A COMPARATIVE STUDY OF THE WEBERIAN APPARATUS IN THE

GENERA DIONDA AND NOTROPIS (CYPRINIDAE)

By

Morgan Emery Sisk

Bachelor of Science

Murray State College

Murray, Kentucky

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GENERA <u>DIONDA</u> AND <u>NOTROPIS</u> (CYPRINIDAE)

Thesis Approved:

Geo. A. Moore
_____
Thesis Adviser

Bryant P. Glass
_____

H. I. Featherly
_____

Dean T. MacVicar
_____
Dean of the Graduate School

ii

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PREFACE

It has been common practice in the past to classify fishes on the basis of external morphological structures and easily accessible parts of the internal anatomy. Today, it is essential that fish taxonomists examine more critically the finer details of hard and soft anatomy in order to better understand and more accurately establish true relationships between presently existing groups of fishes. A case in point is the superficial similarity of the genera Notropis and Dionda. The main criterion that has been used in separating these two genera is the long gut in Dionda and a short gut in Notropis. One could take the stand that Dionda is only a Notropis with a long gut. Such a stand has precedent in the genus Pimephales in which the gut length varies intra-specifically.

Within the past decade one geographic population of Dionda was described as a full species of Notropis. Alvarez and Navarro (1953) described Notropis ipni from a southern race of Dionda rasconis (Jordan and Snyder), thus indicating the superficial resemblance of the two genera, according to Hubbs (1956).

The present study involving all of the United States members of the genus Dionda and six common species in the genus Notropis, was undertaken to investigate and describe in detail structural variations existing in the bony elements of the Weberian apparatus of these nine species of minnows. It was hoped that comparison of these osteological structures in the two genera might help understand their relationship.

iv

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

CHAPTER I

INTRODUCTION

According to Krumholz (1943), E. H. Weber in 1820 described a chain
of bones connecting the air-bladder to the inner ear in the old world
catfish, Silurus glanis Linnaeus. The group of fishes possessing this
remarkable structure was named Ostariophysaea by Sagemehl (1891).
Jordan (1929) defined the series Ostariophysi as "fishes with the an-
terior vertebrae modified to connect with the air-bladder and inclos-
ing an organ of hearing."

The general plan of the Weberian apparatus in the ostariophysine
fishes (Text Figure 1) consists of the first four or five anterior
vertebrae modified to form the pars sustentaculum or supporting
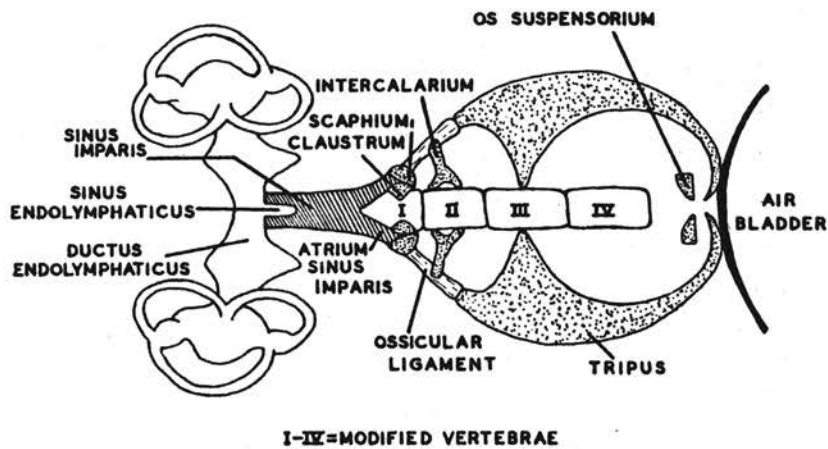
Text Figure 1.

1

mechanism of the apparatus. Associated with the pars sustentaculum are three or four ossicles, small bones connecting the anterior chamber of the air bladder to the inner ear, which are collectively referred to as the pars auditum. These ossicles are thought to be derived from the modified vertebrae. Between the left and right inner ears there is a connecting duct, the ductus endolymphaticus, containing endolymph. Projecting posteriorly from this duct is a median diverticulum, the sinus endolymphaticus. Enclosing the sinus endolymphaticus, but not openly communicating with the sinus or ductus endolymphaticus, is a median tube containing perilymph, the sinus imparis. This sinus divides posteriorly to form a pair of cavities, the atria sinus imparis, whose posterior medial and lateral walls are formed by one or two of the anterior ossicles.

The function of the Weberian apparatus has never been definitely determined. Several theories have been proposed relative to its physiological function: registering changes in atmospheric pressure, serving as an aid to hearing, and functioning as a hydrostatic organ. Recent experiments by Wunder (1936), von Frisch (1938), Poggendorf (1952), and others indicate the apparatus may serve any one or more of the proposed functions.

CHAPTER II

HISTORICAL REVIEW

The present review does not entirely represent a complete coverage
of the literature, since many of the important works concerning the
Weberian apparatus were not available. Therefore, those pertinent papers
available were reviewed and some comments and discussions of the findings
of early workers were taken from them.

Adams (1928) credited Rosenthal with having been the first to ob-
serve the Weberian ossicles although Weber (1820) apparently published
the first paper relative to the apparatus and ossicles which bear his
name. The ossicles from some of the Siluroidea were studied by
Reissner (1859) and Bridge and Haddon (1889, 1892) made valuable contri-
butions to the nomenclature of the Weberian ossicles in their works on
the Siluroidea. Nusbaum (1881) described Weber's apparatus in some of
the Cyprinidae and a few years later the first description by an
American worker, Wright (1884), appeared. Wright's work included a
description of the fused second, third, and fourth vertebrae and the
ossicles from Amiurus catus (Linnaeus). Niazi (unpublished) has pointed
out the doubt injected by Krumholz (1943) when the latter indicated
Wright's material as Amiurus catus (Ameiurus nebulosus). Nusbaum (1908)
described the early stages of the Weberian apparatus in Cyprinus carpio
Linnaeus. Regen (1911), in his classification of fishes in the group
Ostariophysi, discussed in some detail the anatomy of the Weberian
apparatus. Hora (1920) summarized some of his earlier works regarding

the Weberian ossicles in some Cyprinidae. During the middle and late
1920's Chranilov (1926, 1927, 1929, 1930) published several works on the
Weberian apparatus of some of the Cypriniformes. An American, Adams
(1928) worked on the apparatus from Ictiobus urus (Agassiz) and Matveiev
(1929), a Russian, described early developmental stages of the apparatus
from Scardinius erythrophthalmus. Wunder (1936), von Frisch (1938),
and Watson (1939) are recent workers who have contributed to the know-
ledge of the Weberian apparatus. Krumholz (1943) did a comparative study
on the Weberian ossicles from 16 species of North American ostariophysine
fishes and Taranetz (1946) studied 26 species of Cyprinidae from the
Amur River system of Russia. Nelson (1948, 1949, 1955, 1959) has contri-
buted much to the knowledge of the Weberian apparatus, especially in the
catastomid fishes. Mookerjee, Ganguly and Mukerji (1952) worked on the
vertebral column and Weberian ossicles of Esomus dandricus (Ham.) and
a fellow worker from India, Ramaswami (1955 a., 1955 b.), in describing
the skull and Weberian apparatus from several cyprinids, discussed the
superficial morphology of the apparatus in Notropis cornutus. Robins
and Raney (1956) have recently included an examination of the tripus for
possible taxonomic significance in their study of the genus Moxostoma.

Investigators, both past and present, have agreed that the anterior
modified vertebrae represent the pars sustentaculum of the Weberian
apparatus and that the ossicles plus the interossicular ligament makes
up the pars auditum. However, at least three nomenclatural changes,
relative to the ossicles, have been proposed since Weber's original
description of the bones. These proposed names and their authors were
taken from Krumholz (1943) and are as follows:

Claustrum	Stapes	Incus	Malleus	(Weber, 1820)
Claustrum	Steigbugel	Ambos	Hammer	(Mueller, 1853)
Claustrum	Scaphium	Intercalarium	Tripus	(Bridge and Haddon, 1889)
Hinlage	Deckel	Lenker	Hebel	(Thilo, 1908)

Chranilov (1930) suggested that the original nomenclature of Weber be applied to these ossicles. In the United States, however, the nomenclature of Bridge and Haddon is preferred, the advantage being that this nomenclature removes all possible confusion with the nonhomologous ossicles in the mammalian ear.

The derivation of the Weberian ossicles has been and still is, a controversial subject. Many authors have proposed theories relative to their origin, based primarily on their morphology and the position that they occupy in relation to the first four vertebrae. Wright (1884) assumed that they are derived from parts of the anterior vertebrae and ligamentous ossifications. That Wright's ideas were well founded, is confirmed by the results of Watson's (1939) work on the embryonic development of the ossicles in Carassius auratus Linnaeus. His findings are presented in Table I.

Although Ramaswami (1955 b.) commented briefly on and made some few drawings of the Weberian apparatus from Notropis cornutus, no other works have come to the writers attention concerning a detailed study on any of the species included in this paper.

TABLE I

DEVELOPMENT OF THE WEBERIAN OSSICLES

Ossicle	Part	
Claustrum	--	Accumulation of messenchyme in wall of atrium sinus imparis.
Scaphium	a. Concha stapedis	a. Circular disc of messenchyme.
	b. Ascending and articulating processes	b. Basidorsal of first vertebra.
Intercalarium	a. Manubrium incudis	a. Ossification in the inter-ossicular ligament.
	b. Ascending and articulating process.	b. Basidorsal of the second vertebra.
Tripus	a. Anterior process.	a. Basiventral of the third vertebra plus ossification in interossicular ligament.
	b. Articulating process.	b. Basiventral third vertebra.
	c. Main body	c. Mesenchymous mass between third and fourth basiventral.
	d. Transformator process.	d. Rib rudiment of third vertebra plus ossification in the wall of the air bladder.

CHAPTER III

MATERIALS AND METHODS

Collection of Fishes

A total of 126 individuals were examined during the course of this study. Preserved specimens were obtained from the fish collections of Oklahoma State University, with the exception of three specimens of _Dionda diaboli_ which were donated by Doctor Clark Hubbs. Fresh specimens were collected in Oklahoma from the following localities: Lake Texoma (Marshall County), Blue River (Johnston County), Little River (McCurtain County), Red River (Choctaw County), Boomer Creek (Payne County), Beaty's Creek (Delaware County), Big Lee Creek (Sequoya County), Illinois River, Barren Fork Creek, and Tyner Creek (Cherokee County). The nomenclature employed is that of Jordan, Evermann, and Clark (1928) and Moore (1957). The Weberian apparatus was studied from the nine species and one hybrid listed below. Numbers in parentheses indicate the numbers of specimens examined.

Dionda nubila (Forbes). Ozark minnow. (12)

Dionda episcopa Girard. Roundnose minnow. (10)

Dionda diaboli Hubbs and Brown. Devils River minnow. (3)

Notropis (_Notropis_) _percobromus_ (Cope). Plains shiner. (14)

Notropis (_Luxilus_) _cornutus_ (Mitchill). Common shiner. (22)

This is the subspecies currently known as _N. c. isolepis_ Hubbs and Brown.

7

Notropis (Luxilus) zonatus (Agassiz). Bleeding shiner. (14)

 Mr. C. R. Gilbert (personal communication with Dr. G. A.

 Moore) regards N. pilsbryi to be the valid species name.

Notropis (Cyprinellus)venustus (Girard). Blacktail shiner. (16)

Notropis (Cyprinellus) lutrensis (Baird and Girard). Red shiner.

 (20)

Notropis (Cyprinellus) whipplei (Girard). Steelcolor shiner. (9)

Notropis lutrensis X Notropis venustus. Hybrid combination. (6)

Preparation of Specimens for Observation

In dissecting the Weberian apparatus, it was found that fish placed
in a 2% potassium hydroxide solution for a period of 72 hours, macerated
sufficiently to allow removal of the muscle tissue without severing the
ossicles from the vertebral members or disarticulating them. This pro-
cedure proved effective for larger specimens but a need was felt for
some method of locating these components in smaller fish prior to dis-
section. It was suggested by a co-worker that an in toto staining
process be used to facilitate this operation. Hollister's (1934)
alizarin red-S method was modified and tried with success. After the
viscera, eyes, and scales were removed, the specimens were placed in a
2% potassium hydroxide solution for 72 hours. At the end of this
period the alizarin stain was added to the KOH solution until a cherry
red color was obtained. The specimens were allowed to remain in the
stain for an additional 72-96 hours. Dissections were made in most
instances before clearing, but some were removed from the stain,
rinsed in water and cleared in glycerine. Using this procedure,
observation and/or dissection of the apparatus was easily accomplished.

An additional method was employed with limited success. This consisted
of fixing live specimens in a strong brine solution (1/2 pound of table
salt to one pint of water) instead of the usual 10% formalin. Specimens
so prepared literally "fell apart" within 48 hours at temperatures above
26° C. The vertebral members of the apparatus were disarticulated by
this method, but with the aid of a binocular microscope it was possible
to salvage the ossicles and stain them with the alizarin red-S.

The initial attempt to dissect the Weberian apparatus from pre-
served, unstained specimens proved to be futile. Formalin fixed,
alcohol preserved tissue was rendered too hard to be stripped from the
specimens without losing the ossicles or separating them from the
vertebral members of the apparatus. Krumholz (1943) suggested cooking
at 60° C. for 30 minutes, or freezing, before dissection of fresh
material. Both techniques proved to be ineffective when using preserved
material.

Preparation of Illustrations

With the aid of a binocular microscope and camera lucida, charcoal
drawings were made of the ossicles (Plates III and IV, Figures 18 through
26) from the right side of all species examined, except the Notropis
lutrensis X Notropis venustus hybrid. The tripus is shown in dorsal,
the intercalarium in posterolateral, and the scaphium and claustrum in
lateral aspect. The vertebral components of the apparatus from two
species were illustrated from dorsal, ventral, lateral and anterior
views (Plate I, Figures 1 through 8) and the neural complexes from all
species were illustrated (Plate II, Figures 9 through 17) utilizing

the techniques mentioned above. Text Figure 1 is from Chranilov
(1926), with slight modification.

CHAPTER IV

OBSERVATIONS

Examination has revealed that the Weberian apparatus in all
species included in this work are so closely similar that a separate
description of each species is not warranted. For this reason the
apparatus from Notropis cornutus has been described in detail and
compared with the apparatus of the remaining species. The nomencla-
ture proposed by Bridge and Haddon (1889) has been employed in
describing the pars auditum.

Pars Sustentaculum

In N. cornutus the first four vertebrae are involved in the
Weberian apparatus but remain distinctly separate from one another.
The first modified vertebra is securely attached anteriorly to the
vertebra-like articular surface (basioccipital proatlas of Harrington,
1955) of the basioccipital bone. Projecting laterally from the antero-
ventral surface of the first centrum is a pair of short, bony rods,
the modified pleural ribs. These ribs, in all nine species, normally
project at right angles from the base of the centrum but terminate
slightly below the base line of the centrum when viewed anteriorly.
On the dorsolateral surface there is a shallow oval pit to receive the
articular process of the scaphium. On the ventral surface of the
centrum, there is a single median pit of undetermined origin and func-
tion. Neural pedicles and a neural spine, derived from the basidorsals

of the arcualia, are lacking on the first vertebra. The centrum is of the amphicoelous type, the concavity being more pronounced on the posterior one. From the lateral aspect, this first centrum appears to be thicker dorsally than ventrally, because a convex, backward projecting lip, on the dorsal articular facet, fits into a slight concavity on the anterodorsal articular surface of the second centrum.

The second centrum bears a pair of lateral projecting modified pleural ribs, differing from those on the first centrum in that they are broader at their base, longer and directed more posteriad. These ribs are quite variable within the species. They may be incompletely ossified on one or both sides, present varying degrees of dihedral up-sweep, or vary in length. On the ventral surface of the centrum there are three pits, a large median one flanked by two smaller ones. The lateral pits may be quite distinct or appear as mere dimples in the bone. Dorsally, a small pair of median pits is located between a pair of larger pits, the latter pair receiving the articular arms of the intercalariae. Smaller pits and fenestrae are found scattered about the surface of the centrum, but present no constant pattern in the nine species. Neural pedicels, as in the first centrum, are absent from the second centrum. The saddle-shaped neural arch of the second vertebra, deeply notched on its anterior border, lies above the second centrum and extends forward over the first. From the notropid specimens this bone presents a flat to smoothly rounded dorsal profile but in Dionda it bears a slight elevation near the middorsal line, possibly representing a rudiment of the second neural spine.

The neural arch forms the anterior roof of the neural canal and acts as a keystone between the anterior halves of the two neural

pedicles of the third vertebra. The anterior notch provides attachment for strong connective tissue fibers originating from a posterior projecting spur of the exoccipital bones, immediately above the foramen magnum.

The third vertebra lacks the dorsal ribs found on the first two and is approximately equal to their combined lengths. The dorsal surface bears two pyramidal shaped depressions, separated by a bony pitted septum, which receive the ventral bases of the third neural pedicles. From the ventral aspect the third vertebra appears as a typical spool-shaped centrum devoid of pits. The lateral surfaces of the centrum are modified to form deep angular grooves on either side of the posterior two-thirds of the centrum, sloping about 45° from the posterodorsal to the anteroventral region. The articular processes of the tripods fit into these grooves. Above the grooves and separating them from the pyramidal depressions mentioned previously, there is on each side, a bony shelf, terminating as a short spur behind the posterior articulating face of the centrum. This shelf forms the dorsal boundary of the angular groove. The neural pedicles of the third vertebra form the anterior bony walls of the neural canal and may or may not be fenestrated on their outer surfaces. From the lateral view, these pedicles present a profile not unlike that of a mushroom. The dorsal, horizontally expanded cap extends forward above the second centrum to about the latters anterior border. The anterior half of the cap supports the neural arch of the second vertebra. Posteriorly, the expanded cap extends above the third centrum and terminates near the posterior border of the centrum. This posterior half of the cap in articulation with the fourth nerual pedicle provides support for the neural complex described below. The expanded upper portion of the

pedicle narrows ventrally into a stalk, which in turn broadens to form
a pyramidal root. The root rests in the pyramidal depression in the
third centrum. There is a short diverticulum projecting postero-
ventrally from its origin on the anterolateral surface of the pedicle.
This projection serves for attachment of a ligament from the tripus.
The spur-like projection is present in the six notropids but absent in
all species of Dionda. The most conspicuous structure associated with
the third vertebra is the wine-cup-shaped neural complex lying dorsal
to the third and fourth vertebrae and supported by the neural pedicles
of these vertebrae. This unique bone may be divided, for convenience
of description, into three regions: (1) the expanded, hollow, dorsal
cup, (2) the stem, which, from side view is narrower than the cup, and
(3) the base, which broadens ventrally from the stem and articulates
with the neural pedicles of the third and fourth vertebrae ventrally
and with the ventral portion of the fourth neural spine posteriorly.
The dorsal cup is formed by thin bony walls surrounding a deep cavity
which extends down into the stem of the complex. When viewed from
above, this cavity appears laterally compressed. Anteriorly the cup
presents a closed border and from it a median lamina extends forward
and above the neural arch of the second vertebra. Posteriorly the cup
is narrowly open. Dorsally the cup rim is unevenly emarginate and
usually exhibits a deep notch near its posterior border. The cup and
median lamina are securely bound by connective tissue to a posteriorly
projecting process of the supraoccipital bone. Three or four ridges
mark the lateral surface of the stem of the neural complex and provide
for muscular attachment. Small foramina and some fenestrations are
usually scattered among these ridges. The base, if considered

separately from the stem and cup, is slightly convex dorsally and forms the roof of the neural canal above the third and part of the fourth vertebra.

The fourth and last modified vertebra of the pars sustentaculum has a centrum quite similar to the unmodified ones posterior to it. The ventral aspect is spool-like and very slightly pitted on the midline bridge which spans the gap between the two conical halves of the centrum. A ventral process, the modified pleural rib, articulates with the latero-ventral surface of the centrum by means of a pyramidal root which fits into a similarly shaped depression in the centrum. The pleural rib is broad at its proximal end and is directed posteroventrally from the fourth centrum. Before extending past the ventral line of the vertebral column, it turns abruptly and passes anteroventrad, forming an elbow beneath the fifth vertebra. From the elbow the rib narrows toward its distal end and terminates either in a blunt or sharp point or a laterally flattened blade. This distal portion forms approximately a 60° (with extremes of 45° to 80°) angle from the horizontal. Near the elbow of the rib in all species, a small elevation occurs to which a ligament from the third neural pedicle attaches. Issuing from the pleural rib, posteroventral to the elbow, a ventromesiad process, the os suspensorium meets its fellow from the oppo-site side at the midline and turns ventrad, forming a thin triangular, transverse plate as seen from an anterior or posterior view. The post-erior most portion of the tripus (transformator process) is attached to the ventrolateral surface of this bony plate by a thin, triangular muscle, the tensor tripodis. Anteriorly, there is a keel-like process from the basioccipital bone which approaches the plate but does not make contact with it. The ossa suspensoria are not solid bony structures,

there being a jagged open suture where the medial borders of each ventro-
mesiad process from the fourth pleural rib fail to meet. This suture is
bridged by connective tissue which binds the two halves of the ossa sus-
pensoria together. The general shape of the triangular plate and the
suture varies between specimens and the upper regions of the plate
usually present a pitted or fenestrated appearance. The dorsal aorta and
postcardinal vein pass above the ossa suspensoria, immediately beneath the
vertebral column. The anterior chamber of the air bladder lies in close
association with the posterior surface of the ossa suspensoria. Dorsal
to the pleural rib there is a triangular depression and formed by thin
elevated walls on the fourth centrum, which serves to separate the pleural
rib from the neural components of the fourth vertebra and also provides
for muscle attachment. On the dorsal surface of the centrum above the
triangular depression, there appears on each side a pyramidal pit which
receives the roots of the fourth neural pedicles. The neural pedicles
of the fourth vertebra, unlike the preceeding ones, are united dorsally
to form a complete arch over the neural canal and are produced even more
dorsally as a slender spine. The neural spine is similar to the normal
fifth neural spine but is slightly shorter and more erect terminating
just below the dorsal margin of the neural complex. This spine is
attached posteriorly to the prezygapophysis of the fifth vertebra by
connective tissue. A thin, rectangular interneural bone is present in
the muscular tissue above the fourth neural spine and between the neural
complex and fifth neural spine. The neural pedicle, including the spine,
that is, one half of the fourth neural arch, is suggestive in shape of a
fireman's axe. Anteriorly it articulates with the neural pedicle of the
third vertebra and the neural complex. There is a spur-like postzygapo-

physis projecting backwards from the fourth neural pedicle but reaching
only one third of the distance from the neural pedicle to the fifth
neural spine.

Pars Auditum

The pars auditum in <u>Notropis cornutus</u> consists of the usual four
ossicles (Plate III, Figure 18). In anteroposterior sequence the
ossicles are; the claustrum, scaphium, intercalarium, and tripus.

The claustrum is a small bone, resembling a saucer attached to a
triangular base. The base may be likened to a right triangle, with the
hypotenuse forming the posterior border and the apex directed dorsally.
The posterior border is rounded and thick, tapering off to a sharp knife-
like anterior edge. There is an enlarged articular node located at the
point of junction of the hypotenuse and the base line of the assumed
triangle. This articular node fits into a corresponding notch in the
scaphium. The concave, saucer-shaped portion of the bone, or the major
part of the base line, is oriented anterolaterad to form the medial bony
wall of the atrium sinus imparis. The claustrum is securely bound at its
posterior border to the anterior edge of the second neural arch by strong
ligaments which are attached anteriorly to the exoccipitals above the
foramen magnum. The anterior edge is likewise immobilized by the same
ligament to the exoccipitals.

The scaphium acts as a lid covering the claustrum and is hinged at
its posterior border by dorsal and ventral projections in such a fashion
that it operates as a brachiopod valve over the claustrum. For descrip-
tive purposes, the scaphium amy be divided into two parts; the cup, or
concha stapedis, and the vertical articular hinge. The hinge is usually

divided into a lower articular process and an upper ascending process. The concha is roughly heart-shaped in lateral view. Its thin walls form a concave medial surface and a convex outer surface from which a prominent elevation arises near the middle, serving for the attachment of the ossicular ligament. The vertical hinge consists of a bony rod tapering to a blunt point dorsally and a conical articular peg ventrally. Near its middle the rod flattens out and is notched to accept the articular node of the claustrum. There is a tiny perforation of the concha which, in lateral view, opens externally just above the articular peg. The dorsal end of the hinge line rests in the suture formed between the second neural arch and third neural pedicle and is secured by connective tissue. The articular peg fits into a pit on the dorsolateral surface of the first centrum. The scaphium forms the lateral bony wall of the atrium sinus imparis.

The intercalarium, from the posterolateral aspect, is a Y-shaped, triradiate bone which broadens into a deltoid surface in the region where the three radii appear to merge. The dorsal arm, or ascending process, is straight and tapered and is hinged to the anterolateral edge of the third neural pedicle by connective tissue. The ventral arm, or articular process, is much shorter and heavier than the dorsal member. It terminates as a small articular peg which fits into a pit on the dorsolateral surface of the second centrum. The third arm of the intercalarium is longer than the two hinge arms and is directed anteroventrally from the vertebral column. Its terminus is thickened slightly and encompassed by the interossicular ligament. The intercalarium is quite variable, often differing in size or shape from left or right in the same specimen.

The fourth and largest ossicle in the chain is the tripus. In describing the tripus, the ventral and dorsal borders referred to in the text and drawings are seen actually to be the lateral and medial borders when the bone is observed from above and in its articulated state. The tripus may be divided into five regions (Krumholz, 1943): the anterior ramus, the body, the articular process, the posterior ramus, and the transformator process. The anterior ramus is short and stout and is attached to the posterior end of the interossicular ligament. The interossicular ligament thus serves to connect the tripus to the intercalarium and the scaphium. The body constitutes the greater mass of the tripus and exhibits along its ventral half, a series of annulations, doubtless due to deposition of bone during growth. The dorsal contours of the body suggest a triangular shield, at right angles to the long axis of the bone, merging into a concave surface antero-ventrally. The shield region lies in contact with the third vertebra and receives strength from a strut on its anterior face. Along the dorsal portion of the body there usually may be found fenestrations of varying sizes and numbers. The trough-like articular process acts as the fulcrum of the tripus and lies in the groove on the lateral surface of the third centrum. In unmacerated specimens the trough appears to be occupied by cartilage-like material which probably acts as a bearing surface and shock absorber for the articular process. The ventral border of the tripus is smoothly curved fore and aft. Posteriorly, the body tapers to form the posterior ramus. This portion of the tripus is thinner and longer than its anterior counterpart and bends slightly ventromesad towards the air bladder. From the posterior end of this ramus a thin strip of bone, the transformator process, arises and turns

abruptly posteroventrally to become embedded in the tunica externa of the anterior chamber of the air bladder, from which it is derived during embryonic development. Anteriorly, the distal part of the transformator process is connected to the ossa suspensoria by a strong triangular muscle, the tensor tripodis of Bridge and Haddon (1889) and Evans (1924-1925).

CHAPTER V

DISCUSSION AND CONCLUSIONS

The foregoing description of the Weberian apparatus applies to all
nine species of minnows and the hybrid form examined during the course
of this study. The following discussion and descriptions pertain to
generic and specific similarities and differences among the nine species.

The first centrum in the nine species and the hybrid are practically
identical morphologically, being of the amphicoelous type and attached
anteriorly to the proatlas (Plate I). Ramaswami (1955 a.) found that
the first centrum in the Gobioninae presented flat anterior and posterior
facets but no such condition was found to exist in the minnows examined
in this study. In Cyprinus carpio and Ictiobus bubalus, however, a thin
bony disc has been noticed between the anterior facet and the proatlas
so that either the centrum or proatlas appears flat (personal observation).
This is dependent upon the location of the disc, that is, whether it
adheres to the facet or proatlas. This disc is probably ossified noto-
chordal tissue. In the nine minnows a cartilage-like ring was often
noticed between centra, resembling an intervertebral disc and probably
representing the incompletely ossified notochordal material as in the
carp and buffalofish. In several specimens an additional and possibly
noteworthy structure was observed. From the center of many centra
there projected a slender cartilaginous slip, which in some cases appeared
to pass through the center of the next centrum. Upon removal of the slip
from its position between several consecutive centra, a small hole was

21

noticed extending through the centrum, clearly indicating that the slip was the remains of the notochord which had failed to ossify completely in this region.

The first pair of modified ribs spring laterally from the antero-ventral edge of the centrum in all species. From dorsal view they are broad at the base and project laterally forming a right angle with the centrum. The lengths of these ribs are quite variable in all species studied. Specimens were found with one rib twice the length of its opposite fellow, the shorter one seemingly having failed to ossify completely. An attempt was made to correlate the lengths of the ribs with centrum lengths or widths but to no avail. Similarily, the angle of departure of the ribs from the centrum was measured in an attempt to clarify an earlier observation relative to this angle. There seemed to be a greater percentage of notropids in which the rib formed a 30° angle, measured from a horizontal axis with the centrum, than in _Dionda_. After dissecting a greater number of specimens, however, this was found to be another character highly variable in both genera. In general, the first and second pleural rib in _Dionda_ are much slenderer and comparatively longer than their counterpart in the six notropids. The first rib in both genera is securely attached to the supracleithrum by a strong ligament originating from the rib tip.

In all species studied, there occurs a series of pits on both the first and second centra. These pits were constant in location and number in all specimens examined. On the dorsal surface of the first centrum there are two pits to receive the articular pegs of the scaphia. On the ventral surface a single median pit is present. The second centrum bears four pits dorsally, the lateral pair accepting the articular processes of the intercalaria. The median pair are of unknown function but

probably represent centers of ossification of the centrum. Ventrally, three pits are found; one on the midventral line of the centrum and a lateral pair located posterodorsad to the base of each modified pleural rib.

Watson (1939) referred to the structures herein called modified pleural ribs as dorsal ribs. He supported this view by stating "their structures indicate they are ribs, and their position, attached to the middle of the centra and penetrating the muscle points to homology with the dorsal or upper ribs of Esox."... Watson further stated, "They (the dorsal ribs) are not transverse processes or diapophyses since they are firmly attached to the centra while true diapophyses proceed from the neural arch". Yet in his drawings of the goldfish he clearly labeled them transverse processes, possibly indicating he was not sure of their origin. Hyman (1942) has defined diapophyses and parapophyses as lateral projections of the centrum for the attachment of the upper and lower capitula of a two headed rib. Thus neither name may be assigned properly to the lateral projections found on the first and second centra of the Cyprinidae. A more accurate term describing these modified pleural rib would be pleurapophyses. Hyman (1942) stated that a pleurapophysis represents the rib attachment of the vertebra plus the fused rib. Furthermore, Watson's statement relative to the structure and position of the lateral processes and their homology with upper ribs is untenable if Emelianov (1940) is followed. According to Hyman, Emelianov stated that "the ribs may shift their position with regard to the muscles during development, and hence the type of rib cannot be determined by its location in the adult. From this evidence it can be seen that it is quite possible for a pleural rib to become fused to its vertebral

attachment and through a muscular rearrangement change its position from ventral to dorsal. Watson's terminology was followed by Ramaswami (1955 a.) who called them dorsal ribs. Wright (1884), Bridge and Haddon (1889), Hora (1922), Chranilov (1926, 1927), Adams (1928) and Nelson (1948) referred to the ribs as transverse processes. Berg (1947) followed Chranilov in his illustrations taken from the latter author.

Centrum number three has essentially the same form in all species examined.

In the neural pedicle of centrum three were found the first constant differences between Dionda and the six species of Notropis. The pedicle has been described as mushroom-shaped in this study. Near the middle of the dorsal, expanded cap of the pedicle, at the point where it narrows into the stem, a slender, spur-like bone arises and extends postero-ventrally in the six species of Notropis (Plate I, Figure 1). Such a structure is lacking in Dionda (Plate I, Figure 5) and is represented only by a small ridge in approximately the same position. It is believed that this spur and ridge serve for the attachment of a ligament helping to secure the tripus in its articulating position. From the drawings of both Notropis and Dionda it will be noted that one other difference occurs in the neural pedicle of the third centrum (Plate I, Figures 1 and 5). In all species of Dionda the pedicle tends to be longer and slenderer, less stout and heavy in profile than its counter part in Notropis. The anterior edge of the expanded cap of the pedicle in both genera certainly must represent a highly modified prezygopo-physis. This is suggested by its direct articulation with the neural arch of centrum two. In like fashion, the posterior edge would represent a modified postzygopophysis since it articulates with the neural

arch of centrum four. The third neural pedicle in both genera is marked with varying degrees of fenestration and other sculpturing, some of which must serve for muscle attachment.

The unusual saddle-shaped bone referred to in this work is the second neural arch and is quite similar in shape in both Dionda and Notropis. It has been regarded as the neural arch of the first centrum or the fused arches of the first and second by Adams (1928) and by Sarbahi (1932). The fact that the arch lies above both centra (one and two) is strong argument that it does represent the fusion of arches one and two. However, Watson (1939) indicated that the first neural arch is never present in the adult goldfish but is incorporated embryonically in the scaphium. As pointed out previously, the second neural arch articulates with the neural arch and pedicle of centrum three, indicating that it rightfully should be called the second neural arch. Niazi (unpublished thesis) has reported a laterally compressed median blade representing a rudimentary neural spine on the second neural arch of some species in the genus Pimephales. No such structure was noticed in this study although the second neural arch of Dionda does have a slight elevation near the middle (Plate I, Figure 5) which quite possibly represent the minute remains of a neural spine.

Nelson (1948) in his comparative study of the Weberian apparatus of the Catostomidae described the neural complex as an expanded dorsal midsagittal plate formed by the fusion of the lamina and neural spines of the third vertebra plus possible interspinous elements. He made no mention of the fate of the neural spine of the second vertebra. In a later paper, Nelson (1949) referred to the neural complex from Raphiodon vulpinus Agassiz as consisting of the third neural spine and possibly

the second neural spine and/or interspinous elements. Ramaswami
(1955 b.) stated that in N. cornutus the complex represents the fused
second and third neural spines. Although Taranetz (1946) observed the
complex from several cyprinid species and noted specific variation in
its shape, he did not discuss its composition other than to refer to it
as an apophysis on the back of the third vertebra. Watson (1939)
described the neural complex in his embryological study of Carassius
auratus but he did not use the term neural complex. Watson made con-
fusing and contradictory statements relative to the formation of the
neural complex. He found in the embryonic development of the goldfish
a mass of cartilage above the second and third centra. This mass, he
stated, represents the fused nerual spines and basidorsals of the second,
third, and fourth vertebrae along with the first three interspinous
bones, and possibly the neural spine of the first vertebra. In the
adult, the cartilaginous mass becomes the compound neural arch and an
enlarged neural spine closely applied, posteriorly, to the smaller, more
normal shaped spine of the fourth vertebra. Thus, Watson would have the
cartilaginous mass forming two parts; the compound neural arch and spine,
and the fourth neural spine. He did not mention the fourth neural arch
nor do his text and drawings indicate whether or not a fusion exists
between the fourth neural spine and the neural complex. Watson decided
that the compound neural spine represents a fusion of the second and
third nerual spines with the first three interspinous bones and possibly
the neural spine of the first vertebra. He later contradicted this
statement by saying that the first vertebra does not enter into the
cartilaginous mass. In conclusion, Watson contradicted himself once
again by labeling the compound neural spine as the third neural spine,

rather than that of the second and third.

In _Dionda_ and _Notropis_, the following explanation is tentatively proposed to account for the formation of the modified neural arch and spine until a detailed embryological study is made. The fourth neural arch and spine forms independently of the neural complex, even though it is slightly modified in comparison with the fifth. The fact that it is at no point fused to the neural complex would indicate this. The first three interspinous elements, if they are present in the embryo, have fused with the complex spine, probably forming the anterior projecting midsagittal lamina which is attached to the supraoccipital by connective tissue. The neural spine of the second vertebra contributes to the formation of the neural complex because it is absent from the second neural arch or at best is represented by a mere elevation on the arch in one instance and as a thin medial plate in some _Pimephales_ according to Niazi (unpublished thesis). In a great many specimens examined during the course of this study, the ventral border of the neural complex blade approaches very near to the second neural arch before angling antero-dorsally to its terminus. This further suggests that the second neural spine has been arrogated by the neural complex. If, as Watson reported, the first neural spine does not contribute to the neural complex, then it follows that it is lost at some early embryonic stage by reabsorption, or contrary to Watson's findings, does enter into the formation of the neural complex, possibly becoming the most anterior border of the forward projecting blade of the complex.

Taranetz (1946) after studying 26 species of Cyprinidae stated that the conformation of the neural crest (neural complex) differed considerably with each species. Similar results were obtained in comparing the

complexes of the fishes involved in this study. Considerable variation was noticed in the neural complex of the notropid species (Plate I, Figures 9 to 14). Although superficially it would appear that species separation is possible, utilizing the shape of the neural complex, the number of specimens studied was insufficient to warrant definite conclusions regarding taxonomic separation. The Notropis lutrensis X N. venustus hybrids were examined to compare the shape of the neural complex with that of the parent species. Such hybrids exhibit a gray caudal spot, intermediate between the distinct black spot of N. venustus and its absence in N. lutrensis. Since many characters of fish hybrids show intermediacy (Hubbs, 1940) one might expect this condition to obtain here. Upon examination, however, the bone in all six presumed hybrid specimens appeared almost identical to those found in N. venustus. The absence of intermediacy may indicate dominance of N. venustus or suggest the possibility that the specimens in question are not hybrids, but N. venustus with a poorly developed caudal spot. The shape of the neural complexes in the three species of Dionda exhibit very few differences from those of the notropids. Differences in the shape of the neural complex between Notropis and Dionda were noticed and may be mentioned. Plate II, Figures 9 to 17 illustrate that the neural complex of Dionda is a horizontally elongated, boat-shaped structure whereas in the six species of Notropis this bone usually appears to be more vertically elongate and presents a wine-glass profile, the cavity being much deeper than that of Dionda. The shape of the neural complex may reflect the general body shape of the minnow. The species of Dionda are characteristically slender bodied in contrast to the laterally compressed, deeper bodied notropids, except N. percobromus, included in this study. N. percobromus approaches the slender form of Dionda and its neural

complex (Plate II, Figure 14) exhibits a lower more horizontally elongate silhouette than that of the other five species. A detailed study of the complex from other slender-bodied minnows of the genus Notropis, such as N. fumeus, N. ozarcanus and others, may present a neural complex quite similar to that of Dionda. The variation existing in the shape of the neural complex within the genus Notropis is interesting in that one species, N. lutrensis, differs more from the other five notropids, than another of the same genus, N. percobromus, differs from Dionda. Three notropids of the subgenus Cyprinellus, N. lutrensis, N. venustus, and N. whipplei, have morphologically distinct neural complexes (Plate II, Figures 11, 12, and 13). N. lutrensis and N. venustus have radically different neural complexes but are evidently very closely realted since the freely interbreed (Hubbs and Strawn, 1956).

With regard to the fourth vertebra, both genera vary only in minor detail between individual specimens. The neural arch of the fourth verte-bra is complete in having both nerual pedicles united by connective tissue dorsally to form the walls and roof of the neural tube in this region. The pedicles extend above the neural rach dorsally to form the fourth neural spine. This spine resembles the normal fifth neural spine but is reduced in size, never exceeding but often equaling the height of the neural complex. Modified zygapophyses are present on the fourth neural pedicles and are similar to those of the third vertebra, the posterior one, however, is reduced in size. The prezygapophyses articulate with the postzygapophyses of the third neural pedicle and the posterventral surface of the neural complex. The postzygapophyses are attached to the neural arch of the fifth vertebra by connective tissue. The fourth centrum is pierced dorsolaterally by two pyramidal pits into which the bases of the neural pedicles fit. A modified pleural rib articulates with

the ventrolateral surface of the centrum by a pyramidal root fitting into a like depression in the centrum. A thin bony wall separates the lower depression from the one above into which the root of the neural pedicle fits. The ossa suspensoria project ventromesiad from the pleural rib, terminating as a flat triangular plate ("transverse plate", Nelson, 1948). Nelson, in referring to the "transverse plate" formed by the ossa suspensoria, stated; "In the Cyprinidae the ossa suspensoria form the only 'transverse plate' and usually arise separately of the fourth pleural ribs from the ventral surface of the fourth centrum". Ramaswami (1955 a.) apparently shared this view by describing the ossa suspensoria as projections from the ventral surface of the fourth centrum. Watson (1939) would have them as haemapophyses of the vertebra. The above conditions do not apply generally to the Cyprinidae. In addition to Dionda and Notropis, the ossa suspensoria have been observed (personal observations) from Cyprinus, Pimephales, Hybopsis, Hybognathus, Chrosomus, and in none does the centrum give rise to the ossa suspensoria. In every species the pleural ribs seem to be fused to the basiventrals, the latter acting as the rib head in articulating with two or three deep depressions on the ventrolateral surface of the centrum. The ossa suspensoria probably represent an independent outgrowth from the ventromesiad surface of the fourth pleural ribs and are not separate, distinct parts of the centrum. Goodrich (1930) is, therefore, quite correct in referring to the ossa suspensoria of Cyprinus carpio as the "surface of the modified third rib, which presses on the airbladder". The tripus, in its articulation with the body of the third vertebra, curves posteriad beneath the pleural rib of the fourth vertebra and lateral to the ossa suspensoria. The terminus of the tripus, the transformator process, is recurved and imbedded in the tunica externa of the anterior chamber of the air bladder.

Anteriorly, the transformator processes are attached to the posterior surfaces of the ossa suspensoria by the muscular tensor tripodes.

The fifth vertebra is not a part of the Weberian apparatus of _Dionda_ and _Notropis_ but it is of some value to note its relationship to these bones. It is the first normal trunk vertebra posterior to the apparatus. The pleural rib of the fifth vertebra is directed anteroventrally and passes lateral to the pleural rib of the fourth vertebra. The prezygapophyses of the fifth vertebra are attached to the fourth neural spine by connective tissue (Plate I, Figure 1). The first interspinous bone is located above the fourth neural spine and between the neural complex and the fifth neural spine. This bone lies imbedded in the interspinous ligament and is the first of a series of such bones, ranging in number from five to eight in _Dionda_ and _Notropis_, located between successive spines.

In discussing the ossicles of the Weberian apparatus from _Dionda_ and _Notropis_, it must be pointed out that variability is the rule throughout. This variability exists not only within the two genera, but may be found between specimens of a single species. Moreover, it was found that variation occurred in a single specimen as exemplified by the intercalaria from the left and right side of _N. zonatus_ (Plate III, Figure 19). The tripods from the nine species included in this study present two distinct forms; one type in which the anterior and posterior rami are very short and the other form in which the rami are quite long. The lateral border of the tripus may be smoothly rounded from the anterior ramus to the tip of the transformator process or the border may be nearly straight with the transformator separating at a sharp angle from the posterior ramus. Either of the latter two conditions may exist in

combination with the long or short rami. Fenestrations and struts of the tripus offer no help in either specific or generic determination. Fenestrae may occur in abundance on the tripus of one specimen within a species and be totally lacking on another from the same species. The variable length of the anterior rami occurring on the tripods of the nine species may be explained. Apparently the length of the anterior ramus increases with age, brought about by ossification in the interossicular ligament where it attaches to the tripus. This ossification occurs at two additional points in the ligament; at the distal end (manubrium incudis) of the intercalarium and on the external surface of the scaphium where the ossicular ligament attaches. In larger, and presumably older, specimens of both genera the ligament appears to be shorter, the anterior ramus of the tripus longer, the distal end of the intercalarium thicker, and the elevated ligamentous attachment on the scaphium somewhat higher. In one large specimen(153 mm., standard length) of N. cornutus the ossicular ligament was stained by the alizarin red-S at two points within the ligament; one about midway between the intercalarium and the scaphium and the other midway between the intercalarium and the anterior ramus of the tripus. This would indicate the possibility of the ligament ossifying, in fish of maximum age and size, to the extent that the function of the ossicles may be impaired.

The remaining ossicles from all nine species are quite similar in shape and structure. The intercalarium is most variable in both genera, assuming a large assortment of shapes.

The illustrations of these bones (Plates III and IV) do not represent typical ossicles from a certain species but rather point out the similarity existing between the nine species examined during this study.

The results of this work indicate that in _Notropis_ and _Dionda_ the Weberian apparatus is of no taxonomic value, at the generic level, even though differences between the two genera were noted. These differences are not distinct enough to be of taxonomic significance when utilized without considering other intangible generic and specific factors. This is especially true of the neural complexes, as additional work may prove the differences in the shape of the bone to be simply a gradient character from the slender-bodied to the laterally compressed, deep-bodied forms. Nelson (1948) has stated in his work on the Weberian apparatus of the Catostomidae that beyond the tribe level, the Weberian apparatus cannot be considered as a distinguishing criterion even though he found three main morphological forms. The findings herein reported confirm Nelson's results relative to the apparatus.

The Weberian ossicles from _Dionda_ and _Notropis_ are of no value in separating the two genera. The bones are much too closely similar, and have too much intrinsic variability to be utilized as taxonomic tools. Krumholz (1943) stated that the morphology of the Weberian ossicles is stable within a species and that there were differences between genera and even between species referred to the same genus. He further stated that generic and specific distinctions were particularly pronounced in the Eventognathi. Robins and Raney (1956) appear to agree with Krumholz. In their study of the genus _Moxostoma_ they reported that important taxonomic features were found in the Weberian apparatus, particularly the tripus. They made no mention, however, of the number of tripods examined in reaching this conclusion. Results of this study do not agree with the findings of Krumholz and Robins and Raney. A statement from

Taranetz's (1946) work on 26 cyprinid species from the Amur River system
is more applicable to the nine species included in this study. Taranetz
found that there were generic differences, especially in the neural
complex, but that the ossicles showed little range of variation in all
26 species.

Finally, it is concluded that, based on results obtained from this
study, the differences and/or similarities of the Weberian apparatus in
Dionda and Notropis offer inconclusive evidence of their taxonomic
relationship.

CHAPTER VI

SUMMARY

1. The Weberian apparatus from 126 specimens, representing three species of _Dionda_, six species of _Notropis_, and one hybrid combination, were examined during the course of this study.

2. Fresh and/or preserved specimens were stained, using a modification of Hollister's (1934) alizarin red-S method and dissections made. The various osseous components were illustrated in charcoal with the aid of a camera lucida.

3. The Weberian apparatus from these minnows consists of four separate modified vertebrae and four ossicles articulating with the vertebrae.

4. The lateral projections of the first and second centra are regarded as modified pleural ribs fused to the centra. They are regarded as pleurapophysis.

5. The ossicles of all nine species are structurally very similar, and also quite variable in all species.

6. The primary differences existing in the Weberian apparatus between _Dionda_ and _Notropis_ are as follows:

   a. The pars sustentaculum of _Notropis_ is much stouter and heavier than in _Dionda_.

   b. A spur-like diverticulum is present on the third neural pedicle in _Notropis_ but absent in _Dionda_.

c. The neural complex of <u>Notropis</u> is vertically elongate and cup-shaped and in <u>Dionda</u> it is horizontally elongate and boat-shaped.

7. Differences in the shape of the neural complex between the two genera are of dubious taxonomic value and require additional work.

8. Considerable variation exists in the shape of the neural complex within the notropid species. In <u>Dionda</u> specific variation is negligible.

9. The neural complex represents the neural spines of the second and third vertebrae plus fused interneural bones, anterior to the fourth neural spine, if they exist.

10. The tripus is of no taxonomic value in any of the nine species.

11. Variation in the length of the anterior rami of the tripods, thickness of the distal end of the intercalaria and height of the ligamentous attachment on the scaphium are the result of ossification at these points in the interossicular ligament.

12. The intercalaria are the most variable ossicles in all species examined.

13. The ossa suspensoria appear as distinct outgrowths of the fourth pleural ribs and not part of the fourth centrum.

14. Rather than being markedly similar, as might be expected in a subgenus, three species, <u>Notropis</u> (<u>Cyprinellus</u>) <u>lutrensis</u>, <u>N</u>. (<u>C</u>.) <u>venustus</u>, and <u>N</u>. (<u>C</u>.) <u>whipplei</u>, are radically different with regard to their neural complexes.

15. Results obtained from this study provide no conclusive evidence of the taxonomic status of <u>Dionda</u> and <u>Notropis</u>. The general similarity of the Weberian apparatus does, however, indicate the two are closely related.

CHAPTER VII

SUGGESTIONS FOR FURTHER STUDY

1. A thorough embryological study of the Weberian apparatus from two or three cyprinid genera is needed to clear up the existing blurred picture we have if its primordial development.

2. The neural complex of all species of Notropis needs critical examination.

3. More studies concerning variation in species of the large genus Notropis are needed.

4. A comparison of the Weberian apparatus of Dionda with that of Hybognathus would be of importance in view of the fact that the two have been considered congeneric.

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APPENDIX

PLATE I

Figure 1. Lateral view of the pars sustentaculum in N. cornutus including the fifth centrum and neural arch.

Figure 2. Dorsal view of the same structure in N. cornutus minus the fifth centrum and neural arch.

Figure 3. Anterior view of the pars sustentaculum in N. cornutus.

Figure 4. Ventral view of the pars sustentaculum in N. cornutus with the right pleural rib of the fourth centrum removed.

Figure 5. Lateral view of the pars sustentaculum in D. diaboli including the fifth centrum and neural arch.

Figure 6. Dorsal view of the same structure in D. diaboli minus the fifth centrum and neural arch.

Figure 7. Anterior view of the pars sustentaculum in D. diaboli.

Figure 8. Ventral view of the pars sustentaculum in D. diaboli with the right pleural rib of the fourth centrum removed.

Abbreviations:

BNC - Base of the neural complex
C 1, 2, 3, 4, 5 - Centra
CRT - Cartilaginous connective tissue
IS - Interspinous bone
NA 2, 4, 5 - Neural arches
NC - Cup portion of the neural complex
NP3 - Neural pedicle of the third centrum
NS 4, 5 - Neural spines
OS - Ossa suspensoria
POZ - Postzygapophyses
PRZ - Prezygapophyses
R 1, 2, 4 - Modified pleural ribs
SNC - Stem of the neural complex

PLATE I
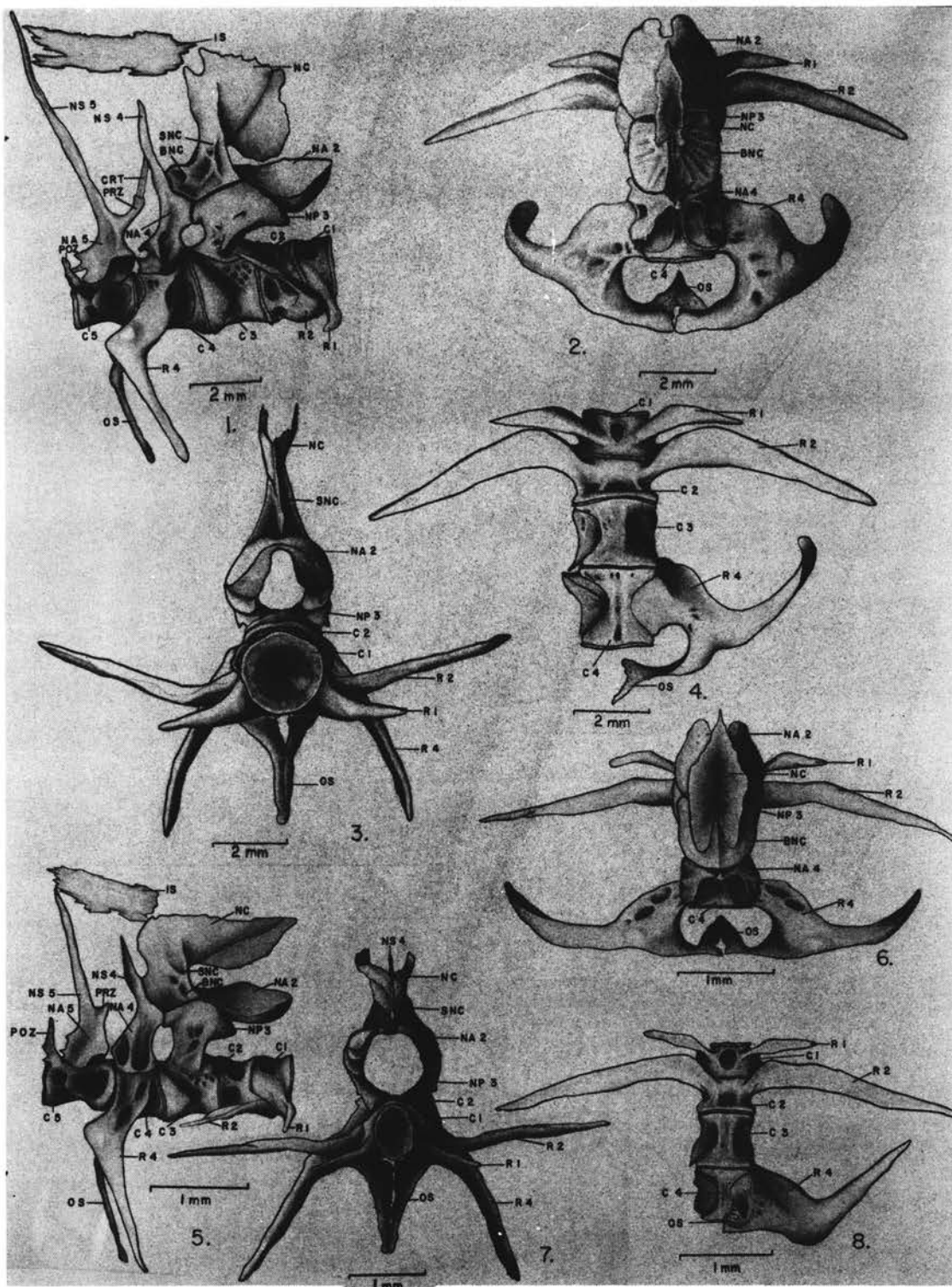
PLATE II

Figure 9.   Neural complex of <u>N</u>. <u>cornutus</u>

Figure 10.   Neural complex of <u>N</u>. <u>zonatus</u>

Figure 11.   Neural complex of <u>N</u>. <u>whipplei</u>

Figure 12.   Neural complex of <u>N</u>. <u>lutrensis</u>

Figure 13.   Neural complex of <u>N</u>. <u>venustus</u>

Figure 14.   Neural complex of <u>N</u>. <u>percobromus</u>

Figure 15.   Neural complex of <u>D</u>. <u>diaboli</u>

Figure 16.   Neural complex of <u>D</u>. <u>episcopa</u>

Figure 17.   Neural complex of <u>D</u>. <u>nubila</u>

PLATE II

Fig.-9.

Fig.-10.

Fig.-11.

Fig.-12.

Fig.-13.

Fig.-14.

Fig.-15.

Fig.-16.

Fig.-17.
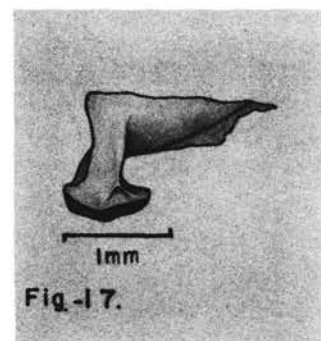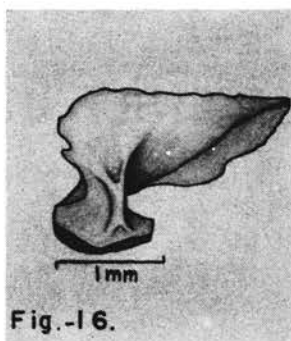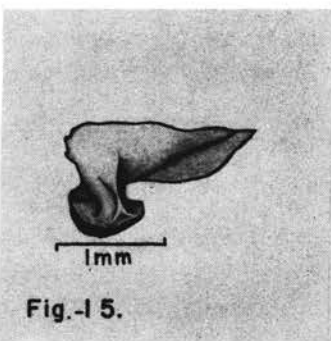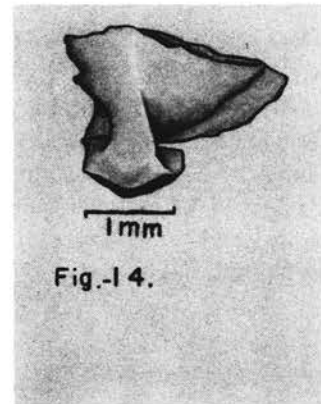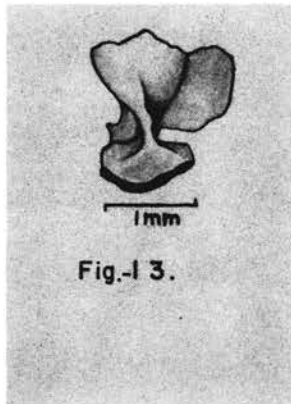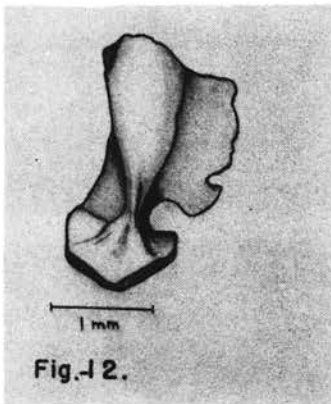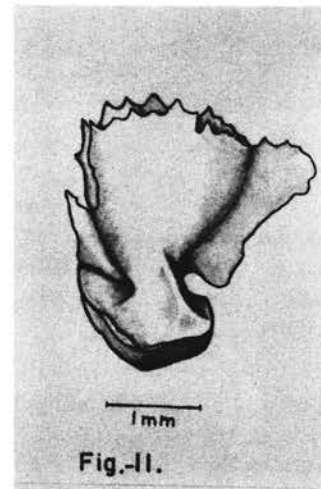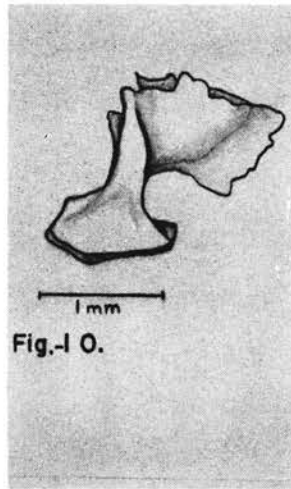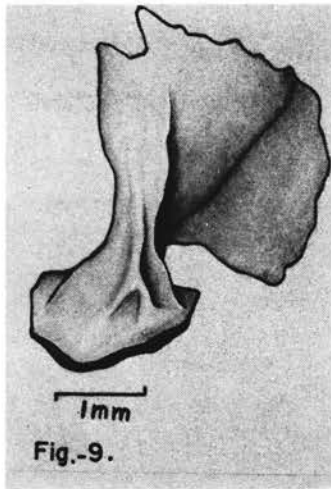
PLATE III

Figure 18. Weberian ossicles in N. cornutus

Figure 19. Weberian ossicles in N. zonatus showing both the left and
right intercalarium from a single specimen as an example
of variation commonly found in this bone

Figure 20. Weberian ossicles in N. percobromus

Figure 21. Weberian ossicles in N. venustus

Figure 22. Weberian ossicles in N. lutrensis

Figure 23. Weberian ossicles in N. whipplei

Abbreviations:

    AP – Articular process
    AR – Anterior ramus
    ASC – Ascending process
    Cm – Claustrum
    CS – Concha stapedis
    Ic – Intercalarium
    MI – Manubrium incudis
    PR – Posterior ramus
    Sc – Scaphium
    TP – Transformator process
    Tr – Tripus

PLATE III

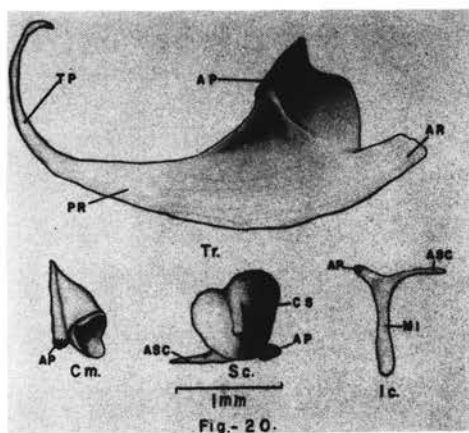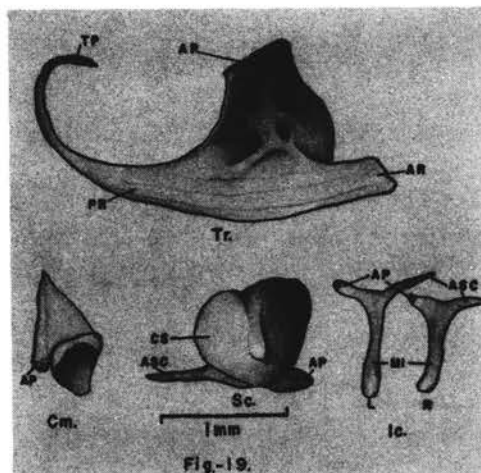Fig.-18.

Fig.-19.

Fig.-20.

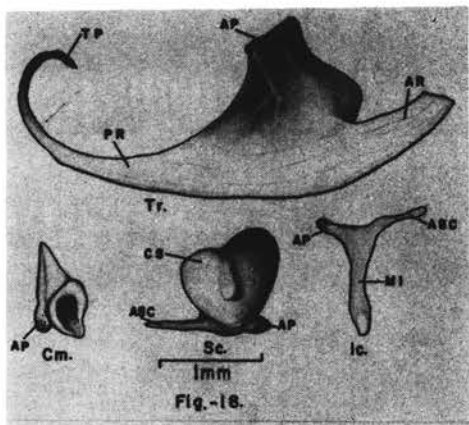Fig.-21.

Fig.-22.

Fig.-23.
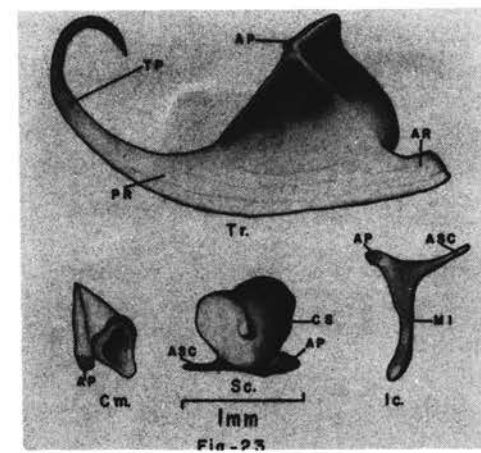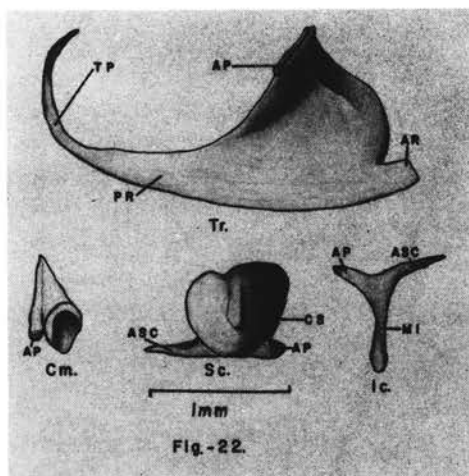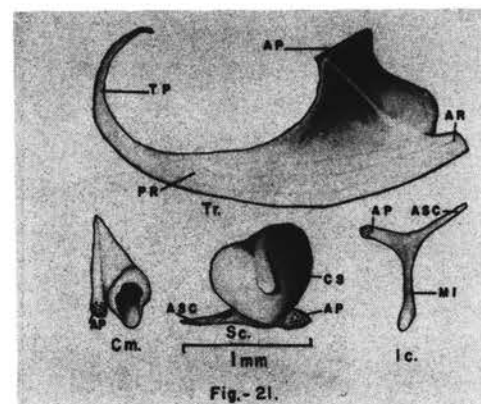
PLATE IV

Figure 24. Weberian ossicles in <u>D</u>. <u>diaboli</u>
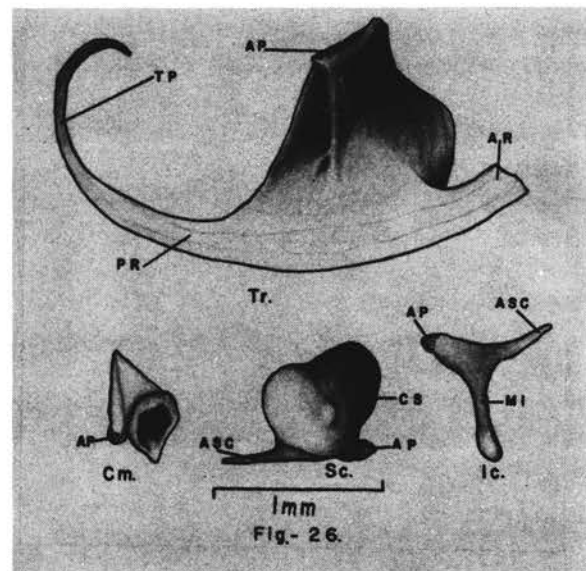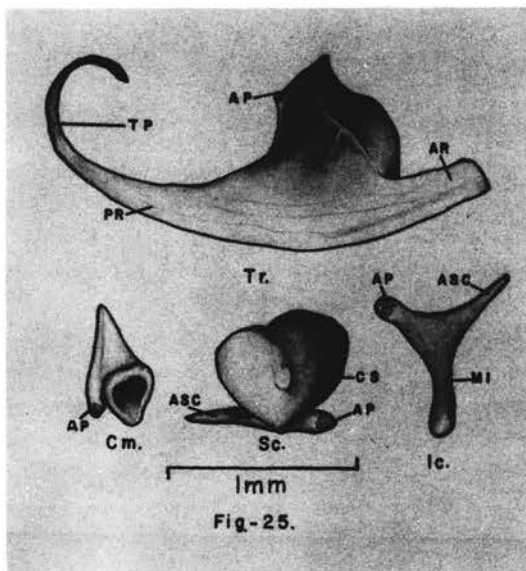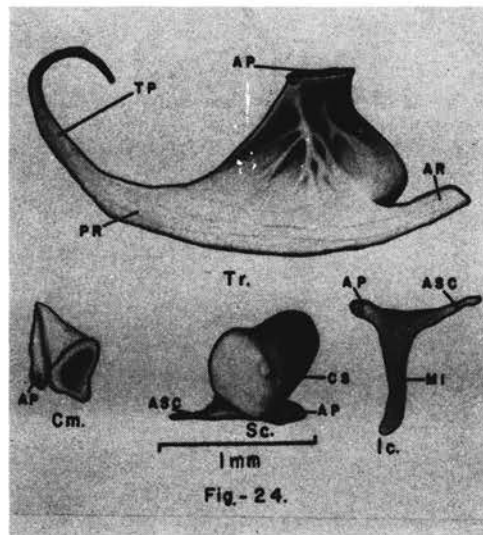
Figure 25. Weberian ossicles in <u>D</u>. <u>episcopa</u>

Figure 26. Weberian ossicles in <u>D</u>. <u>nubila</u>

Abbreviations:

    AP - Articular process
    AR - Anterior ramus
    ASC - Ascending process
    Cm - Claustrum
    CS - Concha stapedis
    Ic - Intercalarium
    MI - Manubrium incudis
    PR - Posterior ramus
    Sc - Scaphium
    TP - Transformator process
    Tr - Tripus

PLATE IV

Fig - 24.

Fig - 25.

Fig - 26.

VITA

Morgan Emery Sisk

Candidate for the Degree of

Master of Science

Thesis: A COMPARATIVE STUDY OF THE WEBERIAN APPARATUS IN THE GENERA
DIONDA AND NOTROPIS (CYPRINIDAE)

Major Field: Zoology

Biographical:

Personal Data: Born at Ashland, Kentucky, April 5, 1930, the son
of Morgan E. and Sadie Mae Sisk.

Education: Attended grade and high school in Paducah, Kentucky;
graduated from Lone Oak High School, Paducah, Kentucky in
1949; received the Bachelor of Science degree from Murray
State College, Murray, Kentucky, with a major in Agriculture,
in August, 1953; attended Murray State College on a part time
basis between September, 1956 and August, 1958 to complete
the required hours for a Biology major; completed the require-
ments for the Master of Science degree from Oklahoma State
University with a major in Zoology, in May 1961.

Professional experience: Teaching experience from 1958 to present
as a graduate assistant in the Department of Zoology, Oklahoma
State University; member of the following organizations; The
American Society of Ichthyologist and Herpetologist, The
Southwestern Association of Naturalists, The Oklahoma Academy
of Science, The Kentucky Academy of Science, Sigma Xi, and
The American Fisheries Society.