

EVOLUTIONARY TRENDS AND POSSIBLE ORIGIN OF THE WEBERIAN APPARATUS

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KEYWORDS: evolution, Weberian apparatus, Otophysi, Ostariophysi.

ABSTRACT

A synthesis of anatomical, paleontological and ontogenetic knowledge of the Weberian apparatus is presented. The primitive state of the Weberian apparatus of the extant otophysan orders is deduced and evolutionary trends are discussed in a functional perspective. Main trends are shortening, reduction of weight, loss of intermediate structures, and ankylosis of anterior vertebral centra. Paleontological and developmental data help to develop a tentative reconstruction of a primitive Weberian apparatus, without a manubrium of the intercalarium. Sagemehl's hypothesis on the origin of the Weberian apparatus, which considers the interossicular ligament as the first structure appearing, provides a basis for a more detailed scenario in which each step leads to a more efficient sound transmitter.

INTRODUCTION

About 6000 teleost species of four very different orders (Cypriniformes, Characiformes, Gymnotiformes and Siluriformes) constitute the Ostariophysi coined by SAGEMEHL (1885), on the basis of (at the time) a single character, the Weberian apparatus (for a recent classification, see FINK & FINK, 1981).

The Weberian apparatus *sensu lato* consists of topographically and mechanically linked specialized structures: 1) modified ventral parts of the labyrinths fused on the midline to form a posterior caecum (sinus endolymphaticus) coated with a lymphatic sac (sinus impar) (for details see DE BURLET, 1934), 2) two symmetrical chains of three ossicles (scaphium, intercalarium, tripus), linked by a ligament (interossicular ligament); the anterior ossicles attach to the sinus impar; the thin posterior recurved end (transformator) of the tripus is imbedded in the wall of the tunica externa of the swim bladder, 3) the ossa suspensoria articulating on the fourth vertebra and firmly attached by the strong ligament suspensor to the transformator tripodis, and 4) the anterior part of the swim bladder covered with the strong fibrous tunica externa. The hind part of the enchondral skull and the four anterior vertebrae are modified as well (best account in CHRANILOV, 1927, 1929).

The Weberian apparatus improves auditory capabilities by transducing sound pressure waves into vibratory movements, which the neuromasts linked to the lower otoliths are able to receive (DE BURLET, 1934; POPPER, 1974; CHARDON & VANDEWALLE, 1989). It probably also works as a transmitter related to pressure sensitivity of the gas bladder (GUYENOT, 1912).

PRIMITIVE STATE OF THE WEBERIAN APPARATUS

Ostariophysi with a Weberian apparatus were called Otophysi by FINK & FINK (1981). Although all members of the extant four otophysan orders are to some extent specialised, comparative anatomy coupled with outgroup comparisons (particularly with gonorhynchiforms) and a functional approach to the primitive versus derived state of the characters, allows a tentative reconstruction of the structures in a common ancestor. Previous attempts (principally ROBERTS, 1973; FINK & FINK, 1981; GOSLINE, 1973; ARRATIA, 1987) are also considered.

A primitive Otophysi (the recently described fossils are excluded here) should possess the following main characteristics (figs 1,2); 1) a long sinus endolymphaticus and a long sinus impar bifurcated posteriorly (CHARDON, 1968), 2) a sinus endolymphaticus covered by interconnecting mesial projections of the exoccipitals (WEITZMAN, 1962; CHARDON, 1968; VANDEWALLE, 1974; DE LA HOZ & CHARDON, 1984), 3) the concha scaphii fitting in a notch in the basi- and exoccipitals, 4) all ossicles and claustrum present and distinct; scaphium and intercalarium with articular and ascendens processes; tripus with a large crescent-shaped transformator, 5) the fourth vertebra with recognizable parapophyses and ribs, the ossa suspensoria being simple anterior limbs (cf. *Brycon meeki*, in WEITZMAN, 1962) free from the anterior vertebra; os suspensor linked to the transformator tripodis by a thick crescent-shaped collagen ligament (ALEXANDER, 1962), 6) the chain of ossicles included in a lymphatic space (saccus paravertebralis, REICHEL, 1927) filled with loose fatty connective tissue (ALEXANDER, 1962), 7) first five vertebral centra conserving some mobility, somewhat shorter than the following ones, the first one being the shortest; reduced parapophyses on the first two centra; first three vertebrae lacking normal basidorsals or basiventrals which seem to be transformed into ossicles (cf. *Brycon fry* in ROSEN & GREENWOOD, 1970), 8) large supraneurals 2 and 3 articulating on, or continuous through cartilage with the basidorsals of the third and fourth vertebrae and the exoccipitals (and probably the supraoccipital) (FINK & FINK, 1981). GAYET (1985) does not consider a contact between the supraneural and the occipital region; this contact was not found in two primitive catfishes *Diplomystes papillosus* and *Wallago attu* (CHARDON, 1968), and in a cyprinid (VANDEWALLE, 1974), 9) a claustrum just above the concha scaphii, continuous through cartilage (or fibers) with the supraneural 2, 10) swim bladder large, physostomous, not reaching the skin on the sides, 11) the camera aerea weberiana of the swim bladder not separated from the hind part (like in catfishes), coated with an ichthyocoll fiber tunica externa (ALEXANDER, 1962) and more extensible than the hind part (GUYENOT, 1909; ALEXANDER, 1959b), 12) tunica externa attached to the parapophyses of the fourth vertebra, 13) a dorsal longitudinal gape in the thick fiber layer of the tunica externa, which is reduced to a thin elastic membrane (ALEXANDER, 1961; CHARDON, 1968; DE LA HOZ & CHARDON, 1984; VANDEWALLE, 1974); an ichthyocoll fiber bundle attaching at a right angle to the transformator tripodis, ensuring transmission of the volume changes of the endodermic inner gas bladder to the ossicles (CHARDON, 1968; DE LA HOZ & CHARDON, 1984) (fig. 3).

Figure 1. Tentative reconstruction in ventral view of a Weberian apparatus presenting the primitive characters of the extant Otophysi. Ventral wall of the swim bladder and endodermic- splanchnopleural bulla are removed, as well as inner fibers of the tunica externa on the right side (see list of abbreviations).

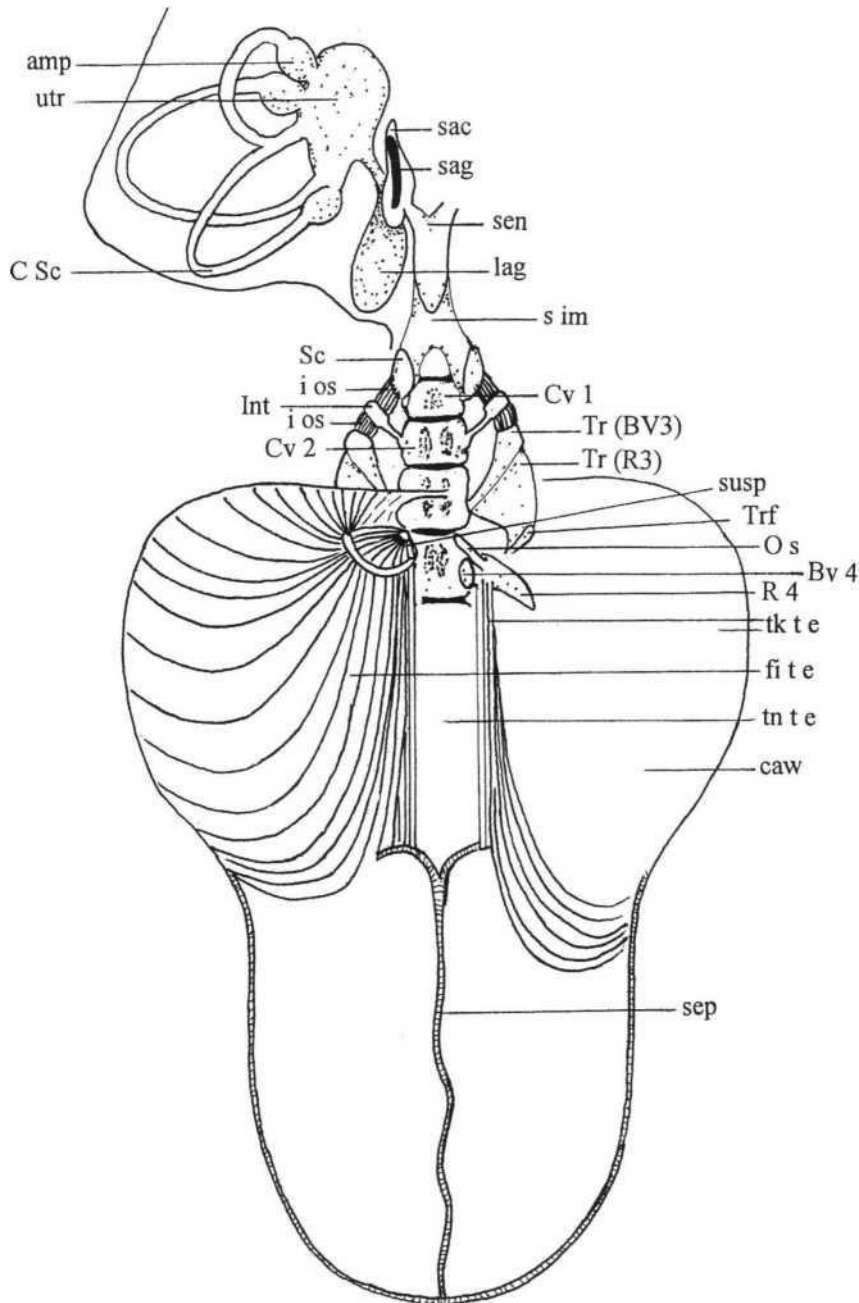


Figure 2. Tentative reconstruction in lateral view of a Weberian apparatus presenting the primitive characters of the extant *Otophysi*.

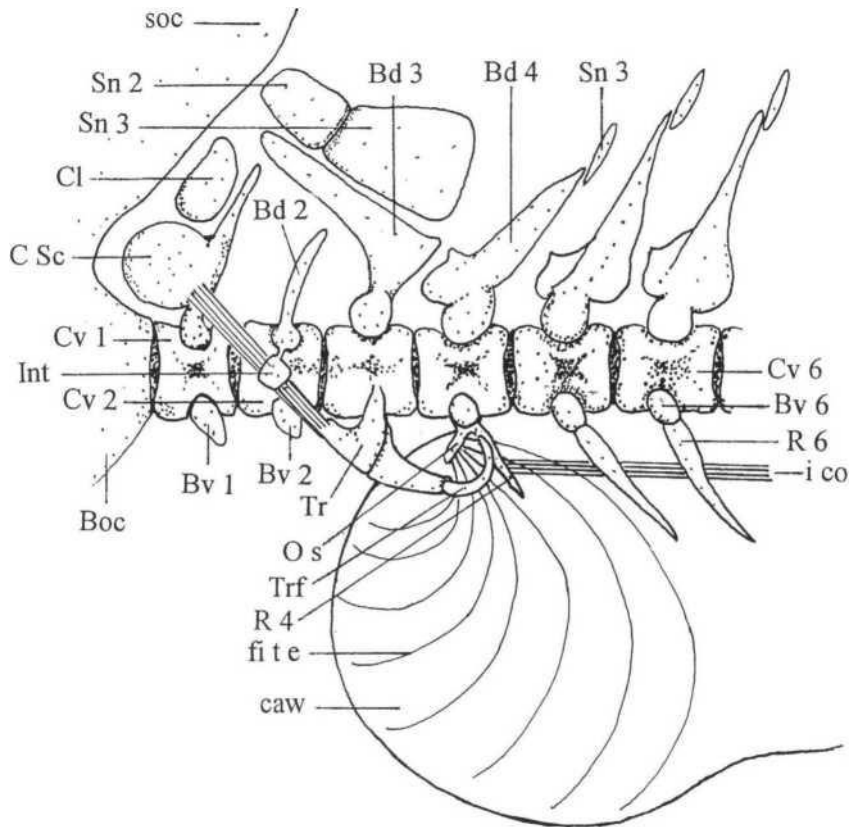
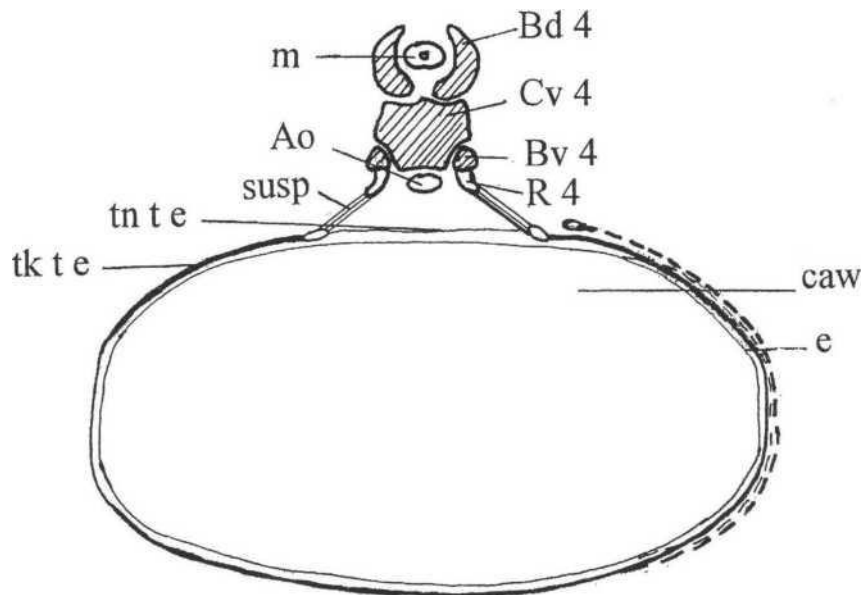


Figure 3. Transverse section at the level of the fourth vertebra through the Weberian apparatus of a primitive 'extant Otophysi'. The effect of pressure decrease (inflation of the bulla, sliding movement of the thick tunica externa and movement of the transformator) is represented in dashed lines.



EVOLUTION OF FUNCTIONAL IMPROVEMENTS OF THE WEBERIAN APPARATUS

The auditory role of the swim bladder is well demonstrated (see for example KLEEREKOPER & ROGGENKAMP, 1959; PLATT & POPPER, 1981). The auditory system may be improved by adding different types of otophysic connections (WOHLFAHRT, 1936; STIPETIC, 1939; BLAXTER, 1981, for the case of clupeids; COOMBS, 1981), which fill the gap between the swim bladder and the labyrinths. The backward elongation of the labyrinths in the Ostariophysi (ROSEN & GREENWOOD, 1970), but also polyphyletic trends such as shortening of the anterior vertebral centra, may also be considered to be functional improvements. The reception of sound pressure waves by the gas bladder may be ameliorated by refinement of its shape and resonance properties. The system may be further improved by reducing damping by the muscles between the skin and tunica externa (BRIDGE & HADDON, 1893; ALEXANDER, 1975), reducing the deformable region of the tunica externa (for instance in catfishes, CHARDON, 1968), modifying the disposition and direction of the fibers of the tunica externa relative to the transformator, and sheltering the gas bladder under the lateral wings of the parapophyses of the fourth and sometimes fifth centra or in a more or less complete capsule (catfishes and cobitids, after CHRANILOV, 1927, 1929; BRIDGE & HADDON, 1893; and gymnotids, DE LA Hoz, pers. comm.).

The inertia of the ossicles may be lowered by reducing their size, loss of the articulares and ascendentes processes of the anterior ossicles, reduction of the intercalarium and shortening of the interossicular ligament (description in CHRANILOV, 1929).

Vibration transmission should be more efficient if the scaphium abuts directly on the sinus endolymphaticus (CHARDON, 1968), and if the saccular otoliths are placed at a right angle to the endolymphatic flow (DE BURLET, 1934; VON FRISCH & STETTER, 1932). The orientation of the hairs of the sensory cells of the neuromasts seem to play a role as well (PLATT, 1977; PLATT & POPPER, 1981; POPPER & PLATT, 1983).

The selective pressures towards improvement of the Weberian apparatus seem to have worked at different degrees and rates in otophysan lineages, particularly in relation to gross

ecological adaptations. A benthic or more pelagic life style, nocturnal or cave dwelling habits, anguilliform shape and locomotion are accompanied with shape and size modifications of the swim bladder, and skeletal reinforcement or weakening, which in most cases seem to have brought about opportunities for progressive functional evolution of the Weberian structures. The same is probably true for the general strengthening and ankylosis of the pectoral region: osseous continuity between the hind part of the skull, ossified Baudelot's ligament, basidorsals of the fourth vertebra, pectoral girdle (GOSLINE, 1977) and radials of the dorsal fin as a firm support for the defensive lockable spines of the pectoral and dorsal fins, for example in Ariidae, Doradidae and Mochokidae (CHARDON, 1968; ALEXANDER, 1965). Such an ankylosis prevents bending of the anterior backbone and thus protects the chains of ossicles from lateral tension. The ankylosis of the anterior centra (BRIDGE & HADDON, 1893) up to the eighth vertebra in the catfish *Doras brevis* has the same effect; fusions of at least centra 2 to 4 is the rule in catfishes, and fusion of two or even four centra is observed in many cyprinids (CHRANILOV, 1927; RAMASWAMI, 1955; VANDEWALLE, 1974).

In no case, the Weberian apparatus became vestigial or lost its biological role (CHARDON, 1968), which seems to indicate the advantage of possessing a Weberian apparatus.

Size reduction (BRIDGE & HADDON, 1894; CHRANILOV, 1929; CHARDON, 1968) is observed in several catfish families. In the superfamily Loricarioidei (CHARDON, 1967) it results in true miniaturization, and cephalisation of the whole Weberian apparatus *sensu lato*, which is housed in the hind part of the apparent neurocranium, as a sort of addition to the labyrinths. The Loricarioidei present a special example of the Weberian apparatus, which deserves experimental investigation. The resonant frequencies (inversely related to the volume of the swim bladder) should be matched to the hearing range (BLAXTER, 1981). The small swim bladder is expected to be poorly sensitive to low frequencies.

DEVELOPMENT OF THE WEBERIAN APPARATUS

Development of the Weberian apparatus was described (sometimes incompletely) in about twenty cyprinids, three catfishes and one characid (KINDRED, 1919; MATVEIEV, 1929; WATSON, 1939; BAMFORD, 1948; ROSEN & GREENWOOD, 1970; KULISHRESTHA, 1977; VANDEWALLE *et al.*, 1989, 1990, 1992; RADERMAKER *et al.*, 1989; BOGUSTKAYA, 1991; COBURN & FUTEY, 1996). Development of the Weberian structures takes place early during the postembryonic phase, before homodynamic ones.

The labyrinths appear in the same way as in non-ostariophysine teleosts, but the left and right primordia extend backward and fuse on the midline, while the sinus impar develops over them from connective tissue (RADERMAKER *et al.*, 1989; GRASSE, 1957).

At first, the origin of the ossicles and ossa suspensoria seems to be clear: scaphium and intercalarium are homologous to the first two basidorsals; tripus and os suspensor represent respectively the third and fourth basiventrals and ribs; centra appear later and are all distinct, even in catfish. But, as shown in table I, most authors recognize a multiple origin of the ossicles, including mesenchyme, intraligamentous ossification and, for the transformator tripodis, ossification of the tunica externa of the swim bladder. It remains dubious whether the reported differences in the developmental origin of the ossicles are true differences or reflect differences in the methods of the authors.

Table 1 – Interpretations by the authors of major original observations about development of the

Weberian apparatus

Authors	Matveiev, 1929	Watson, 1939	Bamford, 1948	Rosen & Greenwood, 1970	Kulshresta, 1977	Radermaker <i>et al.</i> , 1988	Vandewalle <i>et al.</i> , 1990
Orders or suborders	SIL	CYP	SIL	CHA (one late stade)	CYP	SIL	CYP
Claustrum	SD1	mes. os.	not found	SD1	part of BD1 + mes. os.	not found	mes. os.
Scaphium	BD1 + mes. os. (CO)	BD1 + mes. os.	BD1	BD1	part of BD1 + mes. os.	BD1 + sep mes. os.	BD1 + sep mes. os.
INTC tripus	BD2 + os.	BD2 + ilig. os. BV3 + mes. os.	BD2	BD2 + PZ2 BV3	BD2 + ilig. os. BV3	hook on tripus	BD2
TFTP		rib 3 + SWT os.	BV3 + rib 3	rib 3	mes. os.	BV3	BV3
SUSP		outgrowth V4	rib 4	BV4	outgrowth BV4	part of BV4 (or rib?)	part of BV4 (or rib?)

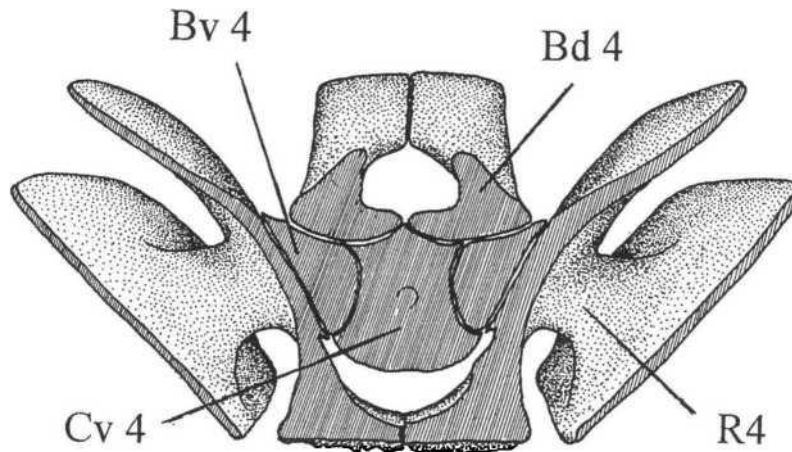
At first, the rudiment of the tripus lies in front of that of the fourth basiventral. Later the ossified transformator process extends backward and crosses a growing anterior limb of the rib of the fourth vertebra, the os suspensor. The tripus and the transformator seem to be drawn backward as if the fibrous bundle attached to the transformator pulls the ossicle while the bladder is inflating.

The fourth basiventral and rib rudiments are at first similar to the following ones even though they develop earlier; but in *Clarias* and *Barbus* (RADERMAKER *et al.*, 1989; VANDEWALLE *et al.*, 1990) an anterior process of the rib grows forward: the os suspensor *sensu stricto*, which WATSON (1939) considers as distinct from the parapophysis and from the rib. The os suspensor develops in very different ways among the Otophysi. In the adult gymnotid *Sternopygus* (DE LA HOZ & CHARDON, 1984) the pleural rib of the fourth vertebra remains clearly distinct from the parapophysis in transverse section, and the os suspensor appears as a ventral branch of the rib (fig. 4).

The paired claustrum appears to result from the transformation of the single first supraneural (GAYET, 1982a; COBURN & FUTEY, 1996).

The tunica externa develops from the two cellular somatopleural sheets, while the splanchnopleura sticks to the endoderm to form the thin and elastic internal bulla (CHARDON & VANDEWALLE, 1989). This explains the presence of blood vessels and muscles in the wall of the bulla. The camera aerea weberiana grows early. The swim bladder appears to be already swollen when the transformator tripodis attaches to it, probably in the same way as in adult Otophysi in which its internal pressure is somewhat higher than in the surrounding water (ALEXANDER, 1962).

Figure 4. Transverse section and hind part in front view of the fourth vertebra of *Gymnotus carapo* to show the limits of the basiventrals and ribs (original drawing by E. De la Hoz, unpublished).



CHEMICAL EVIDENCE

Interesting results were published by ALEXANDER (1961, 1962) about the composition of the swim bladder tunicae and principal ligaments of the Weberian apparatus of the Cyprinidae. The interossicular ligament is made of ichtyocoll and collagen fibers, like the tunica externa. The suspensor ligament is made of mere collagen as well as the band of fibers running forward 'from the inner layer of the tunica externa at the posterior end of the slit and becomes attached as a ventral tunica adventitia to the dorsal aorta'. The ligament joining the dorsal face of the tripus to the parapophysis of the fourth vertebra is made of elastin and probably plays a role in pulling back the ossicle and stretching the interossicular ligament.

BIOGEOGRAPHY OF FOSSIL AND RECENT OTOPHYSI AND OSTARIOPHYSI

Extant Otophysi are primary freshwater fish (DARLINGTON, 1957) with few exceptions (CHARDON, 1967, for a review). The main families are three catfish families (Ariidae, Plotosidae and Aspredinidae) which contain a large percentage of marine species (GREENWOOD *et al.*, 1966). The Otophysi inhabit the fresh waters of all continents. In Australia, New-Zeeland, Madagascar, and other oceanic islands, there are only Ariidae and Plotosidae, seemingly thanks to their euryhaline potentialities. The four classic extant orders are not present on all continents; for example, gymnotiforms are restricted to South America.

The situation is less clear for the fossil representatives from the Cretaceous and early Tertiary of the extant orders (see paragraph on paleontological data). Further findings are expected to bring a more clear view of the repartition in seas or fresh waters, and on continents of the early Otophysi. Five fossil species do not clearly belong to any of the four classical extant orders. Their number remains so low that biogeographical hypotheses are hazardous and depend on the phylogenetic conceptions of the author. GAYET'S (1982a) one is coherent but rests on phylogenetical views which are not shared by other authors (PATTERSON, 1984b; FINK *et al.*, 1984). However, a marine origin of the Otophysi is at present a plausible proposition (TAVERNE, 1995), and a marine origin of one of the extant orders is possible as well (GAYET, 1982a).

The gonorynchiforms, the sister group of the Ostariophysii, are divided by GAYET (1993) into

Gonorhynchoidei and Chanoidei. The Gonorhynchoidei are marine. They include (GAYET, 1993) the genus *Ramallichthys*, *Charitosomus* and *Judeichthys* of which the anterior neural arches are possibly adapted to transmit vibrations to the skull (GAYET & CHARDON, 1987).

The Chanoidei are fresh or brackish water dwellers, probably euryhaline at their origin (GAYET, 1993). Some African families live exclusively in fresh waters (POLL, 1957).

Most ancient fossil gonorhynchiforms were found in deposits from around the Tethys, but since the upper Cretaceous, their known distribution is much broader. The same is true for the extant orders of Otophysi (GAYET, 1982a, 1993; POYATO-ARIZA, 1996).

It must be pointed out that during the late Cretaceous, Gonorhynchiforms and Otophysi, were living in the same regions, but they possessed different types of Weberian apparatus. This includes such gonorhynchiforms like *Ramallichthys* or Chanidae (*sensu* POYATO-ARIZA, 1996) with different 'paraweberian' modes of vibration transmission (ROSEN & GREENWOOD, 1970; GAYET & CHARDON, 1987).

FOSSIL EVIDENCE

Until 1984, all the fossil Otophysi described pertained to the recent orders. Catfish (GAYET, 1988; ARRATIA & GAYET, 1995), are known from the late Cretaceous; characins (GAYET, 1982b) from Oligocène or Miocene deposits (after the review of CARROLL, 1987); gymnotids were recently found in the Miocene of Bolivia (GAYET & MEUNIER, 1991; GAYET *et al.*, 1994); cyprinids are reported from early Eocene and Miocene (CAVENDER, 1991), from early Paleocene and from the upper Cretaceous of Bolivia (GAYET, 1982b).

GAYET (1982a) in her description of the marine gonorynchiform *Ramallichthys orientalis* from the lower Cenomanian proposes that the first and second enlarged basidorsals are a scaphium and an intercalarium, and that the evolution of the Weberian apparatus began in the dorsal part. She also describes *Lusitanichthys characiformis*, a fossil of the same period, and attributes it to the characiforms or to their stem-group. More importantly, it is the first report of a true Weberian apparatus (the species is far better figured in GAYET, 1985). A better preserved 'Weberian' fossil was nicely described soon after, by PATTERSON (1984b). The four typical Weberian ossicles and skull of *Chanoides macropoma*, however, show characteristics that exclude this species from the four extant orders of Otophysi (three orders after FINK & FINK, 1981, who group the catfishes and gymnotids in one single order Siluriformes). Other comparable fossils were described by GAYET (1985) and TAVERNE (1995), with true Weberian ossicles, but with characteristics excluding them from extant orders. Gayet herself however contests that exclusion on the basis of many characters relating the 'Weberian fossils' to cypriniforms and characiforms. TAVERNE (1995) proposes as most parsimonious to consider *Clupavus* as a Characiphysi. FINK *et al.* (1984), and PATTERSON (1984a, b) do not agree with such an hypothesis.

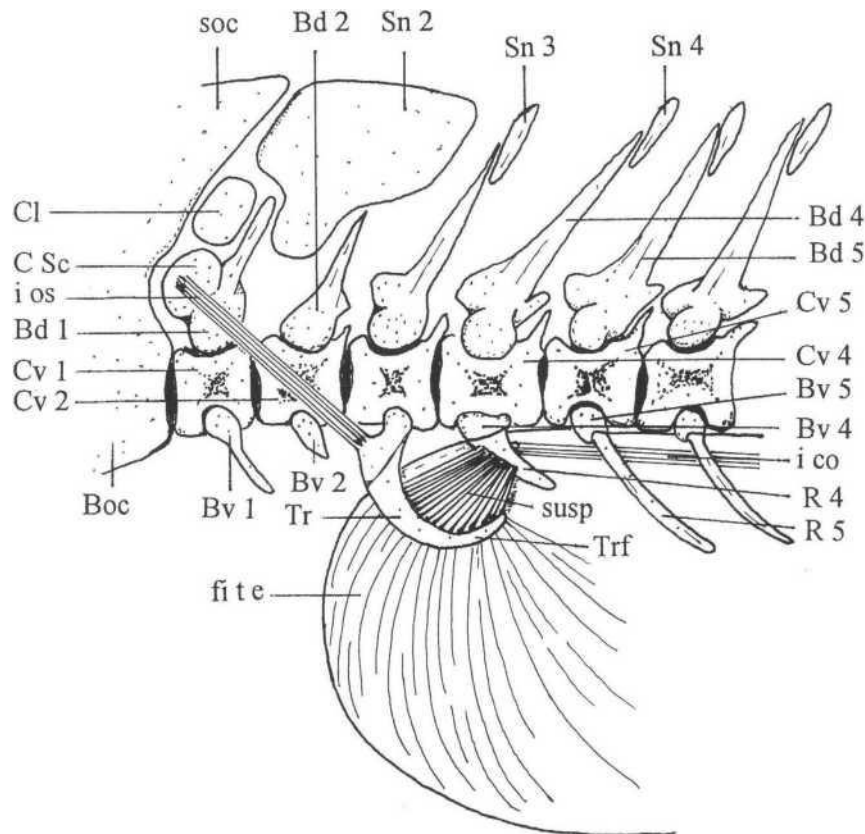
Chanoides macropoma and *Lusitanichthys characiformis*, both carefully described from several relatively well preserved specimens, exhibit four modified anterior vertebrae and ossicles. After a reconstruction (fig. 5) taking into account the articular surfaces and presumed zones of attachment of ligaments, they form a plausible chain of three ossicles and an os suspensor (PATTERSON, 1984b; GAYET & CHARDON, 1987). More hazardous reconstructions of *Salminops ibericus* Gayet and *Eurocharax tourainei* Gaudant (GAYET, 1985), and of *Clupavus maroccanus* Arambourg, 1968 (TAVERNE, 1995) are consistent with

the former results. All five fossil species show specific Weberian characters excluding them from the ancestry of the extant orders and making it somewhat uncertain to classify them all in one homogenous taxon. This situation demonstrated the variety of Weberian structures during the Cretaceous and early Tertiary. It is however possible to present (sometimes very incomplete) reconstructions of the Weberian structures of the five species, which demonstrate that they could work efficiently as an otophysic transmitter (GAYET & CHARDON, 1987).

The ossicles and ossa suspensoria are quite different in *Chanoides* and *Lusitanichthys*. The tripus evolved in *Lusitanichthys* in a more otophysan manner, with a crescentic transformator, while in *Chanoides* it is reduced and probably played a role similar to that of the intercalarium: one more ossicle in the interossicular ligament. *Chanoides* seems to be transformed beyond the otophysan level in the reduction of the basiventral of the third vertebra; its scaphium and intercalarium are otophysan-like but the os suspensor seems to act as a tripus. *Clupavus* was probably *Chanoides*-like in the shape of the os suspensor and scaphium, but more primitive judged by the size of the third centrum and shape of the intercalarium. In *Eurocharax tourainei*, the first centrum is reduced and the tripus is well sized like in *Lusitanichthys*, but a transformator may be absent and the fourth parapophysis seems to lack a differentiated os suspensor: it seems to be short and separated from the rib (not found). More complete knowledge of such fossils is clearly needed.

A tentative list of primitive (plesiomorphic) features relative to the extant orders Otophysi, may be presented. The gonorynchiforms (ROSEN & GREENWOOD, 1970; POYATO-ARIZA, 1996; GRANDE & POYATO-ARIZA, 1995) and the clupeiforms, which are considered as the sister group of Ostariophysi by LECOINTRE (1995) according to molecular data by NELSON (1973), are valuable outgroups for comparisons. ROSEN (1973) included the clupeiforms as well as the Ostariophysi in the Euteleostei (fig. 5).

Figure 5. Hypothetical reconstruction of the hind part of a primitive Weberian apparatus, principally based on the descriptions of *Lusitanichthys* by GAYET (1985a) and *Chanoides* by PATTERSON (1985) and on the development of extant species. Note that the interossicular ligament is not interrupted by a manubrium of the intercalarium.



The primitive features proposed are (in spite of the evident difficulties in the interpretation of the fossils): 1) first two basidorsals and basiventrals 3 and 4 clearly specialized as ossicles, 2) scaphium not extending beyond the rostral margin of the first centrum, 3) intercalarium not part of the chain of ossicles, lacking a manubrium (the part embedded in the interossicular ligament; see below), 4) a large tripus probably with a recurved end, 5) a fourth basiventral poorly transformed into an os suspensor, lacking an anterior limb, 6) the four anterior centra progressively shortened, the first one not being dramatically reduced, 7) a large anterior ($2^d + 3^d$) supraneural in contact with the third neural arch and the occipital region (see for example *Clupavus* in TAVERNE, 1995, fig. 3), 8) parapophyses on the first two centra. *Lusitanichthys characiformis* conserves most of these primitive characters.

ORIGIN OF THE WEBERIAN APPARATUS

Up to the description of the (Weberian) fossils from the Cretaceous, the question of the origin remained very difficult because the basic structure is very constant in extant orders, even in the rare known fossils of these orders. Most hypotheses mainly focused on the problem of the ossicles and eventually the swim bladder, which seemed to be primordial (ROSEN & GREENWOOD, 1970; GAYET, 1982a). Developmental studies were oriented in the same way, except RADERMAKER *et al.* (1989) and VANDEWALLE *et al.* (1989, 1990). The recently described fossils show a broader variety of Weberian structures, including more primitive ones, and they support the developmental data as to the homologies of the ossicles.

An interesting idea was expressed more than a century ago by SAGEMEHL (1885) who proposes that the interossicular ligament was the first Weberian structure to occur in the course of evolution. We propose a coherent and more detailed scenario and some interesting

arguments in favor of it.

In the clupeids, the sister group of the Ostariophysi, an otophysic connection consists of anterior tubular outgrowths of the swim bladder reaching the otic region through the skull. Such a connection is plausible in stem Otophysi, if a precursor of the tunica externa was present (cf. ROSEN & GREENWOOD, 1970). It could work in two ways: by transmitting pressure variations to the labyrinths through the tubes, and by transmitting vibrations through the fibrous peritoneal wall of the same tubes. If the second way of transmission proved more efficient, it possibly developed and improved while the tubes regressed. The net result would be the future interossicular ligament. A strong argument for this is the chemical composition of the interossicular ligament: ichthyocoll and collagen, the same materials as found in the tunica externa (ALEXANDER, 1962). Later on, the ligament attached to the skull around the foramen for the vesical tube. The embryonic material for the concha scaphii fitting the foramen may be provided by one of the cephalic ribs observed in most gonorhynchiforms but not in Otophysi. The concha finds a point of support on the autogenous first basidorsal. This could explain the multiple origin of the scaphium.

At the other end of the ligament the first well developed pleural rib of the gonorhynchiforms is the third one; the tunica externa attaches to it, as does the fourth rib. The 3^d and 4th pleural rib are linked (like the following ones) by a longitudinal collagen ligament. The end of the interossicular ligament submitted the tunica externa to complex stress, which ossified in response to this mechanical load. In this way the transformator tripodis may have appeared, while the third basiventral and rib became the tripus. The suspensor ligament joining the 3^d and 4th ribs is the specialized former intercostal ligament, which is consistent with its collagen composition (see ALEXANDER, 1962).

The particularities of the os suspensor growing from the pleural rib of the fourth vertebra are harder to explain. A comparable anterior limb is present in the fossils *Salminops* (GAYET, 1985) and *Chanoïdes* (PATTERSON, 1984b) but not in *Lusitanichthys* (GAYET, 1985).

The case of the intercalarium is problematical. Among the fossils, its manubrium part (situated in the interossicular ligament) is observed in only one species, *Chanoïdes macropoma*. It is postulated in *Lusitanichthys* by GAYET & CHARDON (1987) but only after a preconceived idea based on the situation in *Chanoïdes*. During the larval development of *Clarias gariepinus* (RADERMAKER *et al.*, 1989) the second basidorsals appear later than the first, third and fourth ones, and keep an aspect of a small basidorsal, while the manubrium seems to be reduced to a small hook on the fore end of the tripus (there is no distinct intercalarium in adult *Clarias*). A manubrium is present in *Barbus* and *Carassius* soon after the appearance of the ligament (or in the same time) (WATSON, 1939; VANDEWALLE *et al.*, 1990).

In the 12 mm *Carassius* (WATSON, 1939, fig. 5) the manubrium is only linked to the second basidorsal by a ligament-like fibrous structure (*ibidem* fig. 2) and it seems to pull on the interossicular ligament, which is bent at this level. Fusion occurs later at the 15 mm stage. After Watson, the absence of an articular process in cobitids and catfishes means that they retain a primitive condition like in goldfish fry, and that the second basidorsal did not participate in the formation of the intercalarium. CHARDON (1968, observation maintained contra FINK & FINK, 1981) and ARRATIA (1987) however describe a complete intercalarium with an articular process in the primitive catfishes Diplomystidae. The intercalarium thus develops late in ontogeny and probably late in evolution, and is also the first to disappear in

cobitids and many catfishes. Its possible function is to sustain and hold the interossicular ligament when the head remains somewhat movable relative to the trunk (CHARDON, 1968).

CONCLUSIONS

1. The basic structure of the Weberian apparatus is particularly constant in the four classical otophysan orders, and subject to convergent evolution, especially in benthic catfishes. No otophysan presents a degenerate or non-functional Weberian apparatus. To the extent that recently described Cretaceous fossils are reconstructed correctly, much larger differences exist between fossils and extant species.
2. The goniorhynchiforms (the Weberian fossils are excluded, because they are true Otophysi) do not possess any kind of Weberian transmission even through the first basidorsal occasionally resembles a concha scaphii.
3. Homologies of the ossicles clearly result from the study of development, but development does not recapitulate much of the evolution.

PERSPECTIVES

The majority of freshwater fishes are Otophysi, but the number of marine species is small. Apart from the Weberian apparatus, the Otophysi do not share any important character which could explain their success. It remains to be explained how a significant improvement of auditory capacities affects competition in fishes and allows a worldwide adaptive radiation. The evolutionary history, development, performance and function of the Weberian apparatus constitutes a major biological question deserving an integrative approach. However, research on the Weberian apparatus, except in the field of auditory physiology, has slowed down since more than thirty years. As a result, a survey of the problem treated as a whole discloses many gaps in our knowledge and perspectives for exciting studies:

- the search for other fossil Otophysi, their careful description and plausible reconstruction,
- in depth study of mechanical transmission by the ossicles, and the role of the tensor tripodis,
- morpho-functional comparison of different kinds of suspensoria,
- ontogenetical studies on the non-vertebral parts of the ossicles, the interossicular ligament and the envelopes of the swim bladder and their attachment to the transformator and os suspensor,
- further comparative studies on the physical properties of the swim bladder (cf. VAITULEVICH, 1977, 1979), on the mechanical significance of the orientation of the fiber bundles and their attachment to the transformator, and of the stiffness of the different regions of the bladder,
- further studies on the adaptation of the Weberian apparatus to pressure changes and its probable role as a pressure-sensitive organ (see for example, WATSON, 1939; ALEXANDER, 1959a, 1966),
- studies on the influence of size and morphological characters of the Weberian apparatus on the auditory capacities, and search for possible relations with ecology and

ethology with special emphasis on the cave dwelling *Otophysi* (for example, CHARDON, 1966; POPPER, 1971),

LIST OF ABBREVIATIONS

Amp	ampulla
Ao	dorsal aorta
Bd 1, 2, ...	basidorsal of first, second, ... vertebra
Boc	basioccipital
Bv 1, 2, ...	basiventral of first, second, ... vertebra
caw	camera aera weberiana
Cl	claustrum
C Sc	concha scaphii
Cv 1, 2, ...	centrum of first, second, ... vertebra
e	endodermic swim bladder plus splanchnopleura
fi t e	fibers of the tunica externa
i co	intercostal ligament
Int	intercalarium
i os	interossicular ligament
lag	lagena
m	medulla
O s	os suspensor
R 4, 5, ...	rib of fourth, fifth, ... vertebra
sac	sacculus
sag	sagitta
scc	semi-circular canal
sen	sinus endolymphaticus
sep	septum
s im	sinus impar perilymphaticus
Sn 2, 3, ...	supraneural of second, third, ... vertebra
soc	supraoccipital
SUSP	ligament suspensor
tk t e	thick tunica externa
tn t e	thin tunica externa
Tr	tripus

Tr (Bv3)	tripus, part homologous to Bv3
Tr (R3)	tripus, part homologous to R3
Trf	transformator tripodis
utr	utriculus

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