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THE VERTEBRAL COLUMN OF THE TRIASSIC FISH *SAURICHTHYS* (ACTINOPTERYGII) AND ITS STRATIGRAPHICAL SIGNIFICANCE

ANDREA TINTORI

Key-words: Triassic, *Saurichthys* (Actinopterygii), Vertebral column, Stratigraphy.

Riassunto. Esemplari appartenenti al genere *Saurichthys* sono relativamente comuni in tutto il Triassico e si rinvencono frequentemente in tutti gli ambienti bacinali con fondali anossici del Norico della Tetide occidentale. Almeno quattro specie possono venire facilmente individuate soprattutto in base alle caratteristiche della colonna vertebrale: tutte mostrano infatti prezigapofisi più sviluppate che nelle specie prenoriche. La lunghezza relativa di questo processo è massima nelle due specie del Norico superiore, raggiungendo una lunghezza pari ad almeno sei segmenti vertebrali. Tale significativa variazione viene messa tentativamente in relazione con un importante cambiamento nella fauna a pesci. La comparsa in massa dei *Pholidophoridae* durante il Norico porta alla sostituzione di gran parte dei piccoli pesci che costituivano il cibo principale dei *Saurichthys*. I Folidofori, erano infatti in grado di nuotare meglio dei Subholostei e dei Chondrostei che popolavano i mari triassici prima del Norico stesso. Essendo la morfologia di *Saurichthys* già ben adattata alla predazione, l'unico cambiamento possibile poteva consistere in un irrobustimento della colonna vertebrale allo scopo di sviluppare una maggior potenzialità di scatto. E' infatti plausibile che le modalità di predazione di *Saurichthys* fossero sostanzialmente simili a quelle degli attuali lucci e barracuda. L'autore evidenzia la possibilità di un utilizzo stratigrafico, sia pure informale, della lunghezza relativa delle prezigapofisi di *Saurichthys*, per lo meno nel Norico.

Abstract. The Norian beds of the Southern Calcareous Alps have yielded at least four species belonging to *Saurichthys*. Their vertebral column has large praezygapophyses, which, in each of these nominal species, attain a different relative length. The latter is inversely proportional to age: in fact, the youngest two, coeval species have the longest praezygapophyses, at least six times as long as a vertebral segment. Such a conspicuous change in an otherwise conservative genus, is here related to a major ichthyofaunal break that saw the flourishing of the *Pholidophoridae*. The relative length of the praezygapophyses can be a very useful stratigraphical means, at least in the Norian (Upper Triassic).

Introduction.

The chondrosteian genus *Saurichthys* is one of the best known Triassic fishes. Detailed papers have been published by Stensiö (1925), Lehman (1952), Griffith (1959, 1962, 1977) and Rieppel (1985); several authors have described specimens from all over

the world (Beltan & Tintori, 1980). Unfortunately, most of the nominal species are based on very scanty or fragmentary specimens, often a single tooth. As a consequence, the taxonomy is very complicated and will certainly need a revision, which is beyond the aim of this paper. For this reason I refer to my new material as *Saurichthys* sp. A and *Saurichthys* sp. B (from the Bergamo Prealps) and *Saurichthys* sp. C (from the Preone Valley; see Tintori et al., 1985). The specimen from the Garza Valley is ascribed to *S. seefeldensis* Strand, 1928 on the base of a comparison with topotypical specimens.

In the Bergamo Prealps several specimens of *Saurichthys* have been collected; they are more or less complete, and one of them is, as far as I know, the longest known *Saurichthys* specimen, its standard length reaching 165 cm. The distinction of two species among them is due to differences in squamation and in the skull post-orbital length-orbital diameter ratio. Furthermore, *Saurichthys* sp. B shows a more slender body than *Saurichthys* sp. A, even though the elements of the vertebral column are stouter. Beltan and Tintori (1980) have already briefly described a specimen of *Saurichthys* sp. A, especially pointing out the dermocranial characters.

Up to the present day only a body fragment of a small saurichthyid is available from the Preone Valley localities, its vertebral elements being clearly different from those of both the Bergamo species. Again, only body fragments of *S. seefeldensis* Strand are taken into account, both from the Seefeld beds and the Garza Valley locality. *S. seefeldensis* is the only Norian species that has been reliably dated, being found with conodonts which indicate a lowermost Alaunian age (*bicrenatus* ammonite zone, sensu Krystyn, 1983; Donofrio et al., in press).

A close investigation of the vertebral column leads to new interesting anatomical considerations as well as to a key to Norian *Saurichthys* species, also useful in stratigraphy.

Previous works.

A detailed description of the vertebral column has been given only for a few *Saurichthys* species (Stensiö, 1925; Lehman, 1952; Griffith, 1959, 1962). According to these authors, the *Saurichthys* vertebral elements show a similar morphology in most species. Paired neural arches, which are present all along the body, are coupled with ossified haemal arches only behind the pelvic fins. Pairs of subsequent haemal arches are always fused, so that their number is only half of that of corresponding neural elements. However Rieppel (1985), giving a detailed restoration of the axial skeleton of three Ladinian (Middle Triassic) species, described for *S. curionii* (Bellotti) a complete series of haemal elements that never fused in couples. The other two Ladinian species had a similar pattern, confirmed by personal observations on undescribed specimens. This configuration seems to be restricted to these three species, even though it may also be present in *Brevisaurichthys osseus* Beltan (Beltan, 1972, pl. 14, fig. B).

Though either the general shape or the dermal skull covering of all the Norian specimens closely resemble those of most of the *Saurichthys* species, a detailed observa-

tion of my material points out a peculiar character which is unknown in all the previously described species. This is the presence of very well developed praezygapophyses (sensu Rieppel, 1985; anterior process or zygapophyses of Stensiö, 1925), comparable in size to the neural spines. Praezygapophyses are known only in few species [*S. ornatus* Stensiö from the Lower Triassic (Stensiö, 1925) and *S. curionii*, *S. macrocephalus* (Deecke), and especially *S. costasquamosus* Rieppel from the Ladinian (Rieppel, 1985)], but they never reach the extension seen in the Norian specimens.

Abbreviations: MCSNB = Museo Civico di Storia Naturale, Bergamo; PT and GT = Dipartimento Scienze della Terra, Milano, field catalogue; MFSNU = Museo Friulano di Storia Naturale, Udine; IGPIU = Institut für Geologie und Paläontologie der Universität Innsbruck; na = neural arches; ns = neural spines; p = praezygapophyses; s = scales.

Paleontological descriptions

Saurichthys sp. A (Fig. 1A, 3I).

Saurichthys sp. A (two specimens, PT2 and MCSNB 6170, from uppermost Calcare di Zorzino, upper Norian) has very stout vertebral elements with neural arches and spines like those of *S. krambergeri* Schlosser (Griffith, 1962), except for the praezygapophyses. The neural spines are distally truncated, wide and very close to each other, so that, without suitable preparation, the praezygapophyses are seldom visible. These latter also are blunt and laterally flattened, with no possibility of relative longitudinal shift in each pair. They are more or less as long as their relative neural spines. The angle formed by the praezygapophyses with the body axis is about 30°, wider than in *Saurichthys* sp. B. Neural spines show a somewhat wider angle, around 35°.

Saurichthys sp. B (Fig. 1B, 2, 3H).

In one specimen of *Saurichthys* sp. B (MCSNB 1906 from uppermost Calcare di Zorzino, upper Norian) more than 157 neural arches are present, small and subquadrate; their size increases rather quickly back to the middle of the abdominal region, then only very slightly. The neural spines follow the same pattern, being 8.3 mm long near the 30th vertebral segment, 12 mm at the 80th and 13 mm in the caudal peduncle. Neural spines are very slender; they slope backwards from the postero-dorsal corner of each neural arch at a 35-45° angle with the body axis. Neural arches lie close to each other; spines are well spaced, so that praezygapophyses are largely visible.

The praezygapophyses occur all along the vertebral column. Since they are directed forwards, I presume they might either be missing or be reduced in the foremost vertebral segments. Unfortunately, because of the dermal bone covering, it has been impossible to observe this region in any of the prepared specimens. The praezygapophyses, like the neural spines, increase in length backwards from the anterior region, from

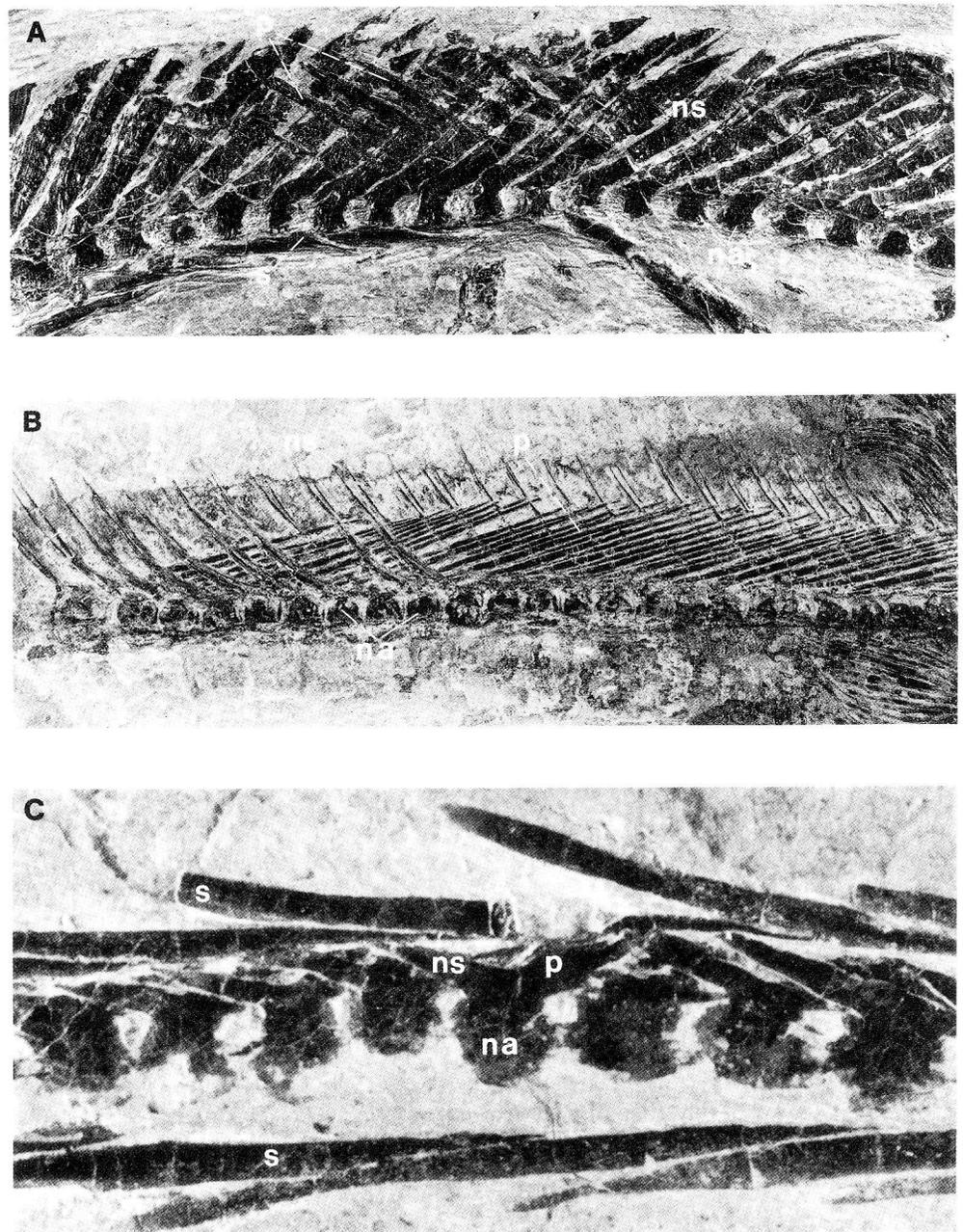


Fig. 1 - Comparison of vertebral column elements in: A) *Saurichthys* sp. A, specimen PT2, s.l. 900 mm, detail of the posterior abdominal region; anterior to the left; x 1.6; B) *Saurichthys* sp. B, specimen MCSNB1906, s.l. \pm 500 mm, detail of the anterior abdominal region; anterior to the right; x 2.7; C) *Saurichthys* sp. C, specimen MFSNU GP1800, s.l. unknown; anterior to the right; x 11.2.

about 12 mm to 16.5 mm near the 80th vertebral segment. They are splint-like, tapering very gently from their base, sloping forwards at an angle of about 15° in the anterior abdominal region and 12° in the pelvic fins region. Each praezygapophysis lies very close to the adjacent ones, in its proximal region, so that only elements from one side are visible. In the same region they must have been transversally gently wavy: this might have caused a median contact between the paired elements. Distally both elements of the pairs are completely visible. This is probably due to partial shifting of a neural arch row during fossilization (Fig. 2).

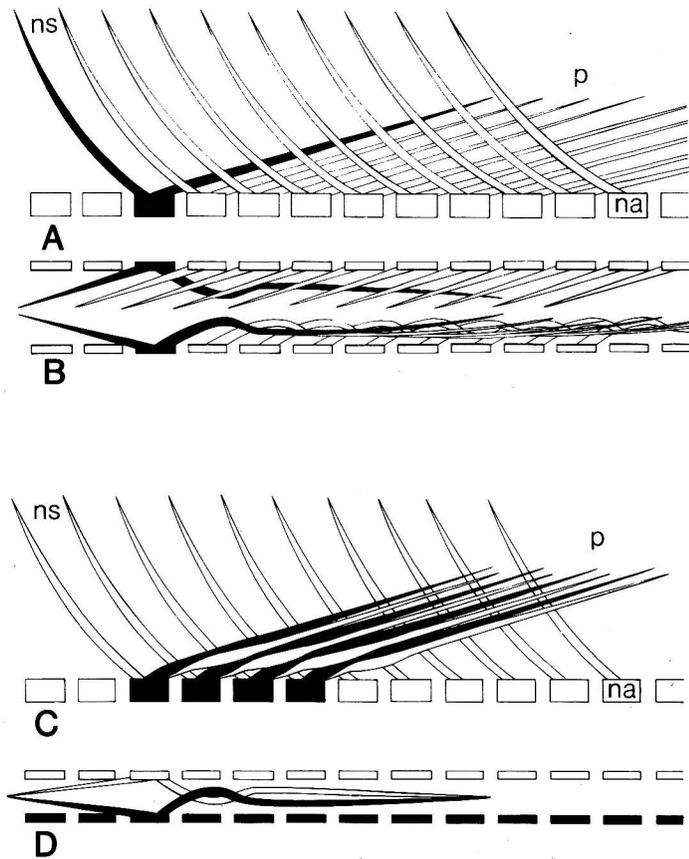


Fig. 2 - *Saurichthys* sp. B. Schematic restoration of a fragment of the vertebral column in the abdominal region, based mainly on specimen MCSNB 1906; anterior to the right. A-B) In life restoration (A, lateral view; B, dorsal view in which the left side shows only neural arches and spines and the right side shows only praezygapophyses; full black is for a complete vertebral segment). C-D) After fossilization (C, lateral view in which no right neural spines have been shown; D, dorsal view; full black is for right vertebral elements).

In the posterior caudal region, both neural arches and praezygapophyses apparently form a lower angle with the body axis, but no detailed observations could be done on my specimens. However, this is consistent with data concerning *S. costasquamosus* (Rieppel, 1985; fig. 42).

Saurichthys sp. C (Fig. 1C, 3F).

This species is so far known only by one specimen (MFSNU GP1800) from Preone Valley (Lower Norian).

It has subquadrate neural arches with slightly concave anterior and posterior edges. The neural spines are short and each one lies in a shallow depression at the base of the following praezygapophysis. These latter look very massive, being medially well expanded. Since both the praezygapophyses and the neural spines slope at a very low angle from the neural arch, the vertebral column results to be a compact, low structure, where elements are closely tied to each other.

Saurichthys seefeldensis Strand, 1928 (Fig. 3G).

This species (specimens GT1 and IGPI P9024) has neural arches and spines very similar to those of *Saurichthys* sp. A, but its praezygapophyses are shorter, measuring about half the corresponding neural spines. The angle between these latter and the body axis is 35°-37°; the praezygapophyses slope at 30° in the Italian specimen and at 45° in the Seefeld one. Such difference is clearly related to the fact that the two studied fragments belong to different parts of the fish body.

Conclusions.

Saurichthys is a long ranging genus, spanning at least 30 M.Y. in the Triassic (Beltan & Tintori, 1980). During this long period the general anatomical pattern changes only in details of squamation and dermal bones. Nevertheless, in the light of the results of the present study, the vertebral column is involved in major changes, at least during the Norian.

As already pointed out, several species have only double haemal arches posterior to the pelvic fins, with absent or very small praezygapophyses. All the Lower Triassic species show this pattern (Stensiö, 1925; Lehman, 1952). Another group of species has small praezygapophyses and single haemal arches all along the body, with well developed haemal spines posterior to the pelvic fins (Rieppel, 1985). Norian species have no haemal arches in front of the pelvic fins and their praezygapophyses became longer and longer during that stage.

The abnormal growth of the praezygapophyses may be considered as a very important derived character, probably connected to a major change in the swimming.

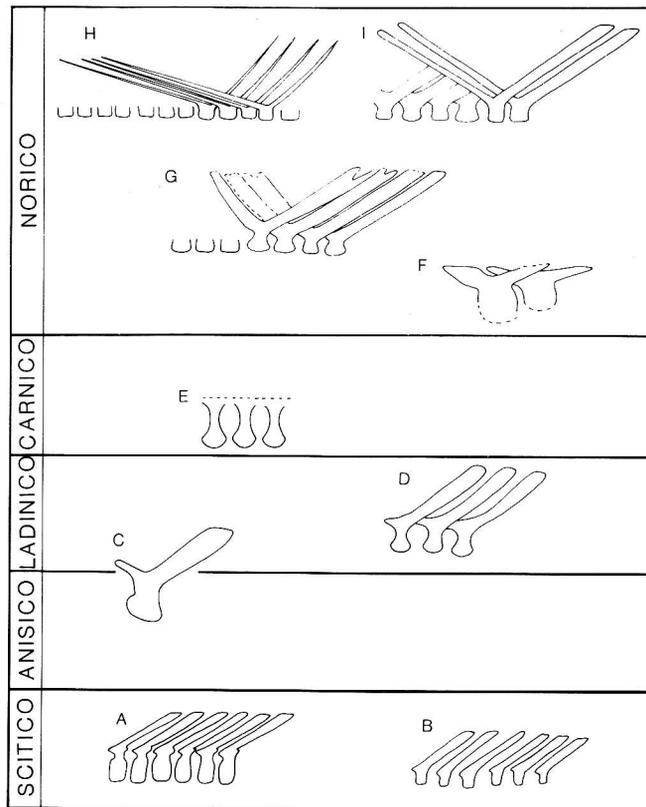


Fig. 3 - The dorsal vertebral elements in some of the best known *Saurichthys* species; anterior to the left.
 A) *Saurichthys ornatus* Stensiö, after Stensiö, 1925;
 B) *Saurichthys madagascarensis* Piveteau, after Lehman, 1952;
 C) *Saurichthys costasquamosus* Rieppel, after Rieppel, 1985;
 D) *Saurichthys curionii* (Bellotti), after Rieppel, 1985;
 E) *Saurichthys striolatus* (Bronn), after Griffith, 1959;
 F) *Saurichthys* sp. C;
 G) *Saurichthys seefeldensis* Strand;
 H) *Saurichthys* sp. B;
 I) *Saurichthys* sp. A.

The *Saurichthys* morphology suggests an *Esox*-like attack pattern, with a well developed forward lunge. *Lepisosteus* shows a similar body shape, but its predation is characterized by sideway striking. Its ability to bend suddenly is probably due to the presence of opistocoelus vertebrae, a unique character of *Lepisosteus* itself.

So, why did this change occur only in the Norian, thus near the end of the history of this conservative genus? Actually, it is coeval with a major ichthyofaunal change. The *Pholidophoridae*, in fact, were increasing in variety and number so much that they outnumbered, by the end of this stage, all the other small fishes on which *Saurichthys*

preyed; during the preceding Triassic time they were mainly "subholosteans" (Rieppel, 1985), worse swimmers than the *Pholidophoridae*. *Saurichthys* had, by that time, acquired a highly specialized shape; it is possible that, to be still competitive in the predation, its inner structures had to become stronger.

A first appearance of this process is seen in *S. costasquamosus* from Lower Ladinian (Rieppel, 1985). Nevertheless it seems to fail: species such as *S. curionii* and *S. macrocephalus*, known from most of the Ladinian (pers. obs.), show less developed praezygapophyses (Rieppel, 1985) and Carnian species have no praezygapophyses at all [*S. striolatus* (Bronn); Griffith, 1959 and pers. obs., and *S. calcaratus* Griffith; Griffith, 1977]. The definite increase in the praezygapophyses size starts only with the Norian *Saurichthys* sp. C and reaches its maximum in the two Bergamo species. In *Saurichthys* sp. C praezygapophyses are as long as only one vertebral segment, in *S. seefeldensis* they are three to four times and in *Saurichthys* sp. A and B up to six-seven times. The hypothesized link between the size of praezygapophyses and the growing of the pholidophorid population cannot be definitely proved, but it appears a plausible solution to the problem.

Whatever the cause of the process, the continuous increase of the relative length in Norian *Saurichthys* praezygapophyses can represent a useful stratigraphical means in this stage. Body fragments of *Saurichthys* are commonly found in Norian basinal black sediments and length of the praezygapophyses can be easily measured after a short preparation. The fact that biostratigraphical means in similar environments are very scarce, increases the importance of praezygapophyses evolution in Norian *Saurichthys*.

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