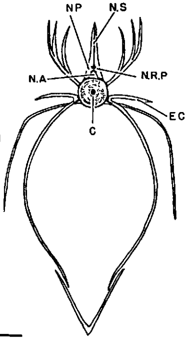


FIG. 21

PLATE VIII

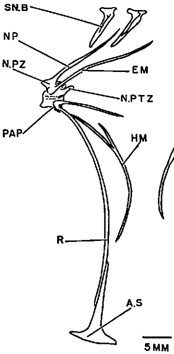


FIG. 22

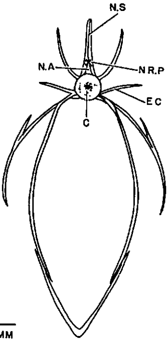


FIG. 23

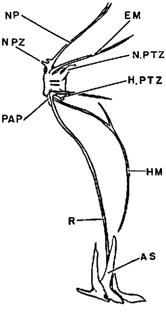


FIG. 24

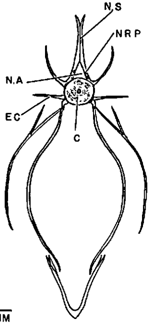


FIG.25

PLATE IX

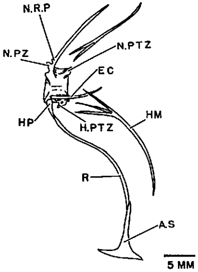


FIG.26

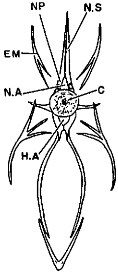


FIG. 27

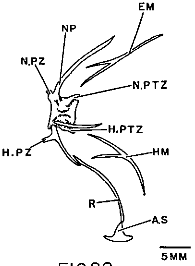


FIG.28

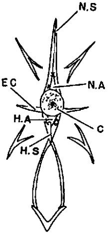


FIG.29

PLATE X

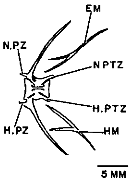


FIG.30

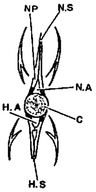


FIG. 31

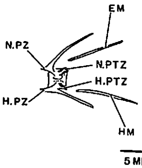


FIG.32

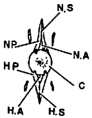


FIG.33

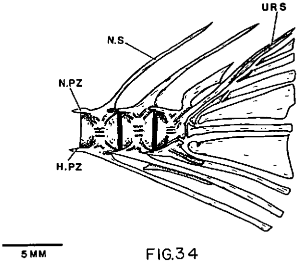


FIG.34

PLATE XI

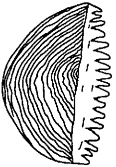


FIG. 35

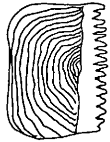


FIG. 37

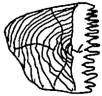


FIG. 39

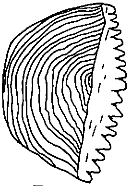


FIG. 36

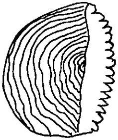


FIG. 38

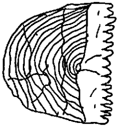
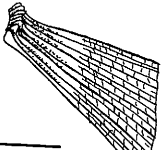


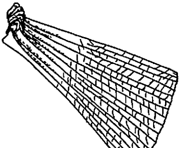
FIG. 40

5 MM



5 MM

FIG. 41



5 MM

FIG. 42