NOTA BREVE - *SHORT NOTE*

STRUCTURE OF THE TAIL OF A PHYTOSAUR (REPTILIA, ARCHOSAURIA) FROM THE NORIAN (LATE TRIASSIC) OF LOMBARDY (NORTHERN ITALY)

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Riassunto. In questa nota viene descritta la morfologia della porzione caudale della colonna vertebrale di uno scheletro completo di Fitosauro (Reptilia, Diapsida, Phytosauria) rinvenuto nel Calcare di Zorzino, di età Norica (Triassico Superiore), nella località fossilifera di Endenna (Zogno, Bergamo). Lo stato di avanzamento del lavoro di preparazione consente una descrizione precisa della morfologia delle vertebre caudali, e del loro numero complessivo. La struttura del cranio, non ancora completamente preparato, fa supporre affinità con il genere *Mystriosuchus*, ma l'attribuzione è per ora ipotetica. La presenza di un' adattamento alla locomozione in acqua più spinto che in altri Fitosauri è testimoniato dalla morfologia delle emapofisi e delle spine neurali, finora non figurata in letteratura per i fitosauri. Può darsi che il fitosauro completo di Endenna appartenga ad una nuova specie, particolarmente adattata all'ambiente marino.

Abstract. The structure of the caudal portion of a vertebral column belonging to a complete phytosaur skeleton is described. The skeleton has been collected from the Calcare di Zorzino (Zorzino Limestone) of Norian (Late Triassic) age, in the small quarry of Endenna (Bergamo, Lombardy, Northern Italy). The specimen is currently being prepared, and only a detailed description of the tail is possible. The exposed portion of the skull, which shows, among other characters, a narrow, flattened snout, suggests possible relationships with the genus *Mystriosuchus*, but preparation of the skull must be finished prior to attempting any classification. The morphology of the tail vertebrae has never been figured for phytosaurs; however, the structure of the tail vertebrae of this specimen reflects a great degree of adaptation toward aquatic life, justifying its description prior to complete preparation. If this specimen represents a new species, it should have been highly specialised toward marine life than other phytosaurs in which the postcranial skeleton is known.
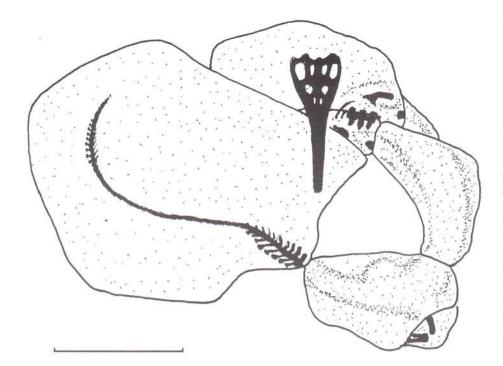
Introduction.

The Norian (Late Triassic) Calcare di Zorzino (Zorzino Limestone) formation yielded an interesting vertebrate fauna (Renesto, 1995a; Tintori, 1995). Finds mainly consist of fishes; however, reptiles, with more than 10 genera are of great importance and often repre-

sent endemic or poorly known taxa. Despite the depositional environment (marine basins amid a carbonate platform; Jadoul, 1986; Jadoul et al., 1992), terrestrial reptiles are more common than aquatic ones, suggesting the presence of land nearby, possibly ephemeral islands with freshwater reservoirs in which insects (Whalley, 1986) and endemic reptiles lived. Marine reptiles are represented by the placodont *Psephoderma* (Pinna & Nosotti, 1989; Renesto & Tintori, 1995) and the thalattosaur *Endennasaurus* (Renesto, 1984, 1992). Among non-marine reptiles, the oldest pterosaurs so far known have been collected (Wild, 1978, 1984; Renesto, 1993), along with odd diapsids like *Drepanosaurus* (Pinna 1980; Renesto, 1994a) and *Megalancosaurus* (Calzavara et al., 1980; Renesto, 1994b) both scansorial reptiles with arboreal habits. The peculiar small prolacertiform, *Langobardisaurus* (Renesto, 1994c) is unknown from other localities, while the sphenodontid *Diphydontosaurus* (Renesto, 1995b) is reported also from the Late Triassic fissure fillings of England (Whiteside, 1986). Remains of aetosaurs and phytosaurs have been found and referred to genera well known from the coeval Stubensandstein Formation (Late Triassic of Germany). *Aetosaurus ferratus* is represented by some fragments of the dorsal armour (Wild, 1991), while phytosaurs were so far known only from an isolated skull without lower jaw, placed in the genus *Mystriosuchus* (Renesto & Paganoni, 1998).

In November 1995, a large, complete, and articulated reptile skeleton was found (Tintori et al., 1996). When it was still covered by matrix, it was tentatively considered a large thalattosaur, owing to the very long tail and the rather short limbs. Initial preparation, however, revealed that it was a nearly four meter long, narrow snouted phytosaur.

Phytosaurs were carnivorous, crocodile-like archosaur reptiles well known from several Late Triassic loca-

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Hungerbühler, pers. comm.). In addition the structure of the caudal vertebrae of this specimen is peculiar for phytosaurs, and the tail has never been figured so far. The structure of the tail, especially the haemapophyses and neural spines, reveals a strong adaptation toward aquatic life, suggesting more marine life habits for this narrow-snouted, gavial-like phytosaur.

lities mainly in the Northern Hemisphere (McGregor, 1906; Gregory, 1962; Chatterjee, 1978; Buffetaut et al., 1988; Ballew, 1989; Hunt & Lucas, 1989; Buffetaut, 1993; Doyle & Sues, 1995) and Madagascar (Chatterjee, 1978).

Phytosaurs are usually associated to freshwater environments and it was assumed (Renesto, 1995a) that also the isolated *Mystriosuchus* skull found in the Endenna locality belonged to a specimen that did not live on the islands close to the basins in which the Zorzino Limestone was deposited, but on more distant continental land, this latter sharing its fauna with the European continent. The new find of the complete and articulated specimen leads us to reconsider this point of view, suggesting instead that the phytosaurs found in the Calcare di Zorzino may well have lived close to the basins, both in freshwater and marine environment, as already suggested by Buffetaut (1993) for the *Mystriosuchus* specimens found in the Norian Dachsteinkalk (Austria), which was deposited in a shallow marine environment.

Preparation is still in progress, but the tail has been exposed almost entirely (only some of the most proximal caudal vertebrae are still covered by matrix), along with part of the skull, cervical vertebrae and ribs. The skull has a narrow, flattened snout, and it may be tentatively referred to the genus *Mystriosuchus*, already known at this locality from an isolated skull (Renesto & Paganoni, 1998). Any attempt of a definitive taxonomic assignment of the specimen, however, must await a more complete preparation. The description of the tail prior to complete preparation of the entire skeleton is justified, because the caudal vertebrae, especially the more distal ones, are unknown or poorly known in many phytosaur genera, particularly from Europe (A.

Systematic palaeontology

Class **R e p t i l i a**
Superdivision **N e o d i a p s i d a** Benton, 1985
Division **A r c h o s a u r i a** Cope 1869
Family **P h y t o s a u r i d a e** Meyer 1861

Genus ? *Mystriosuchus* Fraas, 1896
(Plate 1; Fig. 2-3)

Material. A nearly complete, articulated phytosaur skeleton, about 4 metres long, exposed in dorsal view. Apart some small fragments, the skeleton is preserved on four large slabs and a smaller one (Fig. 1). Only two of the slabs have been prepared so far, revealing the middle and distal portion of the tail and, in part, the skull and some cervical vertebrae. The specimen has been catalogued as MCSNB 10.087 (MCSNB being the acronym of the Museo Civico di Scienze Naturali "E. Caffi" di Bergamo, Lombardy, Northern Italy, where the specimen will be stored after preparation).

Remarks. *Mystriosuchus* is well known from many beautiful isolated skulls and several fragmentary remains of the postcranial skeleton from the German Stubensandstein (Fraas, 1896; Mc Gregor, 1906; Westphal, 1976). The structure of the skull is well documented and useful for classification, in contrast with less known postcranial material. The already prepared portion of the skull of specimen MCSNB 10.087 (Fig. 2) reveals the presence of an uncrested, rather long and narrow snout; external nares close to the orbits and lying presu-
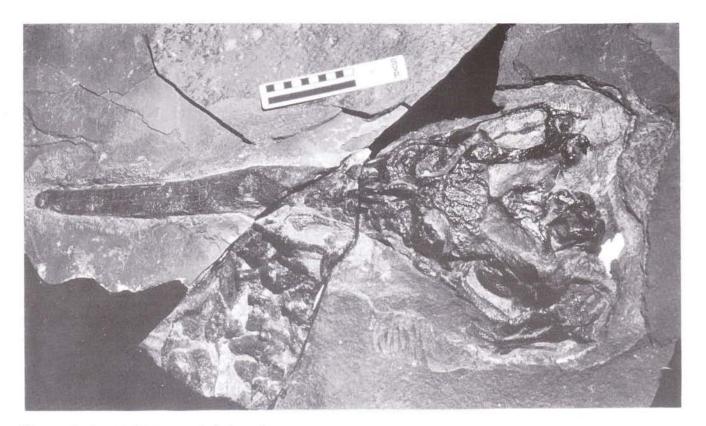
Fig. 2 - Specimen MCSNB 10.087, skull after preliminary preparation, scale bar equals 10 cm.

mably above the antorbital fenestrae; frontals and nasals deeply sculptured, and a compressed, inverted U-shaped parietal-supraoccipital complex, along with a truncated posterior processes of the squamosals. Hunt & Lucas (1989) have cited all these characters as diagnostic for *Mystriosuchus*. The postorbital bar, however, is not so wide as it could be expected in this genus (Hunt & Lucas, 1989) and the snout is proportionally less elongated than usually occurs in *Mystriosuchus* (Fraas, 1896, Mc Gregor, 1906; Gregory, 1962; SR, pers. obs.). The apparently different width of the postorbital bar may be due to preservation (the skull is dorsoventrally flattened; the top of the skull seems to have collapsed during fossilization and some lateral bones are broken or distorted). On the other hand, the skull length/rostrum length ratio for *Mystriosuchus* should range from 65 to 72%, according to Westphal (1976). Specimen MBSN 10.087 with a skull length of ca. 55 cm (approximately half the length of the larger *Mystriosuchus* skulls) and a rostrum length of about 35 cm has a skull length/rostrum length ratio of about 63%, close to with that for *Mystriosuchus*. Other characters are required prior to assessing definitely the taxonomic status of the specimen, but, at present, there seem to be good reasons to include the specimen tentatively in the genus *Mystriosuchus*. No specific assignment is attempted however, even if the peculiar morphology of the tail and the possibly different body proportions may suggest that specimen MCSNB 10.087 belongs to a new species.

The tail.

Description. The cleaned portion of the tail (Fig. 3) is about 144 cm long and 64 caudal vertebrae have been exposed. The more proximal portion of the tail, (lying on another slab) is still embedded in the matrix, for a length of approximately 45-50 cm, while another small part is missing; thus the total length should be about two metres. By comparison with the length of the most proximal centra already prepared, it can be estimated that at least 10-12 caudal vertebrae are still embedded in the matrix, giving a count of ca. 70-75 caudal vertebrae. This number is rather high, since Mc Gregor (1906) figured only approximately 34 caudal vertebrae in his combined reconstruction of a phytosaur (*Mystriosuchus* skull with *Rutiodon* postcranial skeleton). Westphal (1976) quoted an average of 50 and Romer (1956) an average of 40 caudal vertebrae. The long tail of specimen MCSNB 10.087 might reflect the high number of caudal vertebrae typical of primitive archosaurs (Romer, 1956), but much more probably a derived condition, suggesting a greater degree of adaptation for swimming, as detailed in the following section.

The caudal vertebrae are amphicoelous and the ventral outline of the centra is slightly concave; in the proximal exposed portion of the tail both pre-and postzygapophyses are stout with nearly horizontal articular facets. Indeed, the structure of the caudal vertebrae changes distinctly along the series. The more proximal

central in position and have stout, enlarged articular facets. Their distal ends are expanded anteroposteriorly into a "foot"; the ventral margin of this "foot" shows some fluting. At the ?20 th caudal vertebra, the neural spines start to slant posteriorly (Fig. 6). The following caudal vertebrae are exposed in dorsal view, and the associated neural spines are frequently broken or poorly preserved, but a gradual increase of the slanting is clearly detectable. In this region the transverse processes have nearly disappeared, and the centra seem to be mediolaterally compressed. The more distal portion of the tail, from caudal vertebra ?40 to the very end of the tail, is exposed again on its left side (Pl. 1, fig. 1-3). The size of the centra decreases progressively, and the centra themselves are spool-shaped up to the last vertebra, which is triangular. The pre- and postzygapophyses become reduced. The most unusual features are the structure of the neural spines and the haemal arches (Fig. 7 A-B). The neural arches become rather low, while the neural spines are still very long, narrow and strongly slanting posteriorly, overhanging the following centrum and at least half of the further succeeding one. The spines are preserved in natural position and are not broken; their pronounced backward slant represents indeed the original condition, as it is testified by the continuity of marks and pores on the bone surface. The haemal arches become short, and the haemal spines are anteroposteriorly expanded at their ventral margin, forming a sort of expanded "foot" very similar to that of pachypleurosaurids as figured by Carroll & Gaskill (1985). This pattern persists until the very end of the tail, excluding the last two or three vertebrae.

caudal vertebrae (approximately caudal vertebrae 15-20,; Fig 4-5) are exposed in lateral (left) view. They bear high neural arches and spines and very short but stout transverse processes. The neural spines are somewhat expanded at their bases, then show a slightly concave anterior and posterior outline ending with a flattened top. They are extremely thin, in contrast with their height. The haemal spines also are deep and robust, nearly as long as, but narrower than, the neural spines. They are inter-
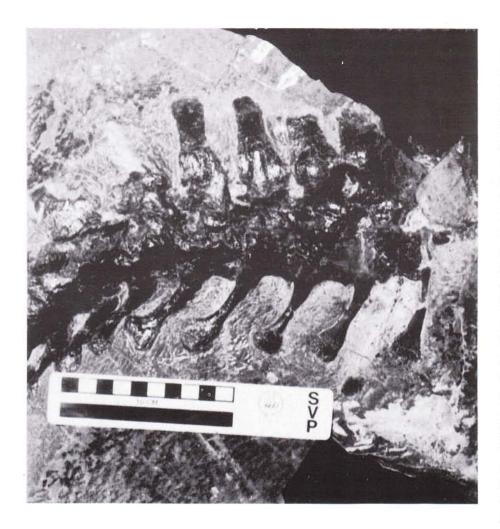
Fig. 4 - Specimen MCSNB 10.087, proximal caudal vertebrae (?12-18), scale bar equals 10 cm.

Functional morphology. Phytosaurs have generally been considered crocodile-like in habits, with some genera more adapted to amphibious or aquatic life than others. According to Westphal (1976), *Mystriosuchus* is possibly the most "aquatic" phytosaur, based on its gavial- like snout and the high and laterally compressed tail (Westphal, 1976). However, even greater adaptation towards aquatic locomotion is suggested for specimen MCSNB 10.087 by both the general shape of the tail and the morphology of its vertebrae. While the lateral compression of the tail ("Rudderschwanz", Westphal, 1976) of *Mystriosuchus* was already known, the distal expansion of the haemal spines along with the backward slanting of the neural spines of the middle and distal caudal vertebrae have never been reported or figured (the same applies to the great length of the tail). In his de-
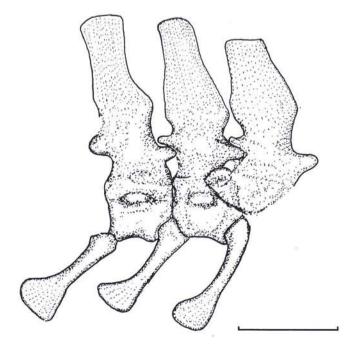

Fig. 5 - Specimen MCSNB 10.087, proximal caudal vertebrae (approximately 15-18th). Scale bar equals 4 cm.
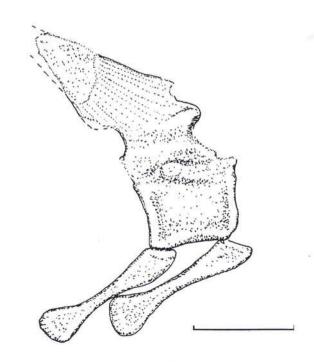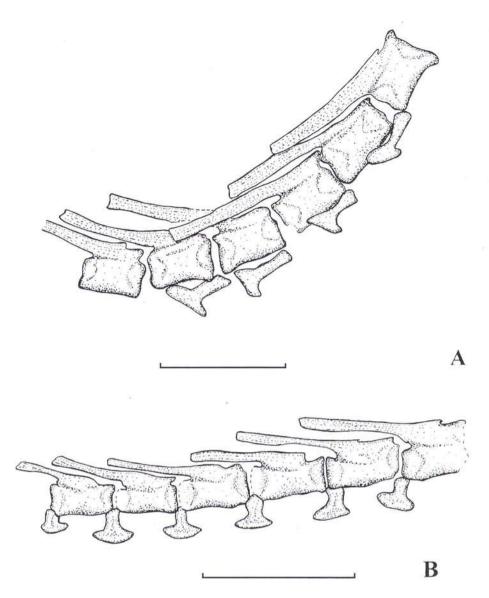
Fig. 6 - Specimen MCSNB 10.087, ?20th caudal vertebra, starting point of the posterior slanting of the neural spines, scale bar equals 4 cm.

A

B

Fig. 7 - Specimen MCSNB 10.087, two series of distal caudal vertebrae (A: ?50-55; B: ?57-62) in which the posterior slanting of the neural spines and the anteroposteriorly expanded haemal spines are visible, scale bars equal 4 cm.

the same category of undulatory swimmers, which are characterised by "Trunk stocky, limbs little modified, tail laterally compressed, but not elongate" (Carroll, 1985, p. 147). Specimen MCSNB 10.087 (and possibly other *Mystriosuchus* specimens?) does not fit many of these characters: the trunk seems more slender than in non-marine crocodiles and in other phytosaurs, the limbs appear to be somewhat reduced (judging from the already prepared portion of a knee joint) and finally the tail is elongate. All these characters point to another of Carroll's (1985) categories of swimmers, which includes some nothosaurs, along with other aquatic diapsids, such as *Hovasaurus* and *Claudiosaurus*, more spec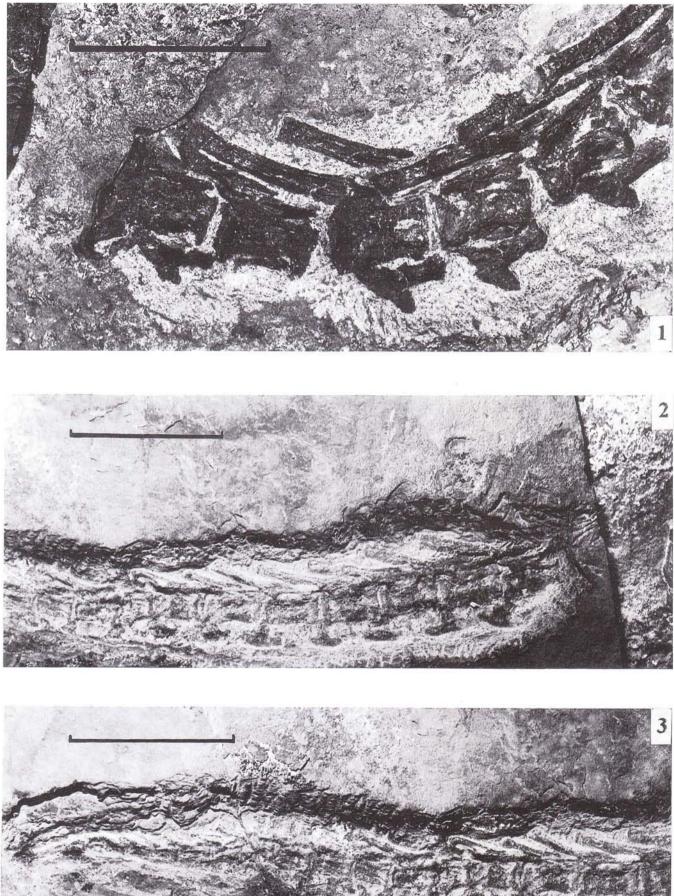ialized toward aquatic life. They show "Neck moderately elongate, trunk not elongate but laterally compressed, limbs somewhat reduced and slightly modified as paddles, tail long and laterally compressed" (Carroll, 1985, ibid.). However, specimen MCSNB 10.087 does not show any particular elongation of the neck nor are the limbs modified as paddles, rendering its classification in Carroll's scheme rather difficult. It is clear that specimen MCSNB 10.087 represents a step further toward a more aquatic adaptation, compared to other known phytosaurs. It was probably a rather efficient swimmer, and the tail was the main source of propulsion. The "footed" haemapophyses are present in many aquatic reptiles; in some *Neusticosaurus (Pachypleurosaurus)* species (Carroll & Gaskill, 1985; Sander, 1989), they are very similar to the more distal ones of specimen

scription of *Mystriosuchus* Mc Gregor (1906) did not describe the caudal vertebrae and restored those of *Rutiodon* with long but narrow "non-footed" haemal spines along with "normal", vertical neural spines. Westphal (1976) also reported elongated neural spines and chevrons for *Mystriosuchus*, but did not mention any distal expansion or slanting.

The very long and compressed tail (along with the possible presence of rather short and slender limbs) points undoubtedly to axial swimming sensu Braun & Reif (1985), possibly some sort of undulation (caudal subundulatory mode sensu Braun & Reif, 1985). In his survey of aquatic locomotion in diapsid reptiles, Carroll (1985) put the phytosaurs together with non-marine crocodiles, choristoderans and non-armoured placodonts in

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PLATE 1

Fig. 1 - Specimen MCSNB 10.087, distal caudal vertebrae (?51-55), scale bar equals 5 cm.
Fig. 2 - Specimen MCSNB 10.087, distal caudal vertebrae ?57-64. Scale bar equals 5 cm.
Fig. 3 - Specimen MCSNB 10.087, distal end of the tail, scale bar equals 5 cm.

MCSNB 10.087. Haemal spines, that are laterally flattened and anteroposteriorly expanded can easily be explained as adaptation for undulatory swimming, since they offer a greater surface for the insertion of axial musculature. On the other hand, the peculiar backward slanting of the neural spines of the mid- and dorsal portion of the tail is rather unusual and requires an explanation. The great elongation of the neural spines may be related to the need of increasing the surface for thrust and to the development of a strong epaxial musculature to improve lateral undulation, as suggested for *Hupehsuchus* (Carroll & Dong, 1991). The posterior slant of the neural spines, which increases toward the end of the tail, represents a problem, because it probably rendered the region rather stiff. In some Jurassic marine crocodilians (Romer, 1956) a similar pattern is due to the presence of an inverted heterocercal tail fin, in which the stiff distal portion of the tail supports the ventral lobe. In these crocodilians, however, the neural spines of the distal portion of the tail slant backward only up to the beginning of the tail lobe, where the direction of slanting becomes inverted (anterior). Due to the deep ventral bending of the tail, they project vertically, giving probably support to the dorsal lobe of the fin. In addition, a "fan" shape is reported for the haemapophyses, which prevented any possibility of undulation. In specimen MCSNB 10.087, the slanting of the neural spines does not change its direction, and neither is there a tail bend, nor the ventral ends of the haemapophyses are so close to each other. Thus a lobed caudal fin like that of marine crocodiles is not plausible.

Perhaps the slanting is a way to counterbalance the extreme thinness of the neural spines and, toward the end of the tail, of the entire caudal vertebrae. The whole skeleton seems rather lightly built, but this do not contrast with aquatic habits if the animal had not to reach the bottom, but swum and fed at, or near to, the surface of the water (Hildebrand, 1978).

As detailed in the description, the caudal vertebrae become very slender and their thickness is greatly reduced posteriorly. This may be an unusual feature for an aquatic animal, unless light caudal vertebrae are required to save weight, in order to balance a very long tail with respect to a rather short trunk, to avoid pitching "head up". Such a thin tail may have been not very efficient for swimming, unless the posterior slanting neural spines increased the strength of the structure by overhanging each other. As a consequence the centra were linked together in some way and also yawing was reduced, because lateral torsion was hindered by the sequence of overhanging neural spines. The influence of these elongated neural spines on caudal undulation should be investigated (the zygapophyses are greatly reduced allowing good mobility). It may be hypothesised that some stiffness of the distal portion of the tail may have improved thrust (Hildebrand, 1978). In any case, the posterior slant of the neural spines rendered the dorsal outline of the tail rather low, despite to their length. A low tail is present in some aquatic diapsids, which swim by undulation of both the trunk and the tail in a sort of anguilliform swimming pattern (pleurosaurs, some aigialosaurs, and thalattosaurs, Carroll, 1985). According to Carroll (1985), this latter kind of locomotion is more frequent in reptiles and fishes that lived among rocks or muddy bottoms. Their swimming was rather slow and involved neither speed, nor rapid bursts of acceleration (Carroll, 1985), that are required in a gavial-like fish eater. This pattern of locomotion was hindered by the morphology of the neural spines. Caudal undulation associated to a rigid trunk allows perhaps better propulsion in reptiles, but must be associated with a laterally compressed tail in order to obtain effective thrust. It may be hypothesised that the posterior portion of the tail of specimen MCSNB 10.087 might have borne some kind of fin-like expansion in order to increase the efficiency of the whole structure. In conclusion, specimen MCSNB 10.087 represents a phytosaur (possibly a new species of *Mystriosuchus*) highly specialized toward aquatic life, which inhabited seashore and shallow marine environments, feeding upon fishes and possibly other smaller reptiles like *Endennasaurus*, representing one of the top predators in its environment.

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