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A PHYTOSAUR SKULL FROM THE NORIAN (LATE TRIASSIC) OF LOMBARDY (NORTHERN ITALY)

SILVIO RENESTO* & ANNA PAGANONI**

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Riassionto. Viene descritto per la prima volta un cranio isolato di un rettile Fitosauro, rinvenuto nel Calcare di Zorzino, di età norica (Triassico superiore) nella località di Endenna nelle Prealpi Lombarde. Il cranio, per il resto completo, è privo della mandibola ed è stato notevolmente deformato nella sua parte posteriore. È stata tuttavia possibile una descrizione che ha consentito di attribuirlo con ragionevole certezza al genere Mystriosuchus, probabilmente M. planirostris, già noto da eccellenti esemplari della formazione tedesca dello Stubensandstein. Questo cranio rappresenta uno dei rari rettili di grosse dimensioni rinvenuti nelle località fossilifere del Norico lombardo, essendo stati rinvenuti solamente un esemplare completo di fitosauro lungo 4 metri, ancora in preparazione e un esemplare del rettile Placodonte Psephoderma alpinum lungo circa due metri.

Abstract. An isolated phytosaur skull found in the Calcare di Zorzino (Norian, Late Triassic), near the locality of Endenna (Bergamo Prealps, Lombardy, Northern Italy), is described. The skull lacks the mandible and is severely compressed and distorted in its posterior portion. Nevertheless it is possible to ascribe it to the genus Mystriosuchus, likely to Mystriosuchus planirostris, already known on the basis of excellent specimens from the Stubensandstein Formation in Germany. This finding represents one of the rare large reptile specimens found in the Norian fossil-bearing localities of Lombardy, along with a new phytosaur yet to be prepared and a nearly two meters long specimen of the placodont Psephoderma alpinum.

Introduction.

The Norian (Late Triassic) formations of Calcare di Zorzino (Zorzino Limestone) and Argillite di Riva di Solto (Riva di Solto Shale) crop out extensively in northern Italy. Some localities are fossiliferous and have yielded a rich vertebrate fauna of great scientific interest.

The richest fossiliferous unit is the Calcare di Zorzino, deposited in intraplatform basins some hundreds of meters deep and several kilometres wide, surrounded by the huge Dolomia Principale (Hauptdolomit) carbonate platform. The centre of these basins was anoxic, while the margins were in the oxic environment (Jadoul

et al., 1992) and sustained a rich vertebrate and invertebrate life. Fossil findings consist mainly of fishes and are characterised by thousands of superbly preserved specimens, representing a well differentiated community, (Tintori, 1992), with also some previously unknown genera (Tintori & Lombardo, 1996). Reptiles are much rarer, albeit of great interest. Aquatic reptiles include the first complete specimens of the placodont Psephoderma alpinum Meyer (Pinna, 1979, Pinna & Nosotti, 1989, Renesto & Tintori, 1995) and the thalattosaur Endennasaurus (Renesto, 1984, 1992). Despite the depositional environment, terrestrial reptiles are more common than marine forms, offering an insight into the complex faunal community living on the emerged areas surrounding the basins, possibly islands with freshwater reservoirs (Tintori et. al., 1985). The oldest pterosaurs described so far (Wild, 1978; Renesto, 1993) were found associated with fragments of the armour of the archosaur Aetosaurus (Wild, 1991). Other finds are rare diapsids, often unknown from other localities, like the arboreal genera Megalancosaurus (Calzavara et al, 1980; Renesto, 1994a) and Drepanosaurus (Pinna, 1980, 1984; Renesto, 1994b). Two small prolacertiform reptiles related to the tanystropheids and belonging to the new genus Langobardisaurus (Renesto, 1994c) were found along with a tiny specimen of the sphenodontid Diphydontosaurus (Renesto, 1995a).

Most of these reptiles are of small or medium size, excluding the large specimen of *Psephoderma* (Renesto & Tintori, 1995), nearly two meters long, and a newly found complete phytosaur, currently under preparation, that reaches nearly four meters in length (Tintori et al., 1996). The isolated skull described here belongs also to a large phytosaur, as characterised by the elongate, crocodile-like snout, with a long rostrum formed principally by the premaxillae, and by the pattern

[&]quot; Dipartimento di Scienze della Terra dell'Università degli Studi di Milano, via Mangiagalli 34, 20133 Milano, Italy; e-mail: renesto@miucca.csi.unimi.it

Museo Civico di Scienze Naturali "E. Caffi", Piazza Cittadella, Bergamo, Italy.

of other skull bones. Phytosaurs are archosaurs well known from several Triassic fossiliferous localities, mainly in the northern hemisphere, Europe, USA and India (McGregor, 1906; Gregory 1962; Chatterjee, 1978, Ballew, 1989; Hunt & Lucas, 1989; Doyle & Sues, 1995) but known also from fragmentary remains from North Africa (Chatterjee, 1978) and Turkey (Buffetaut et. al., 1988). The phytosaurs were carnivorous reptiles of late Triassic age, which resembled crocodiles both in general shape and possibly in life habits. They are usually considered to be associated with freshwater environments, but it cannot be excluded, at least in the case of our finding, that occasionally they might have visited the seashore, as do some modern crocodiles. Alternatively, it may be hypothesised that the isolated skull belongs to a floating carcass that was swept away by water currents (Renesto 1995b). It is worth mentioning, though, that other findings of phytosaur remains have been reported from brackish environments (Westphal, 1976; Buffetaut, 1993).

The skull described here was found several years ago in the fossiliferous quarry of Endenna, near Zogno (Bergamo, Lombardy, Northern Italy), but it was only mentioned incidentally by Pinna (1987) as possibly belonging to the genus *Mystriosuchus* and no description was provided. Buffetaut (1993) also mentioned the specimen under the name *Mystriosuchus planirostris*, but did not provide any evidence for this identification. At the time the fossil was exposed only on its ventral side. Further preparation by Mr. M. Pandolfi, on staff at the Museum of Natural History of Bergamo, revealed the dorsal side, allowing a complete description and a positive generic attribution, despite the fact that many of the bones of the postnarial region were flattened and crushed.

Systematic Palaeontology

Class Reptilia

Superdivision Neodiapsida Benton, 1985
Division Archosauromorpha Huene, 1946
Subdivision Archosauria Cope, 1869
Order Phytosauria Meyer, 1861
Family Phytosauridae Meyer, 1861
Genus Mystriosuchus Fraas, 1896

Mystriosuchus planirostris (Meyer), 1863

Pl. 1

1863 Belodon planirostris von Meyer, p. 244 1896 Mystriosuchus planirostris-Fraas, p.15-17 1906 Mystriosuchus planirostris -McGregor, p. 36 Material. An isolated skull, 71.5 cm long from the tip of the snout to the occipital condyle. The skull is transversely broken into three pieces, lacks the mandible and is flattened dorsoventrally so that many bones of the postnarial region are crushed or overlapped. Furthermore, the antorbital fenestrae are obliterated. The left portion is the best preserved and provides the basis for most of the description.

Repository. Museo Civico di Scienze naturali "E.Caffi", Bergamo (Lombardy, Northern Italy). Curator Dr. Anna Paganoni. Catalogue number MBSN 2.

Provenance. Uppermost level of the Calcare di Zorzino (Zorzino Limestone), Norian age (Upper Triassic), in the small quarry of Endenna, near Zogno (Bergamo Prealps, Lombardy, Northern Italy).

Measurements (in cm).

Length of the skull from the tip	
of the snout to the occipital condyle	71.5
Lenght of the rostrum	54
Number of alveola on the left premaxilla	21
Number of alveola on the left maxilla	20

Description.

The premaxillae (Pl. 1) are long, slender and narrow, only slightly expanded at the anterior tip, which is slightly bent ventrally. The entire outline of the skull bears a gavial-like appearance. The dorsal surface of the premaxillae is smooth and the snout lacks crests or ridges. Both show two medial rounded ridges on the ventral side, separated by a trough in the middle. According to McGregor (1906, p. 38) these features "prevent the close approximation of upper and lower alveolar region and thus serve to prevent the breaking of the teeth when the jaws are forcibly closed". A cavity is visible in cross section along the greater part of the rostrum. The left premaxilla bears 21 rounded alveoli which are spaced, suggesting that the dentition was unserrated. In some cases the margin of the alveolus has a low lateral crest. The teeth are almost completely lost, apart for some elements on the left premaxilla. Fragments of the first tooth, which had to be among the largest, are visible, but its size, judging from that of the alveolus, was not too different from that of the other teeth. The 18th tooth, a very small replacement tooth, which bears a faint posterior carina and delicate fluting, is preserved. The last preserved tooth, the 21st, is crushed, so that only its rounded cross section may be observed. The median margins of the dorsal processes of the premaxillae are very extended posteriorly, nearly reaching the anterior border of the external nares.

The maxillae are extremely difficult to reconstruct, because their dorsal region is crushed and split, and the dorsal outline may not be observed; the antorbital fenestra also is obliterated. About 20 rounded, spaced alveoli are visible on the left maxilla, and their size decreases gradually toward the posterior end of the bone. No teeth are preserved.

Fig. 1



- Mystriosuchus planirostris, isolated skull; A) dorsal, B) ventral views. The entire length of the skull is 71.5 cm.

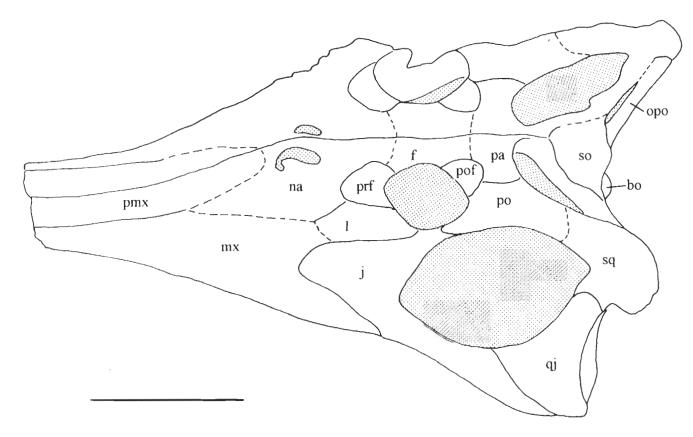


Fig. 1 - Mystriosuchus planirostris, schematic restoration of the pattern of the post rostral region of the skull, from dorsal view. Scale bar equals 10 cm. Fractures were omitted for clarity. Abbreviations are: bo) basioccipital; f) frontal; j) jugal, l) lacrimal; mx) maxilla; na) nasal; opo) opisthotic; pa) parietal; pmx) premaxilla; po) postorbital; pof) postorbitofrontal; prf) prefrontal; qj) quadratojugal; so) supraoccipital; sq) squamosal.

The septomaxillary is difficult to see, due to the shifting and crushing of the bones. The nasals, on the contrary, seem to form most of the margin of the narial openings and are sculptured with grooves and pits in their posterior portion. Their posterior margin meets the prefrontals, the frontals and the wide lacrimals. The narial openings are anteroposteriorly elongate, open anterodorsally and raised with respect to the dorsal profile of the snout, but they do not raise over the level of the skull roof.

The frontals are heavily sculptured and seem to be longer than wide, but their suture with the parietals is not visible, while the sagittal suture between the two bones is clearly detectable. A rounded postfrontal forms, along with the frontal, the posterodorsal margin of the orbit. A large postorbital is present ventrally to this bone.

The parietals seem to be small and rugose in their dorsal portion. The interparietal suture is persistent and a pineal foramen is absent. Posteriorly they contribute, along with the squamosal, to the greatly depressed and reduced upper temporal arcade that is distinctive for the genus (McGregor 1906; Gregory, 1962; Ballew, 1989; Hunt & Lucas, 1989).

The squamosals show a strongly scupltured dorsal portion and form the outer part of the highly modified

post-temporal arcade. The supratemporal bar is formed by postorbital and squamosal that becomes flattened dorsoventrally and moderately stout and wide mediolaterally. A ridge divides the squamosal into lateral and dorsal portions. The posterior process of the squamosal is short and not pointed as in *Pseudopalatus* (Hungerbühler, pers. comm.).

A wide lacrimal meets the large jugal anteriorly. The latter bone bears a posteroventral process that forms most of the ventral margin of the large, lower temporal fenestra and is in contact with the quadratojugal. The dorsal process of the jugal separates the orbit from the lower temporal fenestra and contributes to the formation of the ventral margin of the orbit.

The quadratojugal is subtriangular, it contacts the quadrate and overlaps part of the squamosal. Its surface is smooth.

The ventral surface of the skull is badly crushed and many bones are reduced to splinters, making it very difficult to reconstruct their outlines. For this reason this surface is only superficially described and it is not illustrated.

Palatine bones. The anterior portion of the narrow, elongate vomers is visible, while the choanae are obliterated by bone fragments and are not detectable. The palatines are wide and smooth, and are in contact

medially with the large pterygoids. Part of the left ectopterygoid is preserved. The basisphenoid is heavy and sturdy strong in its distal portion; the junction with the basioccipital is strong and no suture line is visible.

Occipital bones. The foramen magnum is obliterated but it can be reconstructed from the pattern of the surrounding bones. A small triangular supraoccipital is surrounded dorsally and laterally by the parietals, forming an inverted U structure (Ballew, 1989; Hunt & Lucas, 1989). Its surface is slightly concave and rugose for the attachment of muscles. The two exooccipitals are strong and contribute also to the formation of the occipital condyle. They continue lateroposteriorly into the long and stout paroccipital processes of the opisthotic, but no suture is visible between these bones. The paroccipital processes of the opisthotic are surrounded distally by the squamosals and support dorsally the greatly depressed parieto-squamosal arcade. The posttemporal fenestra is reduced to a small slit. The ball-like basioccipital forms most of the condyle.

Discussion.

The characteristics observed in the specimen show that MBSN2 belongs to the Phytosauridae (intended as the group including the last common ancestor of Angistorhinus, Mystriosuchus, Pseudopalatus, Nicrosaurus and Rutiodon) as diagnosed by Ballew (1989) and Doyle & Sues (1995). The diagnostic characteristics visible in MBSN2 are the external nares facing dorsally and the squamosal with posterior and hook-like ventral process. According to Gregory, (1962) and Hunt & Lucas (1989) the following characteristics suggest that MBSN2 belongs to the genus Mystriosuchus: unserrated and probably homodont teeth that decrease in size posteriorly, heavily sculptured skull roof region and greatly depressed, compressed, supratemporal fenestra, inverted U shaped parietal-supraoccipital complex, short and not pointed posterior process of the squamosal, supratemporal openings that are deeply incised into the skull roof and nares which are not raised above the level of the skull roof.

Poor preservation of the region posterior to the nares prevents a detailed comparison with other *Mystriosuchus* skulls, resulting in a tentative specific assignment to *Mystriosuchus planirostris*. "*M. plieningeri*", specimen GPIT stored at the Institut und Museum für Geologie und Paläontologie, University of Tübingen, number 264/001 (Huene, 1922, pls. 12-14) may well represent a different species, but according to Hunt & Lucas (1989) it shows, among other differences with *M. planirostris*, external nares depressed well below the skull table, a characteristic not observed in MBSN2. On the other hand this trait is questioned by Long & Murry (1995)

who state that the nares of specimen GPIT are not significantly more depressed than in *M. planirostris*. However, specimen GPIT has also a much more massive snout (Hunt & Lucas, 1989), large posterior maxillary tooth sockets (Huene, 1911), a shorter prenarial snout and a ventrally bulging rim of the maxillary (Long & Murry, 1995), all characters that are different from those of MBSN 2.

The classification of MBSN 2 as *Mystriosuchus planirostris*, typical of the Middle Norian Stubensandstein fauna, confirms the age determination of the locality, based on fragments of *Aetosaurus* (Wild, 1991).

Palaeoecology.

The elongate, cylindrical snout with conical teeth indicates a piscivorous diet as already pointed out by Hunt (1989), even if an occasional reptile prey cannot be excluded, as reported by Chatterjee (1978) for the long-snouted species Parasuchus hislopi. Mystriosuchus is considered linked, like other phytosaurs, to a continental, freshwater environment, and therefore the finding of MBSN2 amid a marine basin has to be explained. The finding of such isolated remains of animals, common in coeval continental deposits such as the Stubensandstein, like the Aetosaurus scutes and Mystriosuchus skull can be explained as representing sunken parts of decaying carcasses coming from distant life environments, as hypothesised by Renesto (1995b). However, the recent finding of a new, large (4 meter in length) phytosaur (Tintori et al., 1996), possibly another Mystriosuchus, requires changing this scenario. The skeleton of this new specimen is virtually complete and articulate and suggests that the life environment of these animals might have been closer to the basin, and perhaps might have corresponded to the islands (with freshwater reservoirs, Tintori et al., 1985) which surrounded the basin and hosted many endemic reptiles. If this is the case, it cannot be excluded that these phytosaurs became acquainted with a marine environment, preying on the abundant fish fauna of these basins. Further strength to this hypothesis is provided by the discovery of phytosaur remains (possibly Mystriosuchus, Buffetaut, 1993) in the southern part of the Totes Gebirge in Styria (Austria). The specimens were found in the Norian Dachsteinkalk, that is considered as deposited in a shallow marine environment. Among phytosaurs, Mystriosuchus is the most adapted to a piscivorous diet, and thus may have been a mostly aquatic form, which lived in both freshwater and marine environments, like some modern crocodilians. Actually, Crocodylus porosus inhabits both freshwater and marine environments and can swim for several kilometers in the open sea (Ross & Magnusson, 1989); Mystriosuchus may have done the same.

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