ABOUT SOME SKELETAL PARTICULARITIES OF THE FIRST VERTEBRAE RELATED TO THE MODE OF PREY CAPTURE IN *URANOSCOPUS SCABER* (URANOSCOPIDAE)

by

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ABSTRACT. - Feeding in *Uranoscopus scaber* is characterised by bending of the body just behind the head. Bending is related to the organisation of the first five vertebrae: vertebral centra of lesser height fitting one into the next; short, less tilted neural spines, presence of many intervertebral ligaments. Bending of the vertebral column causes the head to rotate upward and the mouth to open just beneath the prey; it also brings the pharyngeal jaws, shifted with respect to each other at rest, to face each other.

RÉSUMÉ. - Particularités squelettiques des premières vertèbres en relation avec le mode de prise de nourriture chez *Uranoscopus scaber* (Uranoscopidae).

La prise de nourriture chez *Uranoscopus scaber* est caractérisée par une pliure du corps, située à l'arrière de la tête. Cette pliure est en rapport avec l'organisation des cinq premières vertèbres: corps vertébraux peu élevés et emboités les uns dans les autres, neurépines courtes et redressées, présence de nombreux ligaments intervertébraux. Cette pliure entraîne une rotation de la tête qui amène la bouche à s'ouvrir vers le haut immédiatement sous la proie et place les mâchoires pharyngiennes, décalées au repos, les unes en face des autres, les rendant aptes à saisir la proie.

Key-words. - Uranoscopidae, *Uranoscopus scaber*, Feeding, Vertebral column.

The stargazer, *Uranoscopus scaber* Linné, 1758, is a Mediterranean fish that feeds by lying in wait for its prey. Its head is flat and wide, corresponding with a benthic life. Buried in the sand almost to its eyes, it attracts its prey by means of a protractile appendix attached to the mandible and waved like a lure (Bauchot and Pras, 1980; Pietsch, 1989). At the right moment, it lunges quickly out of the substrate and catches the prey, or tries to. The lunge is caused by bending between the head and trunk, by 60° and more (Goosse *et al.*, 1995). The aim of the present paper is to examine whether there are special adaptations of the anterior vertebral column that make this bending possible, and to assess changes in the disposition of cephalic skeletal structures as bending occurs. The cephalic skeleton has been described by Pietsch (1989) and will thus not be described again here.

MATERIAL AND METHODS

Twelve dead *Uranoscopus scaber* specimens (standard length between 16 and 25.5 cm) were stored frozen or in alcohol. One was cleared with trypsin and stained with alizarin red for observation of the bony skeleton, the others were dissected and examined with a Wild M10 stereobinocular microscope equipped with a camera lucida and a photographic tube.

Three live specimens (standard length: 17.5, 19 and 22 cm) were acclimated to living and feeding on live prey in an aquarium. They were filmed at 400 fps with a Photosonics 1PL camera (Eastman Kodak High Speed film, 400 ASA, 3200K°).

All specimens studied were from Calvi Bay (STARESO station) and Lion Gulf (Grau du Roy aquarium), France.

Abbreviations used in the figures

BOC: basioccipital	NA: neural arch	POZ: postzygapophysis
E: eye	NS: neural spine	PZ: prezygapophysis
HY: hyobranchial apparatus	OP: opercle	SPNF: spinal nerve foraman
LI 1,2,3,4,5: ligament 1 to 5	PF: pectoral fine	VC: vertebral centrum
MAX: maxilla	PJ: pharyngeal jaw	V1,2,3,4,5,6: vertebra 1 to 6
MD: mandible	PAP: parapophysis	

RESULTS

Movements

Bending of the vertebral column in *Uranoscopus scaber* occurs when a live prey passes above its head (Fig. 1). Bending causes a slight elevation of the trunk and a major lifting of the neurocranium. It always takes less than 3/100 s, after which the fish resumes its initial position at a quite variable speed (32/100 s to 55/100 s).

Vertebrae

The first five abdominal vertebrae display several original features. They bear broader neural spines than the following vertebrae. The first neural spine is shorter than the neurocranium heigth. The length of the neural spines increases from the first to the sixth vertebra and these first neural spines are not tilted as far backward as the following ones. Viewed from the side (Fig. 3), the first four vertebral centra are lower than those of the following vertebrae; they display no prominent parapophyses (Fig. 2).

The first two vertebrae bear no ribs. The first vertebra is longer than the following ones and is attached to the occipital region by short fibres, from the top of the short neural spine to the base of the vertebral centrum; this makes it almost completely immobile. The next three vertebrae are short and their vertebral centra are wider than high. The anterior end of each one is narrower than the posterior end of the preceding one, so that the first four vertebrae interlock. The second, third, and fourth neural arches are situated quite forward on the vertebral centra. The front part of each vertebral centrum is narrower than the rear part of the preceding one. They bear prezygapophyses with extended, outward-turned articulation surfaces. Each of these surfaces is coapted to that of the inward-turned postzygapophysis of the preceding vertebra (Fig. 3).
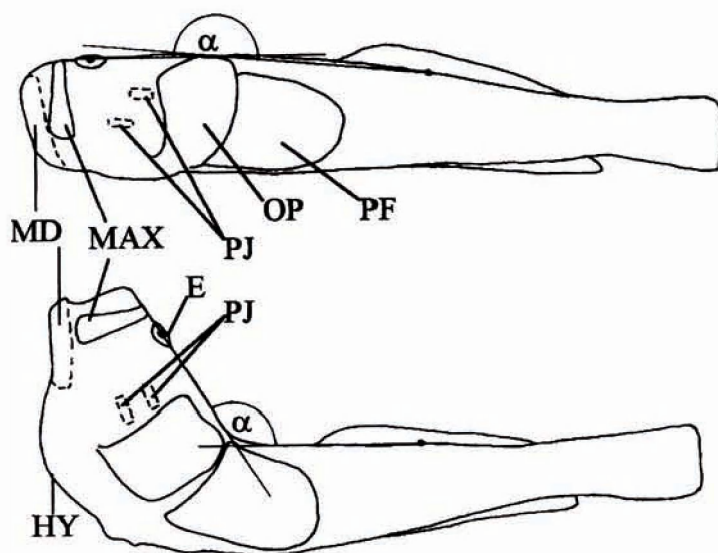
Fig. 1. - *Uranoscopus scaber*. Schematic lateral views showing above, the fish lying in wait for its prey, and below, the fish with raised head, when the mouth is wide open and bending is maximal. The prey has already been sucked into the buccal cavity. The drawings were made from frames of a film made at 400 frames per second.
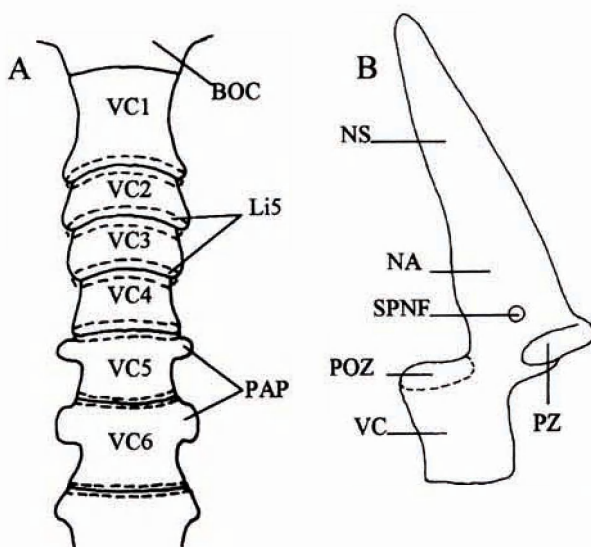

Fig. 2. - *Uranoscopus scaber*. A: Ventral view of the first vertebrae; the interrupted lines show the limits of the Li5 ligaments. B: Lateral view of the second vertebra; the interrupted lines situate the zone where the postzygaphophysis articulates with the prezygapophysis of the next vertebra.

The third vertebra bears a pair of ribs at the upper extremity of the neural arch. The fourth is flanked by ribs, articulated on the lateral walls of the neural arch. Not until the
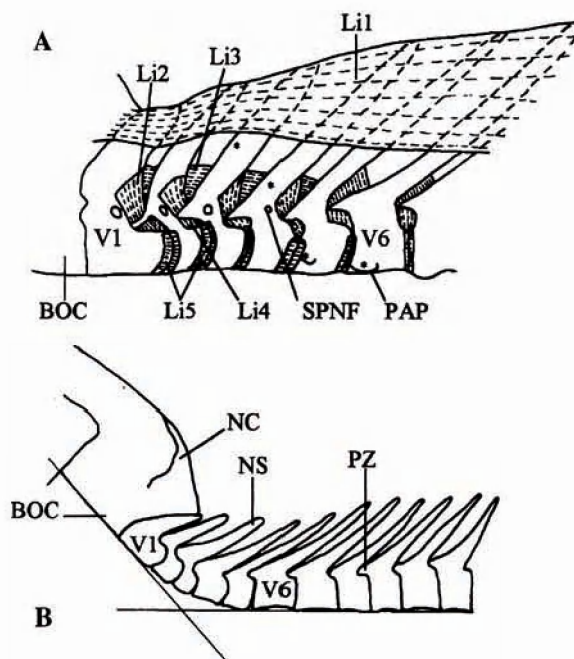
Fig. 3. - *Uranoscopus scaber.* A: Lateral view of the first vertebrae and associated ligaments; B: Lateral view of the positions of these vertebrae when bending exceeds 45°. Asterisks indicate where the ribs articulate with the vertebrae.

fifth vertebra do the ribs appear as usual on the parapophyses. The fifth vertebra looks partially "normal". Although the front of its vertebral centrum is still narrow and flattened, its posterior surface has the same shape as the following vertebra. The parapophyses protrude ventro-laterally at the front of the vertebral centrum. The neural arch is located almost completely above the vertebral centrum and is extended by a more tapered neural spine.

All of the vertebrae are attached to each other by ligaments. A large dorsal septum (Ll.1) encloses the neural spines from the rear to the fifth vertebra; then it thickens and shortens as the height of the neural spines decreases. It attaches to the rear of the neurocranium where it spreads out. A part of the epaxial musculature (wide and voluminous in the back of the head) inserts onto this septum.

Thick ligaments (Ll.2) link each neural arch with the dorsal side of the prezygapophysis of the next vertebra. The first four ligaments are a little more tilted than the following ones, which are wider and thinner. In between the first five vertebrae there is a ligament Ll.3, almost horizontal and partly masked by Ll.2 (completely masked between the next vertebrae). Another thick ligament (Ll.4) links the inner surface of a prezygapophysis with the postzygapophysis and the vertebral centrum of the preceding vertebra. Lastly, each vertebral centrum is linked to the next by a ligament Ll.5 consisting of short fibres. The Ll.5 fibres connecting the first four vertebrae appear longer than those of the following ligaments.

Buccal parts and pharyngeal jaws

One original feature of the buccal and pharyngeal jaws is their position. While the fish is lying in wait, the two buccal jaws are almost vertical (Fig. 1A). Upon bending and prey capture, the neurocranial elevation raises the buccal jaws but the mandible retains practically the same vertical position whereas the maxillaries and premaxillaries become almost horizontal (Fig. 1B). The expansion of the buccal cavity is confirmed by the hyoid depression in comparison with the neurocranium top, but not with the bottom (elevation).

Observed on dead animals, the lower pharyngeal jaws are located forward the upper jaws in extended position (Fig. 1A). In curved position, the upper and lower pharyngeal jaws appear opposite (Fig. 1B).

DISCUSSION

Teleosts have different systems for opening their mouths. Elevation of the neurocranium is one possible system; it is always caused by contraction of the epaxial musculature (Vandewalle, 1978; Liem, 1979; Sibbing, 1982; Westneat and Wainwright, 1989). Elevation of the neurocranium by about 10° during feeding has been described in many fish (Alexander, 1967; Liem, 1979; Lauder, 1979, 1980, 1981; Lauder and Liem, 1981; Sibbing, 1982; Muller, 1987; Westneat, 1994; Vandewalle *et al.*, 1995). This lifting does not seem to require special anatomical features. Some teleosts are capable of a greater elevation of the cephalic region: 35° for *Macrochirichthys macrochirus* (Valenciennes) (Howes, 1979), 40° for *Luciocephalus pulcher* (Gray) (Lauder and Liem, 1981), 50° for *Synanceia verrucosa* Bloch & Schneider (Grobecker, 1983), 40° for Syngnathidae (Bergert and Wainwright, 1997). Lesiuk and Lindsey (1978), Howes (1979) and Lauder and Liem (1981) have evidenced the specialised morphological features of certain teleosts capable of extreme markedly bending of the front of the vertebral column. In all cases the anterior vertebrae are modified, but in different manners. *Macrochirichthys macrochirus* raises its head simply by rotating around the first, reduced vertebra, fitting into the second vertebra (Howes, 1979). In the characoid *Raphiodon vulpinus* (Agassiz), bending can reach 45° and occurs posterior to the first four vertebrae, probably because of the presence of the Weberian apparatus. The fifth vertebra is wide, not very high, and bears a shorter neural spine than the following ones (Lesiuk and Lindsey, 1978). In *Uranoscopus scaber*, the changes in the vertebral column concern the first five vertebrae, which explains why the bending angle can be exceptionally great in this species (Goosse *et al.*, 1995). When the epaxial musculature, fixed on a small occipital crest and a wide occipital region (Piestch, 1989) contracts, vertebrae two to five, being not high, are lifted. This rotation is made possible by the interlocking of the first vertebral centra, the incline of the pre- and postzygapophyses, and the difference in width between the front and rear of the first neural arches, enabling them to cover each other to a certain degree. The structures limiting this rotation are probably the LI.5 ligaments and the neural spines. The subsequent vertebrae, because of their standard morphology, should not enable the vertebral column to curve differently from what is usually observed in teleosts (Lauder, 1979; Sibbing, 1982; Vandewalle *et al.*, 1995). Downward bending of the anterior region of the vertebral column should be minimal slight to impossible in *Uranoscopus scaber*, due to the presence of ligaments LI.1, LI.2, LI.3, and LI.4.

In acanthopterygians, during feeding, the mouth, pointed towards the prey, opens first, after which the buccal cavity, then the opercular cavity dilate, causing the prey to be sucked in. Finally the pharyngeal jaws, facing each other, separate to grasp the prey (Lauder, 1980, 1981; Westneat and Wainwright, 1989; Vandewalle et al., 1992, 1995). In Uranoscopus scaber, the mouth is turned upward. Opening of the mouth without rotation of the neurocranium would protrude the mouth opening, whereas the prey is located above the predator. Rotation of the neurocranium makes it possible to open the mouth upward, (practically) without modifying the orientation of the mandible. The distance between the mandibular and the premaxillaries increases, nevertheless, as upon any opening of the mouth (Alexander, 1967; Lauder, 1980, 1981; Vandewalle, 1980). This requires participation of the ventral musculature of the head (protractor hyoideus and sternohyoideus muscles) to maintain the mandible at its position. Contraction of this musculature is attested by depression of the buccal cavity bottom (ventral part of the hyobranchial system) with respect to the skull. If this did not occur, the mandible would follow at least partially, like the rest of the head, the rotatory motion of the neurocranium. The originality of mouth opening in U. scaber thus does not reside in any special motion of the buccal parts with respect to one another, but solely in the possibility of bending the vertebral column to a larger degree than other teleosts. In the stonefish Synanceia verrucosa, which also lies in wait like U. scaber, bending causes only raising of the head without motion of the body. In the stonefish the mandible is also practically vertical at rest and remains so during opening of the mouth (Grobecker, 1983).

Bending of the vertebral column most probably has a second beneficial consequence. At rest, the toothed plates of the pharyngeal jaws of Uranoscopus scaber do not face each other as in most teleosts (Liem, 1970; Liem and Osse, 1975; Aerts et al., 1986; Gobalet, 1989; Vandewalle et al., 1992); the lower ones are markedly in front of the upper ones. In this position, the pharyngeal jaws would be unable to grasp a prey. Major bending of the front of the vertebral column, causing rotation of the neurocranium, may cause an upward rotation of the upper pharyngeal jaws while the lower ones are retained by the depression of the mouth bottom; this would place the toothed plates one above the other, position enabling them to grasp a prey.

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