A COMPARATIVE STUDY OF THE WEBERIAN APPARATUS

IN THE GENUS PIMEPHALES (CYPRINIDAE)

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CHAPTER I

INTRODUCTION

Although some studies concerning the Weberian apparatus in Cyprinid fishes have been conducted, there is no literature on this subject pertaining to the subfamily Pimephalinae.

This subfamily includes the nominal genera Hyborhynchus Rafinesque, Pimephales Rafinesque and Ceratichthys Baird and Girard. The first two genera are monotypic, including H. notatus and P. promelas respectively. The genus Ceratichthys includes two valid species as currently considered, although Hubbs and Black (1947) recognized C. perspicuus, C. vigilax, C. tenellus, and C. callarchus as comprising the genus.

Ceratichthys callarchus Hubbs and Black, represented only by the holotype, is regarded as a dubius species and is excluded from consideration. Hay (1888) considered Hyborhynchus synonymous with Pimephales. He also called attention to the similarity and taxonomic confusion of Pimephales (=Hyborhynchus) notatus and Cliola (=Ceratichthys) vigilax and noticed variability in the length of the intestine of P. notatus.

Pimephales notatus is intermediate between P. promelas and Ceratichthys. P. promelas has a much longer intestine, with coils and loops, whereas in Ceratichthys the intestine has only a single loop.

Bailey (1951), working with fishes of Iowa, without comment merged the three nominal genera in the genus Pimephales. Cross (1953) demonstrated the need for the reduction of P. perspicuus to subspecies status

under P. vigilax, in accordance with Hubbs' (1951) statement: "Recent work shows that C. perspicuus is conspecific with C. vigilax, as formerly suspected...." which he considered as a source of synonymization.

Cross (1953) examined breeding males of P. perspicuus and P. v. vigilax and reported that the tubercle patterns suggest differences of only subspecific value. Another identifying character which Hubbs and Black (1947) cited for the separation of C. vigilax from C. perspicuus was the degree of exposure of the jaws in breeding males, but Cross (1953) considered this character to be of less taxonomic value than number and arrangement of the pearl organs, because some perspicuus specimens, on the basis of the latter character, had tubercle patterns typical of vigilax.

Hubbs and Black (1947) presented characteristics and phylogeny of the Pimephalinae, suggesting that this subfamily differs from other cyprinids in two respects. These are: (1) the presence of a blunt, rudimentary, spinelike ray attached by a membrane to the first developed dorsal ray, whereas in other American cyprinids the second ray has the form of a thin splint appressed to the third ray; and (2) the limited number of nuptial tubercles in breeding males and their arrangement in one, two, or three transverse rows on the snout, while in other minnows they occur in different patterns.

Ceratichthys has been separated from Pimephales and Hyborhynchus on the basis of its shorter intestine. Hyborhynchus differs from Pimephales in that the former has a more ventral mouth, a more distinct caudal spot and the presence of a temporarily developed barbel-like expansion at the angle of the jaw in breeding males. Also Hyborhynchus

has a complete lateral line compared with the more or less incomplete lateral line of P. promelas. Except that Hyborhynchus has a long gut, it has a more superficial resemblance to Ceratichthys than to Pimephales (Cross, 1953).

For separation of the species of Pimephales the following diagnostic features are considered herein in agreement with Moore (1957).

P. promelas is characterized by the presence of three rows (sometimes a fourth row between the nostrils) of tubercles on the snout of breeding males; caudal spot indistinct or absent; body stout, its greatest depth contained about 3.2-4.0 times in standard length; and nuptial chin tubercles may be present.

Common characteristics for the other three species are: a slender body, its greatest depth contained about 3.9-5.1 times in standard length; a distinct caudal spot; and breeding males with 1-3 rows of nuptial tubercles on the snout. However, they can be differentiated since P. notatus is characterized by: a black peritoneum, or at least black pigment present; upper lip overhung by a fleshy snout, mouth more ventral; and intestine variable in length, but usually with at least one transverse loop across the anterior end of the stomach. P. vigilax and P. tenellus never have a black peritoneum and the gut is always short, without a transverse loop.

P. tenellus differs from P. vigilax in having more distinct crosshatching, the absence of black pigment in the crotches of the dorsal rays and a more slender body.

The absence of osteological consideration in past works, which treat the subfamily Pimephalinae, has prompted this study, with the hope that a basis may be found to support or discourage the generic merger now based on more superficial characters.

CHAPTER II

HISTORICAL REVIEW

The literature concerning the Weberian apparatus has been reviewed
by several writers (Krumholz, 1943, Nelson, 1948, Weitzman, 1954, Bridge
and Haddon, 1889, 1892) and many others. The following literature review
is in part according to the above authors and in part from original
sources, since not all papers written on this subject were readily avail-
able. The review is presented for the sake of completeness.

E. H. Weber (1820) in his paper "De aure et auditu hominis et
animalium," was the first to describe the anatomy of these ossicles,
having found them in Silurus glanis, (but according to Adams, 1928, they
were first seen by Rosenthal). They were named after Weber and termed
the Weberian ossicles (Bridge and Haddon, 1889). The anatomy of the
apparatus in Cyprinus brama was described by Isis von Oken (1821).
Reissner (1859) studied the ossicles in some siluroid fishes and Nusbaum
(1881) gave a description of the apparatus in some Cyprinidae. One of
the first North American investigations was made by R. R. Wright (1884)
when he described these bones in Amiurus catus. Krumholz (1943), in
citing Wright (1884), introduced some doubt concerning Wright's material
by indicating "Amiurus catus (Ameiurus nebulosus)". He may have doubted
the identity of Wright's material or falsly considered A. catus a syno-
nym of A. nebulosus. Bridge and Haddon (1889, 1892) gave the initial
account of the anatomy of the Weberian ossicles of the Nematognathi.

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They called them the "Weberian ossicles" rather than auditory ossicles and described the elastic spring apparatus, "Springfederaparat" of Johannes Muller, 1843, which is an outgrowth of the transverse process of the fourth vertebra in some catfishes. Nusbaum and Sidoriak (1899) described the Weberian apparatus of Cobitis (=Misgurnus) fossilis. In 1908, Nusbaum described the development and morphology of these ossicles in Cyprinus carpio. Evans (1924-1925) contributed a study of the anatomy and physiology of the air-bladder and Weberian ossicles of Cyprinidae. Recent investigators who described the Weberian ossicles are Hora (1922), Chranilov (1926, 1927, 1929, 1930), Adams (1928), Wunder (1936) and von Frisch (1938). In (1943) Krumholz published a comparative study of the Weberian ossicles in North American ostariophysine fishes. Nelson (1948) studied the comparative morphology of the Weberian apparatus of the Catostomidae and called attention to its systematic significance. In 1949, Nelson studied the swim bladder and Weberian apparatus of Raphiodon vulpinus Agassiz and gave notes on some additional morphological features.

Ostariophysaea was the name given by Sagemehl (1891) to include those fishes possessing Weberian ossicles. Jordan (1929) defined the series Ostariophysi as "fishes with the anterior vertebrae modified to connect with the air-bladder and enclosing an organ of hearing." This series includes the nominal orders Eventognathi (suckers, minnows, and loaches), Nematognathi (catfishes), Heterognathi (characins) and Gymnonoti (electric eels, etc.) the latter occurring in the tropical regions of Central and South America.

The nomenclature of the Weberian ossicles proposed by various authors according to Krumholz, 1943, is presented in Table I.

TABLE I

NOMENCLATURE OF THE WEBERIAN OSSICLES PROPOSED BY VARIOUS AUTHORS

Author and Date	Names of Bones in Anterposterior Sequence			
Weber (1820)	Claustrum	Stapes	Incus	Malleus
Mueller (1853)	Claustrum	Steibugel	Ambos	Hammer
Bridge and Haddon (1889)	Claustrum	Scaphium	Intercalarium	Tripus
Thilo (1908)	Hinlage	Deckel	Lenker	Hebel

In the United States the nomenclature of Bridge and Haddon is preferred because it avoids any confusion with the non-homologous auditory ossicles of mammalia.

Three theories concerning the origin of the Weberian ossicles have been proposed. Weber (1820), Trenviranus, Saagman Mulder, Bear and Breschet and other earlier authors considered these ossicles to be homologous with the ear ossicles of mammals. St. Hilaire (1824), Muller (1843), Beaudelot (1868), Sagemehl (1884 a,b, 1891), Bridge and Haddon (1893), Sachs (1912), Nusbaum (1908 a, b), Grassi (1883) and Sidoriak (1898) considered them to be entirely derived from the anterior vertebrae. Wright (1884), held that they are derived in part from ossification of ligaments and in part from the anterior vertebrae.

Many workers supposed that these ossicles originated by the simple detachment of the portions of the anterior vertebrae. All theories were based on morphology which alone is an insufficient guide, as Bridge (according to Watson, 1939) has remarked.

Watson (1939) was the first to study the development of ossicles in the young stages of Ostariophysi (see Table II).

TABLE II

THE ORIGIN OF THE WEBERIAN OSSICLES ACCORDING TO WATSON

Ossicle	Part	Anlage
1. Claustrum	---------	Crescentic accumulation of mesenchyme in wall of atrium sinus imparis.
2. Scaphium	1-Concha Stapedis 2-Ascending and Articulating processes	Circular disc of mesenchyme. Basidorsal of first vertebra.
3. Intercalarium	1-Manubrium incudis 2-Ascending and Articulating processes	(1) Ossification in inter-ossicular ligament. (2) Basidorsal of the second vertebra.
4. Tripus	1-Anterior process 2-Articulating process 3-Main body 4-Transformator process	(1) Basiventral of third vertebra plus ossification in inter-ossicular ligament. (2) Basiventral of third vertebra. (3) Mass of mesenchyme between third and fourth basiventrals. (4) Rib rudiment of third vertebra plus ossification in wall of air-bladder.

Hora (1922) gave the homology of these ossicles as follows: claustrum, a part of neural arch I; scaphium, a part of neural arch I; intercalarium, neural arch II; and the tripus, transverse process plus ribs of III and IV.

Apparently there is some error in Ramaswami (1955) since he mentioned Hyborhynchus notatus, without specific comment concerning its Weberian apparatus, as having pharyngeal teeth 5-5, a count that never

occurs in <u>Pimephales</u>, in so far as known.

CHAPTER III

MATERIALS AND METHODS

Specimens, obtained from the fish collections of Oklahoma State
University were fixed in formalin, preserved in alcohol and stained in
alizarin.

After fixation in formalin or alcohol the specimens were put in
two percent Potassium hydroxide (KOH) for one day, then placed for four
to six days in fresh (KOH) to which a tinge of alizarin was added.
Some specimens, kept in the solution (2% KOH) for ten days, were so
tough that dissection was impossible without breaking some of the
ossicles. It was necessary to keep such specimens for ten to fourteen
days in Potassium hydroxide of a strength greater than two percent.

Dissections were made in water and the dissections preserved in
glycerin. Absolute alcohol for dehydration and toluene for dissolving
fatty tissue also were used.

Serial cross sections of one specimen, (P. tenellus) to illustrate
the relationship between the anterior air chamber and the tripodes,
were made.

Cooking in a solution of two percent KOH, with alizarin added,
was tried as a method for facilitating dissection of tough specimens.
This method proved to be of little use since the specimens disarticu-
lated or partially disintegrated after two days. However, under care-
ful observation the method was to some extent useful since the ossicles
were readily separated from other bony elements.

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Dissections were made under a binocular microscope and drawings executed with the aid of a camera lucida. All drawings were made from the right side of specimens unless otherwise stated.

TABLE III

SPECIMENS USED FOR DISSECTION AND STUDY

Legend: (1) O.A.M. - Museum of Zoology, Oklahoma State University
(2) O.A.S. 1-59 - Field Collection Number
(3) S.L. - Standard length
(4) SWAN-14-1959 - Field Collection Number

	S. L. and Sex		Source
A - P. promelas			
1.	48 m m	♀	OAM 3388
2.	68 m m	♂	OAM 3388
3.	42 m m	♂	Spring Creek
4.	48 m m	♀	Fair Park, Stillwater
5.	55 m m	♀	Fair Park, Stillwater
6.	38 m m	♀	Spring Creek
7.	54 m m	♀	OAM 3388
8.	63 m m	♂	OAM 3388
9.	69 m m	♂	OAM 3388
10.	35 m m	♀	OAM 3388
B - P. notatus			
1.	45 m m	♀	OAM 3178
2.	65 m m	♂	OAM 3178
3.	55 m m	♀	OAM 4580
4.	77 m m	♂	OAM 4580
5.	65 m m	♀	OAM 4580

TABLE III (CONTINUED)

	S. L. and Sex		Source
6.	70 m m	♂	OAM 4580
7.	68 m m	♂	Swan-14-1959
8.	61 m m	♂	Swan-14-1959
9.	48 m m	♀	Swan-14-1959
10.	62 m m	♂	Swan-14-1959
11.	55 m m	♂	Beaver Creek

C - P. tenellus

1.	62 m m	♀	OAM 759
2.	51 m m	♂	OAM 51
3.	50 m m	♂	OAM 884
4.	32 m m	♀	OAM 884
5.	48 m m	♂	OAM 1058
6.	46 m m	♂	OAM 2693
7.	45 m m	♂	OAM 2693
8.	35 m m	♂	OAS 1-59
9.	42 m m	♂	OAM 759
10.	40 m m	♀	OAM 759

D - P. vigilax

1.	60 m m		♂	OAM 4727
2.	40 m m		♀	OAM 4727
3.	55 m m	(1)	♂	OAM 5153
4.	55 m m	(2)	♂	OAM 5153
5.	50 m m	(1)	♀	OAM 4727

TABLE III (CONTINUED)

	S. L. and Sex		Source
6.	50 m m (2)	♀	OAM 4727
7.	69 m m	♂	OAM 4727
8.	59 m m	♂	OAM 4727
9.	65 m m	♂	OAM 4727
10.	50 m m	♀	OAM 4727

CHAPTER IV

GENERAL DESCRIPTION AND RELATIONSHIPS OF THE
WEBERIAN APPARATUS IN PIMEPHALES

The Weberian apparatus in the genus Pimephales consists of two
functional units, Weberian ossicles (Pars auditum) and the supporting
part (Pars sustentaculum).

Weberian Ossicles (Pars auditum)

This unit consists of four ossicles on each side of the first three
vertebrae, named in anteroposterior order the claustrum, scaphium, inter-
calarium, and tripus.

The claustrum (Plate I) is an inverted cup-shaped bone with a
slightly convex triangular crest-like elevation placed externally on
its convex surface. This crest is attached posterodorsally by connective
tissue to the anterolateral surface of the saddle-like neural arch of
the second vertebra. The claustrum covers more than half of the poste-
rior portion of the cavity of the scaphium and leaving an aperature for
communication with the atrium sinus imparis. The atria from both sides
soon join in front forming the sinus imparis which extends forward on
the dorsal surface of the basioccipital to the cranial cavity. The
sinus imparis surrounds the endolymphatic sac which is a median poste-
rior projection of the transverse communicating canal connecting the
sacculi of the membranous labyrinth.

The claustrum arises from an accumulation of mesenchyme cells which become directly ossified and forms the upper part of the inner wall of the atrium sinus imparis. Ventrolaterally the claustrum rudiment is attached to the scaphium rudiment by a thin sheet of mesenchyme, while dorsally it is joined by mesenchyme to the vault of cartilage which lies over the spinal cord. (Watson, 1939).

According to Adams (1928) the claustrum has no physiological relation to the atrial cavities, but merely strengthens the wall of the neural canal behind the exoccipital.

The scaphium (Plate I), as a part described by Krumholz (1943) in North America ostariophysine fishes, consists of four parts:

1. Cup-shaped cavity, concha stapedis, which forms the lateral ventral and posterior surfaces of the atrium sinus imparis

2. A rounded prominence from the outer lateral surface, of the concha, to which the interossicular ligament is attached

3. The ascending process

4. The articulating process

The articulating process is a short knob on the ventroposterior edge and is fitted into a pit on the dorsolateral surface of the first centrum. The ascending process is on a straight line with the articulating process, and extends dorsoposteriorly at about 45° from the vertical. Anteriorly it lies under the second neural arch and posteriorly in front of the anterior edge of the neural pedicle of the third vertebra. It is connected to both of them by a connective tissue. The concave surface of the scaphium is directed anterodorsally toward the spinal cord. From its posterior external surface there is a more or less prominant protuberance to which the interossicular ligament is

attached. As seen from the convex surface, the scaphium bears a
shallow groove extending at right angles from the axis of the ascend-
ing and articulating processes to the anterior rim of the cup.

The majority of investigators are agreed that the scaphium, repre-
sents a modified part of the neural arch of the first vertebra (Hora,
1922). According to Watson (1939), the scaphium arises as an accumu-
lation of loose mesenchyme cells below the claustrum rudiment in the
parasagittal plane, then becomes ossified to form the concha stapedis.
Fused with this is the cartilaginous basidorsal of the first vertebra.
The basidorsal projects dorsally and ventrally, giving rise dorsally
to the ascending process and ventrally to the articulating process.
The outer surface of the concha stapedis rudiment becomes attached to
the interossicular ligament which passes backwards, downwards, and
outwards to become attached posteriorly to the basiventral of the third
vertebra.

The intercalarium, (Plate I) in _Pimephales_ is curved posteriad
near its middle and may be triangular, T-shaped, or an inverted L-
shaped bone. It is connected by the interossicular ligament to the
ventroposterior surface of the scaphium, anteriorly and to the anterior
ramus of the tripus posteriorly. As a rule the intercalarium always
articulates with the centrum of the second vertebra by a rounded artic-
ulating process fitted into a socket on the dorsolateral surface of the
centrum. On the other side of this articular process there is a
slender extension which is directed upward and backward to articulate
with the ventral or lateral surfaces of the third neural pedicle; this
is the ascending process of the intercalarium.

Watson (1939) found that the intercalarium first appears as a

direct ossification in the interossicular ligament quite close to the

concha stapedis rudiment. This ossification becomes the manubrium

incudis. Opposite to it lies the cartilaginous basidorsal of the

second vertebra, the whole intercalarium becoming ossified to form a

unified structure. The basidorsal of the second vertebra gives rise

to the articulating and ascending processes of the intercalarium.

The tripus (Plates II and III) is the largest bone in the series

and consists of four parts. (1) The body, the central part of the

bone, is concave on its ventral and convex on its posterodorsal surface,

with a concave shelf in front. It is more or less fenestrated and has

a bridge extending from the articular process downward in an antero-

lateral direction to the body. (2) The anterior ramus, connected by

the interossicular ligament to the intercalarium, may be long or short,

wide or narrow; it reaches the second transverse process, and in some

specimens overlaps it. (3) The articular process is located on the

medial side of the body and articulates with the ventrolateral surface

of the third centrum anteroventrally to posterodorsally. This process

has a groove along its surface into which a ridge from the lateral

surface of the third centrum is fitted. (4) The posterior ramus, which

is thinner than the anterior ramus, extends posteriorly beneath the

medial extension of the pleural rib of the fourth vertebra. The trans-

formator process is a long, delicate, hook-like recurved extension.

Its posterior edge is embedded in the tunica externa of the anterior

chamber (termed by Chranilov the "Weberian air-chamber") of the air

bladder. Anteriorly the transformator process, near its termination

is connected to the os suspensorium by a small triangular, unstriated

muscle, the tensor tripodis of Evans (1924-1925), Bridge and Haddon (1889).

The apex of the tensor tripodis is connected with the os suspensorium.

The ossicles are thus held in place by the tensor tripodis which immediately pulls the tip of the tripus into position after its displacement through movement of the air bladder wall. Therefore, vibrations are transmitted by changes of tension and not by impact as in mammals.

According to Watson (1939) the origin of the tripus is very complex, its parts originating as follows.

1. The anterior ramus originates from the basiventral of the third vertebra plus ossification in the interossicular ligament.

2. The articulating process is derived from the basiventral of the third vertebra.

3. The main body is derived from a mass of mesenchyme between the third and fourth basiventrals.

4. The transformator process develops from the rib rudiment of third vertebra and an ossification in the wall of the anterior chamber of the air bladder.

By means of this series of bones and the associated ligament, it is possible for the air-bladder to function as a hydrophone which picks up pressure waves over a wide surface of the body wall and transmits them indirectly to the inner ear.

An important thing to be mentioned about the transmission of vibrations from the "Weberian-air-chamber" is, that the pressure in it must be kept at a uniform level. This is effected through inervation of the ductus communicans, surrounded by a powerful sphincter, by a branch of the vagus nerve. Evans (1924-1925), in his experiments, has shown that the change of pressure in the posterior chamber influences the sphincter to close and thus the pressure in the anterior chamber remains

at a uniform level, making response to vibrations possible.

According to Watson (1939), Kuiper (1915) has shown that the de-struction of the Weberian apparatus results in cessations of responses to vibration, but continuation of responses to other types of stimuli. Von Frisch (1938) demonstrated that the sacculus and lagena of Cyprinidae and Siluridae are adapted for reception of sound vibrations carried by the Weberian chain.

Pars Sustentaculum

The pars sustentatulum, which is the supporting unit of the Weberian apparatus, consists of the first four modified vertebrae, none of which is fused with others in Pimephales (Plates III and IV).

The first vertebra is a disc-like centrum with two big, pit-like depressions on its dorsolateral side to hold the articular processes of the scaphia, one very small pit between these in the mid-dorsal surface (present in two species) and one median pit in the ventral surface. This vertebra has two ribs which are not uniform in length or in general shape in the four species. These more or less short ribs usually lie toward the anterior margin of the centrum, extending forward and then bending outward. A long ligament connects their extremities to the posterior edge of the supracleithrum. These ribs are firmly fused to the centrum proximally while distally they penetrate the myotomes. Watson (1939) considered them to be dorsal ribs in the gold fish. The first vertebra lacks a neural arch. An ordinary intervertebral joint articulates it with the conical centrum-like basioccipital proatlas (of Harrington, 1955) of the cranium and also with the body of the second vertebra. The ante-rior face of the centrum is very little concave, and is not circular,

but vertically elliptical in shape. Its posterior face is extended dorsally backward, producing a posterior concavity. The whole centrum is covered by a layer of cartilage which continues above, extends to the skull and surrounds the spinal cord.

The second vertebra (Plate III) consists of a vertebral body, long ribs and neural arch (Plate V). The centrum appears to be concave anteriorly in its ventral portion when viewed dorsally; its ventral surface is produced anteriad because the ribs are placed anteroventrally. Behind each rib there is a big hole for muscle insertion and above these holes there is a moderately large conical pit on each side to hold the articulating process of the intercalarium (Plates III and IV). Also two median small pits are present in some specimens (Plate III). Viewing the body of the centrum dorsally, it seems to be constricted near its posterior face and behind the large lateral holes. The second centrum has one ventral medial pit and, in addition, other pits varying in number and size even among specimens of the same species. The second centrum is amphicoelous and differs from the first in having a saddle-shaped neural arch that is very thick on its anterolateral edge. This arch in some of the species has a rudimentary, laterally-compressed neural spine which in some species is very conspicuous and recognizable (Plate V). This neural arch extends anteriorly over the posterior upper half of the first centrum to which the crest of the claustrum on each side articulates by means of connective tissues (Plate IV). Posteriorly, to some extent, it extends over the third centrum. The ribs of the second are firmly fused to the body anteroventrally (Plate III). They are wide plates near the centrum directed anterolaterally and partially enclosing the first centrum ventrally. Near their extremities they become slender

and are directed slightly posteriad. On the dorsal posterior edge of
the rib, a groove extends a short distance from the centrum. Ventrally
each rib has a very shallow depression, in some specimens.

The peculiarly shaped, ribless third vertebra consists of the
amphicoelous centrum, the neural pedicles and the neural complex (Plates
IV and V). The centrum, viewed laterally, has the aspect of three cones
with their apexes meeting at a common locus in the lateroventral surface.
This configuration, therefore, presents two grooves in the lateral
surface, one extending diagonally about 50^{0} downward and backward, and
usually containing a pit; the other, characterized by a ridge extending
dorsoposteriad about 50^{0} with it. The tripus, having a groove on its
articulating process, fits over the ridge within this groove, producing
a hinge capable of movement in two directions. The upper cone, duplicated
on the opposite side, is inverted and hollow to receive the pyramidal
root of the neural pedicle. The posterior wall of the upper cone extends
posteriad over the posterior face of the centrum (Plate III). The cen-
trum, from dorsal view, exhibits the two above-mentioned inverted cones,
with a narrow and grooved bridge between them. The groove is widest
posteriad, where there is a deep pit, and pointed anteriad. The centrum,
from the ventral aspect shows the anterior and posterior faces joined by
a bridge which narrows near its middle, with more than four small pits.

The neural pedicles (Plate III) consist of three parts. The pyram-
idal roots fit into the upper cones on the dorsolateral surfaces of the
centrum. The stem extends a short distance dorsad and is laterally
slightly concave with a pit near its base; the anterior edge of the stem
is extended as a flange, sometimes as a ventroposterior bony extension,
to be fastened by a ligament to the upper anterior edge of the fourth

pleural rib. The third part of the pedicle is the body which extends anteriorly over the second centrum. Anteriorly the ventral edge of the body is slightly curved upward and forward. Some specimens have a notch in this surface in front of which the ascending process of the inter-calarium lies. The dorsal and anterior edges of the body are very thick. The body articulates anterodorsally with the second neural arch, dorsally with the basal arch of the neural complex and posterodorsally with the prezygapophysis of the neural arch of the fourth, leaving a circular hole between them.

The neural complex, as here treated, (Plate V) is composed of a basal arch, a stem and the boat (so named because of its shape). The basal arch, with a posteriorly indented edge, articulates ventrolaterally with the neural pedicle, anteriorly with the second neural arch and posteriorly with the neural arch of the fourth vertebra, thus covering the spinal cord in this region. The stem extends dorsoanteriad from the basal arch as a compressed crest, which may be very wide, of variable height and extending from the anterior to the posterior edge of the arch. It may be fenestrated and reinforced by struts. The boat is uppermost and open posteriorly. In some specimens the boat is wider and longer than in others, but apparently the shape and size are not correlated with sex. In some species the boat is relatively deep, in others it is shallow. This boat-shaped neural complex has a ventral blade which extends downward and/or forward to be attached ventrally in front of the stem. It is usually raised on a perpendicular stem, but in P. tenellus the stem is inclined forward at about 40° from the horizontal axis of the body. The boat usually extends over the second neural arch. The elements which form the neural complex are the neural spine of the third

vertebra plus, possibly, interspinous elements fused with it. The first interspinous element is long and may be very low; it lies over the posterior end of the neural complex, to the sides of which it is attached by ligaments (Plate IV).

The fourth vertebra is the least modified and consists of the following parts: (1) the centrum (Plate III), (2) the pleural ribs and ossa suspensoria (Plates VI and VII) and (3) the neural arch with its spine (Plate VIII). The amphicoelous centrum, viewed dorsally, contains two pyramidal cavities, one on each side leaving a narrow bridge, widened posteriorly and anteriorly on the middorsal surface. Laterally the centrum presents the aspect of three pyramids, one dorsal, one anterior and one posterior, with their apexes approximating each other. Between the anterior and dorsal pyramids, and directed in the dorsoanterior plane, is a small open subtriangular cavity placed antero-dorsolaterally. The upper posterior part of the articular process of the tripus is placed just in front of this opening and the posterodorsal portion of the wall of the pyramidal cavity of the third centrum extends above it. Under these three pyramidal walls the rest of the centrum is nearly flat. The pyramidal roots of the fourth neural arch (Plate VIII) are fitted into the dorsolateral pyramidal cavities and the articular heads of the pleural ribs are accommodated by the lateroventral cavities. The centrum, from ventral view, has a narrow bridge, wider anteriad, with a median groove and asymmetrically arranged pits (Plate III). The neural arch, above mentioned, has two pyramidal roots, articulating anteriorly with the third neural pedicles by short anterior projections, modified prezyga-pophyses, one on each side, leaving a circular space below their artic-ular surfaces. Anterodorsally they articulate with the posterodorsal

edge of the basal arch of the neural complex. The neural arch, near its base, is invaginated on its anterolateral surface and penetrated by a hole (variable in size in different specimens) which extends into the pyramidal root, without connecting with the neural canal. The neural arch anteriorly extends over the posterior part of the third vertebra, but does not extend posteriorly beyond the fourth centrum. Posteriorly the edge of the neural arch projects as a modified postzygapophysis of variable shape (Plate VIII). The neural spine of the fourth is usually short, directed dorsoposteriorly and is connected by a ligament to the posterior edge of the neural complex. The pleural ribs of the fourth vertebra have dilated articular facets, their heads being nearly pyramidal and bearing slight depressions on their anterior, dorsal and posterior surfaces (Plates VI and VII). Each head extends from the midlateral side of the fourth centrum to the midventral surface. These heavy ribs, widest near their articulation with the fourth centrum extend downward, slightly backward and outward from the fourth centrum. The anterior edge of a rib may or may not have a spine-like projection directed anterodorsally and connected by a ligament to the posteriorly projected process from the base of the stem of the third neural pedicle. The projection, sometimes long and slender, may have two spines on the upper anterior surface of the rib. Usually a depression, just under the articulation of the rib, contains three or four pits separated by struts. From the point where the rib extends anterolaterally, a knob articulates with the proximal part of the fifth "first normal" rib by a strong white ligament. The pleural rib divides into two portions, the rib proper and the os suspensorium. The external surface of the rib proper has a groove on its anterior upper side. The ossa

suspensoria extend posteromesad then turn abruptly downward, without bony connection with each other (Plates VII and VIII). The space be= tween the ossa, filled by connective tissue, is much wider dorsally than ventrally. The ossa suspensoria (Plates VII and VIII) from posterior view are flattened, triangular, fenestrated in the upper, broader portion and exhibit a median depression there.

At the upper edge of the ossa, there are shelf=like extensions, directed posteriad, their median posterior extensions, in some specimens, are present as reduced spines and were called the spines of the ossa suspensoria by Nelson (1948). The space above the ossa suspensoria and beneath the fourth centrum accommodates the dorsal aorta and other large blood vessels. The tunica externa of the air bladder extends as a ribbon forward and downward and is firmly fastened to the posterior edges of the shelves of the ossa suspensoria anteriorly, while dorsally the sides of this ribbon are fastened to the ventral surfaces of the fifth and sixth centra. This forms a tunnel through which the dorsal aorta passes. In some specimens the shelves are represented by small spines or posterior projections, one on each side. The transformator process of each tripus passes beneath the median extension of the fourth pleural ribs, which form the ossa suspensoria, and is recurved anteriad. The tensor tripodis is inserted here and has its origin on the ossa (Evans, 1924=1925).

The fifth is the first unmodified rib=bearing vertebra.

The air=bladder consists of two chambers connected by a narrow duct, the ductus communicans. According to Evans (1924=1925 and 1928) and Watson (1939) the ductus communicans, between the Weberian air chamber and the air bladder proper, is inervated by a special branch

of the Vagus nerve. A powerful muscular sphincter surrounds the ductus communicans, thus serving to control the pressure in the Weberian air chamber. The anterior chamber is connected to the inner ear through the Weberian ossicles. This chamber consists of two coats, the outer connected anterodorsally to the posterior edges of the transformator processes. Anteroventrally this coat exhibits a pear-shaped slit. The internal coat is loosely attached to the lower rough surfaces of the ossa suspensoria, which Evans (1924-1925) called the central plate, thus filling the anterior interval of the slit in the external coat. On either side of this slit the free margin of the external coat, slightly thickened so as to form anterior ligaments, passes downwards to be attached to the blunt extremities of ossa suspensoria ventrally. The outer coat extends backward and covers the anterior chamber to the ductus communicans, the internal coat extending back to form the posterior chamber. The posterior chamber makes connection by means of a long narrow pneumatic duct which opens slightly to the left of the middorsal line of the esophagus behind the pharyngeal bones. This duct issues from the anteroventral surface of the posterior chamber. The air-bladder is retroperitoneal and is located immediately beneath the vertebral column and extending posteriad almost to the end of the 18th vertebra. The peritoneum is completely fused with the posterior chamber at the point where the pneumatic duct emerges.

The various parts of the apparatus are joined in rather complex fashion by ligaments. Dorsally the neural complex, from its anterior edge, is joined by a ligament to the posterior midsagittal edge of the supraoccipital keel. A similar connection is effected, by interspinous ligaments, between the posterior edge of the boat-shaped neural complex

and other neural spines and the first interspinous bone, which is located
posterodorsally from the boat. The exoccipitals are joined medianly by
ligaments to the anterior edges of the second neural arch and the third
neural pedicles over the claustra. The claustrum and the scaphium are
joined by connective tissue in the region between the ascending and arti-
culating processes of the scaphium. Another flat ligament extends from
the epiotic to the posterior sides of the neural complex. A narrow,
very thin and slender ligament extends between the second neural arch
and the posterior upper surface of the crest of the claustrum and passing
over the intercalarium to the upper anterior surface of the fourth pleu-
ral rib. Another ligament passes from the lateral surface on each side
of the first vertebra to the proximal tips of the ribs of the second.
Broad ligaments extend between the fourth pleural ribs and the ossa
suspensoria. The ribs of the first vertebra are connected by ligaments
to the supracleithra.

The basioccipital forms the floor and the side walls of the cavum
sinus imparis, the ventral wall of which is continuous behind with the
conical, posteriorly concave centrum of the subsumed proatlas. Below
and behind the proatlas the basioccipital is produced in an oblique,
posteroventrally directed pharyngeal process, which serves as origin
for the muscles concerned with the retraction of the toothed fifth
ceratobranchials (pharyngeal bones). The pharyngeal process of the
basioccipital extends, below the first three vertebrae and partly under
the fourth. From the dorsal surface of the basioccipital floor, two
thin plates ascend to meet the opposing ventral ridges under the hori-
zontal plates of the exoccipitals above. These form the lateral walls
of the cavum sinus imparis and the medial wall of the adjacent recessus
sacculi.

The pharyngeal process of the basioccipital is laterally compressed posteriad into a vertical plate, except in one species, but widens anteriorly to form, below, a horizontal, ventrally concave masticatory plate which opposes the teeth of the pharyngeal bones. At the broad base of the pharyngeal process, just below the proatlas, the large canal for the dorsal aorta opens dorsoposteriorly.

CHAPTER V

DISCUSSION AND CONCLUSIONS

The previous description applies in a general sense to the genus _Pimephales_. The following descriptions are concerned with specific differences found in the four species.

The first centrum is amphicoelous, with the anterior concavity shallower than that of the posterior face. Ramaswami (1955) working on Gobioninae found that the anterior and posterior facets of the first vertebra, were flat. In _Pimephales_ the anterior facet of the first vertebra often separates from the centrum and remains attached to the proatlas, leaving the impression that the facet is flat.

The first modified ribs are anteriorly placed near the anterior facet on the lateroventral edge of the centrum, in the four species. They project slightly forward near their bases, and then turn laterally. Differences were found in the ratios of the length of the modified ribs of the first vertebra to that of the second vertebra in the four species studied. The average ratios are as follows: _P. notatus_ and _P. promelas_, 1/4.5; _P. tenellus_, 1/3.48; and _P. vigilax_, 1/2.4. The first modified rib in _P. notatus_ is more swollen near its base than that of _P. promelas_. In _P. vigilax_ it is longer and slenderer than in the other species.

In one specimen of _P. promelas_ the ligament which joins the tip of the first rib to the supracleithrum contains a sesamoid bone in the left side.

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The claustrum has exactly the same shape in all four species. The only difference was that the uppermost end of the crest is always pointed in P. vigilax, P. notatus, and P. promelas, whereas in P. tenellus it is usually blunt.

Also, the scaphium shows no variation in the four species, except with regard to the length of the ascending process (Plate I). The species in order from the longest to the shortest ascending processes of scaphia are as follows: P. notatus, P. tenellus, P. vigilax, and P. promelas.

A foramen, of undetermined function, near the bases of the articular processes of the scaphia, is uniformly present in all specimens of all four species examined. This foramen is apparently homologous with those which penetrate into the pyramidal roots of the third neural pedicle and the base of the fourth neural arch. If this is true, it follows that the articular processes of the scaphium and intercalarium are homologous with the pyramidal roots of the third and fourth basidorsals. The ascending processes of the scaphium and intercalarium represent, in all probability, postzygaphophyses of the first and second vertebrae respectively.

The number of pits found in the first centrum in the four species are listed in Table IV.

As previously mentioned, the modified ribs of the second vertebra differ in the four species only with regard to length. The second neural arch always in P. promelas, and usually in P. notatus, possesses a rudimentary laterally compressed neural spine. This feature was not observed in P. tenellus and P. vigilax. This neural spine in some, but not all, specimens of P. notatus is large and conspicuous (Plate V).

TABLE IV

NUMBER OF PITS IN THE FIRST CENTRUM

	Species	Dorsal Surface	Ventral Surface
1.	P. promelas	3	1
2.	P. notatus	Usually 2, Rarely 3	1
3.	P. tenellus	2	1
4.	P. vigilax	2	1

In all species, except P. vigilax, there are four pits in the dorsal surface of the second centrum. There are usually three in P. vigilax, but occasionally only two. In all four species a single pit is found in both ventral and lateral surfaces. The ventral pits lie in the median surface; the lateral ones (large depressions) are located on each side posterodorsal to the modified ribs; the dorsal ones (large and conical) consist of two in dorsolateral position, to accommodate the processes of the intercalaria; and the other two, if present, are located dorsomedially.

The intercalarium, as a part of the second vertebra, shows variation in shape (Plate I). The following description gives the usual shape found in each of the four species.

In P. notatus (Plate I, Fig. 2) the intercalarium is an inverted L-shaped bone with a short articulating process. The ascending process is not straight, but has a slight curvature, extending to the edge of the third neural pedicle to terminate in a notch, described above, where it is fastened by means of a ligament. The terminal end of the manubrium

incudis is swollen and compressed anteriorly and posteriorly
for the attachment of the interossicular ligament. From side
view, before removal from the specimen, the manubrium incudis
is long and slender, with an anterior short extension on its
end.

In P. vigilax (Plate I, Fig. 1 A and B) the intercalarium is a tri-
angular bone with a needle-like ascending process which over-
laps the anteroventral edge of the third nerual pedicle.
Usually the ascending process is needle-like in all the inter-
calaria examined of the species, but in some of the specimens
the portion between the ascending and articulating processes
and the manubrium incudis is less triangular in shape and the
manubrium is more slender, than in P. notatus, but usually it
is wide and stout. The terminal portion of the manubrium
incudis is also anteriorly and posteriorly compressed, but
not swollen.

In P. tenellus the intercalarium (Plate I, Fig. 3) is T-shaped,
with a slender, but not needle-like ascending process over-
lapping the anteroventral edge of the third neural pedicle.
The manubrium incudis is slender and long, with a ball-
shaped, anteroposteriorly compressed terminus for attachment
of the interossicular ligament. The articular process is
longer than in P. notatus and P. vigilax.

In P. promelas the intercalarium (Plate I, Fig. 4) is crescentic
in shape, in that the manubrium incudis is curved upwards,
with a short ascending process on the upper side; this
ascending process articulates with and overlaps the antero-
ventral edge of the third neural pedicle. Usually the

plano-convex termination of the manubrium incudis is circular

or triangular, with the manubrium incudis extending from its

termination to join the ascending and articulating processes.

The third centrum is similar in all four species. The anteriorly

extended portion of the body of the third neural pedicle has a notch in

P. notatus in front of which the end of the ascending process of the

intercalarium is fitted. Also, in this species the anterior lower sur-

face of the convex stem usually extends latero-ventroposteriad to be

attached by a ligament to the anterior projection in the upper portion

of the fourth pleural rib. This lateral extension is similar to that

called the transverse plate by Nelson (1948) in Catostomidae. This

characteristic is always found in P. notatus; is present, but not in

all specimens, of P. promelas; rarely present in P. tenellus; and absent

in P. vigilax. On the posterior lower surface of the stem of the third

neural pedicle, another short projection extending posteroventrally

over the anterior edge of the fourth neural arch, is rarely found.

The boat-shaped neural complexes, though similar, are not alike in

the four species (Plate V). In some of the females it is narrow and

short, whereas it is wide and long in males. It always has one or more

pits in its lateral walls near the lower posterior end and opening into

the bottom of the boat. In general, the shape of the neural complex

shows great variability within the species. The more constant features

are described below.

In P. promelas (Plate V, Fig. 1) the boat is deep, its anterior big

blade extending in front of the boat and stem and over the posterior

portion of the second neural arch, but not reaching over the rudimentary

second neural spine. The stem is wide and short, sculptured by many

pits and bridges for insertion of muscles and ligaments. The boat is open behind. The basal arch has a laterally compressed ridge that extends upward and is connected with the posterior end of the boat, thus completing a unified structure.

In _P. vigilax_ (Plate V, Fig. 2) the neural complex differs from that of _P. promelas_ in that the stem is longer and lacks the broad connection with the anterior projecting plate, which is comparatively deep and extends over the second neural arch. The boat is usually open behind.

In _P. notatus_ (Plate V, Fig. 4) the neural complex is similar to that of _P. vigilax_, but the stem is shorter and broader and the anterior plate is small and not so deep. Usually there is a short, triangular, laterally compressed blade in front and below the boat. The boat is usually closed behind.

In _P. tenellus_ (Plate V, Fig. 3) the boat is usually very shallow, its stem very short and inclined anteriorly. The boat is open posteriorly and anteriorly, except in one specimen in which it is closed anteriorly. The bottom of the boat is gradually inclined posteriad. The blade beneath the boat does not extend in front of the stem.

The tripus, as a part of the third vertebra, shows differences in the four species (Plate II). Generally speaking, the articular process is long and straight, having a posteriorly closed narrow groove. The posterior rami and the transformator processes are horizontal in position, inclined ventrally from their posterior edges, and terminating as anteriorly recurved points just behind the ossa suspensoria. All the specimens, of the four species examined, possess grooves extending from the anterior rami posteriad on the body which is usually

dorsally convex. In front of this convexity a concave shelf extends under the articular process and in front of the body to the anterior ramus. Each species has a bridge extending ventrally from the posterior edge of the articular process to the body. This bridge, in P. notatus, is dorsally branched and usually short. Since, in P. vigilax, P. promelas, and P. tenellus, this structure is usually long, it is useless as a diagnostic character.

The following are good characters of the tripus in the four species.

P. vigilax (Plate II, Fig. 4) is characterized by:

1. The angular shape of the posterior ramus; the nearly flat, little convex, externally and posteriorly flattened body, without fenestrations.

2. The shelf extends only a short way under the posterior portion of the anterior ramus and has a shallow concavity dorsally, anteriorly its convexity is continuous with that of the body.

3. The wide, straight and very slightly curved (in two of 11 specimens) groove of the articular process.

4. The wide and short anterior and posterior rami.

5. The posterior edge of the body is curved upward and slightly forward.

P. notatus (Plate II, Fig. 3) is characterized by:

1. The similar curvature of the posterior ramus and body.

2. The usual absence of fenestration.

3. The dorsal concavity of the shelf extending ventro-anteriad to join the posterior portion of the anterior ramus, and then posteriad at the same level as that of

the body before passing under the anterior ramus where it may branch into reinforcing struts.

4. The straight, shallow and usually narrower (than in P. vigilax) groove of the articular process.

5. The long and wide (less wide than in P. vigilax) anterior ramus.

6. The long posterior ramus.

7. The straight external anterior edge of the body with a curved posterior contour, giving an impression of inward curvature.

P. tenellus (Plate II, Fig. 2) differs from P. notatus in that:

1. The body is usually fenestrated.

2. The external anterior edge of the body is usually concave.

3. The shelf is dorsally deep and anteriorly with struts as in P. notatus.

4. The anterior ramus is long, but shorter than that of P. notatus.

P. promelas (Plate II, Fig. 1) has:

1. A slight but even curvature throughout the outer edge of the tripus.

2. A sharply declivous shelf extending below the posterior portion of the anterior ramus and dorsally with a deep concavity.

3. Usually no fenestration.

The fourth centrum (Plate III) shows no differences among the four species, except that the posterolateral wall of the upper pyramidal

cavities usually project very slightly posterodorsally in P. vigilax and P. tenellus, but does not extend beyond the posterior facet of the centrum.

The pleural ribs in P. promelas project laterally near their termination. They are straight in lateral view, inclined forward and are pointed in both lateral, posterior and anterior views (Plate VI, Figs. 3 and 4). A groove extends on the anterolateral edge from the upper depression, in front of which a wide projection is usually found. In one specimen two spine-like slender projections instead of one were found. The ossa suspensoria are usually bluntly pointed, rarely fenestrated and slightly inclined (18°) forward.

In P. tenellus the pleural rib is slightly curved anteriad and terminated bluntly (Plate VI, Figs. 2 and 4). A groove near the anterior edge, extends downward about two-thirds the length of the rib, in front of which there is a little projection. The fenestrated ossa suspensoria terminate as slender anterior projections at an angle of about (22°) from the horizontal axis of the body.

The perpendicularly-placed ossa suspensoria are fenestrated in P. vigilax and P. notatus, but more so in notatus than vigilax. Also they are slender and pointed in P. notatus, wider and blunter in P. vigilax in which two specimens were found to possess serrations on the internal edge (Plate VII, Figs. 1 and 2).

The rib proper is slender, pointed and anteriorly curved in P notatus (Plate VII, Fig. 3) with a short spine-like projection, absent in P. vigilax which has a heavier and serrately truncate rib (Plate VII, Fig. 4). From the anterior or posterior view the rib is directed at a 45° angle from the sagittal plane in all species, but in lateral view,

of _vigilax_ only, it is sigmoid, being girst directed posteriad and then
anteriad.

The neural arches of the fourth vertebrae have short neural spines
nearly equal in height to the neural complexes. The neural arches,
are plate-like, in their posterior portions, with a depression, near
the base, having a pit on each side penetrating the pyramidal roots
which are fitted into cavities on the dorsolateral surfaces of the fourth
centra (Plate VIII, Figs. 1, 2, and 3). The neural arches project an-
terodorsally and are firmly attached to the posterior projections
(postzygapophyses) of the third neural pedicles by a ligament (Plate
IV, Fig. 1). They are also attached to the posteroventral portion of
the basal arch of the neural complex. The right and left components
unite into one short posterodorsally inclined neural spine. The poste-
rior part of the neural arch , as in the rest of the vertebrae, has no
bony covering, but the neural arch is completed by some sort of con-
nective tissue. In the four species the neural spine does not extend
higher than the neural complex; usually they have the same height except
in _P. tenellus_, which has a very short one. In one specimen of this
species the neural arches are not united, there being two separate
rudimentary neural spines. In _P. promelas_ the spine is compressed an-
teroposteriorly and basally bent posteriad to accommodate the basal
portion of the neural complex. The neural arch usually has two
posterior projections. These projections are usually represented in
P. tenellus by one (rarely two) and in _P. promelas_ by two (the lower
one small). In _P. notatus_ the two are usually united, leaving a
circular pit or foramen and in _P. vigilax_ there is usually one, two
in some specimens and none in others (Plate VIII, Figs. 1, 2, and 3).

The neural spine in P. vigilax is inclined posterodorsally, but straight, pointed and slenderer than that of P. notatus. In some specimens of P. tenellus and P. vigilax the lateroposterior wall of the pyramidal cavity of the fourth centrum projects very slightly above the base of the neural arch. The shape of the projections of the neural arch is very variable, even within a species, showing asymmetry in that there may be none, one or two on either side.

Variations were also found in the shape and posterior projections of the neural arches of other trunk vertebrae (Plate VIII, Fig. 4).

The notochordal canal, in the four species studied, is very clear in the vertebrae posteriad from the fifth. It expands between the successive amphicoelous vertebrae, but is constricted within each centrum as described by Romer (1955) "...so it resembles those of a series of hour glasses set end to end."

The third neural pedicle and the fourth neural arch have anterior and posterior projections, regarded herein as highly modified zygapophyses. The anterior projection of the third neural pedicle, whether curved or straight ventrally, has a wide dorsal surface for ligamentous attachment. Between the third and fourth neural arch, these zygapophyses have been modified in such a way that instead of overlapping they are joined end to end in an immovable suture. The prezygapophyses of the fifth vertebra are always present and connected by ligaments to the posterior edges of the neural arch of the fourth.

Watson (1939), in agreement with Goodrich (1930), regarded the processes which are firmly attached to the first and second vertebrae as dorsal ribs because "their structure indicates that they are ribs, and their position, attached to the middle of the centra and penetrating the muscles points to homology with the dorsal or upper ribs of Esox.......

their origin and structure in the larva is similar to that of dorsal or
upper ribs of pike and some other teleosts." He labeled them, in the
drawing, as transverse processes. Wright (1884), Bridge and Haddon
(1889), Hora (1922), Chranilov (1926 and 1927), Adams (1928), and Nelson
(1948) consider them as transverse processes. Koh (1931) considered them
as ribs. Berg (1947) stated that cyprinoid fishes have no upper ribs;
he called them parapophyses, while Mookerjee (1952) considered them as
lateral processes. Ramaswami (1955) used the terminology of Watson.

In Pimephales they lie toward the anterior margin of the first and,
on the second centrum, are placed low on the anterolateral edge. They
are more ventrally than laterally placed. In Ictiobus niger (personal
observation) they are slender and attached laterally to the anterodorsal
margins of the centra. In Pimephales they are not slender, at least
near the centra. Watson stated that "They are not transverse processes
or diapophyses since they are firmly attached to the centra while true
diapophyses proceed from the neural arch." We cannot regard these
processes as either parapophyses or diapophyses if we accept Hyman's
(1942) definitions of the terms since she stated that they are lateral
projections of the centrum for the attachment of the lower and upper
heads of a two-headed rib respectively. Emelianov (1940) according to
Hyman, stated "the ribs may shift their position with regard to the
muscles during development." Thus the type of rib cannot be determined
by its location in the adult. Accordingly, in spite of what Watson found,
I consider these processes as modified ventral ribs firmly fused latero-
ventrally with the first and second centra. However, this decision
needs to be proved by studying their embryonic development.

The spinal cord in the region of the first vertebra is surrounded

by a cartilaginous, tubular structure fastened to the dorsal surface of the centrum making it impossible to pull the spinal cord through the neural canal, in prepared specimens, without disarticulating its attachment with the centrum. This tube extends forward inside the exoccipital edges and roofing over the exoccipital processes which cover the cavum sinus imparis. This tube has been termed the perineural tube by Mookerjee (1952). Watson (1939) stated that it is a part of the exoccipital, whereas Mookerjee found in his study that this tube and the exoccipitals are quite independent and separate structures; this is completely applicable in the genus _Pimephales_.

According to Adams (1928), the neural arch above the second vertebra is the first arch. It seems more logical to agree with Watson (1939) who found that the first arch is incorporated in the scaphium. The fact that this arch is in articulation with the neural pedicle and neural complex of the third vertebra also supports the idea that it is the second rather than the first.

The neural complex in _Catostomidae_ has been regarded by Nelson (1948) as representing the neural arches and spines of the third plus possible interspinous elements. Ramaswami (1955), without stating reasons for his stand, stated that, in _Notropis cornutus_, it represents the fused second and third neural spines, although he showed that the second and third centra are not fused. Also he mentioned that Sarbahi (1933) considered it as a part of the neural arch and spines of the second and third vertebrae. Adams (1928) mentioned no compound neural spine in _Ictiobus urus_ (= _I. niger_). Watson (1939), in his paper on the embryonic development of the Weberian apparatus in _Carassius auratus_, did not use the term neural complex in describing a similar structure.

He found in the embryo, where the second and third vertebrae are not fused, that there is a cartilaginous mass above these two centra. He found that this mass represents the fused neural spines and basidorsals of the second, third, and fourth vertebrae together with the first three interspinous bones and possibly the neural spine of the first vertebra. This cartilaginous mass found in the embryo becomes, in adult, the compound neural arch and an enormous neural spine closely applied, posteriorly, to a much smaller neural spine belonging to the fourth vertebra. So two parts are formed from that cartilaginous mass, the compound neural arch with a spine, and the neural spine of the fourth. He did not mention the neural arch of the fourth while his drawing and text do not indicate that the neural arch of the fourth is fused with the compound neural arch. Thus, he decided that, the compound neural spine represents the fused neural spine of the second and third with the first three interspinous bones and possibly the neural spine of the first, but later mentioned that the first vertebra does not take part in the formation of the cartilaginous mass. This is contradictory to his previous statements. While concluding this, he labeled this compound neural spine as the third neural spine, another contradictory statement. It is possible that the first three interspinous bones are nonexistent.

In Pimephales the number of these bones, in specimens having different length, is not constant, but it never exceeds eight. This indicates that these bones ossify at different ages; also the posterior-most interspinous bone, if it is the eighth, is usually very tiny. Four interneural bones were found in two specimens of P. tenellus, six in P. promelas, seven in P. vigilax and eight only in two specimens of P. notatus. The present work is not concerned with these bones, but their presence above

the first three vertebrae was not detected. The first interneural bone
is always big and long, extending from the posterodorsal edge of the
neural complex, passing over the fourth neural spine to the upper ante-
rior edge of the fifth neural spine. This large bone may represent the
fusion of two or possibly three interneurals, since occasionally (in two
specimens) there is a very tiny bone just in front of this large inter-
neural and possibly representing the second or third interneural. If
we suppose that these interspinous bones are at some time present above
the first three vertebrae and we are unable to find them, they may be
fused or reabsorbed; otherwise they are absent.

In many ways _Pimephales_ is different from _Carassius_ and _Catostomus_.
In _Pimephales_ the second and third centra are not fused in adults having
a standard length of 32-77 mm. It is not a matter of length as Nelson
(1955) found in _Catostomus_. The neural complex in _Pimephales_ appears to
represent the upper part of the third neural arch and third neural spine
plus an interspinous bone or bones if they exist over the first three
vertebrae. It is of interest in this connection to note that the
neural spines are inclined posterodorsally, the boat extends anteriad.
The boat-shaped structure should, therefore, be a modified fusion of the
neural spine of the third with the interspinous bone or bones if existing.
The term "neural-complex" as used by Nelson (1948) is still appropriate
in the genus _Pimephales_, but in a different sense.

Some confusion in the literature concerning the articulation of
the tripus is evident. Krumholz (1943) stated that the articular process
of the tripus in Eventognathi articulates with the second vertebra.
Nelson (1948) studied the Catostomidae and found the tripus articulated
with the third; other authors have made similar observations. Watson

(1939) found that the second and the third vertebrae are not fused in embryos of <u>Carassius auratus</u>, but that they are in adults. He found that all components of the tripus, except the transformator process, were derived, as could be expected, from the third vertebra with which it articulates (Table II). Krumholz (1943) found a fibrous band between the posterior ramus of the tripus and the body of the fourth centrum in Eventognathi. In <u>Pimephales</u> the articular process of the tripus articulates with the posterior half of the third centrum, as previously stated, but there is no fibrous band connecting the posterior ramus with the fourth centrum. Bridge and Haddon (1889) and Evans (1924-1925) independently introduced the term tensor tripodis to apply to the muscular fibers that extend from the transformator process (not from the posterior ramus) to the os suspensorium (not to the fourth centrum), as is true in <u>Pimephales</u>.

The ossa suspensoria, according to Ramaswami (1955), are a pair of processes projecting from the ventral surface of the fourth centrum. Watson (1939) considered them as being different from the pleural ribs; he derived them from the haemapophyses of that segment. Berg (1940) and Goodrich (1930) regarded them as representing the fourth rib (pleural rib). Adams (1928) found them to be parts of the haemal processes. In <u>Pimephales</u> the ossa suspensoria are firmly fused with the fourth pleural ribs and do not have special grooves in the centrum. They probably arise ventromedianally as an offshoot from the posteromesad surface of the fourth pleural rib. There is no indication that they are separate parts, distinct from the fourth pleural ribs.

Various characters of the Weberian apparatus here considered as critical for the purpose of systematic study are listed in Table V below.

TABLE V

A COMPARISON OF CHARACTERS OF THE WEBERIAN APPARATUS
IN FOUR SPECIES OF PIMEPHALES

Number	Characters	Species			
		P. tenellus	P. notatus	P. vigilax	P. promelas
1.	First rib	Short	Shortest	Longest	Short
2.	First rib / Second rib	1/3.48	1/4.5	1/2.4	1/4.5
3.	Ascending process of scaphium in order of length	2	1	3	4
4.	Pits in dorsal surface of first centrum	2	2	2	2
5.	End of manubrium incudis	Swollen	Swollen	Not Swollen	Slightly Swollen or not
6.	Third neural pedicle				
	A. Ventral anterior edge	Usually long, either straight or curved (variable)	Nearly straight, long, with notch	Long and curved	Short and curved
	B. "Horizontal Plate"	Sometimes Present	Present	Absent	Present

TABLE V (Continued)

Number	Characters	Species			
		P. tenellus	P. notatus	P. vigilax	P. promelas
7.	Neural Complex				
	A. Axis	40° forward	Usually Perpendicular	Perpendicular	Perpendicular
	B. Blade	Small, under boat	Small, in front of boat and, in part, in front of stem	Long, in front of boat	Large, in front of boat and stem
	C. Height in descending order	Low	Higher	High	Highest
	D. Fenestration	4	3	2	1
	E. Depth of the boat	Shallow	Deeper	Deep	Deepest
8.	Tripus				
	A. Outer edge	Anteriorly slightly concave, curved posteriorly	Anteriorly straight, curved posteriroly	Nearly straight, except posteriorly convex	Evenly curved, slightly
	B. Fenestration	Present	Variable, frequently present	Absent	Rare 3 of 10
	C. Anterior and Posterior Rami	Longer, wide	Longest, wider	Short, widest	Long, narrow

TABLE V (Continued)

Number	Characters	Species			
		P. tenellus	P. notatus	P. vigilax	P. promelas
9.	Pleural rib				
	A. Rib proper				
	(1) Curvature	Curved anteriorly	Curved anteriorly	Sigmoid shape	Curved anteriorly
	(2) Anterior Projection	Present	Present, long	Absent	Present
	B. Ossa suspensoria	Fenestrated, and inclined forward (22°)	Narrow, pointed and more fenestrated, perpendicular	Wide, less fenestrated, perpendicular	Fenestrated and inclined forward (18°)

From the table above it is apparent that P. tenellus and P. notatus
are more closely related than they are to either of the other two species.
Characters which indicate this are:

1. The swollen terminal end of the manubrium incudis.

2. The external anterior edges of the tripodes are nearly straight
   in both of them.

3. The anterior and posterior rami of the tripodes are long.

4. The body of the tripus is fenestrated in P. tenellus and there
   is a similar tendency in P. notatus.

5. One specimen of P. tenellus has a neural complex very much like
   that of P. notatus.

6. The blade of the boat in both is small.

7. The number of pits in the dorsal surface of the first centra
   are equal.

8. The ascending process of the scaphium is long in both.

9. The anterior projection of the pleural rib is present in both,
   although it is also in P. promelas.

10. The ventral anterior edge of the body of the third neural
    pedicle in P. notatus is long, straight, and has a notch. It
    is also long in P. tenellus and tends to be straight, but with-
    out the notch.

11. A "horizontal plate", present in P. notatus is also present in
    specimens of P. tenellus.

Some characters suggest that P. promelas and P. vigilax also are
closely related.

1. The ascending processes of their scaphia are short.

2. The tripodes are not fenestrated.

3. The boat-shaped neural complex in both have larger blades.

4. Both species have a high and deep neural complex and in both it is perpendicularly placed.

In one specimen of P. promelas the neural complex has nearly the same general shape as that of P. vigilax.

P. notatus and P. tenellus on the one hand and P. promelas and P. vigilax on the other, exhibit intergrading characters between members of the two groups as follows.

1. The ratio of the length of the first rib to that of the second is the same in P. promelas and P. vigilax.

2. The ascending process of the scaphia intergrade in length as shown in Table V.

3. Fenestration of the tripus is absent in some specimens of P. notatus.

4. The anterior and posterior rami of the tripus is long in P. notatus, P. promelas, and P. tenellus.

5. The pleural rib proper has very much the same configuration in P. tenellus and P. vigilax.

6. A high neural complex is found in both P. vigilax and P. notatus.

7. The second neural arch has a short laterally compressed rudimentary neural spine, in P. promelas and usually in P. notatus.

8. In some specimens the termination of the manubrium incudis is slightly swollen like that usually found in P. notatus and P. tenellus.

9. Pits in the dorsal surface of the first centrum are two in P. tenellus, P. notatus, and P. vigilax.

10. A "horizontal plate" is found in P. tenellus, P. notatus, and
     P. promelas.

From the foregoing discussion it appears probable that these two
groups (P. tenellus and P. notatus) and (P. promelas and P. vigilax)
represent two species groups that have arisen separately in the evolution
of the subfamily Pimephalinae. Each group has an herbivore and a carni-
vore, if intestinal length may be taken with peritoneal color as criteria
of distinction.

As previously indicated, the nominal genus Ceratichthys, including
vigilax and tenellus (C. callarchus being regarded as an abberant example
of tenellus) differs from Hyborhynchus (=Pimephales notatus) and
Pimephales promelas chiefly in possessing a pale peritoneum and a short
gut in contrast to the black peritoneum and long gut in the latter forms.
These characters break down in Hyborhynchus since individuals have vary-
ing degrees of pigmentation of the peritoneum and an intestine of
variable lengths.

The superficial resemblance of P. notatus and P. tenellus is such
that in small specimens, one has to check several characters in order
to make correct specific diagnoses. Each of these forms is slender and
terete, whereas P. vigilax tends to be deeper bodied and chunkier, ap-
proaching P. promelas in this regard. Coupling these similarities with
those concerning the Weberian apparatus, it seems logical to postulate
that the early pimephaline ancestral form diverged to give rise to two
ancestral stocks each of which in turn responded to environmental
stimuli to become, through natural selection, adapted to carnivorous
habit on the one hand and an herbivorous habit on the other. The
ancestral pimephaline stock probably arose with the Notropinae as

herbivorous fishes. The Notropinae, a much larger group, may have arisen from a stock which diverged in a manner similar to the directions taken by the Pimephalinae, to give rise to carnivores (Notropis) and herbivores (Dionda and Hybognathus).

It is of interest, though not exactly parallel, to note here the odd similarity in origin of nonparasitic lampreys from parasitic progenitors. For each of three parasitic species there is a closely related nonparasite (Hubbs and Trautman, 1937).

CHAPTER VI

SUMMARY

1. Ten specimens of Pimephales tenellus, 11 P. notatus, 10 P. vigilax and 10 P. promelas were stained by the alizarin method and dissected. Serial sections were prepared of one additional P. tenellus.

2. The Weberian apparatus includes the first four modified verte- brae, none of which is fused with others.

3. The processes of the first and second vertebrae represent modified ventral ribs firmly fused with the centra.

4. Homologies of structures of the scaphium and intercalarium with structures of the third neural pedicle and fourth neural arch are proposed.

5. The difference between the scaphia in the four species lies in the length of the ascending processes (Table V).

6. The intercalarium shows differences in the length of the ascending process, and the termination of the manubrium incudis. It articulates with the second centrum and the third neural pedicle and is embedded in the interosseus ligament.

7. The second neural arch possesses a rudimentary neural spine in P. promelas and usually in P. notatus.

8. The neural complex is highest in P. promelas and P. notatus which have high side walls of the boat, but a short stem. P. tenellus has a low neural complex because of its low side walls and short stem. P. vigilax has a moderately high boat, but a long stem.

9. The tripus has long anterior and posterior rami in P. notatus, P. promelas, and P. tenellus. They are shorter and wider in P. vigilax. The body of the tripus is fenestrated in tenellus, frequently in notatus, but rarely in promelas and never in vigilax. The contour of the outer anterior edge of the tripus is straight in notatus, slightly concave in tenellus, evenly curved outward throughout in promelas and in vigilax it is nearly straight except at the rear.

10. The transformator process is anteriorly connected to the os suspensorium by means of the tensor tripodis and partially embedded posteriorly in the tunica externa of the Weberian air chamber.

11. The neural complex represents the neural spine of the third vertebra plus the interneural bone or bones, if these exist.

12. The fourth pleural rib has an anterior upper projection in P. tenellus, P. notatus and in some P. promelas.

13. The ossa suspensoria are parts of the fourth pleural ribs. They are, in P. promelas and P. tenellus, inclined slightly forward while in the other two species they are perpendicular.

14. The anterior and posterior projections from the fourth neural arch and the third neural pedicle are proposed as representing pre- and postzygapophyses.

15. The two-chambered air-bladder is retroperitoneal, dorsally connected (slightly on the left) with the esophagus by means of the pneumatic duct which arises from the anteroventral surface of the posterior chamber. The anterior chamber anteriorly exhibits a slit in the tunica externa.

16. A perineural tube of cartilaginous composition, is present in the four species, attached to the dorsal surface of the first centrum

and enclosing the spinal cord over and in front of the first centrum, completing the neural arch in this region.

17. The four species did not exhibit differences at the generic level, they are considered as comprising one genus _Pimephales_.

18. _P. tenellus_ and _P. notatus_ appear to be more closely related to each other than either is to _P. vigilax_ or _P. promelas_.

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APPENDIX

PLATE I

The upper row. The intercalaria of:

Figure 1A. P. vigilax 55 mm ♂ (1) OAM 5153

Figure 1B. P. vigilax 55 mm ♂ (2) OAM 5153

Figure 2. P. notatus 77 mm ♂ OAM 4580

Figure 3. P. tenellas 62 mm ♂ OAM 759

Figure 5. P. promelas 68 mm ♂ OAM 3388

The middle row. The Claustra of:

Figure 5. P. vigilax 69 mm ♂ OAM 4727

Figure 6. P. notatus 70 mm ♂ OAM 4580

Figure 7. P. tenellus 51 mm ♂ OAM 51

Figure 8. P. promelas 55 mm ♀ Fair Park, Stillwater

The lower row. The Scaphia:

Figure 9. P. vigilax 69 mm ♂ OAM 4727

Figure 10. P. notatus 70 mm ♂ OAM 4580
(A) side view to show the concavity.
(B) side view to show the convexity.

Figure 11. P. tenellus 51 mm ♂ OAM 51

Figure 12. P. promelas 55 mm ♀ Fair Park, Stillwater

Legend:

    AS.P.-Ascending process
    AR.P.-Articulating Process
    CO.ST.-Concha stapedis
    CR.-crest
    CP.-cup
    MN.IN.-Manubrium incudis

PLATE-1
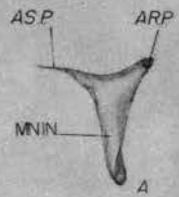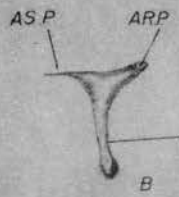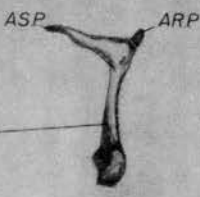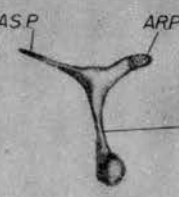
FIG-1 FIG-2 FIG-3 FIG-4

FIG-5 FIG-6 FIG-7 FIG-8

Imm

FIG-9 FIG-10 FIG-11 FIG-12

A B
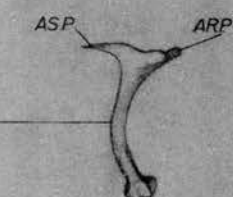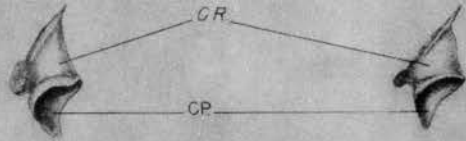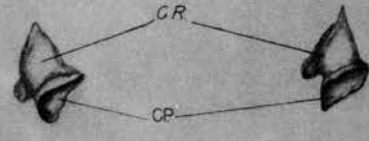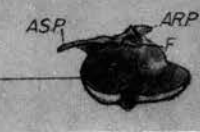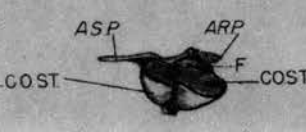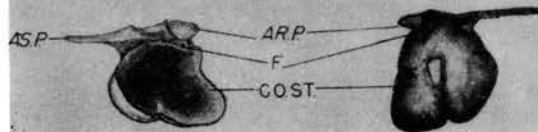
PLATE II

Tripodes of:

Figure 1.   P. promelas 42 mm ♂ Fair Park, Stillwater

Figure 2.   P. tenellus 42 mm ♂ OAM 759

Figure 3.   P. notatus 70 mm ♂ OAM 4580

Figure 4.   P. vigilax 55 mm ♂ (1) OAM 5153

Legend:

    AN.R.-Anterior ramus
    AR.P.-Articulating process
    B.-Body
    G.-Groove
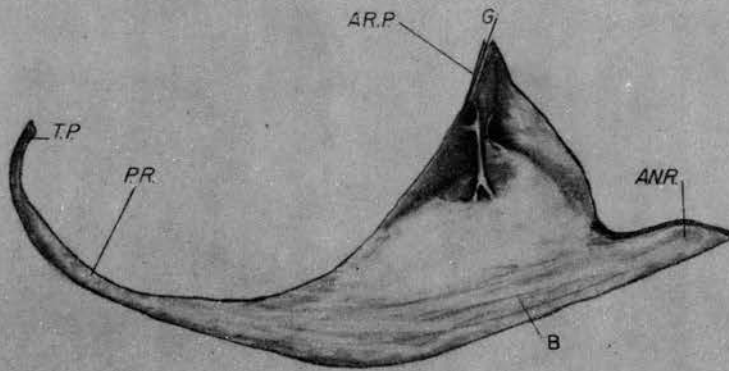   P.R.-Posterior ramus
    T.P.-Transformator Process

PLATE-II

FIG-1

FIG-2

FIG-3

FIG-4

1mm.
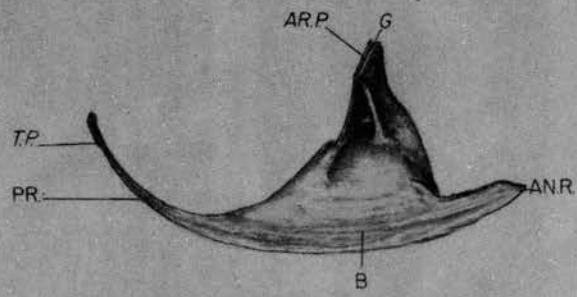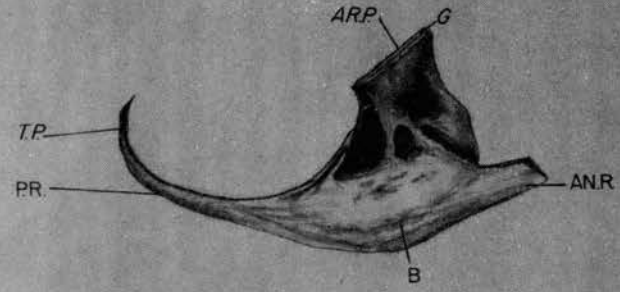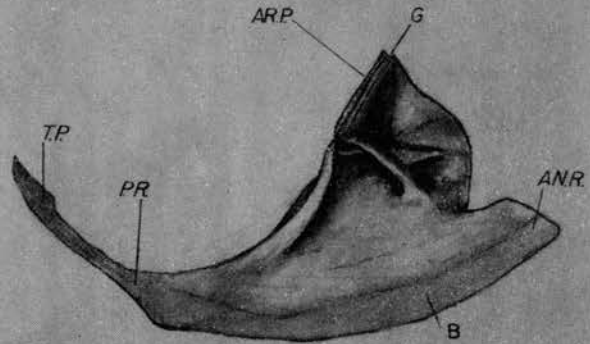
64

PLATE III

Figure 1.   Ventral view of the first four centra of
              P. tenellus 62 mm ♀ OAM 759

Figure 2.   Dorsal view of the first four centra in
              P. tenellus of the same

Figure 3.   The neural pedicle of P. tenellus 51 mm ♂
              OAM 51

Figure 4.   The neural pedicle of P. vigilax 69 mm ♂
              OAM 4727

Figure 5.   The neural pedicle of P. promelas 54 mm ♀
              OAM 3388

Figure 6.   The neural pedicle of P. notatus 65 mm ♂
              OAM 3178

Legend:

  B.-Body
  C1, 2, 3, 4.-Centra
  NCH-Notch
  P.G.-Pyramidal groove
  P.INT-Pit for the articulating process of the intercalarium
  P.R.-Pyramidal root
  P.SC.-Pit for the articular process of the Scaphium
  R1, 2-First and second ribs
  ST.-Stem

PLATE-III

FIG-1 FIG-2 FIG-3 FIG-4 FIG-5 FIG-6

1mm.
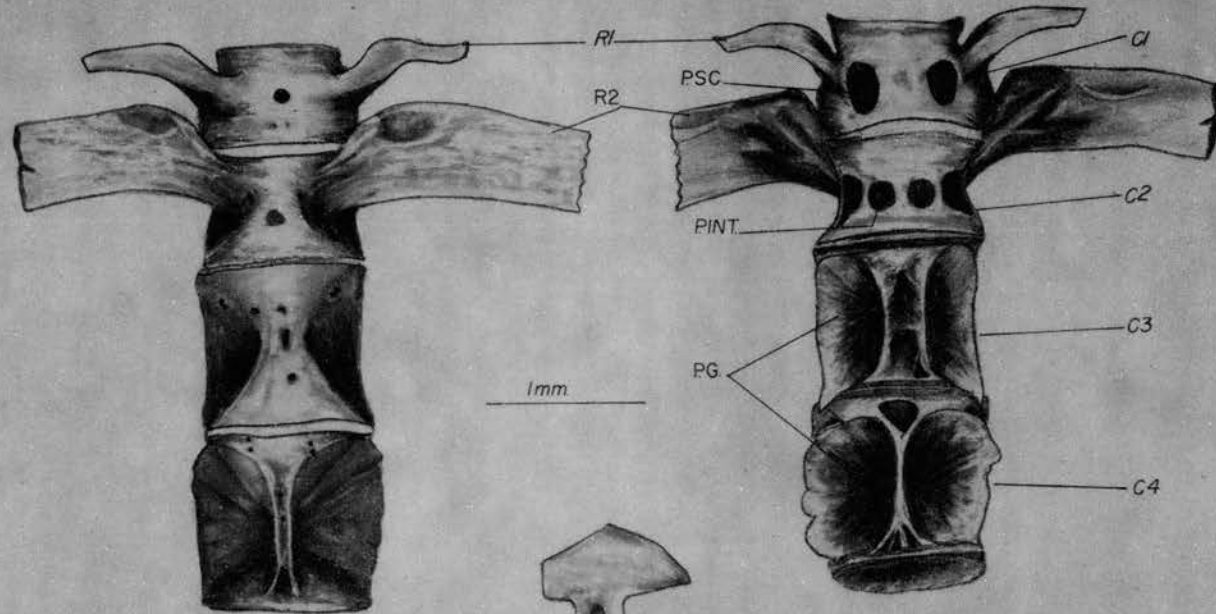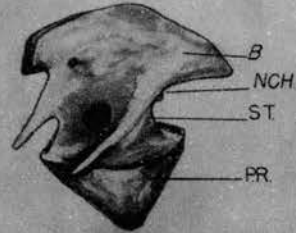
PLATE IV

Figure 1.   Posterolateral view of the Weberian apparatus
             in P. notatus 68 mm ♂ SWAN. 14, 1959

Figure 2.   Dorso-anterolateral view of the first centrum
             with the claustrum and scaphium of the left
             side of P. vigilax 69 mm ♂ OAM 4727

Figure 3.   Posterior view through the external coat of the
             anterior air chamber of P. notatus 48 mm ♀
             SWAN. 14, 1959

Legend:

   A.A.CH.-Anterior air chamber
   C1, 2, 3, 4,-Centra
   CL-Claustrum
   D.AO.-Dorsal aorta
   EX.C.A.CH.-External coat of anterior air chamber
   INTS.B.-Interspinous bone
   INT.L.-Interossicular ligament
   N.C.-Neural complex
   N.SP.-Neural spine
   OS.-Os suspensorium
   PRZYG: POZY.-pre-and postzygapophyses
   R1, 2-First and second rib
   R. 2nd. N.SP.-Rudimentary second neural spine
   SC.-Scaphium
   2nd. N.A.-Second neural arch
   3rd. N.PE.-Third neural pedicle
   T.P.-Transformator process
   T.R.-Tripus
   T.T.-Tensor tripodis

PLATE-IV

FIG-1

FIG-2

FIG-3
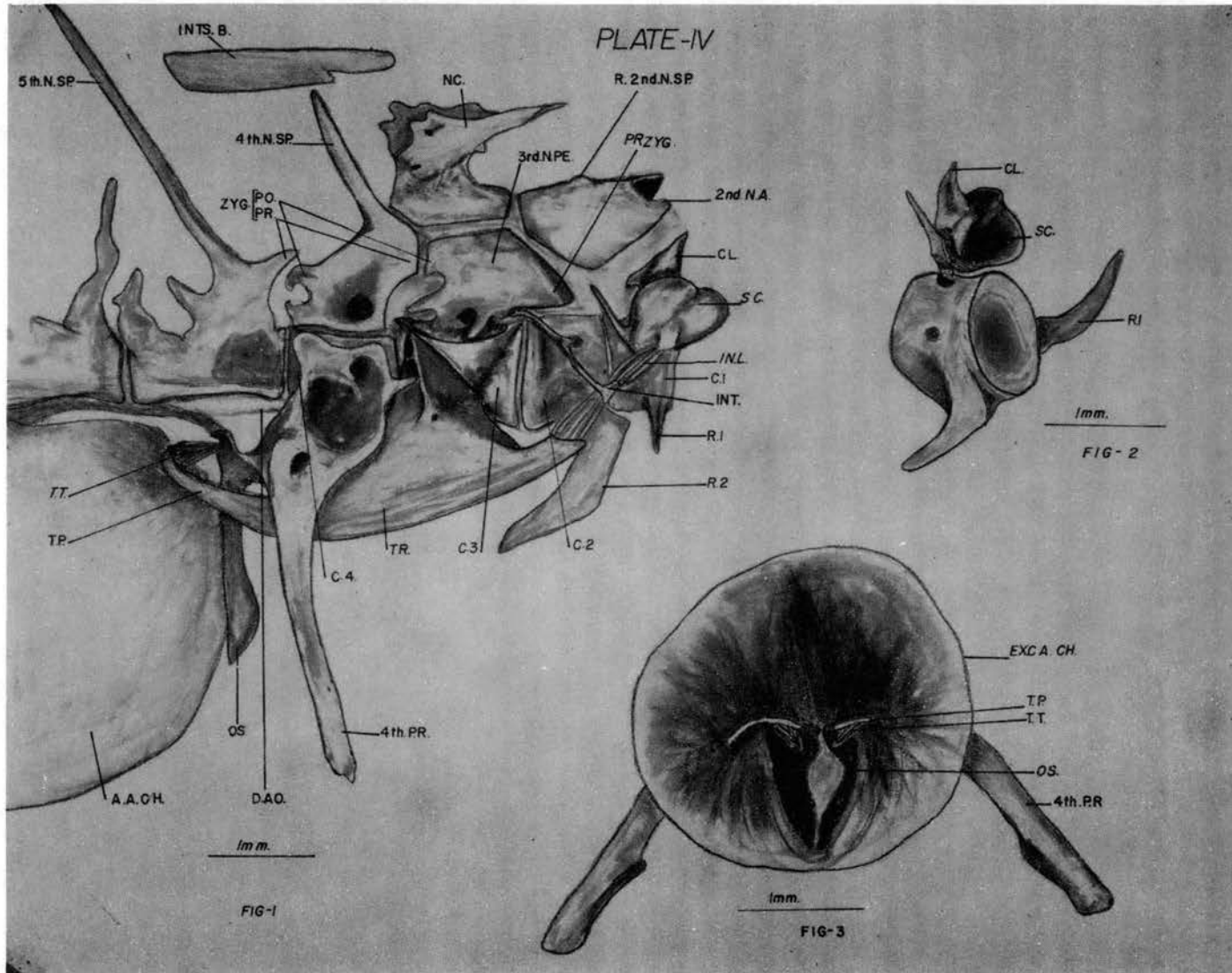
PLATE V

The neural complex of:

Figure 1.   P. promelas 55mm ♀ Fair Park, Stillwater

Figure 2.   P. vigilax 69 mm ♂ OAM 4727

Figure 3.   P. tenellus 46 mm ♂ OAM 2693

Figure 4.   P. notatus 77 mm ♂ OAM 4580

Figure 5.   Second neural arch of P. notatus 62 mm ♂
             SWAN. 14, 1959

Legend:

  B.A.-Basal arch
  BL.-Blade
  BO.-Boat
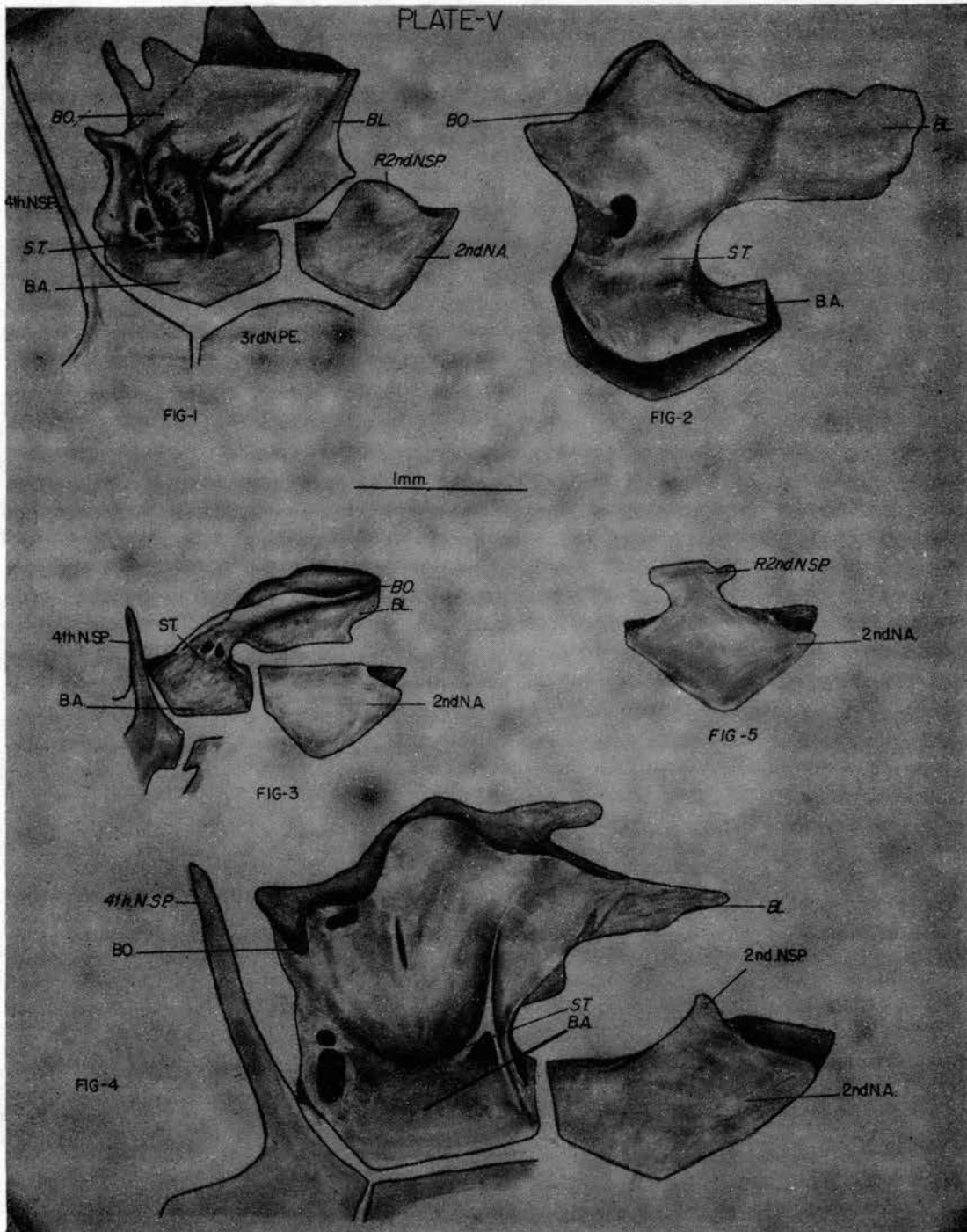 R. 2nd. N.SP.-Rudimentary second neural spine
  ST.-Stem

PLATE-V

PLATE VI

Posterior view of the ossa suspensoria and pleural rib
proper of:

Figure 1. P. promelas 42 mm ♂ Spring Creek

Figure 2. P. tenellus 48 mm ♂ OAM 1058

Figure 3. Side view of the pleural rib proper of
P. promelas 55 mm ♀ Fair Park, Stillwater

Figure 4. Side view of the pleural rib proper of
P. tenellus 48 mm ♂ OAM 1058

Legend:

AR.H.-Articular head
4th P.R.-Fourth pleural rib
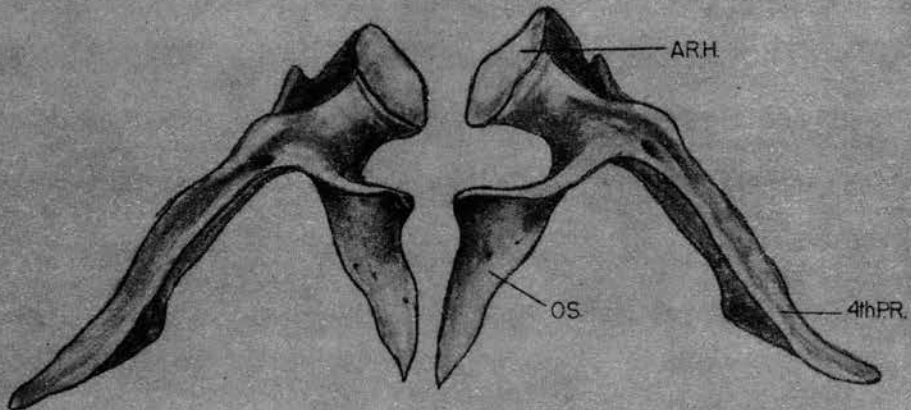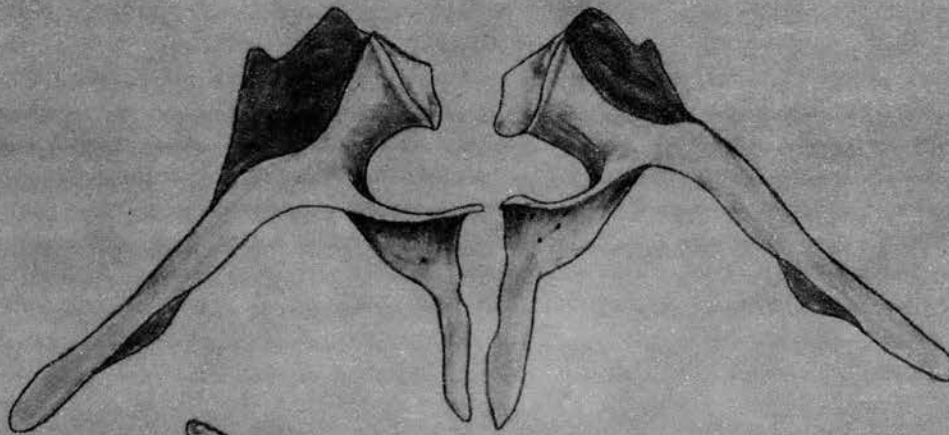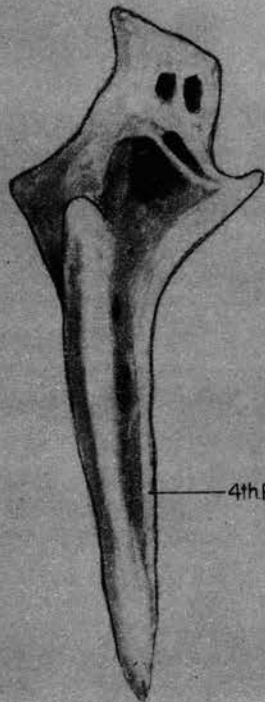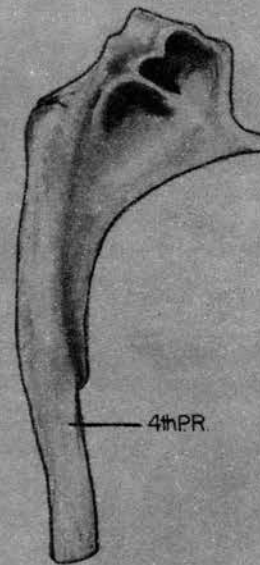O.S.-Os suspensorium

PLATE-VI

FIG-1

FIG-2

FIG-3

FIG-4

PLATE VII

Posterior view of the ossa suspensoria and pleural
rib proper of:

Figure 1.   P. notatus 45 mm ♀ OAM 3178

Figure 2.   P. vigilax 50 mm ♀ OAM 4727

Figure 3.   Side view of the pleural rib proper of
             P. notatus 65 mm ♂ OAM 3178

Figure 4.   Side view of the pleural rib proper of
             P. vigilax 65 mm ♂ OAM 4727

Legend:

  AR.H.-Articular head
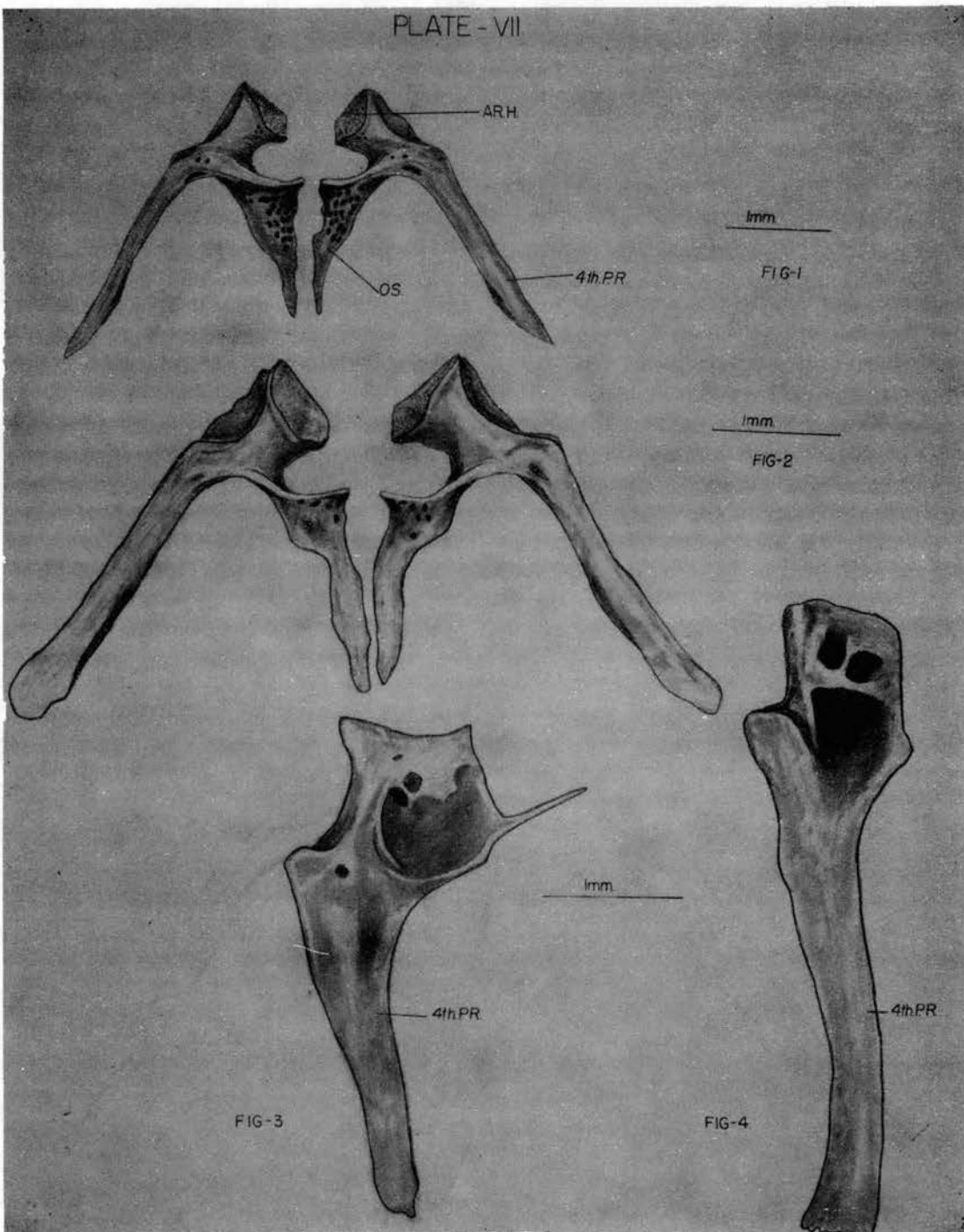 4th.P.R.-Fourth pleural rib
  OS.-Os suspensorium

PLATE - VII

FIG-1

FIG-2

FIG-3

FIG-4

PLATE VIII

Variations in the shape of the neural arches

Figure 1.　　Side view of the 4th neural arch of
　　　　　　P. vigilax 69 mm ♂ OAM 4727

Figure 2.　　Side view of 4th and 5th neural arches
　　　　　　of P. notatus 77 mm ♂ OAM 4580

Figure 3.　　Side view of the 4th and 5th and 6th
　　　　　　neural arches of P. promelas 55 mm ♀
　　　　　　OAM Fair Park, Stillwater

Figure 4.　　Trunk vertebrae of P. vigilax 65 mm ♂
　　　　　　OAM 4727

Legend:

　　INT.M.B.-Intermuscular bone
　　N.SP.-Neural spine
　　NO.CA.-Notochordal canal
　　P.R.-Pyramidal root
　　POZYG.-Postzygapophysis
　　PRZYG.-Prezygapophysis
　　R.-Rib

PLATE-VIII
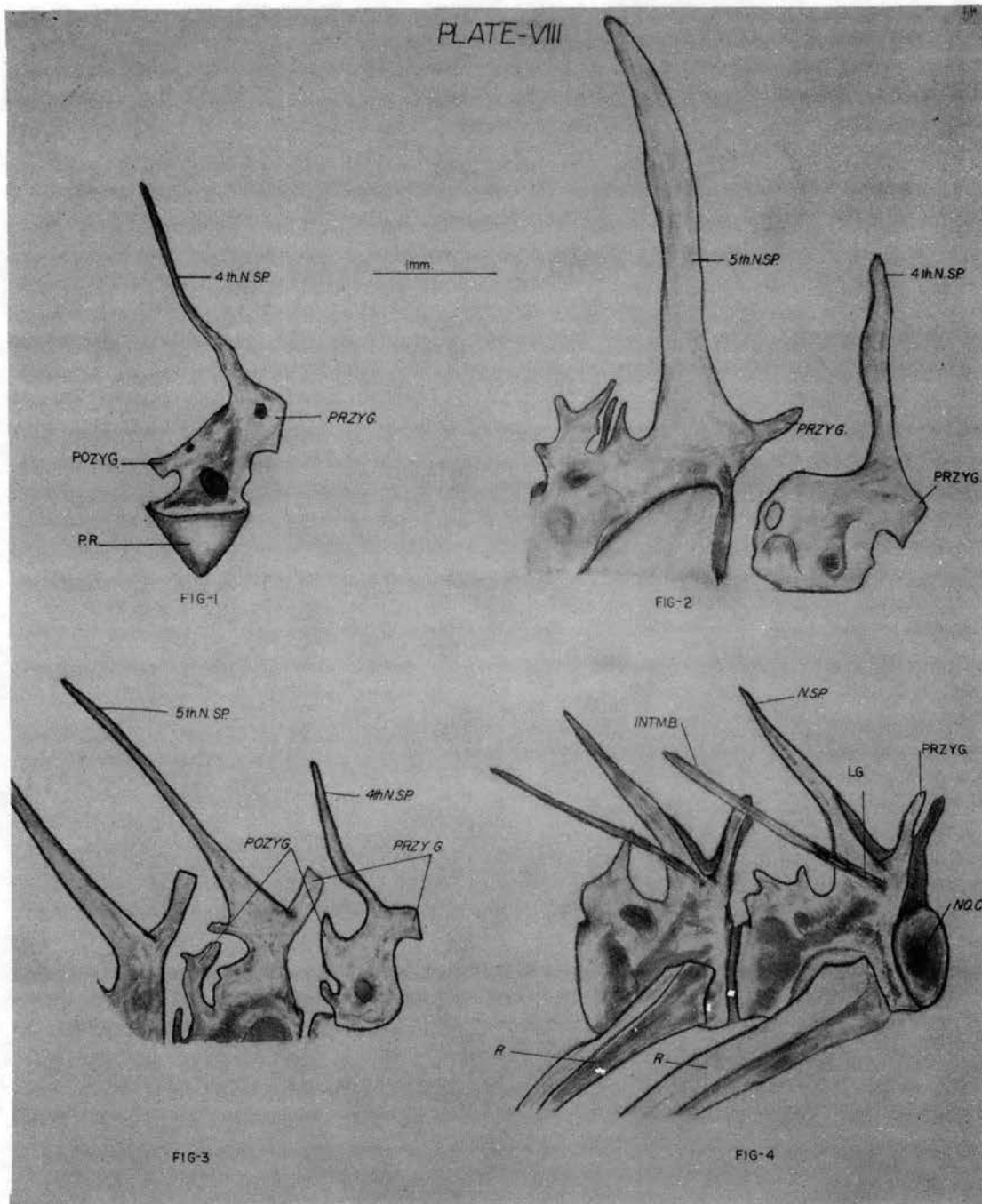
VITA

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