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AQUATIC VARANOID REPTILES FROM THE CENOMANIAN (UPPER CRETACEOUS) LITHOGRAPHIC LIMESTONES OF LEBANON

Up to now, the recently described dolichosaur *Aphanizocnemus libanensis* (Dal Sasso & Pinna, 1997) represented the first and unique published record of fossil reptiles from the Upper Cretaceous of Lebanon (Middle Cenomanian, about 95 MYA). New findings in the same locality (Nammoura) and in another site (Hakel) are now allowing identification of other taxa from the Lebanese lithographic limestones. The material here described is housed at the Museo di Storia Naturale di Milano as part of a considerable collection from Lebanon, mainly consisting of fishes, crustaceans and worms.

At least two different clades of varanoid reptiles are present in the Cenomanian of Lebanon: dolichosaurs and ophiomorphs. Together with the aigialosaurs and the better known mosasaurs, the dolichosaurs represent the crown clade Mosasauroidea, an assemblage of semiaquatic and aquatic squamates which appeared and radiated about 95 MYA within the coastal habitats of the Southern European epicontinental Tethys. Sister group to mosasauroids are considered the snakes, of which the ophiomorphs (the second taxon here described) are thought to be the ancestors.

Dolichosaurs are represented by *Aphanizocnemus_libanensis* and by a second taxon, both consisting of single but striking complete specimens. Among mosasauroid reptiles, the family Dolichosauridae is the less studied, since very few material is known, mostly incomplete and described almost one century ago. In this perspective, the new specimens represent a precious source of information.

Aphanizocnemus is a small sized, lizard-like, slender animal diagnosed by skull with wide parietals and short facial region; tapering body with small girdles; hindlimbs shorter than the forelimbs, especially in the epipodial segments; very long and thin tail. The type specimen MSNM V783 (from Nammoura outcrop), is 286 mm long from the apex of the premaxillaries to the tip of the tail. The vertebral column consists of 178 elements: 36-37 presacral, 10-11 of which are cervical and 25 dorsal, 2 sacral and 141 caudal. The tail alone represents 3/5 of the whole animal. Except for a few elements of the girdles and of the limbs, all the bones look well ossified, but the skull structure, as well as some unusual proportional ratio of the postcranial skeleton, raise some doubts about the attribution of this specimen to an adult individual.

The skull, partly damaged and incomplete, is characterized by extended parietal bones, only slightly narrowing in the posterior third, completely fused medially in one single element. The lower jaw reveals the presence of intramandibular hinge (or splenio-angular joint), an accessory articulation typical of aquatic varanoid lizards (Carroll & deBraga, 1992). The presacral vertebrae show, like in other dolichosaurs and in the ophiomorphs,

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extremely low neural spines, reduced to ridges. Therefore, contrary to Lee (1997) this character is not diagnostic of the Serpentes only but it is synapomorphic with the above mentioned taxa. Moreover, given the undoubted aquatic habits of *Aphanizocnemus* and *Pachyrhachis* (Dal Sasso & Pinna, 1997; Caldwell & Lee, 1997) this character is not strictly related to fossoriality, but it was more likely achieved by snake ancestors during their marine stage (convergency is a less parsimonious interpretation). Other derived characters, such as zygosphene-zygantrum articulations and transverse processes absent in distal caudal vertebrae, are also typical of the mosasauroid-snake clade (Lee, 1997). In the tail of *Aphanizocnemus*, elongate, tiny chevrons and neural spines are caudally oriented. The scapula and the fan-shaped coracoid are very small, but the distal elements of the forelimbs are remarkably elongated; the phalangeal formula is 2-3-4-5-3. The pelvic girdle consists of elements not suturally united and is proportionally even smaller than the pectoral, being as large as two vertebral centra. The pubis is simple and flat, with narrow ventral process. The proximal extremity of the femur has the same size of the shaft, the distal extremity is quite expanded and flattened.

The name *Aphanizocnemus* (from the Greek "aphanizomai" = to disappear, and "knème" = tibia) points out to the most striking feature of this animal. Its tibia, strongly regressed, is a short, compact and almost flat bone, with unclear articular surfaces; There is no trace of the fibula. The phalangeal formula is the same as the manus, but the pes is shorter and stockier. The remarkable shortening of the epipodials, the poor ossification of the tarsus and the dorso-ventral compression of the metatarsals and phalanges create a paddle-like structure. In substance, the hindlimb of *Aphanizocnemus* shows higher affinity with that of a primitive mosasaur than of any other mosasauroid lizard (all known aigialosaurs and dolichosaurs retain relatively unmodified terrestrial limbs, similar to those of present monitors).

The second specimen here described, labelled MSNM V3662, possibly represents another dolichosaur from Nammoura. It is a remarkably complete, articulated skeleton of a varanid-like animal with an extremely long, dorsoventrally expanded tail. Its overall body length is 1037 mm, but the tail alone measures 680 mm. There are 198 vertebrae: 35 presacral, 2 sacral and 161(!) caudal. The presence of only 9 cervical vertebrae within the presacral series should exclude attribution to dolichosaurs sensu strictu (Bell, 1999, pers. com.), but this specimen is very close to the genus Pontosaurus (Hydrosaurus) (Kornhuber 1873), an aquatic varanoid from the Cenomanian of Dalmatia interpreted as a dolichosaur by Nopcsa (1923). With Pontosaurus the new specimen shares several characters, such as skull with large orbits and shortened facial region; elongated neck; neural "ridges" on presacral vertebrae; pachyostotic ribs; well developed limbs, with femora and fibulae distally greatly expanded, well ossified mesopodials, phalangeal formula 2-3-4-5-3; laterally compressed tail, with transverse processes limited to the proximal vertebrae, tall neural spines with rounded apices, caudally inclined with the same angle of the slender, more elongated haemal arches.

According to Lee (1997), the mosasauroid-snake clade (Pytonomorpha (Mosasauroidea+Serpentes)) is corroborated by a number of derived characters. Some of them are evident in specimen V3662: extensive suture at supraoccipital-parietal contact, four or less premaxillary teeth, dorsoposterior process on atlas neural arch, ribs present from the third cervical vertebra on, zygosphene-zygantrum articulations, pelvic elements

not suturally united. On the other hand, the new material from Lebanon reveals that some diagnostic characters listed by Lee (1997) are ambiguous: for instance, there are not "five or more pygal vertebrae", but three in V3662 and only one in *Aphanizocnemus*. Within Pytonomorpha, specimen V3662 has much closer affinity with the Mosasauroidea (Bell 1997, Lee 1997), sharing with them peculiar features such as: dorsal process of premaxillary contacting fused frontals; nasal bones absent (as in mosasaurs, not simply reduced as in aigialosaurs); external nares large and partially retracted; postfrontal and postorbital fused into a postorbitofrontal bone; marginal teeth with high pedestals; lower jaw with splenio-angular joint; dentary straight; quadrate circular, with large, curved suprastapedial process; caudal transverse processes and zygapophyses absent in distal vertebrae; tail dorsoventrally expanded. Finally wide parietals, well developed and ossified limbs, sacral blade of ilium with anterior process are plesiomorphic characters inherited from terrestrial ancestors.

A unique feature of specimen V3662 is the exceptional preservation of skin remains. Mineralized integumentary patches (not simply impressions) composed of still connected, orange-brown scales, outline the skeleton especially along its posterior half. The scales arrangement vary from small (1 to 2 mm in size), elliptical to polygonal, crazy paving, not overlapping elements in the head region, up to a regular network of larger, diamond-shaped, imbricate elements on the hindlimbs and along the tail margin. As marked by the integumentary remains the dorsoventral expansion of the tail is as twice as deeper than the skeletal outline and gives the tail a ribbon-like look. Such a long and deep tail was probably the main propulsive organ, as in most axial subundulatory swimmers.

In the same deposits two snakelike reptiles have also been discovered. These specimens show many characters in common with yet known genus *Pachyrhachis* from the Lowermost Cenomanian of Israel (thus somewhat stratigraphically older): the pattern of preserved skull bones, the elongate, snakelike body, the absence of pectoral girdle, along with the significant reduction of pelvic girdle and hindlimb.

Pachyrhachis is a snakelike reptile known so far from two specimen formerly ascribed to different genera: Pachyrhachis and Estesius (Ophiomorphus) (Haas 1979, 1980). The two genera have been distinguished by Haas mainly because Pachyrhachis shows pachyostotic ribs and mid-dorsal vertebrae, while this condition is absent in Estesius (Ophiomorphus). However Caldwell & Lee (1997) pointed out that this difference might be due to earlier growth stage of the specimen ascribed to Estesius (Ophiomorphus) in which pachyostosis was not yet developed. According to these authors, there are no diagnostic differences between the two specimen permitting the erection of separate genera, therefore they considered Estesius (Ophiomorphus) as junior synonym of Pachyrhachis.

The two specimens here described, labelled V 3660 and V 3661 in the catalogue of the Museo di Storia Naturale di Milano, are definitely smaller than known specimens of *Pachyrhachis*. Specimen V3660, from Hakel outcrop, is the largest one. Its preserved portion is approximately 620 mm in length. The head is missing, and the most posterior portion of the vertebral column is not visible, due to the curling of the same below the trunk region. At least 111 presacral vertebrae can be observed. They are well ossified, but not pachyostotic; the same applies to the ribs, that can be observed starting from the 40th vertebra. They are stout till the 80th vertebra, becoming then suddenly much more slender. Specimen V 3661, from Nammoura, is almost complete and articulated. Unlike previously

described specimens, this new one retains almost the entire tail. Its size is about 300 mm, approximately one half of the (incomplete) preserved portion of specimen V 3660. Up to 157 vertebrae can be observed. Despite their small size the vertebrae are well ossified, while the ribs are very slender. The skull is poorly preserved. The maxillae are the most complete elements and clearly show the presence of well defined alveola for tooth insertion. Apparently the quadrate seems to be much more slender and rodlike than in known specimens of *Pachyrhachis*, but this might be due to preservation bias. Only two elements of the pelvic girdle and posterior limb are present: the left ilium and femur. No traces of other limb bones can be observed, maybe owing to lack of preservation or to the early growth stage of this specimen. Even if posteriormost caudal vertebrae (probably last three-four) are lacking, the tail is however strikingly short (few centimetres estimate) with respect to the rest of the body, 19 caudal vertebrae are preserved and they show a small, low and posteriorly slanting neural spine and a somewhat longer haemal spine gently bent at its distal end.

At present knowledge, most available characters confirm the strict relationships between specimens V 3660, V 3661 and *Pachyrhachis* as described by Haas (1979, 1980) and Caldwell & Lee (1997). This genus is considered of great importance because it seems an almost ideal intermediate between snakes and varanoid lizards on the basis of many synapomorphies (Caldwell & Lee, 1997). Specimens V3660 and V3661 share most of the synapomorphies linking *Pachyrhachis* with snakes, i. e. elongate, snakelike body, with about 150 presacral vertebrae, absence of pectoral girdle and significant reduction of pelvic girdle and hind limb, absence of otic notch, non sutural contact between premaxilla and maxilla, tooth implantation with teeth possibly ankylosed to the rim of discrete sockets. The more reduced ossification or lack of pelvic girdle and limb elements with respect to yet known specimens of *Pachyrhachis*, render specimen V3661 still more snakelike, but it is preferred here to consider this condition as due to lack of preservation or to early growth stage.

In conclusion, the completeness of the new Lebanese material bears very important phylogenetic inferences, providing strong corroboration that the dolichosaurian clade nests within the Mosasauroidea and that the ancestors of snakes are closely related to them. We speculate that closer examination will acknowledge that the ophiomorphs share more derived characters with the dolichosaurs than with other mosasauroids.

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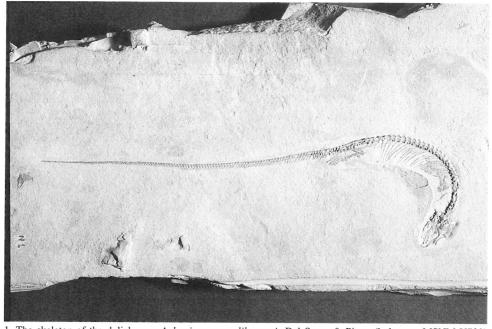
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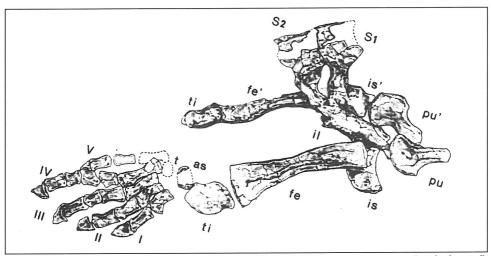
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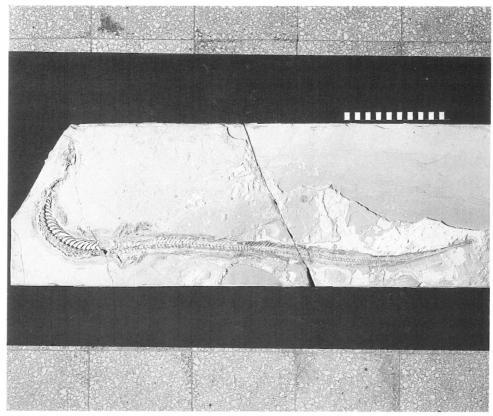
1. The skeleton of the dolichosaur *Aphanizocnemus libanensis* Dal Sasso & Pinna (holotype, MSNM V783) fossilized on the yellowish lithographic limestone from the Cenomanian (Upper Cretaceous) of Nammoura, Lebanon.



2. Sketch of the posterior appendicular elements of *Aphanizocnemus*. Abbreviations: **as**, astragalus; <u>fe</u>, femur; <u>fi</u>, fibula; <u>il</u>, ilium; <u>is</u>, ischium; **mt**, metatarsals; <u>pu</u>, pubis; **S1-S2**, sacral vertebrae; <u>t</u>, tarsal 4; <u>ti</u>, tibia; **I-V**, first to fifth digit.



3. Specimen MSNM V3662, from Nammoura, shows exceptional preservation of the integument. Note the extremely long, dorsoventrally expanded tail.



4. The most complete of the two ophiomorphs, MSNM V3661 (from Nammoura outcrop). Note the elongate thoracic region, the nearly vestigial hindlimbs and the very short tail.

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