

# *American Museum* **Novitates**

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PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

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NUMBER 2428

AUGUST 26, 1970

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## Origin of the Weberian Apparatus and the Relationships of the Ostariophysan and Gonorynchiform Fishes

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### INTRODUCTION

The ostariophysan fishes exhibit a wide range of anatomical and behavioral specializations, and comprise one of the largest and most diverse groups of teleosts. This assemblage contains about one-third of the fishes of the world, and includes animals of such different appearance and habits as the electric eels, the carps, and the armored catfishes. Remarkable for their outward diversity, all ostariophysans possess a specific and complex inner ear-swimbladder connection that involves the first few vertebrae and is called the Weberian apparatus. The phylogenetic integrity of the included species is indicated more by the existence of this bony otophysic connection than by the presence of any other single feature. In 1966 Greenwood, Rosen, Weitzman, and Myers suggested a relationship of the Ostariophysi with the Gonorynchiformes on the basis of shared specializations of the caudal fin skeleton, the occipitocervical region, and the swimbladder. The authors concluded that the resemblances between the two groups of fishes suggest derivation from a common stem,

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and that both groups are tied by ancestry to the salmoniform fishes. The objective of the present report is to consider the relationships of the ostariophysan fishes with particular regard to the phylogenetic significance of early ontogenetic stages of the Weberian apparatus and its associated structures. This particular objective was recently made attainable when we received a collection of exceedingly small specimens of the characid genus *Brycon* from the Bolivian Amazon. In these specimens the Weberian apparatus had not yet developed fully, and skeletal preparations made from them have enabled us to deduce the probable homologies of the Weberian ossicles and associated bony structures. We find that our conclusions are not in complete accord with those of previous students of this subject (see review in Watson, 1939).

### STUDY MATERIAL

On hand from previous studies by the authors were dissections and skeletal preparations of all major groups of elopiforms, salmoniforms, gonorynchiforms, and ostariophysans.

Histological preparations of salmonid, chanid, and characid swimbladders were made using a Masson trichrome stain.

Materials prepared especially for the present work are as follows:

#### CLEARED AND ALIZARIN-STAINED PREPARATIONS

*Brycon* sp. (five juveniles, 9–22 mm. standard length, Río Mamoré, Bolivia).

*Poecilobrycon harrisoni* Eigenmann (five juveniles, 7–21 mm. standard length, aquarium material from S. H. Weitzman).

*Hyphessobrycon scholzi* Ahl (eight juvenile to half-grown, aquarium material from S. H. Weitzman).

*Salmo mykiss* Walbaum [two fingerlings, British Museum (Natural History) No. 1893.2.7.63-72].

#### DRY SKELETONS

*Brycon guatemalensis* Regan (three adults from Guatemala, American Museum of Natural History Nos. 27842, 27809, 21670).

#### ABBREVIATIONS

ac, anterior chamber of swimbladder

avc, anterior vertical semicircular canal

boc, basioccipital

cl, claustrum

crb, cephalic rib

cth, cleithrum

cts, connective tissue sheet

dp, ductus pneumaticus

encrb, intermuscular bone that is partly epineural and partly epicentral

enrb, epineural intermuscular bone  
ep, epural  
eprb, epipleural intermuscular bone  
ept, edge of peritoneal tunic of swimbladder  
exo, exoccipital  
hc, horizontal semicircular canal  
hp<sub>1-6</sub>, hypurals  
in, intercalarium  
inm, intercostal muscle portion of epaxial musculature  
ipt, inner surface of peritoneal tunic of swimbladder  
lat, lateral process  
lig-crb, ligament from pterotic to first cephalic rib  
lig-cth, ligament from pterotic to cleithrum  
lig-int, intercostal ligament  
lig-np<sub>3, 4</sub>, neuro-parapophyseal ligament, numbered to correspond with its vertebra  
lig-oi<sub>1-4</sub>, oblique interneural ligament, numbered to correspond with its vertebra  
lo, lagenar otolith  
na, neural arch  
nsp, neural spine  
opt, outer surface of peritoneal tunic of swimbladder  
os, os suspensorium  
par<sub>2-5</sub>, parapophysis, numbered, when appropriate, with its corresponding vertebra  
parsph, parasphenoid  
pc, posterior chamber of swimbladder  
php, parhypural  
pro, prootic  
pt, peritoneal tunic of swimbladder  
pto, pterotic  
ptt, posttemporal  
pu<sub>1-3</sub>, preural centra  
pvc, posterior vertical semicircular canal  
rb<sub>1, 2, 3</sub>, pleural ribs, numbered from the first rib on the third vertebra  
sb, spongy bone  
sc, scaphium  
scth, supracleithrum  
sd, supradorsal  
sn, supraneural  
so, saccular otolith  
spho, sphenotic  
ten-epx, tendon from first cephalic rib to epaxial musculature  
tr, tripus  
trp, transformator process of tripus  
u<sub>1</sub>, first ural centrum  
un, uroneural  
uo, utricular otolith  
vert<sub>5</sub>, fifth vertebra

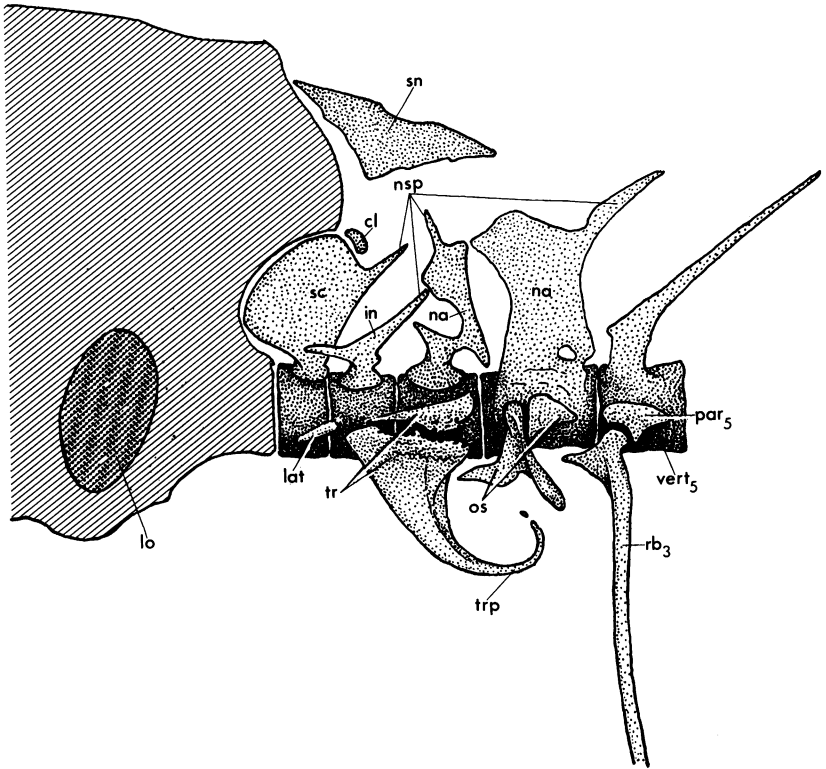


FIG. 1. Incompletely differentiated Weberian apparatus in juvenile *Brycon* sp. of 9 mm. standard length.

### HOMOLOGIES OF THE WEBERIAN APPARATUS

The smallest specimen of *Brycon* examined is 9 mm. in standard length and has a Weberian apparatus in an early stage of differentiation (fig. 1; cf. fig. 2). At this stage, the individual components of the first four vertebrae are still recognizable as vertebral elements. The differentiation that they were obviously undergoing, however, leaves no doubt as to the role each part would have played in the fully formed Weberian apparatus. On the first vertebra the neural arch is expanded and extends into an excavation in the exoccipitals; the paired supradorsal elements (see François, 1966, fig. 12A; and fig. 3, page 5) are directly above this arch and, in this instance, are free from the base of the short neural spine. The two halves of the arch are identified as the presumptive scaphia, and the supradorsals as the presumptive claustra (see also below).

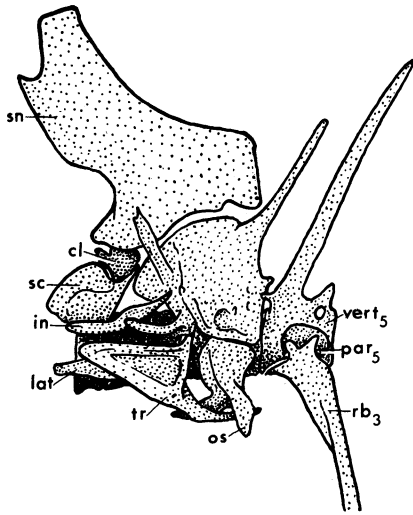


FIG. 2. Fully differentiated Weberian apparatus in adult *Brycon meeki* Eigenmann and Hildebrand, after Weitzman (1962).

On the second vertebra there is a small neural spine and a neural arch with well-developed prezygapophyses. The neural spine is later resorbed, as shown by slightly larger specimens (15–22 mm. standard length), and

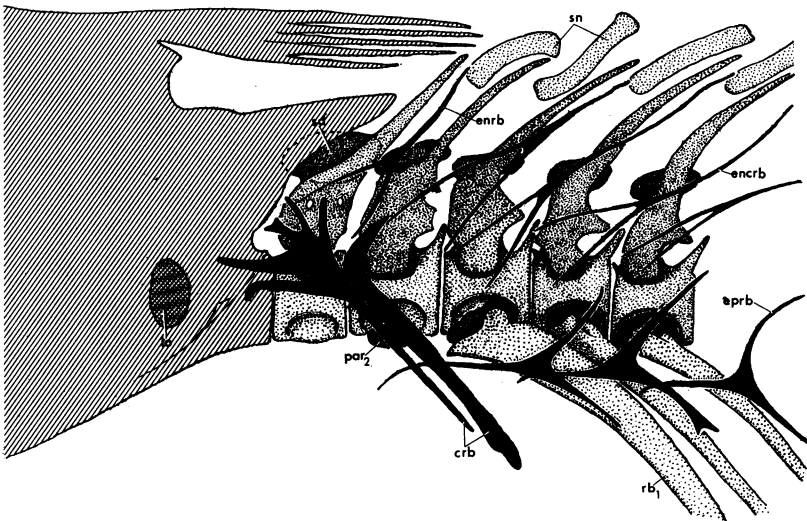


FIG. 3. Occipitocervical region of juvenile *Chanos chanos* (Forskaal) of 25 mm. standard length. Note, especially, the shape and size of the head of the first pleural rib and its parapophysis and the enlarged, anteriormost supradsoral.

the persisting and completely separated halves of the arch and their prezygapophyses form the presumptive intercalaria. The lateral processes of the second vertebra are already well developed in the smallest specimen, and their homology with non-rib-bearing parapophyses is not completely apparent by inspection. Evidence presented below supports this homology, however. On the third vertebra the neural arch and spine are present but much deformed. The most striking feature of the third vertebra is the developing tripus which consists of two distinct components. A comparison of these two elements with the rib and parapophysis of the fifth vertebra leaves little doubt that the compound tripus of *Brycon* is formed from an attenuate parapophysis and from a pleural rib. The rib head is greatly enlarged and expanded forward, whereas the shaft of the rib is greatly reduced and recurved to form the transformator process of the tripus. On the fourth vertebra the parapophysis and rib also are modified, mainly by reduction of the rib shaft, to form the os suspensorium for support of the anterior chamber of the swimbladder. The neural arch of this vertebra is greatly enlarged. The medial, plate-like bone lying free in the tissue above the developing vertebral structures, referred to in ostariophysan terminology as a neural complex, gives no sign of having more than one center of ossification and probably is a somewhat enlarged supraneural (or predorsal) bone. The Weberian apparatus of our figured juvenile specimen may be compared with the fully formed *Brycon* mechanism in figure 2.

There are similarities in certain elements of the anterior vertebrae in the juvenile specimens of *Brycon*, discussed above, and in juvenile and adult *Chanos* (fig. 3). Most noteworthy, is the specialized form of the first pleural rib on the third vertebra. In common with the ostariophysan tripus, the first pleural rib of *Chanos* has an expanded head with a triangular flange projecting anteriorly (homologous with the ventral element of the tripus), as well as an elongate autogenous parapophysis (homologous with the dorsal element of the tripus).

The similarity between the first pleural rib and its parapophysis in *Chanos* with the ostariophysan tripus is enhanced by the association of both the rib and tripus with a thickened peritoneum that surrounds part or all of the anterior chamber of the swimbladder (fig. 4A, C). In ostariophysans the dense guanine-invested connective tissue around this chamber has been identified by various authors as the tunica externa of the bladder, but this identification is in error, as histological preparations of the *Brycon* swimbladder show that a tunica interna, the mucosa, and a tunica externa, the serosa, are present within this membranous covering. In *Chanos* only the anterior tip of the swimbladder is covered

by dense, silvery peritoneum that is firmly supported dorsally by the first rib and more ventrally by the second (fig. 4A). In ostariophysans the dense peritoneal tunic is also supported by the first two ribs, which are modified as the tripus, first rib, and os suspensorium, second rib, (see Alexander, 1962, for a description of these bone-to-membrane contacts).

Other similarities between *Chanos* and *Brycon* are: The protrusion of the anterior margin of the first neural arch forward into a recess formed by the occipital region of the cranium (i.e., the scaphium in *Brycon*; figs. 1, 3); the presence of supraneural (predorsal) elements above the neural spines; the presence of parapophyses not bearing ribs on the second centrum (reinforcing the interpretation of the rodlike lateral process in *Brycon* as a non-rib-bearing parapophysis; figs. 1, 3); the absence of parapophyses and pleural ribs on the first vertebra (although in *Chanos* there is a definite recess in the position of each parapophysis without a sign of an ossified structure in it).

Finally, as noted, the enlarged pair of supradorsal elements present in *Chanos* on the upper border of the neural arch of the first vertebra (fig. 3) are probably homologous with the small elements of similar position, which are identified as the claustra in the juvenile *Brycon*. In the case of both the supradorsal and the claustrum, the bony tissue has a characteristic granular appearance. Paired supradorsal elements are present above the neural arches of all abdominal vertebrae in *Chanos*, as well as in salmoniforms (see François, 1966) and elopoids, but the first supradorsals in *Chanos* are unusually large.

There appear to be no other anterior vertebral specializations of *Chanos* specifically comparable with those in *Brycon*. There are, however, a number of differences, chief of which is the complex series of differentiated intermuscular bones in *Chanos* and other gonorynchiforms that have no counterparts in ostariophysans. These intermuscular bones are in three series: the cephalic ribs (fig. 5), and an upper and lower series of intermuscular bones that are partly epineural, partly epipleural, and partly epicentral in their contacts with the vertebral column (fig. 3). Despite these differences, there does appear to be some degree of functional similarity in the anterior region of the axial skeleton in *Chanos* and *Brycon*. In *Chanos*, for example, the first two pairs of pleural ribs are firmly attached to the outer wall of the anterior peritoneal cover of the swimbladder (fig. 4), and these ribs, in turn, are linked with the enlarged cephalic ribs via sheets of connective tissue and two groups of straplike muscles that are continuous with the epaxial musculature (fig. 5). Anteriorly, the cephalic ribs are firmly associated by ligament and direct

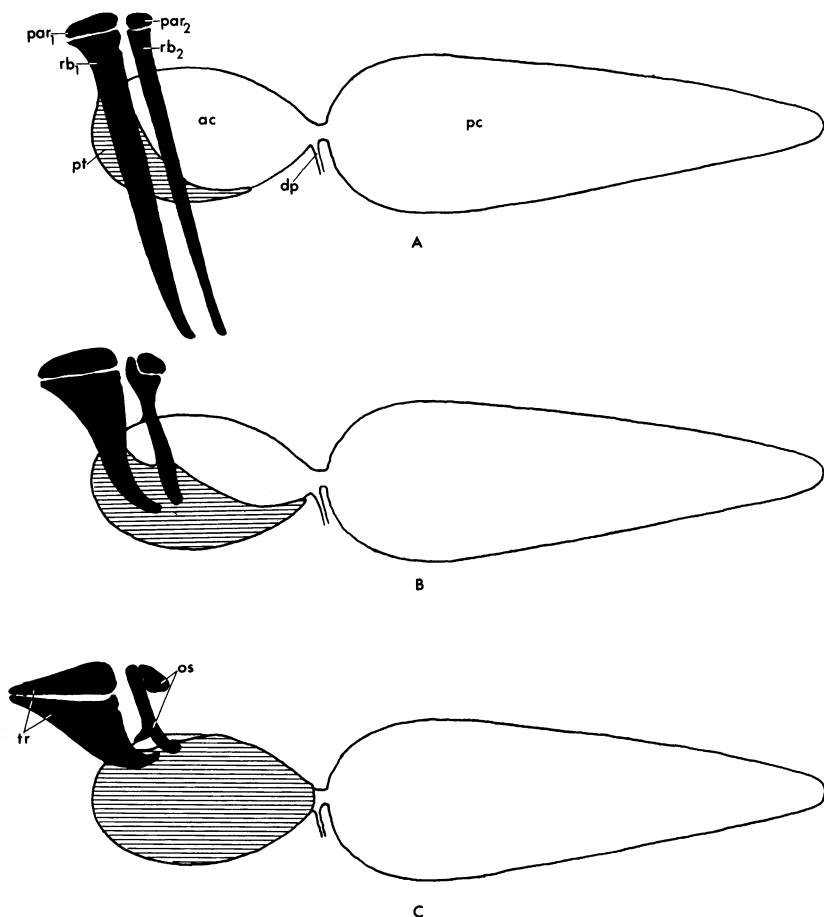


FIG. 4. Diagrammatic hypothetical evolutionary sequence of changes leading to the development, in C, of an ostariophysan tripus, os suspensorium, and peritoneal tunic around the anterior swimbladder chamber. A. Condition of the ribs and peritoneum as in *Chanos*. B. Hypothetical intermediate stage. Anterior to the left.

bony contact with the occipital region of the cranium, the larger of the two cephalic ribs actually touching the outer wall of the lagenar capsule (fig. 6). Posteriorly, the cephalic ribs are associated both with the upper part of the cleithrum and with superficial body musculature.

Although there might be a functional otophysic connection in *Chanos* involving the intervention of enlarged cephalic ribs, there is no real sign



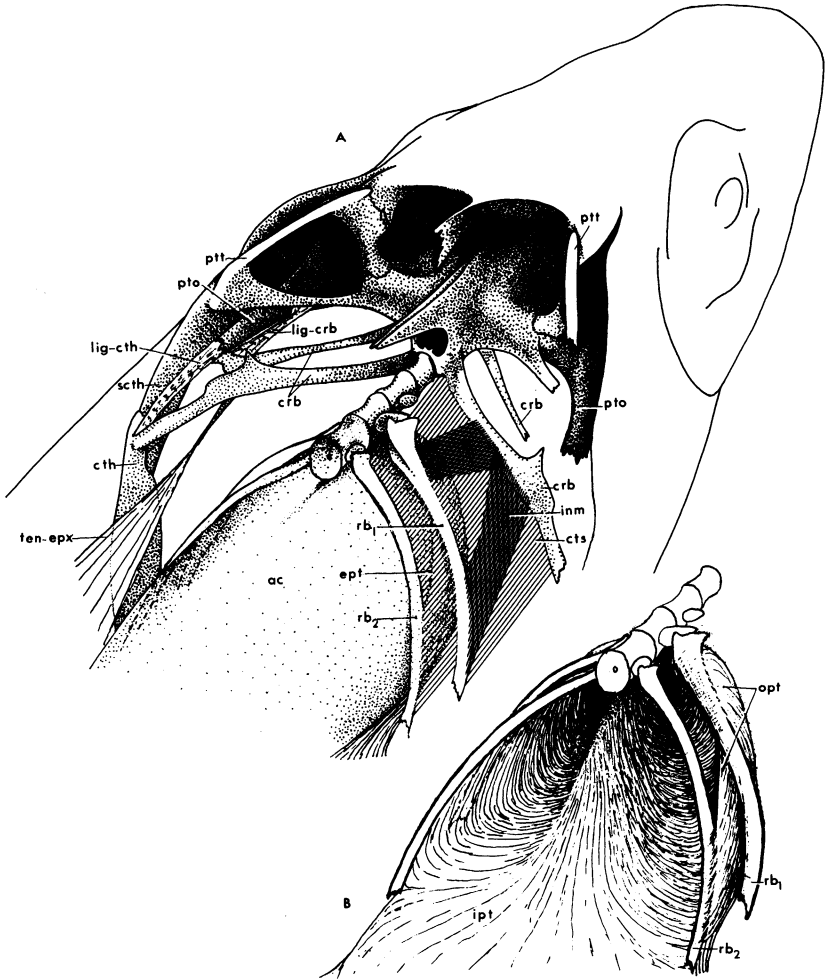


FIG. 5. The occipitocervical region in relation to the swimbladder in *Chanos*. Tip of supraoccipital crest, the right shoulder girdle, and distal ends of all elements on right side cut away. A. Occipitocervical region with swimbladder and with muscles and connective tissues associated with the cephalic and pleural ribs. B. Anterior vertebrae and pleural ribs, without swimbladder, but with peritoneal tunic in position.

of vertebral differentiation that would suggest a condition paralleling the development of Weberian ossicles. This view is contrary to the one expressed by Greenwood et al. (1966, p. 378). The neural arches and

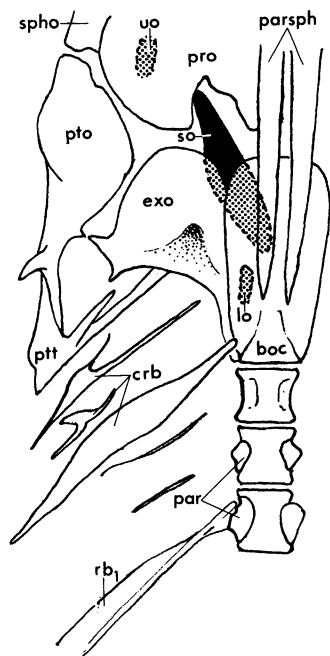


FIG. 6. Ventral view of occipitocervical region in *Chanos*, to show orientation of cephalic ribs and position of otoliths.

spines are, in fact, in a regularly graded series, slightly increasing in size posteriorly, whereas the supradorsal elements decrease in size antero-posteriorly; no prezygapophyses are developed on any neural arch in the series. Moreover, the anterior vertebral centra of *Chanos* appear to be more or less uniform in size and shape, each but the first bearing ventrally, excavations for autogenous parapophyses and, dorsally, excavations for the bases of the autogenous neural arches.

Whereas there are no apparent specializations in the vertebral centra of *Chanos*, there are other gonorynchiform fishes in which the anterior vertebrae do show some modification. For example, in *Gonorynchus* the neural spine of the first vertebra is greatly reduced, but the neural spines of the second and third vertebrae are expanded and platelike relative to the neural spines of the fourth and succeeding vertebrae (Greenwood et al., 1966, text-fig. 8). The centrum of the third vertebra is deeply excavated to receive the movably articulated first pleural rib. This rib has its posterior margin somewhat expanded and platelike. There are no pleural ribs associated with the first and second vertebrae. Neither are there epineural or epicentral intermuscular bones associated with these and the third vertebra. There are, however, peculiar, complex inter-

muscular bones associated with the expanded, ventrolateral margins of the first and second vertebrae. The usual complement of pleural, epipleural, and epineural intermuscular bones occurs on the fourth vertebra. As in *Chanos*, *Gonorynchus* has the first two ribs joined firmly to a dense peritoneal membrane.

The diverse specializations of the anterior vertebrae seen in gonorynchiforms are not known to occur in the generalized salmoniform fishes, namely, the salmonoids, osmeroids, and galaxioids, which possess essentially undifferentiated anterior vertebrae and pleural ribs that form a graded series anteroposteriorly. Furthermore, none of these salmoniform groups has the distinctive cephalic ribs of the gonorynchiforms, nor does any group of salmoniforms known to us have enlarged first pleural ribs, or an intimate association of pleural ribs with the swimbladder or with a specialized anterior peritoneal tunic.

The Gonorynchiformes, alone among the non-ostariophysan physostomous teleosts, possess a swimbladder divided by a distinct constriction into a small anterior and a much larger posterior chamber (fig. 7). We have examined the swimbladder in representatives of all gonorynchiform genera in which this organ is present, and find without exception, that the swimbladder is divided into two chambers. *Gonorynchus* is the only gonorynchiform fish lacking a swimbladder; nevertheless, as described, *Gonorynchus* has the first pleural rib enlarged and articulating in a complex manner with the third vertebra and has the first two ribs supporting a wall-like thickening of the peritoneum.

The over-all similarity between the gonorynchiform and ostariophysan swimbladder in orientation and form is shown in figures 7 and 8.

## EVOLUTION OF THE WEBERIAN APPARATUS

We hypothesize that the gonorynchiforms and ostariophysans are descended from an ancestor in which there was present an adipose fin, a caudal skeleton as in living gonorynchiforms (figs. 9–12), exoccipitals entering the floor of the foramen magnum (required for the development of the ostariophysan endolymphatic system) and participating with the basioccipital in the formation of the first vertebral contact with the occipital region of the cranium, an endolymphatic system as in living chanids (as opposed to the salmonid type; see figs. 13, 14), and numerous intermuscular bones, including cephalic ribs differentiated from the epineural and epicentral series. It is also probable that the hypothetical common ancestor of gonorynchiforms and ostariophysans had begun to differentiate the anterior part of the axial skeleton to some extent, especially in the enlargement of the first pleural rib, and to have had a



FIG. 7. Outline drawing of adult *Chanos chanos* (Forskaal) to show form and extent of swimbladder and position of ductus pneumaticus (arrow).

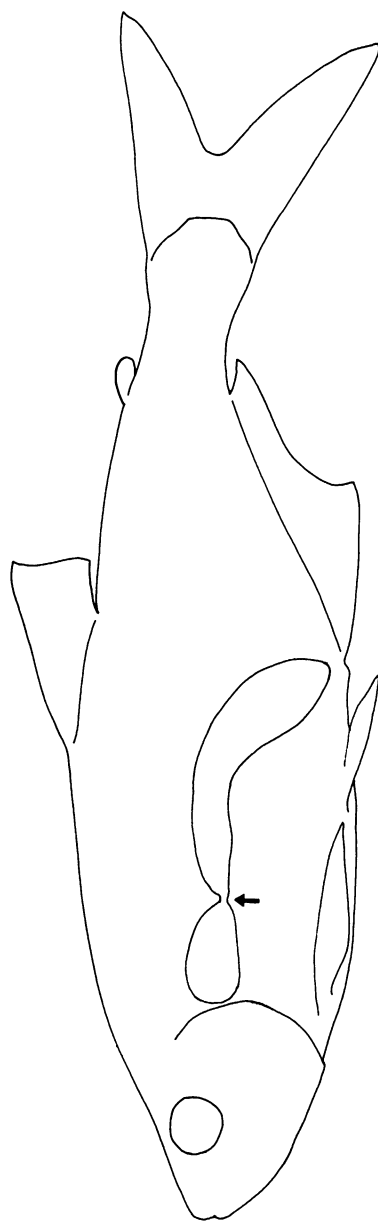


FIG. 8. Outline drawing of adult *Brycon guatemalensis* Regan to show form and extent of swimbladder and position of ductus pneumaticus (arrow).

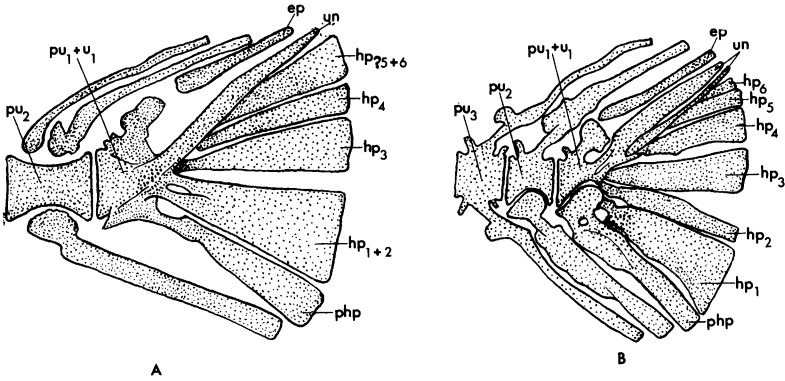


FIG. 9. Caudal fin skeletons. A. *Gonorynchus gonorynchus* (Linnaeus). B. *Chanos chanos* (Forsk.)

swimbladder divided into a small anterior and a larger posterior chamber, the division between the two being at the point of entry of the ductus pneumaticus. Finally, such an ancestor probably had already developed specializations of the labyrinth involving a posterior and medial shift of the sacculi and lagenae. In the ostariophysan lineage a connection was established between the right and left sacculi, thus providing the basis for the evolution of a sinus impar. Intermuscular bones were doubtless lost before, or in connection with, the evolution of the Weberian ossicles.

In the gonorynchiform lineage a different and relatively simple otophysic connection probably was established by hypertrophy and special-

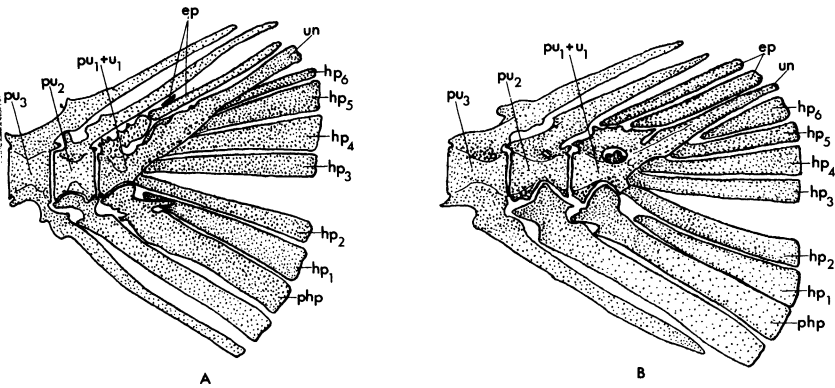


FIG. 10. Caudal fin skeletons. A. *Kneria wittei* Poll. B. *Parakneria* sp.

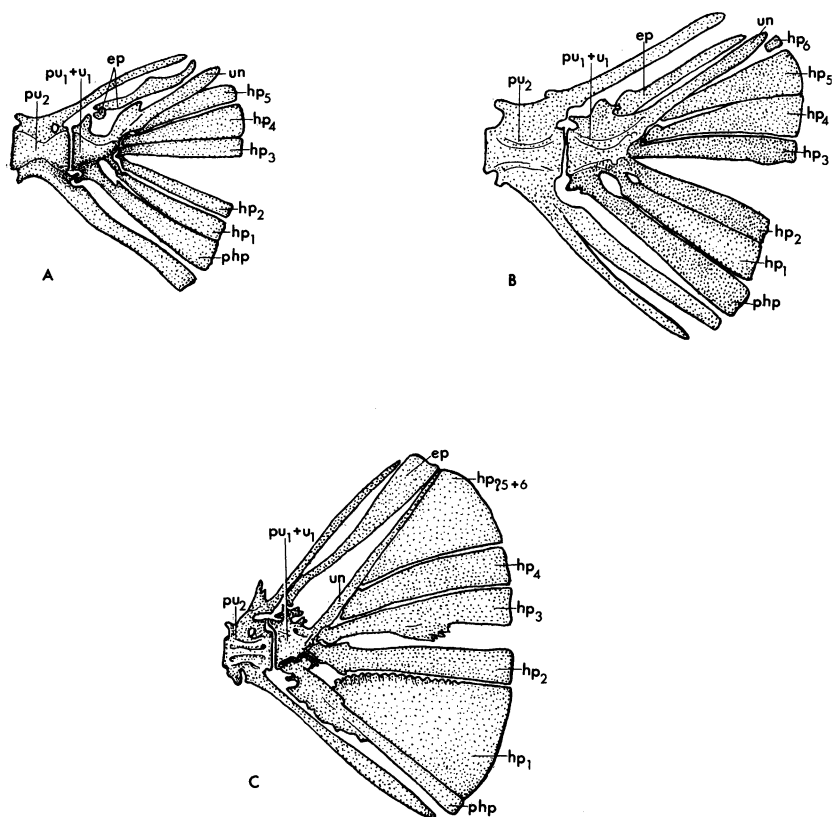


FIG. 11. Caudal fin skeletons. A. *Grasseichthys gabonensis* Géry. B. *Cromeria nilotica* Boulenger. C. *Phractolaemus ansorgii* Boulenger.

ization of the cephalic ribs—an evolutionary solution opposite to that which occurred in the ostariophysans. It is with the exoccipital portion of the lagenar capsule in gonorynchiforms that these modified intermuscular bones, or cephalic ribs, normally make contact (fig. 6). But there is no reason to believe that the initial enlargement and specialization of the cephalic ribs were concerned only with sound transmission. We note that the specialized cephalic ribs are in a position to serve also as a roof for the epibranchial chamber, as well as for effecting a union between the shoulder girdle and the occipitocervical region (fig. 5). Such contacts between the shoulder girdle and the occipitocervical region are both widespread and varied among fishes. There is no evidence to suggest which of these roles can be considered the original one or

even that all three may not have equal importance. As a means of sound transmission, the enlargement of the cephalic ribs appears to be less important than the contact of cephalic ribs with the otic, and in particular, the lagenar region. Because cephalic ribs inserting on the otic region are a feature common to various primitive teleostean lineages, the common ancestor of gonorynchiforms and ostariophysans would also probably have had them present. An ancestor of these two groups might also have shown some enlargement of the lagenar otolith and an elongation and narrowing of the saccular otolith (fig. 14A). It is significant that

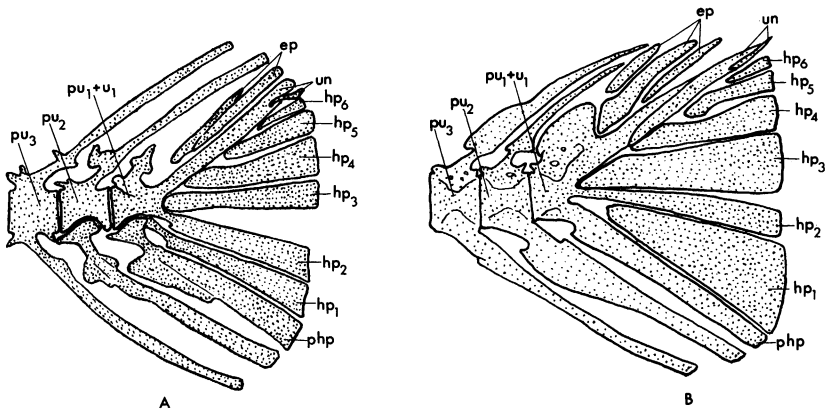


FIG. 12. Caudal fin skeletons. A. *Barbus kersteni* Peters. B. *Brycon meeki* Eigenmann and Hildebrand, after Weitzman (1962).

the lagenar otolith of juvenile and adult *Chanos* is relatively large as compared with the more usual teleostean condition exemplified by *Salmo* (figs. 13, 14). In the labyrinth of the juvenile *Brycon* examined in this study, the lagenar and saccular otoliths had not yet attained their adult configurations, but the saccular otolith was still the larger of the two and both were proportionally very similar to these otoliths of *Chanos* (fig. 15).

For a consideration of the evolution of the Weberian apparatus from the anterior vertebral elements, special note must be taken of the ligaments that join together the parts of the vertebral column in such little-modified animals as *Chanos* and *Salmo* (fig. 16). There are three principal series of ligaments: dorsally, those extending obliquely upward between neural arch and neural spine components, the oblique interneural ligaments; ventrally, those which extend dorsally from the head of a pleural rib and parapophysis to the base of a neural arch, the neuro-parapo-

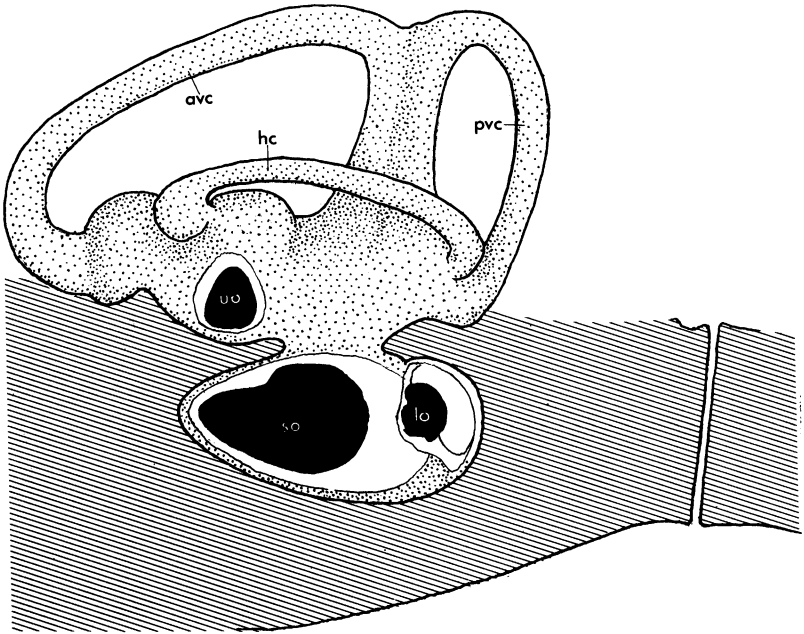


FIG. 13. Left membranous labyrinth of *Salvelinus fontinalis* (Mitchell). Anterior to left.

physeal ligaments; and more ventrally, those which extend obliquely between the pleural ribs in a generally upward direction anteriorly, the intercostal ligaments. Proceeding from the analysis of the parts of the Weberian apparatus given above, it is possible to suggest homologies for the various ligaments associated with the fully formed Weberian ossicles. It is proposed in figure 16 that the scaphium is attached to the occipital region of the cranium by connective tissues homologous with a modified oblique interneural ligament, and the claustrum to the scaphium by some part of this ligamentous bed. Each intercalarium, which is a remnant of the prezygapophysis and neural arch of the second vertebra, would then be attached to the scaphium of its side by the oblique interneural ligament that normally extends between the first and second neural arches. Posteriorly, the intercalarium is attached to the tripus by a very dense, elongate ligament comparable with the oblique interneural ligament that extends between the second and third neural arches and spines combined with the neuro-parapophyseal ligament that would normally connect the parapophysis and neural arch of the third vertebra. Evidence that the tripus-intercalarium ligament is



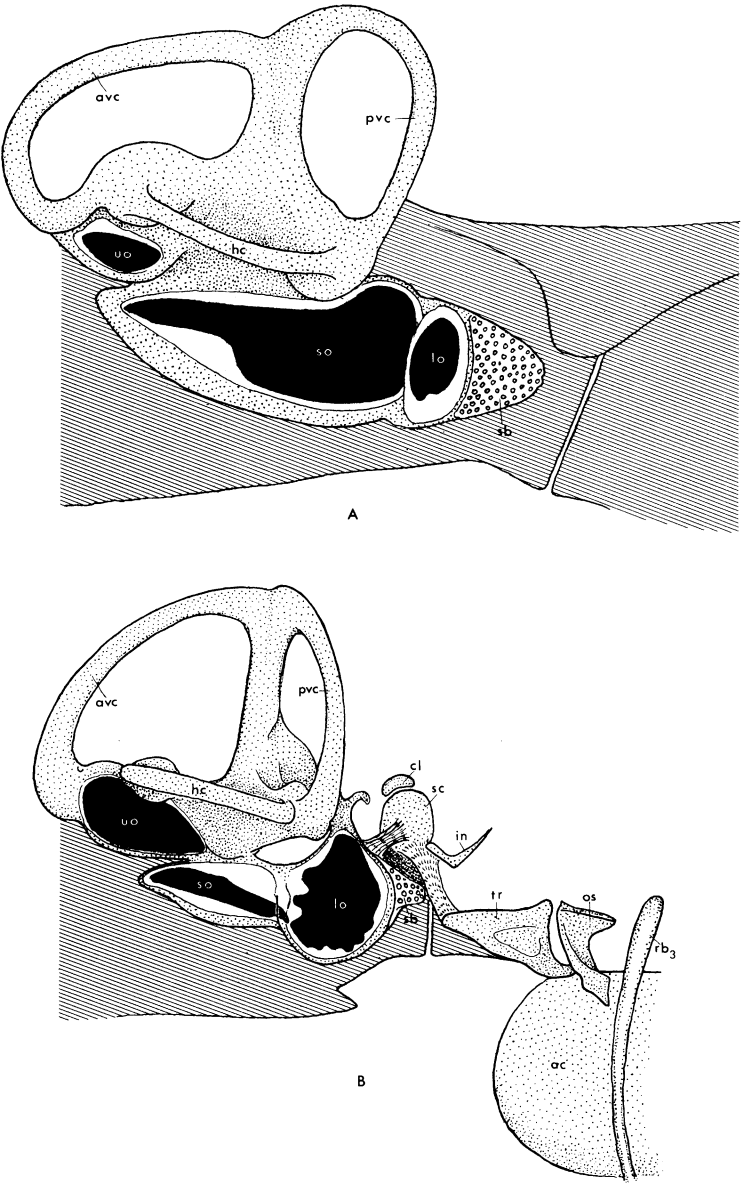


FIG. 14. Left membranous labyrinth in: A. *Chanos chanos* (Forskaal). B. Left membranous labyrinth, Weberian ossicles, first unmodified rib and anterior margin of swimbladder in *Brycon guatemalensis* Regan. Anterior to left.

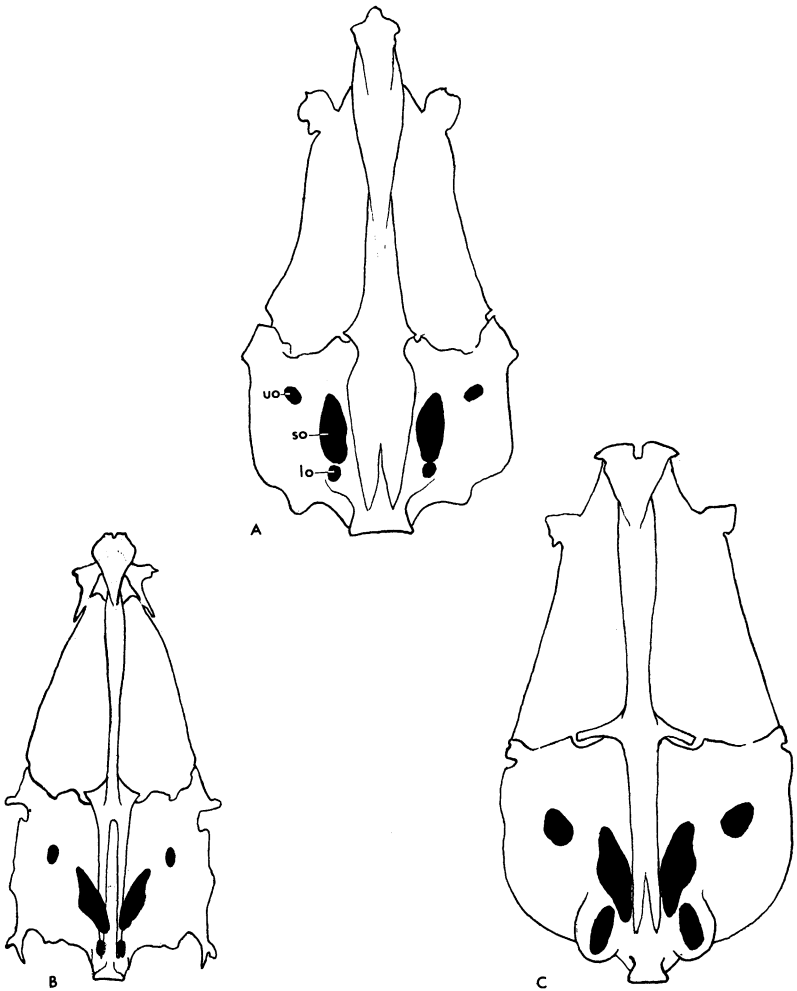


FIG. 15. Outlines of basicrania to show size, shape, and orientation of otoliths in ventral view. A. *Salmo mykiss* Walbaum (fingerling). B. *Chanos chanos* (Forskaal) (half-grown). C. *Brycon* sp. (juvenile, 9 mm. standard length, from Bolivia).

compound, combining neuroparapophyseal and interneural ligaments, is provided by the structure of the neural arch and spine on the third vertebra in the juvenile *Brycon* discussed above. That neural arch and spine are of exceedingly irregular and excavated shape (fig. 1), with the principal excavation being proximal and anterior on the neural arch and

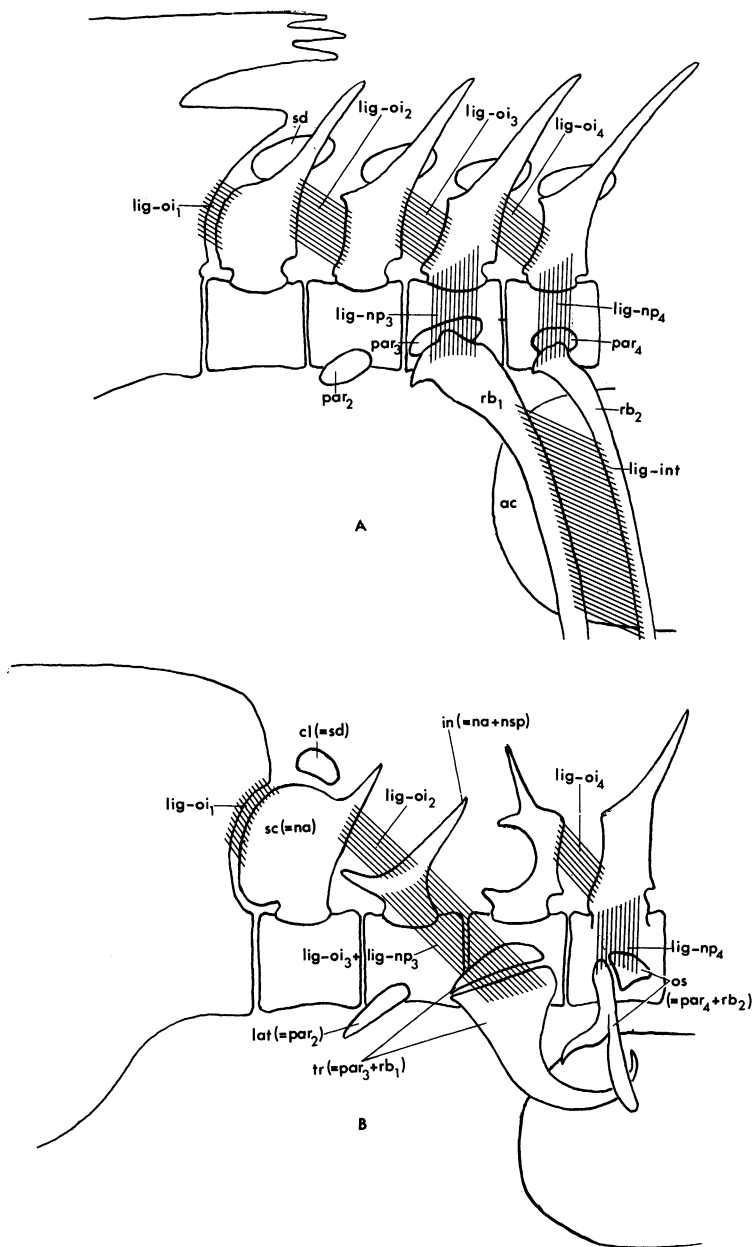


FIG. 16. Diagram to explain hypothesis for homologizing ligaments of occipitocervical region of: A. *Chanos*. B. *Brycon*. See text for explanation.

spine in approximately the position where one would expect the oblique interneural ligament to arise. The irregular growth-form of the neural arch and spine of the third vertebra might well have resulted from the loss of its ligament to the intercalarium-tripus system and the consequent loss of guiding forces during development.

We are unable, of course, to identify with any assurance the selectional and ontogenetic forces responsible for the coordinated changes leading from typical vertebral elements to the assortment of reduced and hypertrophied elements that compose the functional Weberian apparatus. It is evident that many of these changes are reductional, involving the partial or complete suppression of development of some structures and the fusion of others. The principal case of hypertrophy involves the head of the first pleural rib in the formation of the tripus, whereas the intercalarium provides the best example of extreme reduction. Figure 4 summarizes our ideas on the phylogenetic origin of the principal parts of the Weberian apparatus and is, of course, based on the inference that a *Chanos*-like condition of the anterior pleural ribs and swimbladder was present in the ancestor of the ostariophysans. By a gradual shortening of the shafts of the ribs, the dense peritoneal membrane associated with these ribs was drawn upward around the anterior chamber of the swimbladder to form a peritoneal tunic (see above, pp. 6-7, and also Chranilov, 1929, fig. 1). The ribs remained associated with the peritoneal tunic as the tripus and os suspensorium. Because the tips of the shortened first ribs did not actually come together in the midline, the peritoneal tunic did not completely cover the anterior swimbladder chamber dorsally. A small opening remained in the anterior dorsal midline, a slit that characterizes the swimbladder of characoid and cyprinoid fishes (Alexander, 1964, p. 421). The shortening of the first two ribs may have been induced either by an initial tendency of the peritoneum to become adherent to the swimbladder or by an alteration of the ontogenetic environment of the ribs that impeded osteogenesis. The growth outward of the parapophyses of the second vertebra to form elongate lateral processes has the effect of holding the walls of the paravertebral sac away from the midline, and this specialization alone may have been sufficient to affect rib development. What caused the hypertrophy of the parapophyses on the second vertebra is a question that might one day be answered, but we can now at least suggest experiments to test the hypothesis that ectopic rib material should not develop fully in the site of the tripus, and that a presumptive tripus should develop into a normal rib ectopically. Appropriate experimental procedures have already proved feasible in a study by Rosen and Kallman (1959) of the metamorphosis

of the anal fin and its suspension into the gonopodial system of the adult male poeciliid, a study that required the transplantation of developing interhaemal and interneural bones from one part of the fish to another. We have noted that some juvenile characids still have no sign of a developing Weberian apparatus at an experimentally manageable size. For example, in *Poecilibrycon harrisoni* Eigenmann of 7.0 mm. standard length, pleural ribs represented only as dense, hyaline connective tissue in the myosepta are present on all abdominal vertebrae.

### GENERAL CONCLUSIONS

Greenwood et al. (1966) concluded that the two principal lines of evidence suggesting relationship of the ostariophysans and gonorynchiforms are (1) the details of the caudal skeleton, and (2) an otophysic connection in gonorynchiforms functionally comparable, in a broad sense, with the Weberian apparatus of ostariophysans. We still have confidence in the importance of the caudal skeleton as an indicator of this affinity, but disagree that the details of the gonorynchiform "otophysic connection," as then conceived, have great phylogenetic importance. In our earlier publication (Greenwood et al., 1966) we attributed special significance to the highly-developed cephalic ribs in some chanoids as parts of a sound-conducting apparatus. The results of the present study conflict with this simplistic view, and suggest rather that the enlarged cephalic ribs, especially in *Chanos*, may subserve several functions, one of which might be a covering for the posterior chamber of the pharyngeal apparatus, which includes a large epibranchial organ. If the specialized cephalic ribs have developed somehow in response, or in relation, to an epibranchial organ, we are forced to note that such an organ is not widespread among ostariophysans, and that its sparse occurrence does not include any of the most generalized characoids (see Nelson, 1967). Moreover, present evidence on the homologies of the parts of the Weberian apparatus does not involve either the necessity for, or even the presence of, cephalic ribs. It is a cogent fact that no ostariophysan has ever been found to possess a cephalic rib or structure that could reasonably be homologized with one. Instead, what now appears to be crucial is the capability of the gonorynchiform genome for elaborating (1) specialized cervical vertebrae (in *Gonorynchus*) and an enlarged and movable first pleural rib, (2) a reinforced anterior peritoneal wall, supported by the first two pleural ribs, on which the swimbladder impinges (in chanids and kneriids), and (3) a variety of other lesser cervical and occipital specializations that collectively define a trend toward the ostariophysan condition (see pp. 6-7). These attributes provide a basis for pro-

posing an alignment of the gonorynchiforms with the ostariophysans, and the proposal is strengthened by other similarities between the two groups of fishes as discussed both here and elsewhere. The supporting evidence includes the already noted caudal skeleton anatomy, the presence in both groups of fright cells and fright substance, the latter having an experimentally verified functional specificity between members of these groups (Pfeiffer, 1967a, 1967b), a similarly chambered swimbladder in chanoids, in characoids, and cyprinoids, nuptial tubercles in gonorynchiforms and ostariophysans that are histologically distinctive (Wiley and Collette, In press), and a remarkable parallelism in the development of a specialized protrusile mouth in the chanoid *Phractolaemus* and in the characoid *Bivibranchia* (Géry, 1963).

The assembled evidence of homology and parallelism warrants the hypothesis that the gonorynchiforms and the ostariophysans are sister groups. If they are so related, then both groups must be very old, because gonorynchiforms have a fossil record extending into the Upper Cretaceous (Patterson, 1967). The Cretaceous form is a gonorynchid, little different from modern ones, so that a common ancestor of the two groups may be much older still. Unmistakably ostariophysan fossils extend only to the Lower Paleocene (Patterson, 1967).

In our recent classification, the gonorynchiforms are included as an order of the Protacanthopterygii, and the cypriniforms and siluriforms as orders of the superorder Ostariophysi. The Protacanthopterygii would now be a paraphyletic category if our current hypothesis is valid. As the objectives of a phylogenetic classification are not met by maintaining a paraphyletic group (Hennig, 1966, p. 146), the transfer of the Gonorynchiformes from the Protacanthopterygii to the Ostariophysi is recommended. The taxonomic problem resulting from this reallocation was anticipated by Rosen and Patterson (1969): "If . . . the strongest evidence warranted the inclusion of the Gonorynchiformes in the superorder Ostariophysi, there would be no way, in the present hierarchical scheme [i.e., in the classification of Greenwood et al.], of distinguishing the gonorynchiforms from the obviously more closely related cypriniforms and siluriforms. The difficulty lies in the absence of, and in . . . the obvious need for, a collecting category of some sort between the order and superorder . . . The solution to the dilemma seems to . . . lie in the establishment of a descriptive, intermediate category without formal rank, . . . the neutral term 'series.'" An alternative to this solution is the downgrading of the ostariophysans to their former rank as a single order. In so reducing them, however, maintenance of the probably correct phyletic separation of the cyprinoids and characoids from the siluroids

would require either a similar downgrading by one hierarchical step of all ostariophysan groups or the creation of still another informal category at the infraordinal level. Rather than introduce, at this time, yet another higher category into teleostean classification, we elect to use the series concept, as follows:

Superorder Ostariophysi

Series Anotophysi, new name

Order Gonorynchiformes

Suborder Chanoidei

Suborder Gonorynchoidei

Series Otophysi, Garstang (1931)<sup>1</sup>

Order Cypriniformes

Suborder Characoidei<sup>2</sup>

Superfamily Characoidea

Superfamily Gymnotoidea

Suborder Cyprinoidei

Order Siluriformes

## ACKNOWLEDGMENTS

The specimens of *Brycon* on which this study is largely based were collected by Dr. Sydney Anderson, Department of Mammalogy, the American Museum of Natural History, on the American Museum-Bolivian Expedition of 1965, supported by Grant No. DA-MD-49-193-63-G82 of the United States Army Medical Research and Development Command, Office of the Surgeon General, and by the National Geographic Society. Additional characid material was supplied by Dr. Stanley H. Weitzman, Division of Fishes, the United States National Museum, Smithsonian Institution. We are grateful to Dr. Weitzman for his discussions of the work in progress and to Dr. Colin Patterson, Department of Palaeontology, British Museum (Natural History), and Dr. Gareth J. Nelson, Department of Ichthyology, the American Museum of Natural History, for their comments on the typescript. Mrs. Norma Rothman kindly prepared histological sections and Mrs. Avis Rumney helped in the final stages of preparation of the illustrations. The work was supported by a National Science Foundation Grant No. GB-5335 to Rosen.

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<sup>1</sup> The name Otophysi was coined by Garstang (1931) to include fishes with an otophysic connection, but the term has remained unused since that time.

<sup>2</sup> As it is generally accepted that the characoids and gymnotoids had a common ancestry, their relationships to the cyprinoids are better expressed as given here than as treated by Greenwood et al. (1966, pp. 395-396).

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