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Abstract. The apparatus in the adult *Pantosteus plebius* Baird and Girard, the Rio Grande mountain sucker, is complex, particularly so in the modification of the anterior vertebrae. The Weberian ossicles are derived from components of the anterior three vertebrae and from independent connective tissue ossifications. Development is rapid, with the rudiments appearing when the fish are approximately 9 mm. long, and the ossicles reach their mature shape at about the 12 mm. stage.

The Weberian apparatus is characteristic of the largest order of freshwater fishes, the Ostariophysi, a group which includes the suckers, family Catostomidae. The apparatus of the catostomids is complex because of the extreme modification of the anterior vertebrae. The species studied, *Pantosteus plebius* Baird and Girard, is commonly referred to as the Rio Grande mountain sucker and is found only in the mountain streams of the Rio Grande and Mimbres River basins (Koster, 1957).

The Weberian apparatus in the adult *P. plebius* consists of a movable portion, the *pars auditum* or Weberian ossicles and a support, the *pars sustentaculum.*

The *pars auditum* (Figure 1) is composed of four small bones or ossicles and an interossicular ligament. The most anteriorly located ossicles, the *claustrum* and the *scaphium,* form the connection of the Weberian apparatus to the internal ear. The interossicular ligament links the scaphium with the intermediately located bone, the *intercalarium,* and with the most posterior bone, the *tripus,* which is connected with the anterior wall of the air bladder or swim bladder.

The *tripus,* the largest of the ossicles, is a sickle-shaped bone, whose body or main portion has three processes or rami. The articular process extends laterally from the body of the tripus to the centrum of the third vertebra. The medial end of this process is flared and fits into a deep groove that runs vertically across the lateral side of the centrum. The posterior process or ramus extends from the body to the air bladder where it tapers into a thin, delicate extension that is embedded in the *tunica externa* of the air bladder. This slender prolongation of the posterior ramus is the transforma-

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tor process. It passes through the tissue of the air bladder and curves sufficiently so that its tip projects forward out of the tunica externa. The anterior process or ramus extends forward from the body of the tripus and is united with the other bones of the series by the interossicular ligament.

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

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

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

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

The connection between the Weberian ossicles and the ear is formed by the *scaphium* and the *claustrum* and the *atrium sinus impar*. The scaphium forms a lateral part and the claustrum a dorsolateral part of the wall of the sinus, which is an extension of the perilymph spaces of the ear.

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

The *pars sustentaculum* (Figures 2-6) includes the first four vertebrae, all of which are highly modified from the pattern of the remaining trunk vertebrae. The centra of the second, third, and fourth vertebrae are fused. The supradorsal or neural spine elements of these three vertebra form a large, continuous neural spine that is the most dorsal portion of the pars sustentaculum. The distal ends of the second and fourth ribs are joined.

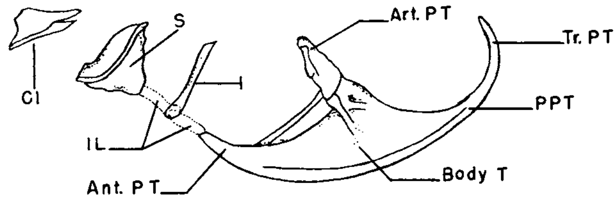

Fig. 1

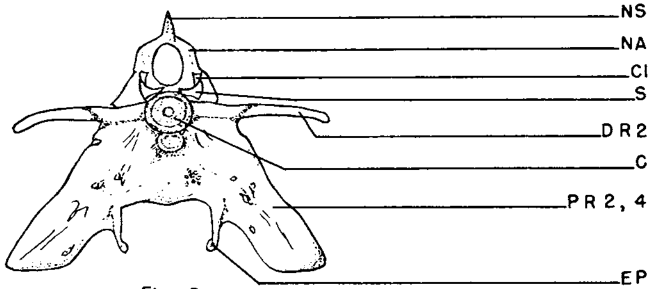

Fig. 2

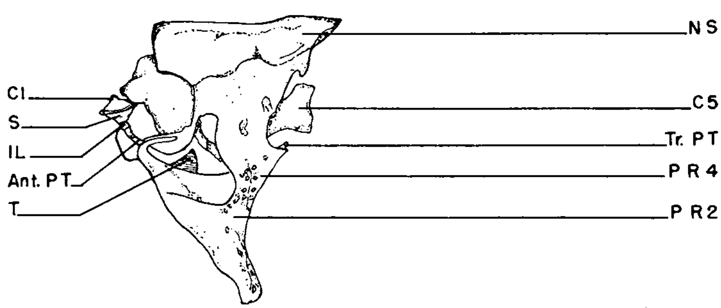

Fig. 3

Figure 1. Dissected Weberian ossicles. *Cl*, claustrum; *S*, scaphium; *I*, intercalarium; *IL*, interossicular ligament; *Ant. PT*, anterior process of the tripus; *Art. PT*, articular process of the tripus; *Body T*, body of the tripus; *PPT*, posterior process of the tripus; *Tr. PT*, transformator process of the tripus.

Figure 2. Anterior view of the Weberian apparatus. *NS*, neural spine; *NA*, neural arch; *DR 2*, dorsal rib of the second vertebra; *C*, centrum; *PR 2, 4*, pleural ribs of the second and fourth vertebrae; *EP*, esophageal process.

Figure 3. Lateral view. *C 5*, centrum of the fifth vertebra.

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

The centrum of the second vertebra bears two processes. A trans-

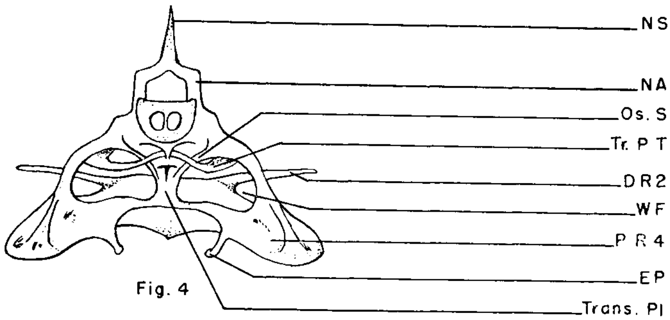

Fig. 4

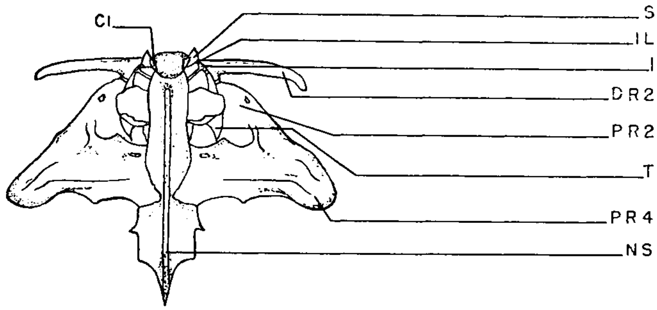

Fig. 5

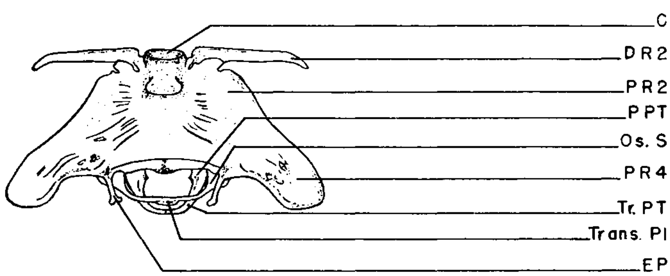

Fig. 6

Figure 4. Posterior view. *Os. S.* os suspensorium; *WF,* Weberian fenestra; *Trans. Pl,* transverse plate.
Figure 5. Dorsal view.
Figure 6. Ventral view.

verse process, which represents a modified dorsal rib (Watson, 1939) is directed laterally and slightly posteriorly (Figures 5 and 6), while a heavy, plate-like process, which represents a strongly modified ventral rib (Watson, 1939), extends ventrally and caudally and fuses with the similarly modified rib of the fourth vertebra. The two ventral ribs of the second vertebra also fuse with one another beneath the centrum. The plate thus formed has a pair of posteriorly directed projections that are termed esophageal processes (Figure 2) because of their proximity to the lateral walls of the esophagus.

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

The fourth vertebra possesses a single, much enlarged rib that passes ventrally and forms, by its fusion with the ventral rib of the second vertebra, a complex structure that lies in contact with the anterior wall of the air bladder. Between the angle formed by the two ribs and the centra of the second, third, and fourth vertebrae, there remains an opening, the Weberian fenestra, through which the *tripus* passes. The ventral ribs of the fourth vertebra give off at their bases the *ossa suspensoria,* which together form a transverse plate (Figures 4 and 6). The *tunica externa* of the air bladder is continuous with this plate.

The initial description of the apparatus was by Weber (1820). Three works dealing with the morphology of the Weberian apparatus treat with the Catostomidae. Adams (1928) described the apparatus in *Ictiobus urus.* Krumholz (1943) studied the apparatus of North American ostariophysines including eleven catostomids. Nelson (1948) compared the Weberian structures in catostomids with reference to their significance in systematics. The most recent embryological study is that of J. M. Watson (1939) wherein he compared the development of the ossicles as seen in the goldfish with that described by previous authors.

The Weberian apparatus of the family Catostomidae has had relatively little attention other than the paper by Nelson (1948) which deals with morphology and systematics. The development of the apparatus in the catostomids apparently has not been studied previously, and this paper attempts to describe the origins of the Weberian ossicles and to trace the developmental path of the apparatus to its mature condition.

Materials and Methods

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

Transverse, frontal, and sagittal sections of larval fish were prepared by standard histological techniques. Methylene blue and alizarin stains yielded the best tissue differentiation. Small specimens cleared in xylene and viewed whole showed the apparatus distinctly. Skeletons of adult fish were prepared by dipping the specimens into boiling water and removing the softened flesh or by clearing the flesh with potassium hydroxide and staining the bone with alizarin. Development was traced from the adult condition, through successively younger stages, to the earliest recognizable beginnings of the Weberian apparatus. (Figures 7, 8, 9, and 10.)

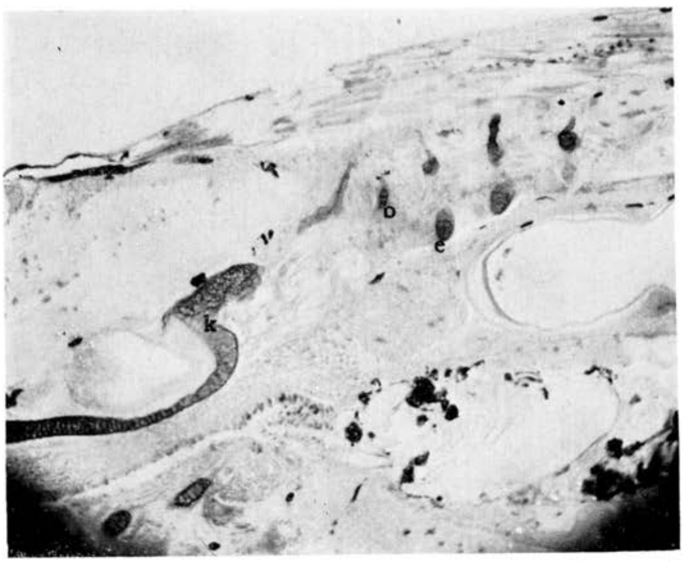

Figure 7. Photomicrograph of *Pantosteus* embryo at stage 1. (Sagittal) *b*, second basidorsal; *e*, third basiventral; *k*, skull.

Development of the Apparatus

The Weberian ossicles of *Pantosteus* are formed both from modified vertebral arch components and from other connective tissue elements. The arcualia of the vertebrae are cartilaginous and de-

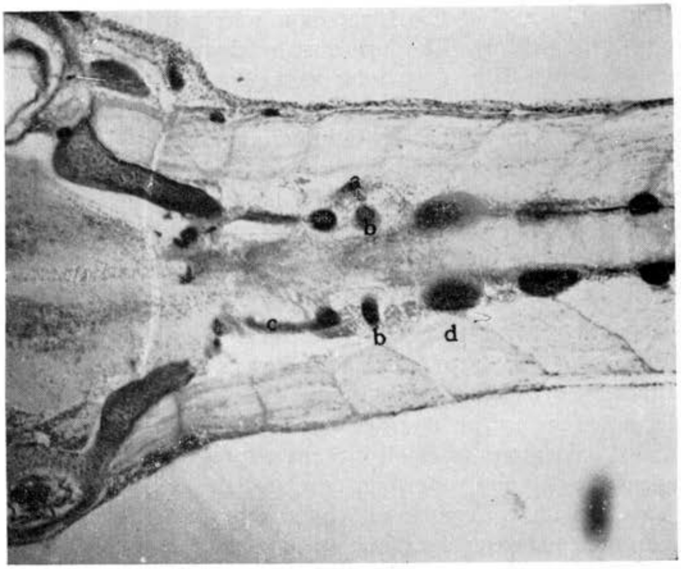

Figure 8. Stage 2. (Frontal) *a*, manubrium incudis rudiment; *b*, second basidorsal; *c*, rudiment of concha stapedis; *d*, third basidorsal.

Figure 9. Stage 4. (Sagital) *f*, scaphium; *g*, interossicular ligament; *h*, manubrium incudis of intercalarium; *i*, anterior process of the tripus.

velop first at the anterior end of the vertebral column and develop posteriorly in regular sequence except for the first and second vertebrae where basiventrals do not occur. Vertebral elements are the chief or sole contributors to the *scaphium*, *intercalarium* and *tripus*.

The *claustrum* is derived from mesenchyme and does not pass through a cartilaginous stage.

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

1. First appearance of the arcualia of the vertebrae as groups of cartilage cells lying alongside the notochord.
2. Arcualia and connective tissue elements present in position of future ossicles.
3. Fusion of the elements of each ossicle.
4. Ossicles assume mature shape.
5. Ossification of ossicles complete.

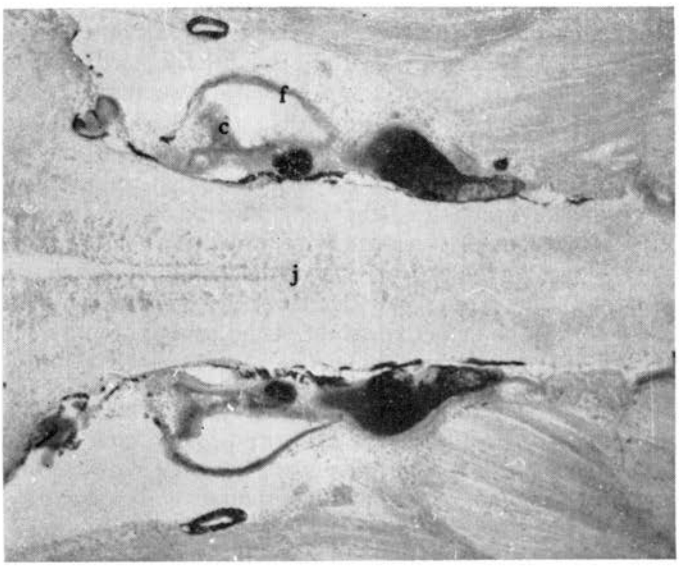

Figure 10. Stage 5 (Frontal) *c*, claustrum; *f*, scaphium; *j*, spinal cord.

Tripus. The *tripus*, which is the most complex of the ossicles in its beginning, has a threefold origin. The major portion of the bone is contributed by the basiventral of the third vertebra. The basiventral first appears at 9 mm. The articular process, body, and much of the anterior and posterior processes form from this beginning. The distal portion of the anterior process is formed by ossification within the interossicular ligament. The transformator process and the more caudal portion of the posterior ramus share as their rudiment a mass of cartilage in the position of the dorsal rib of the third vertebra. The anterior and posterior processes and the transformator rudiment are visible at about 9.5 mm. By the 10 mm. stage the various elements have fused into a single, arch-shaped structure. Stage 5 has been reached by 15 mm., although the articular process remains cartilaginous through 30 mm.

Intercalarium. As in other Ostariophysi, the shaft of the *intercalarium* of *Pantosteus* arises from the basidorsal of the second vertebra, and, in agreement with Watson's (1939) finding in the goldfish, a small island of bone in the interossicular ligament forms the *manubrium incudis*. The two elements are distinct at 9.5 mm., but at 10 mm. are completely fused. The shaft of the bone has ossified by the 11 mm. stage.

Scaphium. Contrary to the results of other authors working upon different groups, the *scaphium* of *Pantosteus* has but a single definite rudiment, the basidorsal of the first vertebra. At the earliest stage at which a rudiment can be detected, there is a rod of cartilage consisting of only a few cells, which projects anteriorly from the basidorsal. As seen in sagittal sections, the cartilaginous rod and the basidorsal proper make an L-shaped structure of cartilage. It is directed obliquely, dorso-anteriorly, from the horizontal plane, and as it falls in the same plane as do the walls of the *concha stapedis* in older specimens, we may conclude that the cartilaginous rod is the beginning of this structure. The rod is present within a densely arranged mass of mesenchyme which no doubt contributes to the substance of the ossicle. The history of the scaphium begins in the 9 mm. stage when a few cartilage cells are seen lying next to the notochord. The definitive aspect of the bone is seen by 11 mm. and stage 5 is reached by 15 mm.

Claustrum. The *claustrum,* smallest of the ossicles, also has a single origin. In *Pantosteus* the claustrum forms from an ossification of mesenchyme in the position of the *saccus paravertebralis,* the sheath that surrounds the anterior vertebrae and separates them from the musculature. The bone develops later than the others. The rudiment cannot be detected until 10 mm. while a fully developed claustrum is not present until 12 mm.

Interossicular Ligament. During the time when the ossicles are taking form, the interossicular ligament, which connects the *scaphium, intercalarium,* and *tripus,* makes its appearance. Dense mesenchyme is present in the future position of the ligament by 9.5 mm., and the fibrous nature of the ligament is clear in sections of 10 mm. fish.

Pars Sustentaculum. The only representative of the vertebral column in *Pantosteus* of 8 mm. and younger stages is the notochord. The arcualia first appear around the notochord at 9 mm. The supporting parts of the apparatus appear at the same time as do the ossicles and by 12 mm. are completely formed in cartilage.

The spinal canal in the region of the first vertebra is roofed over by an arch, the so-called "ring of cartilage." This ring is not visible in sections until the ossicles are completely formed. In fish of 12 mm. it is visible above the spinal cord as an extension of the cranium, and by 20 mm. the ring extends posteriorly to the junction of the first and second centra. The more lateral parts of the area normally occupied by the first neural arch are formed by the *claustra,* which are mostly posterior to the ring in sections of 10 mm. to 12 mm. fish.

Discussion

Three general theories of the origin and development of the Weberian apparatus have been proposed. Weber (1820) believed the ossicles to be homologous with the mammalian ear bones. The traditional belief is that they represent modified portions of the first three vertebrae, and the more recent studies indicate that connective tissue ossifications supplement the vertebral rudiments. The results of this study are in accord with the last theory.

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

All three of the origins of the *tripus* have been disputed. Krumholz (1943) concluded that the tripus articulated with the second vertebra. It is the third basiventral that contributes the articular process, and therefore, it is the third vertebra with which the tripus articulates. The transformator process has been called an ossification in the *tunica externa* of the air bladder (Wright, 1884), or this plus the dorsal rib of the third vertebra (Watson, 1939). The process arises at the junction of the third myoseptum with the horizontal skeletogenous septum, the normal position of a dorsal rib. Since the third vertebra in the adult bears no ribs, we may conclude that part of the tranformator process represents the third dorsal rib. Watson (1939) believed the anterior process of the tripus to be lengthened by ossification in the interossicular ligament, a process that is also seen in *Pantosteus.*

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

The modified ventral process of the fourth vertebra has had a complex history of suggested homologues. The process has been termed a haemal process (Adams, 1928), a transverse process (Wright, 1884), and a pleural or ventral rib (Watson, 1939). Because the modified ventral process articulates with the centrum in the fashion typical of a pleural rib (Goodrich, 1939), one may conclude that the process represents a pleural rib.

The ventral rib of the second vertebra, like that of the fourth, is clearly homologous with the pleural rib of a trunk vertebra.

The *ossa suspensoria* occupy the positions of hemopophyses, and are so termed by Watson (1939). However, even during development, the os suspensorium is never distinct from the fourth pleural rib.

The esophageal processes are mentioned only by Mateviev (1929) and Nelson (1948) and are difficult to determine as to their homology. The processes arise from the second pleural ribs. As the plate formed by the two second pleural ribs is uninterrupted, it is possible that the esophageal processes represent extensions of the hemopophyses incorporated into the flat plate. It is also possible that in many ostariophysines the esophageal processes have no homologues but have evolved separately in those groups which possess a very complex *pars sustentaculum*.

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