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The Development of the Weberian Ossicles in *Pantosteus Plebius*

John Lawrence Butler

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THE DEVELOPMENT OF THE WEBBERIAN OSSICLES
IN PANTOSTEUS PLEBIUS

By
John Lawrence Butler

A Thesis
Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science in Biology

The University of New Mexico

1959



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A Test

Submitted to the Faculty of the

Department of the Agriculture

Master of Science in Biology

The University of New Mexico

1922

This thesis, directed and approved by the candidate's committee, has been accepted by the Graduate Committee of the University of New Mexico in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

E. Castetter
DEAN

May 27, 1957
DATE

Thesis committee

William J. Koester
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facilities for the making of X-ray films, and gave suggestions ...
and criticism indispensable in the preparation of this report.
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for his photographic assistance.

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Chapter I

INTRODUCTION

The Weberian ossicles form a chain of tiny bones that connect the air bladder and the ear of many freshwater fishes. It is thought that the ossicles are derived at least in part from the vertebrae and that they serve to transmit vibrations or changes in hydrostatic pressure to the ear from the air bladder or swim bladder.

The Weberian apparatus, which was first described by Weber in 1820, is characteristic of the largest order of freshwater fishes, the Ostariophysi, a group that includes forty-two families, among which are the minnows, suckers, siluroids, and characids. The apparatus of the family Catostomidae, the suckers, is one of the more complex because the anterior vertebrae are more highly modified than in most other groups. Although the suckers have a more complex form of apparatus, they have received comparatively little study, and this is the first developmental investigation of the Weberian ossicles of any catostomid.

The species studied, Pantosteus plebius Baird and Girard, is commonly referred to as the Rio Grande mountain sucker. It is endemic to the mountain streams of the Rio Grande and Mimbres River basins (Koster, 1957, p. 46).

The Weberian apparatus in the adult Pantosteus plebius consists of a movable portion, the pars auditum, and a support,

THE WEBERIAN

The Weberian is a small, slender, elongated fish, with a pointed snout and a large eye. It is found in the shallow waters of the Amazon basin, where it feeds on small insects and other aquatic organisms. The fish is characterized by its unique shape and its ability to jump out of the water.

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the pars sustentaculum.

The pars auditum (plate 1, figure 1) is composed of four ossicles and an interossicular ligament. Beginning at the anterior end and passing posteriorly, the parts of the pars auditum are: the claustrum, scaphium, interossicular ligament, intercalarium, and tripus. The claustrum and scaphium form the connection of the Weberian apparatus to the internal ear; the interossicular ligament links the scaphium and intercalarium with the tripus, and this, in turn, is connected to the anterior wall of the air bladder.

The tripus, the largest of the ossicles, is a sickle-shaped bone, whose body or main portion had three processes or rami. The articular process extends laterally from the body of the tripus to the centrum of the third vertebra. The medial end of this process is flared and fits into a deep groove that runs vertically across the lateral side of the centrum. The posterior process or ramus extends from the body of the tripus to the air bladder where it tapers into a thin, delicate extension that is embedded in the tunica externa, the outer layer of the air bladder. This slender prolongation of the posterior ramus is the transformator process. It passes through the tissue of the air bladder and curves sufficiently so that its tip projects forward out of the tunica externa. The anterior process or ramus extends forward from the body of the tripus and is united with the other bones of the series by the interossicular ligament.

the same relationship.

The patella (Fig. 1, Table A) is composed of the
osteoid and an interosseous ligament. Beginning at the
anterior end and passing posteriorly, the base of the patella
articulates with the glenoid, humerus, interosseous
ligament, anterior, and posterior. The glenoid and
scapula form the connection of the osseous apparatus to
the internal wall of the interosseous ligament. The
scapula and interosseous with the humerus, and this, in turn,
is connected to the anterior wall of the air bladder.

The radius, the largest of the carpi, is a simple-
shaped bone, whose body or main portion has three processes
at base. The anterior process extends laterally from the
body at the tip of the radius to the center of the third vertebra.
The medial end of this process is flared and lies into a
deep groove that runs vertically across the lateral side of
the center. The posterior process or ramus extends from
the body at the tip to the air bladder where it tapers
into a thin, delicate structure that is embedded in the
anterior extensor, the outer layer of the air bladder. This
slender prolongation of the posterior ramus is the
transverse process. It passes through the lumen of the
air bladder and curves sufficiently so that the tip projects
forward out of the anterior extensor. The anterior process or
ramus extends forward from the body of the radius and is
united with the other bones of the carpus by the

interosseous ligament.

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Plate 1, Figure 1: Dissected Weberian Ossicles.

Plate 1, Figure 2: Anterior View of the Weberian Apparatus.

Plate 1, Figure 3: Colored View of the Weberian Apparatus.

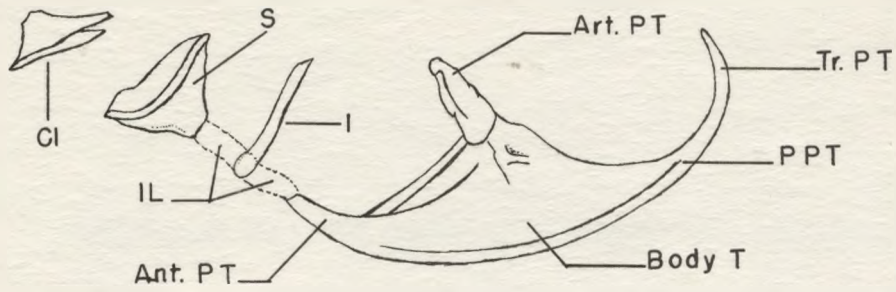


Fig. 1

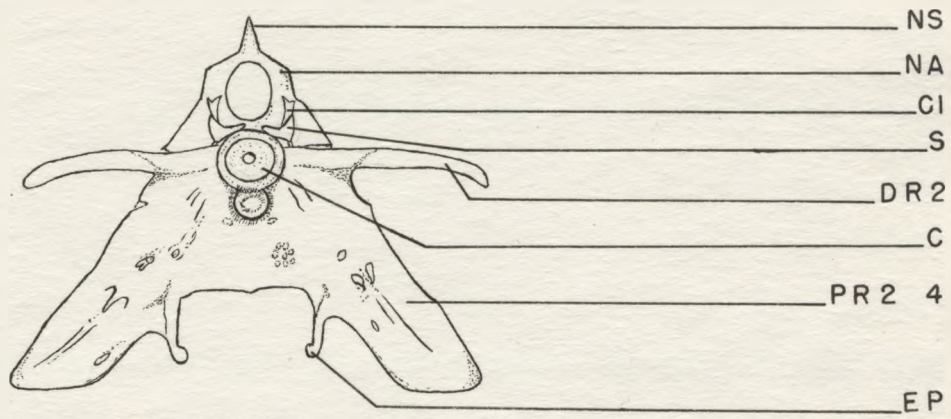


Fig. 2

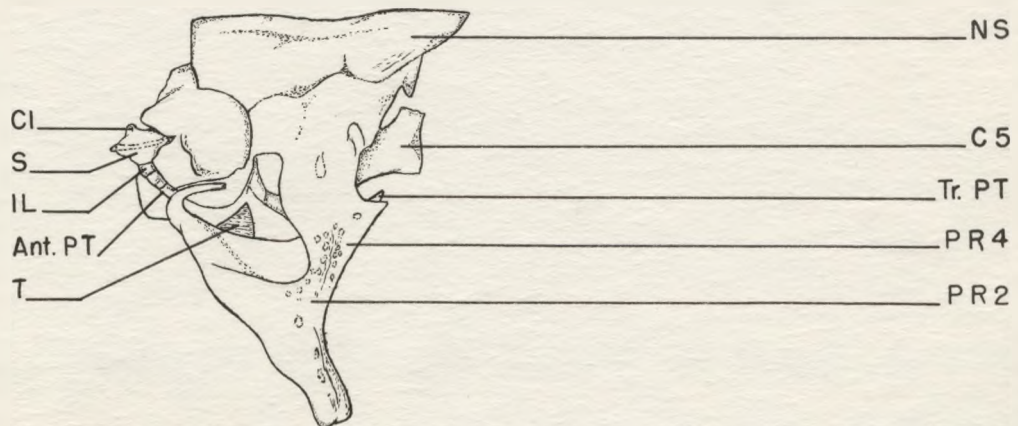


Fig. 3

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ΕΥΡΕΤΕ ΙΙ' ΕΥΡΕΤΕ 3: ΑΝΤΙΣΤΗΝ ΑΓΩΓΗ ΤΗΣ ΜΕΡΕΤΕΥΣ

ΕΥΡΕΤΕ ΙΙ' ΕΥΡΕΤΕ 3: ΔΟΞΟΥ ΑΓΩΓΗ ΤΗΣ ΜΕΡΕΤΕΥΣ ΥΒΔΟΥΚΤΑΙ.

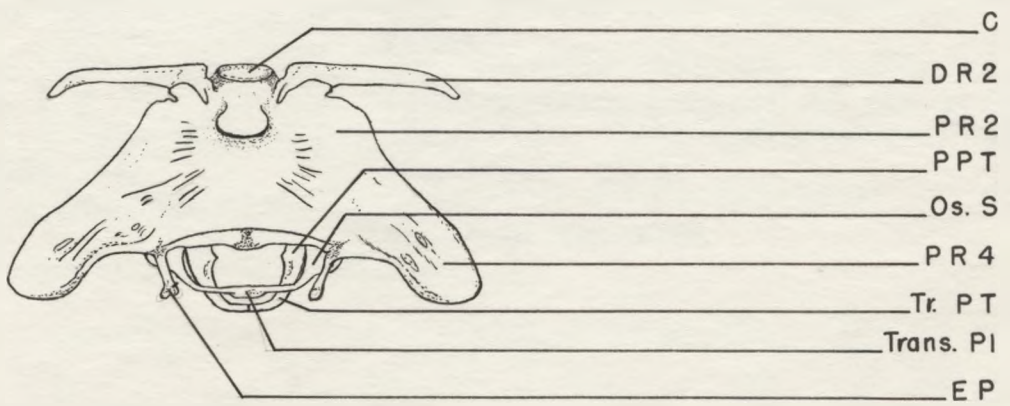
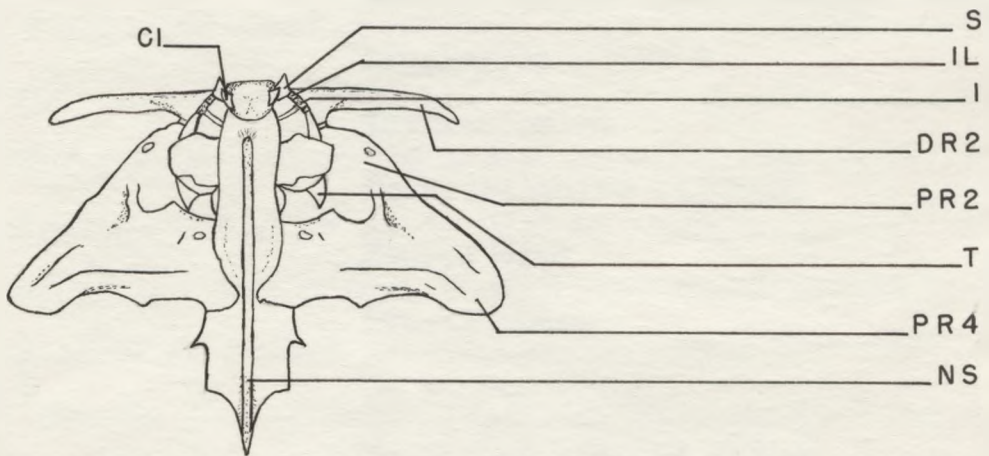
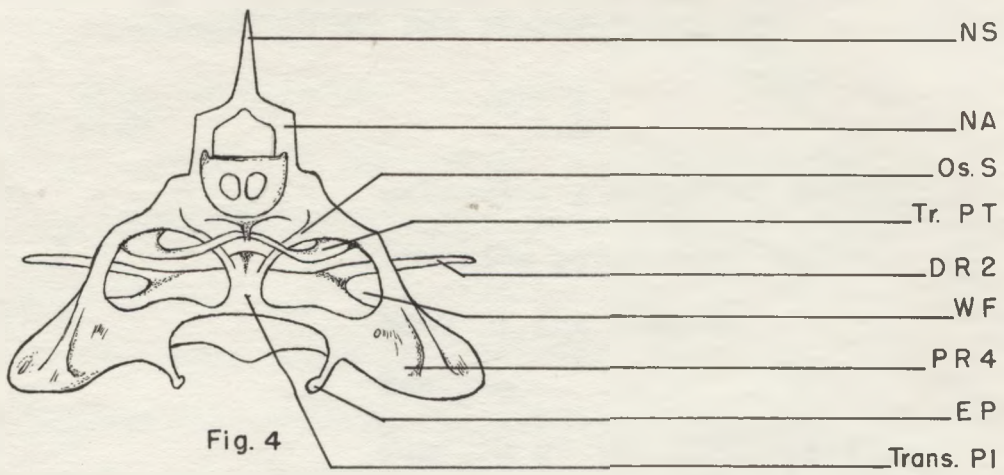
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ΕΥΡΕΤΕ ΙΙ' ΕΥΡΕΤΕ 1: ΕΥΡΕΤΕΥΣ ΑΓΩΓΗ ΤΗΣ ΜΕΡΕΤΕΥΣ

Plate II, Figure 1: Posterior View of the Weberian Apparatus.

Plate II, Figure 2: Dorsal View of the Weberian Apparatus.

Plate II, Figure 3: Ventral View of the Weberian Apparatus.



ABBREVIATIONS FOR PLATES I and II

ABBREVIATION

PART

Art. P T	Articular process of the tripus
Ant. P T	Anterior process of the tripus
Body T	Body of the tripus
C	Centrum
C5	Centrum of the fifth vertebra
C1	Claustum
DR2	Dorsal rib of the second vertebra
BP	Esophageal process
I	Intercalarium
IL	Interossicular ligament
NA	Neural arch
NS	Neural spine
Os. S	Os suspensorium
PPT	Posterior process tripus
PR2	Pleural rib of the second vertebra
PR4	Pleural rib of the fourth vertebra
S	Scaphium
T	Tripus
Tr. P T	Transformator process of the tripus
Trans. Pl	Transverse plate
WF	Weberian fenestra

Plate I, Figure 1: Dissected Weberian Ossicles.

Plate I, Figure 2: Anterior View of the Weberian Apparatus.

Plate I, Figure 3: Lateral View of the Weberian Apparatus.

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Trans. Pl	Transverse plate
WF	Weberian fenestra

ABBREVIATIONS FOR PARTS I AND II

ABBREVIATION	NAME
Art. P. I	Articular process of the atlas
Art. P. II	Articular process of the axis
Body T	Body of the vertebra
C	Centrum
CS	Centrum of the sacral vertebrae
CI	Clinoid
Dors	Dorsal rib of the second vertebra
DP	Dorsal process
I	Intercalarium
IL	Intercostal ligament
NA	Neural arch
NS	Neural spine
Os. S	Os sacrum
PPT	Posterior process of the atlas
PR2	Posterior rib of the second vertebra
PR4	Posterior rib of the fourth vertebra
S	Scapulum
T	Tragus
Tr. P. I	Transverse process of the atlas
Trans. P. II	Transverse process of the axis
Tr.	Transverse

The interossicular, or interosseous, ligament connects the anterior process of the tripus to the intercalarium and to the scaphium. In Pantosteus plebius the ligament is short and is divided into two halves by the insertion of the intercalarium.

The intercalarium is a slender, curved bone that articulates with the second vertebra and extends anteriorly and laterally to join the interossicular ligament. Two regions are distinguished: the shaft and the manubrium incudis, which is the enlarged lateral end that separates the interossicular ligament into two divisions.

The scaphium is a cup-shaped bone bearing three processes. The cup-shaped portion is the concha stapedis. The first of the processes, the central process, arises from the center of the outer convexity of the cup, is aimed laterally on the fish, and is the point of attachment for the interosseous ligament. The second process is directed ventrally and articulates with the second vertebra. The third process, which points toward the head, is an extension of a ridge that runs anteriorly along the cup from the central process.

The claustrum is also somewhat cup-shaped, but the medial depression is much smaller than that of the scaphium. The claustrum lies dorsomedially to the scaphium and is attached to it laterally.

The claustrum and scaphium plus an extension of the perilymph spaces form the connection between the Weberian ossicles and the membranous labyrinth of the ear. The

The interosseous, or interosseous, ligament is a broad
the anterior process of the tibia to the condyle of the
to the scaphoid. In the scaphoid, the ligament is short
and is divided into two parts by the insertion of the
interosseous.

The interosseous is a slender, cord-like structure
with the second vertebra and extends inferiorly and laterally
to join the interosseous ligament. The ligament is
distinguished: the first part is the upper part, which
is the enlarged part, and the second part is the lower part,
ligament into two divisions.

The scaphoid is a trapezoid, more flattened than triangular.
The cup-shaped portion is the upper part. The lateral
the process. The central process, which is the center
of the concave surface of the art. is fixed inferiorly in the
tibia, and is the point of attachment for the interosseous
ligament. The second process is directed vertically and
articulates with the second vertebra. The third process,
which points toward the art., is an extension of a ridge
that runs anteriorly along the top of the central process.

The clavicle is a slender, S-shaped bone, and the
medial depression is the medial part, and the lateral
The clavicle lies horizontally in the neck, and is
attached to the scapula.

The clavicle and scapula are the bones of the
pectoral girdle, and form the connection between the
axial and the appendicular skeleton of the human body.

perilymph spaces, which occur between the membranous labyrinth of the internal ear and the bone of the cranium, extend posteriorly from each ear. The extensions from the two sides join and form the atrium sinus impar, which surrounds the dorsal half of the spinal cord back as far as the first vertebra. The scaphium forms a lateral part, and the claustrum a dorsolateral part, of the wall of the sinus.

The Weberian ossicles have three points of articulation with the vertebral column. These points, which act as fulcra for the movement of the ossicles, lie at the medial ends of the ventral process of the scaphium, shaft of the intercalarium, and articular process of the tripus.

The pars sustentaculum (plates I & II) includes the first four vertebrae, all of which are highly modified from the pattern of the remaining trunk vertebrae. There is much fusion of the parts. The centra of the second, third, and fourth vertebrae are coalesced. The supradorsal or neural spine elements of these three vertebrae form a large, continuous neural spine that is the most dorsal portion of the pars sustentaculum. The distal ends of the second and fourth ribs are joined.

The first vertebra is a thin disc without ribs or other projections. Only the centrum is present and it is greatly flattened antero-posteriorly.

The centrum of the second vertebra bears two processes. A transverse process, which represents a modified dorsal rib (Watson, 1939, p. 463), is directed laterally and slightly

peritrophic spaces, which occur between the membrane labyrinth of the lateral ear and the bone of the cranium, extend posteriorly from each ear. The extensions from the two sides join and form the auricular space, which surrounds the dorsal half of the spinal cord back as far as the first vertebra. The scapula forms a lateral part, and the clavicle a dorsolateral part, of the wall of the sternum. The Weberian ossicles have three points of articulation with the vertebral column. These points, which are as follows for the movement of the ossicles, lie at the medial ends of the ventral process of the scapula, a part of the intercalarium, and anterior process of the clavicle. The para vertebral column (column I & II) includes the first four vertebrae, all of which are highly modified from the pattern of the remaining trunk vertebrae. There is such fusion of the parts. The centrum of the second, third, and fourth vertebrae are separated. The scapula of the second spine elements of these three vertebrae form a large, continuous neural spine that is the most dorsal portion of the para vertebral column. The distal ends of the second and fourth ribs are joined. The first vertebra is a ribless rib without ribs or other projections. Only the centrum is present and it is greatly flattened antero-posteriorly. The centrum of the second vertebra bears two processes. A transverse process, which represents a modified dorsal rib (Watson, 1908, p. 403), is directed laterally and slightly

posteriorly (plate II, figures 2 & 3), while a heavy, plate-like process, which represents a strongly modified ventral rib (Watson, 1939, p. 456), extends ventrally and caudally and fuses with the similarly modified rib of the fourth vertebra. The two ventral ribs of the second vertebra also fuse with one another beneath the centrum. The plate thus formed has a pair of posteriorly directed projections that are termed esophageal processes (plate I, figure 2) because of their proximity to the lateral walls of the esophagus.

The third vertebra lacks transverse and ventral processes. A deep, vertical groove in the lateral surface of the centrum receives the articular process of the tripus.

The fourth vertebra possesses a single, much enlarged rib that passes ventrally and forms, by its fusion with the ventral rib of the second vertebra, a complex structure that lies in contact with the anterior wall of the air bladder. Between the angle formed by the two ribs and the centra of the second, third, and fourth vertebra, there remains an opening, the Weberian fenestra, through which the tripus passes. The ventral ribs of the fourth vertebra give off at their bases the ossa suspensoria, which together form a transverse plate (plate II, figure 2). The tunica externa of the air bladder is continuous with this plate.

posteriorly (plate 12, figure 2, 3), while a deep, wide
liver process, and a transverse, and a small, rounded, and
tip (plate 12, figure 4), which is situated at the
and fused with the anterior, posterior, and lateral
ventrals. The two ventrals are of the same size and shape
and with one another beneath the anterior. The dorsal
process has a pair of posteriorly directed processes that
are termed posterior processes (plate 12, figure 5) because
of their proximity to the dorsal side of the organism.
The third ventral is a transverse and very broad
a deep, ventral groove in the middle of the dorsal
receives the anterior process of the liver.
The fourth ventral process is a single, small, rounded
tip that passes ventrally and later, by the liver, with the
ventral tip of the second ventral and the dorsal tip of the
liver in contact with the anterior wall of the air bladder.
Between the right lateral of the two tips and the ventral of
the second, third, and fourth ventrals, there is a small
opening, the lateral opening, which is called the liver.
process. The ventral tip of the fourth ventral is a
at their bases the posterior processes. When combined with a
transverse plate (plate 12, figure 6), the ventral extension
of the air bladder is continuous with this plate.

Chapter II

HISTORICAL SURVEY

Shortly after the initial description by Weber (1820) in his "De Aure et Auditu Hominis et Animalium. Pars. 1. De Aure Animalium aquatiliu," the apparatus was described in various species by several authors. Among the early investigators, Huschke (1822), St. Hilaire (publication of 1824, cited from Watson, 1939), Müller (1842), and Beaudelot (1868) were notable.

From his work on Siluris glanis, Weber (1820) judged the function of the apparatus to be related to audition and concluded that the ossicles were homologous with the mammalian ear bones. He therefore referred to them as the auditory ossicles. Three of the individual bones he called the malleus, incus, and stapes after their supposed mammalian homologues. The fourth bone, with no supposed counterpart in the mammals, Weber termed the claustrum.

Many of the investigators of the nineteenth century shared Weber's view and adopted his terminology, but some did not. St. Hilaire (vide Watson, 1939, p. 464), Müller (1842, pp. 323-328) and Beaudelot (1868, pp. 87-109), for example, disputed the homology of the ossicles with the ear bones of mammals and instead considered them to be parts of the anterior vertebrae. However, it was Bridge and Haddon (1889, 1892) who gave impetus to this concept which later

replaced that of Weber. They described the Weberian apparatus of ninety-two species of siluroids and replaced the misnomer "auditory ossicles" with a new term, Weberian ossicles, in honor of the investigator who first described them. They proposed the now commonly used terms, tripus, intercalarium, and scaphium, as substitutes for the names properly associated with the mammalian ear bones. The term claustrum used by Weber for the additional bone was retained by these authors. Bridge and Haddon (1892, p. 143) also suggested a hydrostatic function for the air bladder and the ossicles.

Not only did Müller realize that the ossicles were derivatives of the vertebrae, but he also was the first to conclude that the Weberian organ had systematic importance. He concluded that several externally diverse groups, the siluroids, cyprinids, and characids, were related because of the presence of this complex apparatus. In 1885, Sagemehl (pp. 1-119) used the Weberian apparatus as a taxonomic character with which to separate many fish from their earlier categories and combine them in a new group, the Ostariophysi.

Certain investigators, especially Wright (1884, pp. 249-250) who worked with Amiurus [= Ictalurus] catus, believed that the Weberian ossicles were not entirely derived from the vertebrae, but that connective tissue ossifications also contributed to the definitive structures. Wright first discovered the fused condition of the second, third, and fourth vertebrae, a condition found to a greater or lesser extent in all the Ostariophysi.

replaced that of ... of almost two species ... "advisory ... of the investigation ... proposed the ... and ... with the ... Weber for the ... Hodge and Hudson (1957, p. 1483) also suggested a ... function for the ...

Not only did Miller realize that the ... of the ... He concluded that ... alaroid, ... the presence of this complex ... (pp. 1-116) used the ... character with which to ... categories and ...

Certain investigators, ... who worked with ... the Weberian ... vertebrate, but that ... contributed to the ... discovered the ... fourth ...

... ..

The nomenclature in common usage in the literature published in German is the result of the work of Thilo (1908). For the term malleus as used by Weber, Thilo (1908, pp. 780-787) proposed the term Hebel; for the incus, Lenker; for the stapes, Deckel; and for the claustrum, Einlage. Thilo's experiments with pressure convinced him that the function of the Weberian apparatus was hydrostatic.

The apparatus in a catostomid, Ictiobus urus, was described briefly by Adams (1928). Adams (1928, p. 117) concluded that only the first three vertebrae were involved in the Weberian apparatus and that it was the third rather than the fourth ventral rib that was highly modified around the tripus and the anterior end of the air bladder.

Chranilov (1927, 1930) used the Weberian apparatus as an aid in classification within the order Ostariophysi.

Two more recent works, dealing with morphology of the Weberian apparatus, treat with the Catostomidae. Krumholz (1943) studied the Weberian apparatus of North American ostariophysines including eleven members of the Catostomidae. Nelson (1948) compared the Weberian structures in catostomids with reference to their significance in systematics.

The first complete embryological study was that by Nusbaum in 1908 on Cyprinus carpio, family Cyprinidae. He thought that the first three vertebrae formed part of the skull and that the ossicles were entirely derived from the fourth and fifth vertebrae. According to Nusbaum's interpretation the intercalarium was derived from the fourth

vertebra and the tripus from the fifth.

Matveiev (1929, pp. 464-465) agreed with Wright that the ossicles originated both from modified vertebrae and from other connective tissue elements. Matveiev discovered in Scardinius erythrophthalmus, a cyprinid, evidence that led him to conclude that both the intercalarium (1929, p. 501) and the scaphium (1929, p. 503) have dual origins.

The most recent work of an embryological nature is that of J. M. Watson (1939) on another cyprinid, the goldfish. In his excellent paper, Watson compared the development of the ossicles as seen in the goldfish with that described by previous authors. He corroborated the concept that both vertebral and connective tissue elements have a part in the origin of the ossicles. He (Watson, 1939, p. 453) discovered that an arch of cartilage dorsal to the first vertebra is continuous with the exoccipital bones of the cranium; this cartilaginous arch he called the "cartilage ring." In addition Watson (1939, p. 456) believed that the transverse processes of the second vertebra are homologous with dorsal ribs, that the ventral processes of the second and fourth vertebrae are homologous with pleural or ventral ribs, and that the ossa suspensoria are homologous with hemopophyses.

The Weberian mechanism has received considerable study of a morphological nature but much less attention has been given to developmental and physiological aspects. Among the studies concerned primarily with the function of the ossicles and the air bladder, the papers of Kuiper (1915)

and Evans (1925) are outstanding. Kuiper (1915, pp. 572-582) observed the reactions of fish to pressure changes, variations in light intensity, hydrostatic disturbances, and vibrations, both before and after the Weberian organ had been disrupted. He agreed with Weber that the organ was associated with the hearing of fishes. Evans (1925, pp. 547-574), studying many ostariophysines, discovered more evidence corroborating Weber's theory. Bridge and Haddon (1892, p. 142) thought the ossicular arrangement too lax to conduct rapid vibrations, but Evans found the Weberian organ capable of such. He also determined that it was possible for the air bladder to receive faint changes in the pressure impinging upon the sides of the fish. These changes were, he postulated, transferred to the internal ear by the ossicles. Subsequent investigators have been in agreement with Kuiper and Evans.

Other than the paper by Nelson (1948), which dealt with adult morphology and systematics, the Weberian apparatus of the family Catostomidae has had relatively little attention. The development of the apparatus in the catostomids apparently has not been studied previously. It is the purpose of this paper to describe the origins of the Weberian ossicles as seen in a common New Mexican catostomid, Pantosteus plebius, and to trace the developmental path of the Weberian apparatus to its mature condition.

Chapter III

MATERIALS AND METHODS

The specimens used in this study were from two sources. The majority were collected during June, 1958, from the backwaters of the Jemez River and the San Antonio Creek near Jemez Springs, New Mexico. The remainder of the fish studied were reared from eggs obtained from adults taken in the two above mentioned streams. After artificial fecundation, the eggs were incubated and the young raised in tanks at 16° C. Eight days were required for development before hatching. The larvae at hatching were approximately 8 mm. long and three days later were 9 mm., the size at which cartilage formation was apparent in the vertebral column of field-collected specimens. However, in aquarium-raised specimens, cartilage did not appear in the vertebrae until the fish were 10 mm. long. In general the aquarium-raised fish were about 1 mm. longer than the stream-reared specimens in a comparable stage of development. Therefore, a fish raised indoors reached a length of 11 mm. before it showed the same bone formation as a fish of 10 mm. collected from the normal habitat. All measurements quoted in this paper were taken from field-collected specimens.

The larval fish were either fixed in Bouin's fluid and preserved in 70% alcohol or were fixed and stored in 10% formalin. Transverse, frontal, and sagittal sections for

Chapter III

MATERIALS AND METHODS

The specimens used in this study were from two sources.

The majority were collected during June, 1955, from the backwaters of the James River and the San Antonio Creek near James Springs, New Mexico. The remainder of the fish studied were reared from eggs obtained from adults taken in the two above mentioned streams. After artificial insemination, the eggs were incubated and the young reared in James M. 1955. Night days were required for development of the larvae. The larvae at hatching were approximately 3 mm. long and three days later were 5 mm. long. The first cleavage formation was apparent in the ventral column of cells collected specimens. However, in specimens reared specimens, cartilage did not appear in the ventral until the fish were 10 mm. long. In general the specimens reared fish were about 1 mm. longer than the stream-reared specimens at a comparable stage of development. Therefore, a fish reared in the stream reached a length of 11 mm. before it showed the same bone formation as a fish of 10 mm. collected from the stream habitat. All measurements quoted in this report were taken from field-collected specimens.

The larval fish were either fixed in Bouin's fluid and

preserved in 70% alcohol or were frozen and stored in 10%

formalin. Transverse, frontal, and sagittal sections for

microscopic examination were prepared by standard histological techniques. Methylene blue and alizarin stains yielded the best tissue differentiation.

To study the ossicular apparatus in adults and juveniles, several types of preparations were used. Skeletons of large adult fish were prepared by the use of dermestid beetles and were bleached in ammonia. Some skeletons were prepared by dipping specimens into boiling water and removing the softened flesh from the bones. Other adult specimens were treated with alizarin as a stain for bone, cleared with potassium hydroxide, and stored in glycerine. A fourth method, which differentiated between bone and cartilage, involved staining the cartilage with methylene blue, macerating the flesh with potassium hydroxide, and staining the bone with alizarin.

Development was traced from the condition found in the adult, through successively younger stages, to the earliest recognizable beginnings of the Weberian apparatus.

microscopic examination were prepared by standard techniques. Histological sections were stained with hematoxylin and eosin (H&E) and mounted on glass slides.

To study the cellular response to injury and inflammation, several types of procedures were used. In some cases, adult fish were prepared by the use of a standard procedure and were bled at intervals. Some specimens were prepared by dipping specimens into boiling water and removing them. Colored fish from the same source were used as controls. Treated with alaric acid, cleared with potassium hydroxide, and stored in glycerine. A fourth method, which differentiated between normal and injured, involved staining the cartilage with a special stain, processing the tissue with potassium hydroxide, and staining the bone with alaric acid. Development was noted from the condition found in the adult, through successively younger stages, to the earliest recognizable beginning of the reaction against the

Chapter IV

DEVELOPMENT OF THE APPARATUS

The traditional belief concerning the development of the Weberian ossicles is that they represent modified portions of the first three vertebrae. Recent studies indicate a more complex history of development. In addition to modifications of the three anterior vertebrae, other connective tissue elements contribute to the rudiments of the ossicles. These non-vertebral elements are of two types, masses of mesenchyme cells in which membranous bone is later formed and ligament which later ossifies.

In an embryological study, the vertebral rudiments are best discussed in terms of the arcualia of the vertebrae rather than as ribs or transverse processes, because complete structures such as ribs are not present in the younger stages. The arcualia or arch components that fuse to form a typical vertebra are the basidorsal and interdorsal, which are paired components of the upper or neural arch, and the basiventral and interventral, which are paired components of the lower or hemal arch. Only the basidorsals and basiventrals are involved in ossicle construction.

Basidorsals and basiventrals may be either mesenchymatous or cartilaginous (Watson, 1939, p. 462), but both are entirely cartilaginous in Pantosteus plebius. The basidorsals and basiventrals develop first at the anterior end of the

vertebral column and develop posteriorly in regular sequence. Basiventrals do not occur in the first and second vertebrae. The first basiventral to appear, the third, is a contributor to the tripus. It was found that ossification of the basidorsals and basiventrals does not occur until the fish reach a length of 30 mm. In Pantosteus there is no evidence of distinct interdorsals or interventrals.

In the discussion of the homologies of the various parts of the apparatus, it is necessary to refer to the time of development. Thus far, length in millimeters of fish collected from their normal habitat has been used to designate any given stage of development. Because there is difference in length of specimens at a definite level of ossicle formation between fish raised in aquaria and those raised in streams, the specimens have been designated according to five standard stages:

1. First appearance of the arcualia of the vertebrae as groups of cartilage cells lying alongside the notochord. This stage is approximately the same as Balinsky's "stage 32" (1948, p. 337).
2. Arcualia and connective tissue elements present in position of future ossicles.
3. Fusion of the elements of each ossicle complete.
4. Ossicles assume mature shape. Stages 2, 3, and 4 occur during and before Balinsky's "stage 33" (Ibid.).
5. Ossification of all ossicles complete. Balinsky's "stage 36" (Ibid.) is approximately the same as this stage.

The stages described by Balinsky, even though intended to apply to the Cyprinidae, fit the steps in development of

vertical column and develop posteriorly in regular succession.
Basivertebral do not occur in the first and second vertebrae.
The first basivertebral to appear, the third, is a small triangle
to the triquetrum. It was found that basivertebral occur on the
basivertebral and basivertebral, does not occur until the fifth
reach a length of 10 mm. In *Parastichus* there is no evidence
of distinct intervertebral or intravertebral.

In the discussion of the development of the vertebral column
of the specimen, it is necessary to refer to the time of
development. This fact, though in relation to the
collected from this series, is not to be confused
any given stage of development. The stages are as follows:
in length of specimens as a definite level of growth
formation between them, which is apparent and that is seen in
specimens, the specimens were used in the following order:
five standard stages:

1. First appearance of the vertebrae, the vertebrae
are grouped in vertebrae only, but the vertebrae are
notochord. This stage is usually the same
as Hildebrand's "Stage 1" (1911, p. 111).
2. Basivertebral and intervertebral in the specimen present
in position of vertebrae stages.
3. Position of the elements of each of the vertebrae.
4. Ossified vertebrae present in the specimen, the
to occur in the vertebrae, Hildebrand's "Stage 2"
(1911, p. 111).
5. Ossification of all vertebrae, the vertebrae
"Stage 3" (1911, p. 111) is approximately the same
this stage.

The stages described by Hildebrand, even though referred to

apply to the specimens, but are not to be confused with the stages described by Hildebrand.

Pantosteus plebius fairly accurately (Koster, unpublished data).

The way in which the centrum of the vertebra develops is not clearly understood. The best explanation is that a cylinder of bone develops within a layer of mesenchyme that surrounds the notochord and its sheaths (Goodrich, 1930, pp. 43-44). The arcualia have only a small share in the formation of the centrum, but a thin layer of cartilage surrounds the bony layer at the 25 mm. stage.

Vertebral elements are the chief or sole contributors to three of the four ossicles: the scaphium, intercalarium, and tripus. The fourth bone, the claustrum, is derived entirely from mesenchyme and does not pass through a cartilaginous stage.

TRIPUS. The tripus (malleus of Weber), which is the most complex of the ossicles in its beginning, has a threefold origin. The major portion of the bone is contributed by the basiventral of the third vertebra. The articular process, body, and much of the anterior and posterior processes form from this beginning (plate VI, figure 2). The distal portion of the anterior process is formed by ossification within the interossicular ligament. That ossification of the posterior end of the interossicular ligament contributes to the anterior process can be detected by comparison of the length of the ligament in plates V, figure 1 and plate IX, figures 1 and 2. In early stages the transformator process can be seen to have an origin

distinct from that of the rest of the tripus; this origin is shared with the more caudal part of the posterior ramus. The transformator rudiment, a mass of cartilage in the position of the dorsal rib of the third vertebra, is seen on plate VII, figure 2 before its fusion with the third basiventral.

The first rudiment of the tripus to appear is the third basiventral, which appears first at the 9 mm. stage. The additions to the anterior and posterior processes and the transformator rudiment are visible at about 9.5 mm. By the 10 mm. stage the various elements of the tripus have fused into a single, arch-shaped structure. Ossification of the bone is nearly completed by the 15 mm. stage, but the articular process remains cartilaginous through the 30 mm. stage.

INTERCALARIUM. The slender spicule of bone, called by Weber (1820, p. 87) the incus and by Bridge and Haddon (1889, p. 317) the intercalarium, is chiefly a derivative of the second vertebra. As in other Ostariophysi, the shaft of the intercalarium of Pantosteus arises from the basidorsal of the second vertebra. However, in agreement with Watson's (1939, p. 457) finding in the goldfish, the intercalarium of Pantosteus has a second origin. This is a small formation of bone, which forms the manubrium incudis, in the interosseous ligament. Thus, the manubrium incudis is membranous while the shaft is vertebral in origin. The two elements are distinct at 9.5 mm. but at 10 mm. are completely

fused. The shaft of the bone has ossified by the 11 mm. stage. This is much earlier than ossification of the part of the basidorsal that forms the neural arch.

SCAPHIUM. Contrary to the results of other authors working upon different groups, the scaphium of Pantosteus has but a single contributing element, the basidorsal of the first vertebra. At the earliest stage at which a rudiment of the scaphium can be detected, there is a rod of cartilage, which consists of only a few cells, that projects anteriorly from the basidorsal. As seen in sagittal sections, the cartilaginous rod and the basidorsal proper make an L-shaped structure of cartilage. This cartilaginous rod is directed obliquely, dorso-anteriorly, from the horizontal plane, and as it falls in the same plane as do the walls of the concha stapedis in older specimens, we may conclude that the cartilaginous rod is the beginning of the concha stapedis. The rod is present within a mass of mesenchyme more densely arranged than the surrounding tissue. As development progresses, the basidorsal extends dorsally to form the second neural arch, and the cartilaginous rod, as it elongates beyond the concha stapedis, forms the anterior process of the scaphium.

The history of the scaphium begins in the 9 mm. stage when a few cartilage cells are seen lying next to the notochord. The definitive aspect of the bone is seen by 11 mm. and ossification is complete by the 15 mm. stage.

CLAUSTRUM. The claustrum, the smallest of the ossicles, also has a single origin. Historically, the origin of the

used. The shaft of the bone has been lost by the time
stage. This is much earlier than would be expected of the
of the posterior that forms the neural arch.

SCAPHIUM. Contrary to the usual opinion, the scaphium
working upon different groups, the scaphium of *P. laticosta*
has but a single constituting element, the scaphium of the
first vertebra. At the earliest stage it is a single element
of the scaphium can be detected, there is a line of division
which consists of only a few cells, that separates the scaphium
from the posterior. As seen in sagittal section, the
cartilaginous rod and the posterior element with only a single
structure of cartilage. This cartilaginous rod is directed
obliquely, dorso-anteriorly, from the posterior to the
as it falls in the same plane as the wall of the vertebral
arches in other species, the scaphium is a single element
rod is the beginning of the canal rod. The
is present within a mass of mesoderm which is only slightly
than the surrounding tissue. As development progresses
the posterior extends dorsally to form the second neural
arch, and the cartilaginous rod, at its anterior end, the
canal rod, forms the anterior process of the posterior
The history of the scaphium rod is that it is a single
when a few cartilage cells are seen lying back to the
notochord. The definitive aspect of the bone is reached by
it and ossification is complete by the time the animal is
CLAVICLE. The clavicle, the anterior of the scaphium

also has a single origin, the scaphium, the scaphium of the

claustrum has been the biggest puzzle to investigators. It has been described as a derivative of the skull, as a part of the first neural arch, and as an accessory cartilage. In Pantosteus the claustrum has no formation in cartilage; it forms as a direct ossification of connective tissue elements, not connected with, nor derived from, the vertebrae. The anterior vertebrae are surrounded by a sheath, the saccus paravertebralis, that separates them from the musculature. The spinal cord is surrounded, in the position to be occupied by the sheath in later stages, by a thick layer of loosely packed mesenchyme. Clumping together of some of the cells of this layer dorsal to the scaphium, plus subsequent ossification, forms the claustrum. The rudiment of the claustrum lies dorso-lateral to the spinal cord and the adult bones occupy part of the position of the first neural arch.

The claustrum develops later than the other ossicles. The rudiment cannot be detected until 10 mm. (plate V, figure 2). Plate VII, figure 1 shows the ossicle partly mesenchymatous and partly osseous while the scaphium directly below is partly osseous and partly cartilaginous. A fully developed claustrum is not present until the 12 mm. stage.

INTEROSSICULAR LIGAMENT. During the time when the scaphium, intercalarium, and tripus are taking form, the interossicular ligament, which connects the three, makes its appearance. Dense mesenchyme is present in the future position of the ligament by 9.5 mm. and the fibrous nature

of the ligament is clear in sections of 10 mm. fish (plate V, figure 1).

PARS SUSTENTACULUM. The only representative of the vertebral column in Pantosteus of 8 mm. and younger stages is the notochord. The arcualia first appear around the notochord at 9 mm.

The first vertebra develops neither ribs nor neural arch. The spinal canal in this region is roofed over by an arch, the so-called "ring of cartilage." The "cartilage ring" is not visible in sections until the ossicles are completely formed. In fish of 12 mm. the "cartilage ring" is visible above the spinal cord as an extension of the cranium. By 20 mm. the "cartilage ring" extends posteriorly to the junction of the first and second centra. The more lateral parts of the area normally occupied by the first neural arch are formed by the claustra, which are mostly posterior to the "cartilage ring" in sections of 10 mm. to 12 mm. Pantosteus. The component, which in the trunk vertebrae would ordinarily form the neural arch, gives rise to the scaphium.

The second vertebra develops the two ribs typical of a fish vertebra, a dorsal or intermuscular rib, and a ventral or pleural rib. The dorsal rib develops in the junction of the horizontal and vertical skeletogeneous septa. The pleural rib is directed posteriorly as well as ventrally. During development the two pleural ribs of the second vertebra broaden, flatten, and fuse to form a plate, inclined

.....

45° from the long axis of the body (plate I, figure 3). It is at the ventral edge of this plate that the pleural ribs of the fourth vertebra join. The esophageal processes arise medially to the suture line of the second and fourth ribs and project posteriorly and slightly ventrally. Part of the basidorsal, or neural arch, element of this vertebra is modified to form the intercalarium and a part forms the anterior section of the cartilaginous mass that develops into the compound neural arch and spine of the second, third, and fourth vertebrae. In young stages the centrum of the second vertebra is distinct from those of the third and fourth vertebrae, but later the three centra fuse into the so-called "compound vertebra" of the adult. However, even in the adult, the sutures are visible.

The third vertebra lacks processes of any type. The neural arch elements fuse with those from the second and fourth vertebrae to form a compound neural arch and spine. The ventral part of the arch flares laterally from the centrum and gives the appearance of a short transverse process. The ventral and dorsal ribs of this vertebra are absent. Their rudiments, the basiventral and a mass of cartilage in the position of the dorsal rib, form much of the tripus.

The fourth vertebra develops a single pair of processes, the ventral ribs, that develop into expanded plates and fuse with the ventral ribs of the second vertebra. This accessory part of the Weberian apparatus appears at the

same time as the ossicles and by the 12 mm. stage is completely formed in cartilage. The rudiments of the ossa suspensoria, which are projections from the bases of the ventral or pleural ribs, can be seen next to the anterior wall of the air bladder at 10 mm.

same time as the addition of the new material is being
formed in cavities. The addition of the new material
which are produced from the mass of the material of
pleural ribs, and in some cases the material will be
air bladder as in the

COLLON CONTAINING
EVIDENCE
FBI
LABORATORY

Chapter V

DISCUSSION

Three general theories of the origin and development of the Weberian apparatus have been proposed. Weber (1820) believed the ossicles to be homologous with the mammalian ear bones; St. Hilaire (1824), Müller (1842), Beaudelot (1868), Bridge and Haddon (1893), and Nusbaum (1908) thought the ossicles were formed by simple separations of parts of the anterior vertebrae; and Wright (1884), Matveiev (1929), and Watson (1939) concluded that connective tissue ossifications supplemented the modified portions of the vertebrae in the development of the ossicles. The results of this study are in accord with the last theory. The dual origin is best seen in the intercalarium (plate IV, figure 2).

The development of the ossicles in Pantosteus is very rapid; the passage from stages one to four in any one series occurs within the length increase of a single millimeter. The basidorsals and basiventrals appear at 9 mm. and the two previously described elements that fuse to form the intercalarium have joined by the 10 mm. stage. Most of the very rapid development of the ossicles takes place between the lengths of 9.5 mm. and 10 mm. Watson (1939, pp. 452, 458) found cartilaginous basidorsals and basiventrals in goldfish of 8 mm., but the elements of the intercalarium were not fused until 15 mm.

Three general theories of the origin of the
of the hepatic apparatus and the associated
believed the condition to be due to a congenital
ear bones; St. Wilkie (1904), Smith (1905),
(1868), Briggs and Lewis (1911), and Jackson (1918) and
the condition was caused by some abnormality of
the anterior vertebrae; and others (1912, 1913, 1914,
and Watson (1919) suggested that a congenital
ossification of the cartilage of the
vertebrae in the cervical region was the cause.
of this study and in accord with the results of
origin is best seen in the cervical region.
The development of the condition is a
rapid; the process from stages one to four
occurs within two to three months of birth.
The condition is characterized by a rapid
two previously described conditions. The
intercalation have been found by the present
very rapid development of the condition
the lengths of 3.5 mm. and 5 mm. (Watson, 1919, p. 417).
458) found cartilaginous bodies in the
Goldfish of 3 mm. and 5 mm. and the condition
were not found in the

All three of the origins of the tripus have been disputed. Krumholz (1943, p. 36) concluded that the tripus articulated with the second vertebra, but plate VII, figure 2 shows that much of the bone is derived from the basiventral of the third vertebra, and therefore, it is the third vertebra with which the tripus articulates. The transformator process has been called an ossification in the tunica externa of the air bladder (Wright, 1884, p. 249) or this plus the dorsal rib of the third vertebra (Watson, 1939, p. 461). The transformator process arises at the junction of the third myoseptum with the horizontal skeletogenous septum, the normal position of a dorsal rib. Since the third vertebra of the adult bears no ribs, we may conclude that part of the transformator process represents the third dorsal rib. Plate VII, figure 2 shows the basiventral and rib rudiments before their fusion. Watson (1939, p. 461) believed the anterior process of the tripus to be lengthened by ossification in the interossicular ligament, a process that is also seen in Pantosteus.

The two elements that contribute to the intercalarium are entirely separate at stage two (plate IV, figure 2). Plate IV, figure 2 also demonstrates that ossicle formation involves both vertebral and other connective tissue elements. A connective tissue contributor (lateral element seen on plate IV, figure 2) is the manubrium incudis, and the vertebral element is the basidorsal (plate IV, figure 2) of the second vertebra. The next stage in the development of

...the second vertebra. The first ...
vertebral element is the first ...
plate IV, figure 3) is the ...
A connective tissue ...
involves both ...
plate IV, figure 3 also ...
are entirely ...
The two ...
is also seen in ...
ossification in the ...
anterior process of the ...
before their ...
plate VII, figure 2 shows the ...
transformer process ...
of the adult ...
normal position of a ...
myoelectric with the ...
transformer process ...
of the third vertebra ...
bladder (...
called an ossification in the ...
the ...
vertebra, and ...
much of the ...
with the second vertebra, ...
Krumholz (1943, p. 30) ...
The space ...

the intercalarium is the fusion of the two parts, as shown on plate VIII, figure 1.

There are two parts to the scaphium, which seemingly develop independently of one another during the first stages, but it is questionable if there are two distinct origins for the bone. According to Matveiev (1929, p. 503) a mass of mesenchyme appears anterior to the basidorsal, and ossification in this mass produces the concha stapedis or cup-shaped part of the scaphium. Watson (1939, p. 457) concurs with this idea. Sections of Pantosteus show a mass of mesenchyme and within this a cartilaginous rod that is continuous with the cartilage of the basidorsal. If the cartilaginous rod were distinctly separate from the basidorsal, we might conclude a dual origin for the scaphium, but at its first appearance the rod is continuous with the basidorsal. Therefore, it seems more likely that the scaphium arises from a single rudiment, the first basidorsal.

The first vertebra of Pantosteus has no neural arch. Because the cartilaginous "ring" that lies dorsal to the spinal cord is continuous with the cranium, the origin in Pantosteus is in agreement with Watson's (1939, p. 453) explanation that the "ring" is an extension of the exoccipitals.

A second cartilaginous mass becomes visible earlier in development than does the "cartilage ring" and forms a roof over the spinal cord dorsal to the anterior half of the second vertebra. The fate of this mass is to become part of the larger mass of cartilage that forms the compound neural

the interstitial in the ... on plate VII, figure 1.

There are two points to ...

develop independently of ...

but it is questionable ...

the bone. According to ...

mesenchyme appears ...

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cup-shaped part of the ...

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basal. There is ...

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The first ...

Because the ...

spinal cord is ...

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explanation that ...

A second ...

development then ...

over the spinal ...

second vertebra. ...

the lower ...

spine and arch of the second, third, and fourth vertebrae. The entire mass has been interpreted as a part of the skull (Nusbaum, 1908, pp. 530-531), as a complex of the neural spines of the first three vertebrae plus the first three interspinous bones (Matveiev, 1929, p. 477), and as a complex of the basidorsals of the second, third, and fourth vertebrae plus probable contributions from the first three interspinous bones (Watson, 1939, p. 455). Sections of Pantosteus show that there is no connection between the cartilaginous mass and the skull. Findings of this study are in agreement with Watson's results concerning contributions from the basidorsals, but there are no indications of distinct interspinous bones. Therefore, it is necessary to attribute the cartilaginous mass to the basidorsals.

The modified ventral process of the fourth vertebra has had a complex history of suggested homologues. The vertebra possessing this complex ventral process has been called the third vertebra by Adams (1928, p. 117) and Krumholz (1943, p. 36), probably because they did not recognize that the second and third centra are fused. The process has been termed a hemal process (Adams, 1928, p. 117), a transverse process (Wright, 1884, p. 250; Bridge and Haddon, 1889, p. 311), and a pleural or ventral rib (Watson, 1939, p. 456). Because the modified ventral process articulates with the centrum in the fashion typical of a pleural rib as described by Goodrich (1939, pp. 34-44), one may conclude that the process represents a pleural rib.

spine and arch of the sacrum. The entire mass has been removed as a part of the study.

(Husman, 1908, p. 100, 101, 102, 103, 104, 105, 106, 107, 108, 109, 110, 111, 112, 113, 114, 115, 116, 117, 118, 119, 120, 121, 122, 123, 124, 125, 126, 127, 128, 129, 130, 131, 132, 133, 134, 135, 136, 137, 138, 139, 140, 141, 142, 143, 144, 145, 146, 147, 148, 149, 150, 151, 152, 153, 154, 155, 156, 157, 158, 159, 160, 161, 162, 163, 164, 165, 166, 167, 168, 169, 170, 171, 172, 173, 174, 175, 176, 177, 178, 179, 180, 181, 182, 183, 184, 185, 186, 187, 188, 189, 190, 191, 192, 193, 194, 195, 196, 197, 198, 199, 200, 201, 202, 203, 204, 205, 206, 207, 208, 209, 210, 211, 212, 213, 214, 215, 216, 217, 218, 219, 220, 221, 222, 223, 224, 225, 226, 227, 228, 229, 230, 231, 232, 233, 234, 235, 236, 237, 238, 239, 240, 241, 242, 243, 244, 245, 246, 247, 248, 249, 250, 251, 252, 253, 254, 255, 256, 257, 258, 259, 260, 261, 262, 263, 264, 265, 266, 267, 268, 269, 270, 271, 272, 273, 274, 275, 276, 277, 278, 279, 280, 281, 282, 283, 284, 285, 286, 287, 288, 289, 290, 291, 292, 293, 294, 295, 296, 297, 298, 299, 300, 301, 302, 303, 304, 305, 306, 307, 308, 309, 310, 311, 312, 313, 314, 315, 316, 317, 318, 319, 320, 321, 322, 323, 324, 325, 326, 327, 328, 329, 330, 331, 332, 333, 334, 335, 336, 337, 338, 339, 340, 341, 342, 343, 344, 345, 346, 347, 348, 349, 350, 351, 352, 353, 354, 355, 356, 357, 358, 359, 360, 361, 362, 363, 364, 365, 366, 367, 368, 369, 370, 371, 372, 373, 374, 375, 376, 377, 378, 379, 380, 381, 382, 383, 384, 385, 386, 387, 388, 389, 390, 391, 392, 393, 394, 395, 396, 397, 398, 399, 400, 401, 402, 403, 404, 405, 406, 407, 408, 409, 410, 411, 412, 413, 414, 415, 416, 417, 418, 419, 420, 421, 422, 423, 424, 425, 426, 427, 428, 429, 430, 431, 432, 433, 434, 435, 436, 437, 438, 439, 440, 441, 442, 443, 444, 445, 446, 447, 448, 449, 450, 451, 452, 453, 454, 455, 456, 457, 458, 459, 460, 461, 462, 463, 464, 465, 466, 467, 468, 469, 470, 471, 472, 473, 474, 475, 476, 477, 478, 479, 480, 481, 482, 483, 484, 485, 486, 487, 488, 489, 490, 491, 492, 493, 494, 495, 496, 497, 498, 499, 500, 501, 502, 503, 504, 505, 506, 507, 508, 509, 510, 511, 512, 513, 514, 515, 516, 517, 518, 519, 520, 521, 522, 523, 524, 525, 526, 527, 528, 529, 530, 531, 532, 533, 534, 535, 536, 537, 538, 539, 540, 541, 542, 543, 544, 545, 546, 547, 548, 549, 550, 551, 552, 553, 554, 555, 556, 557, 558, 559, 560, 561, 562, 563, 564, 565, 566, 567, 568, 569, 570, 571, 572, 573, 574, 575, 576, 577, 578, 579, 580, 581, 582, 583, 584, 585, 586, 587, 588, 589, 590, 591, 592, 593, 594, 595, 596, 597, 598, 599, 600, 601, 602, 603, 604, 605, 606, 607, 608, 609, 610, 611, 612, 613, 614, 615, 616, 617, 618, 619, 620, 621, 622, 623, 624, 625, 626, 627, 628, 629, 630, 631, 632, 633, 634, 635, 636, 637, 638, 639, 640, 641, 642, 643, 644, 645, 646, 647, 648, 649, 650, 651, 652, 653, 654, 655, 656, 657, 658, 659, 660, 661, 662, 663, 664, 665, 666, 667, 668, 669, 670, 671, 672, 673, 674, 675, 676, 677, 678, 679, 680, 681, 682, 683, 684, 685, 686, 687, 688, 689, 690, 691, 692, 693, 694, 695, 696, 697, 698, 699, 700, 701, 702, 703, 704, 705, 706, 707, 708, 709, 710, 711, 712, 713, 714, 715, 716, 717, 718, 719, 720, 721, 722, 723, 724, 725, 726, 727, 728, 729, 730, 731, 732, 733, 734, 735, 736, 737, 738, 739, 740, 741, 742, 743, 744, 745, 746, 747, 748, 749, 750, 751, 752, 753, 754, 755, 756, 757, 758, 759, 760, 761, 762, 763, 764, 765, 766, 767, 768, 769, 770, 771, 772, 773, 774, 775, 776, 777, 778, 779, 780, 781, 782, 783, 784, 785, 786, 787, 788, 789, 790, 791, 792, 793, 794, 795, 796, 797, 798, 799, 800, 801, 802, 803, 804, 805, 806, 807, 808, 809, 810, 811, 812, 813, 814, 815, 816, 817, 818, 819, 820, 821, 822, 823, 824, 825, 826, 827, 828, 829, 830, 831, 832, 833, 834, 835, 836, 837, 838, 839, 840, 841, 842, 843, 844, 845, 846, 847, 848, 849, 850, 851, 852, 853, 854, 855, 856, 857, 858, 859, 860, 861, 862, 863, 864, 865, 866, 867, 868, 869, 870, 871, 872, 873, 874, 875, 876, 877, 878, 879, 880, 881, 882, 883, 884, 885, 886, 887, 888, 889, 890, 891, 892, 893, 894, 895, 896, 897, 898, 899, 900, 901, 902, 903, 904, 905, 906, 907, 908, 909, 910, 911, 912, 913, 914, 915, 916, 917, 918, 919, 920, 921, 922, 923, 924, 925, 926, 927, 928, 929, 930, 931, 932, 933, 934, 935, 936, 937, 938, 939, 940, 941, 942, 943, 944, 945, 946, 947, 948, 949, 950, 951, 952, 953, 954, 955, 956, 957, 958, 959, 960, 961, 962, 963, 964, 965, 966, 967, 968, 969, 970, 971, 972, 973, 974, 975, 976, 977, 978, 979, 980, 981, 982, 983, 984, 985, 986, 987, 988, 989, 990, 991, 992, 993, 994, 995, 996, 997, 998, 999, 1000)

of the sacrum. The entire mass has been removed as a part of the study.

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The ventral rib of the second vertebra, like that of the fourth, is clearly homologous with the pleural rib of the trunk vertebrae, both because of its type of articulation and because of its position internal to the hypaxial muscle mass.

The horizontal projection of the second vertebra has been termed a transverse process by most early investigators and a dorsal rib by Watson (1939, p. 456). In Pantosteus the position of the projection at the junction of the myoseptum with the horizontal skeletogenous septum verifies its homology with a dorsal rib.

The ossa suspensoria occupy the position of hemopophyses, projections from the ventral side of the centrum representing remnants of the hemal arch, and are so termed by Watson (1939, p. 456). However, even during development, the os suspensorium is never distinct from the fourth pleural rib.

The esophageal processes are mentioned only by Matveiev (1929, p. 482) and Nelson (1948, p. 230) and are difficult to determine as to their homology. The process arises from the second rib component of the second and fourth pleural rib complex. As the plate formed by the two pleural ribs of the second vertebra is uninterrupted, it is possible that the esophageal processes represent extensions of the hemopophyses incorporated into the flat plate. It is also possible that in many ostariophysines the esophageal processes have no homologues but have evolved separately in those groups which possess a very complex Weberian apparatus.

The results of the study have been summarized in the following table. The data show that the average yield of the crop was 1.5 tons per hectare. This is a significant increase compared to the previous year's yield of 1.2 tons per hectare. The increase is attributed to the use of the new fertilizer and the improved irrigation system. The results also show that the new fertilizer is more effective than the old one, as it resulted in a higher yield per unit of fertilizer used. The improved irrigation system also played a role in the increase in yield, as it ensured that the crops received adequate water throughout the growing season. The study concludes that the use of the new fertilizer and the improved irrigation system is a promising way to increase crop yields and improve the efficiency of fertilizer use. The results of the study are summarized in the following table.

Year	Fertilizer (kg/ha)	Irrigation (mm)	Yield (tons/ha)
1970	100	100	1.2
1971	100	150	1.5
1972	150	150	1.8
1973	150	200	2.1

The results of the study are summarized in the following table.

1974

Chapter VI

SUMMARY

The development of the Weberian ossicles, a series of small bones that carries vibrations from the air bladder to the internal ear, was studied in various stages of the Rio Grande mountain sucker, Pantosteus plebius, a member of the family Catostomidae.

The Weberian apparatus in the adult has two divisions, a pars auditum, which consists of the Weberian ossicles proper, and the pars sustentaculum, which consists of the modified four anterior vertebrae that support the ossicles.

Microscopic examination of sections through young fish indicated that the ossicles are derived from the arcualia or arch components of the first three vertebrae plus other connective tissue elements. The tripus has a threefold origin, from the basiventral of the third vertebra, from a mass of cartilage in the position of the dorsal rib of the third vertebra, and from an ossification of the posterior end of the interossicular ligament. The intercalarium forms from two beginnings, the basidorsal of the second vertebra and an ossification in the center of the interossicular ligament. The scaphium has a single origin, the first basidorsal. The claustrum is derived by direct ossification within a mass of mesenchyme that is apparently unrelated to any vertebra. Except that the scaphium has a single rather than a dual origin, the development of the ossicles in the

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The development of the vertebral column in the

small bones that are fused with the axis and the

the intervertebral disc, was seen in the vertebrae of the

Grande Montagne, California, and the

family Catantopidae.

The specimen was found in the same locality as the

a pair of the same species, which were found in the

proper, and the pair was found in the same locality as the

modified form of the same species, which was found in the

Microscopic examination of the section of the

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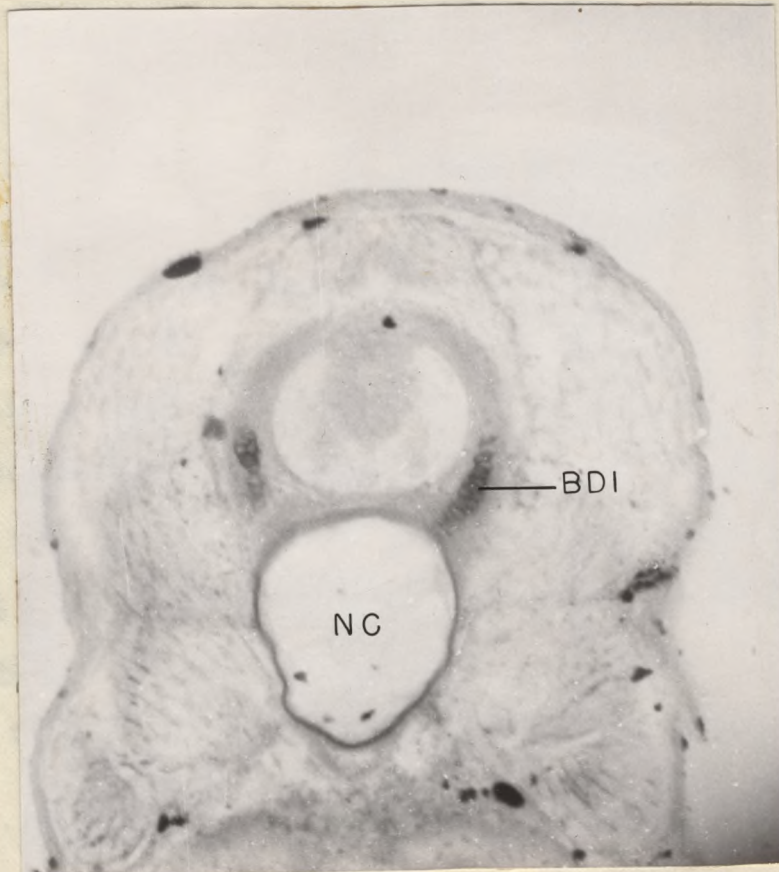
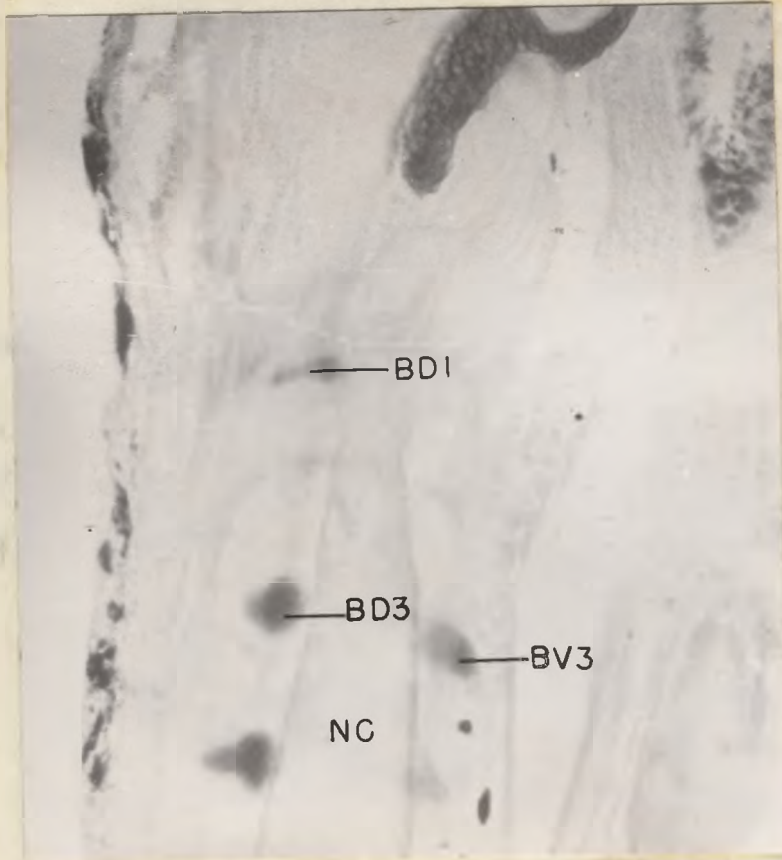
within a mass of cartilage in the section of the section of the

any vertebrae. The section of the section of the section of the

than a dual nature, the section of the section of the section of the

catostomid species Pantosteus plebius is similar to that described for the two cyprinids, Carassius (Watson, 1939) and Scardinius (Matveiev, 1929).

Development of the pars sustentaculum in Pantosteus does not vary greatly from that described by Watson (1939) in the goldfish, even though the anterior vertebrae are considerably more modified in the suckers. The cartilaginous "ring" over the first vertebra is a cranial extension and the mass of cartilage that forms the neural arch and spine of the second, third, and fourth vertebrae is definitely formed from the basidorsals of those vertebrae. The ventral processes of the second and fourth vertebrae fuse and form the Weberian fenestra and a complex rib combination. These ribs are true pleural ribs. The ossa suspensoria represent hemopophyses of the fourth vertebra. The homology of the esophageal processes is not clear, but they may represent hemopophyses of the second vertebra or may have evolved separately and without involving vertebral elements.



— NC —

Plate IV, Figure 21. Photomicrograph of a transverse section of a Pentastoma embryo at stage 1 (text, pp. 22-23); methylene blue and alizarin staining; orange filter; 120 X. BD2, basidorsal of the second vertebra; CM, cartilaginous mass; NC, notochord.



Plate IV, Figure 22. Photomicrograph of a transverse section of a Pentastoma embryo at stage 2 (text, pp. 22-23); methylene blue and alizarin staining; orange filter; 120 X. BD1, basidorsal of the first vertebra; BD2, basidorsal of the second vertebra; BD3, basidorsal of the third vertebra; CS, concha; MI, mandibular invagination. The two elements that contribute to the invagination, the second basidorsal and the mandibular invagination, are visible before fusion.



— MI —

Plate IV, Figure 1: Photomicrograph of a transverse section of a Pantosteus embryo at stage 1 (text, pp. 22-23); methylene blue and alizarin stains; orange filter; 150 X. BD2, basidorsal of the second vertebra; CM, cartilaginous mass; NC, notochord.

Plate IV, Figure 2: Photomicrograph of a frontal section of a Pantosteus embryo at stage 2 (text, pp. 22-23); methylene blue stain; orange filter; 150 X. BD1, basidorsal of the first vertebra; BD2, basidorsal of the second vertebra; BD3, basidorsal of the third vertebra; CS, concha stapedis portion of the scaphium; MI, manubrium incudis. The two elements that contribute to the intercalarium, the second basidorsal and the manubrium incudis, are visible before fusion.

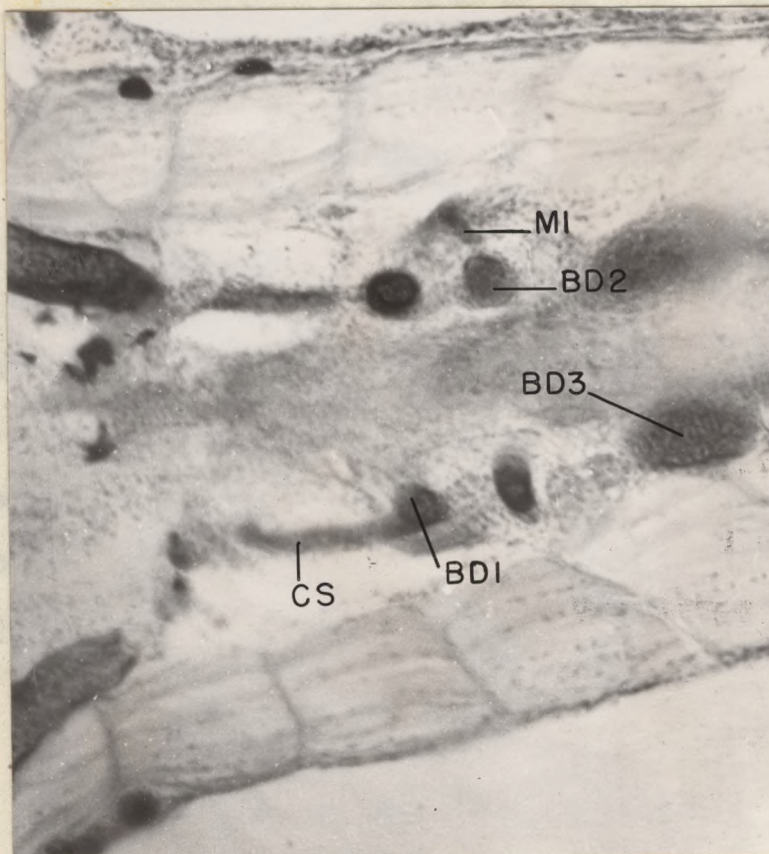
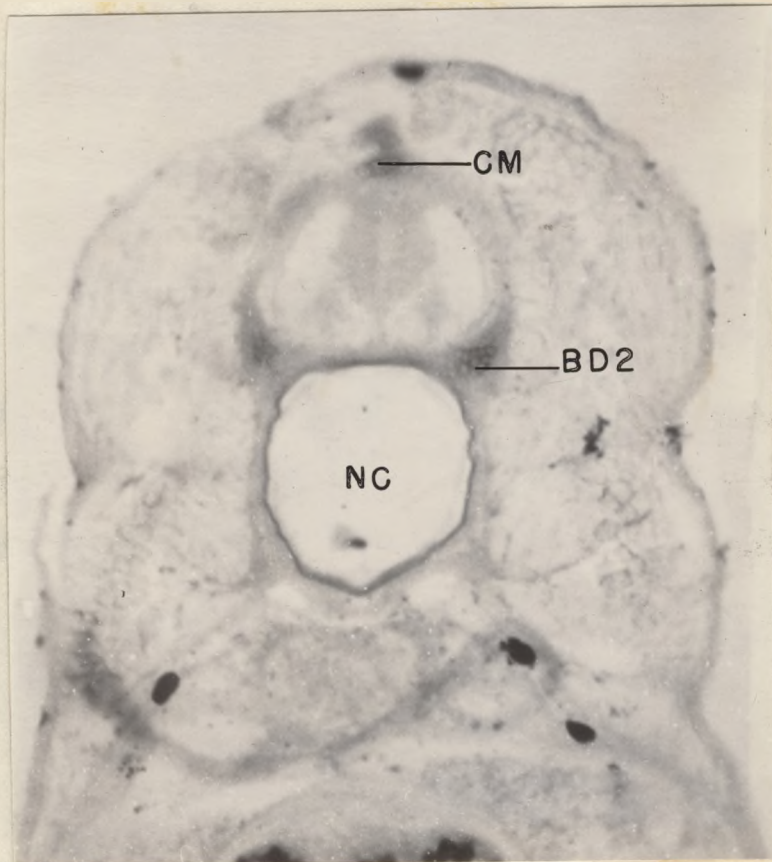




Plate V, Figure 1: Photomicrograph of a frontal section of a Hemistene embryo at stage 3 (text, pp. 22-23); methylene blue stain; range filter; 150 X. BDS, basidorsal of the second vertebra; IL, intersegmental ligament; S, scapulum.



Plate V, Figure 2: Photomicrograph of a sagittal section of a Hemistene embryo at stage 3 (text, pp. 22-23); methylene blue stain; range filter; 150 X. HDL, basidorsal of the first vertebra; BDS, basidorsal of the second vertebra; BDS, basidorsal of the third vertebra; CI R, rudiment of the clavicle; OM, cartilaginous mass.

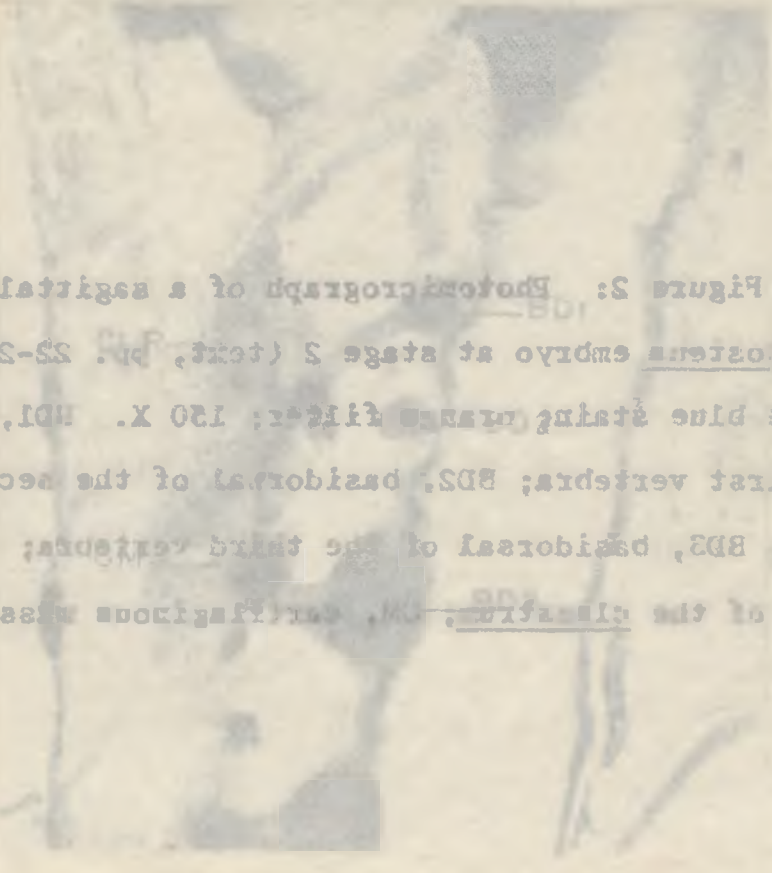


Plate V, Figure 1: Photomicrograph of a frontal section of a Pantosteus embryo at stage 2 (text, pp. 22-23); methylene blue stain; orange filter; 150 X. BD2, basidorsal of the second vertebra; IL, interossicular ligament; S, scaphium.

Plate V, Figure 2: Photomicrograph of a sagittal section of a Pantosteus embryo at stage 2 (text, pp. 22-23); methylene blue stain; orange filter; 150 X. BD1, basidorsal of the first vertebra; BD2, basidorsal of the second vertebra; BD3, basidorsal of the third vertebra; C1 R, rudiment of the claustrum; CM, cartilaginous mass.

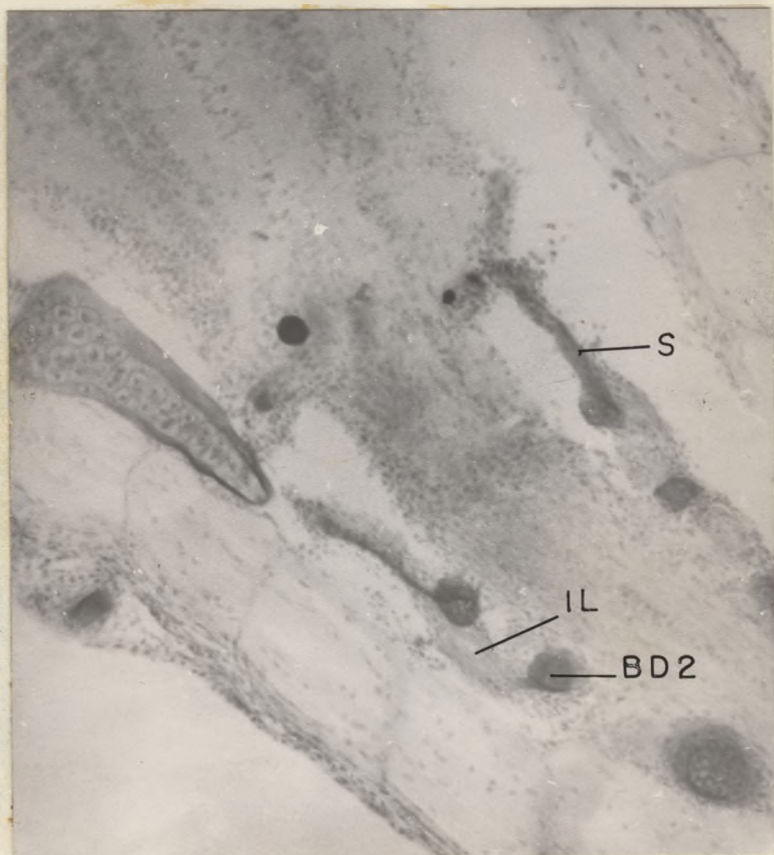




Plate VI, Figure 1: Photomicrograph of a sagittal section of a Pantodon embryo at stage 2 (text, pp. 22-23); methylene blue and alizarin stains; orange filter; 150 X. BDL, basidorsal of the first vertebra; see skull. The rod of cartilage that extends anteriorly from the first basidorsal is visible on this photograph. This rod of cartilage is the rudiment of the condyle region of the acanthium.

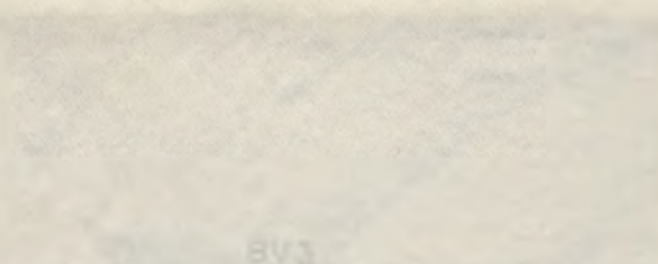


Plate VI, Figure 2: Photomicrograph of a sagittal section of a Pantodon embryo at stage 2 (text, pp. 22-23); methylene blue stain; orange filter; 150 X. BV3, basiventral of the third vertebra; BV4, basiventral of the fourth vertebra; Tr. T, rudiment of the translocator process of the tripes, which is the dorsal end of the third vertebra.



Plate VI, Figure 1: Photomicrograph of a sagittal section of a Pantosteus embryo at stage 2 (text, pp. 22-23); methylene blue and alizarin stains; orange filter; 150 X. BD1, basidorsal of the first vertebra; Sk, skull. The rod of cartilage that extends anteriorly from the first basidorsal is visible on this photograph. This rod of cartilage is the rudiment of the concha stapedis portion of the scaphium.

Plate VI, Figure 2: Photomicrograph of a sagittal section of a Pantosteus embryo at stage 2 (text, pp. 22-23); methylene blue stain; orange filter; 150 X. BV3, basiventral of the third vertebra; BV4, basiventral of the fourth vertebra; Tr. T, rudiment of the transformator process of the tripus, which is the dorsal rib of the third vertebra.



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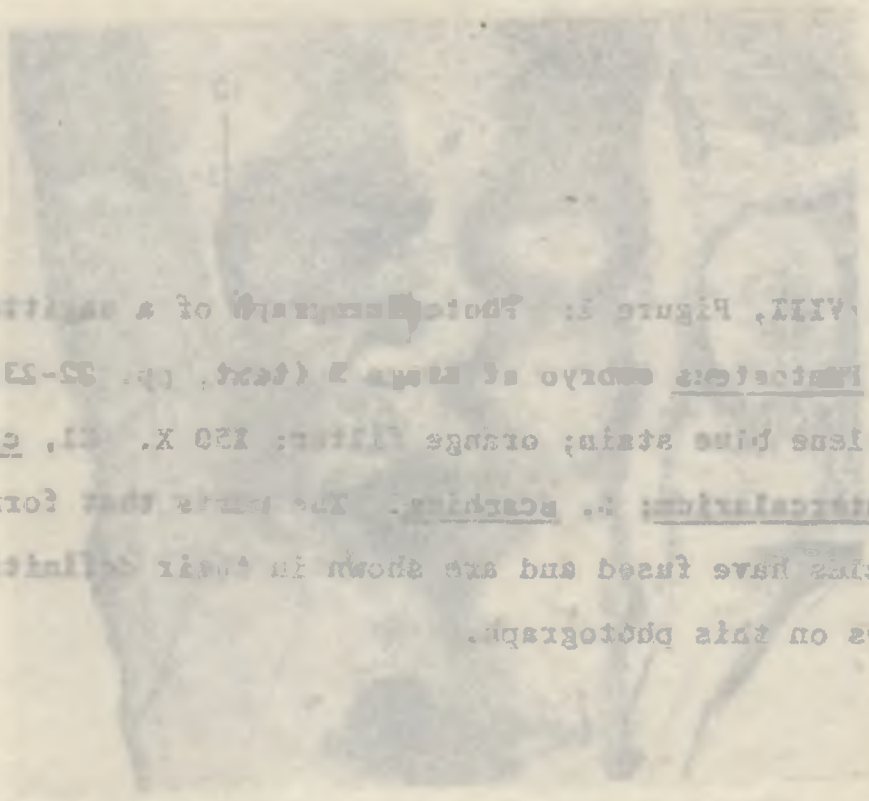


Plate VIII, Figure 2: Photomicrograph of a sagittal section of a Pentastacus embryo at stage 2 (text, pp. 22-23); methylene blue stain; orange filter; 150 X. II, clausium; I, intestinalis; S, scaphium. The bones that form the ossicles have fused and are shown in their collective shapes on this photograph.

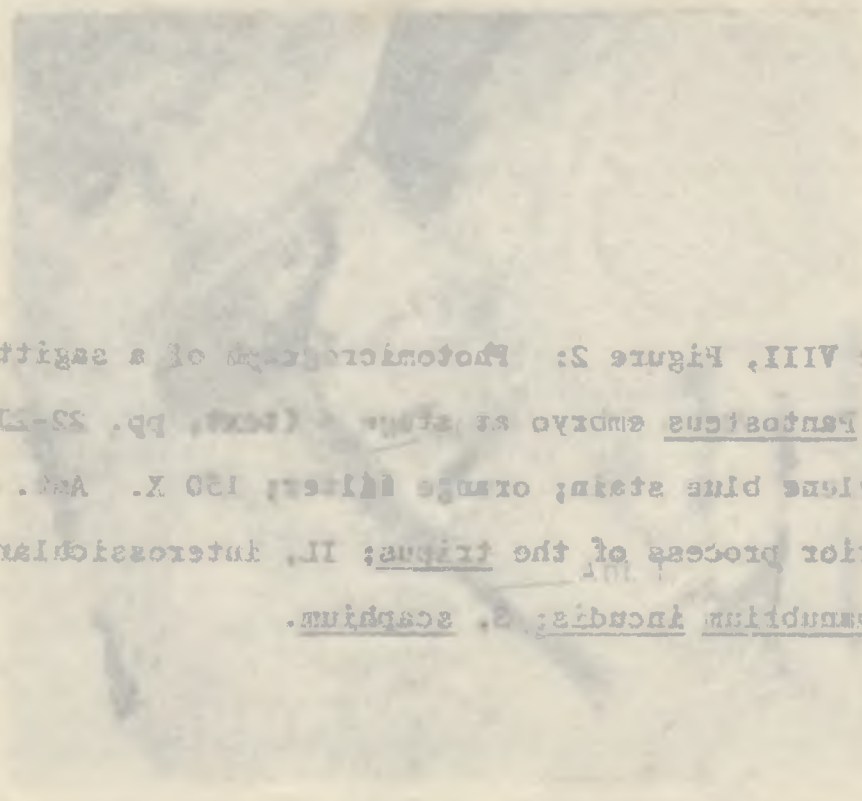


Plate VIII, Figure 2: Photomicrograph of a sagittal section of a Pentastacus embryo at stage 2 (text, pp. 22-23); methylene blue stain; orange filter; 150 X. Ant. T., anterior process of the triquetrum; IL, interossicular ligament; MI, mandibular incus; S, scaphium.

Plate VIII, Figure 1: Photomicrograph of a sagittal section of a Pantosteus embryo at stage 3 (text, pp. 22-23); methylene blue stain; orange filter; 150 X. Cl, claustrum; I, intercalarium; S, scaphium. The parts that form the ossicles have fused and are shown in their definitive shapes on this photograph.

Plate VIII, Figure 2: Photomicrograph of a sagittal section of a Pantosteus embryo at stage 4 (text, pp. 22-23); methylene blue stain; orange filter; 150 X. Ant. T, anterior process of the tripus; IL, interossicular ligament; MI, manubrium incudis; S, scaphium.



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Plate IX, Figure 1: Photomicrograph of a frontal section
of a Panosteus embryo at stage 2 (text, pp. 22-23);
methylene blue and alizarin staining; 120 X. CI, claustrum;
2, scapula; 3C, axial cord.



Plate IX, Figure 2: Photomicrograph of a frontal section
of a Panosteus embryo at stage 2 (text, pp. 22-23);
methylene blue and alizarin staining; 120 X. BV3, basiventral
of the first vertebra; BDS, basidorsal of the second vertebra;
BV2, basiventral of the third vertebra; I, intercalarium;
2, scapula.

Plate IX, Figure 1: Photomicrograph of a frontal section of a Pantosteus embryo at stage 5 (text, pp. 22-23); methylene blue and alizarin stains; 120 X. Cl, claustrum; S, scaphium; SC, spinal cord.

Plate IX, Figure 2: Photomicrograph of a frontal section of a Pantosteus embryo at stage 5 (text, pp. 22-23); methylene blue and alizarin stains; 120 X. BD1, basidorsal of the first vertebra; BD2, basidorsal of the second vertebra; BV3, basiventral of the third vertebra; I, intercalarium; S, scaphium.

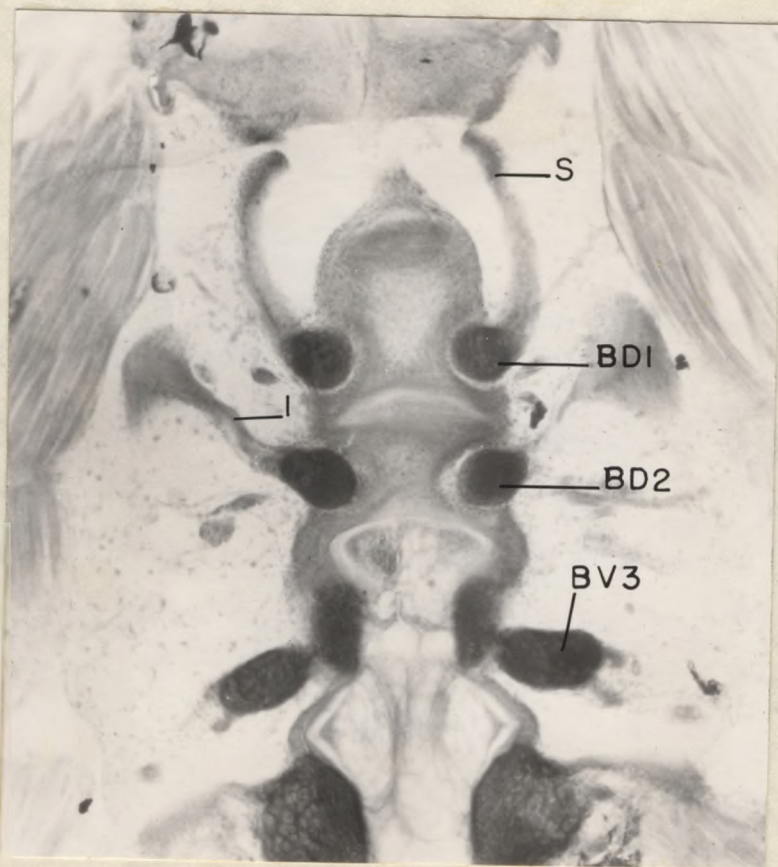
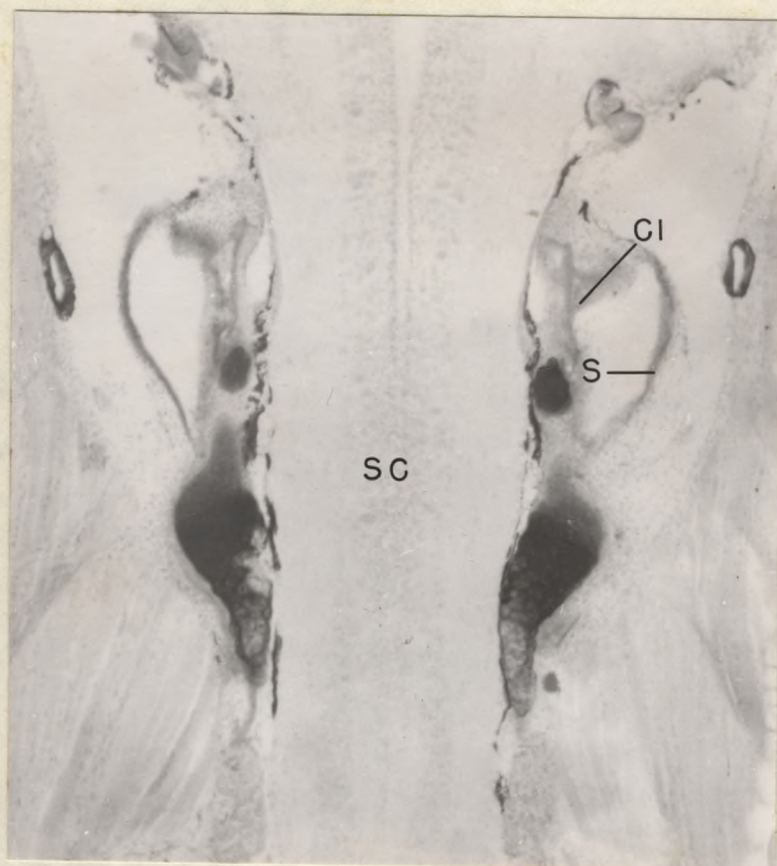




Plate X, Figure 1: Photomicrograph of a frontal section of a Penaeus embryo at stage 5 (text, pp. 22-23); methylene blue and alizarin stains; 120 X. SK, skull; T, tricus.



Plate X, Figure 2: Photomicrograph of a frontal section of a Penaeus embryo at stage 5 (text, pp. 22-23); methylene blue and alizarin stains; 120 X. SK, skull; T, tricus; T.P., posterior process of the tricus; SK, skull; T, tricus.

Plate X, Figure 1: Photomicrograph of a frontal section of a Pantosteus embryo at stage 5 (text, pp. 22-23); methylene blue and alizarin stains; 120 X. Sk, skull; T, tripus.

Plate X, Figure 2: Photomicrograph of a frontal section of a Pantosteus embryo at stage 5 (text, pp. 22-23); methylene blue and alizarin stains; 120 X. DR2, dorsal rib of the second vertebra; PT, posterior process of the tripus; Sk, skull; Tr. T, transformator process of the tripus.

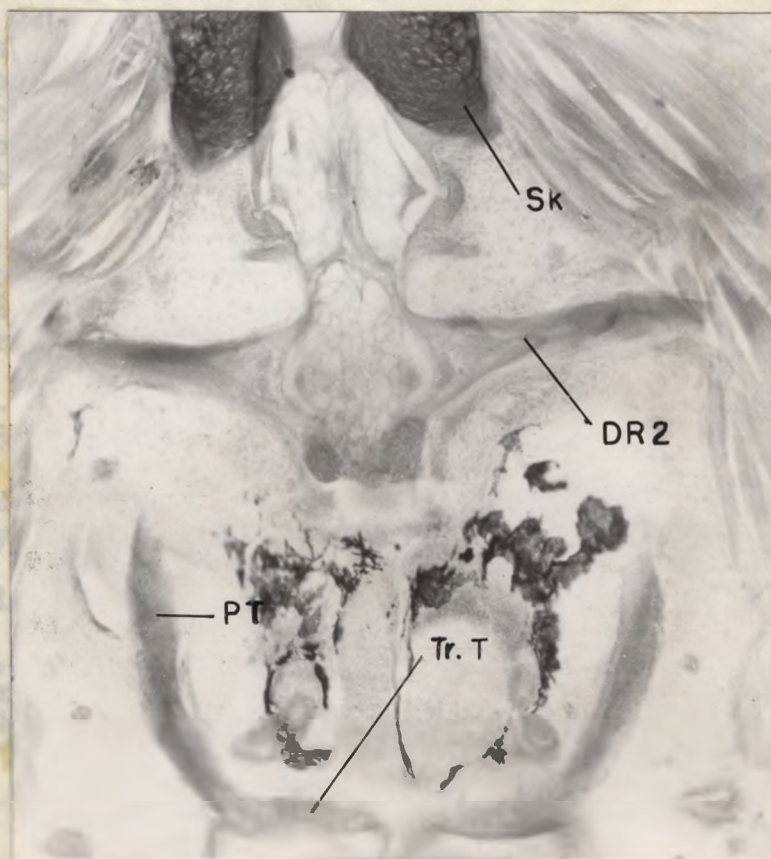
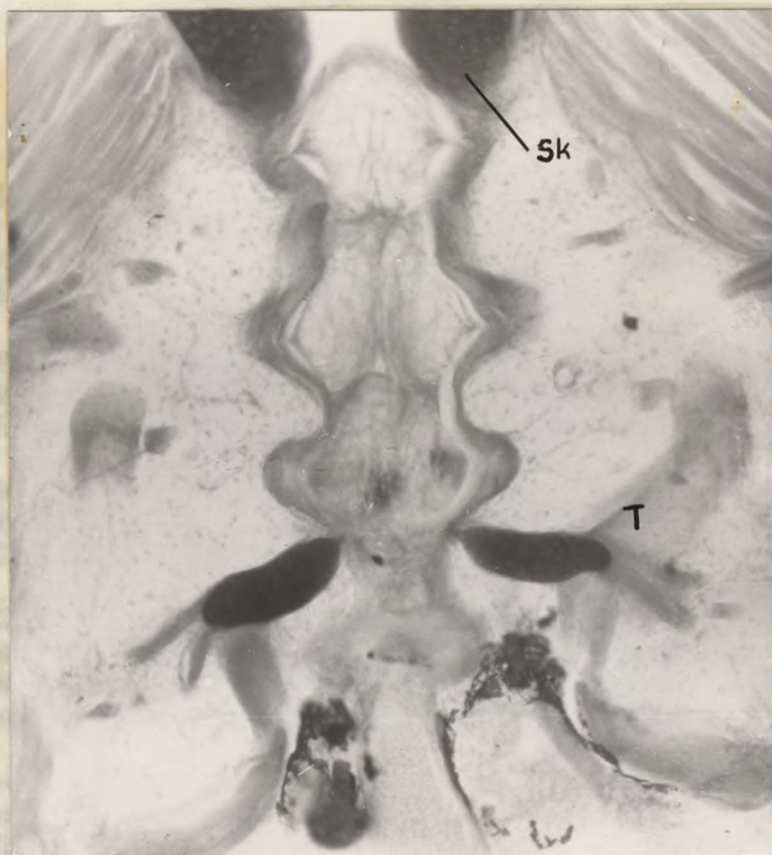


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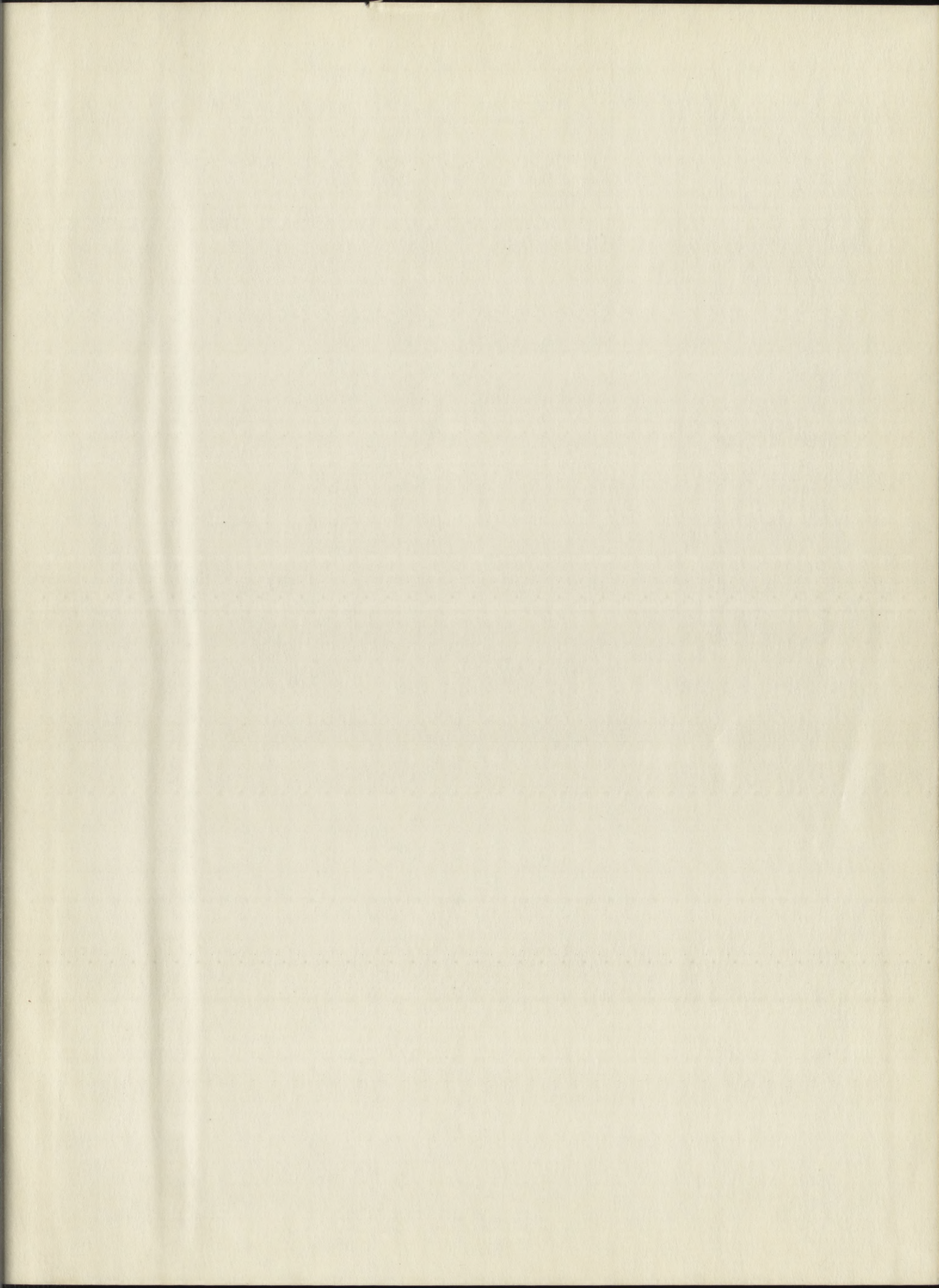
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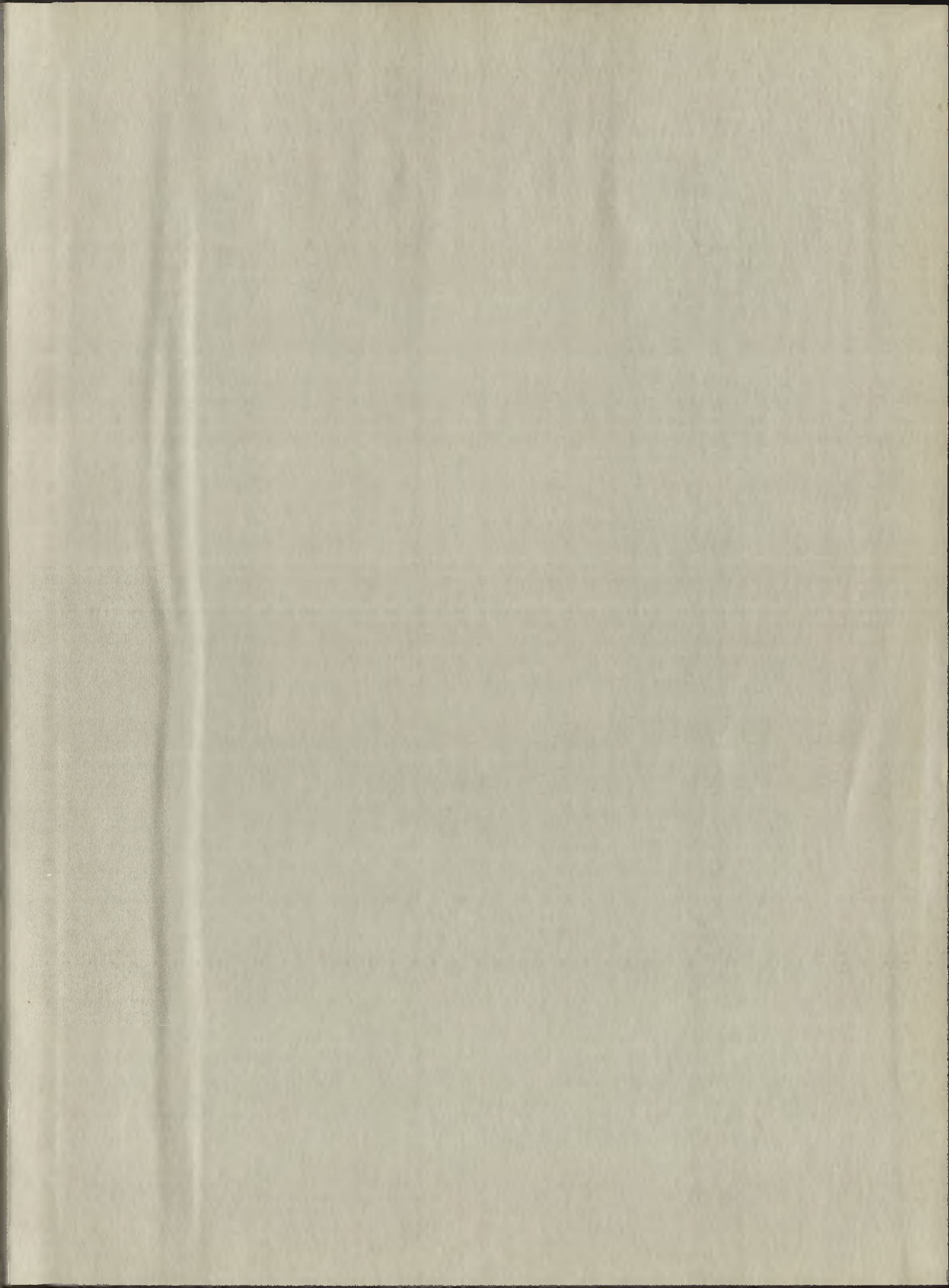
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