

PREDATORS AND PREYS: A CASE HISTORY FOR *SAURICHTHYS (COSTASOURICHTHYS) COSTASQUAMOSUS* RIEPPEL, 1985 FROM THE LADINIAN OF LOMBARDY (ITALY)

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To cite this article: Tintori A. (2019) - Predators and preys: a case history for *Saurichthys (Costasaurichthys) costasquamosus* Rieppel, 1985 from the Ladinian of Lombardy (Italy). *Riv. It. Paleontol. Strat.*, 125(1): 271-282.

Keywords: Predation; Preys; Scavenging; *Saurichthys*; Middle Triassic; Lombardy; Taphonomy.

Abstract: A large specimen of *Saurichthys (Costasaurichthys) costasquamosus* from the lower Ladinian of the Northern Grigna mountain is described. It is an incomplete specimen, lacking the caudal region, and showing gut content. This latter consists of totally scattered remains of at least two specimens of adult *Ctenognathichthys bellottii*, a medium size fish quite common in this fossil assemblage. *Saurichthys* has been always considered an active predator on small fishes, but it cannot be the case for this specimen, with remains in the gut are totally disarticulated and evenly scattered all along the abdomen. Scavenging on floating carcasses is proposed, the hypothesis being also supported by the common preservation of *Ctenognathichthys* as incomplete individuals. Although the *Saurichthys* specimen shows some “in situ” disarticulation, caudal region elements are totally missing on the slab yielding the anterior part of the fish. As for other large *Saurichthys* specimens from the same site, it is supposed that this is the result of a predation by a much larger marine organism, possibly an ichthyosaur.

INTRODUCTION

Although predation is often considered as a key factor in life history, especially during the recovery after large crises, such as the Permian/Triassic one (Benton et al. 2013; Motani et al. 2015), it is rarely discussed in detail regarding the predator/prey relationships and, even more rarely, proved by actual fossil specimens. In the marine environment, apart from the tetrapods that usually were at the top of the trophic level, especially due to the very large size they could achieve, a few large fishes could be considered as top predators, or even apex predators before the emergence of marine reptiles (Late Early Triassic) and mammals (Eocene).

Saurichthys (*sensu* Tintori 2013a) is a long-lasting, large predatory fish spanning the whole Triassic stratigraphical range (Tintori et al. 2013b, 2014a; Romano et al. 2012) with its First Occurren-

ce (FO) still in the Late Permian of China (Liu & Wei 1988). Though *Saurichthys* always attracted paleontologists, it is just in the last few years that there has been a blooming of papers on both taxonomy and functional morphology of this genus, mostly following the new findings in southern China (Wu et al. 2009, 2011; Tintori et al. 2014b) and Europe (Kogan et al. 2015; Maxwell et al. 2015; Tintori 2013a; Werneburg et al. 2014). The new interest in Middle Triassic species from China prompted new works also on coeval European material, from old and new localities (Tintori 2013a; Maxwell et al. 2015; Renesto & Stockar 2015) as well as on Early Triassic taxa (Kogan 2011; Kogan et al. 2016; Tintori et al. 2014b). *Saurichthys* has been always considered as a top predator, among Triassic fishes, together with *Birgeria*, that shows almost the same stratigraphic distribution, but could reach a much larger size, although with proportionally much shorter jaws (pers. obs. on Middle Triassic specimens from southern China).

However, the first direct record of a *Saurichthys* predation was in Boucot (1990, p. 298, Tintori written communication 1982, but see also Rieppel 1985) related to a specimen from the Norian Zorzino Limestone in Lombardy (Italy). Predation capabilities in *Saurichthys* have been always inferred from the head shape and the usually powerful dentition made of conical teeth of different size along the distal two-thirds of the jaws. Size and stoutness of the teeth are most probably related to the relative elongation of the antorbital region of the jaws and the general size of the species. Large species with quite short snout, such as *S. (Costasaurichthys) costasquamosus* Rieppel, 1985 (Fig. 1), show very large teeth (Rieppel 1985; this paper) while small species with very thin and elongate jaws, as *S. striolatus* (Bronn, 1858) from the basal Carnian of NE Italy (Griffith 1959; pers. obs.), have very tiny teeth. Such relationships between teeth size and jaws length are due to biomechanical and functional features (thin jaws cannot support large struggling prey), and can be very useful to differentiate species also because apparently this character is not affected too much by the ontogenesis (Rieppel 1992). Apart from tooth size of the largest teeth, *Saurichthys* dentition is characterized by the presence of more than a single tooth row on each jaw, differentiation in tooth size and shape along the distal third respect to the median one (the proximal third being usually edentulous) of the jaws and contemporary presence of teeth of at least three size groups although spaced in different way (Rieppel 1985, 1992; Werneburg et al. 2014; Wu et al. 2009, 2011).

Thus, in the last years, the interest about this genus was not only for its complicate taxonomy, but also on its swimming biomechanics (Tintori 1990; Gozzi 2006; Maxwell & Wilson 2013; Kogan et al. 2015) and predation habits (Tintori 2013b; Renesto & Stockar 2015; Kogan & Romano 2016).

Regarding predation, *Saurichthys* has been always considered as the top fish active predator for the Triassic (Tintori 2013b), although specimens with gut content are not so commonly recorded (Renesto & Stockar 2015; Kogan & Romano 2016; Hitij & Tintori 2010, pers. obs. on Norian and Late Anisian specimens), especially if compared to modern similar predator fishes such as lepisosteids or the garfish *Belone*, where 75% of collected specimens shows some gastric content (Zorica & Čikeš

Keč 2012). However, Kogan & Romano (Fig. 4D, E, 2016) showed a “predated” *Saurichthys* inside a somewhat larger conspecific specimen. In my opinion, these two specimens are too close in size to be considered in a real predator/prey relationship, but most probably just two specimens in the same nodule, as sometimes happens in the Madagascar remains. Actually, *Saurichthys* skull is not very wide: although the lower jaws articulate at the far end of the skull, so that the gape is very elongate, it seems improbable that they can manage such a large prey skull and elongate body. Furthermore, the skull of *Saurichthys* is rigid, the rostro-premaxilla-maxilla complex being totally sutured to the preopercular bone, as in most non-neopterygian actinopterygians, and the branches of the lower jaw are distally well sutured. On the other hand, Kogan et al. (2014) already pointed out that for *Saurichthys* “preying” on large congeneric specimens was “lethal” as is proved by an apparently high ratio of fossils with such preys, sometimes still not totally engulfed. However, only a few Early and Middle Triassic *Saurichthys* appear to have this predation habit (Kogan et al. 2014; Renesto & Stockar 2015; Kogan & Romano 2016) while no such finds are recorded in the European Late Triassic or Chinese Middle Triassic *Saurichthys* (pers. obs.). Norian *Saurichthys* as well as most Middle Triassic species, appear to prefer small preys that were swallowed as complete, usually head first (Boucot 1990; Renesto & Stockar 2015 and pers. obs.). In this latter case, it is common that preyed fishes belonged to different taxa, although they show a very similar size (Renesto & Stockar 2015 and pers. obs.).

Regarding *Birgeria*, the other genus considered as top predator among the Triassic fishes, only one specimen has been recorded with a gut content, although the preys were originally considered as “embryos” (Beltan 1980). As already discussed by Bürgin (1990) and Lombardo & Tintori (2005), the two supposed preyed small fishes cannot be considered as *Birgeria*; furthermore they belong to two different genera. *Birgeria* shows a totally different anatomical plan compared to *Saurichthys* and possibly it is to be considered as a suspension feeder by suckering or filtering in open waters, but also possibly nearby the bottom, through the large gape that allows to flare its gills to suck in water and prey into its “bucket mouth” (Gozzi 2006; Lombardo & Tintori 2005; Tintori et al. 2014a;

Tintori & Lombardo 2018).

The comparison of the predator/prey size ratio between *Saurichthys* and neopterygians, especially teleosts, must take into consideration the strong kinetic skull structure in these latter fishes, thus allowing capture of very large preys, even more than half the predator length. Common examples for fossil teleosts are *Eurypholis boisieri* Pictet, 1850 specimens from the Cretaceous of Lebanon, that often show well preserved (undigested) large preys (pers. obs.). However, probably the most famous specimen is the “fish-within-a-fish”, *Xiphactinus audax* Leidy, 1870 (FHSM VP-333) at the Sternberg Museum of Natural History with a large *Gillicus arcuatus* Cope, 1875 (FHSM VP-334) as stomach contents. *Xiphactinus* is about 4 m long, while the prey is about 1.8 m. *Xiphactinus* head is quite small compared to the body length, making easy to engulf the prey through latero-ventral enlargement, compared to the very elongate, but narrow, stiff skull of all species of *Saurichthys*, where the only possible movement is the lowering of the mandible.

However, *Saurichthys* was not only “preyed” by conspecific/congeneric individual, but some of the largest specimens from the Buchenstein Formation of the Grigna Mountains (Lombardy, Italy), the Besano Formation in the Monte San Giorgio area (Italy/Switzerland) and the Zorzino Limestone (Lombardy, Italy) show traces of lethal predation possibly by a much larger organism. Tintori (2013a, Fig. 2) already pointed out that the skull of the holotype of *S. grignae* Tintori, 2013 has been smashed. For the same species also an isolated tail has been reported (Tintori 2013a, Fig. 4), so that two out of three specimens were clearly subjected to peri-mortem traumatic events, which can be related only to a predation by a larger animal. Also *S. rieppeli* Maxwell et al., 2015 shows obvious traces of predation in the smashed skull of the holotype (Maxwell et al. 2015, Fig. 2B), although the authors interpreted the skull itself as “disarticulated” (Maxwell et al. 2015, p. 891). However, “disarticulation” implies the scattering of single bones or skeletal parts, usually owing to bioturbation, and/or presence of currents, at sea bottom, especially when some oxygen was present. This is often the case for the Besano Formation vertebrates remains (Tintori 1992) preserved in the bituminous shale layers (Lombardo 1999), but it is not for the holotype of

S. rieppeli, where all the postcranial skeleton is totally articulated, down to the very end of the fin rays (Maxwell et al. 2015, Fig. 4). Similarly, the largest (about 160 cm in total length) complete specimen (MCSNB4883) of *S. deperditus* (Costa, 1862) from the Zorzino Limestone shows the same pattern in the skull preservation (pers. obs. on the specimen in the exhibit in the Bergamo Museum of Natural History “Caffi” - MCSNB). No other taphonomic process other than predation is able to damage the head or the body of a large *Saurichthys*, or crush such a powerful skull as those of *S. grignae* or *S. deperditus*, yet leaving complete and totally articulated complex and delicate structures like fin rays. A large ichthyosaur could have been a possible predator for *S. grignae*: although no remains have been found in the Grigna site itself, a fragmentary specimen of a large (4–6 m long) shastasaurid ichthyosaur (R. Motani, Davis, US, pers. comm.) is known from the Buchenstein Formation of Seceda (Gardena, Dolomites, Italy) (Kuhn-Schnyder 1980). Also, rare large ichthyosaurs are recorded from the slightly older Besano Formation (Sander 1989; Dal Sasso & Pinna 1996). Moreover, one medium size *Saurichthys* specimen (GMPKU-P-3281) from the Panxian Fauna (Pelsonian-Middle Anisian) of southern China shows the posterior part of the skull with the opercle still in anatomical position, but lacking the region anterior to the orbit, of which a few fragments can be seen on the slab (Fig. 3), being probably another evidence of predation in the skull. Again, as in the *S. grignae* and *S. rieppeli* holotypes, there are no scattered disarticulated bones, but just bone fragments. Furthermore, along the breach in the lower jaw two large notches, that can be considered as tooth-marks, are well visible. In this case, the possible predator of *Saurichthys* could be *Mixosaurus panxianensis* Jiang et al., 2006, a rather small ichthyosaur with a small set of enlarged teeth in the posterior half of the jaws (Jiang et al. 2006, fig. 4, 7).

A *S. (Costasaurichthys) costasquamosus* specimen (MPUM 9547), showing both gastric content and evidence of having been itself predated (Fig. 2), is here reported for the first time. Also, for the first time, it is shown that *Saurichthys* appears to be able of scavenging on large dead, floating fishes, as the gut is filled by scattered bone and scales belonging to at least two individuals of the same species, *Ctenognathichthys bellottii* (De Alessandri, 1910).

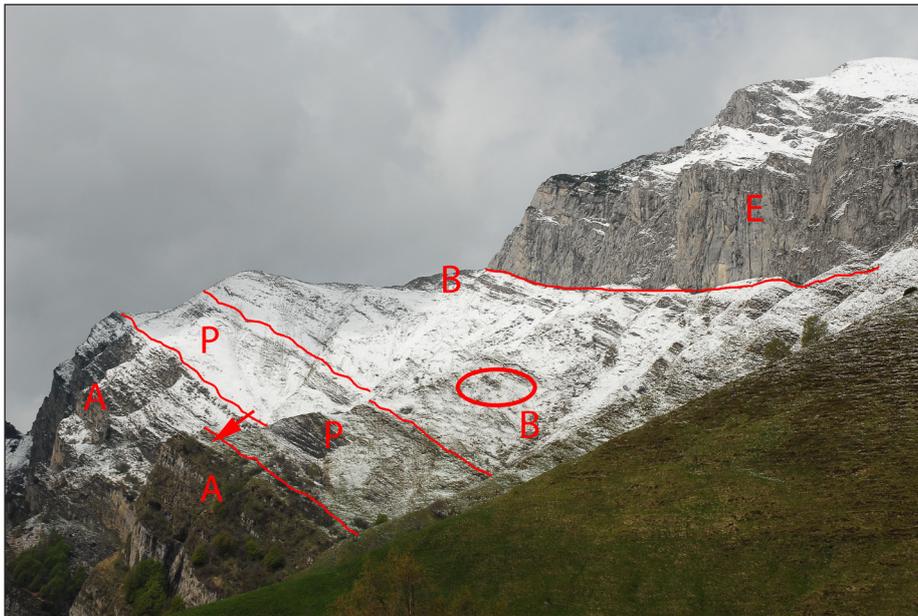


Fig. 1 - The stratigraphy at the Scudo Tremare under the weak snowfall of May 3, 2007. Picture taken by the author during a field trip together with Maurizio Gaetani. A - Angolo Limestone + indifferenziated Bellano Formation at top; P - Prezzo Limestone; B - Buchenstein Formation; E - Esino Formation (S. Calimero Member); ellipse - excavation site for the fish horizon; arrow - Brachiopods Bank.

GEOLOGICAL SETTING AND PALEOENVIRONMENT

The Buchenstein Formation is present only in the northernmost of the three thrust sheets making the Grigna group, and it crops out along the southern slope of this unit (Fig. 1), corresponding to the Northern Grigna (Gaetani et al. 1992). This formation consists essentially of regularly stratified limestones, with bed thicknesses between 10 and 30 cm, locally laminated or somewhat marly and/or rich in black chert nodules or thin beds. The color is usually light-grey/brown at weathered surfaces and dark grey to black in fresh fractures. Intercalations of light-yellow, orange, or red pyroclastics ranging in thickness from one to about 40 cm occur. The total thickness of the unit in the Northern Grigna ranges from 100 to 150 meters. The lower part of the unit is somewhat nodular, although the fossiliferous horizon is made of planar beds, and contains lenses or thin layers of black chert; between the limestone beds there are clayey or marly joints possibly originated from tuffaceous material. The Buchenstein Formation is locally covered by the Esino Formation, the stratigraphic boundary marked by a gradual transition from stratified dark limestones to massive white limestones, during the filling of the basin by progradation of the Esino carbonate platform (S. Calimero Member). Conodont dating indicates a Fassanian (Early Ladinian, upper *curionii* zone) age, just above the Anisian-Ladinian boundary (Tintori 2013a).

The Buchenstein Formation was deposited in an intra-platform basin characterized by more or less extended low oxygen to anoxic conditions in its deeper part. The basin, probably more than 200 m deep, was bordered by the carbonate platform of the Esino Formation; thin to coarse bioclastic debris flows washed into the basin and accumulated along the slope and at the basin center in quiet, oxygen-poor settings (Gaetani et al. 1992; Tintori 2013a).

The Northern Grigna Buchenstein Formation depositional area was at least about 10 km wide, given the outcrops, which are restricted to this mountain in western Lombardy, but probably it extended further east (Gaetani et al. 1992). Nearby, along the western and northern slopes of the Northern Grigna, a different basinal unit deposited during most of the Ladinian, the Perledo-Varenna Limestone. This latter unit is mainly made by black limestones, from thin bedded to thick bedded, but the uppermost part, the Perledo Member, is much more thin bedded and marly. From this succession, mainly in the 19th century, several fishes and marine reptiles have been collected. The so called "Perledo Fauna" is actually made of at least three different assemblages based on comparison to the different vertebrate assemblages from the Monte San Giorgio paleontological site (Tintori & Lombardo 1999). The Monte San Giorgio is about 35 km west of the Northern Grigna and further west the Cunardo Formation proves the existence of another Early Ladinian basin, again with marine vertebrate

remains (Lombardo et al. 2006). *S. (Costasaurichthys) costasquamosus* has been recorded from the Besano Formation in Monte San Giorgio, the Perledo-Varenna Limestone and the Buchenstein Formation in the Northern Grigna (Rieppel 1985; Tintori 2013a), proving that this species was present in environments that were somewhat different. The Besano Formation basin was rather shallow and small (Bernasconi 1994), while both the Perledo-Varenna and Buchenstein ones were quite deeper and larger (Gaetani et al. 1992), although the true size is impossible to state due to lack of preserved margins in the outcropping area. Anyway, all these basins were surrounded by shallow water carbonate platforms (San Salvatore Dolostone to the west and Esino Formation in the Grigna Mt.). Rocks deposited in all these basins record anoxic-disaerobic bottom conditions with only superficial waters suitable for vertebrate life as exchanges were possible through the shallow sills (Tintori 1992; Gaetani et al. 1992). Thus, despite the different physiography of the single basins, the life conditions for coastal epipelagic vertebrates were very similar everywhere, explaining the presence of the same species of *Saurichthys* in the different basins at the same time. However, it must be underlined that also *Ctenognathichthys bellottii*, a clearly demersal fish based on its very peculiar dentition, is present in the Besano Formation, the Perledo-Varenna Limestone (from where the holotype come from) and the Buchenstein Formation (Bürgin 1992; Tintori 1998, 2013a). The presence of both *S. (Costasaurichthys) costasquamosus* and *C. bellottii* in different assemblages allowed Tintori (1998) to establish that these assemblages had to be very close in age and that the paleoenvironments were very similar also along the margin of the basins themselves.

The locality providing the specimen herein studied has been discovered in 1981 during a student field excursion led by Maurizio Gaetani. 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 (Grigna Settentrionale, locally called also Grignone/Big Grigna), few kilometers north of Lecco (Lombardy, N. Italy). However, it was only in 2003 that excavation started. From this fossiliferous horizon, more than 1500 fish remains have been collected during five years of excavation. Several specimens of demersal mid-sized subholo-

steans, such as the rare *Stoppania* (Lombardo et al. 2008) and the quite common *Ctenognathichthys*, have been collected, as well as a few very large (up to 1.5 m) *Saurichthys*, with at least three different species (*S. grignae* Tintori, 2013, *S. (Costasaurichthys) costasquamosus* Rieppel, 1985 and a still undescribed new one). Many miniature fishes belonging to the genera *Placopleurus*, *Habroichthys* and *Peltopleurus* were found mainly on mass mortality surfaces, implying sudden changes in the environmental conditions, possibly related to volcanic activity as suggested by the presence of thin ash layers (Pasquare & Rossi 1969; pers. obs.). Most material is still waiting the time consuming preparation as the limestone matrix is very hard as it is often rich in chert, but at least ten fish species should be present. Relatively rare decapod crustaceans and thylacocephalans have been found, the latter being the only strictly benthic organism other than the asteroid *Trichasteropsis* sp. ind. (Blake et al. 2017). Other complete macrobenthos remains are very rare, including only a few fragments of bivalves other than *Daonella*. Brachiopods and crinoids have been recorded by fragments, as the rock yielding the fossils can be considered mostly a biocalcarene. A different vertebrate level, a few meter above the already exploited one, has been discovered in 2015. So far, only a fragment of a large *Birgeria* has been collected, but no further researches have been carried out. Fish fragments have been recorded also in other outcrops in the upper part of the Buchenstein Formation in the area.

TAPHONOMY AND DESCRIPTION

The subject of this study is a specimen of *S. (Costasaurichthys) costasquamosus* from the Northern Grigna excavation: it consists of the skull and the anterior part of the body, down to the pelvic fins region, with the posterior part missing (Fig. 2). The preserved part of the fish is about 65 cm long, the skull being 25-26 cm excluding the opercle. The specimen has been mechanically prepared with a final buffering with diluted acetic acid as a final highlighting of the elements.

The total length of the complete specimen is supposed to be at least 95-100 cm, thus much larger than the recorded specimens from Monte San Giorgio (Rieppel 1985). Probably the specimen was already incomplete when it arrived at the sea

Fig. 2 - *Saurichthys* (*Cosmasaurichthys*) *ostanquannensis* Rieppel, 1985 from the Lower Ladinian of the Northern Grigna Mt. (Lecco, Italy). Specimen MPUM 9547. Note the concentric change of color around the rostral region of the skull, indicating the different sediment laminae in which this region sank. Scale bars = 1 cm-2 cm.



bottom, as we could not find the posterior region nearby, but then it suffered an important phase of disarticulation before the final burial. Actually, although the preserved part shows quite an important reworking, most of the bones and scales are visible inside a small area around the vertebral column that remained articulated until the posterior breakage. The specimen lies close (about 1 mm) to the upper surface of the layer, with its right side resting on the bottom. As the upper surface of the bed shows clear evidence of slippage between adjacent beds, the thickest part of the specimen (i.e. the postorbital part of the skull) has been exposed and involved in the shear movement, thus being not so nicely preserved. Another peculiar taphonomical feature regards almost all the prepared large *Saurichthys* specimens from this site (Tintori 2013a), which are mostly in lateral view. The tip of the skull is usually downward inclined, as this part sank into the sediments (Fig. 2), while the posterior part of the skull, and eventually the body, remained on the bottom surface. The hypothesis is that the sediments had to be very soft; the narrow anterior part of the rostrum, bearing large teeth, relatively heavy, could not be supported and sank into the sediment, for about two cm in the specimen under study, while the enlarged orbital/postorbital regions and the body had a surface large enough to remain lying on the soupy bottom surface. Although this meant a much longer preparation of this region, it allows a very nice preservation owing to the very fast burial. The postorbital region is badly damaged as it surfaces at the top of the layer and it was involved in the shearing (see above).

The cutting off of the vertebral column is not very sharp, but neural and haemal elements are confused, as well as sparse mid rows scales and fragments of fin rays. The absence of the whole posterior part of the body contrasts with the setting of the trunk neural elements as well as the right flank scales which appear to be wholly articulated, thus, cannot be considered as related to bioturbation or other possible events that happened at the bottom.

Skull and dentition

The left side of the skull is perfectly articulated and the lower jaw rests against the upper one so that the mouth is almost totally closed. Teeth

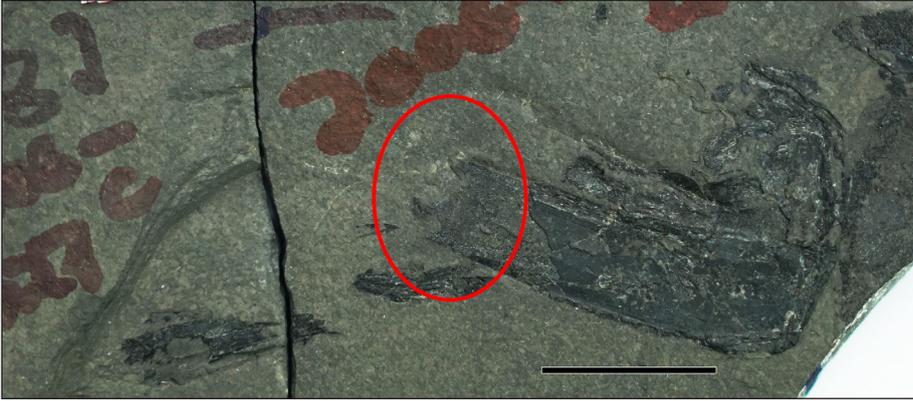


Fig. 3 - *Saurichthys* sp. ind. From the Upper Member of Guanling Formation (Middle Anisian), Yangjuian Village (Xinmin District, Guizhou Province, China). Specimens GMPKU-P-3281. Note the opercle still articulated while the anterior part of the skull is missing. Red circle for the tooth marks on the broken lower jaw. Scale bar = 2 cm

are well visible and, as already shown in Rieppel (1985) the large ones are really powerful being proportionally very large. These latter are close to each other in the distal part of the jaws, while they become more spaced in the middle part and disappear in the proximal third (below and behind the orbit), which is edentulous. This pattern is usual for such a predator, especially when the antorbital region is relatively short and stout (Kogan & Romano 2016; Rieppel 1985; Wu et al. 2009; pers. obs. on *S. deperditus*). Medium size teeth are also present as well as an almost continuous lateral (labial) row of small, peg-like teeth. Shallow notches along the lateral edge of the oral margins allow the large teeth to slide outside when the mouth closed. The large teeth seem to be somewhat internal in the distal third of the jaw, with medium sized ones possibly lateral to them. In the middle part, the big teeth become more and more lateral, getting very close to the row of small teeth. This pattern is present in both upper and lower jaws.

The large teeth are over 5 mm high and still at 115 mm from the tip they are this size, although the largest are at about 50 mm from the tip. Afterwards, the size decreases gently and the large teeth become more and more spaced-out.

Medium size tooth row is medial to the large one. Size of these teeth is uneven, although it is not possible to state if they are just in different growth stages or fully grown.

Postcranial skeleton

The postcranial skeleton is preserved up to posterior to the pelvic fins region (Fig. 4). It appears to be split along the ventral midline, the left side of the body being scattered above its dorsal outline, while the right lateral scales and the vertebral elements being fully articulated. Most of the

area ventral to the vertebral column is plenty of scattered skull bones and scales, without any regular pattern. These elements are present well outside the supposed ventral margin of the body cavity and a few of them can be seen also among the left lateral line scales that lies disarticulated dorsal to the right lateral line scale row. These scales show the typical *S. (Costasaurichthys) costasquamosus* shape, with a small median part yielding the lateral line canal and dorsal and ventral very elongate splint like (up to more than four cm each in the most anterior scales) regions.

The vertebral column shows a breakage a few centimeters behind the skull and it is made by just the neural elements until the pelvic fin region. The neural spines are well expanded, making a continuous “wall”, and show an alternation between larger and smaller elements, which is typical of several Middle Triassic *Saurichthys* species (Wu et al. 2011). A well-developed praezygapophyses is present all along the preserved part. A few scattered haemal elements from the pelvic region are preserved: they are quite slender and probably have a 1:1 ratio respect to the neural arches. Nothing more can be said about the region posterior to the pelvic fins as the specimen is missing this part due to a traumatic event (Fig. 5).

A few sparse lanceolate scales from the mid dorsal/ventral rows are also recorded (Fig. 5).

Gut content

Following the taphonomic analyses, the bones and scales, not belonging to *Saurichthys*, found all along the abdominal region of the specimen are interpreted as gut content due to their position. Usually, the small fishes preyed by *Saurichthys* lie along the vertebral column, anterior to the pelvic fins, and appear still quite well identifiable



Fig. 4 - *Saurichthys* (*Costasaurichthys*) *costasquamosus* Rieppel, 1985 from the Lower Ladinian of the Northern Grigna Mt. (Lecco, Italy). Specimen MPUM 9547. Abdominal region showing the gut content made of *Ctenognathichthys bellottii* (De Alessandri, 1910) remains. Red ellipse: the breakage in the vertebral column. White ellipses: the three *Ctenognathichthys bellottii* maxillae. Scale bar = 1 cm.

(Renesto & Stockar 2015, pers. obs. on Norian specimens) as they appear more or less complete,



Fig. 5 - *Saurichthys* (*Costasaurichthys*) *costasquamosus* Rieppel, 1985 from the Lower Ladinian of the Northern Grigna Mt. (Lecco, Italy). Specimen MPUM 9547. The far end of the specimen showing the cutting off. Scale bar = 2 cm.

depending on their position. In this specimens skull bones and scales are almost evenly scattered from just back to the head to the pelvic region. The peculiar morphology and ornamentation (Bürgin 1992; Tintori 1998) allow to ascribe these remains to adult *Ctenognathichthys bellottii* specimens (Fig. 6). As three maxillaries have been detected, at least two *Ctenognathichthys* specimens had to be involved (Fig. 4).

All the elements preserved as gut content are isolated, no skull bones or scales being articulated to each other. There is no special order in the distribution of the single elements, so that, for instance, the three recorded *Ctenognathichthys* maxillae are respectively at the anterior end of the abdominal region (just behind the cleithrum), in the middle and just in front of the pelvis (Fig. 4). There is clearly a mixing of dermal skull bones and scales all along the abdominal region, making difficult to think preys that have been engulfed as complete specimens. The size of the bones point to *C. bellottii* specimens of average adult size, i.e. around 15-20 cm in total length.

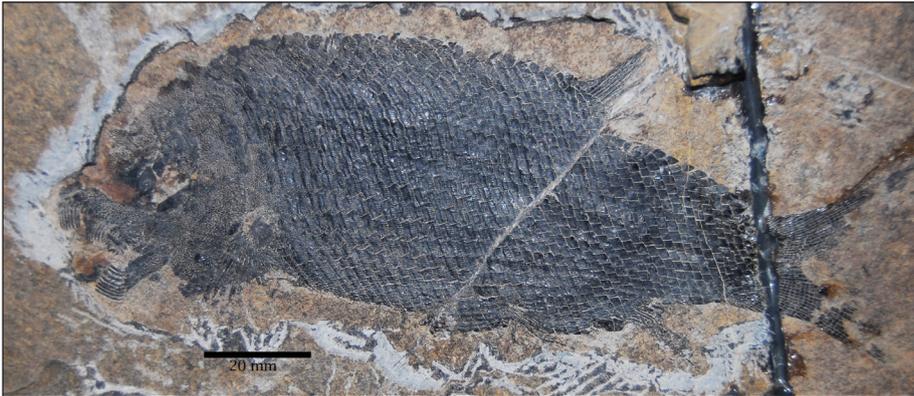


Fig. 6 - *Ctenognathichthys bellottii* (De Alessandri, 1910) from the Lower Ladinian of the Northern Grigna Mt. (Lecco, Italy). Specimen MPUM 10119. This is the only almost totally articulated and complete specimen so far prepared from the Grigna site.

DISCUSSION

The find of scattered bones and scales belonging to at least two large fish specimens in the whole abdominal region of a large *Saurichthys* (*Costasaurichthys*) *costasquamosus* appears to be an unusual one for this genus. Actually, so far, only *Saurichthys* with complete preyed fishes, mostly quite small compared to the size of the predator, are known (Renesto & Stockar 2015, pers. obs. on Ladinian and Norian specimens). The engulfed remains belong to *Ctenognathichthys bellottii*, the most common middle sized species of the assemblage recovered from the Buchenstein Formation site in the Northern Grigna. Most *Ctenognathichthys* specimens from this site show different degrees of disarticulation in both the skull and the body and sometimes part of the specimens are missing too. This kind of preservation can be related to the beginning of decomposition during an after-death floating (Schäfer 1972). Most Triassic actinopterygians, being provided by ganoid scale covering, were probably too heavy to float, although it was possible in some case such as for medium size *Paralepidotus* from the Zorzino Limestone (Tintori 1992). It is here supposed that also *Ctenognathichthys* specimens could float, losing some of the dermal bones, or scales and distal elements of the fin rays. After floating, what remained of the specimens sank to the bottom and the single elements could be easily displaced (Schäfer 1972) as seen in most *Ctenognathichthys*. Such disarticulation opposes the usual preservation of smaller and larger species as almost completely articulated specimens. However, this is also different from that of preyed *Saurichthys*, where, apart from the smashed region

affected by the bite (see also Tintori 2013a), the preserved part is usually well articulated. *S.* (*C.*) *costasquamosus* was probably able to bite floating decaying *Ctenognathichthys*, taking each time just a mouthful from the carcasses. Scavenging by large predatory fishes appears not commonly recorded. However, Kammerer et al. (2006, p. 1028) cited the alligator gar (*Atractosteus spatula*) as “avid scavenger”, while the close *Lepisosteus osseus* is “almost entirely piscivorous”. Considering that further decomposition could carry on inside the gut when the remain of the preyed *Saurichthys* reached the bottom, it is presumed that each skeletal element could become totally isolated during that process.

In the case under study, in the postcranial region of *Saurichthys* there is an evident asymmetry between the right and left sides in the degree of articulation of the preserved part. It was possible that a gut so packed with food could develop large quantities of gas from decay that made the abdomen to blow up along the ventral midline and reversing open the left side. This could explain the position of the left lateral line scales together with a few *Ctenognathichthys* elements from the gut itself while the right side, probably embedded in the soft bottom, and the robust vertebral column, remained totally articulated. It appears impossible that the decomposition and the subsequent blow could mix and scatter the gut content in such the recorded way starting from complete preyed *Ctenognathichthys* specimens. On the other hand, apart from the “lethal predation” on large congeneric fishes (Kogan & Romano 2016), all other reported *Saurichthys* with identifiable gut content show quite small fishes (Renesto & Stockar 2015; Boucot 1990, pers. obs.). Complete adult, 15-20 cm long,



Fig. 7 - *Saurichthys*, with *Ctenognathichthys* in its mouth, being caught by an ichthyosaur (Art work by G. Danini).

Ctenognathichthys are considered unsuitable to be engulfed by a *Saurichthys* with a 25 cm long head, leaving apart the fact that the gut content is made of remains of at least two *Ctenognathichthys* specimens.

The missing caudal region of the specimen under study cannot be related to the partial decomposition but appear to be related to a severe injury that probably was also the cause of the death of the specimen. It is here supposed that for a big predator, it was easier to attack a large and elongate fish, cutting it in large slices and trying to swallow what remains in its mouth. This way of predation is seen also today when large barracudas prey on fishes too large to be swallowed as a whole (Porter & Motta 2004, but see for instance also Hirshcharters 2009; Mila 2010; Millet 2013).

However, as this preyed *Saurichthys* is very large, being among the largest fishes of the assemblage (see also Tintori 2013a), it is presumed that no other fishes were able to attack similar big specimens.

CONCLUSIONS

Saurichthys (*sensu* Tintori 2013a) was a long lasting predator, spanning for more than 50 My across the P/Tr boundary to, probably, the Tr/J crisis. This is more or less the same time interval shown by other top-predator fish such as fresh water gars (*Lepisosteus/Atractosteus*) well known already in the Eocene Green River Fauna, or marine *Sphyraena* (Casier 1966), the latter being present in the Eocene of Bolca (Italy) with the species *Sphyraena bolcensis* Agassiz, 1833-1844. As a long lasting genus, different species show recurrent changes in skull and body proportions, mostly related to different life environments and predation technics. The same could be seen in *Lepisosteus/Atractosteus* species (Kammerer et al. 2006). "It seems likely that multiple evolutionary events of jaw lengthening and shortening have occurred over the course of gar evolution", the last sentence of Kammerer et al. (2006, p. 1030) paper is well applicable also to *Saurichthys*. If we add that *Saurichthys* shows differences not only in skull proportions, but also in body scale covering and vertebral column structures, it is clear that different *Saurichthys* species had different swimming skills and predation behavior patterns. Thus, even if so far *Saurichthys* has been considered as an active predator catching mostly small live fishes, *S. (Costasaurichthys) costasquamosus*, with its relatively short and thin jaws and very large teeth, was probably a scavenger, or, at least, it could easily scavenge on floating dead fishes such as *Ctenognathichthys* (Fig. 6), other than chasing small fishes as most of the other *Saurichthys* species. This behavior could be similar to that of some modern *Lepisosteus/Atractosteus* species (Kammerer et al. 2006), although these fishes show a peculiar lateral strike at quite low speed in complex habitat (Porter & Motta 2004). Most probably, *Saurichthys* lunged head-on like *Sphyraena barracuda* (Kammerer et al. 2006) or *Belone* (Kogan et al. 2006).

Regarding the predation on large size *Saurichthys*, it appears that several specimens from the Northern Grigna site have been damaged (Tintori 2013a), possibly by a much larger predator. So far, from the Buchenstein Formation of the whole Alpine region, only the very fragmentary remains of a large (4-5 m length) shastasaurid ichthyosaur have been recorded from the Gardena Valley (Dolomites, Italy).

Acknowledgments. Excavations in the Northern Grigna have been mostly supported by the Comunità Montana Valsassina, Valvarone, Val d'Esino e Riviera through the financial support for excavations and preparation of a few specimens from 2003 to 2009. The field work has been supported also by a 2004 PRIN/COFIN project "Paleobiogeografia e biostratigrafia dei Vertebrati Triassici della Bioprovincia tetideica" to the author. Special thanks to C. Lombardo, P. and E. Pacor, M. Tentor, I. Shchurenko, S. Rossignoli and T. Hitij for the very hard work in the field: their irreplaceable help made the excavation so successful. I must acknowledge again S. Rossignoli for his very accurate preparation of this *Saurichthys* specimen. Art drawing by G. Danini. Picture of the Chinese specimen by Zhou Min (PKU). Thanks to two reviewers, their comments helped in improving the paper, and to the handling editor G. Carnevale. Last, but not the least, my warmest memory of Maurizio Gaetani: he was my mentor and then colleague and friend, always supporting the VP researches that I went through during my career.

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