

A COMPLETE SPECIMEN OF *MYSTRIOSUCHUS* (REPTILIA, PHYTOSAURIA) FROM THE NORIAN (LATE TRIASSIC) OF LOMBARDY (NORTHERN ITALY)

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Abstract. A complete and nearly articulated new phytosaur specimen is described in detail. The skeleton, about 4 metres long, has been collected from the uppermost level of the Calcare di Zorzino (Norian, Upper Triassic) in the small quarry of Endenna (Bergamo, Northern Italy).

Available characters of the skull allow assignment of this long-snouted, uncrested phytosaur to *Mystriosuchus planirostris* Von Meyer, 1863. The postcranial anatomy, detailed here for the first time for this species, suggests a stronger adaptation to aquatic life in *Mystriosuchus* than in other phytosaurs, and may increase available data to improve our knowledge of the systematic relationships among phytosaurs.

The discovery of this nearly complete skeleton in a marine intraplatform basin suggests that a short post-mortem transport of the carcass occurred and thus this phytosaur may have lived whether in a fresh water environment or in a shallow marine habitat, close to emerged lands.

Riassunto. In questo lavoro viene descritta in dettaglio l'osteologia di un nuovo esemplare di fitosauro, completo e in perfetta connessione anatomica.

Lo scheletro, di circa 4 metri di lunghezza, è stato rinvenuto nei livelli superiori del Calcare di Zorzino, affioranti nella località fossilifera di Endenna (Zogno, Bergamo) e appartenenti al Norico (Triassico Superiore).

Sulla base di alcuni caratteri presenti nel cranio possiamo attribuire questo esemplare alla specie *Mystriosuchus planirostris* Von Meyer, 1863, già segnalata nella stessa località fossilifera sulla base di alcuni osteodermi e di un cranio isolato (esemplare MBSN 2 del Museo Brembano di Scienze Naturali San Pellegrino).

La descrizione dello scheletro post-craniale completo di *M. planirostris*, approntata qui per la prima volta, apporta numerosi nuovi dati utilizzabili nella tassonomia del gruppo e mostra come questa specie presentasse un adattamento alla vita acquatica più marcato di quanto si osservi negli altri fitosauri conosciuti. Il fatto che lo scheletro descritto sia stato rinvenuto completo ed articolato nei sedimenti marini di un bacino intrapiattaforma, porta a supporre che l'animale in vita potesse vivere sia in acque dolci che in ambienti di mare basso, in prossimità della linea di costa.

Introduction

The Norian (Late Triassic) vertebrate localities from Northern Italy (Fig. 1) are of worldwide interest for the diversity and preservation of their faunas. The main fossiliferous unit is the Calcare di Zorzino (Zorzino Limestone) which was deposited in intraplatform basins surrounded by the Dolomia Principale (Hauptdolomit) carbonate platform.

The geological setting of the Lombardian Norian has been studied in detail (Jadoul 1986; Jadoul et al. 1992, 1994) since the discovery of the fossil localities. The Zorzino Limestone was deposited in several small semigraben basins inside a huge carbonate platform which extended from Spain to Greece. Basins, deep and several kilometers large, were created by transtensive tectonics, probably related to the rifting of the Ligurian-Piedmont Ocean (Jadoul et al. 1994). Being surrounded by very shallow waters, the basins had restricted circulation which led to anoxic conditions at the bottom and in the deepest parts of the basins (Tintori 1992). These basins were connected to the open sea only through tidal channels which acted as ecological barriers for larger nectonic organisms (e.g. the huge Late Triassic ichthyosaurs). The carbonate platform which surrounded the basins was probably poorly inhabited because of the warmer and more salted waters. Organic mounds surrounded the basins and occasionally emerged forming ephemeral islands that were colonized by the cheirolepidiacean conifer *Brachyphyllum*, a plant which can survive also in brackish waters.

All fossils collected from the Zorzino Limestone must be considered allochthonous, even if they are mostly marine organisms. In fact they lived either in the oxygenated upper layer of water or close to the basin mar-

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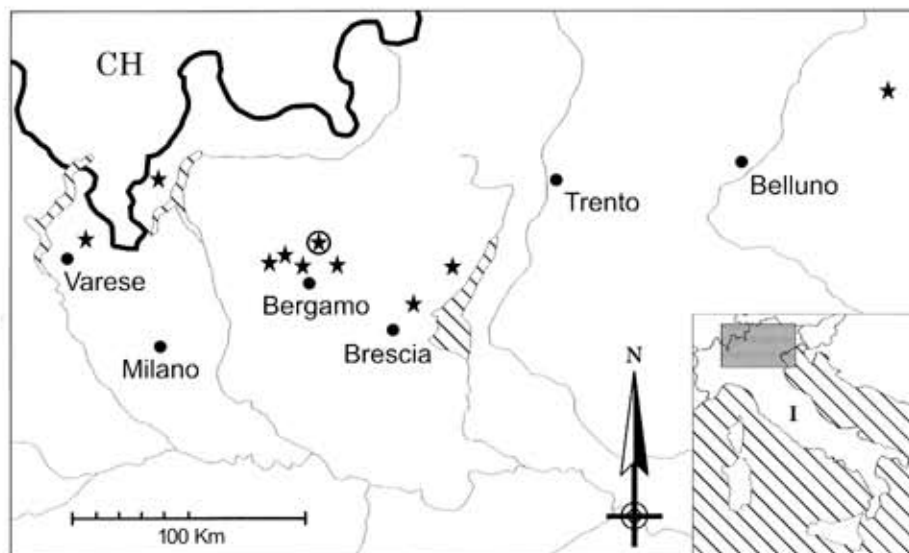


Fig. 1 - Geographical distribution of the Norian (Late Triassic) localities in Northern Italy. The black stars indicate the outcrops of the Calcare di Zorzino (Zorzino Limestone); the circled black star indicates the quarry of Endenna (near Zogno, Bergamo), where the specimens MCSNB 10087 and MB-SN 2 have been found. Modified from Tintori et al. 1985.

gins. The fossil record is represented by mainly nectonic forms but benthic and terrestrial organisms have also been found, allowing the restoration of the life both in the shallow marine environments and on the ephemeral islands close to the basins.

The Zorzino Limestone fish fauna is perhaps the richest of the Triassic with at least 30 different genera already described or under study (Tintori 1981, 1983, 1990; Tintori & Sassi 1992; Tintori & Lombardo 1996). Many yet undescribed new taxa are housed in the collections.

Reptiles are much rarer than fishes, but represented by important and peculiar genera, including of the oldest pterosaurs so far known (Wild 1978): *Eudimorphodon*, *Peteinosaurus* and possibly *Preondactylus*.

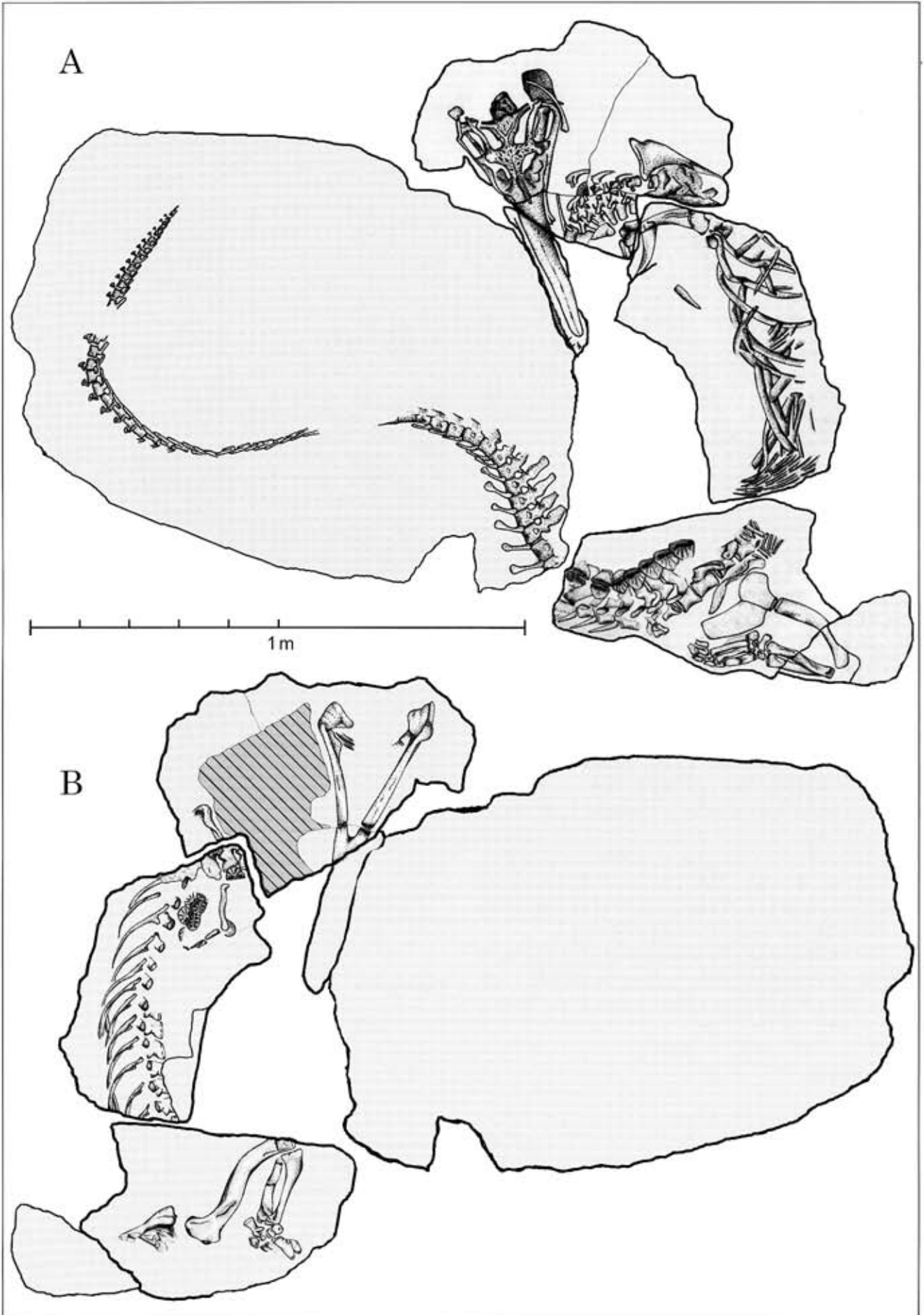
Despite the preservational environment, terrestrial reptiles are more common than aquatic ones both in number and diversity. Fully or predominantly aquatic reptiles are represented by *Endennasaurus* (Renesto 1992, 1994c) and the cyamodontoid placodont *Psephoderma* (Pinna 1979; Pinna & Nosotti 1989). Terrestrial reptiles are represented by the aetosaur *Aetosaurus* (Wild 1991), the sphenodontid *Diphyodontosaurus* (Renesto 1995), the prolacertiform *Langobardisaurus* (Renesto 1994a; Renesto & Dalla Vecchia 2000) and by at least three different genera of drepanosaurids: *Drepanosaurus* (Pinna 1980, 1984; Renesto 1994b), *Megalancosaurus* (Calzavara et al. 1980; Renesto 1994c, 2000) and a still undescribed specimen quoted by Wild (1991) as "*Vallesaurus*" (nomen nudum, see Renesto 2000). All these three genera share skeletal adaptations to arboreal life (Renesto 1994b, c). A few elongate vertebrae have been considered by Wild (1980) as cervicals of a small species of the prolacertiform genus *Tanystropheus*: *T. fossai*.

In our fossiliferous localities, phytosaurs were represented only by an isolated skull ascribed to *Mystriosuchus* sp. (Renesto & Paganoni 1995) and a few osteoderms (pers. obs.) until 1995, when a large and complete

phytosaur skeleton (Fig. 2) was discovered in the locality of Endenna (Fig. 1). Phytosaurs are archosaurs well known from several Triassic localities in Europe, North and South America, India, North Africa, Thailand and Turkey (Westphal 1976; Chatterjee 1978; Buffetaut & Ingavat 1982; Buffetaut et al. 1988; Ballew 1989; Buffetaut 1993; Long & Murry 1995; Kischlat et al. 2002). They were carnivorous reptiles which resembled modern crocodiles in general shape and possibly in life habits. Usually they are found associated with freshwater environments but in some cases they may have lived at the seashore, as testified by findings in brackish environments (Westphal 1976). Despite the abundance and diversity of phytosaur specimens, complete skeletons are very rare (Chatterjee 1978) and most taxa are known mainly by very incomplete specimens often consisting only of the skull.

The importance of the new specimen thus lies mainly in its completeness that allows a detailed description of the whole morphology of this specimen (a preliminary note on the peculiar structure of the tail was already published by Renesto & Lombardo 1999) greatly enhancing previous knowledge about the postcranial skeleton of phytosaurs in general and *Mystriosuchus* in particular.

Fig. 2 - *Mystriosuchus planirostris* Von Meyer, 1863. Specimen MCSNB 10087, drawing of the whole skeleton. A) Right side of the main part of the body and the dorsal side of the skull. B) Left side of the body and the ventral side of the skull. For abbreviations see appendix.



Systematic Palaeontology
Reptilia

Archosauria Cope, 1869

Crurotarsi Sereno and Arcucci, 1990

Phytosauria Jaeger, 1828

Phytosauridae Jaeger, 1828

Pseudopalatinae Long and Murry, 1995

There are different views about the assignment of *Mystriosuchus*. Some authors consider this genus as belonging to the Subfamily Pseudopalatinae (Ballew 1989; Hungerbühler 2002), while others regard it as an independent radiation from more basal taxa and assign it in a distinct Subfamily, the Mystriosuchinae Von Huene, 1915 (Long & Murry 1995). In this paper we follow the first assessment which is, at present, the more widely accepted one.

Genus *Mystriosuchus* Fraas, 1896

Type species: *Mystriosuchus planiostris* Von Meyer, 1863

***Mystriosuchus planiostris* Von Meyer, 1863**

Pls. 1-4

Material examined: specimen MCSNB 10087 of the catalogue of the Museo Civico di Scienze Naturali "E. Caffi" di Bergamo (Lombardy, Northern Italy), consisting of a nearly complete and articulated skeleton of a narrow snouted phytosaur.

Specimen MBSN 2, of the Catalogue of Museo Brembano di Scienze Naturali San Pellegrino (Bergamo, Northern Italy) consisting of an isolated skull lacking the lower jaw.

Locality: The small quarry of Endenna, near Zogno (Bergamo, Northern Italy). In the I.G.M. System the fossiliferous locality is placed in Foglio n° 33, Quadrante III, Orientamento N.E., Tavoleta Zogno.

Horizon and age: Uppermost level of the Calcare di Zorzino (Zorzino Limestone), close to the boundary with the Argilliti di Riva di Solto; Middle Norian; Upper Triassic.

Measurements

Measurements (in millimeters or in degrees) of the specimen MCSNB 10087 are listed in Tab. 1. The numbers preceded by a question mark are measured on crushed or partially preserved portion of the skeleton. (°) The length is measured from the tip of the rostrum to the occipital condyle; (?) distance between the two most lateral edges of the squamosals; (°) angle subtended between the axis of the centrum and the axis of its relative neural spine. For abbreviations see Appendix.

Total length	3760	Chevron length	65,5
Trunk length	865	<i>Distal caudal vertebrae</i>	
Caudal length	1920	Centrum length	23,5
<i>Skull</i>		Centrum height	12,5
Length	555	Neural arch height	6
Width	120	Neural spine length	52,5
Prenarial length	7350	Neural spine thickness	5,5
Rostrum width (tip)	30	Angle s-c	5°-10°
Rostrum width (base)	58	Chevron length	20
Nostril length	52	<i>Shoulder girdle</i>	
Interorbital width	34,5	Scapula height	723
<i>Cervical vertebrae</i>		Sc length at the base	10
Centrum length	42	Interclavicle width	35
Centrum height	27	<i>Pelvic girdle</i>	
Neural arch height	21	Iliac blade length	150
Neural spine height	63,5	Ischium length	140
Neural spine thickness	23	Ischium plate wide	68
Angle s-c	90°	Pu anterior border length	90
<i>Trunk vertebrae</i>		<i>Anterior limbs</i>	
Neural spine height	28	Humerus length	200
Neural spine thickness	36	H diameter of the shaft	20
Angle s-c	90°	Radius length	100
<i>Sacral vertebrae</i>		Ra diameter of the shaft	20
Centrum length	55	Ul diameter of the shaft	22
Centrum height	30	<i>Posterior limbs</i>	
<i>Proximal Caudal vertebrae</i>		Femur length	270
Centrum length	40	Fe diameter of the shaft	35
Centrum height	30	Tibia length	145
Neural arch height	27,5	T diameter of the shaft	
Neural spine height	64	Fibula length	22
Neural spine thickness	15	Fi diameter of the shaft	19
Angle s-c	90°	Mi length (1°-2°-3°)	25-68-79
<i>Central caudal vertebrae</i>		<i>Osteoderms</i>	
Centrum length	33,5	Elliptical os major axis	45
Centrum height	29	Elliptical os minor axis	31
Neural arch height	10	Carina thickness	6
Neural spine height	80,5	Pentagonal os major basis	45
Neural spine thickness	29	Pentagonal os height	35
Angle s-c	60°-70°	Carina thickness	5

Tab. 1 - Measurements taken on specimen MCSNB 10087.

Description

Skull

Owing to compression during fossilization the skull (Fig. 3, Pl. 1) is heavily flattened dorsoventrally, in contrast to most known phytosaur skulls which are usually laterally compressed (Mc Gregor 1906) or three dimensionally preserved (Long & Murry 1995). The overall morphology is typical of slender snouted phytosaurs (Hunt 1989). The rostrum is long, narrow and undoubtedly uncrested. Its anterior tip is missing, lacking the spoon-like expansion. The preserved portion of the rostrum reaches 63% of the whole cranial length, giving a gavial-like appearance to the skull. The isolated skull labelled as MBSN 2, from the same locality, which is virtu-

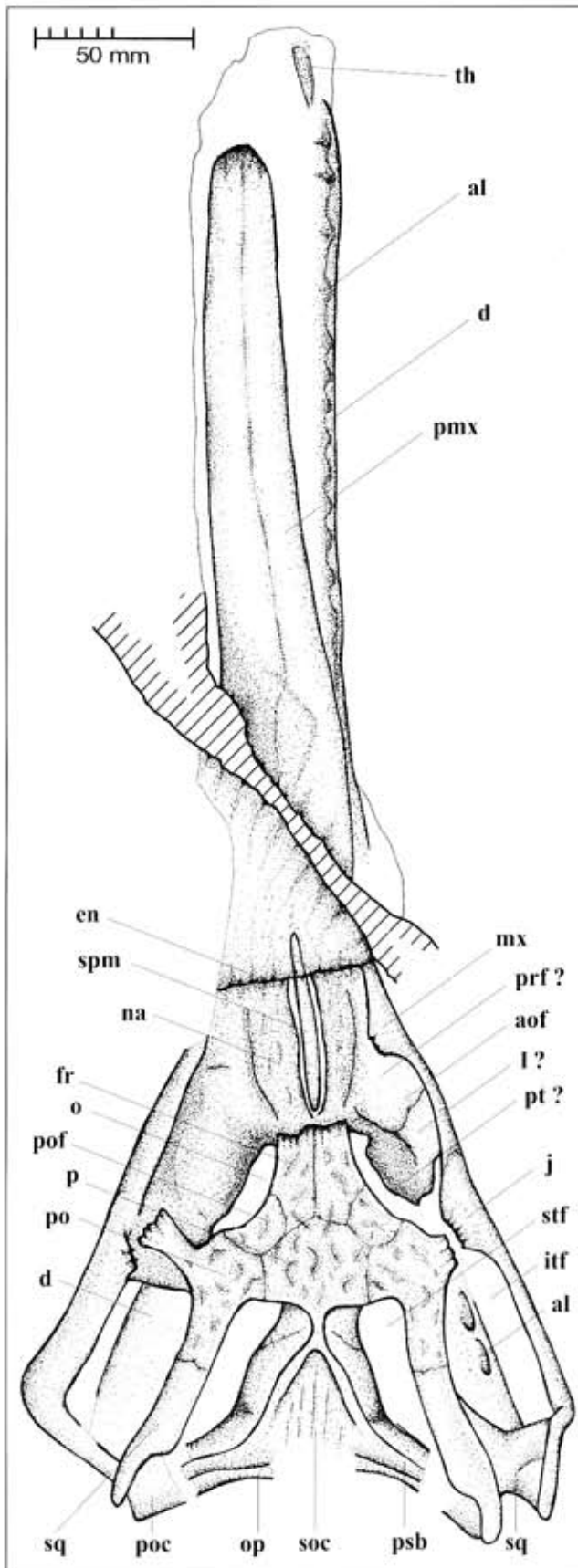


Fig. 3 - *Mystriosuchus planirostris* von Meyer, 1863. Specimen MC-SNB 10087, drawing of the skull in dorsal view. The edges of the stone slabs, in which the specimen is preserved, are highlighted with inclined lines. The bones not belonging to the skull are omitted. For abbreviations see appendix.

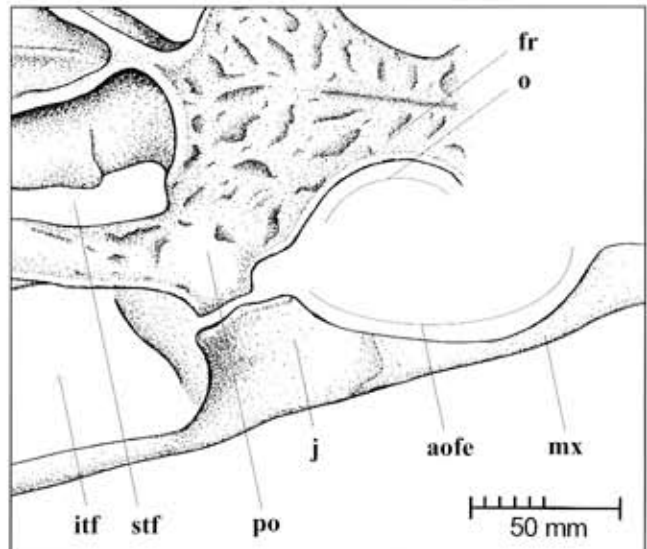


Fig. 4 - *Mystriosuchus planirostris* Von Meyer, 1863. Specimen MC-SNB 10087, detail of the skull in dorso-lateral view. The lacrimal and the ascending process of the maxilla, forming the bony bar between the antorbital fenestra and the orbit, are broken. The dorso-ventral compression has brought the dorsal edge of the orbit nearer to the ventral edge of the antorbital fenestra. For abbreviations see appendix.

ally identical in shape and can thus be considered as conspecific, shows a complete rostrum that reaches ca. 75% of the skull length (Renesto & Paganoni 1998).

Premaxillae are slender and greatly elongated, forming most of the rostrum. In dorsal view they are divided from each other by a small groove running along the sagittal plane for the whole length of the rostrum. Because of jaw closure it is impossible to give a count of the alveoli borne by these bones. The suture between premaxillae and nasals is not detectable (Hungerbühler 2002) because the portion of the skull anterior to the orbits, until the base of the rostrum, is broken and telescoped posteriorly approximately for 3-5 cm, as can be evaluated by comparison with the skull MBSN 2 (Fig. 1 of Renesto & Paganoni 1998).

The maxillae form little part of the posterolateral portion of the rostrum then, caudally, they become divided into two branches. The horizontal one forms part of the ventral margin of the antorbital fenestra and then meets the jugal. The ascending branch, only partially preserved, forms the anterodorsal margin of the antorbital fenestra. This latter, however, cannot be observed, being nearly completely obliterated by the dorsoventral flattening of the skull (Fig. 4).

The jugals are "V" shaped in lateral view, with anteriorly pointed apices that meet the maxillae in the middle of the antorbital fenestrae. The horizontal rami of the jugals are stout and form the main part of the lower temporal bars. Only the proximal portion of the ascending ramus is preserved due to the dorsoventral flattening (Fig. 4). In lateral view, the jugals are wide in their basal portion, forming stout arches between the antorbital fenestrae and

the lower temporal fenestrae, and become more slender towards the postorbital processes, with which form the posteroventral margin of the orbits.

The nasals, lacrimals and prefrontals are poorly preserved, thus they cannot be described in detail. Nevertheless, the nasal openings are detectable; they are cranio-caudally elongated and narrow, divided from each other by thin and straight septomaxillae, which form their medial borders. Owing to the dorsoventral compression, it is impossible to ascertain if the nares, in lateral view, opened at the same level, or below the skull roof, and if their cranial portion faced anteriorly (Ballew 1989; Hungerbühler 2002).

The bones of the skull roof are heavily ornamented with deep grooves and sinuous keels, placed randomly. These elements are coossified, thus the sutures are represented only by faint lines, which are difficult to be distinguished.

The frontals are sub-trapezoidal, arranged with the main basis facing medially and the minor basis forming part of the medial borders of the orbits. Their anterior portions are not preserved while the posterior ones meet the parietals medially and the postfrontals laterally. A small groove runs straight along the interfrontal suture line.

The postfrontals are small crescentic elements forming with their concave borders the posterodorsal margins of the orbits.

The parietals show approximately the same shape and arrangement as the frontals. They meet the postfrontals and postorbitals laterally and form the anterior and lateral margins of the supratemporal fenestrae posteriorly. The suture between the parietals is completely obliterated by their fusion and there are no evidence of a pineal foramen. Because of the compression of the skull it is impossible to see the extent to which these bones participate to the narrow and depressed parietosquamosal bars (McGregor 1906; Hungerbühler 2002).

The postorbitals, in dorsal view, consist of an anterior ornamented portion that forms the posterodorsal margin of the orbits, and a smooth caudal portion that meets the squamosal, forming a slender upper temporal bar. The postorbital processes are narrow and they bend anteriorly toward the jugals.

The squamosals are clearly divided by horizontal ridge into a lateral and dorsal portion. Their lateral portions are heavily crushed as it occurs for the quadratojugals. The dorsal portions of the squamosals are subrectangular in dorsal view and, in contrast with the other bones of the skull roof, have smooth surfaces. The posterior processes of the squamosals (*sensu* Hungerbühler 2002) are short, not reaching 10 mm in length.

The dorsal surface of the supraoccipital is visible in dorsal view, surrounded by the two divergent parietosquamosal bars. This surface is rough and shows slight cranio-caudally directed carinae for the insertion of the nuchal musculature. The exoccipitals and the opisthot-

ics are completely coossified and no sutures are visible between them. The paroccipital processes are stout and dorsally they support the depressed parietosquamosal bars for their whole length. In caudal view the posttemporal fenestrae are reduced to narrow slits but, due to the preservation, their outline is not detectable (Hungerbühler 2002). The basioccipital and the occipital condyle are obscured by the atlas complex.

Some poorly preserved bones of the palate, tentatively identified as the posterior portions of the pterygoids, can be observed in dorsal view through the antorbital fenestrae-orbital openings; the ventral surface of the palate is still embedded in the matrix with the exception of the quadrate processes of the pterygoids (Fig. 5C, Pl. 1B).

Lower jaw. The lower jaw (Fig. 5C, Pl. 1B) lies in anatomical connection with the quadrates, concealing them. The dentaries are long and slender and show a wide mandibular symphysis that spans from the preserved tip of the rostrum to the level of the anterior border of the nostrils. Their forked caudal ends form the anterodorsal and anteroventral margins of the mandibular fenestrae but, due to preservation, the sutures with the angulars and the surangulars are not detectable. As for the premaxillae and maxillae, it is impossible to establish the number of alveoli. The angulars and surangulars border, respectively, the posteroventral and posterodorsal margins of the subelliptical mandibular fenestrae (Fig. 5A). Due to the dorsoventral compression, it is difficult to detect their exact outline, however, they seem to be three to four times longer than high. The surangulars are collapsed horizontally, thus observing the skull in ventral view they show their concave and rough lingual surfaces, that are the points of insertion for the temporal muscles. The posteriormost extremities of the mandibular rami end with poorly developed retroarticular processes.

Dentition. Only some teeth of the right mandibular ramus, from the tip of the rostrum to the anterior level of the mandibular fenestra, are exposed in lateral view (Fig. 3, Pl. 1A). Most of the dentary teeth, excluding the posteriormost ones, show the same morphology (Fig. 5B). They are sharp, conical, high and slender, with their axis slightly bent postero-medially. The surfaces of their crowns are prominently fluted from the basis to the apex. The poorly exposed posteriormost teeth (Fig. 5A), placed near the level of the mandibular fenestra, seem to be shorter, stouter and slightly medio-laterally compressed than the more anterior ones (Hungerbühler 2002).

Vertebrae and ribs

The vertebral column (Fig. 2A) consists of at least 25 presacrals, 2 sacrals and 74 caudals. It is almost complete and the elements are preserved nearly articulated. Most of the vertebrae are exposed in lateral view apart for those of the middle portion of the tail, which are exposed in dorsal view.

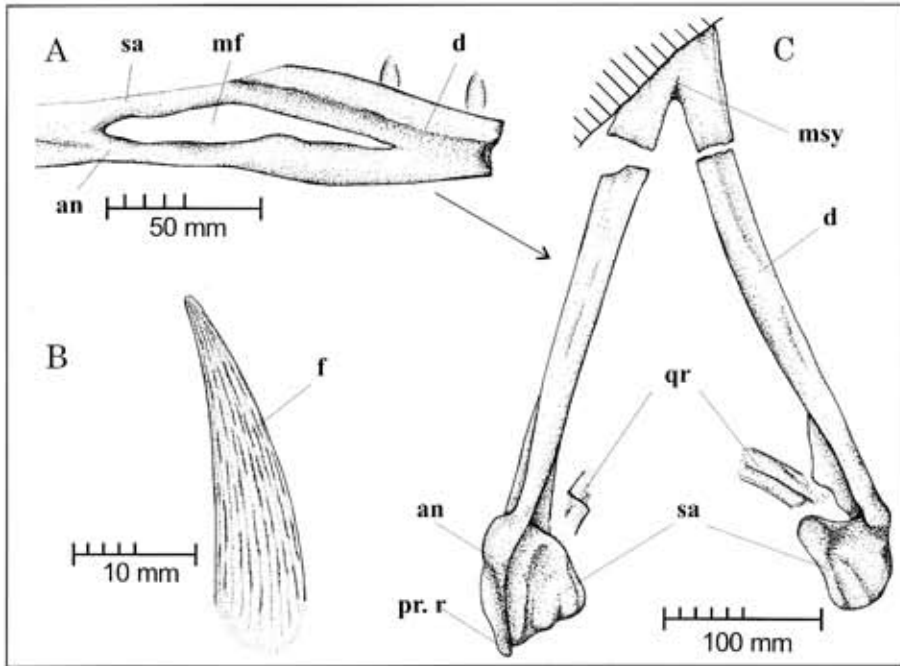


Fig. 5 - *Mystriosuchus planirostris* Von Meyer, 1863. Specimen MCS-NB 10087. A) Lateral view of the right mandibular ramus; the suture lines between the bones are undetectable. B) Lateral view of the crown of a conical teeth placed in the anteriormost portion of the dentary. C) Lower jaw in ventral view; the edge of the slab is highlighted. For abbreviations see appendix.

Cervical vertebrae. The atlas and axis are separated; the atlas lies close to the occiput of the disarticulated skull (Pl. 1A), while the axis is still connected with the rest of the vertebral column. Little can be seen of the atlas complex because of the poor preservation. The anterior part of the axis is missing, while the posterior portion is preserved (Fig. 6), showing part of the centrum and the posterior portions of the neural arch and neural spine. The centrum is stout and its posterior articular surface is slightly concave. The diapophyses and parapophyses are not preserved but, judging from the position of the capitulum and tuberculum in the axis ribs (Fig.

10B), they should have been placed close to each other. The preserved portion of the neural spine shows that it was low and stout, more expanded craniocaudally than those of the following cervical vertebrae.

The postaxial cervical vertebrae (Fig. 6) show platycoelous centra (sensu Romer 1956), with subrectangular lateral outlines, embayed at their ventral margins. The parapophyses are subcircular in shape and placed lateroventrally, near the anterior margins of the centra. Due to fragility of the matrix, it is impossible to clear off the matrix enough to establish if hypopophyses were present as has been reported for other phytosaur specimens (McGre-

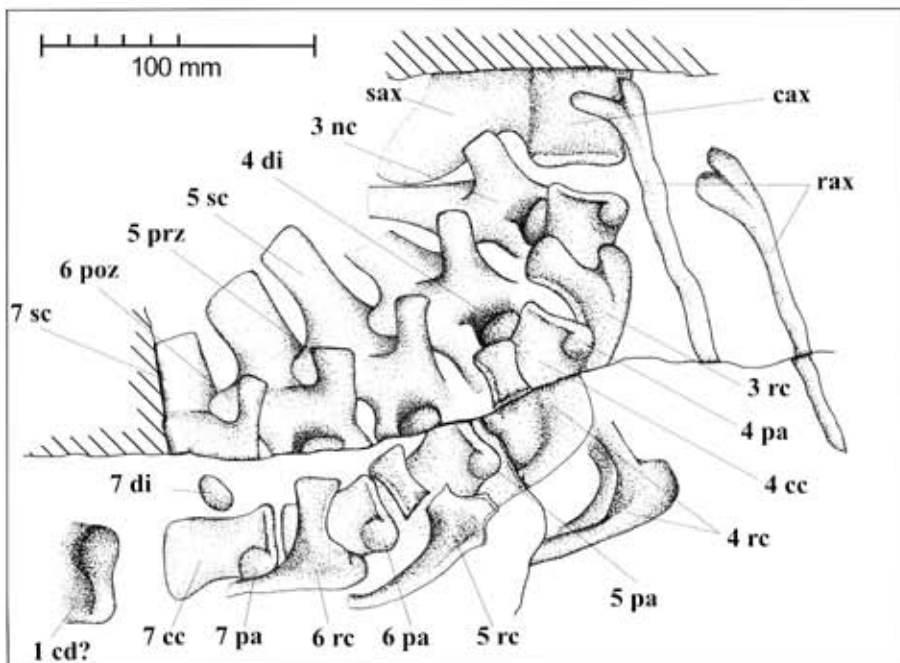


Fig. 6 - *Mystriosuchus planirostris* Von Meyer, 1863. Specimen MCS-NB 10087. Cervical vertebrae in right lateral view. The edge of the slab is highlighted. For abbreviations see appendix.

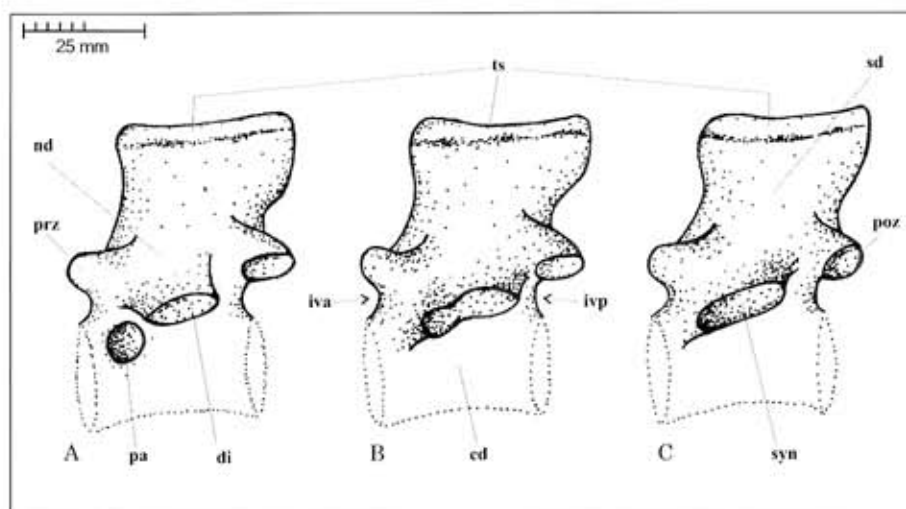


Fig. 7 - *Mystriosuchus planirostris* Von Meyer, 1863. Specimen MC-SNB 10087, drawing of the three main morphologies of the dorsal vertebrae with hypothetical reconstructions of the centra. A) Vertebra of the anterior portion of the trunk. B) Vertebra of the middle portion of the trunk. C) Vertebra of the posterior portion of the trunk. For abbreviations see appendix.

gor 1906). No intercentra are present. The neural arches are subrectangular in lateral view, only slightly higher than long. The pedicels of the neural arches are fused with the centra, with no evidence of neurocentral sutures. The zygapophyses are stout and bear nearly vertical articular facets, suggesting a considerable vertical mobility of the neck. The diapophyses are short processes, sub-oval in shape, which lie at the base of the neural arches. The neural spines are high and slender (2.2 times higher than wide), and directed perpendicularly relatively to the centra.

Due to the pattern of preservation it is rather difficult to establish where the transition from cervical to dorsal vertebrae occurs; in fact the base of the neck and the anteriormost portion of the trunk lie on the margins of two separate stone slabs and the overlapping scapula obscures details. The seventh vertebra (Fig. 6), judging by its general morphology, is probably a cervical while the eighth one is poorly exposed and its identity is thus not determinable, making it impossible to resolve uncertainties in other published reports of cervical counts in phytosaurs (7-9 according to McGregor 1906 and Westphal 1976; 8-9 according to Romer 1956; 8 for Chatterjee 1978).

Dorsal vertebrae. At least 17 dorsal vertebrae are present (Fig. 7, Pl. 2B). Due to fragility of the stone slab it was not possible to prepare completely the dorsal centra. In the dorsal series, the neural spines are subrectangular in shape, much lower (2 times wider than high) and stouter than those of the cervical vertebrae. Their dorsal edges are rough and slightly expanded to increase presumably the insertion area of the ligamentum supraspinosum and of the ligament complex which connects the axial skeleton to osteoderms, as occurs in crocodiles (Frey 1984, 1988). Neural arches, low and subrectangular, bear stout zygapophyses with horizontal articular facets; those allow good lateral mobility to the trunk, quite the opposite of what occurs in the neck. Diapophyses and parapophyses change their shape and placement area through the dorsal series. In the anterior dorsal vertebrae (Fig. 7A) the diapophyses are well developed processes which project

laterally and horizontally from neural arches, while the parapophyses are placed laterally on the centra, near their anterior margins. The parapophyses become gradually closer to the diapophyses proceeding in cranio-caudal direction (Fig. 7B) and, in the posteriormost dorsal vertebrae, these processes become fused into wide synapophyses (Fig. 7C).

All the dorsal vertebrae are lightly built and show no signs of pachyostosis.

Sacral vertebrae. The two sacral vertebrae (Fig. 8A, Pl. 3A) are exposed in ventro-lateral view, thus nothing can be observed of the neural spines. The centra are platycoelous and there are no evidences of anchilosis between them. Close to the neural arches, stout pleurapophyses are present, formed by the complete fusion of the sacral ribs with the transverse processes. These processes expand distally, forming a wide area for the articulation with the iliac blade. Also these processes do not show any kind of coossification for strengthening the pelvic girdle.

Caudal vertebrae. The tail (Fig. 9C, Pl. 3A-4) consists of at least 74 vertebrae and reaches about 192 cm in length (51% of the whole length of the specimen, 2.2 times longer than the trunk). As already noticed in a previous work (Renesto & Lombardo 2000), this vertebral count is much higher than what was reported in the literature (34 to 50, McGregor 1906; Romer 1956; Westphal 1976; Chatterjee 1978). Throughout the tail the shape of the caudal vertebrae changes substantially, making it possible to distinguish at least three different morphologies.

In the first 17 caudals (Fig. 9D, Pl. 3A-4A) the centra are platycoelous, with a subrectangular lateral outlines (1.2 times longer than high), and slightly embayed at their ventral margins. Chevrons, starting from the fourth caudal, are intercentral in position and loosely connected to the centra. The height of the haemal spines is equal to that of the neural spines, forming a deep and laterally flattened tail. The distal end of each haemal spine is cranio-caudally expanded forming a sort of "foot" that widens

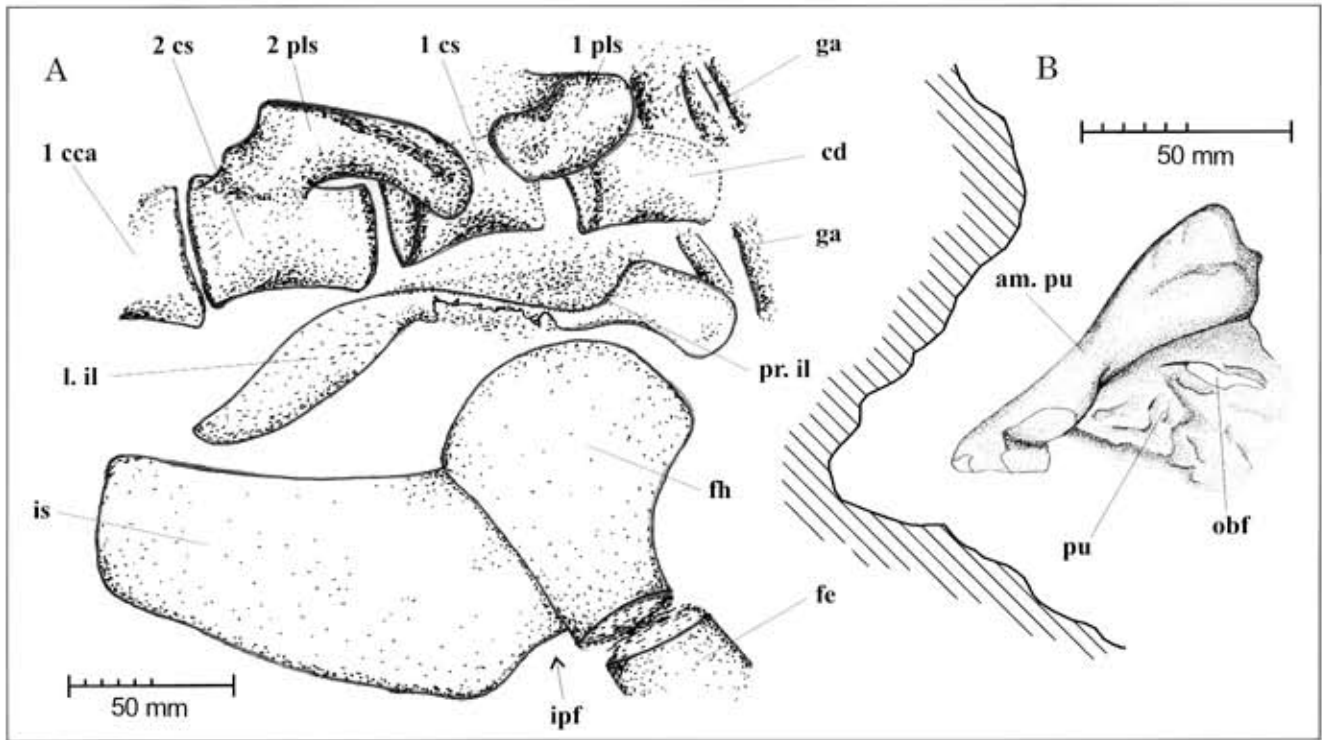


Fig. 8 - *Mystriosuchus planirostris* Von Meyer, 1863. Specimen MCSNB 10087. A) Sacral ribs in ventrolateral view; right ischium and iliac blade in lateral view. B) Lateral view of the left pubis; the edge of the slab is highlighted. For abbreviations see appendix.

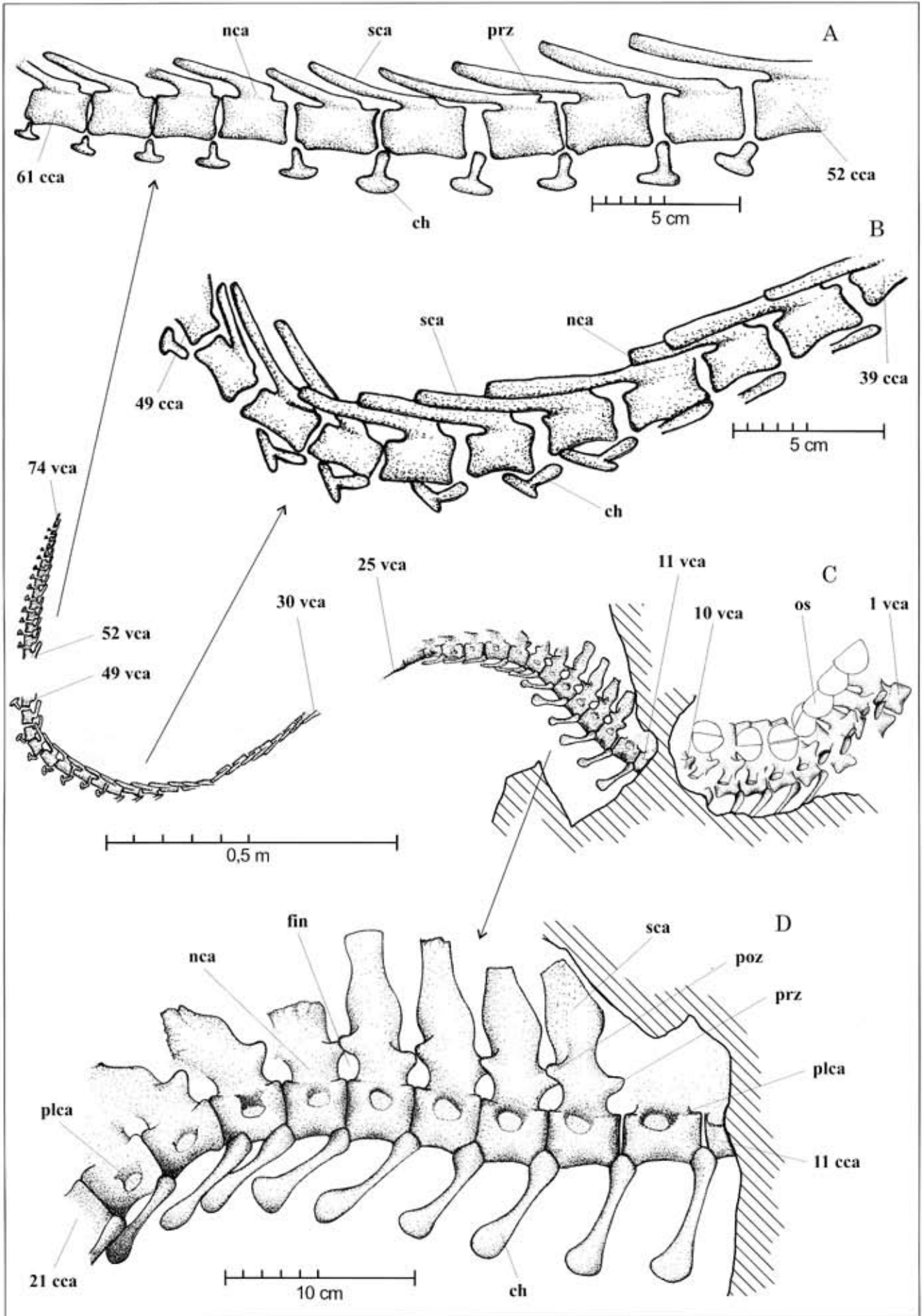
the area for the attachment of the hypaxial musculature. Neural arches are stout, subquadrangular in lateral view and are firmly sutured with the centra. The zygapophyses are prominent and show horizontal articular facets. Stout pleuroapophyses are well developed until the 10th caudal vertebra. Thereafter their size decreases rather rapidly, but they are identifiable to at least the 18th caudal vertebra. The neural spines belonging to the first nine caudal vertebrae (Pl. 3A) are very high (4.3 times higher than wide), sub-rectangular in lateral view and perpendicular to the centra, with rough dorsal edges to house the insertion of the ligamentum supraspinosum. The neural spines of the 9th to 18th vertebrae (Fig. 9D, Pl. 4A) are sub trapezoidal in lateral view and narrow toward their distal end; a slight carina runs ventrodorsally on their lateral surface, strengthening them towards lateral bendings and possibly increasing the insertion area for the interspinosus muscle.

From the 18th caudal vertebra until approximately the 28th-32th (this area is poorly preserved thus the transition point cannot be established with more precision), the neural spines and chevrons start to slant posteriorly and this slanting become more and more pronounced caudally (Pl. 4A).

Posterior to the 32th caudal vertebra (Fig. 9A-B, Pl. 4B), the centra are small, platycoelous and subrectangular in lateral view (roughly twice long than high). The neural arches are very low and bear vestigial pre and postzygapophyses that do not meet each others. The neural spines

are narrow but very long (at least 2 times the length of corresponding centrum) and, in their first halves, they are almost horizontally (craniocaudally) oriented, bending slightly dorsally in their distal portion. As a consequence, the distal end of each neural spine overhangs at least one and sometimes more than one of the following centra. This structure is peculiar and has not been reported for other phytosaurs. Possibly this pattern rendered the posterior portion of the tail rather stiff. The haemal arches are small and show an inverted "T" shape, similar to that one of some sauropterygians (Carroll & Gaskill 1985; Sander 1989) and some Jurassic marine crocodylians (Fraas 1902).

Ribs. The ribs of the atlas and axis (Fig. 10B) are described for the first time for a phytosaur. The ribs of the atlas are holocephalous with capitulum and tuberculum fused together, their shaft is long and narrow and it spans for the first three centra. The ribs of the axis are dicocephalous, with capitulum and tuberculum placed very closely but separated. They also show a long and narrow shaft which is shorter, however, than the atlantal ribs, being as long as two adjacent centra. The following cervical ribs (Fig. 10A) are "hatchet" shaped (sensu McGregor 1906). That is, in lateral view, they look like an axe, these latter being much wider in their anterior portion, followed by short and slender posteriorly directed shafts (as long as a centrum). At the anterior tip of each rib, a cranial process is present, that outreaches the anterior border of the centrum. In the medial surface of the



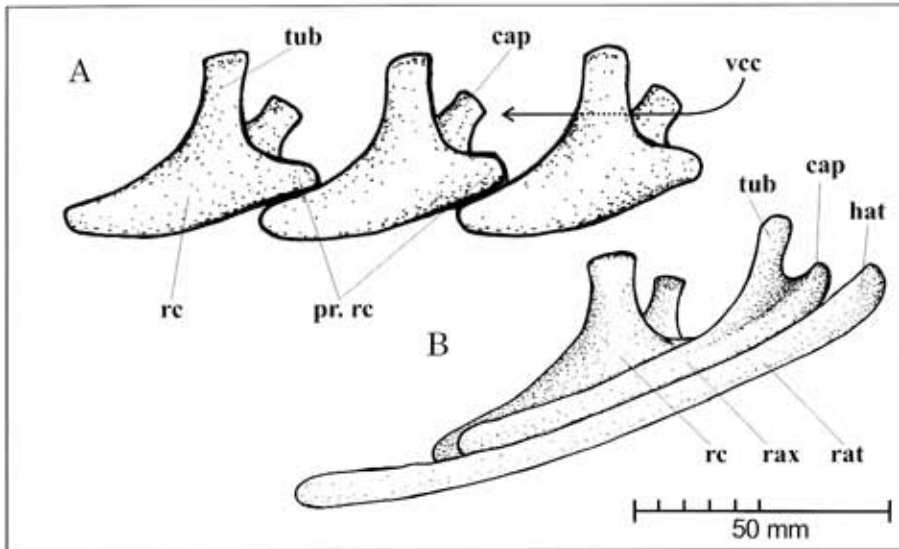


Fig. 10 - *Mystriosuchus planirostris* Von Meyer, 1863. Specimen MCS-NB 10087, reconstruction of the cervical ribs in articulation. A) Lateral view of three right ribs showing the overlapping between their anterior processes and their posteriormost portions of the shafts. B) Atlas rib, axis rib and third cervical rib in right lateral view, showing the complete overlap between these elements. For abbreviations see appendix.

rib shaft, a slight groove can be noticed. The tubercula and capitula are well developed and widely spaced. The last cervical ribs cannot be observed, possibly obscured by the overlying scapula.

All dorsal ribs (Pl. 2B) are dichoccephalous, but the distance between capitulum and tuberculum decreases gradually proceeding caudally. Proximally, the rib shaft bears on its dorsal surface a slight carina, possibly representing the process for the insertion of intercostal muscles. The curved outline of the dorsal ribs does not change along the dorsal series and no lumbar region is differentiated. Ribs are slender thus exhibiting no pachyostosis.

Several disarticulated gastralia (Pl. 2A-3A) are present in the abdominal region. They are rod-like, sub-circular in cross section and, like the dorsal ribs, not pachyostotic.

Girdles and limbs

Shoulder girdle. The shoulder region is the worst preserved part of the entire skeleton. Only the right scapula, lacking its distal end, and the cranial part of the interclavicle can be observed. The scapula (Fig. 11A) shows an expanded base, which bears a narrow but rather elongate scapular blade. Close to the base, on its medial surface, a crescent-shaped crest marks the articular area for the coracoid. In lateral view, the scapular blade slants posteriorly and becomes increasingly thin towards its dorsal extremity. The interclavicle (Fig. 11B, Pl. 2B) is dorso-ventrally flattened with its anterior portion less laterally expanded with respect to what has been reported for

other phytosaurs, in which this structure is distinctly "T" shaped (McGregor 1906; Chatterjee 1978; Long & Murry 1995). Two embayments on the sides of the anterior margin of the interclavicle housed the medial tips of the clavicles.

Anterior limb. The anterior limbs (Fig. 12-13, Pl. 2) are exposed in ventral view and lie in articulation. However they are found on two separated slabs and so their preservation is poor. The humerus (Fig. 12-13A, Pl. 2A) is short (74% of the length of the femur) and narrow, with a gentle bending of the shaft and a poorly developed deltopectoral crest. Its proximal head is expanded forming a wide convex articular area. Its distal head bears two convex articular areas for radius and ulna, separated from each other by an embayment. A well developed ectepicondylar process is present and, as for other archosaurs, the entepicondylar foramen is absent.

The radius (Fig. 13B, Pl. 2B) is a short (50% the length of the humerus) and slender bone, showing an almost straight shaft and an unexpanded distal end. Proximally, a radial tuberosity meets the ulna. This latter bone (Fig. 12, Pl. 2A) is stouter and slightly longer than the radius; its medial margin is concave, whereas the lateral one is nearly straight. The proximal head is obscured, but in this region the shaft widens distinctly, suggesting that it was well expanded, forming a wide articular surface for the humerus. The distal head of the ulna (Fig. 13B, Pl. 2B) is larger than that of the radius, and it shows a convex semicircular outline. No carpals are preserved despite the size of the specimen and the complete of ossification of

Fig. 9 - *Mystriosuchus planirostris* Von Meyer, 1863. Specimen MCSNB 10087. A) Close up of the caudal vertebrae from the 52nd to the 61st, showing the overlapping of the neural spines. B) Close up of the caudal vertebrae from the 39th to 49th. C) Drawing of the whole tail in right lateral view; the edges of the two slabs are highlighted. D) Close up of the caudal vertebrae from the 11th to the 21st. For abbreviations see appendix.

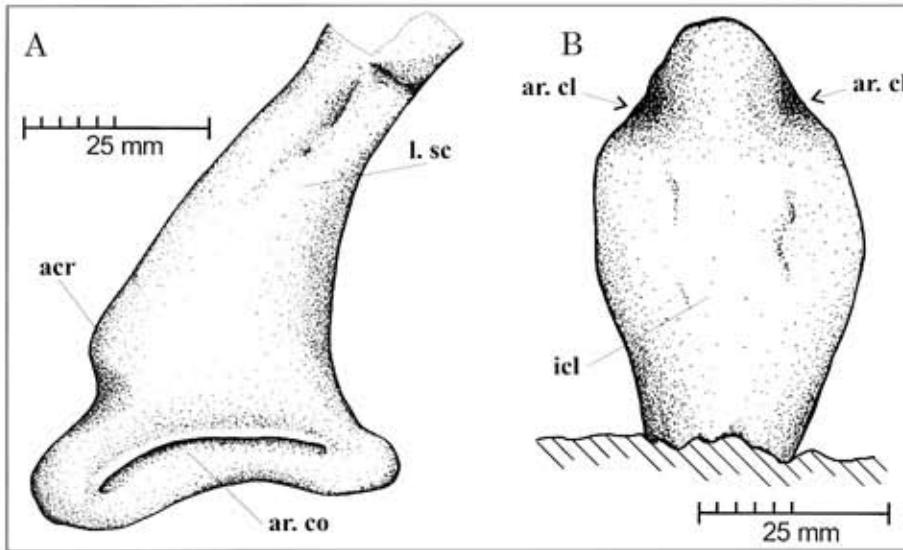


Fig. 11 - *Mystriosuchus planirostris* Von Meyer, 1863. Specimen MCSNB 10087. A) Right scapula in medial view; the break point of the scapular lamina is represented with a dotted line. B) Cranial portion of the interclavicle; the edge of the slab is highlighted. For abbreviations see appendix.

the other bones, suggesting that MCSNB 10087 was fully-grown. Carpal elements are virtually unknown in other phytosaurs (McGregor 1906; Chatterjee 1978) thus it can be hypothesized that these bones did not ossify even in the adult, but were retained in cartilage.

The manus (Fig. 13B, Pl. 2B) is poorly exposed due to its folded position and to the fragility of the matrix which hindered further preparation. Two metacarpals and four to five phalanges of different digits are present but more precise identification is impossible. As a consequence no phalangeal formula for the manus can be given.

Pelvic girdle. Concerning the ilium, only the iliac blade (Fig. 8A, Pl.3A) is clearly visible. In dorsolateral view, it shows the same extension of the puboischiatic plate and its preacetabular region is approximately half the length of the postacetabular portion. The postacetabular portion tapers posteriorly, ending in a pointed process. Just above the acetabulum, the iliac blade bears

a laterally projecting tabular process, probably the point of origin of the iliotibialis muscle (Romer 1956; Hutchinson 2001a).

The pubis (Fig. 8B, Pl.3B) is subrectangular in shape with a thickened anterior margin and, close to the acetabular region, it bears a wide obturator foramen. The ischium (Fig. 8A, Pl. 3A) is posteriorly elongate. The ventral end of its anterior margin loses contact with the pubis forming a puboischiadic opening (Mc Gregor 1906).

Hind limb. The hind limbs are nearly complete and preserved in articulation. The right one (Fig. 14B, Pl. 3A) is exposed in dorsal view while the left one (Fig. 14A, Pl. 3B) is visible from its ventral side. Only some elements of the tarsus and pes cannot be observed in detail.

The femur is rather slender and short being about 7,5% of the length of the whole preserved skeleton (Farlow & Britton 2000). We anticipate that this ratio would have been even smaller in the living animal, because its total length would have been higher due to the presence

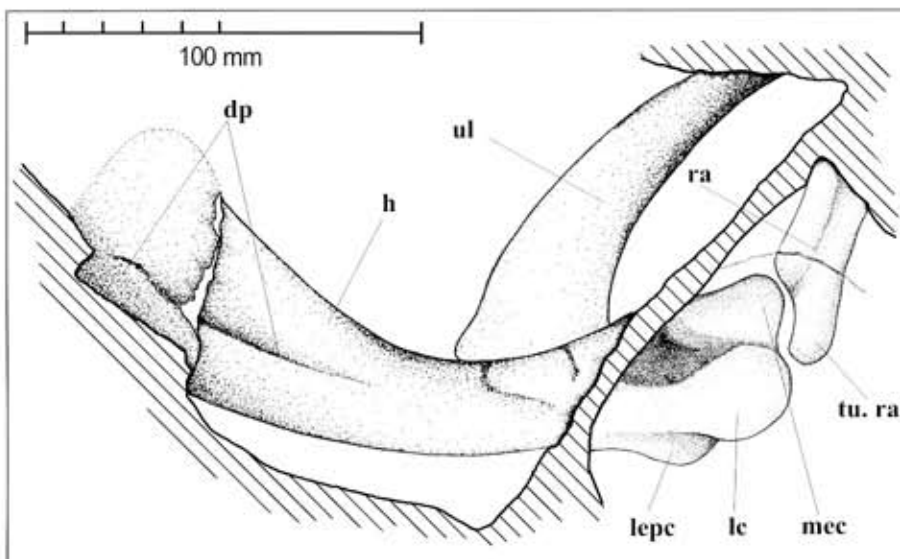


Fig. 12 - *Mystriosuchus planirostris* Von Meyer, 1863. Specimen MCSNB 10087, ventral view of the stilopodium and zeugopodium of the right forelimb; the edges of the two slabs are highlighted. For abbreviations see appendix.

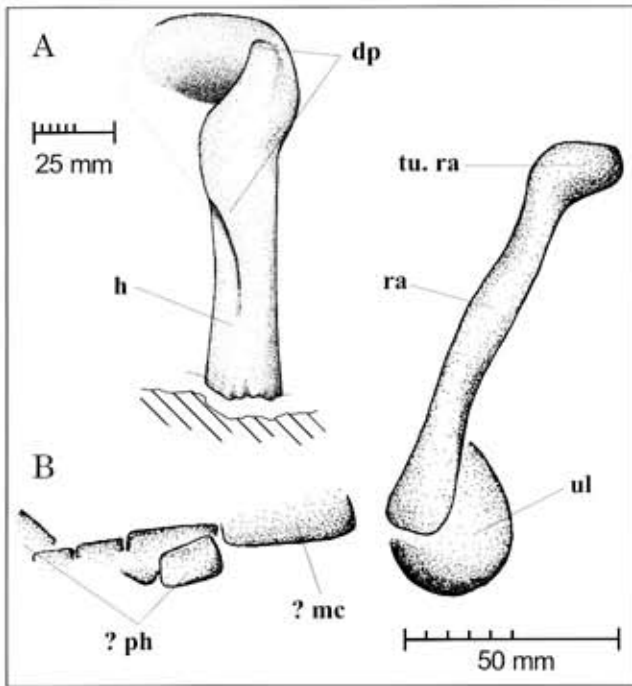


Fig. 13 - *Mystriosuchus planirostris* Von Meyer, 1863. Specimen MCSNB 10087, elements of the left forelimb. A) Ventral view of the humerus head and of the proximal portion of its shaft; the edge of the slab is highlighted. B) Zeugopodium and elements of the manus; the carpals are not preserved as they probably remained cartilaginous also in mature specimens. For abbreviations see appendix.

of articular cartilages between the centra of the vertebrae (Hoffstetter and Gasc 1969). The shaft shows a more pronounced sigmoidal outline than those reported for other European phytosaurs (McGregor 1906; Westphal 1976), but it is very similar to that of the isolated femur which is part of the material referred to *Mystriosuchus planirostris* (Buffetaut 1993, and pers. obs.) collected in the Late Triassic Dachstein Kalk (Austria), housed in Wien Natural History Museum (field number 1986/21/12). The femur of MCSNB 10087 recalls also in its sigmoidal outline those ones ascribed to *Leptosuchus* sp., and *Pseudopalatinae* gen. undet. from the Late Triassic Chinle Formation (Long & Murry 1995; cat. no. UCMP V69131/85100, UCMP V2816/122658). The proximal head is craniodorsally expanded forming a wide convex articular surface, then it gently narrows distally without forming a distinct "neck". The ventral surface of the proximal head (Fig. 14A, Pl. 3B) is slightly concave and rough, forming the intertrochanteric fossa (Romer 1956; Hutchinson 2001b) for the insertion of the puboischiofemoralis muscle. Just distal to the head, a well developed fourth trochanter is visible. This process continues distally into a slight carina, probably for the insertion of the adductor femoris muscle. The distal end of the bone is badly preserved.

The tibia and the fibula are approximately of the same length, the tibia being somewhat shorter but stouter than the fibula. The proximal head of the tibia is enlarged,

sub triangular in cross section and forms most of the articular surface for the femur. The shaft, near the proximal end, is stout and bears a protuberance, probably for the insertion of the iliotibialis muscle (Fig. 14A, Pl. 3B). Distally it becomes narrower forming a moderately expanded distal end that contacts the astragalus. The fibula shows a smaller proximal head than the tibia and its shaft is straight, apart for an embayment of its tibial margin. Under the proximal epiphysis there is a carina (Fig. 14B, Pl. 3A) tentatively interpreted as the iliofibularis trochanter for the insertion of the homonymous muscle (Romer 1956; Hutchinson 2001b). The distal head is only slightly expanded and forms two articular condyles separated by a distinct concavity. The medial condyle is larger than the lateral one and, along with the concavity, forms the articular area for the astragalus. The lateral condyle is more prominent and meets the calcaneum.

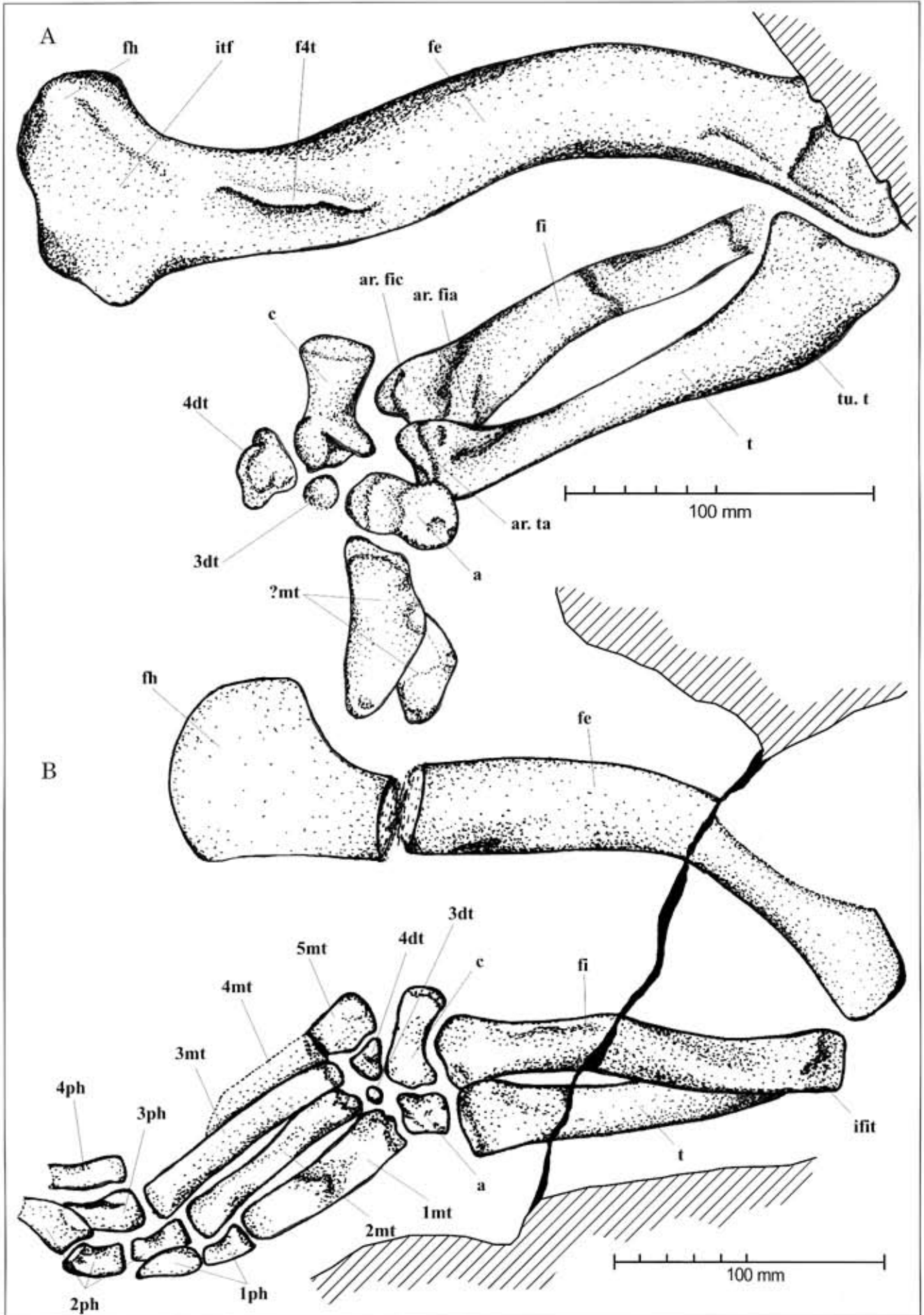
The tarsus (Fig. 14A-B, Pl. 3B) consists of four well ossified bones: the astragalus, the calcaneum and, distal to these latter, the third and fourth distal tarsals. The astragalus is a well developed but short bone with a squared shape. On the dorsal margin it bears the articular surface for the fibular medial condyle and, medially, that one for the tibial condyle. Its lateral surface bears a process that fits into a recess of the calcaneum, forming the typical "crocodile normal" joint. The calcaneum is also well ossified and its medial portion houses the concave articular surface for the astragalus; latero-posteriorly a well developed calcaneal process is present. The third distal tarsal (the medial-distal tarsal sensu Chatterjee 1978) is small and spherical in shape; it meets the astragalus proximally and the metatarsals distally. The fourth distal tarsal (the latero-distal tarsal sensu Chatterjee 1978) is two to three times larger than the distal tarsal three. Proximally it meets both the astragalus and the calcaneum, laterally the hooked fifth metatarsal and distally the third and fourth metatarsals.

The metatarsals (Fig. 14B, Pl. 3A) become longer and thinner from the first to the fourth. The fifth one is proximally expanded and bears a medially directed process which forms the "hook" that meets the fourth distal tarsal.

Only the first two toes (Fig. 14B, Pl. 3A) are completely exposed and they consist of two and three phalanges respectively.

Dermal armour

At least 19 osteoderms belonging to the dorsal armour are preserved in the specimen; 12 osteoderms lie close to the proximal portion of the tail (Fig. 9C, Pl. 3A) and the other seven are visible in the anterior region of the trunk (Pl. 2B). No bony plates are preserved in the throat region as reported for other phytosaurs by McGregor (1906) and Chatterjee (1978); this may represent an artifact due to preservation, but it cannot be excluded that the gular plates were originally absent in the specimen,



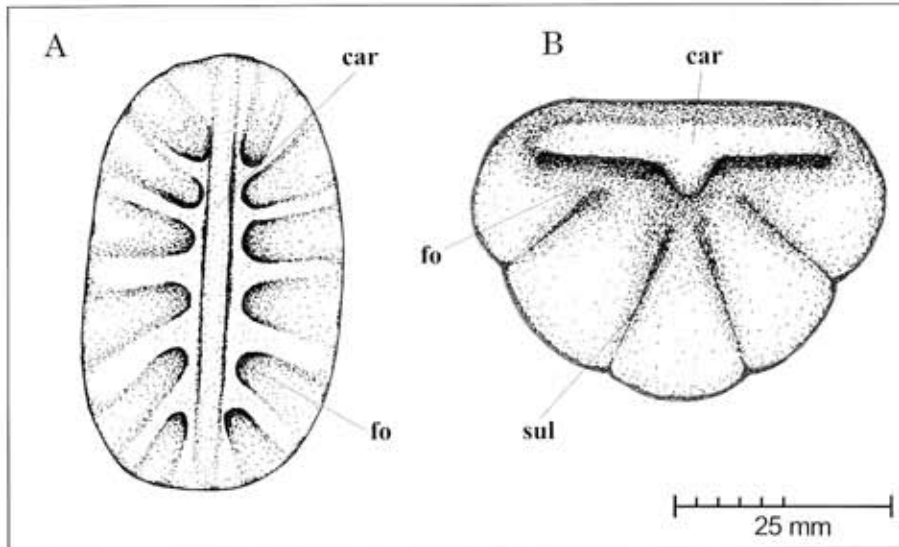


Fig. 15 - *Mystriosuchus planirostris* Von Meyer, 1863. Specimen MCSNB 10087, dermal bones of the dorsal armor. A) Elliptical osteoderm forming two medial rows in the trunk region. B) Subpentagonal osteoderm forming two lateral rows in the trunk region that, differently from the medial ones, proceed in the proximal portion of the tail. For abbreviations see appendix.

being the skeleton generally more gracile than those of other phytosaurs (McGregor 1906; Chatterjee 1978).

In the trunk region, the dorsal osteoderms are aligned in four rows (Pl. 2B) and show two different morphologies. The osteoderms of the two medial rows (Fig. 15B) are subpentagonal in dorsal view, arranged with the main basis medially oriented. A distinct carina can be observed running parallel to the sagittal plane, close to the main basis of the trapezium. Two sub-elliptical concavities are present lateral to the carina and, on the dorsal surface of the plates, a series of shallow sulci radiate from the middle of the carina toward the lateral margins of the osteoderm.

The plates belonging to the two lateral rows are sub-elliptical (Fig. 15A) in dorsal view, arranged with the main axis parallel to the sagittal plane. A distinct carina runs along the main axis of the plates, bordered on each side by six grooves, with some shallow sulci radiating from each groove towards the margins.

From the base of the tail to approximately the 9th-10th caudal vertebra, two rows of subpentagonal plates are present (Fig. 15B, Pl. 3A). Both in the tail and in the trunk, the osteoderms are segmentally arranged. That is, each transverse row of four (in the trunk) or two (in the tail) osteoderms corresponds to one vertebra. Osteoderms do not overlap laterally, but the posterior ends of each osteoderm are slightly superimposed to the anterior ends of the following one.

The relationship of the neural spines in the trunk region (Fig. 7) to the pattern of the dorsal osteoderms is

very similar to what is found in extant crocodiles, where the vertebral column and the dorsal armour are linked together with a strong complex of ligaments (Frey 1988).

Discussion

Some unambiguous features, such as the extreme elongation of the premaxillae and the posteriorly placed external nares (Ballew 1989; Doyle & Sues 1995), point out that MCSNB 10087 belongs undoubtedly to phytosaurs (Phytosauria Meyer 1861). But, though the specimen is nearly complete and in articulation, it is rather difficult to establish its taxonomic position within this group. The whole postcranial skeleton, although extremely useful for ecological and biomechanical research, is of little use for taxonomy because the vast majority of other phytosaurs are known primarily by their skulls. Moreover, in this specimen the skull is strongly flattened dorsoventrally, in deep contrast to what occurs in most other phytosaurs, in which the skulls are preserved laterally compressed (McGregor 1906; Buffetaut 1993) or, due to different diagenetic history, nearly three dimensionally preserved (Long & Murry 1995). Thus many diagnostic characters, used for the identification of different phytosaur taxa, are of difficult application in our case, greatly reducing the possibilities of comparison.

In the present discussion, in order to compensate this lack of available characters, along with data from MCSNB 10087 we add also characters observed in the isolated

Fig. 14 - *Mystriosuchus planirostris* Von Meyer, 1863. Specimen MCSNB 10087, drawing of the hindlimbs as preserved; the edges of the slabs are highlighted. A) Left hindlimb showing the femorus in ventral view and the zeugopodium and pes in anterior view. B) Right hindlimb in dorsocaudal view. For abbreviations see appendix.

skull MBSN 2, from the same locality and fossiliferous level (Renesto & Paganoni 1998). This skull, previously assigned to *Mystriosuchus cf. planirostris* is virtually identical to the skull of MCSNM 10087, with which it shares the overall shape and size, and among other characters, the pattern of the frontal and occipital region, the morphology of the temporal fenestrae. All these characters testify that MCSN 10087 and MBSN2 can be considered as conspecific. MBSN 2 is better preserved, showing also the bones of the palate and, above all, is latero-dorsally flattened, allowing the observation of some additional diagnostic characters.

According to present knowledge of phytosaur relationships (Westphal 1976; Chatterjee 1978; Ballew 1989; Long & Murry 1995; Hungerbühler 2002) we can find in MCSNB 10087 and MBSN 2 some diagnostic characters that allow us to ascribe them to the genus *Mystriosuchus*, as listed here.

Long prenarial snout. MCSNB 10087 lacks the tip of the snout and shows the skull table and the external nares slightly shifted forward, thus making difficult to establish the right ratio between the length of the rostrum and the cranial length. Measuring the skull as it is preserved, that is underestimating the real ratio, we notice that the prenarial portion of the snout forms about the 63% of the whole cranial length, a value close to the range of 65%–72% considered diagnostic for *Mystriosuchus* (Westphal 1976). The better preserved MBSN 2 falls within this range of variability, showing a ratio of about 70%.

Slit-like interpremaxillary fossa. In MBSN 2 the palatal surface of the premaxillae, between the rows of the alveoli, bears two rounded longitudinal ridges, separated by a trough (the interpremaxillary fossa). More anteriorly the narrowing of the snout, and close apposition of the two ridges, reduces the interpremaxillary fossa to a thin slit.

Reduced posterior processes of the squamosals. The posterior processes of the squamosals (sensu Hungerbühler 2002) project minimally (less than 10 mm) behind the lateral extremity of the paroccipital process of the opisthotic.

Posttemporal fossae strongly reduced. The strong depression of the parieto-squamosal bars and, consequently, their close contact with the opisthotics, reduces the posttemporal fossae to narrow slits.

Squamosal well divided into an horizontal and vertical plane. In MCSNB 10087 a prominent longitudinal ridge divides the squamosal into an horizontal surface, flat and smooth, and into a vertical surface, forming part of the posterior border of the infratemporal fenestra.

Skull roof bones deeply sculptured, with pits prevailing over ridges. The external surfaces of the bones of the skull roof and of the narial region are, in both specimens, deeply ornamented by a complex of anastomosed weak carinae and sulci. In dorsal view the sulci seems "to prevail" over the carinae, that is the first ones span over a wider surface of the bones than the second ones.

Within the genus *Mystriosuchus*, MCSNB 10087 and MBSN 2 cannot be ascribed to *M. westphali* Hungerbühler and Hunt 2000 since they lack diagnostic characters for that species and, in addition, they show significant differences in the general morphology of the skull. In the studied specimens the rostrum is clearly uncrested (crested in *M. westphali*, Hungerbühler & Hunt 2000) and less massive, mainly in the portion at the level of the antorbital fenestrae (massive in *M. westphali* Hunt & Lucas 1989). The posterior teeth of the upper jaw are not enlarged in comparison with the anterior ones and they are only slightly laterally compressed (stouter and distinctly compressed in *M. westphali* Hungerbühler 2000).

A comparison with *M. planirostris* is rendered difficult because the majority of the diagnostic features for this species have been established on the basis of descriptions of laterally compressed skulls. In MCSNB 10087 and MBSN 2, the dorso-ventral flattening obscured most of the important unambiguous characters such as, for example, the concave profile of the prenarial area; the anterior portion of the nasal openings that faces anteriorly; the parieto-squamosal bars depressed by more than 30% of skull height; the raised antero-lateral borders of the supratemporal fenestrae.

However, MCSNB 10087 and MBSN 2 share with *M. planirostris* other characters, but these are not unanimously considered as diagnostic for that species.

Parieto-squamosal bars reduced. The depressed parieto-squamosal bars are definitely more slender than the stout paraoccipital processes, to which they are closely associated for their whole length. This character is controversial, having been considered alternatively as a synapomorphy of the pseudopalatine more derived than *Nicrosaurus* (node M in Ballew 1989; unnamed node in Hungerbühler 2002) or as acquired independently into two different groups of phytosaurs, the *Paleorhinus-Mystriosuchus* lineage and the *Angistorhinus-Pseudopalatus* lineage (Chatterjee 1978; Hunt & Lucas 1989; Long & Murry 1995). However the morphology of the parieto-squamosal bars and the general shape of the supratemporal fenestrae seem to be more closely related to *M. planirostris* than to the other phytosaurs which show these features. In these (e. g. the species belonging to the genus *Pseudopalatus*) the supratemporal fenestrae are greatly reduced and not visible in dorsal view. In MCSNB 10087, the supratemporal fenestrae are widened by deformation due to the anterior shifting of the skull roof bones and thus are not useful for comparison. In MBSN 2, they maintain approximately the original morphology and they are well visible in dorsal view.

The pattern of the dentition in the upper jaw. Observing the alveolar morphology of MBSN 2 and the exposed teeth of MCSNB 10087, we can say that in the upper jaw the teeth have approximately the same size but show some changes in their morphology proceeding cranio-caudally. As in *M. planirostris* (Hungerbühler 2000), the majority of the maxillary and premaxillary

teeth are conical, with high crowns and rounded cross-sections, whereas the posteriormost maxillary ones are shorter and slightly compressed laterally. According to Hungerbühler (2000), future in-depth study on phytosaur dentition will probably point out that this kind of pattern could be present also in many other slender snouted phytosaurs, previously described generally as homodont (Hunt 1989).

Nevertheless, the possibility that our specimens belong to other taxa of slender snouted phytosaurs is not feasible in our opinion, considering some evident differences in the skull architecture.

In the middle Carnian phytosaurs of North America and Eurasia (subfamily Paleorhininae Long & Murry, 1995 and subfamily Angistorhininae Camp, 1930), the external nares are less caudally shifted than in MCSNB 10087 and MBSN 2.

Phytosaurs of subfamily Rutiodontinae Long & Murry, 1995 of the late Carnian of North America show the parieto-squamosal bars close to the level of the skull roof bone, while in our specimens they are well depressed below this level.

In the Norian forms of North America (subfamily Pseudopalatinae Long & Murry, 1995) the supratemporal fenestrae are not visible in dorsal view, being recessed below the skull deck, and the postorbito-squamosal bars are wide; in MCSNB 10087 and MBSN 2 the supratemporal fenestrae are well visible in dorsal view and the postorbital-squamosal bars are narrow.

In the slender snouted ecomorph of *Nicrosaurus*, the species *N. meyeri* Hungerbühler & Hunt, 2000, from the coeval localities of Württemberg (Southwest Germany), the postorbito-squamosal bars are wider than those of MCSNB 10087 and MBSN 2, and the supratemporal fenestrae are distinctively narrower.

No significant differences can be found between the skulls of our specimens and those ascribed to *M. planirostris*. Only the postorbito-squamosal bars (the postorbital bars of Hunt and Lucas 1989) seems to show, in dorsal view, some differences in its width. In *M. planirostris* the postorbito-squamosal bars are wide with regard to supratemporal fenestrae while, in MBSN 2 and particularly in MCSNB 10087, they are more slender. Also, in this case, this discrepancy may be due to the differences in the pattern of preservation of the specimens (Renesto & Lombardo 1999).

In summary, several characters support the assignment of MCSNB 10087 and MBSN 2 to the genus *Mystriosuchus* Fraas, 1896. Concerning the specific attribution, we must consider that (1) the characters most accepted as diagnostic for the species *M. planirostris* are either obliterated or altered by the dorso-ventral compression of the specimens, (2) although some features shared with *M. planirostris* can be found also in other phytosaurs belonging to the "dolichorostral type" (Hunt 1989), the systematic attribution of MCSNB 10087 and MBSN 2 to any "dolichorostral phytosaur" other than *M. planirostris* is rejected due to the pres-

ence of other differences, (3) there are instead no significant differences between our specimens and those ascribed to *M. planirostris* that can not be interpreted as resulting from the different mode of preservation of the specimens.

For these reasons we can ascribe the specimens MCSNB 10087 and MBSN 2 to the species *Mystriosuchus planirostris* Fraas, 1896 with some confidence. This classification confirms the preliminary hypotheses (Renesto & Paganoni 1998; Renesto & Lombardo 1999) and it is also consistent with the age determination of the locality as Middle Norian (Wild 1991).

The skulls of MCSNB 10087 and MBSN 2 provide no additional informations to solve the problematic phylogenetic relationships between *M. planirostris* and the other phytosaurs at the suprageneric level.

Conclusion

Due to its completeness, the description of specimen MCSNB 10087, adds significant knowledge to the postcranial anatomy of *Mystriosuchus*. On the systematic aspect, additional data on the postcranial skeleton may reveal useful to solve controversies about phylogenetic relationships among phytosaurs, and represent a basis for further comparison with other nearly complete specimens, for which the postcranial skeleton is still undescribed (cf. Long & Murry 1995). MCSNB 10087 provides also useful data for a detailed study of functional morphology and paleoecology of these reptiles (Gozzi & Renesto in prep.).

Several morphological features, such as the tail structure and the limb-trunk proportions of MCSNB 10087, indicate that *Mystriosuchus planirostris* was more adapted to aquatic life than other known phytosaurs (Renesto & Lombardo 1999), giving further support to the hypothesis that at least some phytosaurs lived in marine environments (Buffetaut 1993), like Liassic marine crocodiles. The Norian intraplatform basins, in which the Zorzino Limestone was deposited, were separated from the open sea by tidal channels which possibly represented ecological barriers for the huge Late Triassic ichthyosaurs (Tintori 1995), more adapted to epipelagic life. Their absence in these Bahama-like lagoons may represent an ecological opportunity for other large aquatic or semi-aquatic predators like these gavial-like phytosaurs.

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REFERENCES

- Ballew K. (1989) - Phylogenetic analysis of the Phytosauria from the Late Triassic of the western United States, pp. 309-339 in S. G. Lucas & A. P. Hunt (eds.) - Dawn of the Age of Dinosaurs in the American Southwest. New Mexico Museum of Natural History, Albuquerque.
- Buffetaut E. (1993) - Phytosaurs in time and space, pp. 39-44 in Mazin J. M. & Pinna G. (eds): Evolution, ecology and biogeography of the Triassic reptiles. *Paleont. Lombarda*, N. S., 2, Milano.
- Buffetaut E. & Ingavat R. (1982) - Phytosaur remains (Reptilia, Thecodontia) from the Upper Triassic of North-Eastern Thailand. *Geobios*, 15: 7-17, Lyon.
- Buffetaut E., Martin M. & Monod O. (1988) - Phytosaur remains from the Cenger Formation of the Lycian Taurus (Western Turkey): stratigraphical implications. *Geobios*, 21: 237-243, Lyon.
- Calzavara M., Muscio G. & Wild R. (1980) - *Megalancosaurus preonensis* n. g. n. sp., a new reptile from the Norian of Friuli. *Gortania*, 2: 59-64, Udine.
- Carroll R. L. & Gaskill P. (1985) - The nothosaur *Pachypleurosaurus* and the origin of plesiosaurs. *Phil. Trans. Roy. Soc. London B*, 309: 343-393, London.
- Chatterjee S. (1978) - A primitive parasuchid (phytosaur) reptile from the Upper Triassic Maleri Formation of India. *Palaentology*, 21: 83-127, London.
- Doyle K. D. & Sues H. D. (1995) - Phytosaurs (Reptilia: Archosauria) from the Upper Triassic New Oxford Formation of York County, Pennsylvania. *Journ. Vert. Paleont.*, 15: 545-553, Lawrence.
- Farlow J. O. & Britton A. (2000) - Size and body proportions in *Alligator mississippiensis*: implications for archosaurian Ichthyology. *Paleont. Soc. Korea Spec. Pub.*, 4: 189-206, Seoul.
- Fraas E. (1896) - Die schwäbischen Trias-Saurier nach dem Material der Kgl. Naturalien-Sammlung in Stuttgart zusammengestellt. Stuttgart (Schweizerbart Festgabe des Königl. Nat. Kabinetts in Stuttgart, 42). *Versamml. Dt. Geol. Ges. Stuttgart*, 1-18, Stuttgart.
- Fraas E. (1902) - Die Meerkrokodilier (Thalattosuchia) des oberen Jura unter spezieller Berücksichtigung von *Dacosaurus* und *Geosaurus*. *Palaentographica*, 49: 1-72, Stuttgart.
- Frey E. (1984) - Aspects of the biomechanics of crocodylian terrestrial locomotion, pp. 93-97 in 3th Symposium on Mesozoic Terrestrial Ecosystems, Wolf-Ernst Reif & Frank Westphal (eds), Tübingen.
- Frey E. (1988) - Anatomie des Körperstammes von *Alligator mississippiensis* Daudin. *Stuttgarter Beitr. Naturk.*, Ser. A (Biologie), 424: 1-106, Stuttgart.
- Gregory J. T. (1962) - The genera of phytosaurs. *Am. Journ. Sci.*, 260: 652-690, New Haven.
- Hoffstetter R. & Gasc J. (1969) - Vertebrae and Ribs, pp. 201-310 in Gans C. (eds) - Biology of the Reptilia, 1, Academic Press, London.
- Hunt A. P. (1989) - Cranial morphology and ecology among phytosaurs, pp. 309-339 in S. G. Lucas & A. P. Hunt (eds.) - Dawn of the Age of Dinosaurs in the American Southwest. New Mexico Museum of Natural History, Albuquerque.
- Hungerbühler A. (2000) - Heterodonty in the European phytosaur *Nicrosaurus kapffi* and its implications for the taxonomic utility and functional morphology of phytosaur dentition. *Journ. Vert. Paleont.*, 20(1): 31-48, Lawrence.
- Hungerbühler A. (2002) - The Late Triassic Phytosaur *Myrstriosuchus westphali*, with a revision of the genus. *Palaentology*, 45: 377-418, London.
- Hungerbühler A. & Hunt A. P. (2000) - Two new phytosaur species (Archosauria, Crurotarsi) from the Upper Triassic of Southwest Germany. *N. Jb. Geol. Palaont. Mb.*, 2000(8): 467-484, Stuttgart.
- Hunt A. P. & Lucas S. G. (1989) - New genotype designations for the phytosaurs *Myrstriosuchus* and *Rutiodon*, with a discussion of the taxonomic status of *Myrstriosuchus*, *Clepsysaurus* and *Rutiodon*, pp. 340-348 in S. G. Lucas & A. P. Hunt (eds.) - Dawn of the Age of Dinosaurs in the American Southwest. New Mexico Museum of Natural History, Albuquerque.
- Hutchinson J. R. (2001a) - The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). *Zool. Journ. Linn. Soc.*, 131: 123-168, London.
- Hutchinson J. R. (2001b) - The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). *Zool. Journ. Linn. Soc.*, 131: 169-197, London.
- Jadoul F. (1986) - Stratigrafia e paleogeografia del Norico nelle Prealpi Bergamasche Occidentali. *Riv. It. Paleont. Strat.*, 91(1985): 479-512, Milano.
- Jadoul F., Berra F. & Frisia S. (1992) - Stratigraphic and paleogeographic evolution of a carbonate platform in an extensional tectonic regime: the example of the Dolomia Principale in Lombardy (Italy). *Riv. It. Paleont. Strat.*, 98: 29-44, Milano.
- Jadoul F., Masetti D., Cirilli S., Berra F., Claps M. & Frisia S. (1994) - Norian/Rhaetian stratigraphy and paleogeographical evolution of the Lombardy Basin (Bergamasco Alps). Excursion B1. 15th IAS Regional Meeting, Ischia, Italy.
- Kischlat E. E., Unilasal A. V. B., Lucas S. G. & Maciel L. (2002) - First record of phytosaurs in the Upper Triassic of South America. *Journ. Vert. Paleont.*, 22 (supplement): 74A, Lawrence.
- Long R. A. & Murry A. M. (1995) - Late Triassic (Carnian and Norian) Tetrapods from the Southwestern United States. Bulletin 4, New Mexico Museum of Natural History and Science, Albuquerque.
- McGregor J. H. (1906) - The Phytosauria, with a special reference to *Myrstriosuchus* and *Rhytidodon*. *Mem. Am. Mus. Nat. Hist.*, 9: 30-101, New York.
- Pinna G. (1979) - Il cranio di un giovane Placochelide (*Psephoderma alpinum* Meyer, 1858) del Norico Superiore di Endenna (Bergamo). *Atti Soc. It. Sc. Nat.*, 120: 195-202, Milano.
- Pinna G. (1980) - *Drepanosaurus unguicaudatus*, nuovo genere e nuova specie di Lepidosauro del Trias alpino. *Atti Soc. It. Sc. Nat.*, 121: 181-192, Milano.
- Pinna G. (1984) - Osteologia di *Drepanosaurus unguicaudatus*, Lepidosauro triassico del sottordine Lacartilia. *Mem. Soc. It. Sc. Nat.*, 24: 7-28, Milano.
- Pinna G. & Nosotti S. (1989) - Anatomia, morfologia funzionale, paleoecologia del rettile Placodonte *Psephoderma alpinum* Meyer, 1858. *Mem. Soc. It. Sc. Nat.*, 25: 17-50, Milano.
- Renesto S. (1992) - The anatomy and relationships of *Endennasaurus acutirostris* (Reptilia, Neodiapsida), from the Norian (Late Triassic of Lombardy). *Riv. It. Paleont. Strat.*, 97: 409-430, Milano.
- Renesto S. (1994a) - A new Prolacertiform reptile from the Late Triassic of Northern Italy. *Riv. It. Paleont. Strat.*, 100: 285-306, Milano.

- Renesto S. (1994b) - A reinterpretation of the shoulder girdle and anterior limb of *Drepanosaurus unguicaudatus* (Reptilia, Diapsida). *Zool Journ. Linn. Soc.*, 111: 247-264, London.
- Renesto S. (1994c) - *Megalancosaurus preonensis*, a possibly arboreal archosauriform from the Norian (Late Triassic) of Northern Italy. *Journ. Vert. Paleont.*, 14: 38-52, Lawrence.
- Renesto S. (1995) - A sphenodontid from the Norian (Late Triassic) of Lombardy (Northern Italy): A preliminary note. *Modern Geology*, 20: 149-158, Malaysia.
- Renesto S. (2000) - Bird-like head on a chameleon body: new specimen of the enigmatic diapsid reptile *Megalancosaurus* from the Late Triassic of Northern Italy. *Riv. It. Paleont. Strat.*, 106: 157-180, Milano.
- Renesto S. & Dalla Vecchia F. (2000) - The unusual dentition and feeding habits of the prolacertiform reptile *Langobardisaurus* (Late Triassic, Northern Italy). *Journ. Vert. Paleont.*, 20: 622-627, Lawrence.
- Renesto S. & Lombardo C. (1999) - Structure of the tail of a phytosaur (Reptilia, Archosauria) from the Norian (Late Triassic) of Lombardy (Northern Italy). *Riv. It. Paleont. Strat.*, 105: 135-144, Milano.
- Renesto S. & Paganoni A. (1998) - A phytosaur skull from the Norian (Late Triassic) of Lombardy. *Riv. It. Paleont. Strat.*, 104: 115-122, Milano.
- Romer A. S. (1956) - The osteology of the Reptiles. Vol. of 771 pp. University of Chicago Press, Chicago.
- Sander M. P. (1989) - The pachypleurosaurids (Reptilia, Nothosauria) from the Middle Triassic of Monte San Giorgio (Switzerland) with the description of a new species. *Phil. Trans. Roy. Soc. London B*, 325: 561-666, London.
- Tintori A. (1981) - Two new Pycnodonts (Pisces, Actinopterygii) from the Upper Triassic of Lombardy (N. Italy). *Riv. It. Paleont. Strat.*, 86: 795-824, Milano.
- Tintori A. (1983) - Hyspysomatic Semionotidae (Pisces, Actinopterygii) from the Upper Triassic of Lombardy (N. Italy). *Riv. It. Paleont. Strat.*, 88: 417-442, Milano.
- Tintori A. (1990) - The vertebral column of the Triassic fish *Saurichthys* and its stratigraphical significance. *Riv. It. Paleont. Strat.*, 96: 93-102, Milano.
- Tintori A. (1991) - Durophagous vertebrates from the Late Norian of southern Alps. Abstract in 7th International Symposium on the Study of Early Vertebrates, Parc de Miguasha, Quebec, Canada.
- Tintori A. (1992) - Fish Taphonomy and Triassic anoxic basins from the Alps: a case history. *Riv. It. Paleont. Strat.*, 97: 393-408, Milano.
- Tintori A. (1995) - The Norian (late Triassic) Calcarea di Zorzino fauna from Lombardy (N. Italy): the state of the art. pp. 139-142 in II International Symposium on Lithographic Limestones, July 1995, Cuenca.
- Tintori A. & Lombardo C. (1996) - *Gabanellia agilis* gen.n. sp.n. (Actinopterygii, Perleidiformes) from the Calcarea di Zorzino of Lombardy (North Italy). *Riv. It. Paleont. Strat.*, 102: 227-236, Milano.
- Tintori A. & Sassi D. (1992) - *Thoracopterus* Bronn (Osteichthyes: Actinopterygii): a gliding fish from the Upper Triassic of Europe. *Journ. Vert. Paleont.*, 12: 265-283, Lawrence.
- Tintori A., Muscio G. & Nardon (1985) - The Triassic fossil fishes localities in Italy. *Riv. It. Paleont. Strat.*, 91: 197-210, Milano.
- Westphal F. (1976) - Phytosauria, pp. 99-120 in O. Kuhn (ed.): *Handbuch der Paläoherpetologie*, 13. Gustav Fischer Verlag, Stuttgart.
- Wild R. (1978) - Die Flugsaurier (Reptilia, Pterosauria) aus der Oberen Trias von Cene bei Bergamo, Italien. *Boll. Soc. Paleont. It.*, 17: 176-256, Modena.
- Wild R. (1980) - Neue Funde von *Tanystropheus* (Reptilia, Squamata). *Schweiz. Palaeont. Abh.*, 102: 4-31, Basel.
- Wild R. (1991) - *Aetosaurus* (Reptilia, Thecodontia) from the Upper Triassic (Norian) of Cene near Bergamo, Italy, with a revision of the genus. *Riv. Mus. Civ. Sc. Nat. Bergamo*, 14: 1-24, Bergamo.

APPENDIX

List of the abbreviations used in the figures.

Skull: al) alveolum, an) angular, aof) antorbital fenestra, d) dentary, en) external naris, fl) fluting of the dental crown, fr) frontal, itf) infratemporal fenestra, j) jugal, l) lacrimal, mf) mandibular fenestra, msy) mandibular symphysis, mx) maxilla, na) nasal, o) orbit, op) opisthotic, p) parietal, pmx) premaxilla, po) postorbital, poc) paraoccipital process, pof) postfrontal, pr. r) retroarticular process, prf) prefrontal, psb) parietosquamosal bar, pt) pterygoid, qr) quadrate ramus of the pterygoid, sa) surangular, soc) supraoccipital, spm) septomaxilla, sq) squamosal, stf) supratemporal fenestra, th) tooth.

Axial skeleton: c) centrum, cap) capitulum, cax) centrum of the axis, cc) centrum of cervical vertebra, cca) centrum of caudal vertebra, cd) centrum of dorsal vertebra, ch) chevron, es) centrum of sacral vertebra, di) diapophysis, fin) foramen intervertebralis, ga) gastralia, hat) holocephalous head of the atlas rib, iva) incisura vertebralis cranialis, ivp) incisura vertebralis caudalis, ne) neural arc of cervical vertebra, nca) neural arc of caudal vertebra, nd) neural arc of dorsal vertebra, pa) parapophysis, plca) pleuroapophysis of caudal vertebra, pls) pleuroapophysis of sacral vertebra, pr. rc) anterior process of cervical rib, prz) prezygapophysis, poz) postzygapophysis, rat) rib of the atlas, rax) rib

of the axis, rc) rib of cervical vertebra, s) neural spine, sax) neural spine of the axis, sc) neural spine of cervical vertebra, sca) neural spine of caudal vertebra, sd) neural spine of dorsal vertebra, syn) synapophysis, tub) tuberculum, ts) thickened tip of neural spine, vca) caudal vertebra, vcc) vertebrocostal canal.

Appendicular skeleton: a) astragalus, acr) acromial process, am. pu) anterior margin of the pubis, ar. co) articular surface for the coracoid, ar. cl) articular surface for the clavicle, ar. fia) fibular articular surface for calcaneum, ar. fic) fibular articular surface for astragalus, ar. ta) tibial articular surface for astragalus, c) calcaneum, dt) distal tarsal, dp) deltopectoral crest, fe) femur, fh) head of the femur, fi) fibula, f4t) fourth trochanter, h) humerus, icl) interclavicle, ifit) iliofibular trochanter, ipf) ischiopubic fenestra, itf) intertrochanteric fossa, is) ischium, l. il) iliac blade, l. sc) scapular lamina, lc) lateral condyle, lepc) lateral epicondyle, mc) metacarpal, mec) medial condyle, mt) metatarsal, obf) obturator foramen, ph) phalanx, pr. il) process of iliac blade, pu) plate of the pubis, ra) radius, t) tibia, tu. t) tibial tubercule, tu. ra) radial tubercule, ul) ulna.

Dermal armor: car) carina, fo) fossa, os) osteoderm, sul) sulcus.

PLATE 1

Myriosuchus planirostris Von Meyer, 1863. Specimen MCSNB 10087. A) Skull in dorsal view. B) Skull in ventral view. Inclined lines on light-grey background represent the portions of the stone slab strengthened by resin.

PLATE 2

Myriosuchus planirostris Von Meyer, 1863. Specimen MCSNB 10087. Two sides of the stone slab in which the region of the trunk and elements of the anterior appendicular skeleton are preserved. A) Right side of the trunk region and elements of the right forelimb. B) Dorsal vertebrae with associated ribs in left view and elements of the left forelimbs.

PLATE 3

Myriosuchus planirostris Von Meyer, 1863. Specimen MCSNB 10087. Two sides of the stone slab in which are preserved the pelvic region, the hindlimbs and the proximal portion of the tail. A) Right forelimb in dorsal view, base of the tail in right lateral view, pelvic girdle and sacral vertebrae in right-lateral view. B) Left forelimb in ventral view and left pubis in lateral view.

PLATE 4

Myriosuchus planirostris Von Meyer, 1863. Specimen MCSNB 10087. A) Stone slab that bears the tail from the 11th caudal vertebra up to its end. B) Close up of the portion of the tail from the x caudal vertebra up to the x.

