CONTRIBUTIONS TO THE FUNCTIONAL MORPHOLOGY OF FISHES

PART IV. THE LOCKING MECHANISM OF THE DORSAL SPINE OF THE CATFISH *SYNODONTIS ZAMBESENSIS* PETERS

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INTRODUCTION

The content of this paper represents part of an investigation into the functional morphology of the dorsal fin-spine of *Synodontis zambesensis* Peters, 1852, commonly known in this country as the 'squeaker'. The genus *Synodontis* is generally placed in the family Mochokidae, which includes some of the more specialised catfish. This investigation was conducted by the first author during 1966. Towards the end of the same year Alexander's excellent paper on 'Structure and function in the catfish' (1965) became available, in which the mechanism of the locking dorsal spine of *Pimelodus* of the family Pimelodidae, a 'fairly primitive catfish' was described. Alexander maintains that 'the skeletal structures and muscles associated with the dorsal spine in most catfish closely resemble those of *Pimelodus*', but draws attention to certain differences in *Synodontis*, namely the different arrangement of nuchal plates, the fact that the first and second proximal radials of the dorsal fin are separated proximally and the different origin of the erector muscle of the first ray, which is on the posterior surface of the skull instead of on the neural spine of the fourth vertebra. Work on *Synodontis* fully confirms Alexander's theory for the mechanism of 'locking' of the spine, but the mechanism of 'unlocking' appears to be different from that in *Pimelodus*. This process involves the use of an extra and hitherto undescribed muscle, and seems to us to warrant a short report.

Dissections and skeletal preparations were performed on five formalin-preserved specimens of *S. zambesensis*. In the descriptions which follow, Alexander's terminology for the skeletal parts will be used.

THE ANATOMY OF THE LOCKING-SPINE APPARATUS (FIGS. 1–3).

With the exception of the points mentioned above, the skeletal parts of the apparatus are very similar to those of *Pimelodus* and will be but briefly summarised.

The defensive spine (the second ray) is triangular in cross-section and 6–8 cm. in length. Its base is broadened laterally and provided with three condyles, of which the median one, according to Alexander, represents the second distal radial and articulates on the distal end of the second proximal radial. The lateral condyles articulate on the lateral distal processes of the second proximal radial (Fig. 2). Immediately above the median condyle the spine is pierced by a foramen running antero-posteriorly, through which passes a ring of bone, here termed the articulatory ring, continuous with the dorsal end of the second proximal radial (Fig. 1). The movement of the spine is thus largely restricted to the saggital plane.

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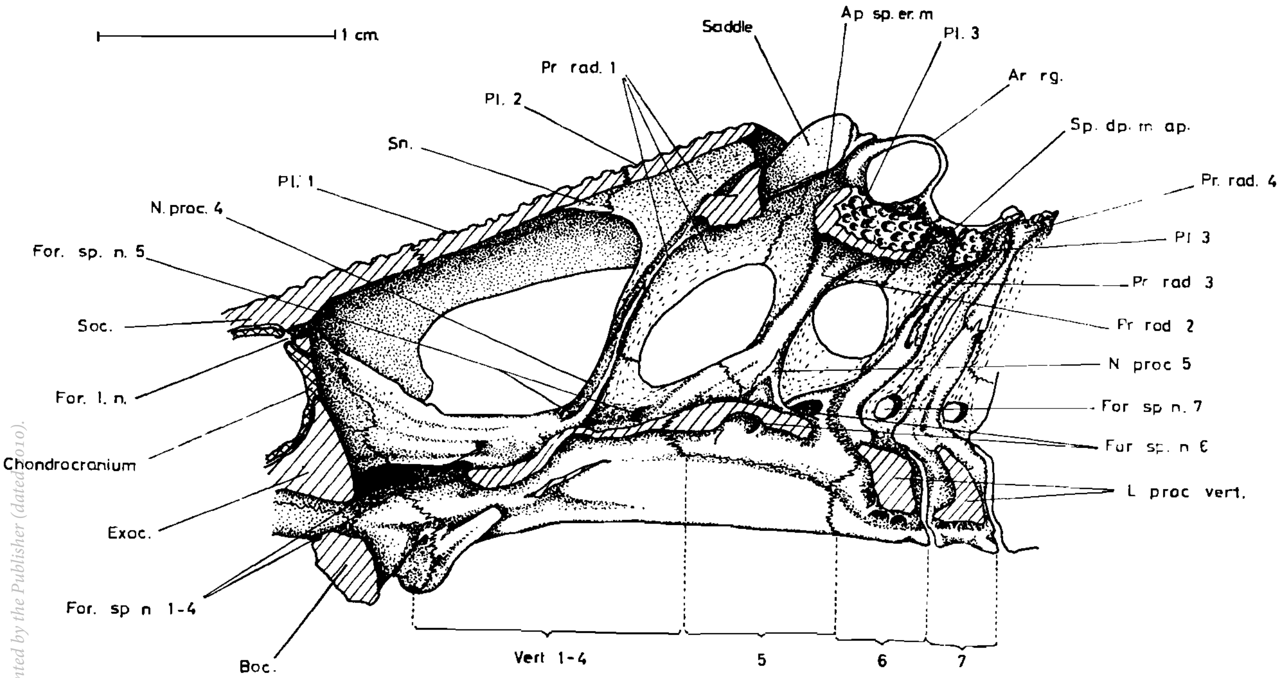

Figure 1. Lateral view of the postcranial skeleton of the left side, with the nuchal shield and parapophyses of the vertebrae cut away (cut edges striped). For abbreviations see p. 94.

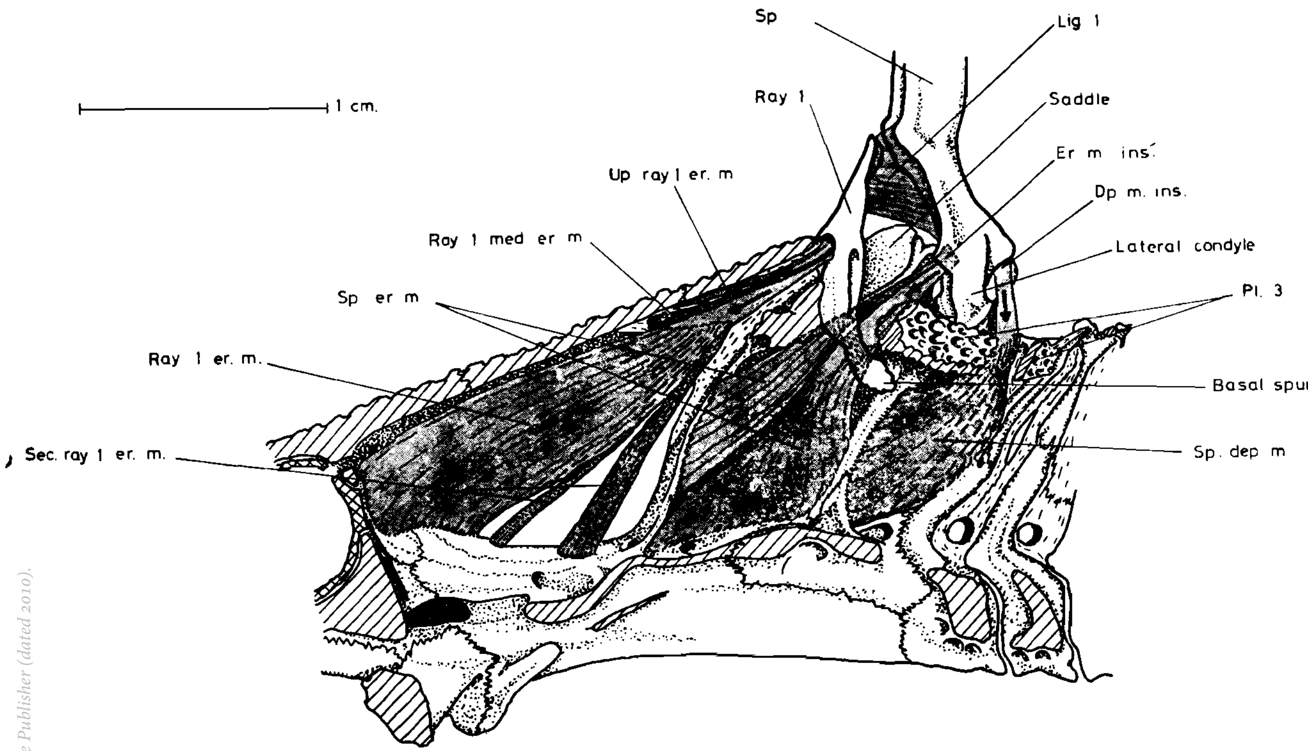

Figure 2. Lateral view of the postcranial region as in figure 1, but including the musculature of the first ray and the spine. The levator of the first ray is omitted here and shown separately in figure 3. For abbreviations see p. 94.

The first ray forms the locking mechanism for the spine and is firmly connected to the anterior surface of the latter by a very tough unstretchable ligament (Figs. 2 & 3, *lig. 1*). The first ray is short (1–1½ cm.) and in the shape of an inverted V. In its 'locked' position the distal undivided part projects vertically from the nuchal shield immediately in front of the spine, and its basal spurs fit through openings in the nuchal shield and curve backwards below it so that their ventral tips lie one on each side of the second proximal radial (Fig. 2). From this position the first ray can slide upwards and backwards into the 'unlocked' position over a boss or 'saddle' formed by the first distal radial, thus allowing depression of the spine. Movement in the lateral plane is impossible.

The first distal radial (the 'saddle') is fused to the distal end of the first proximal radial, and the first and second proximal radials, which are obliquely orientated and practically parallel to one another, are sutured to the neural spines of the fourth and fifth vertebrae (Fig. 1). All of this region is roofed over dorsally by the large nuchal plates which extend laterally around the locking mechanism to the level of the third proximal radial.

The musculature of the spine (ray 2) is very similar to that of *Pimelodus*. Two pairs of powerful erector muscles originate on the first and second proximal radials and on the fourth neural arch, their area of origin filling all the space between the first and second proximal radials. The muscles narrow to tendons which cross the medial surface of the lower limb of the first ray and emerge through the same openings in the dorsal surface to insert on the anterior surface of the spine dorso-lateral to the median condyle (Fig. 2, *sp. er. m.*). One pair of depressor muscles originates on the second and third proximal radials and on the fifth neural arch and emerges through a pair of posterior openings in the nuchal shield to insert on the posterior surface of the spine (Fig. 2, *sp. dep. m.*).

These two groups of muscles can effectively raise and lower the spine. No inclinator muscles are present and sideways movement is restricted by the nature of the articulation and the presence of a pair of ligaments stretching from the lateral condyles to the nuchal shield (Fig. 3, *lig. 2*).

The muscles of the first ray are more extensively modified. The erectors include one large component on each side, originating on the posterior surface of the skull and the anterior neural arches, and a number of minor components, some originating ventrally on the neural arches and some dorsally on the nuchal shield. These muscles narrow to tendons which pass through a special passage above the lateral distal process of the first proximal radial to insert on the anterior surface of the first ray (Fig. 2, *Ray 1 er. m.*).

No sign of depressor or inclinator muscles could be found, though the movement of the first ray is controlled by a ligament stretching from its lateral surface to the nuchal shield (Fig. 3, *lig. 3*).

Dissection, however, revealed the presence of another muscle, here termed the levator muscle of the first ray (Fig. 3). The origin of the muscle extends over the lateral surfaces of the third to fifth proximal radials. From here the muscle runs forwards, narrowing rapidly to a long tendinous band situated lateral and superficial to the erectors and depressors of the spine and embracing the basal spur of the first ray. Anteriorly the tendon divides to insert partly on the dorsal end of the first proximal radial and partly on the lateral distal process of the second proximal radial. In this position, thus, the basal spur of the first ray, when 'locked', projects down into the centre of the tendon as into a sock. There is no direct attachment of

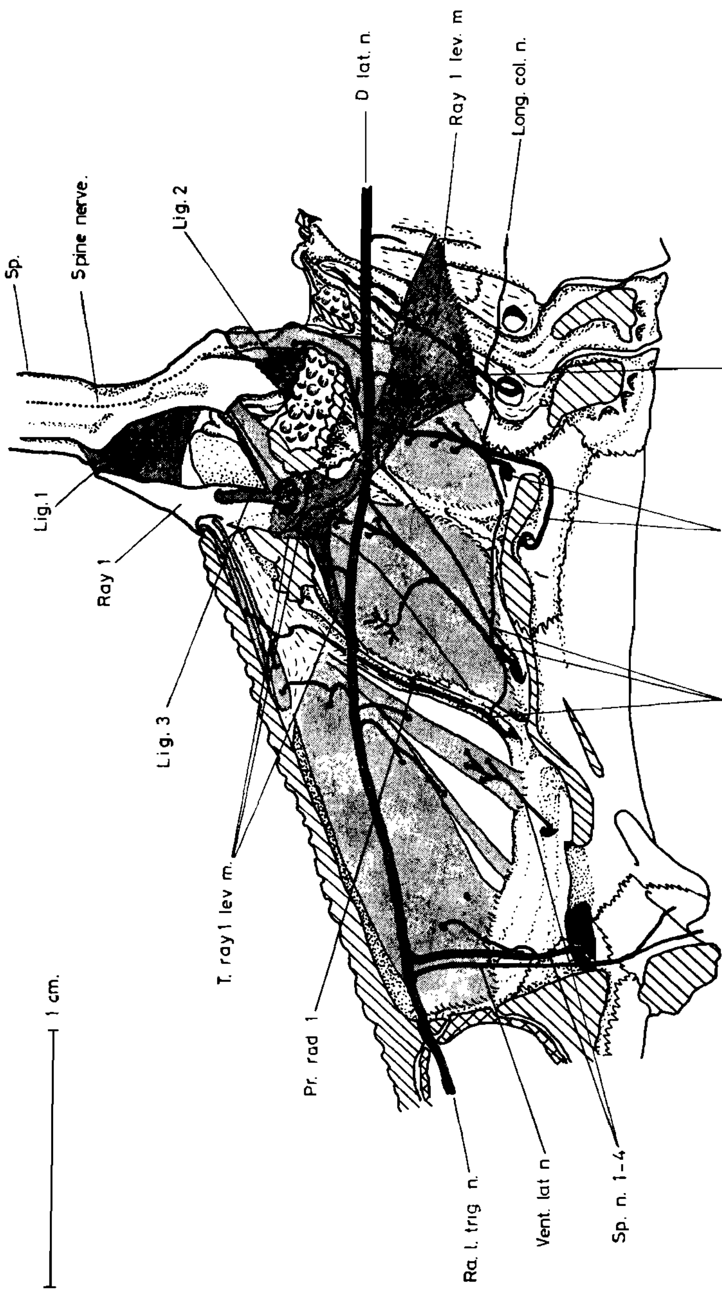

Figure 3. Lateral view of the postcranial region as in figure 1, but including the levator muscle of the first ray and the innervation of the area. The outlines of the muscles shown in figure 2 are indicated. For abbreviations see p. 94.

the tendon to the spur other than by very loose connective tissue. It is evident from the position of the tendon, and can be demonstrated by pulling on the muscle, that contraction of the muscle tightens the tendon and exerts a thrust on the basal spur of the first ray in an upwards and slightly backwards direction. For this reason the muscle has been named the levator of the first ray. Manipulation of a partly dissected specimen shows that if the spine is pressed backwards and the tendon is then pulled the first ray is lifted in its bony socket and the mechanism is 'unlocked'.

DISCUSSION

In *Synodontis* the spine is raised and lowered by its erectors and depressors exactly as in *Pimelodus*. The mechanism of the first ray, however, is very different. In *Pimelodus* the first ray is provided with erectors and also small depressors, both originating on the fourth neural spine. Alexander maintains that contraction of either or both of these muscles pulls the first ray forwards and downwards over its saddle so bringing it into its locked position, from which it cannot be extracted by any external force. Since the spine is firmly held to the first ray by ligament, it too is locked in the erect position. So far the arrangement in *Synodontis* is consistent, except that the musculature can be said to be more advanced in that the erectors have increased in size and shifted their origin forward onto the skull, and the depressors have disappeared entirely.

It is in the unlocking mechanism that *Synodontis* differs markedly from *Pimelodus*. As Alexander correctly states, the only force which can unlock the first ray is a vertical one, pushing up the basal spurs through their bony sockets. A horizontal force only tends to lock the mechanism more firmly. In *Pimelodus* such a vertical force is said to be provided by the resultant of the horizontal forward pull of the erectors of the first ray and the oblique upwards and backwards pull of the spine acting through the ligament attaching it to the first ray. This theory therefore implies that the erectors of the first ray have changed their function and not only cause erection of the ray, but also contribute to its depression (or unlocking) when acting together with the depressors of the spine. It is apparent that a vertical force could not be produced in the same way in *Synodontis*, for the pull of the erectors of the first ray is not horizontal but obliquely downwards and forwards, and moreover the main axis of the ligament connecting the spine and the first ray is almost horizontal. A resultant of their forces would thus be obliquely downwards and backwards, the very action that the whole locking mechanism is designed to resist. We therefore maintain that the necessary vertical force is provided by the curious muscle here termed the levator of the first ray, which on contraction raises the basal spurs of the first ray. The resultant of this force and the backward pull on the ligament attaching the first ray to the spine (due to the depressor of the spine) would be in an upward and backwards direction and would efficiently extract the first ray from its socket and allow depression of the spine (Fig. 4). It is then not necessary to assume a changed function for the erector of the first ray.

The evolutionary origin of the levator of the first ray is debatable. There are two possibilities. Firstly, it might be a modified depressor of the first ray, but considering the completely different orientation of the fibres, and the fact that in *Pimelodus* the depressor is already reduced, this is unlikely. Secondly, it might be a slip which has separated off from the lateral body musculature. Dissection shows that the anterior apex of the cone of the medio-dorsal moiety of the body musculature (using Shann's terms, 1919) is fastened to the distal end of

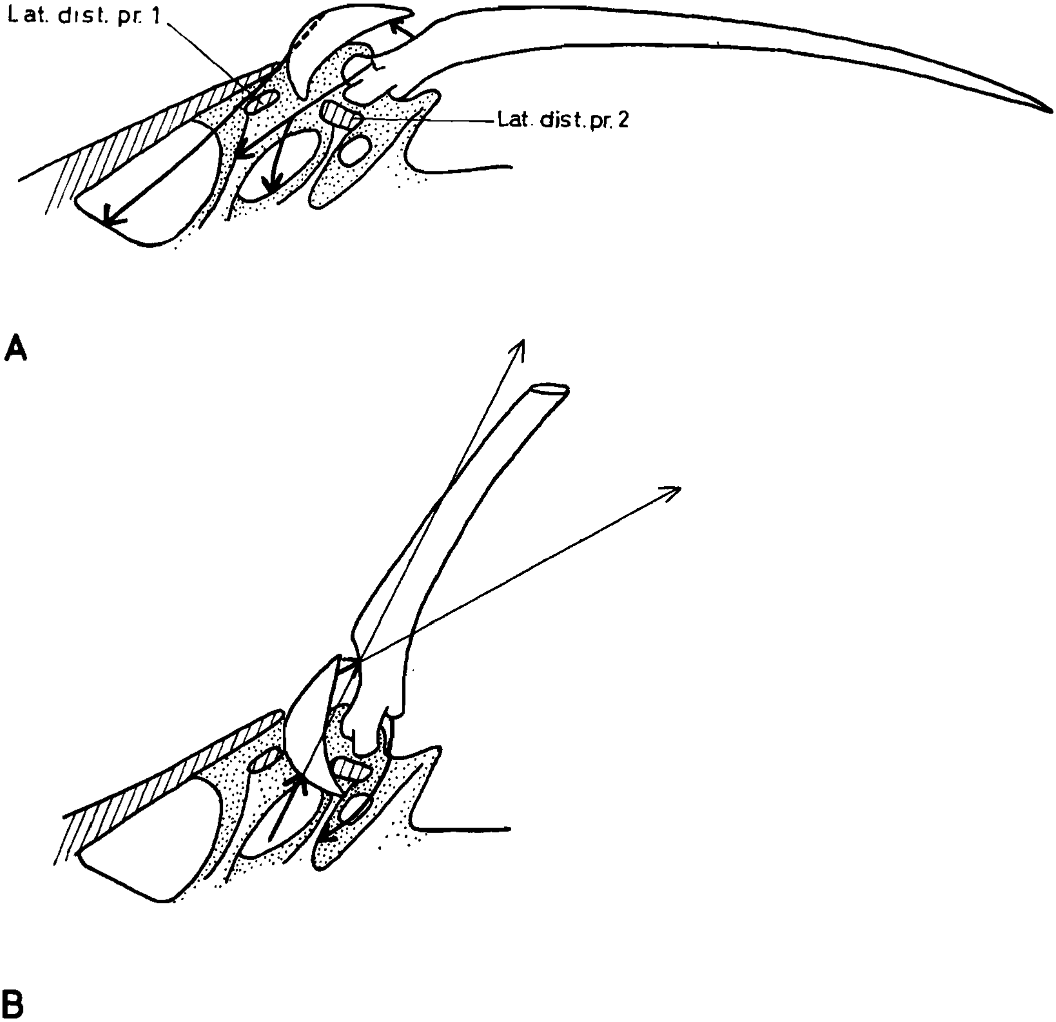

Figure 4. Diagram of the first ray and spine, A, in the depressed position showing the forces responsible for erection and locking, and B, in the erect position showing the forces responsible for unlocking and depression.

the second proximal radial; while the anterior apex of the cone of the laterodorsal moiety is fastened to the neural spine of the fourth vertebra (which is sutured to the first proximal radial). This suggests that the first myomere of the mediodorsal moiety may have become modified as the levator, retaining its attachment to the first proximal radial. It is possible that during the normal behaviour of the fish erection and locking of the spine are associated with a stationary position or 'freezing' of the body when danger threatens, and that unlocking occurs when the fish swims off once more if the levator muscle is to move in rhythm with the normal body myotomes.

It will be interesting to discover whether such a muscle occurs in other species of catfish

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SUMMARY

The structure and mechanism of the locking dorsal fin-spine is described for *Synodontis zambesensis*, an 'advanced' catfish of the family Mochokidae, and compared with that of *Pimelodus*, a 'fairly primitive' catfish of the family Pimelodidae. The locking mechanism of the spine was found to be very similar in the two, but the unlocking mechanism was different, *Synodontis* possessing a special muscle for the purpose, namely the levator of the first ray.

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ABBREVIATIONS USED IN THE TEXT FIGURES

Ap. sp. er. m.	Aperture for spinal erector muscle
Ar. rg.	Articulatory ring
Boc.	Basioccipital
D. lat. n.	Dorsal branch of lateralis nerve
Dp. m. ins.	Insertion of the depressor muscle of the spine.
Er. m. ins.	Insertion of the erector muscle of the spine
Exoc.	Exoccipital
For. l. n.	Foramen for lateralis nerve
For. sp. n.	Foramen for spinal nerve
Lat. dist. pr. 1, 2.	Lateral distal processes of the first and second proximal radials
L. proc. vert.	Lateral process (parapophysis) of vertebra
Lig. 1, 2, 3	Ligaments 1, 2 and 3 (see text)
Long. col. n.	Longitudinal collector nerve
N. proc.	Neural spine
Pl.	Nuchal plate
Pr. rad. 1–4	Proximal radials 1–4
Ra. l. trig. n.	Ramus lateralis trigeminus nerve
Ray 1 *er. m.*	Main erector muscle of the first ray
Ray 1 *lev. m.*	Levator muscle of the first ray
Ray 1 *med. er. m.*	Median erector muscle of the first ray originating on the inner longitudinal partition of the bony tunnel
Sec. ray 1 *er. m.*	Secondary erector muscle of the first ray
Sn.	Supraneural
Soc.	Supraoccipital
Sp.	The defensive spine (second ray)
Sp. dep. m.	Depressor muscle of the spine
Sp. dp. m. ap.	Aperture for the depressor muscle of the spine.
Sp. er. m.	Erector muscle of the spine
Sp. n.	Spinal nerve
T. ray 1 *lev. m.*	Tendons of the levator of the first ray
Up. ray 1 *er. m.*	Upper erector muscle of the first ray originating on the upper wall of the bony tunnel
Vent. lat. n.	Ventral branch of lateralis nerve
Vert.	Vertebra