

A NEW SPECIES OF *SAURICHTHYS* (ACTINOPTERYGII) FROM THE MIDDLE TRIASSIC (EARLY LADINIAN) OF THE NORTHERN GRIGNA MOUNTAIN (LOMBARDY, ITALY)

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Abstract. A new species of *Saurichthys* is described. It comes from an Early Ladinian fossil-bearing bed lying in the middle-lower part of the Buchenstein Formation on the Northern Grigna southern slope (Pasturo, Lecco). This new species differs from the several other Middle Triassic species in the remarkable size (more than 130 cm in length), in the presence of a grid structure made by the dorsal elements of its vertebral column, and in the posteriorly enlarging endoskeletal elements of both dorsal and anal fins. Moreover, only two longitudinal scale rows distinguish this taxon; together with the grid structure of the dorsal vertebral column, this character was previously observed only in Norian species (Late Triassic). The early appearance of these features in a Ladinian species opens a new, serious discussion on the evolutionary trends of *Saurichthys*, which is a very important genus, inhabiting the seas and lakes all over the world from the latest Permian to the end of the Triassic.

Riassunto. Una nuova specie di *Saurichthys* viene descritta dal livello fossilifero rinvenuto nella parte medio-bassa della Formazione di Buchenstein sulla Grigna Settentrionale (Pasturo, Lecco) databile al Ladinico Inferiore. La nuova specie si distingue dalle molte altre del Triassico Medio per le sue notevoli dimensioni, oltre i 130 cm di lunghezza, la presenza della struttura 'a griglia' negli elementi dorsali della colonna vertebrale e per gli elementi endoscheletrici delle pinne dorsale e anale che aumentano di dimensioni posteriormente. Una ulteriore importante caratteristica è la presenza di sole due file longitudinali di scaglie, carattere che, come la struttura 'a griglia', era finora conosciuto solo in specie del Norico (Triassico superiore). La presenza in una specie ladinica di caratteri che secondo diversi autori sarebbero dovuti apparire solo nel Triassico Superiore, apre un'ampia discussione sui trend evolutivi di questo importante genere, che è presente dalla fine del Permiano alla fine del Triassico nei mari e nei laghi di tutto il globo.

Introduction

The Middle Triassic of Lombardy yields a number of fossiliferous sites very rich in marine vertebrates. Among them, the Monte San Giorgio area (today split by the boundary between Italy and Switzerland) is the most important, as several fossiliferous levels are concentrated in a very small area of about 20 square km. The Swiss side of Monte San Giorgio has been inscribed in the Unesco World Heritage List in 2003, joined by the Italian side in 2010. Other Italian new sites are being exploited in the last years (Lombardo et al. 2005) and one of these is proving especially rich in fishes and crustaceans (Tintori et al. 2004; Lombardo et al. 2008; Tintori in progress): it lies on the southern slope of the Northern Grigna Mountain (Lecco). Here, a very interesting level in the lower Buchenstein Formation yielded many fish taxa which are commonly found in the Middle Triassic of the Tethys as well as a few new taxa, of which one is described in this paper. Though lying only 30 km east of Monte San Giorgio (Fig. 1), the basin of the Buchenstein Formation on the Northern Grigna had quite different characteristics: more important volcanoclastic sedimentation (Pasquarè & Rossi 1969), deeper bottom and the fact of being surrounded by a wide carbonate platform (Esino Formation), now forming the bulk of the Grigna Mountains. Because the layers yielding the fishes consist of fine calcarenite, the site is believed to have been situated on the slope between the platform margin and the deepest part of the basin.

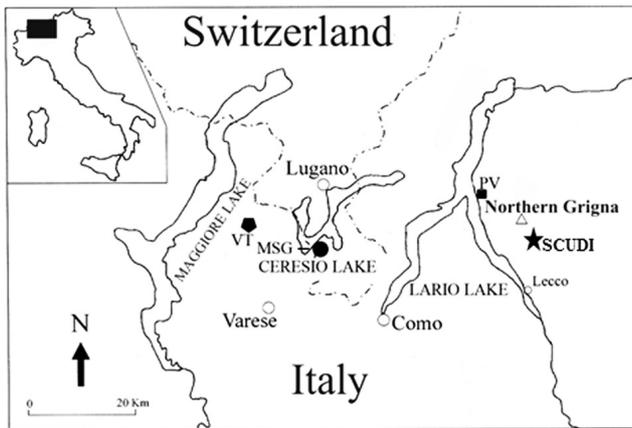


Fig. 1 - Geographical maps of western Lombardy (North Italy) with the four major Middle Triassic vertebrate areas. From East to West: ★ Northern Grigna, this paper; ■ Perledo-Varenna; ● Monte San Giorgio; ◆ Valcuvia/Valtravaglia.

This basin lay also very close (7 km to the south) to the area where the black limestone beds of the Perledo-Varenna Formation deposited for most of the Ladinian (Gaetani et al. 1992), including vertebrates which are among the first marine Mesozoic vertebrates described in Italy (Balsamo-Crivelli 1839; Bellotti 1857). Most specimens, in fact, had been recovered around the middle XIX century. Though a precise stratigraphic record of the so-called Perledo Fauna is not available, Tintori and Lombardo (1999) suggested it comprises at least three different major fossil assemblages, covering most of the Ladinian. We have a similar situation in the Monte San Giorgio area, but the detailed excavations carried out in this important site have allowed a much better stratigraphic classification of its fossil content. Only few species seem to come from the lower part of the Perledo-Varenna Formation, possibly coeval to the vertebrate level of the Buchenstein Formation and the uppermost Besano Formation/lower Meride Limestone. *Ctenognathichthys bellottii* (De Alessandri 1910; Tintori 1998a) and *Saurichthys costasquamosus* (Rieppel 1985) are by far the most common. In the Perledo area, more taxa come from the late Ladinian rocks and they are also found in the Kalkschieferzone (upper Meride Limestone) on Monte San Giorgio (Tintori 1990a; Tintori & Lombardo 1999; Lombardo 2001). Other than for the Perledo-Varenna vertebrates, the Northern Grigna was famous in the past for the invertebrate faunas: molluscs and brachiopods (Stoppani 1858-1860; Rossi Ronchetti 1959, 1960; Gaetani 1969; Mantovani 2002) in particular.

Regarding the new locality, it was during a student field excursion led by M. Gaetani in 1981 that the author found some scattered fish remains in the lower Buchenstein Formation (Early Ladinian) near Scudo

Tremare, on the southern slope of the Northern Grigna Mountain (locally called Grignone, or Grigna Settentrionale), few km north of Lecco (Lombardy, N. Italy). For many years after, the researches on Middle Triassic vertebrates were focused on Monte San Giorgio and the exploitation of this potentially interesting new target was left aside. Only in the fall of 2003 a small excavation was started in the site. The results were so promising that during the summer of 2004-5 and 2007-9 larger excavations were carried out, producing over 1500 fishes as well as a few crustaceans and a single star-fish. This latter is the only one so far found in the Middle Triassic outside the German Muschelkalk. Yet, not a single reptile remain has ever been found.

Most specimens show poor preservation, but a few can be nicely prepared, allowing detailed descriptions. Some may be considered as new taxa, some other will permit a better description of previously known species. Noteworthy are several interesting subholosteans and basal neopterygians (Lombardo et al. 2008) as well as some very long (more than 1 m) *Saurichthys* (*S. costasquamosus* and the new species herein described). Many small fishes are found on mass mortality surfaces, implying sudden changes in the environmental conditions, possibly caused by the volcanic activity testified by the presence of thin ash layers (Pasquarè & Rossi 1969 and pers. obs.). The find of relatively large crustaceans (Tintori in progress), though quite rare, was a surprise: they are almost totally missing in most alpine Middle Triassic Lagerstätten, with few exceptions like the new Anisian localities in Slovenia (Križnar & Hitij 2010). In the southern Chinese sites, on the contrary, they are fairly common (Luoping, Yunnan Province, pers. obs.). It is interesting noting how in our new site crustaceans are usually found in beds where fishes are missing or very rare; conversely, they are missing (or present as small fragments) in the main fish-bearing beds. Even though they are not associated with any other organisms, in one case at least (bed 48), we believe that some crustacean remains lying together on the upper bedding plane are due to a dramatic event. The site is situated along the first creek east of Baita dello Scudo, a small stone shelter used by local hunters. The total thickness of the fossiliferous level is about 135 cm, including some barren beds. Locally the presence of slumped beds has prevented the regular splitting along the broad lamination, also impeding a detailed search.

The total section of the Buchenstein Formation was carefully described by Pasquarè and Rossi (1969), but they had no paleontological aims. Though at the time the whole section was much better exposed, we can place our fossil-bearing level inside Level 46 of Pasquarè and Rossi (1969: p. 21, fig. 5) using as marker the concentric nodular chert occurring a few meters

below a greenish ash level (Level 49). These peculiar chert nodules are found just below our fossiliferous level and the greenish cineritic level is a few meters above it. The lithology does not actually look like it was likely to yield well-preserved vertebrates: it is a well-bedded grey limestone with thin, black chert beds and nodules, and only a broad internal lamination. Thin clay/marly levels may separate the limestone beds; each bed sometimes is hardly split following the frequently rather faint lamination. Most limestone beds are made of fine biocalcarene and their surface is frequently covered by a thin layer of brown weathered clay, possibly of volcanic origin (Pasquarè & Rossi 1969). The bedding plane can be slightly stylolitic, accounting for the poor preservation of the fishes lying on it, too poor to enable other than a generic attribution. The best-preserved fossils are those lying just below the bed surface, covered by a very thin layer of weathered marly limestone, or in the middle of the bed itself. In this case they can be exclusively detected in section, after the slab is broken, and the preparation requires to be absolutely careful because the rock is very hard and often uneven, due to the presence of chert. So far, only 2/3 of the over 1500 specimens have been identified at least at genus level, while the remaining 1/3 is waiting for preparation as they just show up in section.

In the last few years, other new Middle Triassic sites in northern Italy (Braies Dolomites, Valcuvia/Valtravaglia, Gardena Valley) as well as in Slovenia (Hitij et al. 2010) and southern China (Sun et al. 2008, 2009, 2012; Motani et al. 2008; Jiang et al. 2009; Tintori et al. 2008, 2010a, 2012; Wu et al. 2009) reveal that during that time at both ends of the Tethys conditions were often favourable to the preservation of marine vertebrates, implying at least a bottom low oxygen content at regional scale. However, at present, Early Ladinian fossiliferous horizons seem to be present only in the central Southern Alps. Also, we are now aware that all the approximately coeval sites, even when belonging to close-by basins, yield slightly different assemblages. Anyway, a certain number of genera (*Colobodus*, *Habroichthys*, *Peltopleurus*, *Placopleurus*, *Marcopoloichthys*, *Saurichthys* itself, etc.) are common to most Middle Triassic marine sites all over the world (Tintori et al. 2010b). As throughout the Tethys area we already have a few vertebrate fossiliferous levels in the Pelsonian, Late Ladinian and Early Carnian (Tintori et al. 2008, 2009, 2010, submitted) we anticipate the basal Ladinian of Eastern Tethys (the South China Block) yielding levels coeval to the Grigna site; actually, we may already have found some, like Luoping, but we cannot be sure because of their still imprecise dating.

Stratigraphy, correlations and paleoenvironment

The fossil-bearing outcrop was sampled for conodonts; the sample analysis picked out *Pseudofurnishius priscus* Sadeddin, 1990 and *Budorovignathus troempyi* (Hirsch, 1971) (Lombardo et al. 2008). On the strength of these species presence, the fish levels are dated to the upper *curionii* zone (Fassanian), close to the Anisian-Ladinian boundary (Nicora & Rusconi 2007). An Early Ladinian age is also supported by the stratigraphic position: the Anisian/Ladinian boundary in Lombardy is traditionally placed around the base of the Buchenstein Formation (Gaetani pers. com.).

The presence of abundant *Habroichthys* and *Placopleurus* (sometimes in mass mortality surfaces such as in Grigna) is considered typical of the Early Ladinian in Western Tethys (Lombardo et al. 2005). *Ctenognathichthys bellottii* represents a good index-species for this time interval as well, being very common in Grigna (type locality is the near-by Perledo area), in the upper Besano Formation, in the lower Meride Limestone (Cava Inferiore level) and in the Prosanto Fm. (Bürgin & Herzog 2002). A group of taxa comprising the three cited genera, 'large' *Peltopleurus* species and other subholosteans (*Peltoperleidus*, *Peripeltopleurus*, *Stoppania*) found in all the above cited levels except Cava Inferiore (Bürgin 1999; Lombardo et al. 2008), can be regarded as the part of the earliest Ladinian fish assemblage which is widespread throughout the Western Tethys. *Habroichthys*, *Peltopleurus*, *Placopleurus* go further, reaching the other end of the Tethys, in South China, where some of them are found until the Upper Ladinian (Lin et al. 2011; Tintori et al. 2012; Tintori et al. in press). The stratigraphic position of the fish level on the Northern Grigna Mountain is confirmed by the find of *Saurichthys costasquamosus*, as yet known from the upper Besano Formation, the Perledo-Varenna Formation and the Prosanto Formation (in the Swiss Graubünden) but not from the lower Meride Limestone, where other *Saurichthys* species are very common (Rieppel 1985, 1992).

Taxa such as *Colobodus* and *Ptycholepis*, frequently found in the upper Besano Formation, are missing in the younger Ladinian levels: this may be due to a different environment, as we find them again in Early Carnian rocks all over the Tethys (Rusconi et al. 2007; Tintori et al. in press).

Thus, a preliminary identification of part of the material collected in the new Northern Grigna excavation site suggests this vertebrate level may be coeval with those belonging to the Prosanto Formation (Bürgin et al. 1991; Bürgin 1999), the basal Cunardo Formation of Valtravaglia (Lombardo et al. 2005), the lower Perledo-Varenna Formation (Tintori & Lombardo 1999), the Montral-Alcover (C. Lombardo pers. comm.)

and, for the Monte San Giorgio area, the uppermost Besano Formation and, perhaps, the vertebrate-barren San Giorgio Dolomite; therefore, it is older than the Cava Inferiore beds in the lower Meride Limestone. The Buchenstein basin, quite a small one, was rimmed by the carbonate platform now making the Esino Formation; no more than 5–7 km of this platform separated it from the basin of the Perledo-Varenna Formation. The northern and western margins were not far from the present position of the fossiliferous site (possibly 1–2 km, M. Gaetani pers. comm.), while the basin opened toward E-NE. Thus, we assume that a well-oxygenated sea bottom was close-by; it was rich in benthonic organisms, among which the crustacean thylacocephalans, the star-fishes as well as the necto-benthonic fishes (like the common *Ctenognathichthys* and the much rarer *Stoppania*) that could feed on small organisms living on/in the soft bottom and/or incrusting organisms and calcareous algae. Since the fossil-bearing beds consist of a fine biocalcarene, we think a belt of bioclastic sand deposited on the upper slope between the platform and the deeper water; this was an ideal bottom for a rich community composed of worms, molluscs, brachiopods, echinoderms, foraminifers and crustaceans forming the base of a fairly complex food-web. Monotypic mass mortality surfaces prove that small fishes such as *Habroichthys* and *Placopleurus* most probably lived in schools. Superficial waters were inhabited by large predator fishes like *Saurichthys*, and probably also by larger reptiles; though not yet found in this site, in fact, they are known from the lower Buchenstein Fm. in the Gardena Dolomites, where remains of the large ichthyosaur *Cymbospondylus* were collected (Kuhn-Schnyder 1980, pers. obs.). *Saurichthys* is present on the Northern Grigna with at least three different species. Only one of them was already known, *S. costasquamosus*, quite common in the upper Besano Formation and in the basal Perledo-Varenna Formation (Rieppel 1985). Several *Saurichthys* specimens are rather large: *S. costasquamosus* reaches over one meter, while the new species described in this paper is 135 cm or more. A third species may be somewhat smaller, but is still relatively large for the Middle Triassic time (Rieppel 1985, 1992).

Inside the vertebrate bed of the Buchenstein Formation the specimens preservation is not constantly good: we observe complete fishes in some layers, while in some other remains are rather scattered (this especially applies to middle-sized fishes). What we infer is that conditions supporting the vertebrate fossilization only temporarily occurred in the lower/bottom part of this intra-platform trough during the time interval corresponding to the vertebrate bed.

A very preliminary taphonomic study evidences a limited bioturbation in some beds, with bones irregularly scattered. Some specimens (i.e. one *S. costasqua-*

mosus and at least some *Ctenognathichthys*) look as if the side originally touching the bottom was well preserved, while the upper side had a variable share of scattered skeletal elements. This is quite different from what happens in the Besano Formation, where, due to sea-bottom currents (Tintori 1992), the loose bones and scales are always found backwards respect to the fish head. On many bed surfaces isolated bones and scales are very common, implying that the body of dead fishes floated for a significant time, completely (or almost completely) decaying. On the other hand, the way the star-fish has been preserved, with the complete series of ventral spines, suggests that in some periods (corresponding to a few layers) the bottom conditions were very favourable to the preservation of totally articulated specimens. In conclusion, we believe the bottom environment did not usually allow a 'perfect' preservation, suggesting the boundary oxic/anoxic zone was right at the sediment/water interface. Small fluctuations in the low oxygen content of the bottom water could allow temporary totally anoxic conditions. We think the investigated area at the deposition time was around the boundary between the oxic and the anoxic zones, the totally anoxic one being probably in the deepest part of the basin itself, a few km north-eastwards. Then, considering the paleoenvironmental restoration of the Buchenstein basin, if we could follow the fossiliferous level toward the deepest part of the basin, we would find better preserved specimens.

An interesting taphonomical feature regards large *Saurichthys*. The tip of the skull is usually downward inclined, as this part sank into the bottom, while the posterior part of the skull and the body remained on the bottom surface. The hypothesis is that the sediment was very soft; the narrow anterior part of the rostrum, bearing large teeth, was relatively heavy and sank into the sediment for at least one cm. More detailed taphonomic analyses are underway, as more specimens are being prepared.

Material and methods

Three specimens have been considered: only one shows remains of the skull, though its preservation does not allow any anatomical description. On the other hand, the characters of the postcranial skeleton are more than sufficient for a comparison with the known species.

Standard length of the largest and most complete specimen (the holotype, MPUM 9546) is about 135 cm, making it the largest complete *Saurichthys* so far described from the Middle Triassic. Though lacking an articulated skull, this specimen has the whole lower jaw preserved, which lies upside down rotated (together with the pectoral fins) relative to the vertebral column. Some fragments of dermal skull bones are scattered around, implying that the skull was smashed before the fish reached the bottom, while some fragments remained connected to the body by means of soft tissues. Predation is supposed to be the cause of this damage; the same can be said for paratype MPUM 11209, consisting of an isolated tail, almost perfectly preserved even in the distal part of the lepidotrichia, but showing a sharp cut in the caudal pedicle (Fig.

4). A similar cut is observed in a *S. costasquamosus* specimen from the same level, lacking all the caudal region. The third studied specimen, the paratype MPUM 11210 is a fragment consisting of the anterior part of the body: it shows the vertebral column for a length of about 400 mm (probably up to just in front of the median fins) as well as the median scale rows. All three specimens show a well-developed grid structure in the neural elements of the vertebral column, which are totally different from those of *S. (Costasaurichthys) costasquamosus* and of a third *Saurichthys* species from this same fossiliferous level.

All the material was mechanically prepared, mostly by means of air scribe PaleoTools Micro-Jack 2 and 4 while the final polishing of details was carried out by hand mounted steel needles. In a few areas, a final cleaning with diluted acetic acid was also performed. Zoom binocular microscope Wild M-5 has been used all along the preparation. Pictures are by Nikon D-200 with macro Nikkor 60 mm lens.

Institutional abbreviations. MPUM: Museo di Paleontologia Università degli Studi di Milano.

Anatomical abbreviations. afr, anal fin radials; dfr, dorsal fin radials; hs, haemal spines; mds, mid-dorsal row scales; mn, mandible; mvs, mid-ventral row scales; mx, tip of the maxilla; na, neural arches; ns, neural spines; pz, praezygapophyses.

Systematic Paleontology

The genus *Saurichthys*, originated in the latest Permian (*Eosaurichthys* following Liu and Wei 1988), is among the long-living Triassic Actinopterygian genera. It is well known all over the world, mainly from shallow marine environments, but also from continental waters (Beltan & Tintori 1980; Rieppel 1985, 1992; Tintori 1990b; Gozzi 2006; Kogan et al. 2009). Other similar long lasting genera are *Birgeria*, also spanning most of the Triassic (Gozzi 2006), *Peltopleurus* and *Marcoploichthys*, from Middle Anisian to at least middle Norian (Tintori et al. 2008); all these taxa apparently never left the marine environment.

The original material used by Agassiz to erect *Saurichthys apicalis* Agassiz, 1834 was rather poor. For this reason and because the scientific approach was largely different from the present, during the XIX century authors used to describe a new 'genus' in every locality: for example *Ichthyorhynchus* (Bellotti, 1857), *Belonorhynchus* (Bronn, 1858) and *Giffonus* (Costa, 1862). Later on, after Stensiö published his paper on the Early Triassic fossil fishes from Svalbard (Stensiö 1925), most authors decided to retain the name *Saurichthys* for all the Triassic species, despite their huge number and the wide time spanning from the Induan, to the Rhaetian (Beltan & Tintori 1980; Rieppel 1985). Later on Beltan (1972) erected two new genera on specimens from the Ladinian of Mont-ral-Alcover (Spain); Liu and Wei (1988) described as *Eosaurichthys chaoi* a species from the latest Permian and Wu et al. (2011) erected the genus *Sinosaurichthys* for some Anisian species from southern China. However, the Permian species is rather similar to some Early Triassic ones bearing an almost complete scale covering (pers. obs.). The Spanish material is quite poorly preserved: more recent observations (C. Lombardo, pers. comm.) make us suppose that anatomic

differences should be exclusively attributed to the preservation degree. The new Middle Triassic Chinese material ascribed to the new genus *Sinosaurichthys* by Wu et al. (2011) is evidently composed of closely similar species, but the differences from all the other known *Saurichthys* species are really few. However, the erection of a new genus to distinguish them from *Saurichthys* is untimely without a complete revision of the genus, because the bases on which the genus itself should be split need for clarification. Actually, Romano et al. (2012) already stressed the uselessness of erecting a new genus. In conclusion, *Saurichthys* is here considered a well-known, though very complex, long lasting genus. For the sake of stability, we suggest the use of the subgeneric category to encompass closely similar species. For instance, *Saurichthys (Eosaurichthys)* subg. n. for *E. chaoi* and *S. madagascariensis*, considering *S. (Eosaurichthys) chaoi* comb. n. as the type-species of the new subgenus. These two species in fact are very similar, as already suggested by Liu & Wei (1988), mainly because they both show a complete body scale covering. Also *S. aff. S. dayi* (Kogan 2011) might be ascribed to this new subgenus. *Saurichthys (Sinosaurichthys)* subg. n. should be used for some of the new Anisian species from southern China (Wu et al. 2011). *S. (Sinosaurichthys) longipectoralis* comb. n. is to be considered the type species of the new subgenus as it was already the type species of the genus *Sinosaurichthys* (Wu et al. 2011). Other new subgenera can be erected considering important synapomorphies: *S. (Lepidosaurichthys)* subg. n. for the Early Triassic *S. ornatus*, *S. wimani*, *S. elongatus*, *S. dayi* and *S. toxolepis* on the basis of the presence of some more scales in between the main four/six longitudinal rows in the anterior region. *S. (Lepidosaurichthys) toxolepis* comb. n. is here considered as the type species of the new subgenus owing to the recent detailed description of the postcranial elements by Mutter et al. (2008). *S. (Costasaurichthys)* subg. n. is erected for the Middle Triassic *S. costasquamosus* and *S. paucitrichus* that have peculiar, very elongate, thin flank scales associated with four other scale rows. Though, this kind of elongate flank scales might represent a somewhat primitive character. *S. (Costasaurichthys) costasquamosus* comb. n. is chosen as type species of the new genus. It is highly probable that other species can be grouped into monophyletic subgenera but a complete phylogenetic analysis is beyond the aim of this paper.

Rieppel (1992) made a first attempt to establish the phylogeny of the *Saurichthys* species, but the results were apparently very strictly time-related. Since then, some new species based on complete specimens have been erected or got a better description. The new data reveal that many of Rieppel's (1992) conclusions regarding the general evolutionary trends in *Saurichthys* (increasing size, reduction in segmentation of the median

fins rays, reduction in number of longitudinal scale rows) are not correct, even if Schmid and Sánchez-Vilagra (2010) and Romano et al. (2012) tried to support the idea using some of the Middle Triassic species.

Subclass **Actinopterygii** Cope, 1887

Order **Saurichthyiformes** Aldinger, 1937

Family Saurichthyidae Owen, 1860 [sensu Stensiö 1925]

Genus *Saurichthys* Agassiz, 1834

Type species: *Saurichthys apicalis* Agassiz, 1834

***Saurichthys grignae* sp. n.**

Figs 2-6, Pl. 1

Diagnosis (*apomorphies): Very large *Saurichthys* species, well over 120 cm in S.L.; head short, about 1/5 of the total length, caudal pedicle very low and shorter than the dorsal fin insertion*. About 175 vertebral segments, neural spines enlarged and contiguous with a first change in inclination just behind the pelvic fins and a second stronger one at the median fins level, praezygapophyses well developed, as long as the neural spines up to five vertebral segments at least in the abdominal region. Two scale rows, the mid-dorsal and the mid-ventral ones, the mid-ventral being anteriorly lacking. No enlarged scutes in front of the caudal fin*. Paired fins large, made of more than 40 lepidotrichia, unsegmented in the pectorals and with a single segmentation for some of the pelvic rays. Long-based median fins*, dorsal and anal made of at least 65 lepidotrichia each*, caudal up to about 90 rays* almost equally subdivided in epichordal and hypochordal lobes; segmentation up to 4 times in dorsal and anal fins, only one in some of the longest caudal fin rays*; most lepidotrichia are distally branched in an asymmetrical way*. Median fin endoskeleton with proximal radial increasing in size backward*, with the last element very large, extending backward and lying almost parallel to the vertebral column*.

Etymology: from the Northern Grigna Mountain, which yields this species as well as many other complete *Saurichthys* specimens collected around 1840 in the Perledo area, these latter being among the first described complete *Saurichthys* specimens.

Holotype: specimen MPUM- 9546, an almost complete specimen lacking only part of the tail (lost during the recovery of the specimen) and with the skull totally smashed.

Paratype: MPUM 11210 body region of a quite large specimen, MPUM11209 caudal region.

Age and Stratigraphical distribution: Early Ladinian (Middle Triassic), Buchenstein Formation.

Geographical distribution: Northern Grigna Mountain (Pasturo, Lecco, Italy).

Description

The skull. The holotype skull is completely smashed and various bone fragments are scattered on a quite wide surface. No disarticulated isolated bones are visible, implying that the damage cannot be ascribed to decomposition processes: in this case the skull bones would end up completely disarticulated. Furthermore, skull disarticulation is not easily observed in *Saurichthys* (pers. obs.) even in specimens from other localities. No skull present in the paratypes.

The whole lower jaw is preserved in the holotype: it is at least 225 mm long, quite short relative to the total

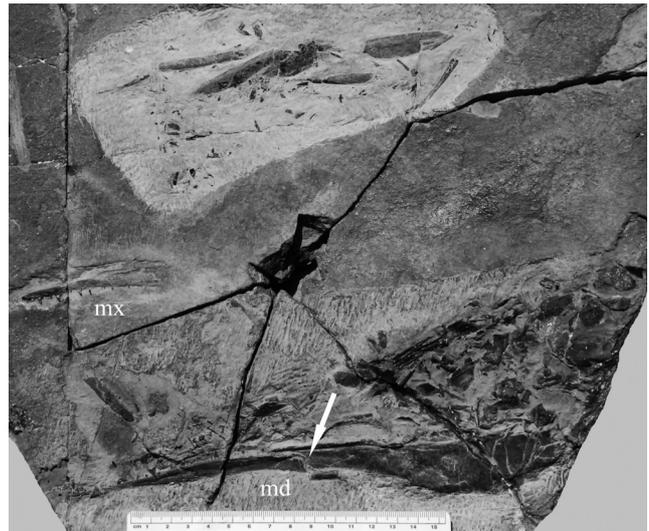


Fig. 2 - The smashed skull of the *S. grignae* sp. n. holotype MPUM 9546. The arrow points to a fracture with possible overlapping of the two halves of the lower jaw. Note that, a part from the almost complete lower jaw, all other remains are made of just fragments and not of disarticulated bones. Scale in cm.

length of the specimen (1350 mm); though, a breakage may indicate a partial overlapping of the anterior part on the posterior one. The teeth are not well visible; as usual in short-headed *Saurichthys*, they are quite large, alternating with smaller ones. Large teeth are also present on what it is interpreted as the fragment of the anterior tip of the upper jaw (fig. 2).

Paired fins. The pectoral fins are made of about 40-45 rays, all of them unsegmented as it is normal in apparently all the other *Saurichthys* species. Though not well preserved in its distal part, the fin probably had a round posterior outline: the length of the anterior rays increases rapidly and then decreases very gradually.

Like all the fins in this new species, the pelvic fins are very large: each one is made by at least 36 rays. Some of the longest (about 10) show a single segmentation whilst all the others are unsegmented. Branching probably started at about the 15th ray and usually occurred twice.

Median fins. The dorsal and anal fins, inserting opposed to each other, are fairly large and tremendously long-based (somewhat more than the length of the whole caudal pedicle), but their most peculiar characters are in the endoskeleton. The haemal arches in the region are disrupted up to the end of the fins, while the neural spines are still strictly connected to each other owing to their peculiar grid structures (see below). For both neural and haemal spines a very distinct change in size and angulation is well visible at about half of the fins length, where the proximal radials also have their major change in shape. Body height dramatically decreases just at the end of the fins, where the posteriormost lepidotrichia of the anal fin are well preserved. On the whole, the ray

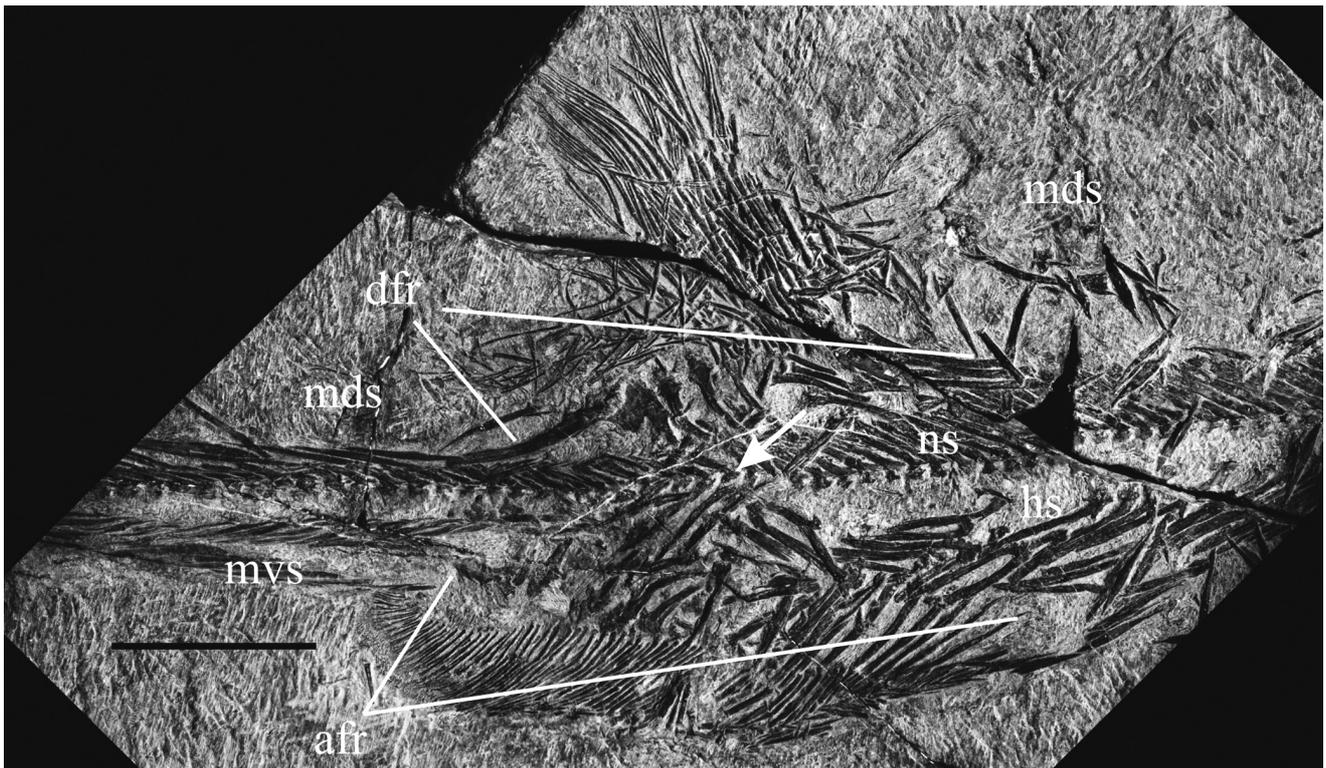


Fig. 3 - Dorsal and anal fin area in the *S. grignae* sp. n. holotype MPUM 9546. Note that the haemal elements are somewhat disarticulated anterior to the end of the anal fin and the distal part of the fin itself is bent below its proximal part. The arrow points to the sudden change in the shape of the neural elements.

number of dorsal, anal and caudal fins in *Saurichthys* is very high, about 65.

The endoskeleton of the dorsal fin is poorly preserved: some elements are not exactly in anatomical position. Anyway, it is clear that the posteriormost proximal radials become stouter and stouter, especially in their distal region. The last two radials are very peculiar. The last one with normal orientation has an axe-shape, with a very large posterior expansion at the distal end; the very last one is much longer than the previous ones and shows a reverse orientation, its proximal region pointing backward while lying on the top of the shortened neural spines of the caudal pedicle. No clear traces of independent baseosts are visible (see Rieppel 1985, 1992), but the enlarged distal region of the posteriormost elements can be interpreted as baseosts and axonosts that became 'fused' in single radials. This conclusion is especially supported by the last elements of the anal fin, where at least part of the distal region has a somewhat different surface from the 'stem' proximal part. Some lepidotrichia are well preserved: they branch very distally up to four times. The subdivision is not symmetrical and the posterior branch usually subdivides more proximally than the correspondent anterior one, even if this is not mandatory. Segmentation concerns only the proximal part, before the lepidotrichium branches:

three to four long segments make this proximal part, followed by a very long distal segment (Fig. 3).

The anal fin is made of rather thin lepidotrichia. The distal region of the anterior half of the fin is almost destroyed or bent below the proximal part (possibly due to the twisting of the body relative to the head), while the posterior half shows complete lepidotrichia. About 65 lepidotrichia make the fin: the first 25 are contiguous to each other, as usual in *Saurichthys* (Rieppel 1985, 1992; Gozzi 2006), the remaining ones are rather spaced. Each ray is made of elongate segments and branches twice (at least the posteriormost ones) in the very distal part. The fin outline is tentatively considered as a low triangle with a very gentle anterior side and a steeper, but not vertical, posterior one. Modified mid-ventral scales are present at the base of the fin as basal fulcra, and a few fringing fulcra should lie on the first lepidotrichium, at least in its proximal-medium part. Better preserved than in the dorsal, the radials of the anal fin are 15. They can be subdivided into two groups: an anterior one of about 10 elements and a posterior one made of 5 very large plates. The anterior radials are long and slender and gently increase in width backwards, up to the point where elements suddenly become much broader, with a very enlarged distal end. The last element is much longer than the previous four

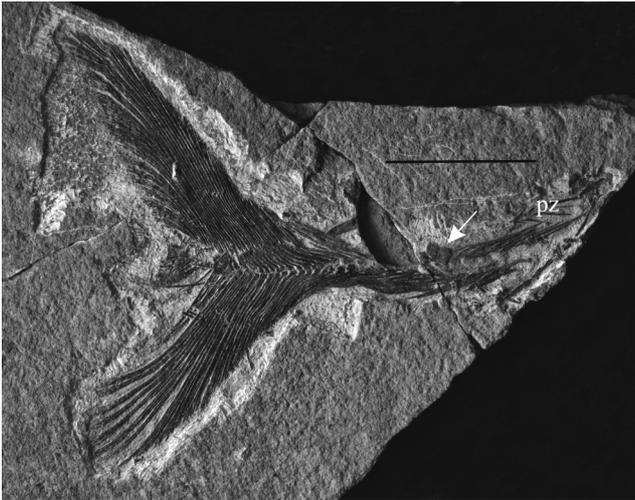


Fig. 4 - The tail of *S. grignae* sp. n. (specimen MPUM 11209). The specimen is made just of the tail, the body had been 'cut' just behind the dorsal and anal fins, leaving well visible the 'praezygapophyses'. The arrow point to a couple of *Ctenognathichthys* scales. Scale bar: 50 mm.

ones and lies with the proximal end pointing backward, like in the dorsal fin.

The caudal fin is well preserved in paratype MPUM 11209, while in the holotype only part of the dorsal lobe is preserved. In this paratype it is clearly visible that most lepidotrichia are unsegmented; the approximately 10 rays making the tip of the dorsal and ventral lobes show a single segmentation. The broad shape of the tail is a very large triangle, only gently forked. The fin is very high compared to the depth of the caudal pedicle, with a ratio of about 8:1; in MPUM 11209 in fact the tail is about 16 cm while the pedicle is little more than 2 cm. On both dorsal and ventral edges there is a very gradual shape-shift from the mid-dorsal and mid-ventral scales to the first lepidotrichia that are very short and unbranched (procurrent rays following Arratia (2008)). From the dorsal edge there are about eight of such rays, followed by 15 lepidotrichia that become longer and longer to the tip of the dorsal lobe. Branching in these rays occurs only ones or twice, the anterior branch being thinner than the posterior one. Some of the longest among these rays show a single segmentation. The upper posterior margin of the caudal fin is formed by the very delicate end of about 20 rays that branch four-five times and shorten regularly, especially in the proximal, unbranched region. Thus the dorsal lobe consists of about 43 rays, of which the shortest eight are not branched.

The ventral lobe is almost symmetrical to the dorsal one; in specimen MPUM 11209 the number of rays inside each ray group (short unbranched, 1-2 branching, more than 2 branching) is a little different. About 12 are the short rays at the base of the ventral lobe, followed by 10 longer and longer ones, branching once or twice.

Other 25 lepidotrichia complete the ventral lobe. Like in the dorsal, the first branching rays show a single segmentation.

Since only specimen MPUM 11209 has a complete tail (Fig. 5), we cannot confirm that the dorsal rays insert at the end of the neural spines; the ventral rays insert at the base of the haemal spines, as it is observed on the specimen. We believe the ratio between rays and vertebral elements can be two to one, at least in the anteriormost lepidotrichia.

Vertebral column. The length of the vertebral column in the holotype is about 100 cm: it consists of 175-180 neural elements, of which about 160 can be counted before the beginning of the caudal fin. The structure is very stout in the dorsal part. Like in all the *Saurichthys*, there is a complete row of neural elements; the haemal ones start from the insertion of the pelvic fins (at about the 80th segment), where the anal opening was placed. The haemal arches correspond one to one to the neural elements, though appearing somewhat larger. The haemal spines are slender and about as long as the corresponding neural spines.

Unfortunately, the firsts 35 neural spines are not well preserved because the slab split in part and counterpart during the recovery. However, it seems the first spines are rather slim and more or less as long as the following ones. Starting from the 30-35th neural spine they get much larger and form a continuous 'wall' up to the 130th, approximately at half the dorsal/anal fins insertion. At that point, the neural spines suddenly become shorter and they almost lay down on the neural arch region. Something similar had to happen to the haemal elements: at the end of the anal fin they lean against the notochord at very low angle and they are strictly abutting to each other. Furthermore, the neural spines rotate along their long axis: while laterally expanded in the trunk region, they become transversally enlarged in the caudal region.

Each neural element displays a well-developed anteriorly pointing element (praezygapophysis in Tintori 1990b). This is as long as 5-6 vertebral elements anterior to the pelvic fins, getting shorter in the caudal region where both the neural spine and the 'praezygapophysis' are reduced to the length of 3-4 elements. In the trunk region the praezygapophyses form a lower angle than the neural spines with the notochord. The resulting structure is called 'grid structure' (Tintori 1990b; Gozzi 2006), clearly visible both on the holotype (at the dorsal fin level especially) and paratype MPUM 11210 (Figs 3, 6, 7). The 'grid structure' of the neural region is apparently present up to the very end of the vertebral column.

The paratype MPUM 11210 distinctly shows another sudden change in the elements supporting the caudal fin: although still abutted to each other, the neur-

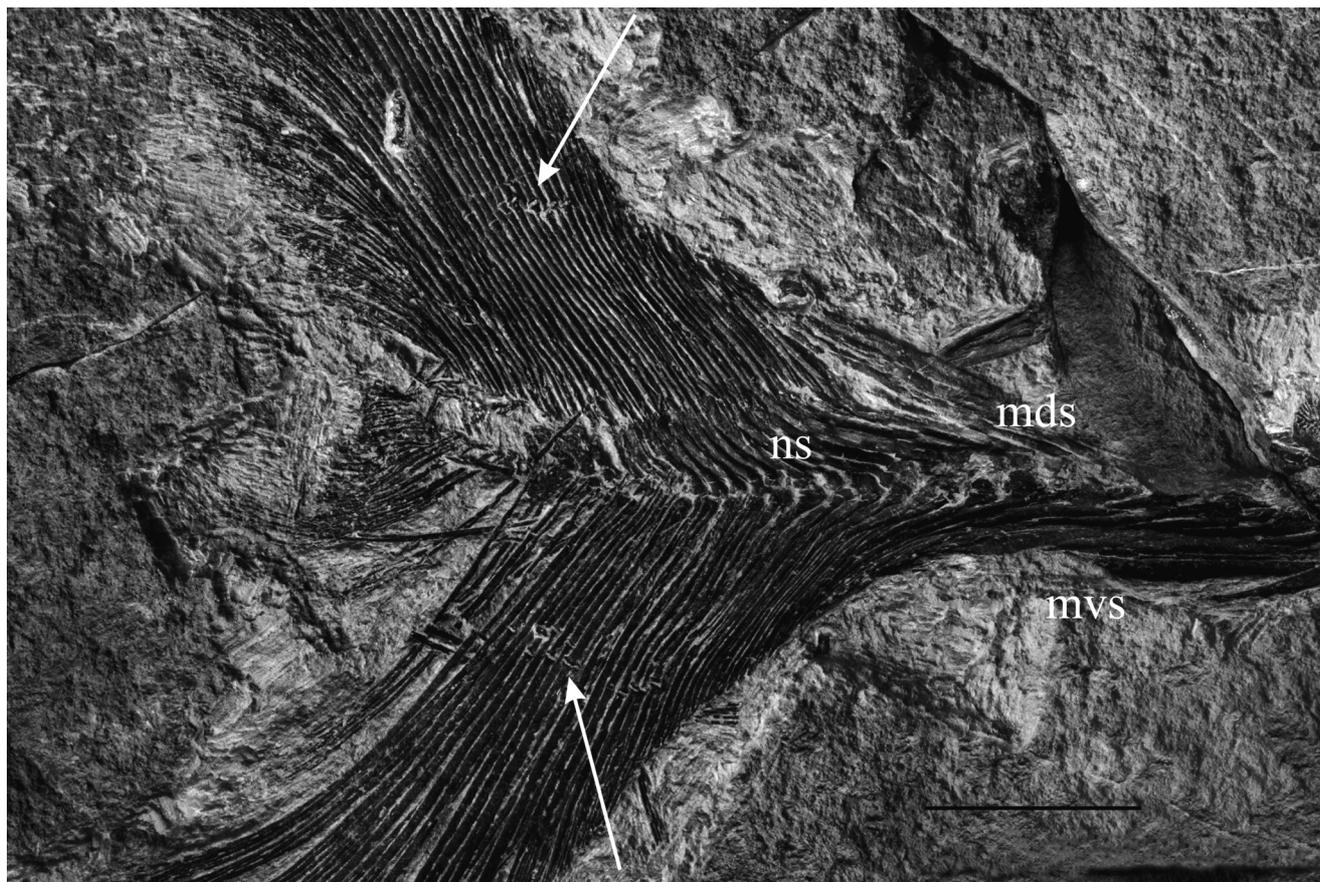


Fig. 5 - Detail of the tail of *S. grignae* sp. n. (specimen MPUM 11209). Arrows point to the single joint in some of the longest rays in both dorsal and ventral lobe.

al spines change again the angle with the notochord, gradually reaching about 90°. They also become shorter and shorter toward the end of the tail. Each neural spine of the tail is also transversally expanded and strictly connected with the adjoining ones. At present it is impossible to state if this happens to the haemal spines either since they are covered by the proximal end of the ventral lobe lepidotrichia.

Scales. Only two scale-rows are present, the mid-dorsal and the mid-ventral. Scales are all elongated, with a small (about 1/3 of the length of the single scale) exposed area covered by little ganoine tubercles. No major modifications can be seen throughout the body and the posteriormost scales are not enlarged as caudal scutes either. The mid-dorsal row is complete from behind the skull to the tail. The mid-ventral row was missing in the anteriormost region: though it is fully articulated in front of the pelvic fins, no traces of it are detected immediately behind the pectoral fins. No differences seem to be present between corresponding mid-dorsal and mid-ventral scales but for the anal loop. The scales of the mid-row and the vertebral elements have one-to-one ratio in paratype MPUM 11210, at least along most of the trunk region. Behind the dorsal

and anal fins, the scales lie very close to the distal end of both neural and haemal spines, supporting the hypothesis that the caudal pedicle had to be much lower than the anterior part of the body.

Discussion

The size of *Saurichthys* spans from the smallest species, the Carnian (Late Triassic) *S. striolatus*, barely reaching 20 cm in total length, to the largest known specimens of *S. deperditus* (= *S. krambergeri* = *S. sp. A* in Tintori 1990b; see also Gozzi 2006), from the Norian, whose total length is over 160 cm. However, very large species (over 120 cm) are also found in Early Triassic (*S. dayi*). In Middle Triassic we have at least the new species here described. These data prevent us from speculating about a general increasing size trend during the Triassic. I suggest to assume approximately 40 cm as the maximum length for a *Saurichthys* complete specimen to be considered small, 40 to 80 cm for medium size, 80 to 120 for large and over 120 cm for very large size.

The head/total length ratio is also largely variable in the adults: usually around 40-30%, the highest values applying to the smallest species such as *S. striolatus*, it

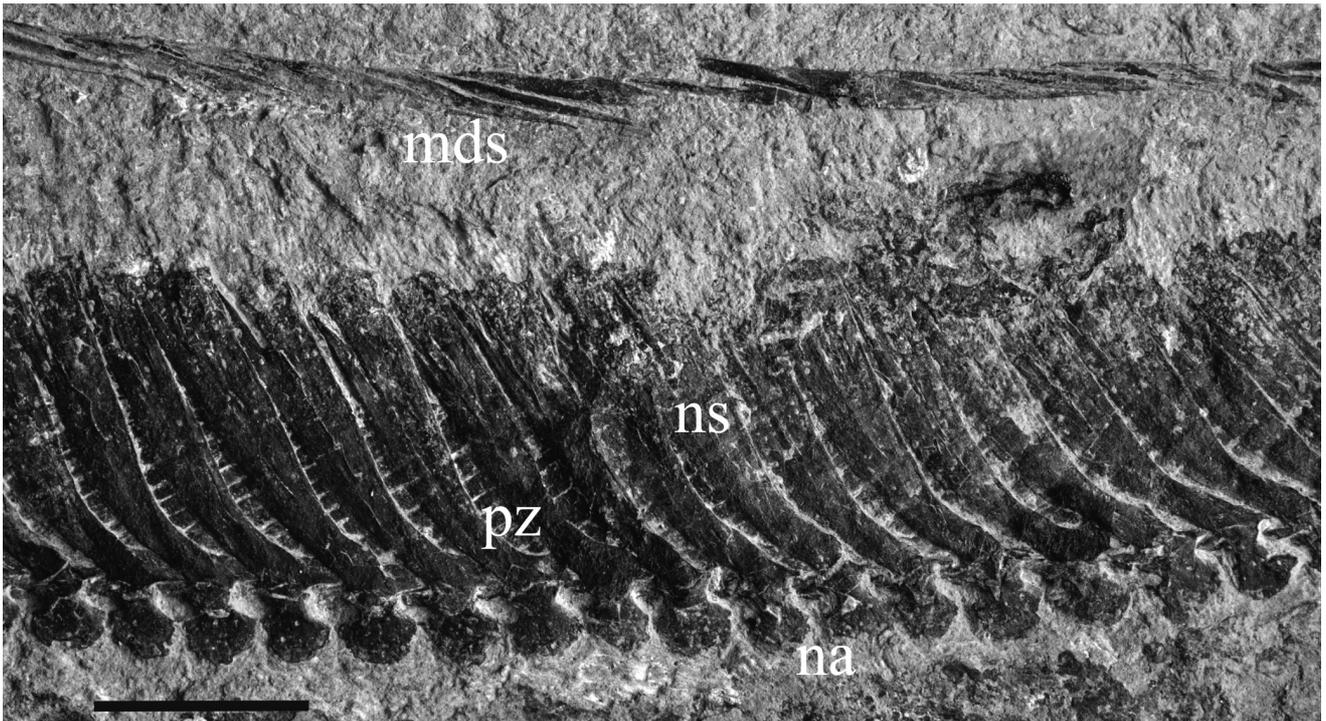


Fig. 6 - Detail of the vertebral column of *S. grignae* sp. n. (specimen MPUM 11210) showing the flattened neural spines and the much narrow, medial ‘praezygapophyses’. Note the different angle the two structures make to the nothocord.

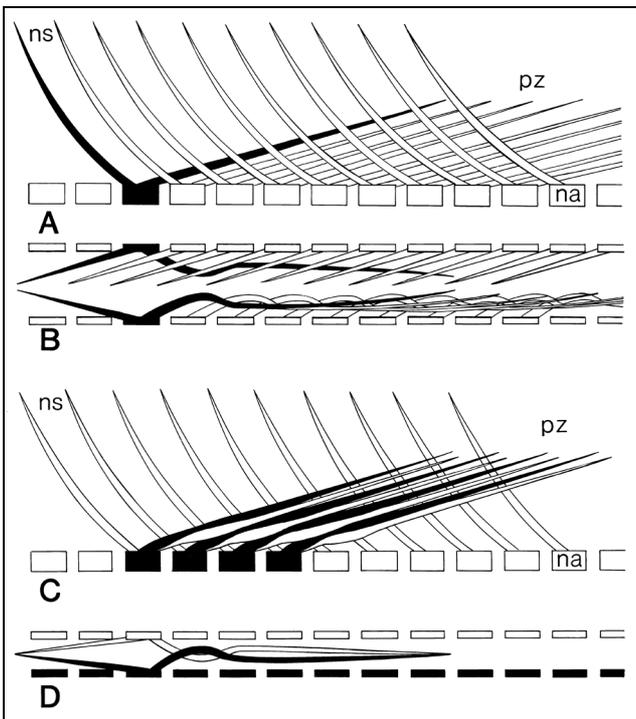


Fig. 7 - Restoration of the grid structure in the Norian species. After Tintori (1990).

can be as low as 20% in this new, very large species. The ratio then appears related to the total length of the adults, through an inverse proportion. In very small juvenile specimens skull length can be about 50% of the total length, at least in the Middle Triassic (pers.

obs.), in accordance with the values observed in other Triassic fishes (Tintori 1996; Tintori & Lombardo 1999).

Teeth shape and size are different in the various species and seem to be related to the head stoutness. Species showing a relatively short and powerful preorbital region usually bear large teeth, such as *S. (Costasaurichthys) costasquamosus* n. comb. (Rieppel 1985 and pers. obs.) or *S. sp. n. B* from the Norian Zorzino Fauna (pers. obs.). Species with a remarkably elongate and thin preorbital region show tiny teeth: for example *S. (Costasaurichthys) paucitrichus* n. comb. (Rieppel 1992) from around the Anisian/Ladinian boundary, and the Carnian *S. striolatus* (pers. obs.). This might depend on the different size/kind of prey, which proved to be rather small relative to the specimen size (pers. obs. on Norian specimens from Northern Italy) even if in some Ladinian species there is evidence of a different predatory habit (Tintori in prep., from this same fauna).

Skull roof bones, especially parietals, are highly variable in number and shape as well as branchiostegal rays, that are usually very few (three to one or even none in the new ‘genus’ erected by Wu et al. 2011).

Scale covering varies from complete in the Late Permian/Early Triassic *S. (Eosaurichthys)* to 6 rows (ventro-laterals, lateral-lines, mid-dorsal and mid-ventral) to 4 down to 2 scale rows (mid-dorsal and an incomplete mid-ventral). So far, the reduction to two rows was surely recorded only in the Norian *S. sp. n. B* (Gozzi 2006 and pers. obs.). The coeval *S. deperditus* (= *S. krambergeri* in Rieppel 1992) has also very small

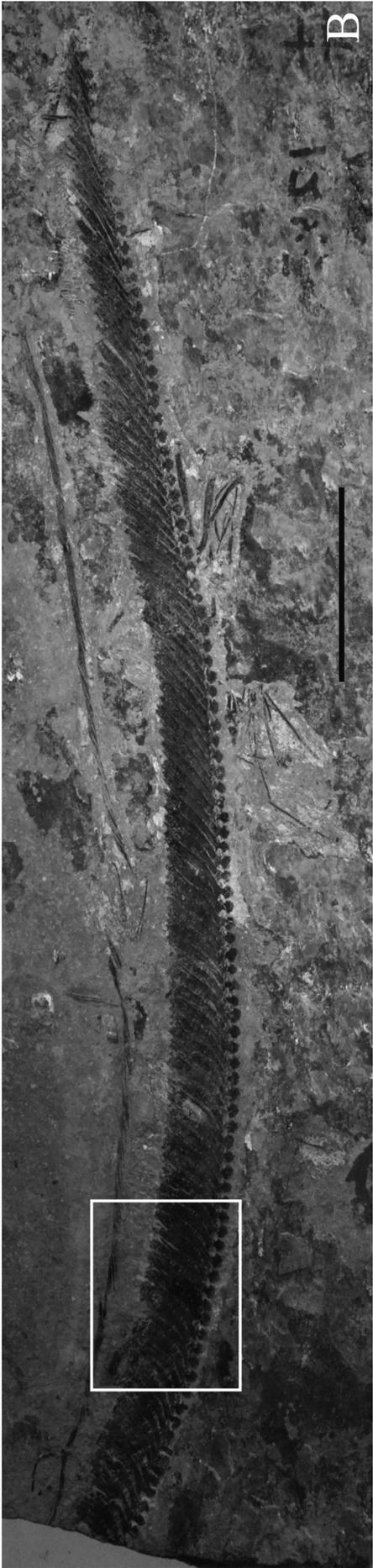
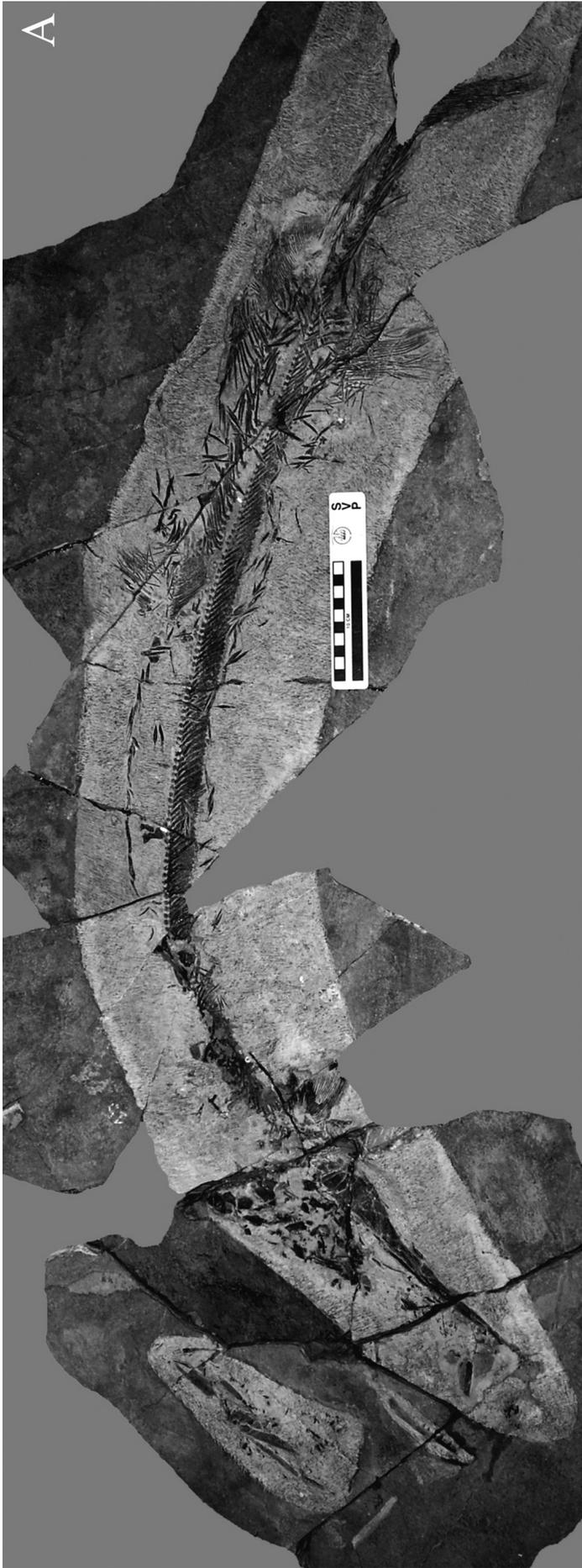


PLATE 1

The holotype of *S. grignae* sp.n. (specimen MPUM 9546). Scale bar in cm. B) The vertebral column of *S. grignae* sp.n. (specimen MPUM 11210). The square includes the area enlarged in Fig. 6.

lateral line scales at least in the caudal region, but this character has been observed in a single specimen (Gozzi 2006). However, if most coeval species have six lateral rows, in the new Early Ladinian species the reduction has already reached the stage of two median rows. As a consequence, according to the information we currently have, we rule out the possibility of regarding the decrease in scale-rows as an evolutionary trend, with inference on phylogenetic relationships as in Schmid & Sánchez-Villagra (2010) and Romano et al. (2012). Only a generally wider scale covering in the Early (pre-Spathian) Triassic species is evident.

After Rieppel's papers (1985, 1992), the segmentation of the median fin rays has also been identified as having an evolutionary trend, especially in the caudal fin. But, again, this character seems to be highly variable, even in coeval species. For instance, in the Norian *S. deperditus* there are up to 15 segments in the longest caudal lepidotrichia, while in the coexisting *S. sp. n. B* the same rays are unsegmented like in some Early Triassic species (*S. toxolepis* and *S. dayi*, Mutter et al. 2008) or in the Carnian *S. calcaratus* and *S. striolatus* (Griffith 1959, 1977, pers. obs.). In the Middle Triassic species the variability is almost as wide, from two segments in the new species here described, to eight in *S. (Costasaurichthys) costasquamosus* n. comb. coming from the same level, to more than ten in the somewhat older *S. dawaziensis* (Wu et al 2009).

It is also worth noting that in *Saurichthys grignae* sp. n. the anal and (probably) the dorsal fins appear composed of two functional parts: the anterior one, with strong lepidotrichia supported by rather thin radials, and a posterior one, much more delicate but with overabundant endoskeletal elements. It seems evident that such large radials cannot have the only function of bearing the posteriormost very thin and short lepidotrichia of both the dorsal and anal fins. As already pointed out, this 'hinge-line' is just where neural spines show a sudden change in inclination, also supporting a different function in the anterior and posterior halves of the fin. A similar endoskeletal support to the dorsal and anal fins is observed in the Jurassic saurichthyid *Saurorhynchus brevirostris*, where the posterior half of the fins is supported by a large 'basal plate' (Hauff 1938). Also in a new Spathian species (Tintori et al. submitted), the posterior parts of the dorsal and anal fins are supported by an enlarged scale (mid-dorsal and mid-ventral). The posterior support with the low-angled neural and haemal spines, as well as the eventual elongated praezygapophyses are all modifications whose common result is to make the caudal pedicle very stiff, enabling it to work as a paddle when springing for the prey.

The grid structure described in the vertebral column of the Norian species (Tintori 1990b) was thought to derive from the need for improving their swimming/

predation capability following the radiation of many new neopteygians, such as the pholidophorids, and also the origin of several new groups (Tintori 1998b). Actually, a very similar structure is now found in this new species of Early Ladinian age, approximately 20 Ma older than the Norian species. As a consequence, the relationship between the development of these structures and the origin of more advanced fishes is not credible anymore because the Early Ladinian fauna is a typical Triassic Middle Fish Fauna (TMFF) which was already well established at latest in the Pelsonian (Middle Anisian) (Tintori et al. in press). Is this very peculiar structure just related to very large species? If this was eventually true, the possible phylogenetic meaning should be clarified; certainly, the trend supposed by Tintori (1990b) should be discarded.

Gozzi (2006) thought the grid structure in *Saurichthys* had the aim of stiffening the vertebral column to provide a better elasticity of the whole structure. This could ensure some energy saving, especially during the burst to reach the chasing speed, allowing a longer acceleration phase. Thus, Gozzi (2006) interpreted the very large *S. deperditus* not as a simple ambush predator, but as a fish able to pursue its prey at high speed for a longer distance: longer, for example, than the modern barracuda. Beside the comparable predation mode, the similarity in the grid structure between the Norian species and *S. grignae* sp. n. may be addressed to the very large size of both; but actually not all the very large species are equipped with this feature. *S. (Costasaurichthys) costasquamosus* n. comb. (Rieppel 1985 and pers. obs. on very large specimen from the same site yielding *S. grignae* sp. n.), for example, is not. A further outcome of a very stiff vertebral column is to minimize the drag during the high speed chase, because the whole anterior part of the body is easily kept straight (Gozzi 2006).

Further detailed investigations in the vertebral column and scale covering are needed: it is now evident that the postcranial skeleton of *Saurichthys* is proving more and more important, not only from a paleobiological point of view, but also in the systematics, and, possibly, in the restoration of phylogenetic relationships.

Finally, *Saurichthys* is a very elongate fish, with a pointed head more or less elongate in its preorbital region, a body with posteriorly placed median fins and a high variability involving fins endoskeleton, shape and structures of the vertebral elements and scale covering. This latter spans from being complete to just two incomplete longitudinal scale-rows. The importance of the genus *Saurichthys* is not only related to its cosmopolitan distribution throughout a period of at least 50 Ma, but also to the fact that almost every Triassic fish-bearing level yields more than one species. In the new

Grigna site the vertebrate bed, less than 1 m thick, has already given three species.

Indeed, several species are still undescribed; they come from various fossil-bearing levels: the Northern Grigna, the Norian (Late Triassic) Zorzino Limestone (Gozzi 2006) and Forni Dolostone (Tintori 1990b), and some other. We certainly need to progress in the knowledge of the *Saurichthys* (Kogan 2011; Romano et al. 2012) coming from Early Triassic rocks, where they are not as common as in the Middle/Late Triassic assemblages. For instance, *Saurichthys* is apparently missing in the pre-Spathian Early Triassic of Southern China, like *Bobasatrania* (see Tintori et al. in press). Though Romano et al. (2012) wrote that the maximum differentiation of the *Saurichthys* species occurred in the Early Triassic, the last extraordinary finds in southern China and in the Alps suggest this maximum must be postponed to the Anisian and Early Ladinian. Also, we underline that the small number of species of *Saurichthys* from the late Ladinian to the end of the Triassic (Romano et al. 2012) could also depend on the number of sites yielding fish faunas, which is much lower than in the case of the Early and Middle Triassic.

The specimens coming from the Lower Ladinian beds of the Buchenstein Formation on the Northern Grigna show a certain number of characters which are both unusual among the Middle Triassic species and unique among all the other *Saurichthys* species. It is worth remembering that the fossils here described almost exclusively consist of postcranial material; though, as already pointed out, they are more than enough to settle a proper systematics.

S. grignae sp. n. shows only two longitudinal scale rows. This is considered as the most specialized scale covering because all the pre-Spathian Early Triassic species show a complete or almost complete scale covering, and most Middle Triassic species have six rows. Currently, the species bearing two scale-rows which we know of are only the Norian ones (Tintori 1990b; Gozzi 2006). These latter species share with the new species a well-developed 'grid structure' in the vertebral column, though in the shape of the neural elements *S. sp. n. B* is totally different from that of *S. grignae* sp. n., being very thin rather than laterally enlarged. Furthermore, *S. sp. n. B* is much shorter: of medium size, usually reaches 60-70 cm (pers. obs.). The other Norian species, *S. deperditus*, shares with *S. grignae* sp. n. the shape of neural elements and the very large size of adult specimens (Tintori 1990b; Gozzi 2006). On the contrary, great differences between them are, for instance, the number of fin rays, much lower in *S. deperditus*, and the fin rays segmentation, much higher in this latter species. While *S. grignae* sp. n. shows only a single joint in a few rays, in fact, *S. deperditus* has up to 15 segments in the longest rays of the caudal fin.

We find a comparable low segmentation of the median fins in *S. (Lepidosaurichthys) dayi* n. comb. and *S. (Lepidosaurichthys) toxolepis* n. comb. from the Early Triassic, *S. calcaratus* and *S. striolatus* from the Carnian, all of them with no segmentation, and in *S. sp. n. B* from the Norian, which has unsegmented caudal fin rays while dorsal and anal fins show up to three segments each (pers. obs.). However, the two former species bear an almost complete scale covering of the body, *S. striolatus* is the smallest known species, barely reaching 20 cm in total length, and *S. calcaratus* is also quite small (40 cm) and has 4 scale rows.

S. grignae sp. n. is also different from the species here ascribed to the subgenus *S. (Sinosaurichthys)* as the Chinese species have 6 scale rows, modified pectoral or median fins, no 'grid structure' in the vertebral column.

The endoskeleton of the dorsal and anal fins with radials growing in size backward described in *S. grignae* sp. n. is a feature that has never been observed in any other species; it is probably related to the dramatic decrease in body depth along the posterior half of the dorsal and anal fins, perhaps down to half the depth in front of the median fins themselves. In the caudal pedicle, in fact, both neural and haemal elements are very low-angled and transversally expanded. Furthermore, the mid-scale rows are much closer to the distal end of the spines than they are in front of the dorsal and anal fin. All this made the functional structure very stiff together with the tail, where at least the neural spines are so strictly connected that it seems impossible that the tail itself could freely bend. The stiffness of this region provided by the vertebral column is probably the cause of the lack of modified scales (scutes) in the mid-dorsal and mid-ventral rows.

It follows that we need to erect the new species *Saurichthys grignae* sp. n. to allocate the new specimens herein described.

Conclusions

Every new species erected on well preserved specimens brings to light new characters and peculiarities which make the variability of the genus *Saurichthys* ever grow.

Most characters defining the different species concern trophic specialization (teeth size and shape and their distribution along the oral margins, skull proportions) and swimming features (vertebral column and median fin structures): for this reason the author believes it worthwhile to keep a single genus name rather than starting to split the genus itself in a probably very high number of new genera. Nonetheless, a subgeneric partition is here proposed to supply a nomenclatural

support to the grouping of species appearing very similar to each other. Anyway a phylogenetic analysis of the interrelationships of all the *Saurichthys* species is beyond the goal of this paper.

A number of characters observed in *S. grignae* sp. n. were previously ascribed only to the youngest *Saurichthys* species: the presence of only two median scale rows and a well-developed grid structure are the most evident. These features are related to a peculiar mode of chasing the preys, as Gozzi (2006) already supposed for the two large to very large Norian species. Following Gozzi (2006), we believe *S. grignae* sp. n. could chase its preys at high speed over a rather long distance. On the contrary, *S. (Costasaurichthys) costasquamosus* n. comb., about the same size and living side by side with *S. grignae* sp. n., had 6 scale rows and no grid structure, which probably made it just capable of very short bursts, likewise to the vast majority of the *Saurichthys* species.

The peculiar endoskeleton of the dorsal and anal fins in *S. grignae* sp. n. suggests the presence of a hinge

at that point; this could enable the anterior part of the body to keep the swimming direction with only a gentle lateral bending, while behind the hinge the caudal pedicle functioned as a totally rigid unit, owing to the low-angled praezygapophyses, neural and haemal spines.

Once again *Saurichthys* performed large adjustments in its postcranial skeleton in order to achieve a wide variety of swimming and chasing capabilities.

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