

The first description of *Halisaurus* (Reptilia Mosasauridae) from Europe, from the Upper Cretaceous of Belgium

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Abstract

This study represents the first extensive description of the skull of species of the genus *Halisaurus* Marsh 1869. *Halisaurus ortliebi* (= *Phosphorosaurus ortliebi* of Dollo, 1889), from the Maastrichtian of Belgium, shows, several character states, including a unique ventral fossa of the parietal. Comparisons are made with the North American *H. platyspondylus*. *H. sternbergi* (Wiman, 1920) is no longer considered as belonging to the genus *Halisaurus*.

Key-words: *Halisaurus*, *Clidastes sternbergi*, taphonomy, taxonomy, phylogeny.

Résumé

Le crâne d'espèces appartenant au genre *Halisaurus* Marsh, 1869 est présenté en détail pour la première fois. *Halisaurus ortliebi* (= *Phosphorosaurus ortliebi* Dollo, 1889) du Maastrichtien belge montre plusieurs caractères intéressants dont une fosse ventrale unique dans le parietale. Une comparaison avec l'espèce nord-américaine *H. platyspondylus* est faite. *H. sternbergi* (Wiman, 1920) n'est plus considéré comme appartenant au genre *Halisaurus*.

Mots-clefs: *Halisaurus*, *Clidastes sternbergi*, taphonomie, taxinomie, phylogénie.

Introduction

Halisaurus material described here represents only the second record of the genus outside of the U.S.A. (the first was recorded in Nigeria by AZZAROLI *et al.*, 1975) and even in the U.S.A. as BAIRD noted (1986b p. 72) "Despite more than eleven decades of collecting effort, *Halisaurus* remains one of the rarest and least well-known of the mosasaurs." The sum-total of the available material consists of no more than isolated and scanty remains, mainly vertebrae and a few fragments of skulls.

Primarily on the basis of the unique frontal bone of *Halisaurus* (see BAIRD & CASE 1966 which includes D. A. RUSSELL's identification of a frontal as that of *Halisaurus platyspondylus*), DOLLO's (1889) *Phosphorosaurus ortliebi* (IRSNB R34, formerly R4671) is reassigned as *Halisaurus ortliebi*. The skull described here, although fragmentary, represents the most substantial material of *Halisaurus* known yet.

Abbreviations

Repository abbreviations:

BMNH, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

IRSNB, Institut Royal des Sciences Naturelles de Belgique, Rue Vautier 29, B-1000 Bruxelles, Belgium.

GPIT, Institut für Geologie und Paläontologie, der Universität Tübingen, Sigwartstrasse 10, D-72076 Tübingen, DBR.

Cranial abbreviations used in the text:

a, angular; ar, articular; che, cerebral hemispheres; cor, coronoid; d, dentary; en, external naris; f, frontal; gl, intermandibular articulation; j, jugal; mx, maxilla; of, olfactory lobe; p, parietal; paf, parietal foramen; pmx, premaxilla; pof, postorbitofrontal; prf, prefrontal; pt, pterygoid; pte, pterygoid teeth; q, quadrate; qpp, quadratic process of pterygoid; sa, surangular; sp, splenial; sq, squamosal; st, supratemporal; sta, stapes; tym, quadratic tympanum.

Stratigraphic position of the material from The Netherlands and Belgium

Halisaurus ortliebi came from the Phosphatic Chalk of Ciply, near Mesvin (Hainaut, Belgium) and *Halisaurus vertebrae*, from St. Pietersberg, near Maastricht, (The Netherlands) (see LINGHAM-SOLIAR & NOLF, 1989 and LINGHAM-SOLIAR 1994a respectively for the geology, palaeoecology and palaeoenvironment)

Systematic Palaeontology

Order SQUAMATA

Family MOSASAURIDAE Gervais, 1853

Subfamily PLIOPLATECARPINAE (Williston, 1897)

Plioplatecarpinae (Williston, 1897)

- 1884 Plioplatecarpidae DOLLO: 653.
- 1890 mosasauriens microrhynques DOLLO: 163.
- 1897 Platecarpinae WILLISTON: 177.
- 1967 Plioplatecarpinae RUSSELL: 148

DIAGNOSIS

See RUSSELL (1967).

Halisaurus* MARSH, 1869.Halisaurus* MARSH, 1869: 395.*Baptosaurus* MARSH, 1870: 3.*Phosphorosaurus* DOLLO, 1889: 68.Generic type. *Halisaurus platyspondylus* MARSH, 1869.

EMENDED GENERIC DIAGNOSIS

Very narrow frontal, subrectangular. Articulating surfaces of cervical and anterior dorsal vertebral centra nearly twice as wide as deep, subrectangular or kidney bean shaped, may be slightly upturned; synapophyses located in centre of lateral surface of cervical centra, occupies somewhat more posterior position in anterior thoracics; ventral border of antero-ventral extension of synapophysis weak and horizontal in anterior cervicals, becomes much enlarged in posterior cervicals and anterior thoracics, extending far below flattened undersurface of centrum; anterior zygapophyses of cervical and anterior thoracics connected by gently rounded, posteriorly des-

cending crest to synapophysis; zygosphenes and zygantra absent; hypapophyseal peduncle located posteriorly on ventral surface of cervical centra, articulation for hypapophysis flat and lenticular, slightly inclined posteriorly, slight tilt of condyle anteriorly.

***Halisaurus ortliebi* (DOLLO, 1889)**
(Figs. 1-5; Pl. 1)1889 *Phosphorosaurus ortliebi* DOLLO: 279-286, pl.10, fig. 6.1991 *Halisaurus ortliebi* LINGHAM-SOLIAR: 663.

HOLOTYPE

IRSNB R34, fragmentary skull, frontal, parietal, prefrontal, postorbitofrontal, quadrate, fragments of pterygoid, fragments of dentary and splenial.

HORIZON AND LOCALITY OF HOLOTYPE

Phosphatic Chalk of Ciply, Upper Maastrichtian, near Mesvin, Hainault, Belgium.

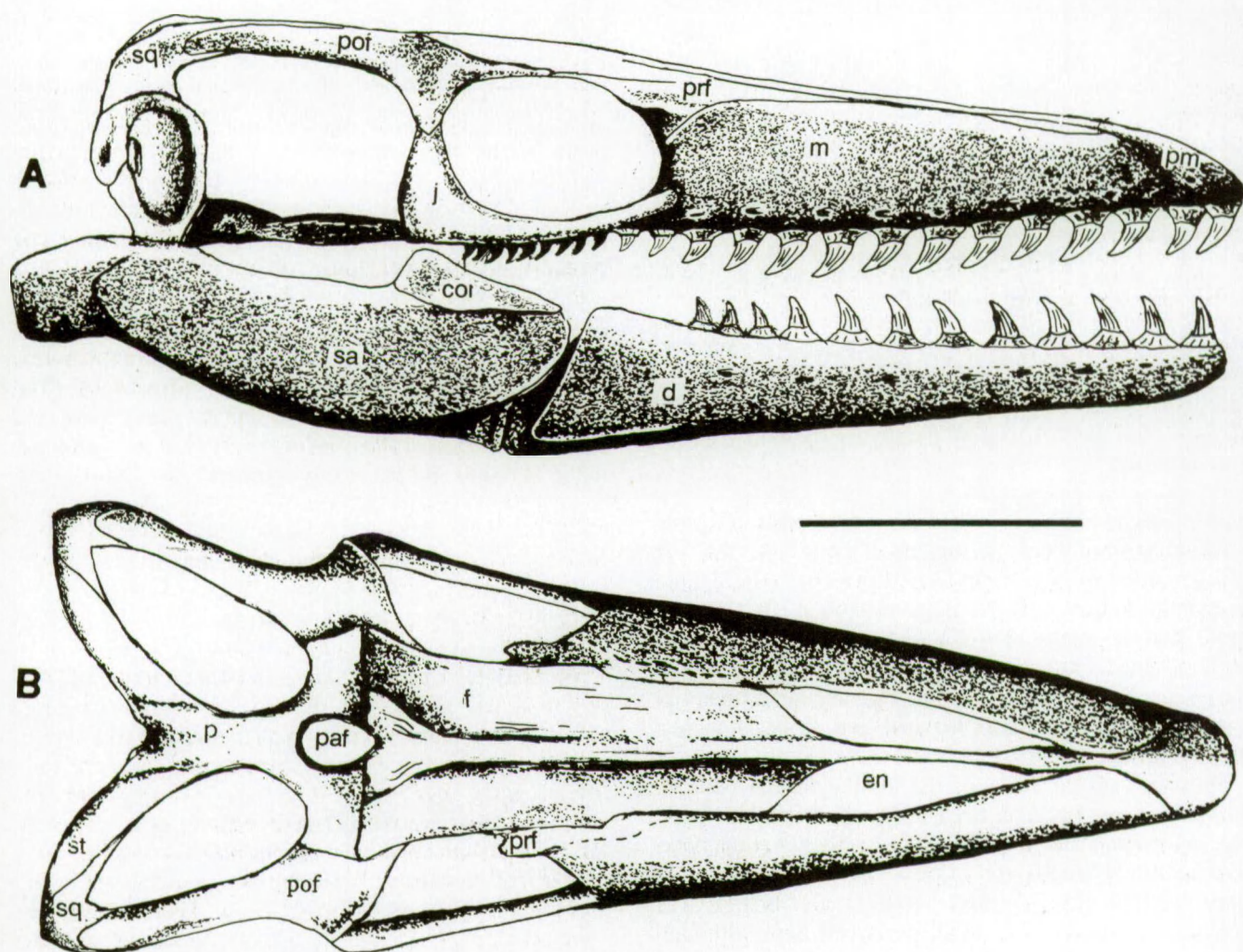


Fig. 1 — Restored skull of *Halisaurus ortliebi* IRSNB R34. A, lateral view; B, dorsal view. Scale bar = 100 mm.

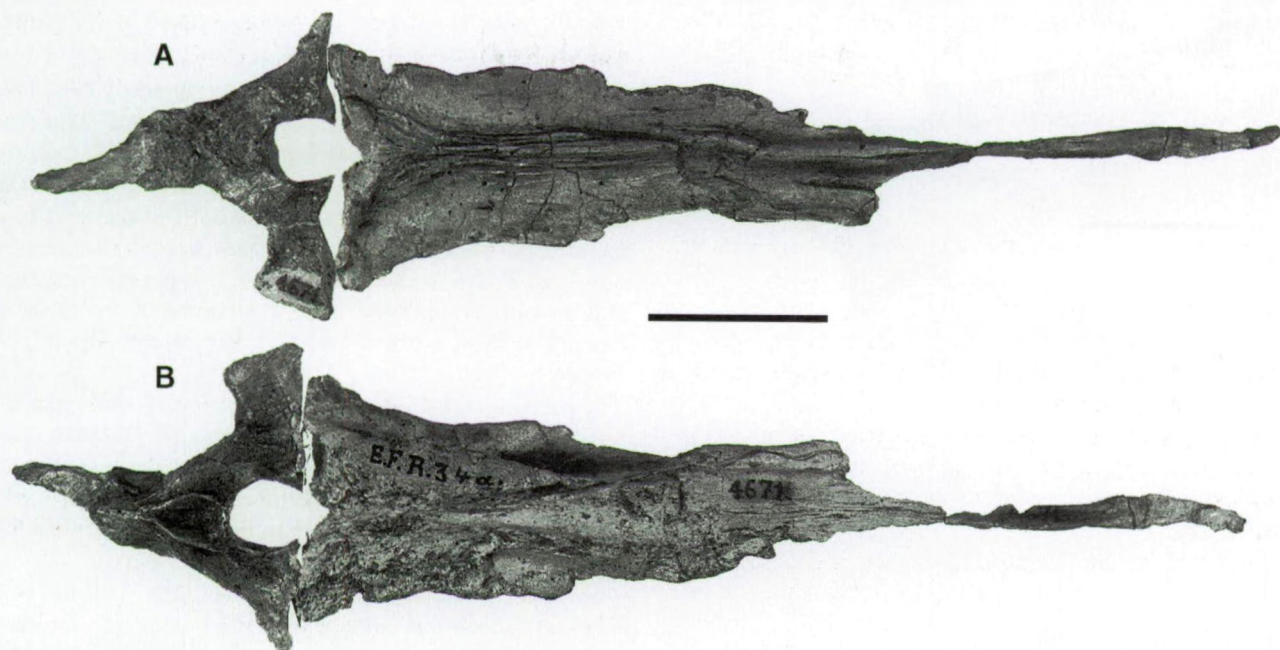


Fig. 2 — Skull table of IRSNB R34. A, dorsal view of parietal and frontal; B, ventral view of the parietal and frontal. Scale bar = 50 mm.

DIAGNOSIS

Large prefrontal, almost entirely overlain by maxilla and frontal. Rounded crest on frontal extends almost the entire length of the bone; sides virtually parallel, slight emargination over orbits. Little evidence of consolidation along mesokinetic axis. Enormous subcircular parietal foramen, most of the margin formed by the parietal; parietal narrow, elliptical excavation on ventral surface behind the parietal foramen. Robust pterygoid, approximately eight posteriorly recurved teeth. Fused supra and infrastapedial processes in a moderate sized quadrate rather than in the usually large quadrate, relatively shallow quadratic tympanum; pinched stapedial pit.

DESCRIPTIONS AND COMPARISONS

Descriptions and restorations are based essentially on the holotype IRSNB R34. Comparisons are made with the North American type species *Halisaurus platyspondylus* (based on RUSSELL, 1967) from the Upper Cretaceous, Greensand, Navesink Formation of New Jersey, Hornerstown. RUSSELL's (1970, p. 369) assignment of *Clidastes sternbergi* to *Halisaurus* is questioned (discussed later) and it is consequently not considered for generic comparative purposes.

SKULL

The skull (Fig. 1 and P1.1) is fragmentary, essentially lacking the dental rami, maxilla, postmandibular units and braincase. The available bones nevertheless indicate a delicate skull approximately 420 mm long that probably tapered to a slender pointed snout (Fig. 1 and P1.1).

Frontal

The frontal in IRSNB R34 (Figs. 2B, D) is exceedingly narrow with an exceptionally short and straight frontoparietal suture. The lateral margins are relatively straight and only slightly emarginate above the orbits. A prominent median crest extending almost the entire length of the bone, dissipates into a delta of fine ridges near the posterior margin. The latter condition has not been described in mosasaurs before. Anteriorly, a long slender medial process forms part of the internarial bar and bounds the postero-medial portion of the external nares. The ventral surface of the bone is considerably eroded but along its midpoint a slight excavation marks the position of the olfactory lobes. Shallow excavations along the lateral borders of the frontal indicate the location for the prefrontal and postorbitofrontal wings. A cleft at the midpoint of the posterior boundary of the frontal represents a small anterior portion of the enormous parietal foramen. Descending processes of the frontal are apparently little developed.

Prefrontal

The prefrontal (Figs. 3A, B) is relatively large and the prefrontal ala or shelf is relatively small. An excavation on its external dorsomedial surface indicates extensive overlap by the frontal. The maxilla overlapped the prefrontal on the lateral surface as far as a distinct dorsolateral ridge, leaving very little of the prefrontal exposed. Poor preservation makes it impossible to determine whether the frontal bordered the orbit or was precluded by the prefrontal and postorbitofrontal wings. However, the excavations on the ventral surface of the frontal and the small size of the prefrontal wing to the maxilla suggest that the prefrontal and postorbitofrontals fitted close to

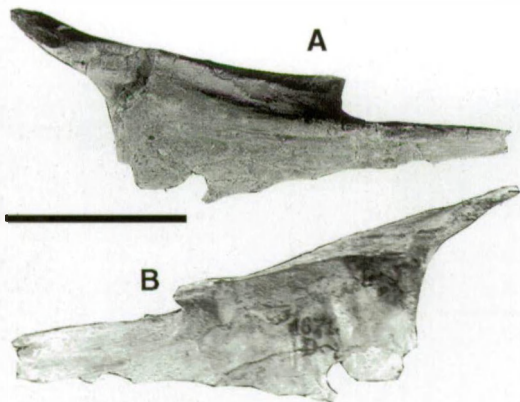


Fig. 3 — Prefrontal of IRSNB R34. A, lateral view; B, medial view. Scale bar = 50 mm.

the lateral margins of the frontal.

Postorbitofrontal

The postorbitofrontal (Figs. 4A, B) is a robust bone. A relatively broad wing underlies the frontal.

Medially, the wing to the parietal is greatly eroded. The ventral wing to the jugal is long and quite robust. The robust posterior wing, forming part of the upper temporal arcade, is exceptionally short, placing the postorbitofrontal a significant distance from the postero-lateral corner of the supratemporal fenestra. Deep striae at its posterior end indicates that the postorbitofrontal and squamosal were clearly broadly united by strong sutures and ligaments.

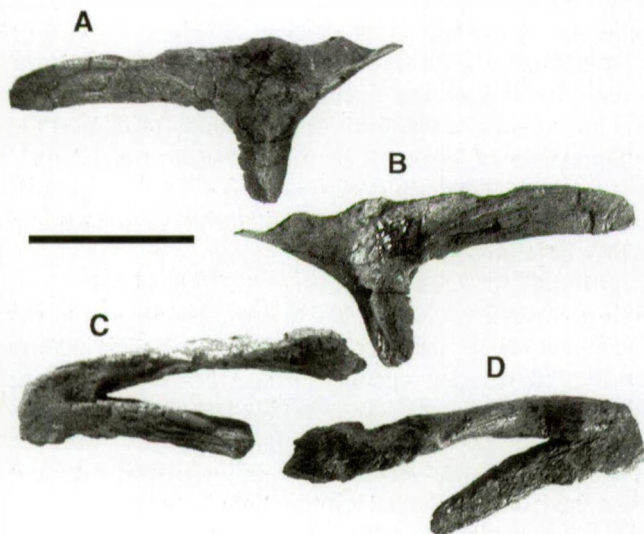


Fig. 4 — IRSNB R34. Postorbitofrontal. A, lateral view; B, medial view. Squamosal. C, dorsal view; D, ventral view. Scale = 50 mm.

Jugal

The vertical arm of the jugal is poorly preserved.

The most notable characters are the laterally broad ala at the junction of the horizontal and vertical axes and absence of a postero-ventral process (Fig. 1A), features similar to those of *Plioplatecarpus houzeau* (LINGHAM-SOLIAR 1994a). On the postero-medial surface a striated excavation marks the point of a ligamentous connection. *Squamosal*. The squamosal (Fig. 4C) is poorly preserved and the only condition of note that can be observed is the heavily striated process leading to the supratemporal.

Parietal

The parietal (Figs. 2A, C) shows several unusual characteristics. The parietal foramen is enormous. It is also large in *Plioplatecarpus*, but unlike *Halisaurus*, at least half of its margin is formed by the frontal. It is, however, more circular in outline in contrast to the ellipsoid configuration in *P. houzeau* (LINGHAM-SOLIAR 1994a).

Anteriorly the parietal table is triangular with the base forming the sutural contact with the frontal. At the apex of the triangle, at approximately the midpoint of the bone, the parietal abruptly constricts and then gives rise to two relatively broad processes that diverge in a gentle curve to the postero-lateral corners of the supratemporal fenestra. Each ramus is vertically flattened and distally striated on the dorsal and ventral surfaces.

Anteriorly the parietal contact with postorbitofrontal is rather broad relative to the generally modest proportions of the bone. Presence of a rather deep elliptical excavation or fossa on the ventral constricted surface of the parietal has not been noted in mosasaurs before. I have noted only one other occurrence in lizards in the literature (ESTES *et al.*, 1988), in *Ctenosaurus pectinata*.

Pterygoid

The pterygoid is poorly preserved. A fragment that includes the tooth row, and one of just the broad posterior wing are present. The two preserved teeth are quite large, pointed and strongly posteriorly recurved. The complete tooth row comprised probably not more than eight teeth. The ectopterygoid process is directed anteriorly at an angle of about 45° degrees.

The quadratic ramus of the pterygoid (Figs. 3C, D), although incomplete, was clearly laterally expanded and flattened dorsoventrally, the medial surface concave and the lateral surface convex. A deep groove extends dorsally along the anterior half of the fragment and a separate groove extends along the postero-lateral flange, flattening out at the posterior termination which is concave. As in other delicately constructed skulls (e.g. *P. houzeau*., LINGHAM-SOLIAR 1994a), this fragment is the stoutest bone preserved in the skull. However, a large quadratic ramus in *P. houzeau* is correlated with a large quadrate while, in contrast, in *H. ortliebi* the quadrate is significantly smaller.

Quadrate

Both quadrates (Figs. 5A, B) are in a poor state of preservation. The suprastapedial and infrastapedial processes are completely fused. The right fragment has broad anterior and dorsal margins and appears to have a shallow

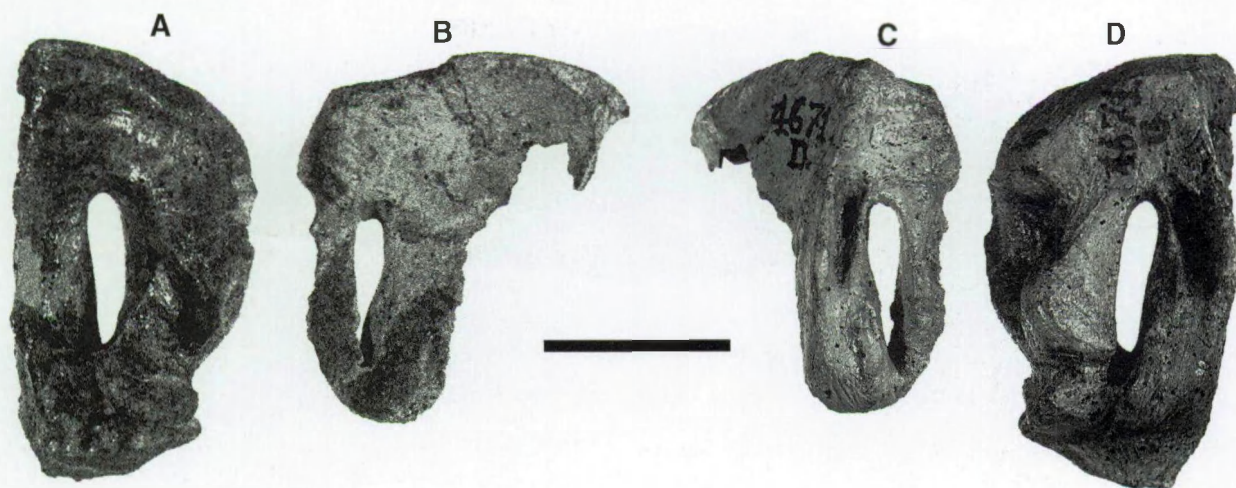


Fig. 5 — Quadrates IRSNB R34. A, B, lateral views; C, D, medial views. Scale bar = 25 mm.

tympanum. However, the partial left quadrate indicates the presence of a moderately deep tympanum suggesting that the shallow tympanum in the right quadrate results from either poor preservation or a pathologic deformation.

Medially the pinched stapelial pit extends parallel to the almost closed quadratic meatus.

Splenial

The bone that is positioned as the angular in IRSNB R34 (P1. 1a) is in fact a fragment of the splenial. It is slender and laterally compressed. Medially there is a large foramen a few centimetres from the posterior termination of the bone. Its posterior articulation is narrow with a slight lip ventrally.

Articular

A small fragment of the articular is present.

It is laterally compressed with the internal surface concave and the lateral surface convex.

POSTCRANIAL SKELETON.

Vertebrae. Vertebral material is not preserved in IRSNB R34. The only probable *Halisaurus* vertebrae from Europe, BMNH 44822 and 42900, are from the Upper Maastrichtian, Maastricht Formation of St. Pietersberg, The Netherlands. In BMNH 42900 the condyle is highly depressed but also somewhat upturned, a unique condition in mosasaurs.

DISCUSSION

Morphology. The frontal of *Halisaurus ortliebi* (Figs. 3B, D) is markedly rectangular even more so than in *Clidastes liodontus* (WILLISTON, 1898; RUSSELL, 1967). However, in the latter unlike in *H. ortliebi*, posterior extensions of the frontal enter the postorbitofrontals and parietal. The relatively short, straight suture of *H. ortliebi* (see, DOLLO, 1889, pl.9, fig. 6 and Fig.), is similar to that of *C. sternbergi* (WIMAN, 1920).

In iguanians generally and in lizards such as xenosaurs, gerrhonotine anguids, and some gynophthalmids and la-

certids strong constriction at the orbits (ESTES *et al.*, 1988) reflects large eyes associated with a highly developed sense of vision. Although the lateral borders are not apparently markedly constricted, narrow proportions of the whole element in *H. ortliebi* makes it reasonable to assume that the eyes were large and that the animal was possibly an active predator.

The exceptionally straight and short frontoparietal suture indicates that mesokinetic movement was quite considerable in *Halisaurus ortliebi*. Indeed the complete disarticulation of all the bones of the skull, although circumstantial, indicates the potential of considerable intracranial mobility.

Fused suprastapedial and infrastapedial processes despite the small size of the quadrates in *Halisaurus ortliebi* (Fig. 5) is puzzling. Previously, such fusion was only known in association with strong crushing jaws of the mosasaurs *Prognathodon* (LINGHAM-SOLIAR & NOLF, 1989) and *Globidens* (RUSSELL, 1975). However, the quadrate of *Opetiosaurus* (e.g. DEBRAGA & CARROLL, 1993, p. 258, fig. 8c) is similar to that of *H. ortliebi*. The character of fusion or near fusion is therefore considered here as a plesiomorphy of mosasaurs with the open state as advanced. Appearance of the fused state in the evolutionary advanced *Prognathodon* and *Globidens* is considered as a character reversal.

The upturned condyle of the vertebrae of *Halisaurus* although unique to mosasaurs is characteristic of varanids and consequently considered here as a plesiomorphy of mosasaurs. *Halisaurus* vertebrae demonstrate several primitive characters, e.g. a relatively larger neural canal and a relatively broader span across the zygapophyses approaching those of less highly modified squamate families, a point also noted by BUKOWSKI (1984).

Systematics and phylogeny

It seems appropriate to place *Halisaurus* in the subfamily Plioplatecarpinae rather than in RUSSELL's Mosasaurinae (1970), for reasons which will be mentioned briefly in the following discussion. This view was also supported by



Fig. 6 — Dorsolateral view of the skull of *Clidastes sternbergi*. Scale bar = 100 mm.

the first cladistic analysis on the Mosasauridae (SOLIAR, 1988).

RUSSELL's (1970) assignment of *Clidastes sternbergi* (Fig. 5) to the genus *Halisaurus* was welcomed by authors such as BAIRD (1986a) on the assumption that the entire morphology of the genus was now available for study. However, for reasons given below, *Clidastes sternbergi* should be excluded from the synonymy list of *Halisaurus*.

The present study of *Halisaurus ortliebi* IRSNB R34 suggests that the differences between it and *Clidastes sternbergi* are so great as to make it highly unlikely that these two species should be included in the same subfamily let alone the same genus. They differ, in common with all known specimens of *Halisaurus*, in two diagnostically important characters, the size of the parietal foramen and its location in relation to the fronto-parietal suture (Fig. 6; for an assessment of the latter character in living squamates and non-squamate lepidosauromorphs see ESTES *et al.*, 1988, pp. 148-149). The parietal foramen in *P. ortliebi* as already noted is amongst the largest in the Mosasauridae (approx. 24 mm in diameter, Fig. 1; see also DOLLO, 1889, pl. 9, fig. 6), exceeded only in another Belgian mosasaur *Plioplatecarpus houzeaui* (DOLLO, 1889, 1894, 1904; LINGHAM-SOLIAR, 1994a), and is bounded anteriorly by the frontal. As noted in WIMAN's (1920, p. 14) description of the parietal foramen in *Clidastes sternbergi*, "The foramen parietale is small and lies on the boundary between the first and second third of the parietale, thus considerably further back than in *Clidastes velox* and other Mosasaurians". Indeed the view that *H. ortliebi* and *C. sternbergi* are not related was discussed briefly earlier (LINGHAM-SOLIAR 1991, p. 663) and is

supported by a cladistic analysis on the origin of mosasaurs (DEBRAGA & CARROLL, 1993).

The relationships of *Halisaurus* are difficult to determine because of the fragmentary nature of the material available. Such poor fossil representation appears quite extraordinary in view of the broad stratigraphic range of *Halisaurus* material, from the Upper Santonian to the Upper Maastrichtian (representing a period of about ten million years). Two factors may provide an explanation; the bones of the skull of *Halisaurus* IRSNB R34 are both highly kinetic and delicate. Rapid *post mortem* disarticulation of the skull may have been followed by severe fragmentation and scattering of the bones.

Halisaurus shares several important characters with *Plioplatecarpus*; a very large parietal foramen, location of the parietal foramen on the fronto-parietal suture, delicate nature of the bones of the skull, an apparently enhanced kinetic skull, depressed vertebral articulations, upturned condyles (as in some varanids) and absence of zygosphenes and zygantra. Inclusion in the subfamily Plioplatecarpinae as previously suggested (SOLIAR 1988) and generic sister status with *Plioplatecarpus* is confirmed in a cladistic analysis (LINGHAM-SOLIAR 1994b). Hence RUSSELL's (1967) inclusion of *Halisaurus* in the Mosasaurinae is rejected here.

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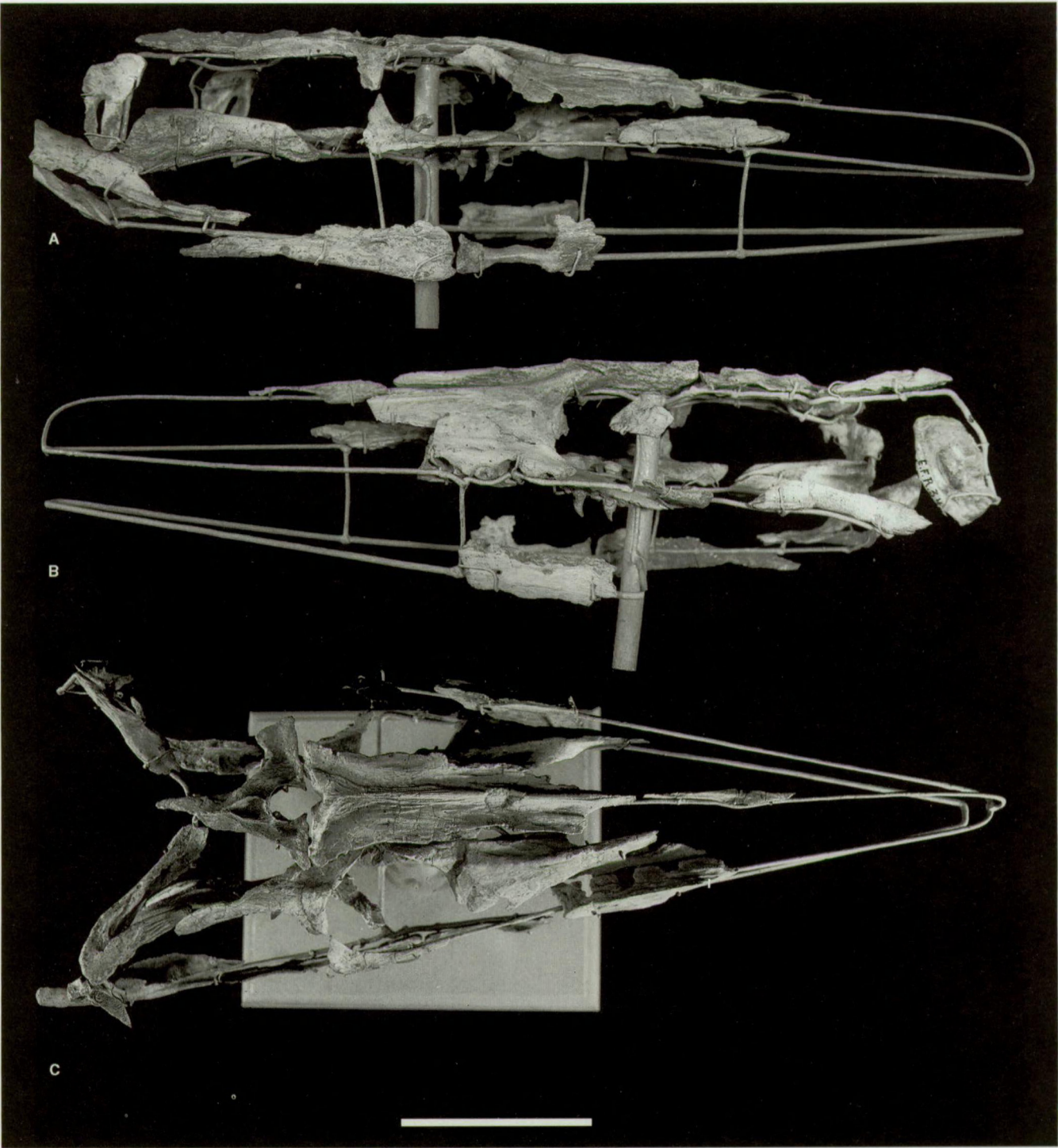
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Explanation of plate

PLATE 1

Skull of *Halisaurus ortliebi* IRSNB R34. A, right lateral view; B, left lateral view; C, dorsal view. Scale bar 100 mm.