MODIFICATIONS AND ASSOCIATED STRUCTURES OF THE FIRST THREE VERTEBRAE IN THE BUFFALO FISH ICTIOBUS URUS.*

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There is a very striking modification of the first three vertebrae in the Cyprinodont fishes, correlated with the swim-bladder and also with the Weberian ossicles, a small chain of bones connected with a hydrostatic function. The modification consists of a great enlargement of the parts of the vertebrae to form a large neural spine region, the Weberian ossicles, a very large and specialized haemal rib structure which supplies a support for the ossicles, cavities for the blood vessels and an anterior base for the swim-bladder. These parts of the vertebrae have been so modified that it has been necessary to study their embryological development to determine their exact homologies, and in some cases, there is still doubt as to their exact origin. This modification of the vertebrae and the development of the ossicles is characteristic of the Cyprinodont fishes, occurring in no other group. Hydrostatic organs exist in other fishes, but they function in a different way and without the aid of special skeletal changes.

The first vertebra is not greatly modified except in the antero-posterior compression of the centrum, which makes this part thin and disc like. A long, thin process extends out from the centrum, paralleling and closely appressed to a similar structure from the second vertebra. The dorsal fact of the centrum is marked by two deep pits that serve as articulations for the ventrally projecting processes of scaphium, the second Weberian ossicle. (Figs. 1, 3 and 4.)

The first vertebra has neural arches but no development of a neural spine. The claustrum, the first Weberian ossicle, is articulated with the antero-ventral face of the neural arch, while the antero-dorsal face articulates with the skull.

The second vertebra is much more modified than the first, with a large neural spine, a strong lateral process and

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highly specialized haemal process and spine. The neural arch projects anteriorly and supports the neural arch of the first, while the neural spine is much enlarged, heavy and broad at the base with a greatly expanded neural spine that is as long as the centra of the three vertebrae. The principal function of this spine is in supplying surface for the muscles. The haemal process is broad and long with a strong attachment to the centrum. This process joins a similar process from the third vertebra to form the expanded haemal structure. A transverse process extends out laterally, paralleling a similar process from the first vertebra. The neural arch supplies the principal articulation for the neural arch of the first vertebra and at its anterior region, supplies an articulation for the third Weberian ossicle, the intercalarium. (See Figs. 3 and 4.) The lateral surface of the centra of both the second and the third vertebra, serve as an articulation for tripus, the fourth ossicle which works on these centra, using them as a fulcrum.

The third vertebra is marked by a long spine from the neural arch, which is pushed posteriorly by the spine of the second. The neural arch is wide but the spine is thin, narrow and closely joined to the posterior face of the second. The haemal process joins with the same structure of the second vertebra as before mentioned, thus forming a large ventral bone with expanded sides. (Figs. 4 and 5.) A pair of small processes are directed posteriorly to aid in the association of the Weberian ossicles with the swim bladder and to form a passage for the blood vessels. This process extends to the posterior end of the fifth vertebra. Laterally the haemal processes of the second and third vertebrae fuse and form a ventrally projecting, triangular structure with a V shaped trough which extends to the ventral end of the bone. The dorsal end is forked in its origin from the two centra. The anterior face is large, irregular and deeply concave. The pharyngeal structures extend into this concavity, while the lateral wing is attached to the posterior face of the cleithrum by muscle. Just ventral to the centra there is a large haemal passage.

The posterior face is much more irregular than the anterior and more varied in its architecture. (Fig. 5). The haemal process extends laterally from the third vertebra, joining a corresponding process of the second. From the latero-ventral region of the third, a part of the haemal process extends ventrally, to form a process that extends along the ventral side of the centra, while a small wing extends ventrally to join the extension of the haemal structure. Two large, lateral fenestra supply openings, through which the most posterior of the Weberian ossicles extend, to come in contact with the swim bladder, while on the median line there is a bony covered passage way for the return of the veins from the head region. (See Fig. 5). Posterior to the three modified vertebrae, the rest assume normal shape and conditions.

Weberian Ossicles.

The Weberian ossicles consist of a small chain of three or four bones that in all Cyprinodonts, lie along the centra of the first three vertebrae. They were first seen by Rosenthal, but they were first described by E. H. Weber in 1820, in a now famous paper entitled "De aure et auditu hominis et animalium." Weber considered the bones homologous with those of the mammalian ear and used the same names in their description, but later study showed that they were different structures and not homologous, so different names were supplied for them. It was shown that the chain is connected with the semicircular canals of the ear and it is now assumed that they have a part in a hydrostatic function, by which the fish is informed of changes in pressure in the swim-bladder. Thilo calls the apparatus a manometer and thinks that the pressure is applied through the bones to the fluids of the brain and spinal cord, where the sensation is registered. It is difficult to see just how this would work and also to determine what special receiving organs would get the sensation through this channel. The Weberian ossicles usually consist of a chain of three or four small bones, the claustrum the most anterior, then follow the scaphium, intercalarium and the tripus. (See Fig. 3.)

The most anterior of the chain, the claustrum, is attached to the neural arch of the first vertebra, facing ventrally and slightly to the posterior. It is firmly sutured to the neural arch so that there is no possible movement, although the suture lines are retained even in very old specimens. The bone is cupped, with expanded lips that meet a similar face on the scaphium. The lips of the two bones meet in a close articulation except for a small opening on the inner side which may be correlated with the hydrostatic function. The origin is not settled, but it is generally considered as having its origin from the skull vertebra according to Goodrich and Nusbaum. Wright considers it as a modification of the spine of the first vertebra. (Fig 2.)*

Scaphium, the second bone of the series, articulates with the claustrum. It also is cup shaped with expanded lips so that it can be closely appressed to the claustrum, or drawn away as the pressure on the swim bladder increases. It has a peg like process on the ventral side which fits, into a corresponding depression on the dorsal side of the centrum of the first vertebra. (Fig. 2.)

When there is a movement of the ossicles, it is on this bearing that the scaphium moves. A ligament attaches it to the intercalarium and finally to tripus.

The third bone of the series, the intercalarium, is a small splint of bone that extends from the ligament that joins the scaphium and tripus, to the anterior part of the centrum of the second vertebra. It serves as a brace for the chain of bones in the ossicle series and holds the bones out from the neural processes. Its origin is the first neural arch according to Goodrich, but others derive it from the neural arch of the second vertebra. It is the incus of Weber. (See Figs. 3 and 4.)

The fourth and the most conspicuous of the ossicles is tripus, which connects the ossicles directly with the swim-bladder. It is a flat, blade like bone, narrowed at the ends, with the anterior end in contact with the other members of the series, through a connective tissue band, while the posterior end is connected with the swim bladder. On the inner or mesial face there is a large bearing at right angles to the main bone, that serves as the bearing for the articulation with the centra of the second and third vertebrae. Extending posteriorly, it passes under the haemal arches of the third vertebra, and comes in contact with the anterior end of the swim bladder. (Figs. 3 and 4.) The bone is nicely balanced on its bearing so that a very free movement is possible, and a slight change in the density of the gas in the swim-bladder will cause a movement of tripus and through it, a movement of the whole series. The origin is given by Goodrich as a modification of the first rib, while Sagemehl gives it as a modification of the third rib.

Mechanically, the Weberian ossicles are beautifully adapted for the purpose that seems to be theirs, of giving the animal notice of changes in depth and consequently of changes in pressure. Correlated with these structures, in the adaptation are the first three vertebrae, which aid in the mechanism by first supplying the material from which the ossicles are made and secondly by developing speciliazations of their parts that will assist the ossicles in performing their function. In no other group is the modification of the vertebrae so striking as in the genus Ictiobus.

While these structures have been studied for years it is quite evident that much remains to be done on them, before they are thoroughly understood. Both developmental and experimental studies should be used to add to our knowledge of the origin of the parts and to clear our ideas of the function of the whole apparatus.

Bibliography (partial).

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Legend.

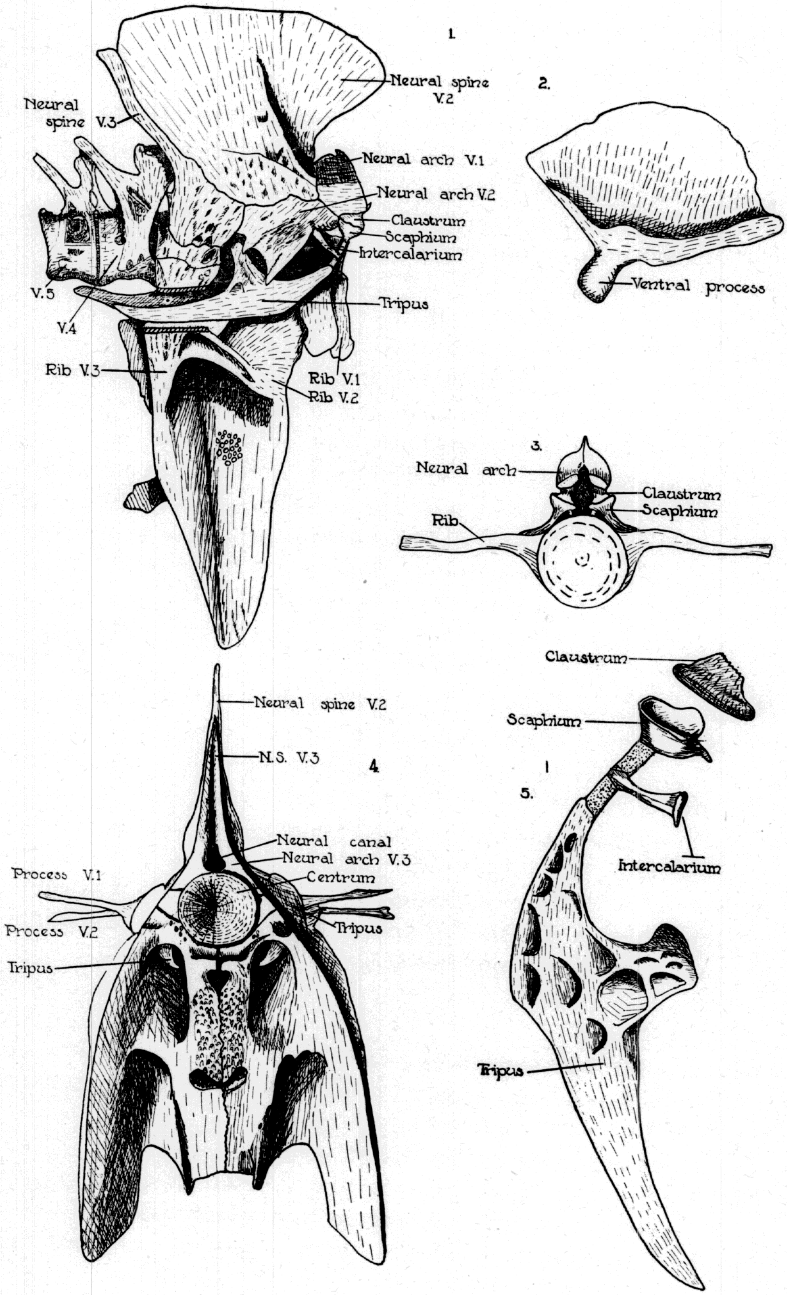
Fig. 1 Lateral view of the first three vertebrae showing the ossicles. A part of the haemal arch is removed. X⅔.

Fig. 2 Dorsal view of the right scaphium. X5.

Fig. 3 Anterior view of the first vertebra showing the position of the claustrum and scaphium. X⅔.

Fig. 4 Posterior view of the third vertebra, showing the relation of the structures in this aspect. X⅔.

Fig. 5 Lateral view of the Weberian ossicles, showing the bones in position. Left side. X5.


1.
Neural spine V.2
Neural spine V.3
Neural arch V.1
Neural arch V.2
Claustrum
Scaphium
Intercalarium
V.5
V.4
Tripus
Rib V.3
Rib V.1
Rib V.2
2.
Ventral process
3.
Neural arch
Claustrum
Scaphium
Rib
4.
Neural spine V.2
N.S. V.3
Neural canal
Neural arch V.3
Process V.1
Centrum
Process V.2
Tripus
Tripus
5.
Claustrum
Scaphium
Intercalarium
Tripus