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ABSTRACT

Modified scales in the cloacal region of two osteolepid rhipidistians are described for the first time. A specimen of Megalichthys sp. (from the Pennsylvanian of Ohio), consisting of an isolated portion of the pelvic region, shows five enlarged scales along the ventral midline: two sets of paired flanking scales and one unpaired central scale. There is no direct evidence of the cloaca in this specimen. In the only known specimen of Sterropterygion brandei (from the Upper Devonian of Pennsylvania), the cloacal position is preserved, and there is one pair of enlarged scales flanking the opening. The modified scales in both genera are interpreted as being secondary sexual characteristics. The apparent absence of scales modified for reproductive functions in other fossil taxa is discussed.

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Very few fossil fishes show any evidence of differentiation of structures in the ventral region of the body that could be interpreted as sexual characteristics. Fossil sharks and some placoderms do, however, show clear evidence of claspers in the pelvic fins (for example, in *Rhamphodopsis*, Miles, 1967) by which males are identified. In the bony fishes, one would expect that the elaborate squamation, which is often extremely well preserved even in fossils of great age, might be expected to show evidence of differentiation in the cloacal region, but this has not hitherto been observed. The purpose of the present communication is to describe the occurrence of modified scales in the region of two osteolepid Rhipidistia (Osteichthyes, Crossopterygii). These modified scales are interpreted as sexual characteristics.

The Rhipidistia is a group of Paleozoic fishes comprising forms of small to rather large size, all of which have well-developed bony scales. In one family in particular, the Osteolepidae, the squamation is especially well developed and bears a thick external coating of shiny cosmine (see Thomson, 1975) and can be studied with great precision. The pattern of squamation of Devonian Osteolepidae has been extensively studied by Jarvik (e.g., Jarvik, 1948) and others, who have provided detailed descriptions of Devonian genera, particularly *Osteolepis*. In none of the existing accounts, however, is there any evidence of modification of the ventral scale pattern in the cloacal region and, indeed, the position of the cloaca is usually difficult to establish in fossil Rhipidistia.

Recently, study of two well-preserved specimens of osteolepid Rhipidistia has yielded new information on this subject. The most striking evidence comes from a Pennsylvanian osteolepid. The specimen consists of an isolated portion of the pelvic region of the trunk, showing both pelvic fins. Because the specimen is incomplete, it can be identified only as *Megalichthys* sp., but it seems essentially identical with *Megalichthys macropomus* Cope. It was collected in the Upper Freeport Shale (Pennsylvanian) at Lisbon, Ohio, by a party from the Cleveland Museum of Natural History (Specimen Number CMNH 8151).

As Figure 1 shows, the ventral side of the pelvic region is completely exposed in this specimen. The ventral surface of the right pelvic fin and the dorsal surface of the left pelvic fin are visible, along with the specialized elongated basal scutes associated with the median side of their insertions on the trunk. It will be observed that, contrary to previous accounts of the rhipidistian exoskeleton (Jarvik, 1948; Andrews and Westoll, 1970), these basal scutes are not part of the fin exoskeleton but are modifications of the squamation of the trunk at their bases. It may be noted also that, although these scutes are close to the cloacal opening, they are not directly associated with it. The distribution and significance of basal scutes is discussed in detail by Rackoff (1976).

In the midline there are five scales that are clearly distinguishable from the rest of the squamation. There is one very large *central scale* located in
Fig. 1. *Megalichthys cf. Macropomus*. Pelvic region showing specialized scales around the cloaca. $afs$ = anterior flanking scales; $cs$ = central scale; $pfs$ = posterior flanking scales. CMNH 8151. $\times$ 1.2. Inset shows diagrammatic reconstruction.

the ventral midline (Fig. 1, $cs$) that is apparently modified from a normal member of the ventral scale row of the midline. It bears a prominent anteroposterior ridge along the posterior portion of its exposed surface. Anterior to this scale is a pair of *anterior flanking scales* (Fig. 1, $afs$) that are moderately enlarged in comparison with adjacent scales and have a modified shape. The posteromedian border of each anterior flanking scale is strongly concave where it overlaps the central scale. Flanking the central scale posteriorly and overlapped by both the central scale and the anterior flanking scales is a pair of *posterior flanking scales* (Fig. 1, $pfs$). These are elongated scales that reach posteriorly to an extent equivalent to the length of more than two of the normal scales adjacent to them. In the specimen at hand, the right posterior flanking scale is missing, but its presence can easily be inferred from the shape of its complete left partner. The posterior part of the posterolateral border of each posterior flanking scale is concave. These two scales overlap a small median scale that, although it cannot be seen in its entirety, seems unmodified.
We interpret these structures as specialized scales surrounding the cloacal aperture which is presumed to lie immediately posterior to the central scale, between it and the unmodified median scale just mentioned.

In the specimen of *Megalichthys* there is no direct evidence of the presence of the cloacal opening. It is fortunate therefore that we are able to confirm our conclusions from a second osteolepid rhipidistian. *Sterropterygion brandei* Thomson is an osteolepid rhipidistian from the Upper Devonian of Pennsylvania. The single known specimen from the Yale Peabody Museum (YPM 6721) has been described briefly by Thomson (1972) and a fuller description of the fish is now completed (Rackoff, 1976). The squamation in the pelvic region of the specimen of *Sterropterygion brandei* is quite well preserved, although certain of the most posterior scales are broken into fragments, making their shape difficult to establish. The relevant portion of the pelvic region is shown in Figure 2. The region of the fish bearing the pelvic fins and cloacal structures is exposed from both sides, the inner surface of the specimen having been prepared so as to reveal the pelvic girdle. Between the two halves of the pelvic girdle there is clearly visible a small cylinder of green matrix set off from the general red sandstone in which the fossil is preserved. It leads directly downwards, and from the other side of the specimen it can be seen to lead to a small opening between the pelvic fins. It is a natural cast of the rectal region of the alimentary tract, leading to the cloaca. The position of the cloaca can thus be fixed with certainty.

Immediately flanking the cloaca anteriorly are two scales that are considerably larger than the other scales in this ventral region. They seem to be homologous with the anterior flanking scales seen in *Megalichthys*. There is, however, no sign of a central scale or posterior flanking scales in *Sterropterygion brandei*.

The modified cloacal scales of both *Megalichthys* and *Sterropterygion* are interpreted as being adaptations connected with the reproductive function, but we cannot make any firm conclusions concerning the relationship of the two described patterns, or the apparent absence of such modified scales in other Rhipidistia. Several possible explanations can, however, be explored. First, the absence of specialized scales in the cloacal region of most known osteolepid Rhipidistia may represent a juvenile condition. This is unlikely; we have examined a very broad size range of specimens of the Permian osteolepid *Ectosteorhachis nitidus* Cope and have found no modified scales even in the largest specimens. Secondly, it is possible that modified scales are characteristic of only one sex. If most known rhipidistians do indeed lack specialized cloacal scales, this would imply a great imbalance in the sex ratio of populations of fossilized fish. However, a third possibility is that modified scales, especially of the weakly modified type seen in *S. brandei*, are in fact present in many fossil specimens but have been overlooked or have not been generally recognized due to displacement (of the
Fig. 2. *Sterropterygion brandei* Thomson. Pelvic region showing specialized scales to the left of the cloaca, displaced to the left, matching right scales missing. *pfs* = posterior flanking scales. YPM 6721. × 2.0. Inset shows diagrammatic reconstruction.
anterior flanking scales). In that case, it could be possible either that all members of a species may possess modified scales, or that sexual differences in presence and in degree of modification may occur. Fourth, the modified scales reported on here may represent a pathological condition, but we do not think that to be the case. There is thus a great need for reexamination of all taxa of Rhipidistia to see whether modifications of the scale pattern in the cloacal region may in fact be present.

We have searched the record of modern fishes for parallels to the development of modified scales in the cloacal region and have been disappointed to find no analogues that would assist us in the interpretation of the structures described here except possibly that reported by Page (1976) in *Percina*.

In summary, modified scales associated with the cloacal region are described for the first time in fossil fishes. In two genera of Osteolepididae, modified scales are found that may be interpreted as secondary sexual characteristics. The apparent absence of such modified scales from specimens of other fossil taxa is an unsolved puzzle.

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