

# The mosasaur *Prognathodon* (Reptilia, Mosasauridae) from the Upper Cretaceous of Belgium

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## Abstract

The osteology of the mosasaurs *Prognathodon solvayi* and *P. giganteus* is extensively described for the first time. *P. solvayi* is known from the holotype IRSNB R33, a complete skull and partially preserved postcranial remains as well as from fragmentary material from specimens IRSNB R107 and IRSNB R108. *P. giganteus* is based wholly on the fragmentary cranial and postcranial remains of the type specimen IRSNB R106. Both species are compared with the North American taxa *P. overtoni* (KU 950, the holotype), *P. ? overtoni* (SDSM 3393), *P. rapax* (AMNH 1490), *? Prognathodon* (FMNH PR 165) and "*Prognathodon*" *crassartus* (AMNH 1562). *P. solvayi* and *P. giganteus* are less similar to each other than are *P. giganteus* and SDSM 3393, referred to *P. overtoni* by RUSSELL (1967), especially with regard to overall shape and size. Because of the very fragmentary holotype material of *P. overtoni* comparisons with it are restricted. Characters critical in the classification of *Prognathodon* (such as dentition, zygosphenes, zygantra and haemal arches) are re-assessed. Re-evaluation of these characters induces changes in the generic assignments of the taxa within the Plioplatecarpinae. "*Prognathodon*" *crassartus* is reassigned to *Plioplatecarpus*. The status of FMNH PR 165, referred to *Prognathodon* by RUSSELL (1970) is questioned on the basis of conflicting diagnostic characters; it is a large plioplatecarpine mosasaur probably more closely related to *Selmasaurus* or *Plioplatecarpus*. *Dollosaurus* IAKOVLEV, 1901 is synonymised with *Prognathodon*. The ecology of *Prognathodon* and certain other mosasaurs of Belgium is discussed and comparisons are made with other aquatic vertebrates.

**Key-words:** *Prognathodon*, mosasaur, Belgium, systematics, feeding, swimming.

## Résumé

L'ostéologie des mosasaures *Prognathodon solvayi* et *P. giganteus* est décrite en détail pour la première fois. *P. solvayi* est connu par l'holotype IRSNB R33, un crâne entier avec des os postcrâniens incomplets, et par les spécimens fragmentaires IRSNB R107 et IRSNB R108. *P. giganteus* est représenté par un matériel crânien fragmentaire et des restes postcrâniens de l'holotype IRSNB R106. Les deux espèces sont comparées avec les taxons nord-américains *Prognathodon overtoni* (KU 950, l'holotype), *P. ? overtoni* (SDSM 3393), *Prognathodon rapax* (AMNH 1490), *? Prognathodon* (FMNH PR 165) et "*Prognathodon*" *crassartus* (AMNH 1562). *Prognathodon solvayi* et *P. giganteus* sont moins semblables entre eux que ne le sont *P. giganteus* et le spécimen SDSM 3393, attribué à *P. overtoni* par RUSSELL (1967) surtout d'après la forme générale et la taille. Les comparaisons sont restreintes avec la dernière espèce dont l'holotype est très fragmentaire.

Les caractères importants de la classification de *Prognathodon* (comme la dentition, les zygosphènes, zygantra et arcs hémaux) sont réévalués. La nouvelle compréhension de ces caractères entraîne des changements dans les attributions génériques de taxons appartenant aux Plioplatecarpinae. *Prognathodon crassartus* est nouvellement attribué à *Plioplatecarpus*. Le

statut du spécimen FMNH PR 165, appartenant à *Prognathodon* selon RUSSELL (1970), est mis en doute d'après des caractères diagnostiques contradictoires; il s'agit d'un grand mosasaure de la sous-famille des Plioplatecarpinae probablement plus proche de *Selmasaurus* ou de *Plioplatecarpus*. *Dollosaurus* IAKOVLEV, 1901 est mis en synonymie avec *Prognathodon*. L'écologie de *Prognathodon* et de certains autres mosasaures de Belgique est discutée et certaines comparaisons sont établies avec d'autres vertébrés aquatiques.

**Mots-clefs:** *Prognathodon*, mosasaure, Belgique, systématique, alimentation, natation.

## Introduction

In 1889a-c, DOLLO described the unusual Belgian mosasaur *Prognathodon*. Although his description was brief and the available material rather complete no additional study of the material has appeared. RUSSELL (1967) in his monograph on North American mosasaurs revised the North American *Prognathodon* species with brief comments on the Belgian forms. As might be expected in such a situation, some errors have been perpetuated. This fuller account will provide needed coverage of these interesting mosasaurs.

## Geological setting and materials

Marine Cretaceous deposits are well exposed in two main areas of Belgium — the Hesbaye-Maastricht district in the north east and the Mons Basin in the south west of the country (Fig. 1).

Both areas have yielded a large number of mosasaur specimens collected and preserved in the Institut Royal des Sciences Naturelles de Belgique.

Mosasaurs were first discovered in the Maastricht area where preservation of the fossil bones is excellent. The bulk of the collections of the IRSNB, however, comes from the Cibly Phosphatic Chalk in the Mons Basin. Here the phosphatic chalk was intensively quarried for the manufacture of agricultural fertilizers during the second half of the 19th century.

In the period between 1880 and 1895, fifty two relatively complete mosasaur skeletons were discovered in various quarries, mainly in Cibly, south of Mons. These were transferred to the IRSNB formerly known as the Musée

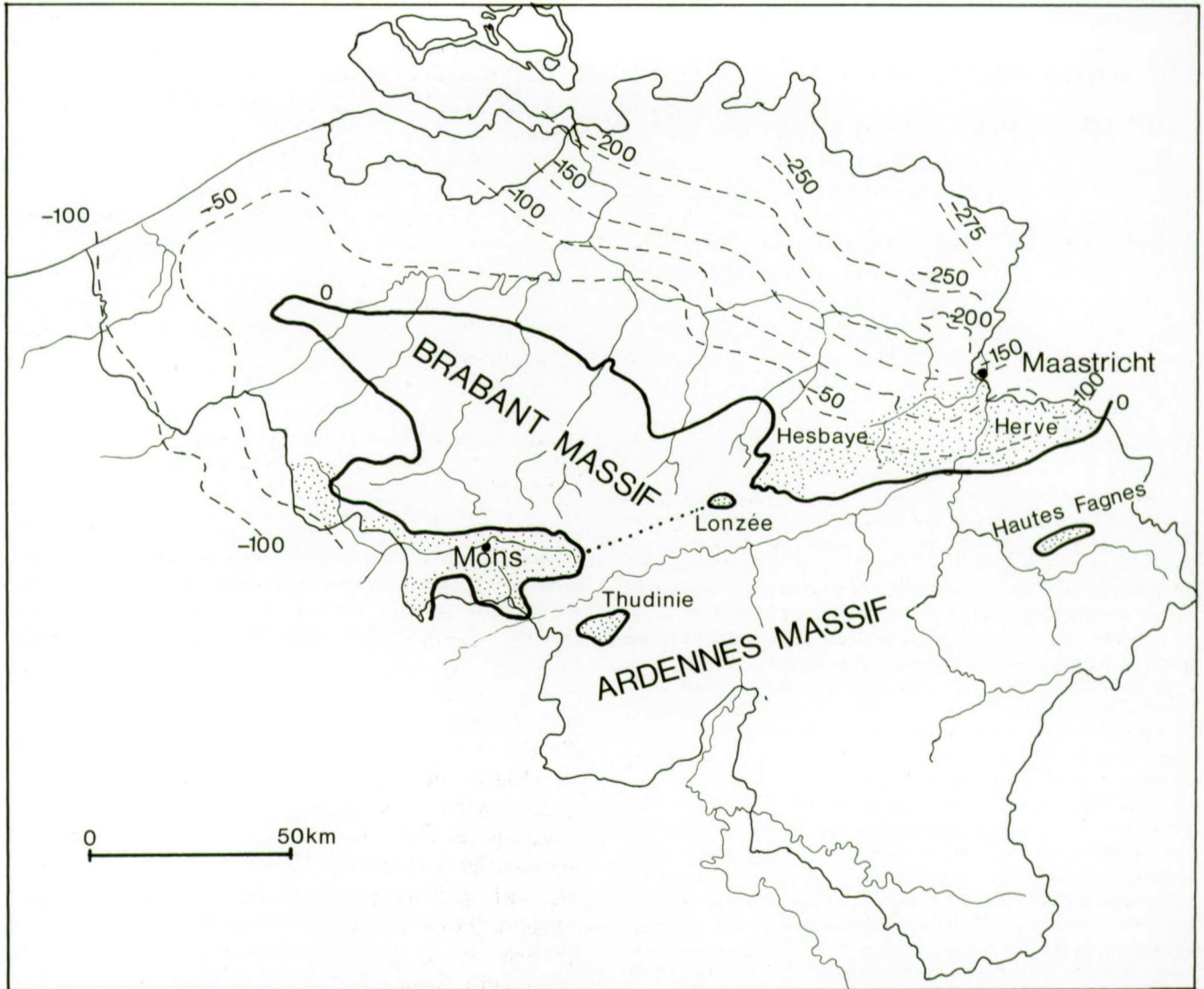


Fig. 1. - Extent of the marine Cretaceous of Belgium and isopaque lines of the Paleozoic substratum. Pointed surfaces correspond to the areas of outcropping (after LEGRAND, 1951 and MARLIÈRE, 1954, modified).

royal d'Histoire naturelle, where they were prepared from their chalk matrix.

In contrast to the material from the Maastricht area, mosasaur remains from the Ciply Phosphatic Chalk are considerably more fragile and abraded, frequently showing extensive postdepositional distortion. Fortunately a number of the specimens were found with significant portions in association, which in many cases allowed fairly accurate reconstructions.

The first specimen to be discovered was that of the gigantic tylosaurine *Hainosaurus bernardi* DOLLO 1885. Subsequently this was followed by a very courteous collaboration between the Institute and the engineers A. LEMONNIER and L. BERNARD of the phosphate exploitation at Ciply. This resulted in the excavation and transfer to Brussels of a total of 52 mosasaur skeletons, besides other vertebrate material such as fishes, turtles and a plesiosaur.

The bulk of the mosasaur material from the Ciply Phosphatic Chalk belongs to the species *Mosasaurus lemonnieri*

DOLLO, 1889, synonymised by RUSSELL (1967, p. 132) with the American species *Mosasaurus conodon* (COPE, 1881). However, at least 6 other species are known from this layer — *Carinodens belgicus* (WOODWARD, 1891), *Hainosaurus bernardi*, *Plioplatecarpus houzeai* (DOLLO, 1889), *Prognathodon giganteus* DOLLO, 1904, *Prognathodon solvayi* DOLLO, 1889 and *Halisaurus* sp.

Although an enormous amount of work was invested in the extraction and mounting of all these specimens, scientific study of this material has been surprisingly limited. In most cases diagnoses and descriptions are brief or restricted to a peculiar point of their anatomy, e.g., the study of the quadrate and associated tympanic membrane in *Plioplatecarpus houzeai* by DOLLO (1904, 1906).

The most brief treatment given to any mosasaur species was that for *Prognathodon giganteus*, for which the full citation of the original description is: "On trouve dans la Craie phosphatée (Sénonien supérieur) des environs de Mons, deux espèces de *Prognathosaurus* [= *Prognatho-*

don,], mais une seule a été caractérisée jusqu'à présent. Voici comment on peut les distinguer :

1. Dents facettées (taille inférieure à 6 mètres) . . . . . *P. solvayi*, DOLLO, 1889;
2. Dents lisses (taille atteignant 10 mètres) . . . . . *P. giganteus*, DOLLO, 1904.

Le première provient de Ciplly; la deuxième de Spiennes". No iconography was used in completing the above diagnosis, which apparently was only intended to provide a name for the skeleton of this large mosasaur for exhibition in the museum hall. The other *Prognathodon* species from the Ciplly Phosphatic Chalk, *P. solvayi* DOLLO, 1889 is based on a fairly complete although abraded skull and partial poorly preserved postcranial skeleton. In the literature, however, only a general view of the skull and a detailed figure of the quadrate was given (DOLLO, 1889) and nothing of the postcranial material.

A lack of information in the literature on *Prognathodon giganteus* and *P. solvayi* was partly responsible for the decision to produce a monograph on them. Besides the species treated here, four North American representatives of *Prognathodon* have been described, *P. overtoni* (WILLISTON, 1897) from the Upper Pierre Formation, Maastrichtian of South Dakota; *P. rapax* (HAY, 1902) from the Navesink Formation, Maastrichtian of New Jersey; *P. crassartus*

(COPE, 1872), from the Lower Pierre Formation, Campanian of Kansas (the status of *P. crassartus* is discussed briefly below in the taxonomic discussion) and an unnamed specimen, cited as *Prognathodon* (FMNH PR 165) by RUSSELL (1970, p. 373) from the Mooreville Chalk, Campanian of Alabama.

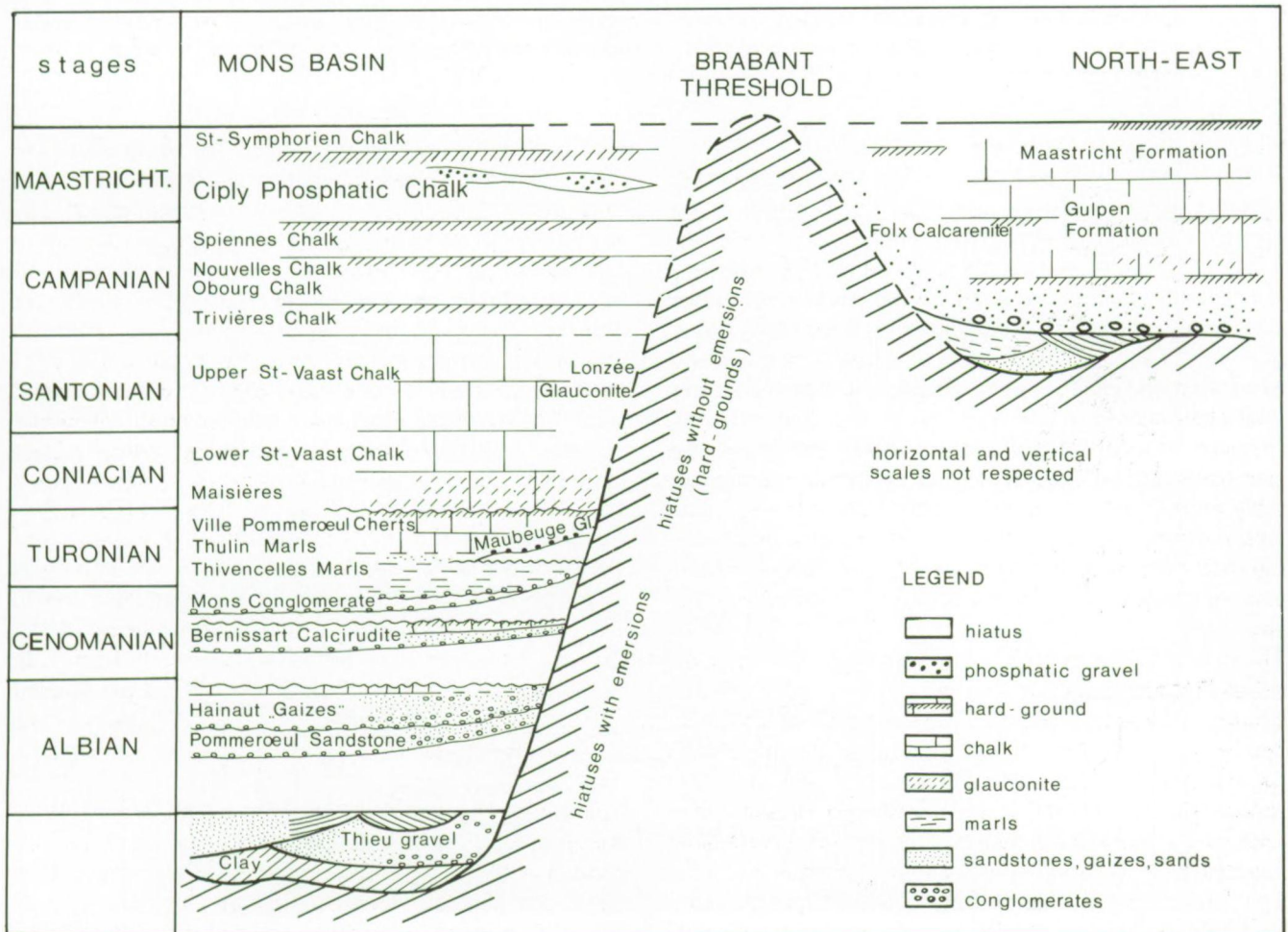
*Stratigraphic position of the material studied and locality data*

In Fig. 2 the stratigraphic position of the Ciplly Phosphatic Chalk is shown in a generalised table of the Belgian Cretaceous deposits.

The formation outcrops on the flanks of several valleys in the area south of Mons, mainly in the municipalities of Cuesmes, Ciplly, Mesvin, Spiennes and Saint-Symphorien (Fig. 2).

The Ciplly Phosphatic Chalk lies on the Spiennes Chalk (Campanian) and is overlain by the Maastrichtian Saint-Symphorien Chalk. This is the succession observed in the centre of the basin, for example under the town of Mons, towards the southern margin of the basin. In the outcrop area the Saint-Symphorien Chalk is lacking and in most parts a disconformable contact occurs between the Ciplly Phosphatic Chalk and the Lower Paleocene Ciplly Calcare-

Fig. 2. - Stratigraphic scheme of the Belgian Cretaceous deposits (after ROBASYNSKI & DUPUIS, 1983, p. 46; modified).



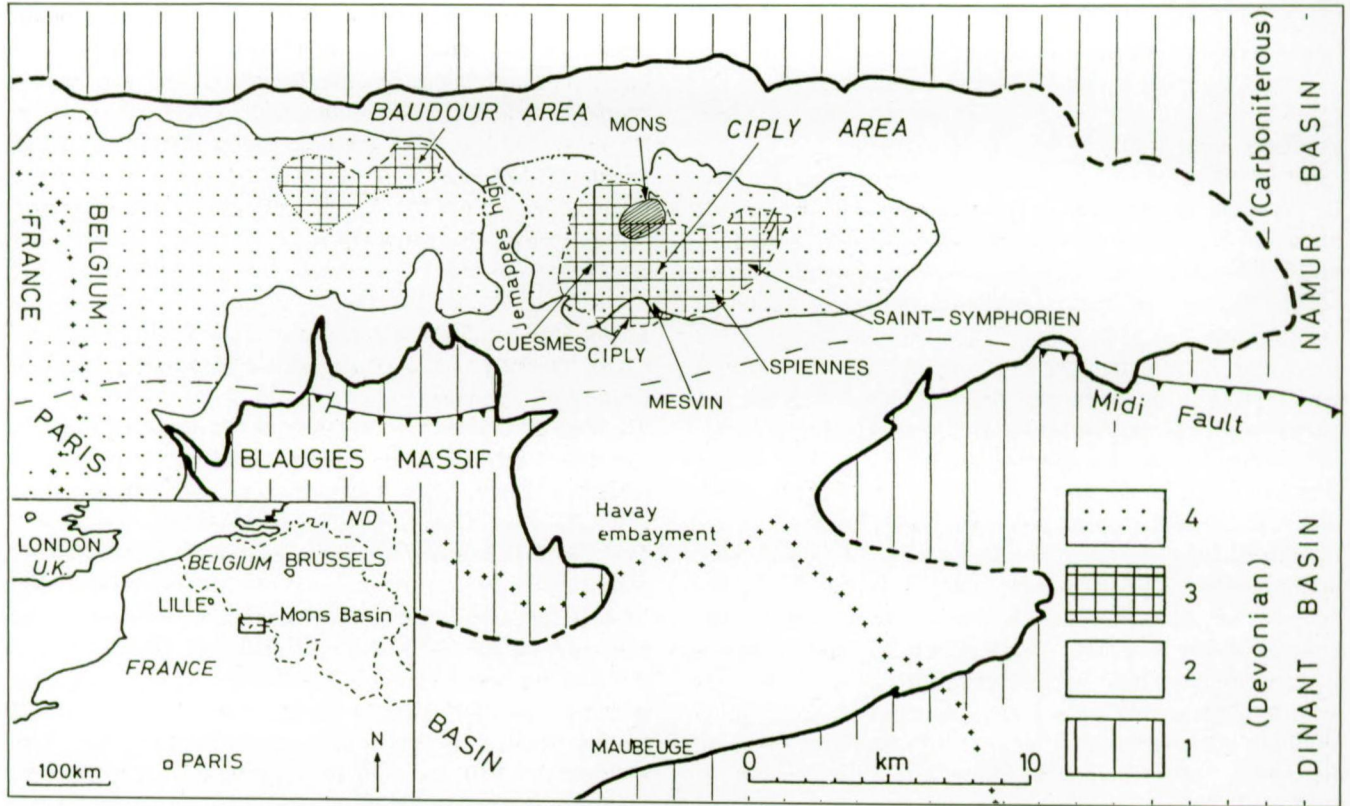


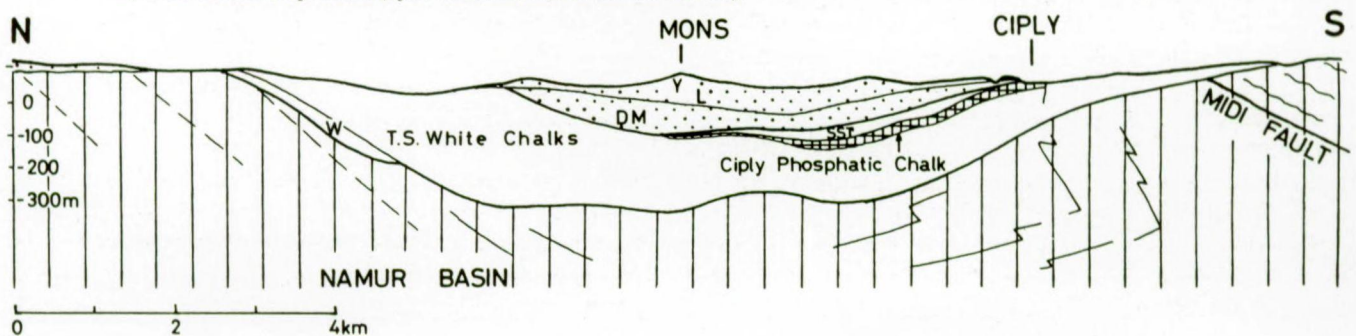
Fig. 3. - Geological sketch-map of the Mons Basin, showing the extent of the Cibly Phosphatic Chalk (Cibly and Baudour areas) and localization of the municipalities cited in the text. 1. Paleozoic basement; 2. Cretaceous marls and white chalk; 3. Maastrichtian Cibly Phosphatic Chalk; 4. Tertiary calcarenites, sands and clays. Note : the largest part of the phosphatic strata in the Cibly and Baudour areas is overlain by Tertiary sediments. The extension of subsurface phosphate is shown under these Tertiary sediments (after ROBASYNSKI & MARTIN, 1988, modified).

nite (= Tuffeau de Cibly; Fig. 3 and 4).

However the same type locality (Cibly) for formations of different age is confusing and does not conform to the directives of modern stratigraphy (HEDBERG, 1976, p. 21, p. 41); these terms are nevertheless used here because they are currently encountered in all the literature on the Upper Cretaceous and Lower Tertiary deposits of the Mons Basin. In point of fact the Cibly Phosphatic Chalk is best exposed in underground galleries of the abandoned Malogne Quarry at Cuesmes. At this site (see Fig. 5; also ROBASYNSKI, GOSSELIN, VANDYCKE & LECLERC, 1988, and Fig. 3 for precise localities), which is close to the former outcropping

area in which phosphate was mined, the thickness of the Cibly Phosphatic Chalk varies between 3 and 8 meters in most of the exposures. A phosphatic basement gravel, called Poudingue de Cuesmes, lies on the Upper Campanian Spiennes Chalk. At several places deep perforations caused by invertebrate burrows in this underlying chalk are observed. Laterally the basement gravel is sometimes divided into two distinct levels, at other points it may even be separated from the basement of the formation by a chalk level. The overlying chalk has a pale brownish colour and contains innumerable minute phosphatic grains (rarely more than 1 mm. in diameter).

Fig. 4. - North-south geological section of the Mons basin with the general setting of the Cibly Phosphatic Chalk (same patterns as in Fig. 3). W Wealden facies; TS Turonian-Senonian white chalks; SST Saint Symphorien Tuffeau; DM Danian and Montian; L, Y Landenian, Ypresian (after ROBASYNSKI & MARTIN, 1988).



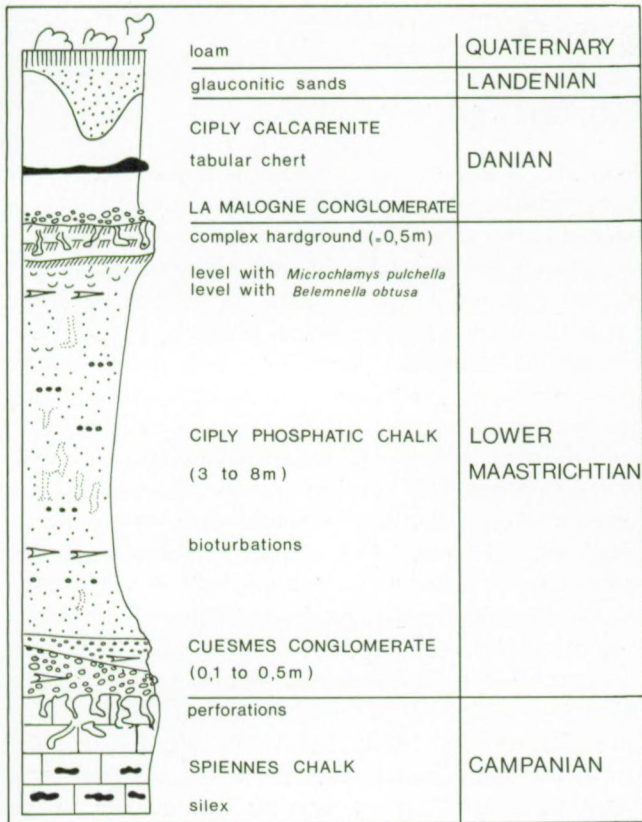


Fig. 5. - Stratigraphic succession of Cretaceous and Paleocene strata in the "La Malogne" underground quarries (after ROBASYNSKI, GOSSELIN, VANDYCKE & LECLERCQ, 1988).

Throughout the formation there are numerous traces of bioturbation. On the top of the formation a hardground is observed, overlain by the Poudingue de la Malogne, which is the basement gravel of the Paleocene Cibly Calcarenite. This contact corresponds to a major hiatus during which the Saint-Symphorien Calcarenite was deposited in other parts of the Basin.

The Poudingue de la Malogne is much richer in phosphate than the underlying Cibly Phosphatic Chalk. The initial mining activities, mainly between 1872 and 1874, were exclusively concentrated in the Poudingue (LECLERCQ & BOUKO, 1985).

Exploitation of the underlying phosphatic chalk started in 1874 in surface extraction. It was at such a surface pit, situated approximately  $x=120.400$ ,  $y=122.900$ , about 0.5 km SW of the centre of Cibly (Fig. 3), that the famous hainosaur skeleton was discovered in 1885. A detailed account of the position of this skeleton appeared in RUTOT & VAN DEN BROECK (1888, p. 229). In this quarry the Cibly Phosphatic Chalk is discordantly overlain by marine Upper Paleocene sand, and the articulated skeleton was found in a subhorizontal position, approximately between 1 and 4 metres below the top of the exposed chalk. Unfortunately at this point the top of the Cibly Phosphatic Chalk is a Late Paleocene erosion surface and because the published section gives no information about the lower limit of the formation it is not possible to indicate the precise level at which the skeleton was found.

For all other mosasaur skeletons from the Cibly Phosphatic Chalk the only locality data available are the municipality names and the names of quarry exploitations; the relative positions and precise stratigraphic levels of the discoveries are unknown. Consequently it is not possible to determine whether there is a distinct mosasaur horizon in the phosphatic chalk, or whether the skeletons were found scattered throughout the formation.

In recent years a renewed interest in phosphorite geology resulted in several papers by ROBASYNSKI and various collaborators. Their reports provide a detailed account of the extension and geometry of the Cibly Phosphatic Chalk deposit (ROBASZYNSKI & MARTIN, 1988), precise localities of the various abandoned quarries and mines (ROBASZYNSKI, POELS & MARTIN, 1988) and descriptions of several sections (ROBASZYNSKI & SUSTRAC, 1988). In figure 21 (p. 38) of the last paper the only place where a mosasaur bone is mentioned at a precise stratigraphic level is from about 1.5 m above the basement of the formation in the Vienne underground quarry,  $x=120.200$ ,  $y=123.250$  at Cibly, but this isolated occurrence is insufficient information on which to determine a mosasaur level.

Most of the mosasaur skeletons were acquired by the Musée royal d'Histoire naturelle around 1890 and come from the municipality of Cibly. The following information on *Prognathodon giganteus* and *Prognathodon solvayi* is available :

*Prognathodon solvayi* - The holotype, R33 (= old register 4672), came from Mesvin, Solvay quarry (same complex of abandoned and partly filled-in quarries near the above cited  $x=120.400$ ,  $y=122.900$  hainosaur locality); it was acquired by the Institute in 1889 (a nearly complete and partly preserved postcranial skeleton with pelvic girdle and tail lacking).

*P. solvayi* - R108 (old register 3201); locality : Spiennes, Houzeau Quarry; acquired by the museum in 1894; comprising jaw and skull fragments, some ribs and vertebrae.  
*P. solvayi* - R107 (old register 4565); locality : Cibly, Solvay Quarry; no precise date of acquisition, probably about 1890. Fragments of skull and dentaries.

*Prognathodon giganteus* - R106 (old register 3103), holotype. Locality : Spiennes, Solvay Quarry. Incompletely preserved skull and remains of postcranial material.

#### *Age of the Cibly Phosphatic Chalk.*

An Early Maastrichtian age has been attributed to the Cibly Phosphatic Chalk by ROBASYNSKI & CHRISTENSEN (1989), on the basis of foraminiferal associations and on the presence of *Belemnella* cf. *B. obtusa* SCHULZ, 1979.

#### *Environmental conditions and taphonomy during the deposition of the Cibly Phosphatic Chalk.*

Most chalk deposits of the Upper Cretaceous correspond to deep neritic facies. A peculiar feature in the lithology of Cibly sediments is the presence of large quantities of phosphate grains. Frequently the presence of phosphates is associated with low rates of sedimentation and shark

teeth or other disarticulated vertebrate remains are common in such deposits. Shark teeth are extremely rare, however, in the Cibly Phosphatic Chalk (HERMAN, 1977, p. 316). Also the presence of many articulated mosasaurs and various other skeletons of large aquatic vertebrates gives a taphonomic picture that is very different from the content of vertebrate remains in a phosphatic deposit (e.g. the Upper Cretaceous and Paleogene phosphates of North Africa, the Neogene phosphates of Florida). A relatively rather rapid sedimentation rate in an area not subject to wave or storm effects seems to be required for the imbedding and preservation of large articulated skeletons, suggesting that water depth of at least 50 m would be required to explain the taphonomy of the Phosphate Chalk of Cibly.

#### Abbreviations

- BMNH = British Museum (Natural History), London, UK  
 FMNH = Field Museum of Natural History, Chicago, Illinois, USA  
 IRSNB = Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium  
 KU = University of Kansas, Lawrence, Kansas, USA  
 NJGS = New Jersey Geological Survey, Newark, New Jersey, USA  
 SDSM = South Dakota School of Mines, Rapid City, South Dakota, USA  
 USNM = United States National Museum, Washington, DC, USA  
 AMNH = American Museum of Natural History, New York, USA

### SYSTEMATIC PALAEOLOGY

Order SQUAMATA OPEL, 1811

Family MOSASAURIDAE GERVAIS, 1853

Subfamily PLIOPATECARPINAЕ DOLLO, 1884

Genus PROGNATHODON DOLLO, 1889

Type species *Prognathodon solvayi* DOLLO, 1889

*Prognathodon* - DOLLO, 1889a, p. 181 & 1889b, p. 214;

*Prognathodon* - DOLLO, 1889, p. 293, pl. 9 figs. 4-5, pl. 10 figs. 8-9;

*Brachysaurus* - WILLISTON, 1897a, p. 96, pl. 8 (preoccupied by HALLOWELL, 1856);

*Dollosaurus* - IAKOVLEV, 1901, p. 518;

*Brachysaurana* - STRAND, 1926, p. 54;

*Ancylocentrum* - SCHMIDT, 1927, p. 59.

There is some confusion concerning the correct generic name for this taxon. In two preliminary notes, DOLLO mentioned the acquisition by the museum of *Prognathodon solvayi* (1889a, p. 181) and provided a provisional diagnosis (1889b, p. 214), but in the subsequent description of the fossil (DOLLO, 1889c, p. 293), he replaced *Prognathodon* with *Prognathosaurus* and used this generic name in all of his subsequent papers. *Prognathosaurus* was also the only name used for this taxon by KÜHN (1939, p. 78) in his mosasaur list in the Fossilium Catalogus. The first subsequent use of the name *Prognathodon* was by RUSSELL

(1967, p. 162) where the priority of *Prognathodon* is apparent from his synonymy.

#### Revised generic diagnosis

Premaxilla with no rostrum anterior to premaxillary teeth. Prefrontal forms large portion of postero-lateral border of external nares; supraorbital wing with heavy triangular ala contacts postorbitofrontal posteriorly above orbit medial to external edge of frontal. Frontal not emarginate above orbits; median dorsal ridge present or absent. Parietal foramen small to moderately large; located anteromedially on small prominence on parietal, closely embraced on either side by short tongues from the frontal; or located on frontoparietal suture. Margins of dorsal parietal surface are parallel as far as the point of divergence of the suspensorial rami, forming a rectangular field. Ventral process of postorbitofrontal to jugal indistinctly separated from moderately well exposed dorsal surface of postorbitofrontal. Postero-ventral process on jugal slightly developed to absent. Squamosal wing to parietal large. Deep groove or foramen on floor of basioccipital for basilar artery. Suprastapedial process fused to infrastapedial process on quadrate. Tympanic ala thick. Stapedial pit nearly circular to elliptical in form. Thirteen to fourteen teeth on dentary. Posterior process on dorsal surface of dentary present, incipient or absent. Dentary terminates abruptly in front of first dentary tooth. Seven to eight teeth on pterygoid. Medial wing from coronoid contacts angular. Anterior process on coronoid abuts over surangular and makes contact with posterior process on dentary; or ends flush with surangular without contacting dentary. Retroarticular process rectangular in outline, medially inflected or laterally facing. Marginal teeth stout, bicarinate and smooth or striated. Zygosphenes and zygantara absent, incipient, or large and functional.

*Prognathodon solvayi* DOLLO, 1889

(Pls. 1-5, 6A)

1889a *Prognathodon solvayi* - DOLLO, p. 181 (name only);

1889b *Prognathodon solvayi* - DOLLO, p. 214;

1889c *Prognathosaurus solvayi* - DOLLO, p. 293, pl. IX, fig. 4 & 5, pl. X, fig. 8;

1909 *Prognathosaurus solvayi* DOLLO, 1889 - DOLLO, p. 103;

1939 *Prognathosaurus solvayi* DOLLO 1889 - KÜHN, p. 78;

1967 *Prognathodon solvayi* - RUSSELL, p. 123.

*Holotype*. - IRSNB R33 (4672), an almost complete skull and incomplete postcranial skeleton comprising thoracic, dorsal and caudal vertebrae, ribs, right and left fragments of scapula and coracoid.

*Referred specimens*. - IRSNB R108 (3201), poorly preserved fragmentary cranial and postcranial material.

IRSNB R107 (4565), incomplete skull. These are very fragmentary remains although the surface preservation is considerably better than in R33.

#### Comparative material

KU 950, fragmentary remains of type species of *Prognath-*

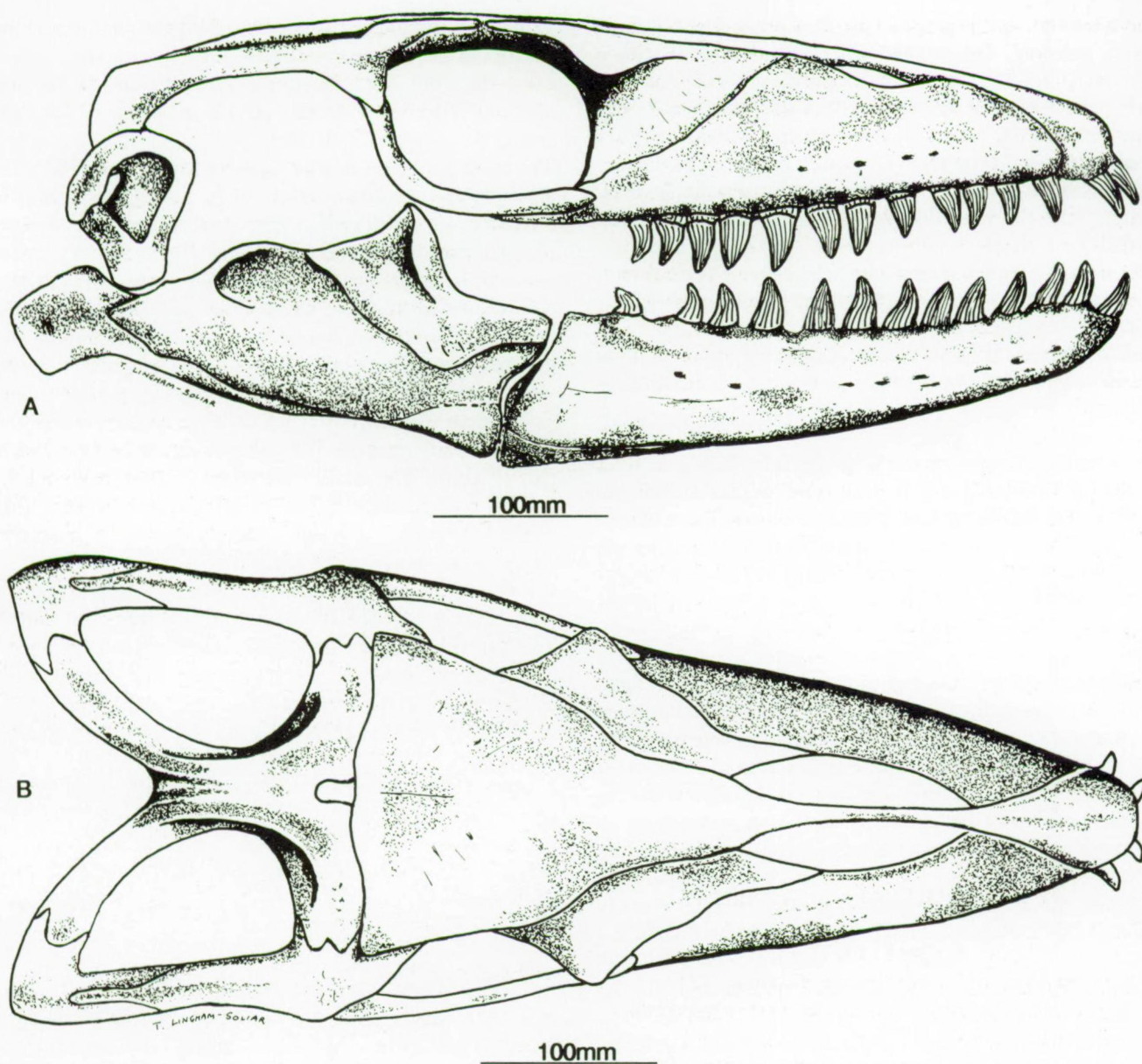


Fig. 6. - Skull and mandibles of *Prognathodon solvayi* (slightly reconstructed after IRSNB R33). A : lateral view; B : dorsal view.

*thodon overtoni* (WILLISTON, 1897).

SDSM 3393, complete, well preserved skull referred to *Prognathodon overtoni* by RUSSELL, 1967.

**Diagnosis.** - Small to medium sized species of *Prognathodon*. Skull broad dorsally, moderately broad laterally. Pre-maxillary teeth highly procumbent, anterior maxillary teeth moderately procumbent; teeth moderately inflated; covered in deep grooves or prismatic. Eight pterygoid teeth; teeth very large with single anterior carinae and bulbous bases. No median ridge on frontal; parietal foramen moderately large; parietal foramen located on fronto-parietal suture with small part on frontal. Fronto-parietal suture almost straight. Deep grooves at juncture of the parietal rami. Coronoid massive with large lateral anterior/posterior wing and large anterior wing medially. Posterior ascending wall of coronoid very deep; coronoid anteriorly does not make

contact with the dentary. Recess on postero-lateral surface of the surangular. Retroarticular process sub-rectangular, laterally compressed, directed laterally. Dentary strongly concave upwards; absence of postero-dorsal process on dentary. Postero-ventral process on jugal absent. Sclerotic ring present. Single foramen on basioccipital for basilar artery. Functional zygosphenes and zygantra on cervical and dorsal vertebrae. Vomers very slender, not fused medially; not fused to palatines posteriorly.

#### DESCRIPTION AND COMPARISONS

##### *Skull*

Although as detailed a description as possible of *Prognathodon giganteus* appears below, the material is very fragmentary and a complete point by point comparison with

the relatively complete skull of *P. solvayi* (IRSNB R33) is not possible. The holotype of *P. overtoni* (KU 950) is also very fragmentary. Consequently, comparisons here will primarily be with the relatively complete skull of *P. overtoni* (SDSM 3393) as described by RUSSELL (1967). Descriptions of the skull of *P. solvayi* are based essentially on the holotype R33. Additional information, however, comes from the more fragmentary material IRSNB R107 and IRSNB R108.

The skull is both broad and deep. The dorsal outline resembles that of *P. overtoni* (SDSM 3393) more closely than does the lateral outline (see Fig. 6 & Pl. 1).

Measurements: length along midline = 600 mm.; width at squamosals = 240 mm.; width across postorbitofrontals = 270 mm.

**Premaxilla.** The premaxilla (Fig. 7) ends bluntly in front of the premaxillary teeth as in all other species of *Prognathodon*. The anterior rostral surface is smoothly continuous with the dorsal surface of the skull. The premaxillary teeth are unique for the genus in their highly procumbent disposition, with only *Prognathodon giganteus* and FMNH PR 165, a specimen referred to *Prognathodon* sp. by RUSSELL (1970), showing some degree of this character. The premaxillary teeth are oriented such that the carinae are laterally and medially directed with the lingual surface approximately a third of the buccal surface. Anterodorsally the shape of the premaxilla is very much as in *P. overtoni* (SDSM 3393), abruptly narrowing posteriorly to a very slender internarial bar (perhaps somewhat accentuated in *P. solvayi*). The external nares are very wide, extending from the third maxillary tooth to about the eight, apparently without the posterior constriction seen in *P. overtoni* (SDSM 3393; RUSSELL, 1967, fig. 89 and our Fig. 6B).

**Maxilla.** The maxilla is ruggedly constructed and is similar to that of *Prognathodon overtoni* (KU 950, SDSM 3393). In lateral view the ventral margin of the maxilla is straight.

A row of foramina extends in a straight line along the maxilla above a horizontal ridge, that presumably represents the gum line. There are 12 teeth on the maxilla although WILLISTON (1898b, pl. 22) indicated 10 for *Prognathodon overtoni* (KU 950).

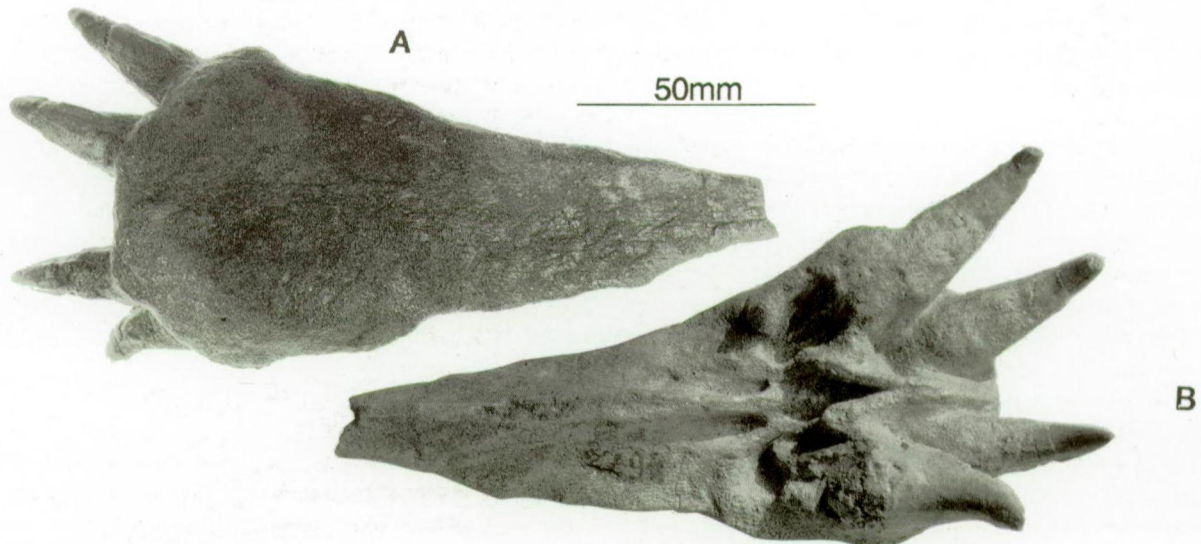
The teeth are large, mostly uniform in size with the most anterior and posterior ones more strongly posteriorly recurved. In addition the first and perhaps the second maxillary teeth are procumbent (see Fig. 6 Pl. 2A). Teeth towards the centre of the tooth row are more vertical when compared with those of the anterior and posterior part of the dental ramus, triangular in lateral configuration and generally more rugged. The tooth crowns possess strong vertical striae, unlike those of *Prognathodon giganteus* and *P. overtoni* (SDSM 3393) which have smooth enamelled surfaces. Judging from WILLISTON's figure of *P. overtoni* (KU 950; 1898b, pl. 22) the tooth crowns may not be entirely smooth but appear to show signs of very fine vertical striations, although examination of the specimen would be necessary to confirm this.

Posteriorly the maxilla tapers abruptly and ends in a sharp point over which the horizontal end of the jugal slides. The last two maxillary teeth, situated on this pointed termination of the maxilla, are very small and stunted. It is conceivable that the corresponding teeth are not preserved in KU 950, perhaps accounting for the low tooth count.

**Lacrymal.** The lacrymal in *P. solvayi* is a V or arrow shaped bone with the point directed anteriorly. It forms the anteroexternal border of the orbit situated medially between the prefrontal and the maxilla. The bone is very well preserved, a condition rarely observed in mosasaurs, (RUSSELL, 1967).

**Frontal.** In dorsal view the frontals of *Prognathodon solvayi* form a very wide, flattened plate giving the skull a broad triangular or heart shaped outline. The lateral mar-

Fig. 7. - Premaxilla of *Prognathodon solvayi* (IRSNB R33). A: dorsal view; B: ventral view.





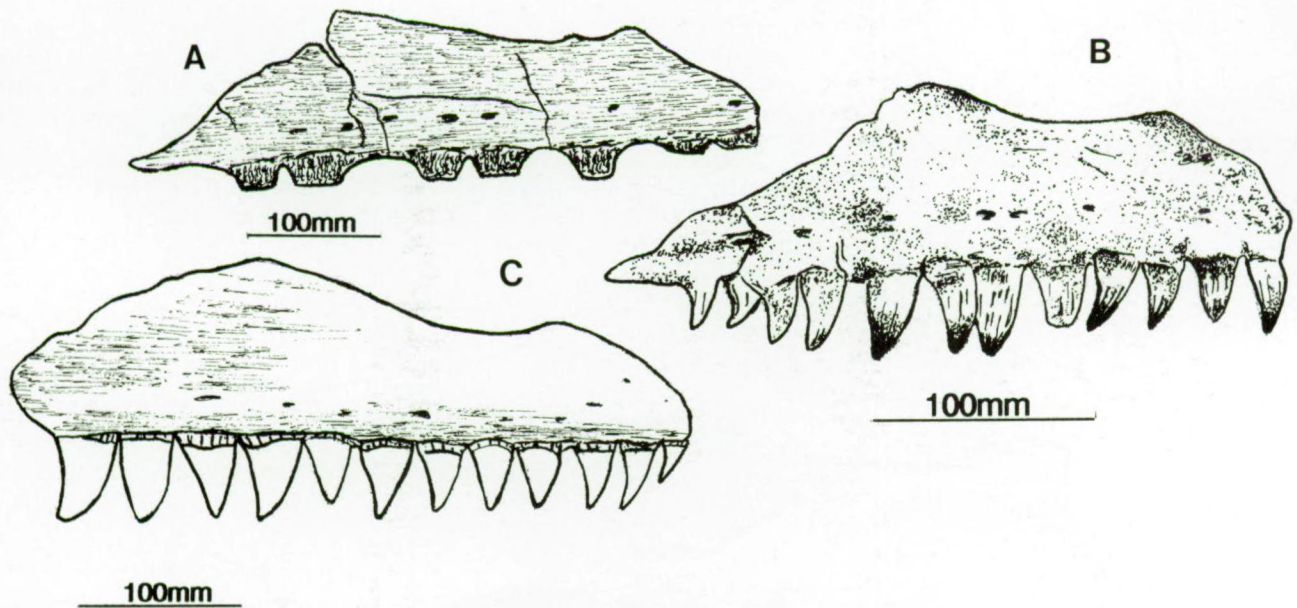
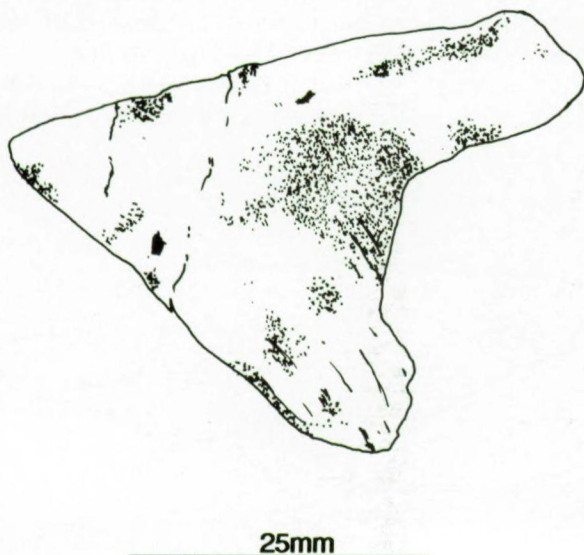


Fig. 8. - Lateral view of right maxilla. A : *Prognathodon overtoni* (KU 950 after WILLISTON, 1898b); B : *P. solvayi* (IRSNB R33); C : *P. overtoni* (SDSM 3393, after RUSSELL, 1967).

gins are moderately convex, only becoming slightly concave towards the anterior border with the prefrontals. RUSSELL (1967) suggested that a median ridge was diagnostic for *Prognathodon* although this is not evident from our material of *Prognathodon solvayi* (see Figs. 6B & Pl. 1B). The fronto-parietal suture is almost straight, a unique condition for the genus.

The general configuration and rugosity of the frontals is very similar to that of *Prognathodon overtoni* (SDSM 3393) but differs in the important condition of the fronto-parietal suture. The posterior border of the frontal in *P. overtoni* (SDSM 3393) sends out two diverging processes or tongues on either side of the parietal foramen (RUSSELL, 1967, fig. 89 & our Pl. 6) forming a U in outline when viewed from the front. A disarticulated posterior fragment

Fig. 9. - Right lacrymal of *Prognathodon solvayi* (IRSNB R33).



of a frontal of *P. overtoni* (KU 950, WILLISTON, 1897a, pl. 8), is too poorly preserved along the fronto-parietal suture to make any reasonable comparison with *P. solvayi*, despite the apparent absence of frontal processes on either side of the parietal foramen. It seems probable though from the above mentioned plate that the frontal processes have been eroded. If this is correct it seems unlikely that the fronto-parietal suture in *P. overtoni* (KU 950) was relatively straight as in *P. solvayi*.

Descending processes of the frontal are little developed representing the general condition seen in mosasaurs. The only mosasaur in which they are known to be well developed is *Goronyosaurus nigeriensis* (AZZAROLI *et al.*, 1972, 1975, SOLIAR, 1988).

GAUTHIER *et al.* (1988) regarded the fairly straight fronto-parietal suture of squamates as ancestral for the group and the roughly W or inverted U shape of lepidosaurs, younginiforms, *Paliguana* BROOM, 1903, kuehneosaurs and rhychocephalians as ancestral for lepidosauromorphs. They noted as well that certain squamates such as mosasaurs (with exceptions) lack straight fronto-parietal sutures (GAUTHIER *et al.*, 1988, p. 47), although they did not analyse the character within the groups. A cladistic analysis of mosasaurs and other squamates will be needed to evaluate the significance of this character.

In mosasaurs a straight fronto-parietal suture is generally associated with a functionally mesokinetic skull occurring in earlier diverging forms, such as *Clidastes* COPE, 1868, *Tylosaurus* MARSH, 1872 and "*Halisaurus*" MARSH, 1869 (IRSNB 4671, LINGHAM-SOLIAR, in prep.). RUSSELL (1964, 1967), however, was among the first to point out that cranial kinesis was gradually reduced in mosasaurs, with complete loss in later forms such as *Mosasaurus* CONYBEARE, 1822. *Plotosaurus* CAMP, 1951 (= *Kolposaurus* CAMP, 1942, preoccupied), *Plesiotylosaurus* CAMP, 1951 and *Prognathodon*.

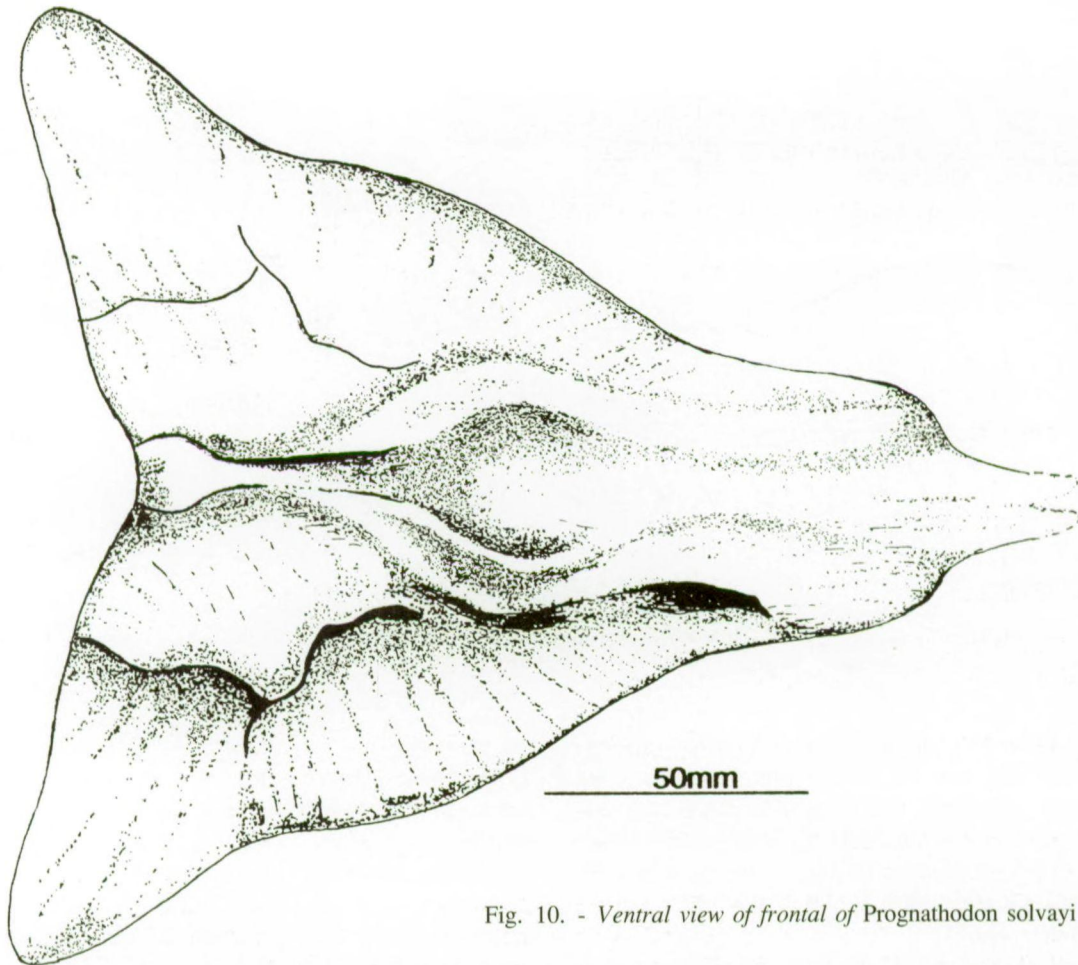


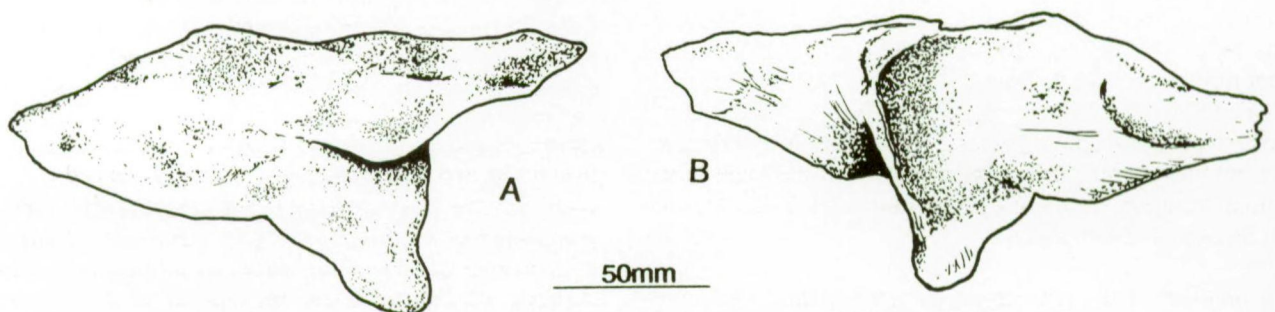
Fig. 10. - Ventral view of frontal of *Prognathodon solvayi* (IRSNB R33).

*Plesiotylosaurus*, *Plotosaurus* (see CAMP, 1942, fig. 13), *Mosasauros* (CAMP, 1942, fig. 13; WILLISTON, 1898, pl. 20) and *Prognathodon overtoni* (SDSM 3393; RUSSELL, fig. 89) all lack straight fronto-parietal sutures, instead they are roughly U shaped when viewed from the front. The notable exception is *Prognathodon solvayi*, in which the relatively straight fronto-parietal suture is interpreted as a reversal within mosasaurs of the plesiomorphic (or ancestral) straight condition of squamates generally. There are notable exceptions in other squamates in which straight fronto-parietal sutures are regarded as a derived character. In the case of amphisbaenians, GAUTHIER *et al.* (1988, p. 47) point out that in the U shaped suture (viewed from behind) previously noted by ESTES and the interdigitated

suture observed by GANS, "... neither of these conditions can be said to be ancestral". In *Platecarpus* COPE, 1869 (belonging to among the earliest mosasaurs) we would interpret the condition of a broad-U shaped suture as more prone to be a convergent character of the genus.

*Prefrontals.* The prefrontal is a fairly extensive bone in *Prognathodon solvayi* and forms a significant portion of the postero-lateral border of the external nares. Laterally a very large ala extends to the anterior margin of the orbits. The contact between the prefrontals and postorbitofrontals (as in *P. overtoni*; RUSSELL, 1967, fig. 90) underlies the frontal, although the frontal actually reaches the orbital margin. Medially the prefrontals are smoothly excavated

Fig. 11. - Right prefrontal of *Prognathodon solvayi* (IRSNB R33). A : lateral view; B : medial view.



forming a deep bowl. At the anterior termination of the bone a further excavation forms the postero-lateral border of the external nares.

The ventro-medial margin of the bone reveals a slight ridge bordering a shallow excavation, which probably marks the sutural contact with the maxilla below. Anterolaterally a further shallow excavation marks the position over which the dorsal border of the maxilla would have fitted.

A large projecting ala on the prefrontal of R33 which although common in marine diapsids is relatively rare in mosasaurs, is also present in *Clidastes* and in aigialosaurs. In contrast to *Prognathodon* though, in both *Aigialosaurus* KRAMBERGER, 1892 and *Opetiosaurus* KORNHUBER, 1901 (see KORNHUBER, 1901) the prefrontals and postorbitofrontals are separated over the orbit, again very similar to the condition seen in *Clidastes*. Contact between the prefrontal and postorbitofrontal occurs in some chamaeleontids, a few scincids, some pygopodids, living species of *Heloderma* WIEGMANN, 1829, a few anguils, some amphisbaenians, and *Lanthanotus* STEINDACHNER, 1878. All other squamates and other lepidisauromorphs in which this character is known lack this contact. (ESTES *et al.*, 1988, p. 43). Given that contact of these bones is rare in other squamates it is likely to be a separate synapomorphy within the Mosasauridae.

**Postorbitofrontal.** The main body of the postorbitofrontal (POF) forms an interdigitated suture with the prefrontal. The frontal and parietal processes are separated from the jugal and squamosal rami, ventrally by a narrow crest of bone. The long process of the POF reaches the end of the supratemporal fenestra above the squamosal, and with the process from the squamosal forms the boundary of the supratemporal fenestra.

**Jugal.** The jugal in *Prognathodon solvayi* is a lightly built, slender bone. Anteriorly it is somewhat laterally flattened and sits on a small shallow depression on the posterior pointed termination of the maxilla, just above the horizontal ridge (gum line) above the tooth row. Posteriorly the horizontal arm curves gently upward at an angle of approximately 75° from the horizontal, terminating at the postorbitofrontal. There is no evidence of a posteroventral process on the jugal.

In these last two points the jugal of *P. solvayi* contrasts strongly with that of *P. overtoni* (SDSM 3393; RUSSELL, 1967, fig. 90) in which the vertical arm rises abruptly at right angles to the horizontal axis. In the latter species also a slightly rounded postero-ventral process of the jugal is present. It nevertheless seems evident that in both species the jugal was probably loosely applied to the maxilla and that movement was probably quite extensive. "*Prognathodon*" (FMNH PR 165; RUSSELL, 1970, fig. 168) has the largest postero-ventral process seen in the Mosasauridae, resembling in this respect the condition of the jugal in the plioplatecarpine mosasaur *Selmasaurus russelli* (WRIGHT & SHANNON, 1988, fig. 4).

**Squamosal.** The squamosal of *Prognathodon solvayi*

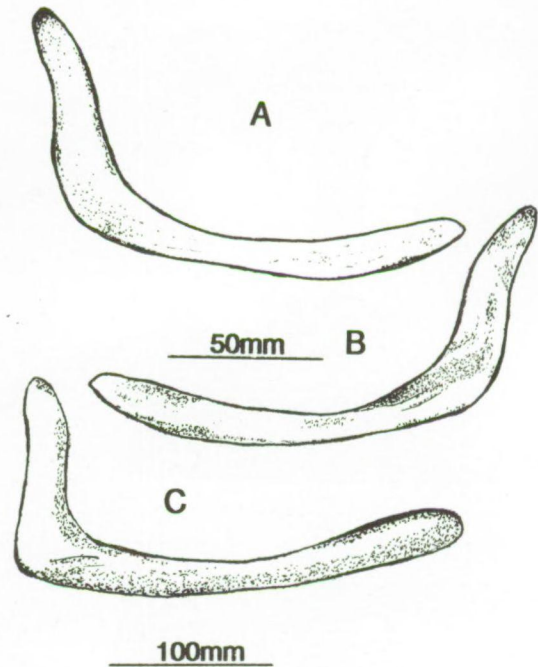


Fig. 12. - Jugal of *Prognathodon solvayi* (IRSNB R33). A & B : lateral and medial views resp.; C : lateral view of jugal of *P. overtoni* (SDSM 3393) after RUSSELL (1967).

(IRSNB R33) is strongly abraded but the signs are that the facet for articulation with the head of the quadrate was fairly strong. IRSNB R108 is better preserved and shows this condition more clearly. The whole bone is more strongly arched laterally than in IRSNB R33.

The supratemporal arcade of IRSNB R33 appears to be slightly bowed dorsally as in *Platecarpus* (see RUSSELL, 1967) and somewhat similar to SDSM 3393 although RUSSELL (1967) described it as straight.

**Palatine.** The palatine and vomer bones are rarely found intact in mosasaur skulls but fortunately are well preserved in *Prognathodon solvayi*. In *Varanus* MERREM, 1820, BAHL (1937) described the palatine as an H shaped bone. RUSSELL (1967) described it in mosasaurs as hexagonal. Neither of these descriptions fits the palatine of *P. solvayi*, which can best be described as an X shaped bone with the base of the X flattened and abutting onto the medial wall of the maxilla. On the anterodorsal surface there are traces of the sutural contact with the maxilla. The postero-lateral projection forms a sutural contact with the anterior part of the pterygoid and a slender anteromedial projection forms part of the medial boundary of the internal nares. Postero-medially the tip of the X curves round to complete the sutural contact with the pterygoid, the whole contact between the two elements being almost V shaped.

Although the V-shaped contact in eublepharid geckos is interpreted as a derived condition (GRISMER, 1988), poor documentation of palatine bones in mosasaurs at present makes it difficult to assess the polarity of this character.

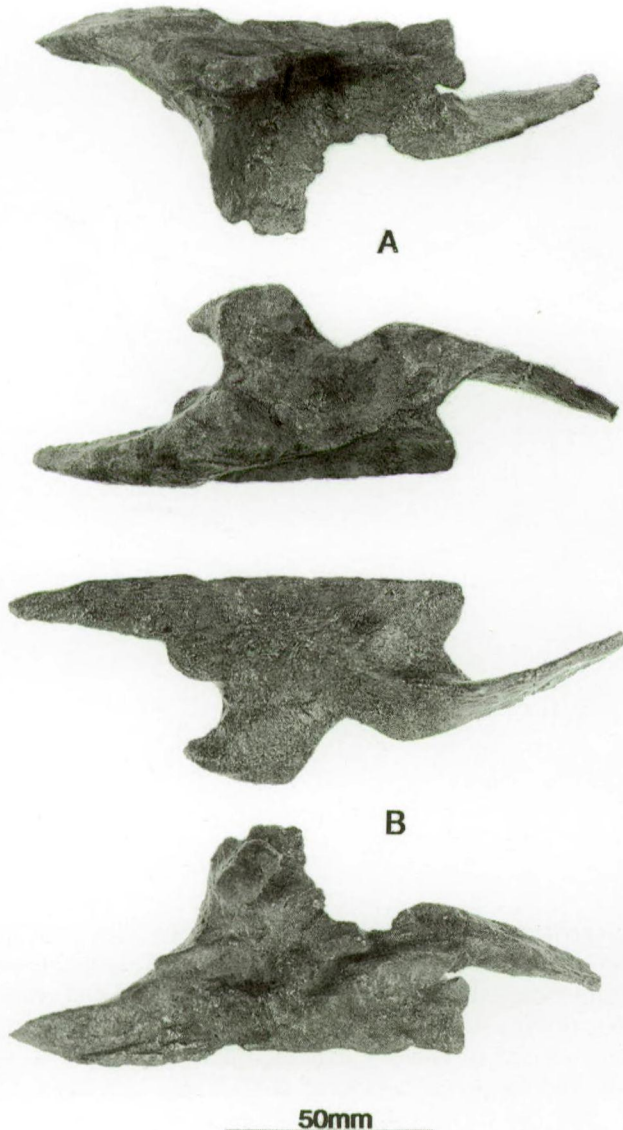


Fig. 13. - Palatine of *Prognathodon solvayi* (IRSNB R33). A : dorsal view of right and left palatines; B : ventral view of right and left palatines.

**Vomers.** The vomers are slender structures forming very narrow points of contact with the anterior medial processes of the palatines. The vomers flatten and broaden somewhat before making contact with the antero-medial wall of the maxilla, thereby completing the fenestra for the internal nares. In *Prognathodon solvayi* the vomers are separate bones and no signs of sutural contact medially are evident. Posteriorly the vomers are not fused to the palatines. Ante-

Fig. 14. - Vomers of *Prognathodon solvayi* (IRSNB R33).



riorly they terminate in slender points that presumably fitted into the narrow excavations on the ventral surface of the premaxilla (see Fig. 7). This particular condition has not been noted before in mosasaurs and may be a consequence of the very slender nature of the vomers.

On the ventral surface of the vomers traces of vertical striae probably mark sutural contact with the nasals, although the latter are not preserved.

A shallow excavation on the antero-ventral surface represents the aperture for Jacobson's Organ. This correlates with RUSSELL's description in mosasaurs (1967, pp. 25-26) in which the aperture for Jacobson's Organ lies between the maxilla and a shallow groove in the side of the vomer, a condition similar to that seen in *Varanus* (see BAHL, 1937).

The position of the groove in *P. solvayi* is near the second maxillary tooth as in *Platecarpus* (see RUSSELL, 1967) although in *Tylosaurus* (see RUSSELL, 1967) it is set further back at about the fourth maxillary tooth.

The vomers of *Prognathodon solvayi* show considerable similarity to those of *Varanus* (see BAHL, 1937) especially in general shape, slenderness and in the anterior pointed termination. In *Platecarpus* (RUSSELL, 1967, fig. 84) the vomers are generally broader and there are probably no more than incipient points anteriorly. In *Tylosaurus* and in certain *Mosasaurus* sp., however, the vomers are slender with long narrow points anteriorly that presumably fitted into ventral excavations on the premaxilla as in *P. solvayi*. It is difficult to discuss the condition of narrow vomers of *Prognathodon solvayi* and of certain other mosasaurs in terms of primitive or derived states. In *Scleroglossa* (see ESTES *et al.*, 1988, p. 151) a wide vomer is regarded as a synapomorphy with reversal in booid and colubrid snakes. A relatively small vomer is present in all non squamate lepidosauromorphs in which it can be determined, except in Younginiformes, in which the vomers are long and thin. The broad skull of mosasaurs such as *Platecarpus* may account for correspondingly broad vomers but the presence of narrow vomers in so broad a skull as that of *P. solvayi* seems anomalous.

Because of the presence of fused vomers in chamaeleontids, pygopodids, and xantusiids as well as in some gekkonids, gymnophthalmids and scincids, the presence of unfused vomers in non squamate lepidosauromorphs led ESTES *et al.* (1988, p. 151) to interpret the unfused state as primitive for squamates. In *P. solvayi* the unfused condition of the vomers with the palatines is unusual in mosasaurs but consistent with the level of development seen in primitive squamates.

**Parietal.** The parietal table is broad with a powerfully constructed temporal arcade. Poor preservation in this part of *Prognathodon solvayi* (IRSNB R33), coupled with apparently a degree of surface abrasion [judging from the somewhat better surface preservation of *P. solvayi* (IRSNB R107, Pl. 2, Fig. B)], makes an assessment of finer details as well as of the true stoutness of the bones difficult to determine. Despite such problems the supratemporal processes are clearly quite robust.

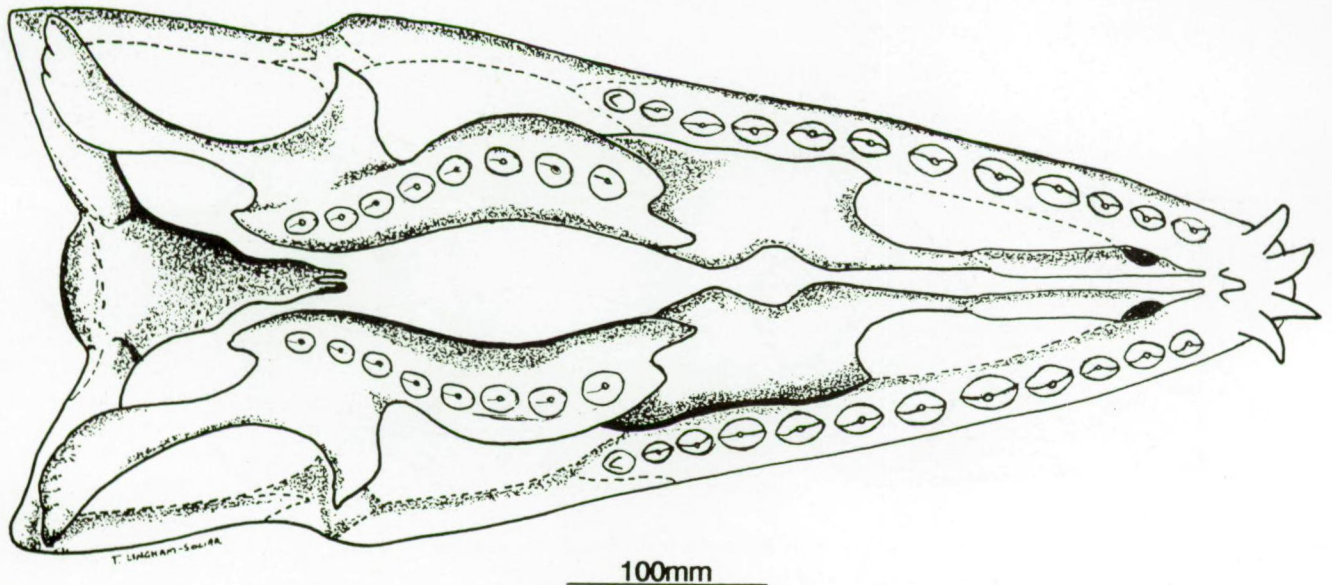


Fig. 15. - Ventral view of the skull of *Prognathodon solvayi* (reconstructed after IRSNB R33).

The supratemporal fenestrae are both long and broad and are very similar to those of *Prognathodon overtoni*. At the juncture of the diverging supratemporal processes of *P. solvayi* the surface is deeply notched a condition not evident in *P. overtoni* (SDSM 3393).

From a point approximately halfway along the length of the element the parietal bifurcates posteriorly, the parietal rami curving towards the quadrate. The rami are broad and externally convex providing strong rugose surfaces for the attachment of the median epaxial musculature. At the anterior end of the parietal, as already mentioned, the fronto-parietal suture is fairly straight although the abraded surfaces and presumably tight sutural contact between the two bones makes the observation of this line very difficult to determine dorsally. It is clearer, however, on the ventral surface which corroborates the above description.

The parietal foramen in *Prognathodon solvayi* is moderately large and situated on the boundary of the parietal and frontal with a small portion of the foramen lying within the frontal.

The size of the parietal foramen and its position on the fronto-parietal suture in *Prognathodon solvayi* contrasts with that seen in *P. overtoni* (SDSM 3393, RUSSELL, 1967, fig. 89) in which it is somewhat smaller and situated within the parietal a little distance away from the fronto-parietal suture. It is, however, difficult to assess the polarity of this character because of extensive homoplasy in both primitive and derived forms of mosasaurs. In squamates in general ESTES *et al.* (1988) regarded the posterior location of the parietal foramen, within the parietal as primitive, although in outgroup comparisons, ETHERIDGE & DE QUEIROZ (1988) suggested that in iguanids, for instance, the primitive location of the parietal foramen is on the fronto-parietal suture and that derived conditions have evolved independently by anterior and posterior displacements of the foramen. The explanation we favour for the character distribution within Mosasauridae is that locations of the parietal foramen on

the fronto-parietal suture is a synapomorphy for mosasaurs with reversal of the character in some forms. The posterior location of the parietal foramen in primitive forms of mosasaurs such as *Clidastes sternbergi* (see WIMAN, 1920) may be plesiomorphic. If RUSSELL's posterior location of the parietal foramen in *P. overtoni* (SDSM 3393) is correct then this may be interpreted as a character reversal. At the moment the polarity of this character is unresolved in mosasaurs and a cladistic analysis is necessary before an attempt can be made to assess it with any degree of confidence.

The general architecture and rugosity of the bones of the temporal arcade indicate a powerful adductor mandibulae musculature. The deep posterior ascending wall of the coronoid in *Prognathodon*, in particular in *Prognathodon solvayi* (see Fig. 24), indicates an exceedingly extensive insertion for the M. adductor mandibulae with presumably a correspondingly broad origin on the stout squamosal elements.

The presence of deep longitudinal notches on the postero-dorsal surface of the parietal at the juncture of the bifurcation of parietal rami (see Fig. 6B & Pl. 1B) is perplexing. Such deep grooves are not commonly seen in mosasaurs in general but appear to be also present in *Mosasaurus missouriensis* (= *M. horridus*, cf. WILLISTON, 1898b, pl. 20) and in a specimen of *Platecarpus coryphaeus* described by MERRIAM (1894, pl. 1). However, it is most conspicuous in the mosasaur *Globidens dakotaensis* in which RUSSELL (1975, p. 245) describes the parietal as "deeply notched posteriorly".

Why it is noticeable in some species and not others is not clear. It is conceivable that the deeply ridged surface provided a particularly strong insertion point for tendons of a powerful median epaxial musculature which may have been better developed in some mosasaurs than others. In *P. solvayi* it would be consistent with the generally powerful development of the skull and associated musculature

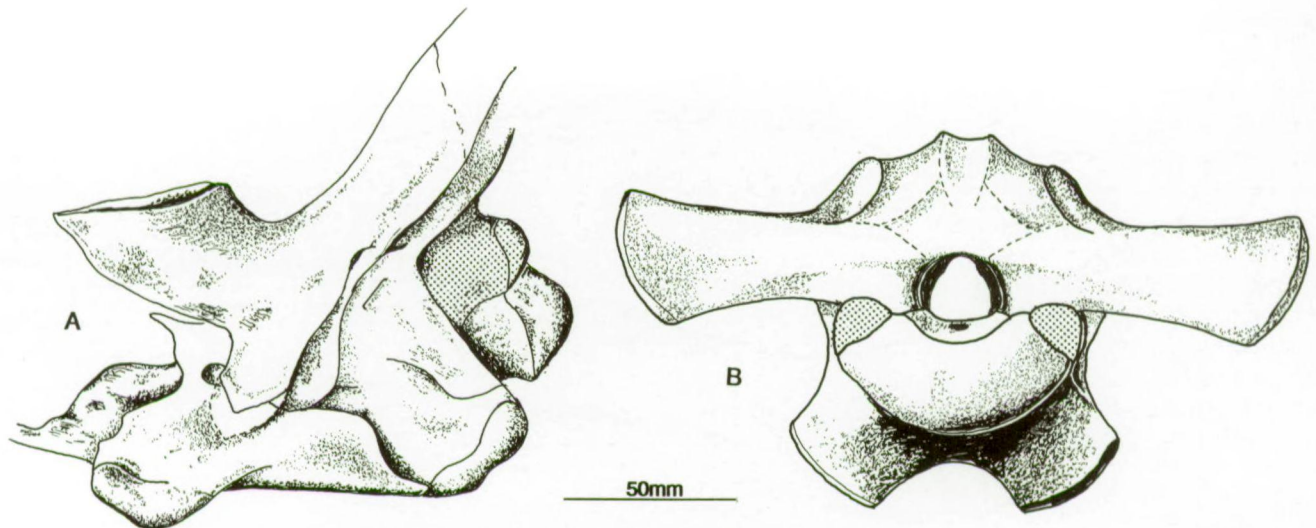


Fig. 16. - Braincase of *Prognathodon solvayi* (IRSNB R33). A : lateral view; B : posterior view.

and may be connected with a strong dentition useful for seizing and gripping tough prey. The presence of very deep notches at the juncture of the supratemporal processes in the parietal of the powerful skull of *Globidens dakotaensis* (see RUSSELL, 1975, p. 245) may support such an hypothesis.

**Basioccipital unit.** It is unfortunate that there is no adequate literature available on the basioccipital unit of *Prognathodon* despite the existence, according to RUSSELL (1967, p. 165), of "a beautifully preserved skull" of *Prognathodon overtoni* in the South Dakota School of Mines. On the other hand the basioccipital unit of *Prognathodon solvayi* is poorly preserved with considerable surface abrasion, as well as being disarticulated in parts, making an assessment of detailed structure especially difficult. Nevertheless several characters are observable.

**Basisphenoid.** The basisphenoid in mosasaurs forms a substantial portion of the floor of the braincase. Owing to poor preservation the basisphenoid and parasphenoid are separated from the basioccipital along the sutural joins. Sutural contacts with the basioccipital posteriorly and the prootic dorsally are also not preserved.

Anteriorly the basiptyergoid process extends ventro-laterally terminating distally in a fairly swollen basal tuber. Antero-medially the dorsum sellae ends in a sharp laterally compressed rostrum. Unfortunately owing to poor preservation it is not possible to comment upon the presence of foramina for the internal basilar and internal carotid arteries or that of the abducens nerve. The vidian canal, along which the external carotid artery and facial nerve extended, is located on the antero-lateral wall of the basisphenoid. In the Mosasauridae, the canal was enclosed by a thin lateral wall of the basisphenoid, which RUSSELL (1967) indicated may be incompletely developed in *Mosasaurus*. Presumably owing to the delicate nature of the lateral wall it is rarely preserved in mosasaurs. In *Prognathodon solvayi* the enclosing wall of the carotid artery is no more than a thin bridge. Whether this results from poor preserva-

tion or represents incomplete development is difficult to determine. The presence of an enclosing wall for the carotid and facial nerve also occurs in *Varanus* (see MERTENS, 1942) although the primitive state in non-squamate diapsids is for the external carotid and facial nerve to lie in an open channel (see ESTES *et al.*, 1988, pp. 153-154). Incomplete development of the enclosing wall of the external carotid and facial nerve in *Mosasaurus* and *P. solvayi* might be interpreted as a character reversal in mosasaurs presuming that the reduction of the wall is not the result of damage.

**Opisthotic-exoccipital.** A segment of the opisthotic is missing revealing a flat, slightly striated sutural contact that was probably cartilaginous in life (see RUSSELL, 1967, fig. 9). In lepidosauromorphs ancestrally the exoccipital fuses to the opisthotic relatively late in development (GAUTHIER *et al.*, 1988, p. 52). In mosasaurs compared to other squamates, however, the fused and unfused state of the exoccipitals and opisthotics varies in different forms although there appears to be no information available on the state in juvenile mosasaurs.

**Prootic.** The prootic is characteristically a triradiate bone in mosasaurs. The anterior ascending arm, the stoutest bone of the element, meets the antero-ventral surface of the parietal along a broad, well preserved, apparently tight horizontal suture. The descending ramus to the dorso-lateral edge of the basisphenoid is very short and appears to have the distal cartilaginous cap absent. The otosphenoidal crest lies just anterior to cranial nerve VII. Ventrally a thick ala overhangs the vidian canal. In *Clidastes* this ala is very thin (see RUSSELL, 1967, p. 34). At the juncture of the ascending and descending rami of the prootic, the exit for cranial nerve V is enclosed in a V shaped incisure. The longest of the three rami of the prootic ascends posteriorly at an angle of approximately 45°. The distal termination is at right angles with the long axis of the skull and in life would have made sutural contact with the supra-temporal bone, which is not preserved in *P. solvayi*.

The cranial foramina on the opisthotic are very poorly preserved, and consequently it is not clear whether a deep medial foramen represents the internal auditory meatus (IAM) or the exit for cranial nerve IX. The interpretation here is that this is the IAM and that a small depression just below it may represent the exit for cranial nerve IX. Because the posterior elements of the opisthotic are absent and the underlying basioccipital is poorly preserved, it is unfortunately not possible to tell whether conjoined cranial nerves X and XI and cranial nerve XII emerged from two separate exits as in *Clidastes* (see RUSSELL, 1967) and *Mosasaurus* or whether they emerged from a single exit as in *Plioplatecarpus* DOLLO, 1882 (DEVILLERS, 1943, RUSSELL, 1967) and *Platecarpus* COPE, 1869 (RUSSELL, 1967).

**Basioccipital.** The ventrolaterally directed basal tuber of the basioccipital is very large in proportion to the rest of the occipital unit and relative to that of other mosasaurs, except perhaps that of *Mosasaurus*. The occipital condyle on the other hand is moderately large. In *Prognathodon solvayi*, just anterior to the occipital condyle, a deep depression indicates the existence of a single foramen that presumably penetrated the medullary cavity, and through which the basilar artery is believed to have entered the basioccipital. Poor preservation ventrally makes it difficult to determine presence or absence of a ventral exit for the foramen.

RUSSELL (1967, p. 30) indicated that unlike in *Platecarpus*, no foramen exists on the floor of the medullary cavity (for the basilar artery) in *Prognathodon*, but that instead the floor seems to have been deeply grooved. Subsequently,

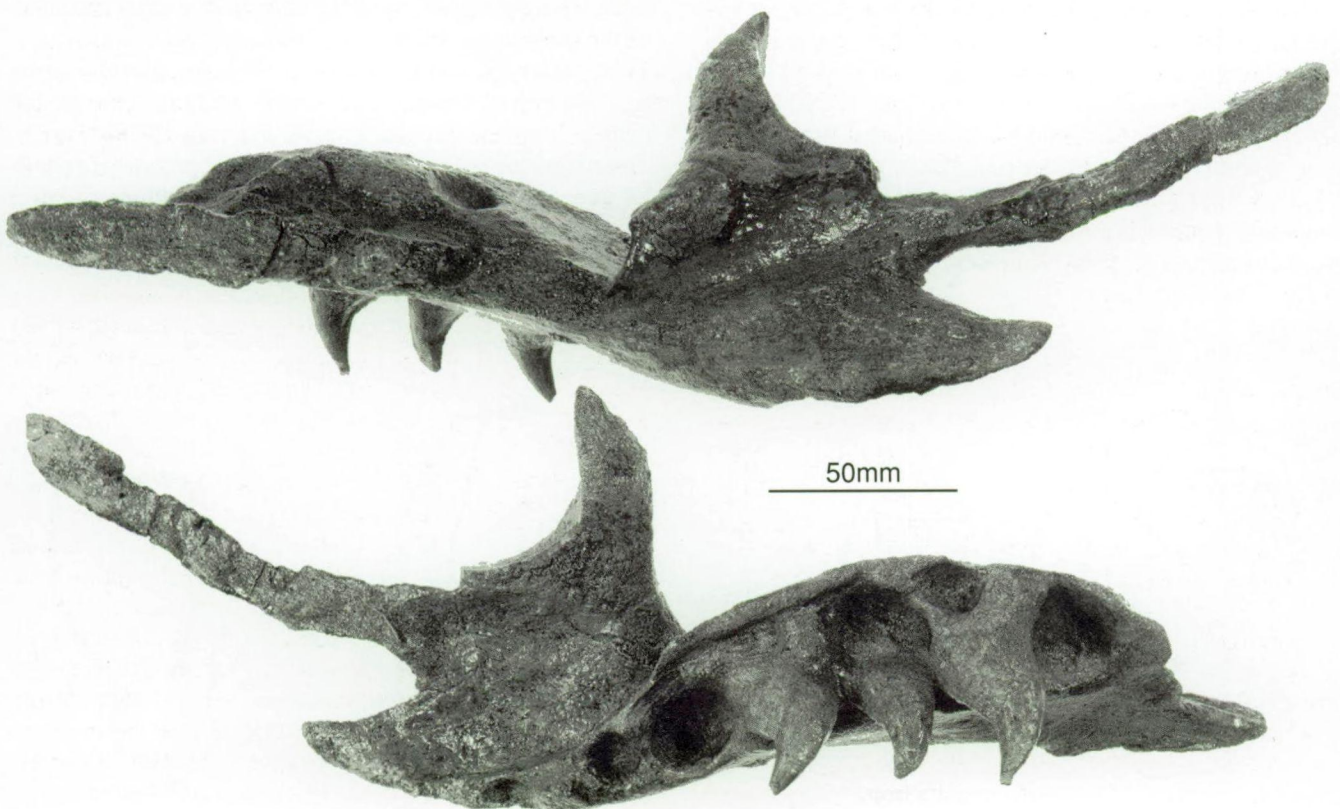
however, he noted the presence of a foramen in FMNH PR 165, questionably referred to *Prognathodon* sp. (RUSSELL, 1970, p. 373).

The presence of foramina for the basilar artery has so far been observed in *Platecarpus*, *Plioplatecarpus*, *Ectenosaurus* RUSSELL 1967, *Selmasaurus russelli*, *Prognathodon solvayi* and "*Prognathodon*" PR165 (all members of the subfamily Plioplatecarpinae) and the African genus *Angolasaurus bocagei* ANTUNES, 1964. The latter genus is generally placed in the Mosasaurinae (see ANTUNES, 1964) but it is almost certainly plioplatecarpine (LINGHAM-SOLIAR, in press). The description of the foramina is, however, quite variable. RUSSELL (1967, p. 149) in his diagnosis for *Platecarpus* stated that the canal for the basilar artery enters the basioccipital and basisphenoid by a large bilobate foramen but does not exit ventrally on the basioccipital. He described a similar bilobate foramen in "*Prognathodon*" (FMNH PR 165). In *Plioplatecarpus marshi*, however, it enters by a large foramen and leaves the basioccipital ventrally also by a large single foramen (DOLLO, 1885b). In contrast the basilar artery of *Plioplatecarpus houzeaui* (DOLLO, 1889) enters by a single foramen and leaves by two smaller foramina.

It is curious that foramina for the basilar artery are found in some members of the genus *Prognathodon* and not in others. A reasonable explanation is that the presence of a canal for the basilar artery represents a synapomorphy for the Plioplatecarpinae with a reversal of the character state in *Prognathodon overtoni* (SDSM 3393). The condition is not known in KU 950, the basioccipital being absent.

DOLLO (1885b) first described the presence of a canal for

Fig. 17. - Right pterygoid of *Prognathodon solvayi* (IRSNB R33). A : lateral view; B : ventral view.



the basilar artery in the basioccipital of *Plioplatecarpus marshi* and correctly identified its association with the basilar artery. He subsequently (1904, p. 211) suggested that, as with the ossified tympanic membrane, the character was "... une adaptation pour plonger à une distance énorme de la surface de l'océan, puisqu'on retrouve une circulation céphalique du même ordre chez les Cétacés." This, however was correctly questioned by DEVILLERS (1943, pp. 14-15) when he indicated the improbability of such a function by pointing out the existence of canals for the basilar artery in non-diving crocodiles and turtles. He also called attention to DOLLO's dubious comparison with cetaceans... "la circulation céphalique était certainement moins bien protégée que chez les Chéloniens et les Crocodiliens et surtout que chez les Cétacés."

**Pterygoid.** The pterygoid is a particularly stout bone in *Prognathodon solvayi* with a broad tooth bearing segment extending over half the overall length of the bone. There are eight pterygoid teeth (represented by three teeth and five tooth bases) although RUSSELL (1967) mentions only seven teeth in his diagnosis for *Prognathodon*. They decrease in size posteriorly, with the first four teeth being particularly large. The teeth have bulbous bases, posteriorly recurved tips and are symmetrical with a single posterior carina.

The extraordinary size of the pterygoid teeth of *P. overtoni* (KU 950) was first noted by WILLISTON (1898b, p. 192), "... the teeth are very large, thus agreeing with the most striking character of the genus *Prognathosaurus*."

The base of the ectopterygoid process is fairly wide, the distal end curving slightly posteriorly. The basisphenoid process arises from a narrow base and despite poor preservation appears to be slender along its entire length with perhaps a fairly narrow wing at the posterior termination. From observations by the senior author of photographs of the pterygoid of *Prognathodon overtoni* (SDSM 3393, DAVID BURNAM pers. comm.) it is clear that the basisphenoid is quite robust in this species. Anteriorly the pterygoid in *P. solvayi* terminates in a V or possibly W shaped boundary that in life formed a sutural contact with the posterior part of the palatine process. On the dorsal surface

a small excavation on the left pterygoid may mark the point of insertion of the epipterygoid bone.

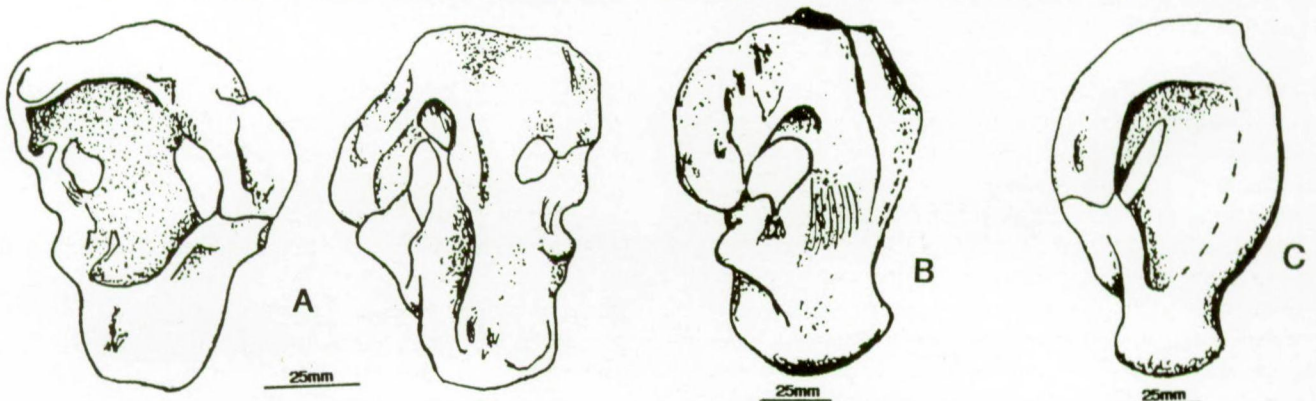
Although all members of the Mosasauridae except *Globidens dakotaensis* RUSSELL, 1975 possess functional pterygoid teeth their relative sizes vary in the different taxa and may upon further study provide useful information on this condition. If one looks at the variation in the presence or absence of palatal teeth among squamates (ESTES *et al.*, 1988), the uniformity of presence in mosasaurs suggests it is a synapomorphy of the group. The loss of functional pterygoid teeth in *G. dakotaensis*, however, is unique in mosasaurs and appears to have arisen as a consequence of its highly specialized form of feeding and as such is interpreted as a character reversal.

**Quadrate.** The quadrate in *Prognathodon solvayi* can best be described as sub-ovoid in lateral view, broad dorsally and narrowing ventrally towards the articular condyle. The suprastapedial and infrastapedial processes are broadly fused near the vertical mid-line of the bone. In lateral aspect the fused processes form a sheer posterior wall for the tympanic ala, in contrast to what appears to be a gently sloping recess in *P. rapax* (NJGS 9827) but is generally similar in this respect to SDSM 3393. A medial view of *P. overtoni* KU 950 (WILLISTON, 1897a), however, reveals a much narrower point of union with the suprastapedial and infrastapedial processes. Unfortunately both this specimen and that of SDSM 3393 are very poorly described in the literature and preclude much further comparison in this respect.

The quadratic condyle is fairly broad laterally in *P. solvayi* but much narrower in SDSM 3393 and *P. rapax*. In *P. overtoni* (KU 950) it appears to be broader laterally and more strongly convex ventrally than in any other members of the genus (see WILLISTON, 1897a, pl. 8).

The anterior surface of the quadrate is broad dorsally tapering somewhat towards the ventral margin. The medial margin is fairly straight as in *P. overtoni* (SDSM 3393). Posteriorly the sides of the suprastapedial process are parallel and somewhat dilated distally. A longitudinal, almost rectangular depression (RUSSELL, 1967) probably marks the point of origin of part of the fibres of the M. depressor

Fig. 18. - Quadrates. A : lateral and medial views of quadrates of *Prognathodon solvayi* (IRSNB R33); B : medial view of quadrate of *P. overtoni* (KU 950, after WILLISTON 1897a); C : lateral view of quadrate of *P. overtoni* (SDSM 3393, after RUSSELL, 1967).





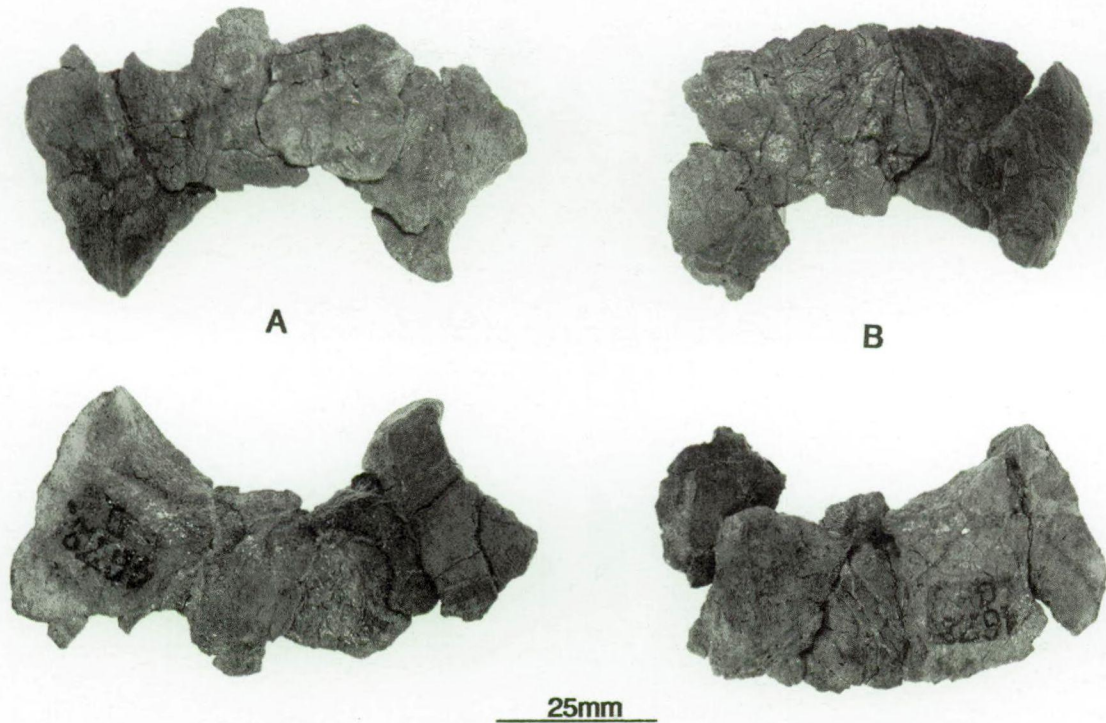


Fig. 19. - Sclerotic ring of *Prognathodon solvayi* (IRSNB R33). A : right lateral and medial views; B : left lateral and medial views.

mandibulae (Fig. 18 & DOLLO, 1889c, pl. 9).

The stapedial pit is ovoid in outline with the broad end uppermost, situated just above the stapedial notch and adjacent to the anterior medial margin.

On the other hand RUSSELL (1967) diagnosed a circular stapedial pit for *Prognathodon*. In life the stapedial pit would have received the processus internus, first described in mosasaurs by DOLLO (1888, pp. 7-8) in the Belgian taxon *Plioplatecarpus marshi*, in which it is preserved in a remarkably intact state. Medially just above the infrastapedial process a slight tuberosity contrasts with the shallow vertical sulcus described in *Prognathodon* by RUSSELL (1967).

A large tuberosity present on the dorso-medial surface of the quadrate is somewhat similar to that found in *P. rapax*. Judging from the deep groove on the opposing squamosal bone (particularly well preserved in *P. solvayi*, IRSNB R108, Pl. 4) it is conceivable that this helped provide a tighter contact between the two elements. The capping of the quadrate by the squamosals in mosasaurs is more consistent with the ancestral diapsid condition (see GAUTHIER *et al.*, 1988), e.g. with that of younginiforms (CARROLL, 1977) and *Paliuana* (CARROLL, 1988) than that of squamates (see ESTES *et al.*, 1988) in which as ROBINSON (1967) pointed out, the quadrate process of the squamosal is reduced to a peg that abuts onto the head of the quadrate along a fenestra or fossa. In *P. solvayi*, however, the deeply grooved squamosal bone and the tuberos counterpart on the quadrate may have in effect had the same functional significance as the peg and fossa in other squamates.

The functional significance of a joint between the head of the quadrate and the squamosal was explicitly demonstrated by SMITH (1980) in *Varanus exanthematicus*. She

showed that the presence of such a joint allowed the pterygoideus muscle to exert maximum force when the jaw was closed. It is suggested here that a somewhat similar quadrato-squamosal joint may have been present in *Prognathodon solvayi* and presumably helped to produce an enhanced force with the jaws in occlusion, similar to that described by SMITH (1980). Such force would be consistent with the rest of the powerfully constructed temporal arcade. In general a powerful quadrato-squamosal joint may reflect an advanced condition of *Prognathodon* and may have arisen more than once in other durophagous mosasaurs such as in the Globidentini. This, however, can only be resolved in a cladistic analysis.

The vertical forces that were probably generated on the quadrate in powerful skulls of durophagous mosasaurs may also account for the broad points of fusion of the suprastapedial and infrastapedial processes and overall robust construction of the element in such forms, exemplified by *Globidens dakotaensis*.

**Sclerotic ring.** The sclerotic ring in *P. solvayi* is preserved only in part, consisting of five scleral ossicles in each ring. The function of the scleral ossicles is to maintain the shape of the cornea and support the sclera in the region of Brucke's muscle responsible for affecting accommodation in the lacertilian eye (RUSSELL, 1967, p. 58).

Unfortunately owing to the presence of only five scleral ossicles in each eye it is not possible to establish the patterns of overlap. Imbrication of the individual ossicle has been found to be diagnostically significant in for example sceloporine iguanids with a large number of iguanids exhibiting "... an ossicle arrangement in which there are 14 ossicles of approximately equal size..." (DE QUEIROZ,

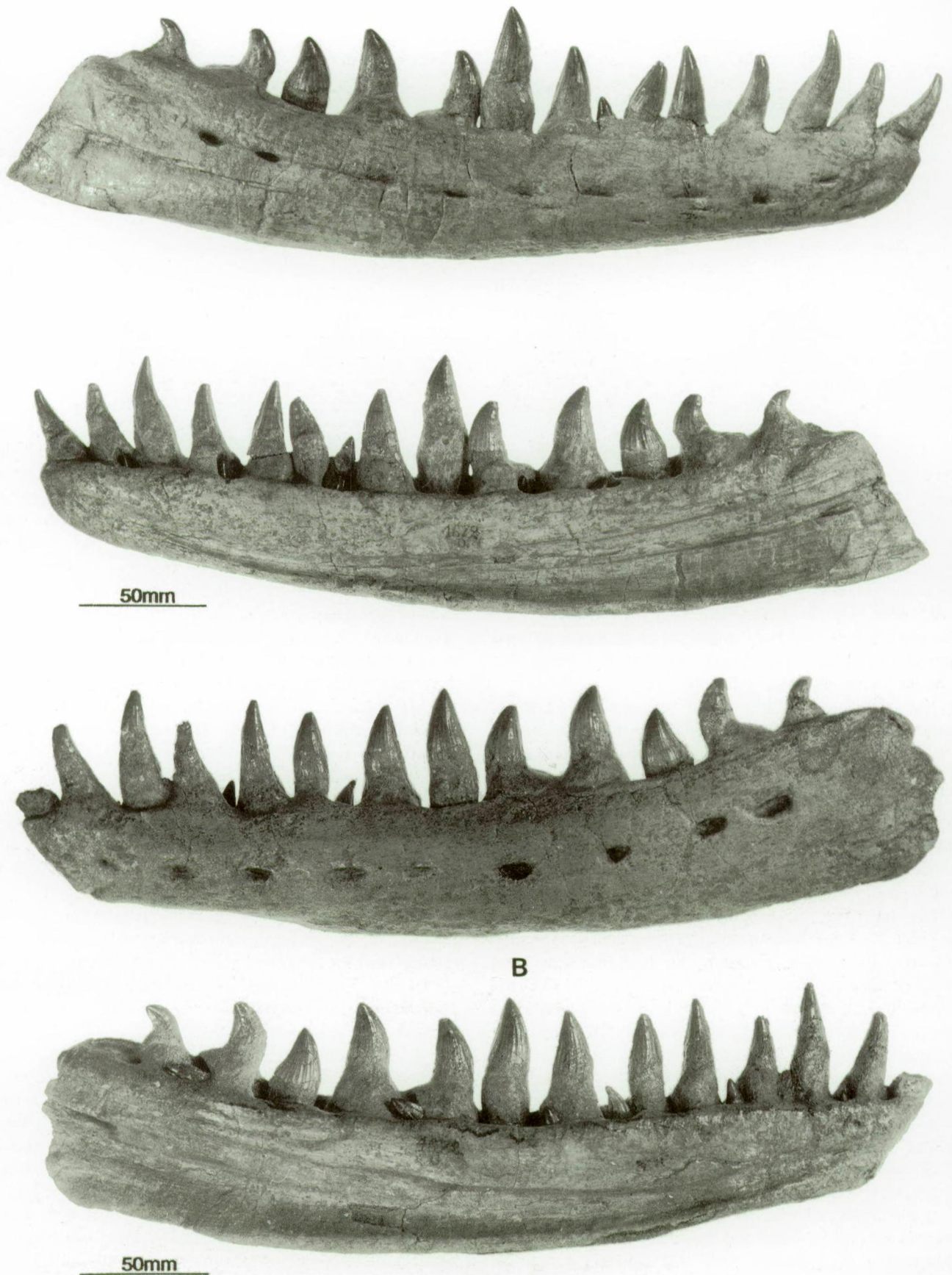


Fig. 20. - Lateral and medial views of dentary of *Prognathodon solvayi* (IRSNB R33). A : right dentary; B : left dentary.

1982, p. 302) and with different degrees of reduction and losses. In a beautifully preserved sclerotic ring of *Mosasaurus hoffmanni* (private collection of R. Garcet), PLISNIER-LADAME & COUPATEZ (1969) worked out the complex series of imbrications in this specimen and concluded, "Le mode d'imbrication des différentes plaques, notamment, nous paraît de première importance, car il constitue un élément essentiel dans l'identification de pièces fossiles." (p. 263).

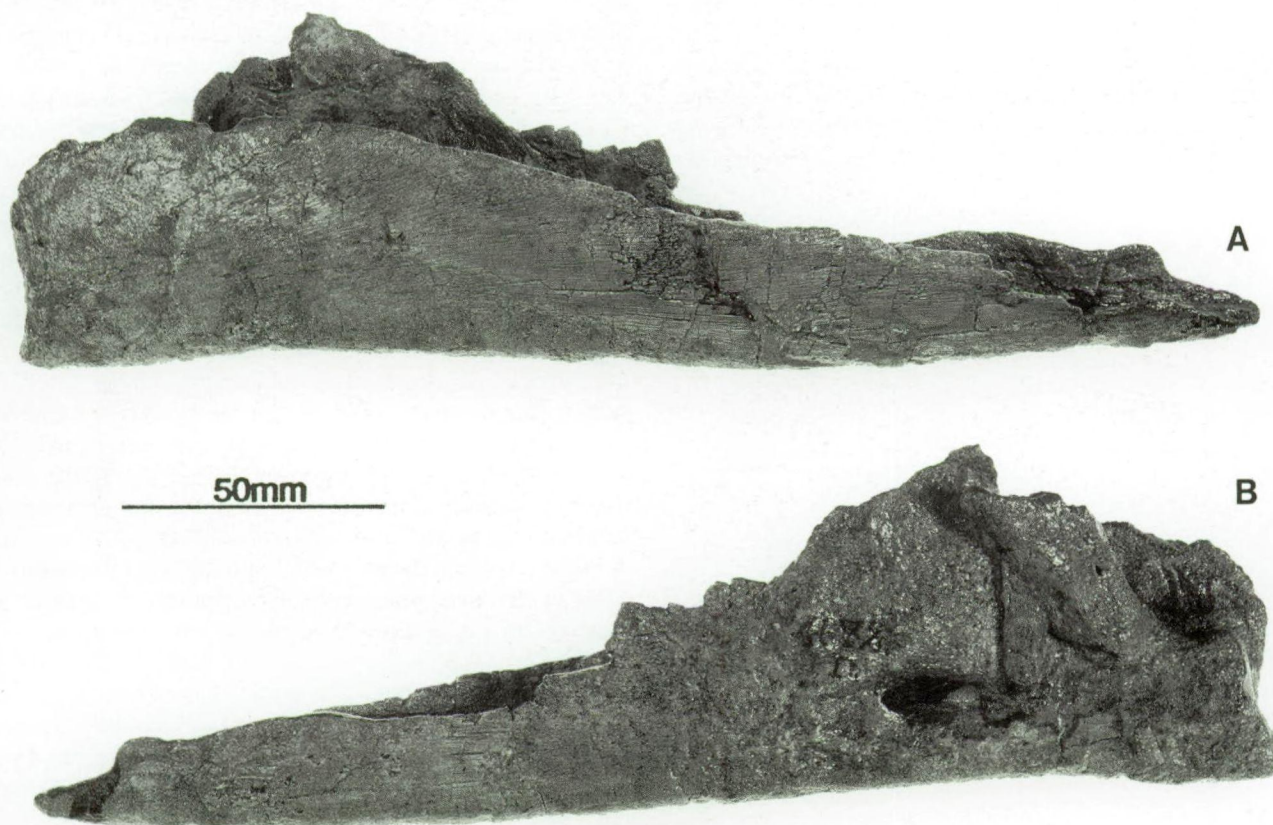
With regard to the character state ESTES *et al.* (1988), basing their outgroup analysis on *Sphenodon* GRAY, 1872 which has 16 scleral ossicles, considered more than 14 to be plesiomorphic and 14 or fewer to be a synapomorphy for Squamata. For diagnostic purposes, however, it is necessary to know the natural position of the sclerotic ring before the character state of the patterns of ossicle overlap may be determined (ESTES, pers. comm.). More data will therefore have to be available in mosasaurs before the character can be assessed in this group.

**Dentary.** The dentary of *Prognathodon solvayi* as in all members of the genus is a particularly stout bone. The most striking feature is the strong concavity of the dental margin and the highly procumbent anterior teeth. Both of these characters are also evident in the referred material of *P. solvayi* (IRSNB R108, Pl. 3). The fragmentary nature of IRSNB R107, however, makes it hard to tell if the dental margin in this specimen was curved or not. The anterior teeth of R107 (Pl. 2) appear, like IRSNB R33 and R108, to be procumbent.

A row of fairly large foramina extends along almost the entire length of the dental ramus at about the vertical midpoint of the bone and curves upwards anteriorly and posteriorly to parallel the dorsal margin of the bone. Anteriorly the dentary terminates abruptly in front of the teeth as in all other members of the genus.

The dental margin in *P. giganteus* (IRSNB R106) appears to be fairly straight although the fragmentary nature of the dental ramus makes it difficult to determine with certainty. RUSSELL's figure of *P. overtoni* (SDSM 3393; 1967, fig. 90) shows a similar upward concavity of the dental margin when compared with *P. solvayi* although perhaps a little less accentuated and WILLISTON described the upper dental margin of *P. overtoni* (KU 950) as "extraordinarily concave". KUES & LUCAS (1985), however, in their identification of "*Prognathodon*" from fragments of mosasaur bones from the Lewis Shales of Colorado, described a dentary with a large edentulous process of approximately 45 mm. This would be unique for *Prognathodon*. A large edentulous projection is characteristic, as they noted, of the Tylosaurinae. The fragmentary and poorly preserved state of the material makes the identification questionable. Their assignment of this material to *P. overtoni* is based on the presence of fused haemal arches in their material and on RUSSELL's diagnosis that the condition is unique to *P. overtoni* (outside of the Mosasaurinae). This is incorrect; the condition also occurs in *Dollosaurus lutugini* (see IAKOVLEV, 1901; TSAREGRADSKII, 1935), a plioplatecarpine mosasaur and is here recorded in *P. giganteus*. Unfortunately the caudal vertebral region is not preserved in *P.*

Fig. 21. - Splenial of *Prognathodon solvayi* (IRSNB R33). A : lateral view; B : medial view.



*solvayi*. It seems quite reasonable to suppose that fused haemal arches may be the usual condition of the genus *Prognathodon* and not the exception as suggested by RUSSELL (1967, 1970).

It is conceivable that the material discussed by KUES & LUCAS (1985) belongs to a large species of the genus *Plesiotylosaurus* CAMP, 1942 (see CAMP, 1942, pl. 4) in which the dentary has a somewhat similar edentulous projection and the teeth are large and inflated. There is to our knowledge no caudal vertebra available belonging to this genus and consequently no record of whether the haemal spines are fused or not.

In SDSM 3393, as already mentioned, the posterior dorsal margin of the dentary terminates in a small projection of bone in the form of a tubercle that meets the anterior termination of the coronoid. In *Prognathodon overtoni* (KU 950) this projection is considerably smaller and meets the surangular instead. *P. solvayi* on the other hand lacks this process entirely, which seems to suggest a more primitive condition, but this kind of judgement would essentially require a cladistic analysis.

*Splénial*. The splénial is a long laterally compressed bone that tapers anteriorly extending to approximately two thirds of the dentary with the medial ala of the splénial sheathing the mandibular channel. A large foramen on the postero-medial surface transmitted the inferior alveolar nerve (RUSSELL, 1967) into the mandibular channel. The splénial extends just past the posterior extremity of the dentary. It makes contact with the anterior tuberos process of the angular by a fairly shallow laterally compressed articulating surface forming a moderately weak ball and socket joint.

*Angular*. The tuberos process of the angular forms a vertically moveable joint with the splénial, the articulation surface being somewhat taller than broad. The lateral wing of the angular is overlapped from above by the surangular

Fig. 22. - *Right angular of Prognathodon solvayi* (IRSNB R33). A : lateral view; B : medial view.

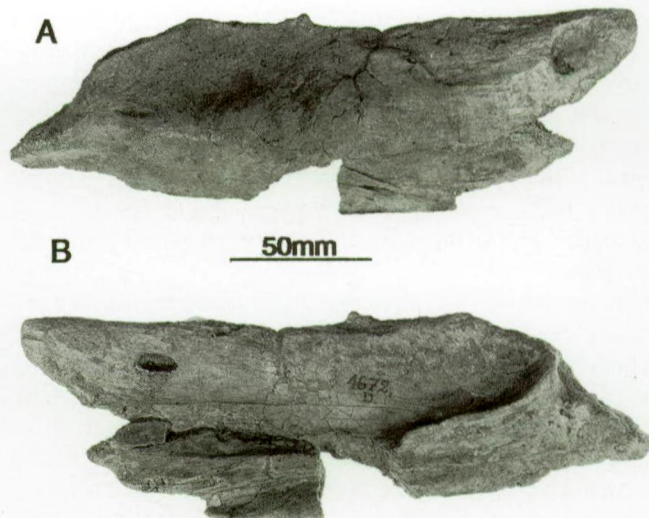
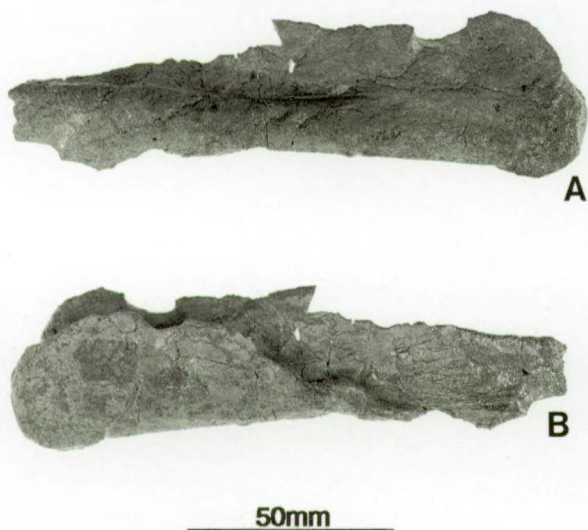


Fig. 23. - *Right surangular of Prognathodon solvayi* (IRSNB R33). A : lateral view; B : medial view.

but the medial wing that normally covers the ventromedial side of the prearticular is poorly preserved.

*Surangular*. The surangular is a long, laterally flattened bone in *Prognathodon solvayi*, tapering and pointed both anteriorly and posteriorly. The postero-dorsal tongue of the surangular terminates at the postero-external corner of the glenoid fossa. Postero-laterally a broad excavation, the presence of which is unusual in mosasaurs (see Fig. 23), may suggest an increased musculature, specifically the Mm. adductor mandibulae externus medialis et superficialis, M. pseudotemporalis profundis and the M. adductor mandibulae posterior. On the antero-dorsal surface a sharply defined recess for the coronoid is observed.

The long and somewhat anteriorly pointed surangular of *P. solvayi* is generally present in most squamates and non squamate lepidosauromorphs (see ESTES *et al.*, 1988, pp. 155-156). In *P. solvayi* the anterior termination of the surangular was probably relatively close to that of the anterior process of the coronoid, a similar condition to that found in *Lanthanotus* and *Varanus* (see ESTES *et al.*, 1988, p. 156) as well as that of certain other mosasaurs. GAUTHIER (1982) and ESTES *et al.*, (1988) related this condition to the extent of development of the intramandibular hinge. A similar interpretation may explain the condition found in mosasaurs; in certain taxa, such as *P. overtoni* (SDSM 3393) and *M. hoffmanni* extension of the surangular onto the dentary could reasonably be interpreted as suppression or modification of the intramandibular hinge.

A slight crescent shaped depression close to the anterior point of the surangular probably represents an artifact of crushing as it is not observed on the left surangular.

*Coronoid*. The coronoid is a saddle shaped bone in mosasaurs and is particularly prominent in *Prognathodon solvayi* relative to that of other mosasaurs including members of the genus *Prognathodon* in which the element is generally well developed.

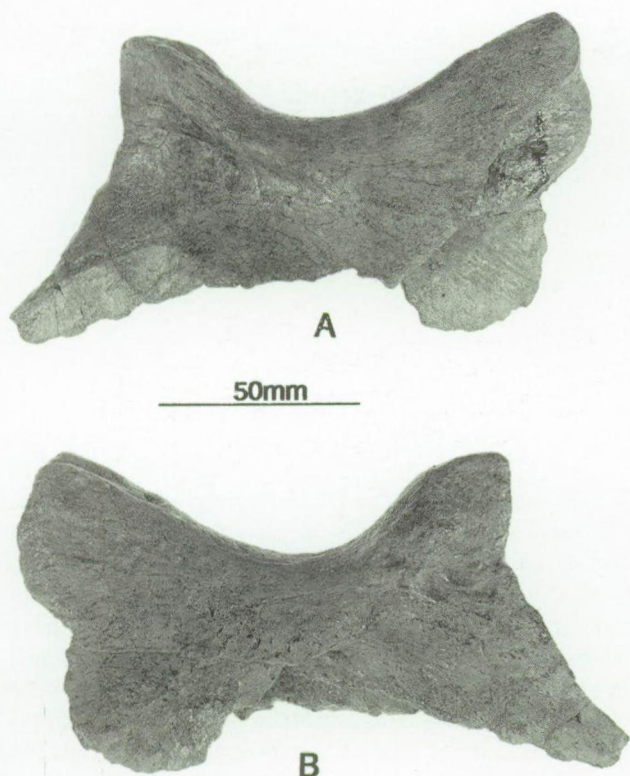


Fig. 24. - Right coronoid of *Prognathodon solvayi* (IRSNB R33).  
A : lateral view; B : medial view.

In the IRSNB mounted exhibit of the skull of *P. solvayi* the coronoid is clearly misplaced far posteriorly on the surangular (Fig. 6 & Pl. 1). In life, in this species, it would have been firmly sutured to the dorsal surface of the surangular in a more anterior position. A well defined excavation on the lateral wall of the surangular clearly marks such a position.

Laterally the coronoid is quite considerably flattened and is particularly deep posteriorly. The dorsal part of the saddle is narrow from side to side with the edges rounding smoothly onto the lateral and medial sides. From about the mid-point of the bone the dorsal margin extends horizontally towards the anterior termination. The anterior wall of the coronoid eminence (see Fig. 24) sweeps up at about an angle of  $75^\circ$  from the horizontal to an acute point, sharper than in *P. giganteus* or *P. overtoni* (SDSM 3393). It then descends posteriorly, abruptly almost vertically at first and then more gradually at an angle of about  $45^\circ$ , to the dorsal edge of the surangular. In *P. overtoni* (KU 950) the dorsal margin of the coronoid buttress is more gently rounded than in either *P. solvayi* or SDSM 3393 (see RUSSELL, 1967, fig. 90).

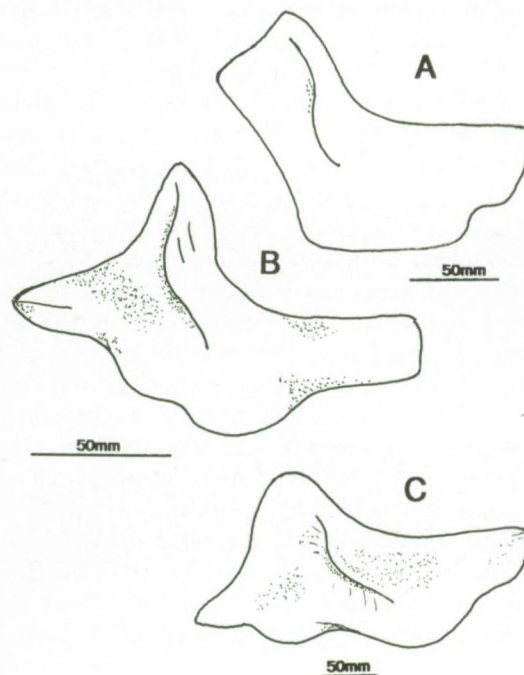
The lateral wings of the coronoid are very extensive in *P. solvayi* with a large posterior and somewhat smaller anterior wing. In *P. overtoni* (SDSM 3393) there appears to be a single antero-lateral wing (see RUSSELL, 1967, fig. 90 and our Pl. 6). Although the distal tips of the wings are absent the general configuration suggests that specimens referred to *P. solvayi* probably match more closely conditions in KU 950 than in SDSM 3393. Medially the anterior

wing of the coronoid is large with the posterior wing somewhat smaller.

The coronoid of *P. solvayi* nevertheless shows many general similarities to that of *P. overtoni* (SDSM 3393) in overall shape, the high coronoid buttress and large lateral and medial wings. The differences lie essentially in degree, and to a lesser extent shape, with the above conditions considerably accentuated in *P. solvayi* — the coronoid buttress is almost twice as deep and the lateral wings of the coronoid somewhat broader.

There are certain character state discordancies between *P. solvayi* and *P. overtoni* (SDSM 3393) that are noteworthy. In *P. solvayi* the coronoid was situated a little further back on the surangular with the posterior lateral wing of the element probably skirting the excavation on the posterolateral surface of the surangular; the anterior process of the coronoid presumably ended flush with the anterior termination of the surangular. This is, as already noted, indicated by the shape of the coronoid and the recess for it on the surangular. Such a condition contrasts sharply with that of *P. overtoni* (SDSM 3393; RUSSELL, 1967, fig. 90) in which the anterior process of the coronoid appears to have projected forward above the surangular and abutted against a small process on the postero-dorsal surface of the dentary. In *P. solvayi* the process on the postero-dorsal surface of the dentary is absent and contact between the coronoid and the dentary as in *P. overtoni* (SDSM 3393) seems unlikely. The incipient posterior process on the dentary in *P. overtoni* (KU 950) suggests a contact intermediate between that of *P. overtoni* (SDSM 3393) and *P. solvayi*. Ancestrally in araeoscelians, younginiforms, archosauromorphs and rhynchocephalians (GAUTHIER *et al.*, 1988,

Fig. 25. - Lateral view of right coronoid. A : *Prognathodon overtoni* (SDSM 3393 after RUSSELL, 1967); B : *P. solvayi* (IRSNB R33); C : *P. overtoni* (KU 950 after WILLISTON, 1898b).



p. 53 and fig. 3L) the coronoid is a fairly small subtriangular bone with a low coronoid eminence. The derived condition in squamates is in contrast, a uniquely modified bone sitting on top of the posterior mandibular unit, extending laterally and posteromedially, with a prominent process that extends down the prearticular to form the antero-medial margin of the mandibular fossa. Gauthier *et al.* (1988, p. 53) pointed out, however, that the condition has been modified in some squamate groups such as mosasaurs, in which the postero-medial process has been lost, leading to greater intramandibular movement. This difference between varanids and mosasaurs had been pointed out by previous authors (RUSSELL, 1964, 1967; CALLISON, 1967). In *Varanus* the components of the dentary and post dentary unit are tightly sutured together, effectively forming a single mandibular unit. The presence of an anterior extension of the coronoid in Varanoidea is regarded by ESTES, de QUEIROZ & GAUTHIER (1988) as a synapomorphy for the group. Intramandibular movement is reasonably interpreted as a derived state of the Mosasauridae, with very little apparent change during the evolution of the group despite the loss of cranial mobility along the mesokinetic and metakinetic axis in some later forms. However, the anterior projection of the coronoid and the dentary process in SDSM 3393 is interpreted here as an early stage in the evolution of a tighter intramandibular joint of later forms.

A similar example of suppression of intramandibular movement is seen in *Mosasaurus hoffmanni*. Here the prearticular and a small anterior projection of the surangular slotted tightly into the dentary anteriorly, with the coronoid firmly sutured over the surangular and posterior termination of the dentary.

Other factors may have functioned in the tightening of the intramandibular hinge, for instance the very large antero-medial wings of the coronoid in *Prognathodon solvayi* which seems was sutured with the angular in life. A large antero-medial wing of the coronoid is also observed in the well preserved skull of *P. overtoni* (SDSM 3393, RUSSELL, 1967, p. 162). Similarly in *Mosasaurus hoffmanni* the posterior coronoid wing is fairly extensive medially, although not large enough to bridge the mandibular fossa. However, the anterior wing is massive extending ventrally and clearly making sutural contact with the angular. The whole lower jaw was consequently a much tighter fitting unit (cf. BMNH cast of the holotype of *M. hoffmanni*). In *M. hoffmanni* the whole lower jaw is frequently found intact as a single unit and in other cases the jaws are broken off at the intramandibular joint rather than dislocated, which although circumstantial suggests a particularly tight joint. This is a reasonable supposition because in such massive mandibles as those of *M. hoffmanni*, loose joints and weak sutures between individual components would greatly weaken the whole jaw and render it liable to severe dislocations. As a consequence of which a more tightly constructed and efficient lower jaw in some forms of mosasaurs appears to have developed.

The contact between the anterior process of the coronoid and the posterior dentary process in *Prognathodon overtoni*

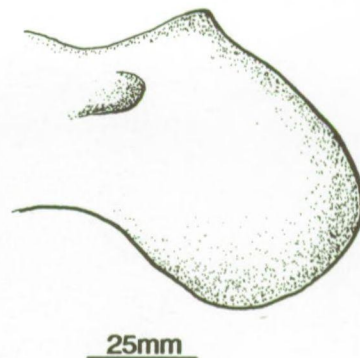


Fig. 26. - Retroarticular process of *Prognathodon solvayi* (IRSNB R33).

(SDSM 3393) may be considered an early stage of a character reversal in mosasaurs, to a condition similar to that seen in *Varanus* in which the anterodorsal cleft of the coronoid clasps the dorsal flange of the dentary. An interpretation of this reversal and of the condition noted in *Mosasaurus hoffmanni* is that they represent separate autapomorphies of these taxa although clearly a condition that needs to be examined in a cladistic study of mosasaurs.

A high posterior buttress of the coronoid as in *Prognathodon solvayi* is seen in several squamate reptiles e.g. *Varanus* and the related aigialosaurid *Opetiosaurus* KORNHUBER, 1902 (RUSSELL, 1967). Absence of a high coronoid buttress is interpreted as a synapomorphy of the Mosasauridae. Given the conditions seen in this region in other mosasaurs, it is possible that the high coronoid buttress of *P. solvayi* is a character reversal and an autapomorphy of the taxon.

*Articular.* The articular is a slender bone in *Prognathodon solvayi*. Anteriorly no trace of the prearticular process remains, presumably because of poor preservation. Posteriorly it forms part of the mandibular fossa, which skirts the medial edge of the glenoid cavity and terminates in the retroarticular process. In *P. solvayi* the retroarticular process conforms to the general description of a "moderately heavy, rectangular bar of bone..." (RUSSELL, 1967, p. 54).

In *P. overtoni* (SDSM 3393), however, the retroarticular process is medially inflected and dorsoventrally flattened, similar to that of *Platecarpus ictericus* (RUSSELL, 1967, figs. 37-38). In both *Prognathodon solvayi* and *P. overtoni* (KU 950) the retroarticular process is laterally compressed and laterally facing, essentially rectangular in configuration.

*Dentition.* Of all the characters the dentition of *Prognathodon solvayi* manifests the greatest difference from that of other members of the genus. The tooth crowns are generally large and quite strongly striated (Fig. 27A). The anterior teeth are more procumbent than in any other mosasaur. The premaxillary teeth are almost horizontal and the anterior dentary teeth only slightly less so (Fig. 6A).

In addition to deep striae the better preserved albeit fragmentary material of *P. solvayi* (IRSNB R107, Fig. 27B)

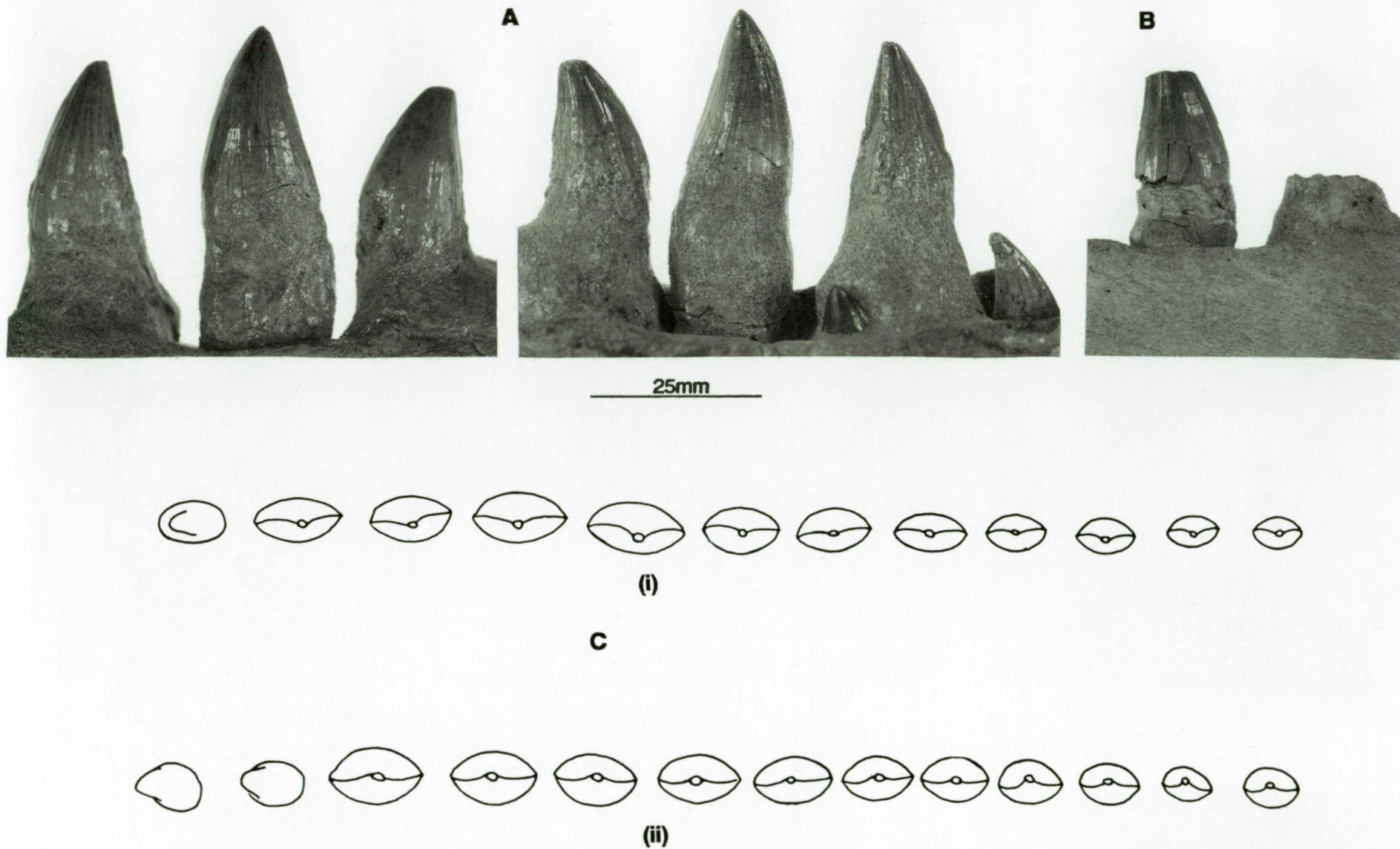


Fig. 27. - Dentition of *Prognathodon solvayi*. A : tooth crowns of IRSNB R33; B : tooth crown of IRSNB R107; C : cross-sections (taken at the base of the crown) of marginal teeth of IRSNB R33 : C I : right maxilla, C II : right dentary.

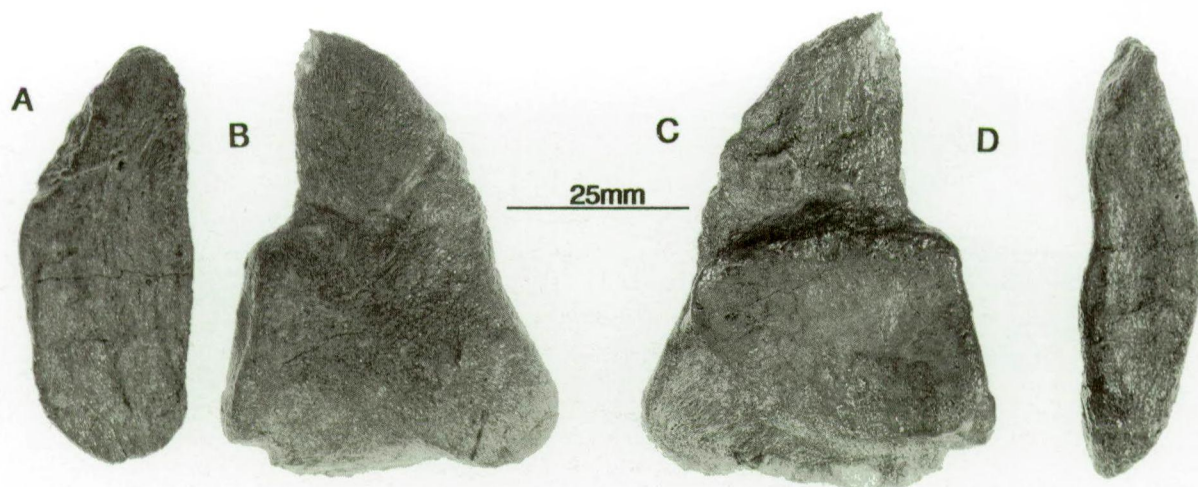


Fig. 28. - Atlas vertebra of *Prognathodon solvayi* (IRSNB R33). A : ventral view of intercentrum; B : lateral view of neural arch; C : medial view of neural arch; D : anterior view of intercentrum.

reveals that tooth crowns may also have been somewhat prismatic with seven to eight prisms on the external surface. It is harder to tell with any confidence the number of prisms on the internal surface, a common problem in mosasaurs.

In *P. solvayi* the teeth are more slender at the anterior end, broader and triangular towards the middle of the dental ramus, decreasing in size towards the posterior end with the last two teeth rather stunted. The tooth crowns are only moderately inflated (Fig. 27C).

In contrast in *P. overtoni* (SDSM 3393) the teeth increase in size consistently in an antero-posterior direction and are somewhat less posteriorly recurved. In *P. overtoni* (KU 950, WILLISTON, 1898b, pl. 22) on the other hand, save for the penultimate tooth base which is larger, all the remaining ones appear to be fairly uniform in size.

*Prognathodon* species show a degree of variation in tooth number. There are 12 teeth on the maxilla of *P. solvayi* and 13 on the dentary. *P. overtoni* (SDSM 3393, see

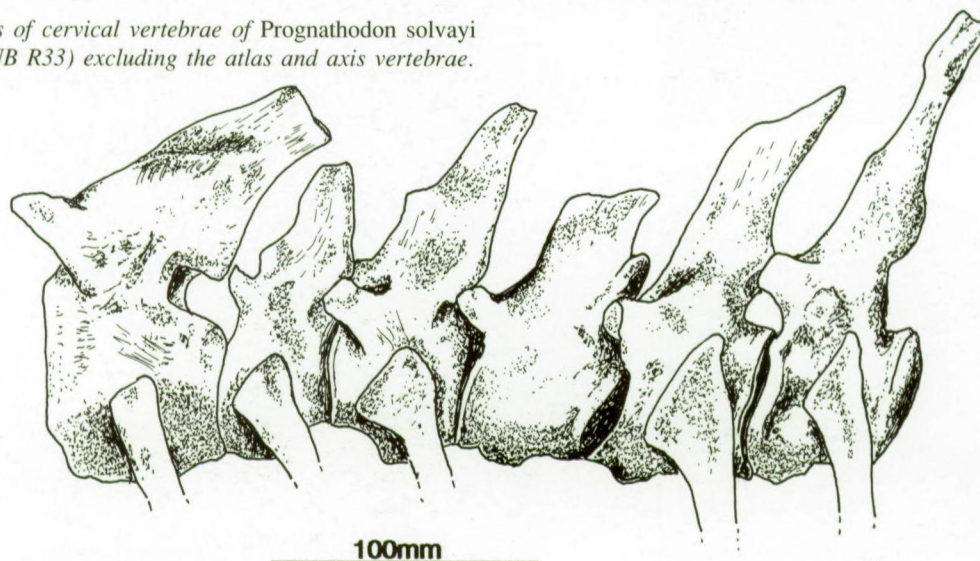
RUSSELL, 1967, fig. 90) has in contrast 14 dentary teeth. WILLISTON'S (1898b) account of the number of teeth in KU 950 is somewhat contradictory. In 1897 he indicated that a previous comment (for which he gives no reference) was incorrect and that the number of dentary teeth should be 13 - 14. Subsequently (1898b) he suggested the number to be 12 or 13. Based on his figure (1898b, pl. 22) 13 seems to be a reasonable estimate.

#### Postcranial skeleton

The vertebrae are poorly preserved and considerably distorted in some parts. The only caudal vertebrae present are the pygals. The approximate vertebral formula is : atlas, seven cervicals including the axis, 30 trunk, 5 pygals.

*Atlas*. All four elements of the bone, which appear to be of typical mosasauroid proportions, are present. The intercentrum lacks a hypapophyseal peduncle.

Fig. 29. - Series of cervical vertebrae of *Prognathodon solvayi* (IRSNB R33) excluding the atlas and axis vertebrae.





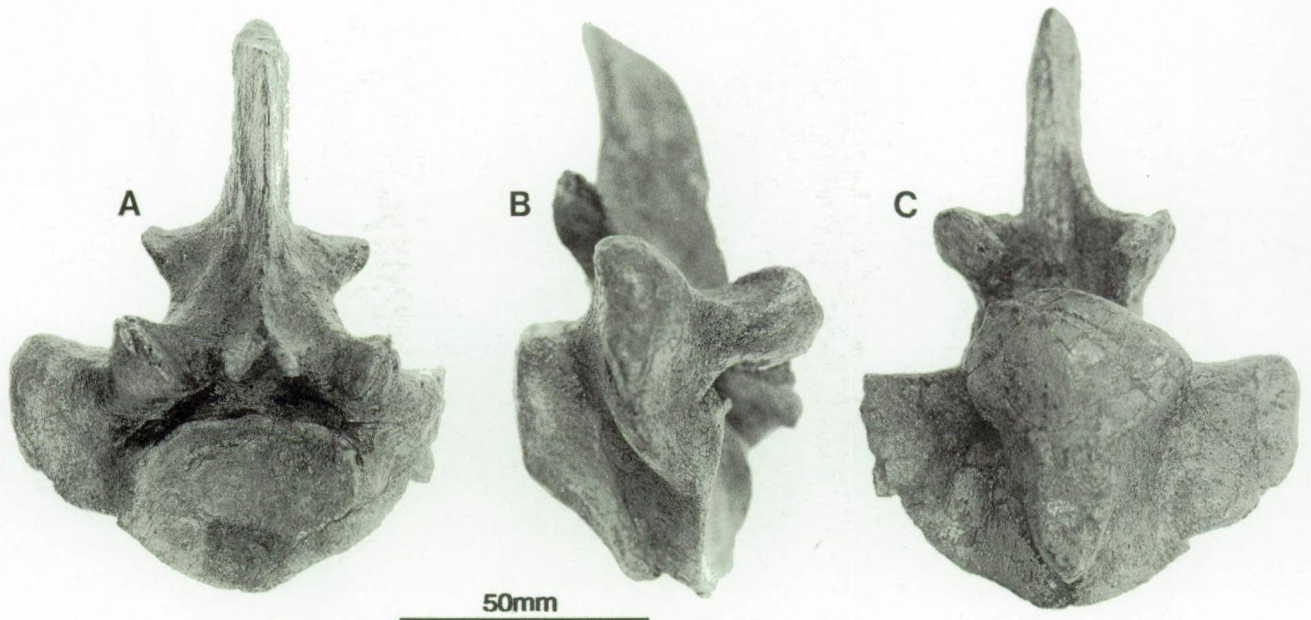


Fig. 30. - Cervical vertebra of *Prognathodon solvayi* (IRSNB R33). A : anterior view; B : lateral view; C : posterior view.

**Axis.** The axis vertebra is crushed and distorted but appears to have had a fairly broad posteriorly directed neural spine; the centrum is too badly crushed and distorted for comment.

**Cervicals.** All the cervicals are extensively crushed and distorted. Apart from the axis vertebra they all bear zygosphenes and hypapophyses. The largest zygosphenes occur on C5; they are fairly long and narrow with pointed tips. The zygantra on the same vertebra are long, deep, similarly shaped excavations. Centrum articulations are generally taller than broad and approximately heart-shaped.

The first cervical has strong pre and post zygapophyses which decrease in size posteriorly. On the last cervical the anterior zygapophyses are stronger than the posterior zygapophyses. The neural spines are tall and are directed posteriorly although this condition may be exaggerated owing to distortion in preservation. All the cervicals bear

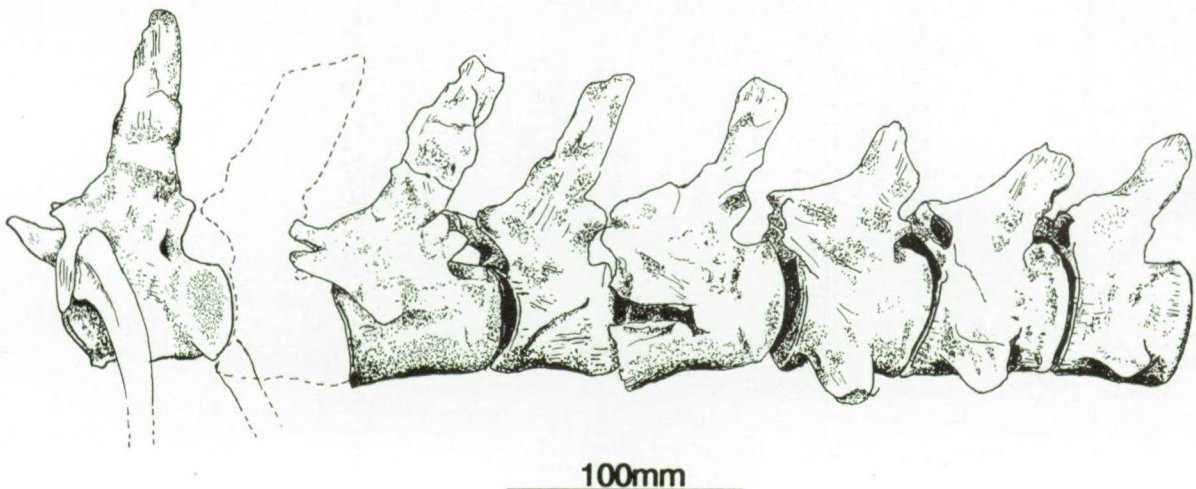
vestigial ribs.

**Trunk.** There are approximately 30 trunk vertebrae but owing to poor preservation the following information is occasionally based on a composite of data from the first six dorsals which are somewhat better preserved. The centra are moderately long, subcircular to almost heart shaped. However, owing to severe distortion it is hard to determine depth of the articulating surfaces or the lengths of the centra with any certainty. Anterior and posterior zygapophyses are not as well developed as in the cervicals. Large zygosphenes and zygantra are present, especially on the anterior dorsals.

The synapophyses appear to be situated fairly high up on the centrum and are quite strong in the first six dorsal vertebrae. Neural spines, although battered and fragmentary appear to be shorter than in the cervicals.

Further along the trunk series of vertebrae articulating

Fig. 31. - Series of lumbar vertebrae of *Prognathodon solvayi* (IRSNB R33).



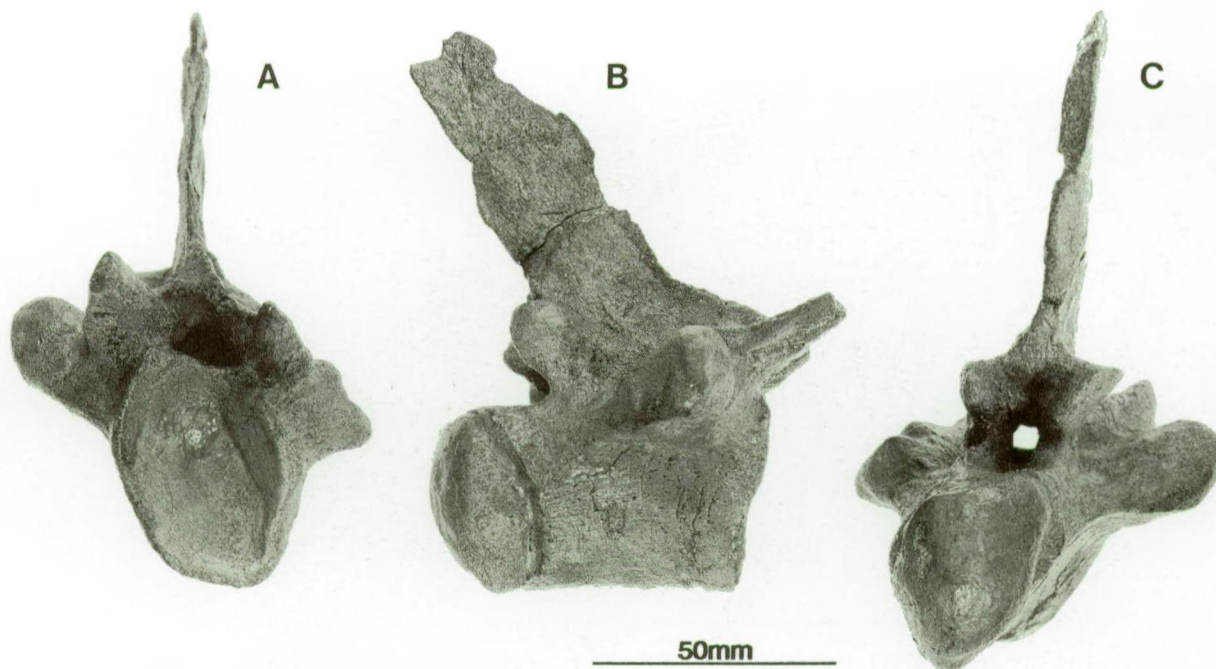


Fig. 32. - Anterior lumbar vertebra of *Prognathodon solvayi* (IRSNB R33). A : anterior view; B : lateral view; C : posterior view.

surfaces are deep and taller than broad. The synapophyses gradually decrease in size posteriorly moving from a dorso-lateral position on the centrum to a more central position. Zygapophyses are quite strong up to about the ninth dorsal vertebra. They decrease in size rapidly thereafter and from approximately the 14th vertebra they are only vestigial with the last five dorsals too severely compressed dorso-ventrally to make any valued comment regarding these articulations.

*Pygals.* The pygals, which appear to be incorrectly positioned at the end of the column in the reconstruction (presumably because of separation of the elements during the taphonomy of the animal), are better preserved, perhaps as a consequence of the displacement.

The transverse processes are broad and very long. The centra are short. Articulating surfaces are subcircular. Neural spines on the pygals are relatively long. The occurrence of zygosphenes and zygantra in the Lepido-

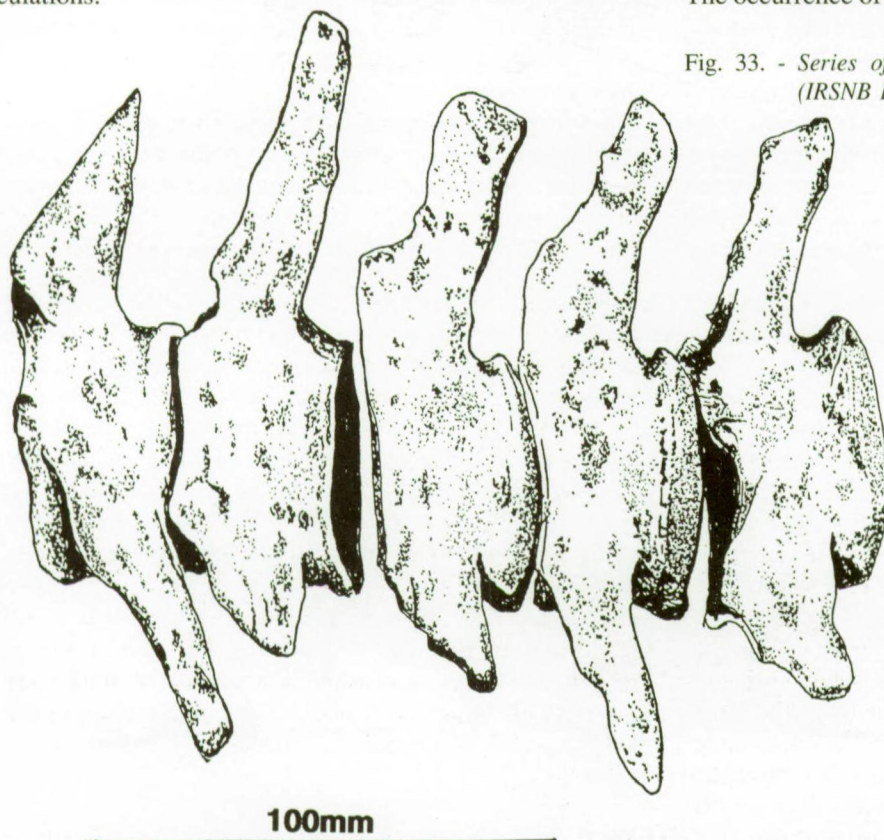


Fig. 33. - Series of pygal vertebrae in *Prognathodon solvayi* (IRSNB R33).

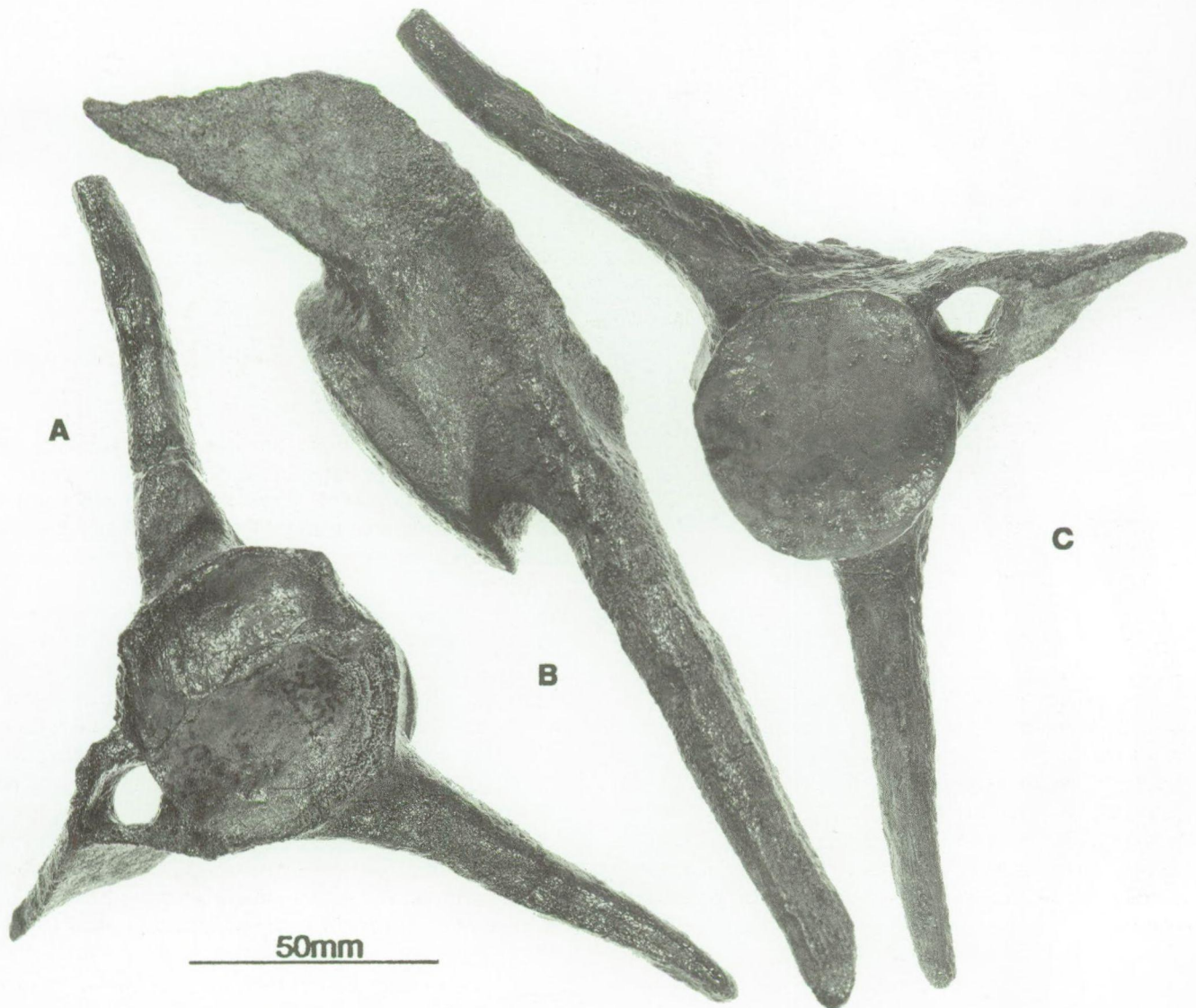


Fig. 34. - Pygal vertebrae of *Prognathodon solvayi* (IRSNB R33). A : anterior view; B : lateral view; C : posterior view.

sauromorpha is very varied. The presence of additional articulations on the midline of the neural arch between the zygapophyses occurs in younginiforms, (CURRIE, 1981). In *Sphenodon* GRAY, 1872 and many squamates, zygosphene and zygantra-like processes are present, a condition which BENTON (1985, p. 136) suggests may be homologous with the additional articulations on the midline of the neural arch of, for example, the younginiforms. In snakes on the other hand the zygosphenes and zygantra are elevated on the neural spine medial to, but distinctly separate from the zygapophyses, a similar condition seen in mosasaurs. Determining the polarity of the presence of zygosphenes and zygantra in mosasaurs is a considerable problem but probably no less so than in some other groups. In preference to regarding loss of zygosphenes in Anguimorpha, Acrodonta and Gekkota as three separate synapomorphies ESTES *et al.* (1988) believed the presence of zygosphenes and zygantra to be primitive for squamates. We have adopted a similar position regarding the character of zygosphenes and zygantra in mosasaurs. Provisionally they may be considered primitive for mosasaurs because of their occur-

rence in the early mosasaurs *Clidastes*, *Mosasaurus* and *Platecarpus*, with loss in the later forms, *Plotosaurus*, *Plioplatecarpus* and *Halisaurus* regarded as derived. The Tylosaurinae on the other hand represented by individuals from some of the earliest mosasaur horizons (*Tylosaurus nepaeolicus* from the Coniacian, RUSSELL, 1967, and *Hainosaurus peminensis* from the early Campanian, NICHOLLS, 1988) to the latest horizons (*Hainosaurus bernardi* from the Maastrichtian) show a lack of, or rudimentary zygosphenes and zygantra. The variation in the presence or absence of zygosphenes and zygantra in mosasaurs presents a problem in determining the polarity of the character. An hypothesis of relationships within mosasaurs is therefore necessary to establish whether or not absence of zygosphenes and zygantra is a synapomorphy of mosasaurs, a possible sister group of squamates. Presence of zygosphenes and zygantra, however, is tentatively regarded as a character reversal in *P. solvayi* and *P. giganteus*.

*Ribs.* The largest rib processes preserved are probably on



Fig. 35. - Ribs of *Prognathodon solvayi* (IRSNB R33).

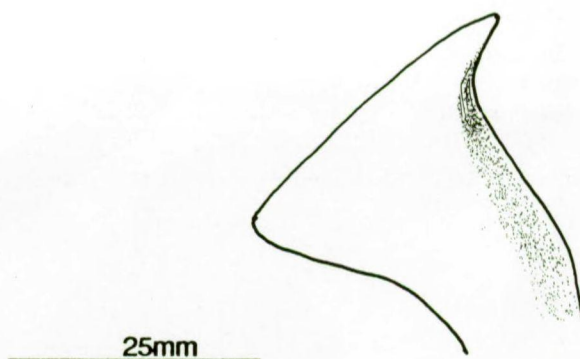
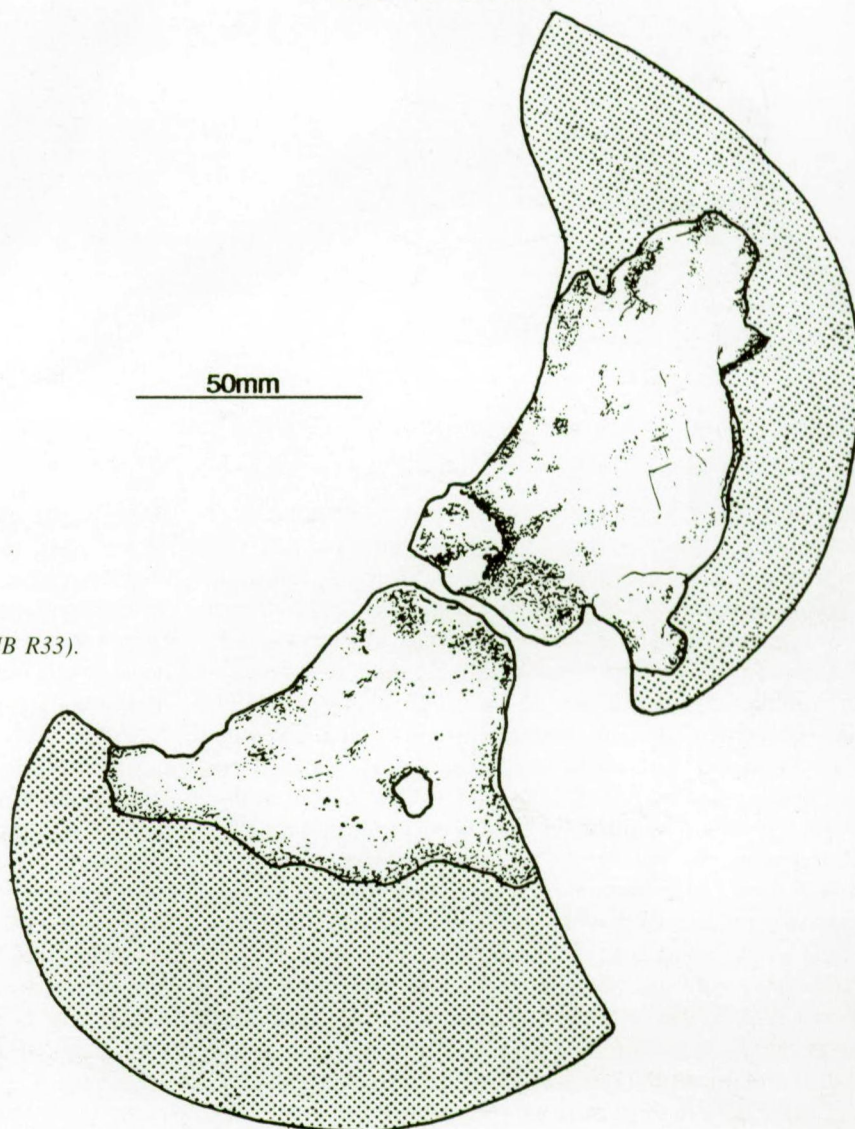


Fig. 36. - Articulation head of rib of *Prognathodon solvayi* (IRSNB R33).

dorsal vertebrae two, three, four, six and seven. They are fairly slender and preservation generally is quite poor. All the vertebrae possess single articulation heads which are fairly narrow with perhaps the widest belonging to the second dorsal vertebra, measuring approximately 32.2 mm.

Fig. 37. - Reconstruction of right scapulo-coracoid of *Prognathodon solvayi* (IRSNB R33).



*Scapula.* The scapula is incomplete and poorly preserved, and probably represents about half of its original size. The superior border of the blade-like fan of the scapula seems to have been directed anteriorly with the anterior edge short, possibly half that of the posterior edge. The glenoid fossa is concave and divided into a ventro-lateral and ventro-posterior surface.

*Coracoid.* The coracoid is abraded and very fragmentary, represented by a proximal segment of possibly no more than a third of the original size.

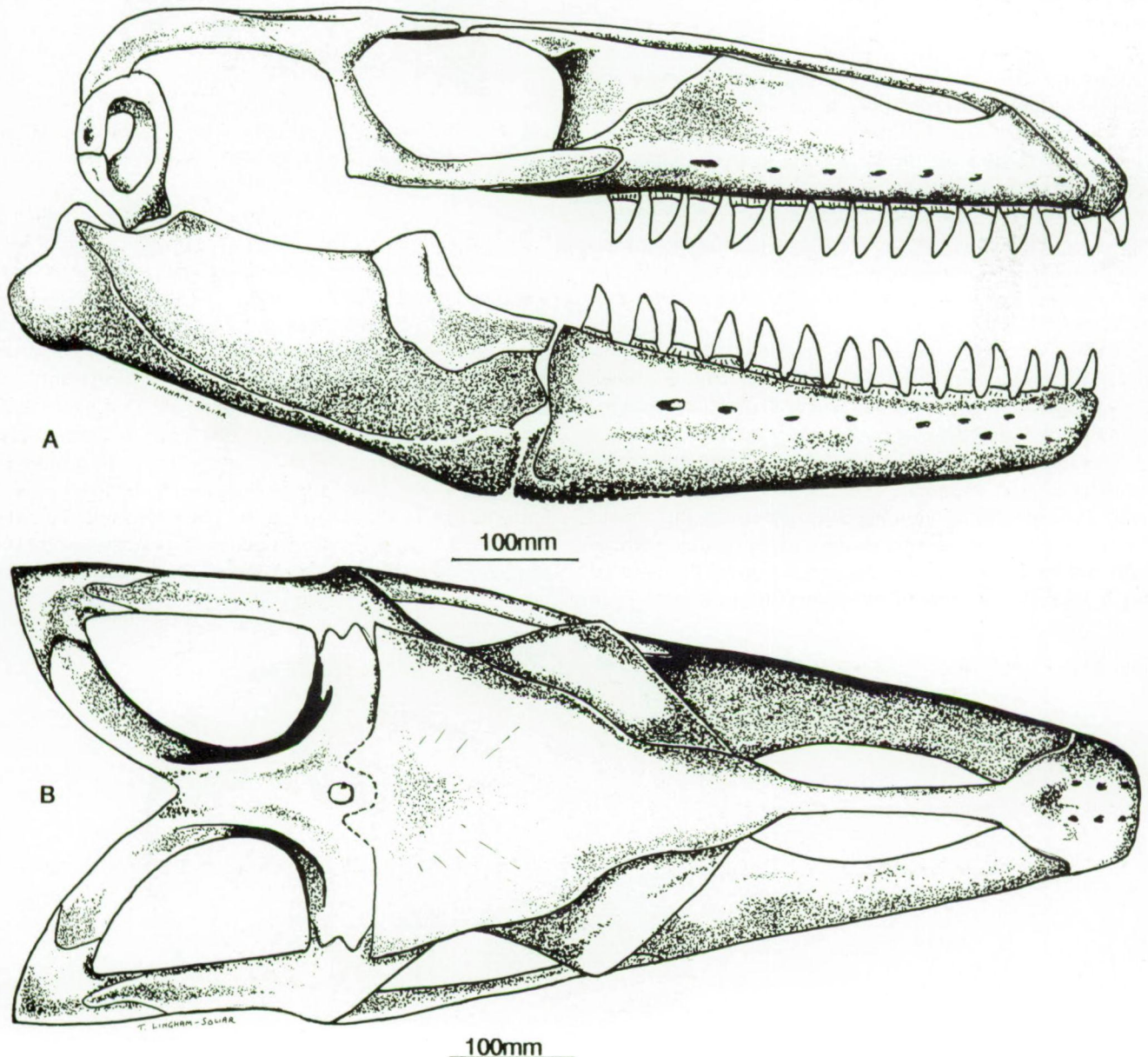
The glenoid cup is worn and appears to be flat although this may be the result of poor preservation. The coracoid foramen although large, the irregularity of its outline suggests that it may have been exaggerated by weathering and abrasion. It is not possible to say with any certainty what the fan of the coracoid was like and the reconstruction in this respect is somewhat speculative.

*Prognathodon giganteus* DOLLO, 1904  
(Pl. 6B, 7)

1904 *Prognathodon giganteus* - DOLLO, p. 213;  
1909 *Prognathodon giganteus* DOLLO, 1904 - DOLLO, p. 103;  
1967 *Prognathodon giganteus* RUSSELL, 1967, p. 123.

*Material.* - Holotype, IRSNB R106. Incomplete skull comprising premaxilla, anterior and posterior fragments of maxilla, fragments of prefrontals, three maxillary teeth, fragment of jugal, fragment of quadrate, two ossicles of sclerotic ring, fragments of right and left dentaries with six tooth crowns, fragment of splenial, surangular, distorted fragment of articular and retroarticular process, fragment of angular and fragment of coronoid; incomplete post-cranial skeleton comprising thoracic vertebrae, dorsal, posterior lumbar and caudal vertebrae, ribs, fragment of coracoid.

Fig. 38. - Skull and mandibles of *Prognathodon giganteus* (substantially reconstructed after IRSNB R106). A : right lateral view; B : dorsal view.



*Diagnosis.* - Plioplatecarpine mosasaur with the following characters: foramina marking the premaxillary exits of the ophthalmic ramus of the fifth cranial nerve situated near the midline of the bone; anterior narial emargination starts at a point just adjacent to the second maxillary tooth; articular condyle short; coronoid very small with restricted medial and lateral wings; anterior wall of the quadrate straight; quadratic condyle concave ventrally; quadratic meatus large.

#### DESCRIPTION AND COMPARISONS

##### Skull

The description of the skull of *Prognathodon giganteus* is based entirely on the fragmentary remains, of IRSNB R106. The skull has an estimated length of 1050 mm. and is laterally very broad and blunt-nosed, similar in configuration to that of *P. solvayi* and the North American species and unlike the sharp conical shape of the vast majority of other mosasaurs. The skull table is not preserved but from the available bones it is apparent that the dorsal surface was broad.

*Premaxilla.* The premaxilla is short, dorsally broad and despite a missing fragment across the anteriormost tip of no more than a few millimetres, it is reasonably certain that the termination of the premaxilla in front of the premaxillary teeth was blunt. A dorsal crest is absent. The foramina on the premaxilla marking the exits of cranial nerve V (ophthalmic branch) are situated uniformly toward the mid-line, an arrangement comparing closely with that of a *Prognathodon*-like premaxilla of slightly smaller proportions (BMNH 39939).

In FMNH PR 165, a specimen of possibly similar proportions to *P. giganteus*, RUSSELL (1970, fig. 167) described the anterior teeth of the dentary and premaxilla as procumbent. To our knowledge it is the only American mosasaur to manifest this condition which was first noted in its most extreme form in *P. solvayi* (DOLLO, 1889b). Although the premaxillary teeth are missing in *P. giganteus*, the second tooth of the right premaxilla shows a slight forward inclination and based on this and the inclination of the anterior tooth sockets, the teeth of the premaxilla may have been

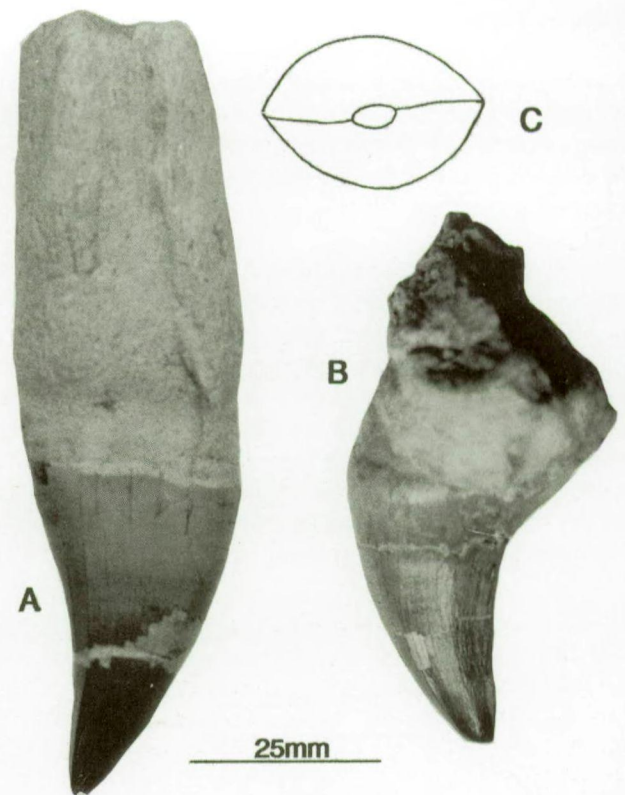
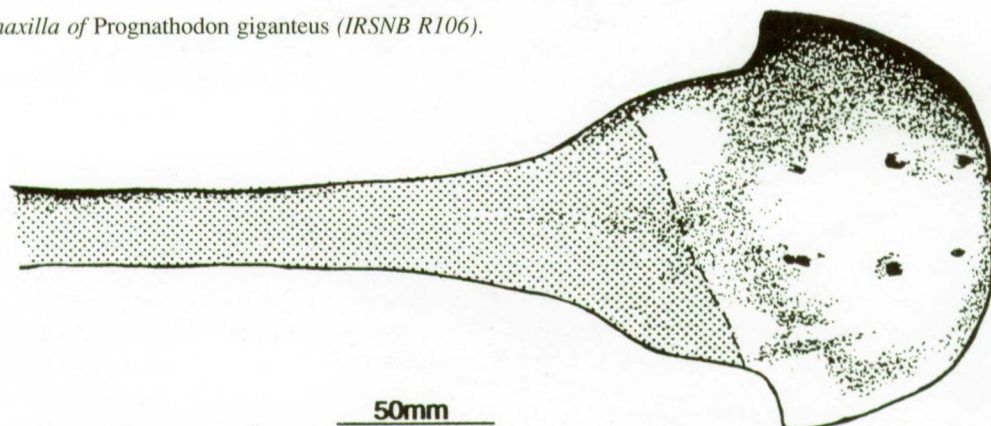


Fig. 40. - Tooth crowns of *Prognathodon giganteus* (IRSNB R106). A: buccal view; B: lingual view; C: cross-section (taken at the base).

somewhat procumbent, although probably not as extreme when compared with *P. solvayi*.

The teeth of *P. giganteus* are large, quite powerful in appearance and generally triangular in shape with somewhat posteriorly recurved tips. They are bicarinate with subequal buccal and lingual surfaces. In horizontal cross-section the tooth is subcircular and bears a close resemblance to WILLISTON's (1897a) cross-section of a tooth of *P. overtoni* (KU 950). The teeth appear to be more or less uniform in size along most of the jaw ramus although this assessment is an inference based on an incomplete number of preserved teeth and tooth bases of the maxillae and dentaries.

Fig. 39. - Premaxilla of *Prognathodon giganteus* (IRSNB R106).



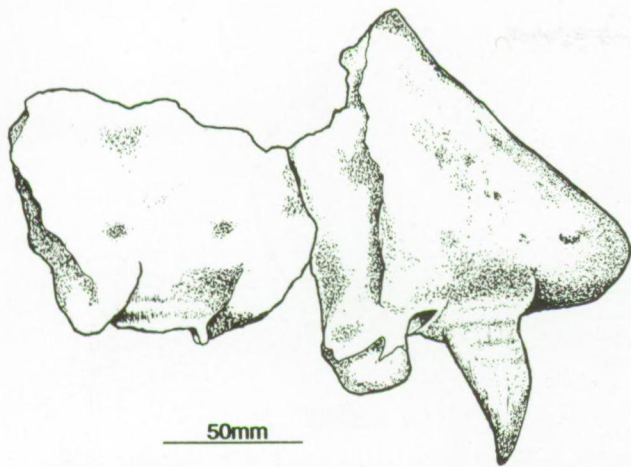


Fig. 41. - Anterior fragment of right maxilla of *Prognathodon giganteus* (IRSNB R106).

Tooth surfaces are enamelled and appear to be covered in very fine vertical striae. This may on the other hand be an artifact of preservation caused by cracking of the enamel. RUSSELL (1970, p. 374) on the other hand described the enamel in *P. giganteus* as smooth but he may have based his statement on DOLLO's (1904, p. 213) brief comment to that effect. KUES *et al.* (1985) also mention fine anastomosing striae in teeth which, however, are questionably referred to *Prognathodon*. RUSSELL (1970) noted that the teeth in "*Prognathodon*" FMNH PR 165 have vertical prisms presumably as in *P. solvayi* although the status of this specimen is questioned and will be mentioned later. Perhaps the only truly smooth teeth in *Prognathodon* belong to *P. overtoni* (SDSM 3393, see RUSSELL, 1967). It is clear though that there is some variation in tooth surfaces among members of the genus and that between such extremes of tooth crown surfaces of *P. overtoni* (SDSM 3393, with smooth surfaced teeth) and *P. solvayi* (with markedly striated teeth) there may be some intermediate types.

**Maxilla.** The maxilla are represented only by fragments (see Fig. 41) although some useful characters are visible. The suture between the premaxilla and maxilla is fairly unusual. It commences by rising briefly in an anterior direction, then turning posteriorly, describing a short, strongly convex curve. From this point it rises steeply posteriorly at an angle of approximately  $45^\circ$  until it reaches the external narial emargination, which commences unusually far forward, adjacent to the second maxillary tooth. From here it presumably continued to slope posteriorly at a geometrically decreasing angle. The narrow ventral margin of a large fragment of the prefrontal indicates that the postero-lateral wall of the maxilla in *P. giganteus* may have been somewhat similar to that of *P. solvayi* but narrower than in SDSM 3393. A posterior fragment of the maxilla indicates that the termination of the maxilla was pointed as in *P. solvayi*, a condition which is not evident in RUSSELL's figure (1967, fig. 90) which shows the maxilla of *P. overtoni* ending abruptly. The exits of the terminal branches of the cranial nerves of the maxilla (Vth)

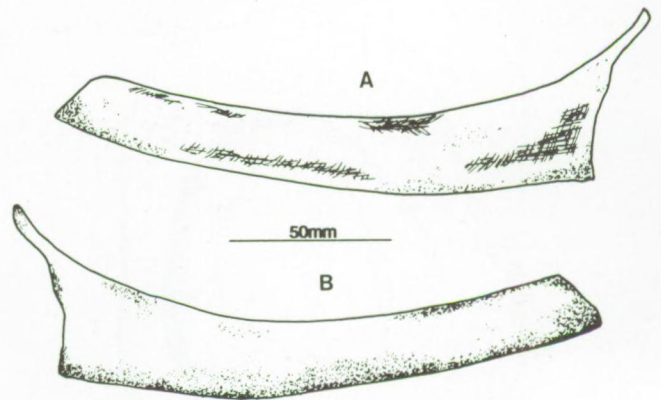


Fig. 42. - Fragment of right jugal of *Prognathodon giganteus* (IRSNB R106). A : medial view; B : lateral view.

emerge as a row of foramina just above a ridge, presumably the gum line.

**Prefrontal.** The prefrontal in *Prognathodon giganteus* is represented by a large left fragment which appears to be almost entire, and a smaller right fragment. Long anterior extension of the left prefrontal suggests that it may have bordered a large part of the external nares although the fragmentary nature of the adjacent bones makes this hard to confirm conclusively.

**Jugal.** Only the horizontal arm of the jugal remains; the anterior and posterior extremities are absent. The arm is long, fairly slender and laterally convex, flattening towards the anterior end. The curvature upwards of the jugal from a point approximately mid-way along the horizontal axis is very slight, suggesting that the vertical arm curved in a gentle arch as in *P. solvayi* rather than a sharp right angle as in *P. overtoni*.

On the medial surface posteriorly, a shallow depression ridged dorsally by a nubbin of bone probably marks the jugular contact with the ectopterygoid. RUSSELL (1967, p. 24) indicated that this was probably a sliding joint in mosasaurs, although WRIGHT & SHANNON (1988, p. 105) noted an exception in *Selmasaurus* WRIGHT & SHANNON, 1988, in which the "... medio-ventral surface [of the jugal] is strongly sutured for articulation with a matching surface on the lateral face of the ectopterygoid." Posterior to this depression there is a meshwork of fine striations that presumably mark the point of attachment of the quadratomaxillary ligament.

**Quadrate.** The quadrate is not well preserved and is represented by the anterior half to two thirds of the bone (see Fig. 43). What remains, however, seems to indicate that the quadrate of *Prognathodon giganteus* was significantly different from that of other *Prognathodon* species. The anterior wall of the quadrate seems to be quite straight when compared with the convex anterior wall of other species of *Prognathodon*. Although incomplete, it appears

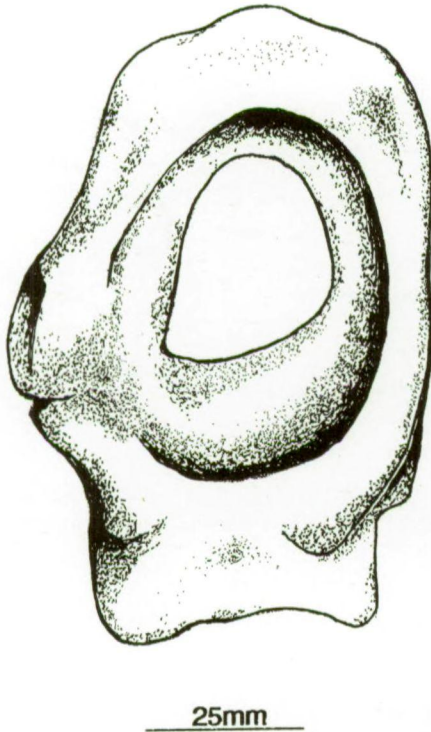


Fig. 43. - Reconstruction of right quadrate of *Prognathodon giganteus* (IRSNB R106).

that the quadratic meatus was very large, approximately 45 mm. long vertically and 35 mm. wide (estimated) horizontally. It is relatively much smaller in all other members of the genus.

In *P. solvayi* the quadratic meatus is a little wider than in *P. overtoni* (SDSM 3393) in which it appears as a narrow slit in lateral view, adjacent to the union of the suprastapedial and infrastapedial processes. In CHAFFEE'S (1939) figure of *P. rapax* (his *Ancylocentrum hungerfordii*) the meatus is somewhat comparable to that of *P. giganteus*, being fairly large, subcircular and more centrally positioned but still much smaller in size.

The quadratic condyle is unusual, being fairly narrow laterally and concave ventrally. In other *Prognathodon* species the quadratic condyle varies from gently to strongly convex (RUSSELL, 1967, p. 49). The tympanic ala, although not well preserved may have been as thick as in other members of the genus judging by the depth of the available fragment of the tympanum. It is not possible to determine either the size of the suprastapedial process or presumable contact with the infrastapedial process.

**Dentary.** The dentaries, although crushed and fragmentary, were obviously massive and stoutly constructed. The second tooth and first tooth base of the left dentary suggest that the anteriormost teeth were procumbent.

The alveolar margins of the dentaries, although fragmentary, suggest they were straight unlike those of *Prognathodon solvayi* and *P. overtoni* (SDSM 3393 and KU 950) in which they are strongly concave (*Campylorhynchus* condition of WILLISTON, 1898b) and to a lesser extent that of



Fig. 44. - Fragment of right splenial of *Prognathodon giganteus* (IRSNB R106), posterior view.

"*Prognathodon*" PR 165 (RUSSELL, 1970, p. 373), which appears somewhat concave.

**Splenial.** All that remains of the splenial is a small fragment of the posterior termination of the bone that articulates with the angular (Fig. 44 & Pl. 4). Nevertheless, it is sufficient to show that it was a relatively slender bone, laterally compressed and bearing a resemblance to the splenial of FMNH PR 165 (RUSSELL, 1970, p. 373) and that of *Prognathodon rapax* described by BAIRD (1986, fig. 5).

**Postmandibular unit.** The largest fragment of the available skull material is the posterior mandibular unit (hereafter PMU) comprising the surangular, angular, coronoid, articular and prearticular. The posterior region of the PMU is crushed involving vertical fracturing of part of the surangular along the long axis of the bone with a large part of the surangular abraded posteriorly.

The shape of the PMU is quite unusual in its rectangular lateral outline in contrast to the cone shaped outline of this unit in other mosasaurs. The retroarticular process in *Prognathodon giganteus* is short, and lies close to the main body of the articular. It is semicircular and laterally compressed. On the ventral surface a crest appears to be present although it is not certain whether or not it may be an artifact of crushing. RUSSELL (1967, p. 54), however, mentions "an articular questionably referred to *Globidens* (USNM 4993)", with a large tuberosity on its ventral margin that may have served for the attachment of the depressor mandibulae or sphinctor colli muscles. It is probable that the crest in *P. giganteus* served a similar function, forming insertion points for these muscles, which normally have points of origin on the anterior cervicals. In *Globidens*, however, it is a somewhat broader tuberosity, presumably a consequence of the highly specialized jaws and dentition.

The glenoid fossa is quite deep, more so at the anterior margin. Just posterior to the glenoid fossa the articular margin descends quite abruptly towards the retroarticular process, which, however, may be exaggerated owing to dislocation of the fragments.



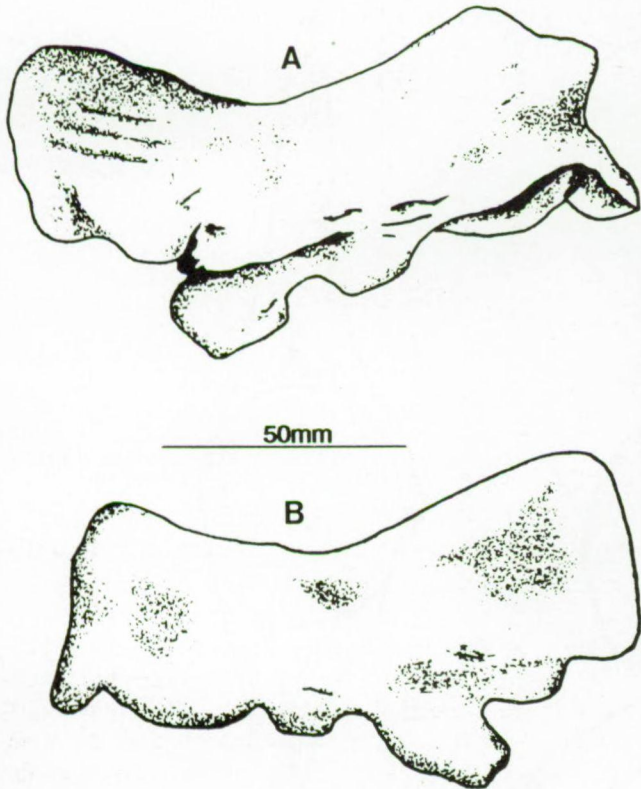


Fig. 45. - Left coronoid of *Prognathodon giganteus* (IRSNB R106). A : medial view; B : lateral view.

**Coronoid.** The coronoid is very small relative to the rest of the PMU, in strong contrast to conditions in other *Prognathodon* species, especially *P. solvayi* in which the coronoid is massive with extensive lateral and medial wings (Fig. 45). In *P. giganteus*, there are traces of the lateral and medial wings, but poor preservation makes it difficult to assess their size with any certainty, although they were

probably not extensive.

The main body of the coronoid is saddle shaped with fairly steep anterior and posterior slopes. Horizontal scarring on the postero-medial surface of the coronoid buttress marks the points of tendinous insertions of the *M. adductor externus* muscles which originate in the temporal arcade of the parietal unit. This muscle was probably quite powerful in *Prognathodon* (see RUSSELL, 1967) and responsible for providing strong bite forces. In *Varanus* a small part of the tendinous insertion is on the surangular (BAHL, 1937; FRAZZETTA, 1962; RUSSELL, 1967) and it is possible that owing to the relatively small size of the coronoid in *P. giganteus*, a larger segment of the tendinous insertion may have likewise been on the surangular, but poor preservation in this area makes it difficult to confirm.

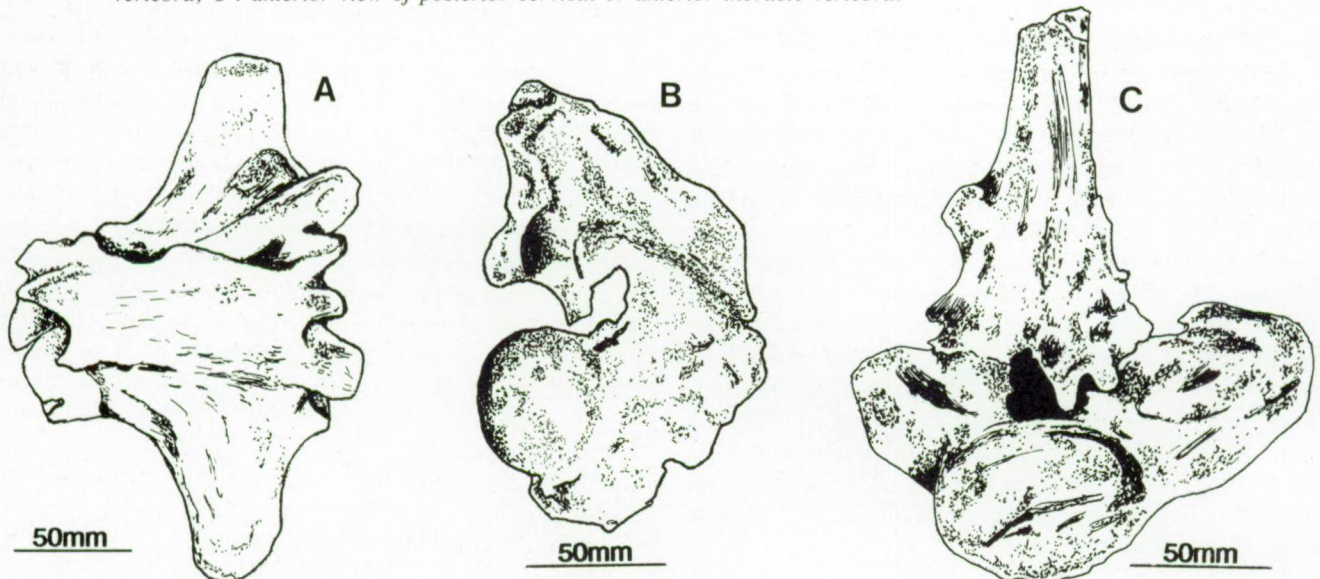
A large shallow excavation on the dorsal proximity of the postero-medial wall probably was the insertion point of a segment of the bodenaponeurosis which connects the *M. pseudotemporalis superficialis* with the coronoid.

#### Postcranial skeleton

Although RUSSELL (1967, p. 164) briefly mentioned the "excellent postcranial material" of *Prognathodon* from Belgium, the material unfortunately falls short of this description. We assume the comment was mistakenly based on DOLLO's (1889c, pp. 293-294; 1890, p. 163; 1917, p. 20) sometimes brief descriptions. The poor postcranial material applies to *P. solvayi* but especially to *P. giganteus*. Despite such poor preservation of the vertebrae of *P. giganteus*, however, they demonstrate some very important characters and help to clear up errors in previous interpretations.

**Axis vertebra.** The anterior part of the centrum as well as a fragment of the neural spine of the axis vertebra are not

Fig. 46. - Vertebrae of *Prognathodon giganteus* (IRSNB R106). A : dorsal view of posterior lumbar vertebra; B : lateral view of axis vertebra; C : anterior view of posterior cervical or anterior thoracic vertebra.



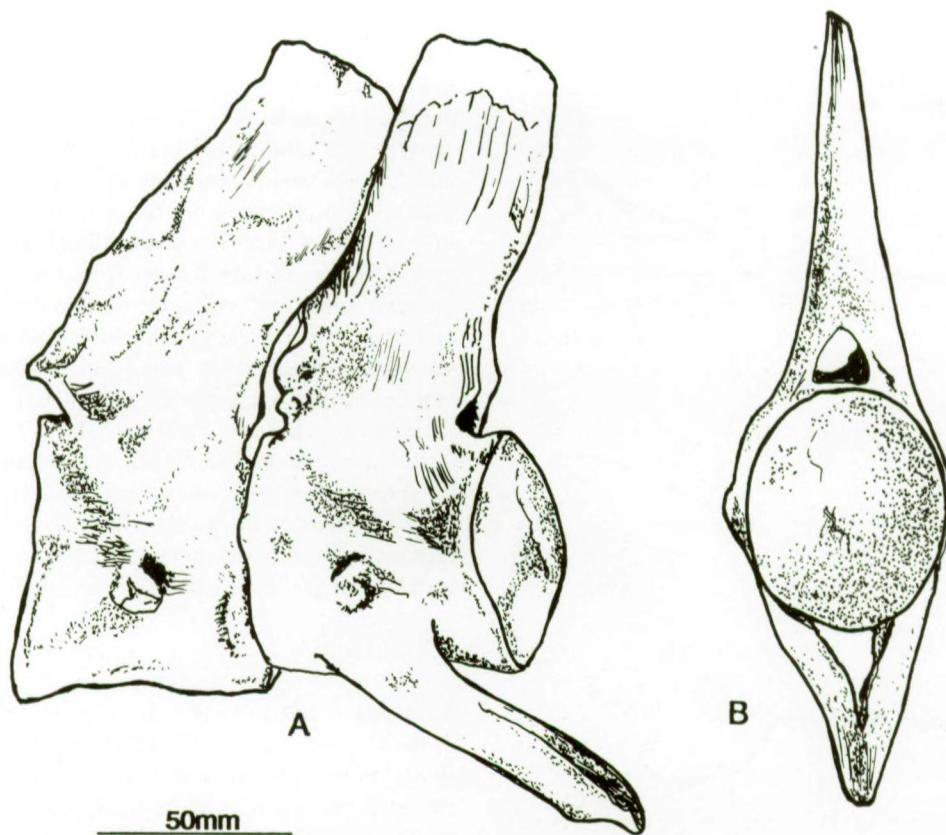


Fig. 47. - Two associated caudal vertebrae of *Prognathodon giganteus* (IRSNB R106); the lower portion of the right haemal arch is reconstructed.

preserved. Posteriorly, the articulation surface of the centrum is a deep well preserved condyle that presumably fitted into a correspondingly deep cotyle on the succeeding cervical vertebra. The latter is represented only by a fragment of the hypapophyseal peduncle. The posterior zygapophyses are fairly well developed but the corresponding prezygapophyses are absent. The neural spine although poorly preserved is almost entire and is posteriorly inclined.

*Cervical vertebra.* In a posterior cervical vertebra the size of the zygosphenes are approximately one quarter the size of the zygapophyses. The vertebra is badly distorted with the left side severely crushed and twisted. Despite this distortion, which has left the zygosphenes twisted and displaced somewhat from their position above the neural canal, they are quite well preserved, and may best be described as globular or tear-drop shaped projections. Unfortunately, owing to severe crushing in the posterior part of the vertebra, the zyantra are not visible. The zygosphenes of *Prognathodon giganteus* are massive even in relation to well developed zygosphenes of *Clidastes*, "*Platecarpus*" *intermedius* and *Ectenosaurus*. This is significant when for instance we consider it alongside RUSSELL'S (1967, p. 75) comment that in *Ectenosaurus* zygosphenes "... may attain a size as great as one sixth that of the zygapophyses..."

*Trunk vertebrae.* Quite unusually for a posterior trunk

vertebra the zygosphenes are even larger than those of the anterior trunk or cervical vertebrae. The vertebra shows other quite considerable differences compared with the anterior dorsals. The vertebral centrum is dorso-ventrally flattened with correspondingly flattened zygosphenes, but whether this is the result of post-mortem deformation or represents a genuine condition is not clear. Nevertheless the zygosphenes are massive, being about one half the size of the zygapophyses. Posteriorly the zyantra are clearly marked as deep excavations into which the zygosphenes of the succeeding vertebrae would have fitted.

RUSSELL (1967, pp. 75, 164) stated that zygosphenes in the cervical vertebrae of *Prognathodon* are "very small or absent...", a condition that had also been noted by previous authors (COPE, 1875, p. 153; WILLISTON, 1897a, p. 96). They are in fact present, and generally large in the Belgian forms. The zygosphenes in *P. giganteus* are unusually large, and although most of the vertebrae are missing or in a poor state of preservation, they are clearly present in several posterior cervicals and anterior and posterior trunk vertebrae. Zygosphenes and zyantra also occur in *P. solvayi*, thus clarifying a character that has caused considerable taxonomic confusion.

The very nature of the zyantra in mosasaurs, which are often no more than shallow excavations, accounts for their poor preservation even when the corresponding zygosphenes are prominent. This is the case except in such genera as *Clidastes* and *Ectenosaurus*. In *Clidastes*, the zygosphenes are not only relatively large in general but also have

well defined articular surfaces. A small *Clidastes* specimen BMNH 2946 observed by the senior author reveals that the zygantra are not simple excavations but bear matching articular surfaces for the zygosphenes, very similar to the condition seen in snakes and in some lizards. This condition is also present in *Mosasaurus lemonnieri* (IRSNB 3127 and IRSNB 3186).

**Caudal vertebrae.** One of the best preserved vertebrae in the poorly preserved postcranial remains belongs to the posterior caudal series. The vertebra is complete and undistorted. The neural spine is tall, laterally broad and posteriorly directed. The centrum is longer than deep. The articulation surfaces of the centrum consists of a fairly deep condyle and cotyle that are taller than wide. A small nubbin of bone represents the vestigial remains of the transverse process. The most important character, however, is the presence of fused haemal arches which are also evident on two fragments of vertebrae further along on the column. The latter character, like that of the zygosphenes, is of fundamental importance to the taxonomy of *Prognathodon* and has likewise been inaccurately reported in the literature. WILLISTON (1898b) observed striking resemblances between DOLLO's "*Prognathosaurus*" and the North American type specimen of *Prognathodon overtoni* (KU 950), and suspected that the two genera were identical. WILLISTON remained in doubt, however, because of confusion as to whether or not the chevrons were fused. WILLISTON (1898b) stated that the chevrons are co-ossified in the type of *P. overtoni* (KU 950), adding that DOLLO (1889b, p. 298) had originally indicated this to be the case in "*Prognathosaurus*" but had contradicted it on the following page by saying that the chevrons were free. This is a mistake on the part of WILLISTON because DOLLO throughout his comparison of *Prognathodon solvayi* with other mosasaurs (1889b, pp. 295, 296, 297, 298), clearly indicated that the chevrons are co-ossified to the vertebrae: e.g. "Par ses os chevrons, qui sont coossifiés avec les vertèbres..." (p. 295). WILLISTON's ambiguity has, however, caused confusion in the taxonomy of this genus. Unfortunately we have not been able to locate any caudal vertebrae of *P. solvayi* in the IRSNB collections and consequently cannot comment on whether haemal arches were fused or not in this particular species. The presence of fused haemal arches in *P. giganteus* is, however, perfectly clear.

### Taxonomic conclusions

The present study of the Belgian species of *Prognathodon* suggests a different view of both Old and New World species from that given by RUSSELL (1967, 1970).

*P. solvayi* and *P. giganteus* are regarded as very distinct species. *P. giganteus* seems to show greater similarity to the North American form SDSM 3393 referred to *P. overtoni*. *P. solvayi*, however, possesses several unique characters not observed in other species of the genus.

Functional zygosphenes and zygantra are present in *Prognathodon* with the possible exception of *P. overtoni*

(SDSM 3393). Fused haemal arches are present uniformly in all known caudal vertebrae of *Prognathodon* and thus *P. overtoni* (SDSM 3393) is not the exception, as suggested by RUSSELL (1967, 1970). In order to clarify the latter statement it is necessary to re-evaluate three taxa, "*Prognathodon*" *crassartus*, FMNH PR 165 referred to *Prognathodon* sp. by RUSSELL (1970) and "*Dollosaurus*" *lutugini*. In 1872 COPE (p. 278) named *Liodon crassartus*, which he subsequently described more fully as *Platecarpus crassartus* (1875, pl. 26). He noted that the humerus is "a most remarkable bone, having the outline of that of *Clidastes propython*, COPE but very much stouter, the anterior-posterior dimensions of the proximal extremity being greatly enlarged." (COPE, 1875, p. 153). WILLISTON (1898b, p. 180), however, in his monograph on American mosasaurs declared, "The species does not belong in the genus *Platecarpus*...". Instead, apart from the presence of free chevrons on the caudal vertebrae, he believed it to have strong relationships with his *Brachysaurus* (= *Prognathodon*), adding that it would perhaps be even better placed in DOLLO's *Prognathosaurus* (= *Prognathodon*). In a major revision of the systematics and morphology of American mosasaurs, RUSSELL (1967) appears to have been influenced by WILLISTON's misgivings by assigning COPE's *Platecarpus crassartus* to *Prognathodon*.

Comparison by the senior author of excellent figures on the material of *Platecarpus crassartus* (COPE, 1875, pl. 26, referred to *Prognathodon* by RUSSELL, 1967), with previously unidentified mosasaur material (BMNH R5868, partly represented in Fig. 50) consisting of a humerus, fragment of basioccipital, articular, quadrate, phalanges, tooth, and numerous vertebrae (from Arkansas, Marlbrook Marl) indicates that *Prognathodon crassartus* is almost certainly not referable to *Prognathodon*.

Specimen BMNH 5868 clearly belongs to the genus *Plioplatecarpus*, indicated by the highly diagnostic quadrate, basioccipital and numerous vertebrae of the vertebral series (LINGHAM-SOLIAR, in prep.). The well preserved humerus, however, is the most remarkable element of the material, being very powerfully constructed, with a massive pectoral crest, the largest recorded in the Mosasauridae. It closely resembles a poorly preserved humerus of the holotype specimen of *P. marshi* (IRSNB R38). DOLLO (1888, see explanation for plate VI) made particular reference to the proximal and distal elements of the bone, "pour montrer le caractère massif de l'os, caractère qui le distingue de la partie correspondante du *Lestosaurus* et du *Platecarpus*." What is most relevant is that this specimen is almost identical to the humerus of "*Prognathodon*" *crassartus* and shows little similarity to the humerus of *P. overtoni* (KU 950) figured by WILLISTON (1897d, p. 8, fig. 6). The vertebrae of BMNH R5868 also bear a very close resemblance to those of "*Prognathodon*" *crassartus*. In view of such strong diagnostic evidence, "*Prognathodon*" *crassartus* seems to be clearly referable to *Plioplatecarpus*.

FMNH PR 165, *Prognathodon* of RUSSELL (1970), is not referable to *Prognathodon* on the basis of the following characters: (i): Quadrate "... appears to closely resemble that of *Platecarpus* ..." (RUSSELL, 1970, p. 373). (ii) Bilo-

	<i>PROGNATHODON SOLVAYI</i>	<i>P. GIGANTEUS</i>	<i>P. OVERTONI</i> (SDSM 3393)	<i>P. OVERTONI</i> (KU 950)
Premaxilla	Ends bluntly. Anterior rostral surface smoothly continuous with dorsal surface of skull. No observable foramina for cranial nerve V.	Ends bluntly. Anterior rostral surface smoothly continuous with dorsal surface of skull. Foramina in parallel row either side of midline.	Ends bluntly. Anterior rostral surface smoothly continuous with dorsal surface of skull.	Absent.
Maxilla	Robust. Ventral margin straight. Tapers to a point posteriorly. External nares commence 2-3 max. tooth.	Appears robust. Ventral margin probably straight. External nares 2.	Robust. Ventral margin straight. External nares commence 3-4 max. tooth.	Robust. Ventral margin straight. Maxilla tapers to a point. External nares commence 2-3 max. tooth.
Frontal	No median ridge. Fronto-parietal suture almost straight.	Absent.	Median ridge present. "U" shaped fronto-parietal suture.	Fronto-parietal suture probably "U" shaped.
Postorbital-frontal	Extends to dorsal surface of squamosal.	Absent.	Extends to dorsal surface of squamosal.	Absent.
Jugal	Horizontal and vertical arms form a gentle curve. Postero-ventral process absent.	Arms probably at right angles.	Horizontal and vertical arms meet at right angles. Small postero-ventral process.	Absent.
Parietal	Parietal foramen large. Located on fronto-parietal suture. Deep grooves at juncture of parietal rami.	Absent.	Parietal foramen small. Located entirely within parietal. Junction of parietal rami smooth.	Parietal foramen probably small. Probably "U" shaped fronto-parietal suture.
Quadrate	Suprastadial and infrastadial processes broadly fused. Small oval meatus. Narrow convex condyle. Deep tympanum.	Very large meatus. Concave condyle. Deep tympanum.	Supra- and infrastadial processes broadly fused. Small constricted meatus. Narrow convex condyle. Deep tympanum.	Supra- and infrastadial processes broadly fused. Round meatus. Broad convex condyle. Deep tympanum.
Dentary	Dorsal margin highly concave. Posterior process on dentary absent.	Dorsal margin seems relatively straight.	Dorsal margin highly concave. Fairly large posterior process on dentary.	Dorsal margin highly concave. Incipient posterior process on dentary.
Surangular	Long, laterally flattened, tapering at both ends. Depression posteriorly for increased musculature. Recess for coronoid anteriorly.	Relatively broad both anteriorly and posteriorly.	Somewhat similar to that of <i>P. solvayi</i> in shape.	Absent.
Articular	Retroarticular process laterally compressed and laterally directed.	? laterally compressed.	Retroarticular process dorso-ventrally compressed and medially inflected.	Retroarticular process laterally compressed and laterally facing.
Coronoid	Large. Massive anterior and posterior wings laterally and anterior wing medially. Lateral wing may be slightly emarginate distally. Anterior process of coronoid ends flush with anterior process of surangular.	Very small coronoid. Lateral and medial wings small.	Similar to <i>P. solvayi</i> except eminence somewhat smaller. Lateral wing not emarginate distally. Anterior process abuts over surangular and makes contact with dentary.	Similar to <i>P. solvayi</i> except eminence is somewhat smaller and more rounded. Lateral wing may be emarginate. Incipient anterior process on coronoid.
Dentition	Teeth, 13 dentary, 12 maxillary, 8 pterygoidal. Marginal teeth - bicarinate, anteriorly highly procumbent, deeply striated or prismatic, anteriorly and posteriorly posteriorly recurved, moderately inflated. Pterygoidal teeth uncarinate, posteriorly recurved.	Marginal teeth smooth moderately inflated (less than KU 950) somewhat posteriorly recurved. Dentary teeth uniform in size?	Teeth, 14 dentary, 12 maxillary, 7 pterygoidal. Marginal teeth bicarinate, vertical, inflated, smooth, posteriorly recurved, increase in size posteriorly. Pterygoidal teeth very large.	Teeth, 13 dentary, ? 10 maxillary, smooth, inflated, bicarinate, probably uniform in size along ramus. Pterygoidal teeth very large and posteriorly recurved.
Vertebrae	Cervical and trunk vertebrae heart-shaped condyles; pygals, sub-circular. Zygosphenes/zygantra large and functional. Haemal spines not known.	Cervical condyles sub-circular, somewhat depressed. Caudal vertically elliptical. Haemal spines fused. Zygosphenes/zygantra large and functional.	Zygosphenes and zygantra incipient or absent. Haemal spines fused to centrum.	Cervical vertebrae heart-shaped. Pygal and caudal condyles sub-triangular. Zygosphenes and zygantra incipient or absent. Haemal spines fused.

Fig. 48. - Table of comparison of skull and jaw characters of *Prognathodon solvayi*, *P. giganteus*, (IRSNB R106), *P. overtoni* (SDSM 3393) and *P. overtoni* (KU 950).

bate channel on basioccipital for basilar artery. (iii) The "premaxilla is short and broad and is very similar to that of *Platecarpus*" (RUSSELL, 1970, p. 373). (iv) Haemal arches on vertebrae are free. (v) Massive postero-ventral process on the jugal.

The main characters RUSSELL (1970) used to refer FMNH PR 165 to *Prognathodon* appear to have been the bluntly terminating dentary and procumbent anterior teeth of the dentary and premaxilla. These conditions, however, also appear in *Plioplatecarpus* (DOLLO, 1889c, pl. 10).

The above characters indicate that PR 165 is a plioplatecar-

pine mosasaur possibly belonging to a large species of either *Selmasaurus* (see WRIGHT & SHANNON, 1988) or *Plioplatecarpus*. RUSSELL's (1970, p. 374) statement inadvertently supports our tentative assignment, "It is apparent from the foregoing description that the *Selma Prognathodon* may be distinguished from all known species of the genus with the exception of *P. [Prognathodon] crassartus*." Referral of *P. crassartus* to e.g. *Plioplatecarpus* makes this statement more understandable.

"*Dollosaurus*" *lutugini* (IAKOVLEV, 1901) shares most characters with *Prognathodon* (see RUSSELL's diagnosis 1967,

Measurements	<i>P. solvayi</i>	<i>P. giganteus</i>	<i>P. overtoni</i> (SDSM 3393)	<i>P. overtoni</i> (KU 950)
Length of skull along mid-line	600	e. 850	702	
Width of frontals between orbits	137	e. 250	188	
Length between 1st and 6th maxillary tooth	132	(245)	167	222
Height of quadrate	90	(130 - 140)	119	145
Length of lower jaw	660	(1150)	867	1146
Length of dentary	350	(610)	472	650
Length between 1st and 6th dentary tooth	122	(235)	167	193

Fig. 49. - Table of skull and jaw measurements in *Prognathodon solvayi*, *P. giganteus* (IRSNB R106), *P. overtoni* (SDSM 3393) and *P. overtoni* (KU 950), all in mm, e: estimated values, approximate values between brackets.

p. 70) but was excluded on the basis of two characters: the presence of large zygosphenes and zygantra and "... great enlargement of the first two dentary teeth..." (RUSSELL, 1967, p. 170).

Presence of functional zygosphenes in *Prognathodon* invalidates the first distinction. The second distinction is highly questionable (see IAKOVLEV, 1901, fig. 2 & our Fig. 51). The possession of fused haemal arches in "*Dollosaurus*" adds further evidence to support relationship with *Prognathodon*. Consequently *Dollosaurus* is here synonymised with *Prognathodon*.

*Prognathodon solvayi* demonstrates several characters that may be regarded as primitive for the genus — an almost straight fronto-parietal suture, a relatively flexible intra-mandibular joint, striated, moderately inflated teeth and a deep coronoid buttress.

THURMOND (1969, p. 75) first noted on sound diagnostic characters, that *Platecarpus curtirostris* is a form closely

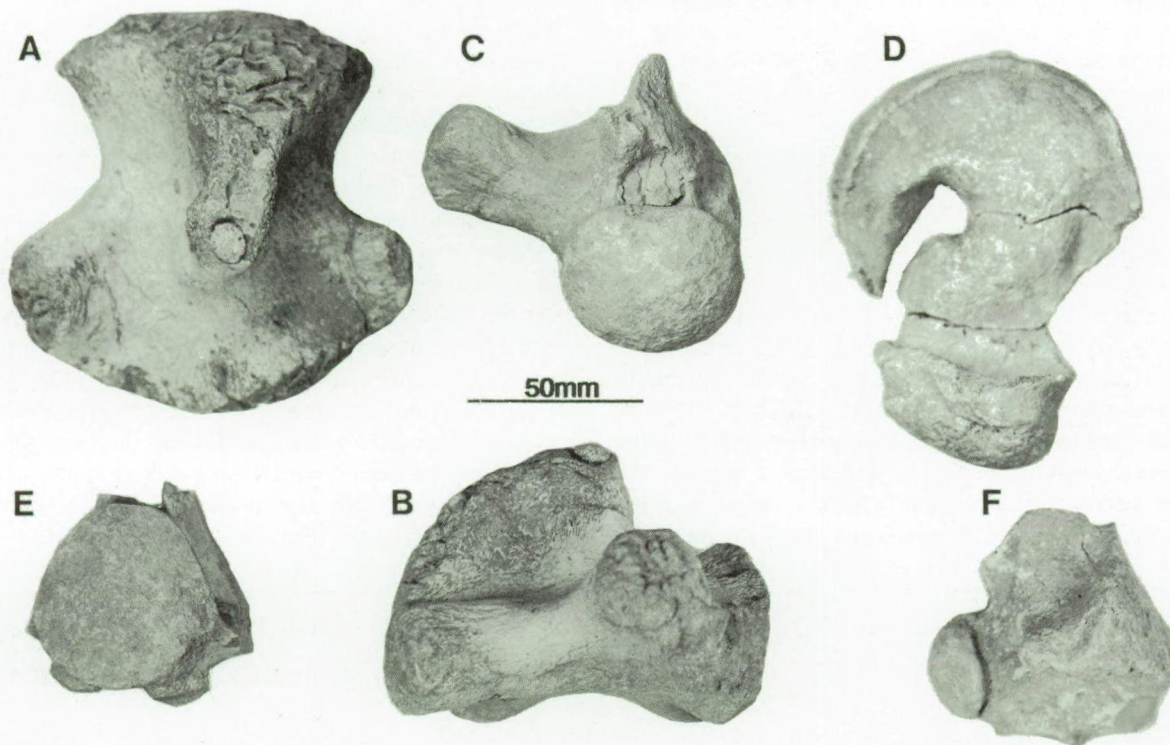
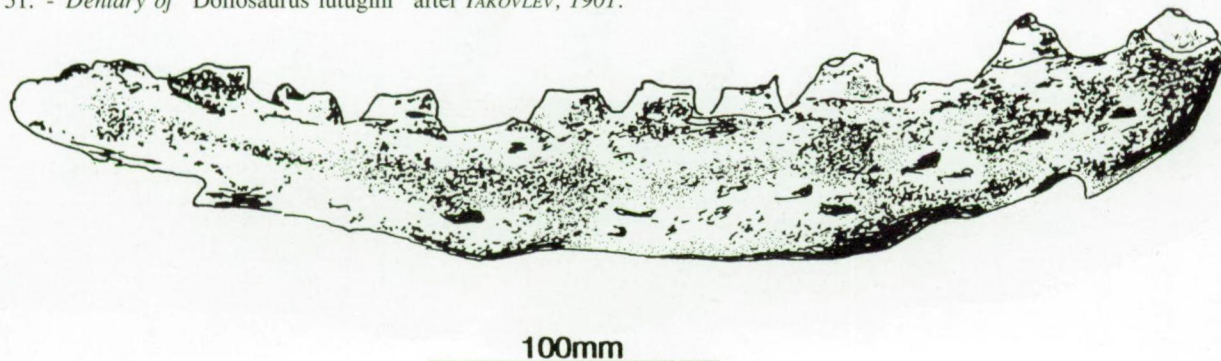


Fig. 50. - *Plioplatecarpus* sp. (BMNH R5868). A: flexor aspect of humerus; B: profile of humerus; C: posterior view of dorsal vertebra; D: lateral view of right quadrate; E: posterior view of caudal vertebra; F: cervical vertebra.

Fig. 51. - Dentary of "*Dollosaurus lutugini*" after IAKOVLEV, 1901.



related to *Platecarpus ictericus*, and probably descend from it. He added that the differences between these species suggest that *P. curtirostris* is a morphological intermediate between *P. ictericus* and *Prognathodon*. Characters expressed by *P. solvayi* such as deeply striated tooth crowns, slightly inflated teeth and moderately sized skull and body indicate that it may be the closest intermediate form between *Platecarpus curtirostris* and later species of *Prognathodon*.

It is noteworthy that in both North America and Europe, *Prognathodon* is represented by large and small forms: *P. giganteus* and *P. solvayi* in Europe and by *P. overtoni* (KU 950, the type) and SDSM 3393 (referred to this species by RUSSELL, 1967) in North America. Judging from this and the characters already discussed it is possible that KU 950 and SDSM 3393 are two different species but a closer examination of the material is necessary before a re-evaluation can be made (see Fig. 49).

Many of the complex characters of the mosasaurs discussed in this paper make it clear that a cladistic analysis is necessary in order to resolve them. The senior author is at present engaged in such an analysis of the European and African mosasaurs.

### Palaeoecology

#### *Feeding in mosasaurs*

Several authors (RUSSELL, 1964, 1967; CALLISON, 1967; WRIGHT & SHANNON, 1988) concluded that intracranial mobility in mosasaurs was reduced or completely lost in later or more derived forms. RUSSELL (1967, p. 65) indicated that kinesis was not an essential element in the feeding mechanism of mosasaurs and that "... perhaps the inertia of the bodies of larger prey or the viscosity of the aqueous medium in which mosasaurs lived impaired the

usefulness of the kinetic mechanism..." Furthermore inertial feeding as described by GANS (1961), whereby the prey is shifted towards the gullet using the inertia of the organism, was rejected by RUSSELL (1964, 1967) as ineffective in underwater swallowing and subsequently WRIGHT & SHANNON (1988) also excluded it on presumably the same grounds. In a rejoinder to RUSSELL, GANS (1969) made several noteworthy comments on inertial feeding, three of which may be summarized as follows:

- 1) Tossing small food objects in the air;
- 2) Releasing food object followed by upward acceleration of the jaws to the object;
- 3) Rotating the snout about an instant centre located near the braincase or neck region and sawing off the prey in chunks.

The first two methods could conceivably have been employed by mosasaurs in surface feeding. It is possible also that the third method may have been adapted by some forms of mosasaurs to underwater feeding and it will be briefly mentioned later.

The problems of underwater feeding have been discussed in detail in the literature (GANS 1961, 1969; RUSSELL, 1967) but perhaps one advantage should be mentioned. BRAMBLE & WATER (1985) noted (and observed in *in vivo* experiments on *Chelydra serpentina*) that aquatic turtles such as *Chelydra*, *Chrysemys* and some *Clemmys* cannot continue feeding unless permitted to submerge their heads in water. The intraoral and pharyngeal fluid pressure evidently played an important part in deglutition in these forms and may have also facilitated underwater feeding in mosasaurs. Probably the most important advance in mosasaur feeding, however, was behavioural, involving selective feeding and in the handling of manageable sizes of prey rather than indiscriminate attempts at swallowing the largest possible food item. This development probably occurred concomitantly with a reduction and eventual loss of a functionally kinetic skull in later forms of mosasaurs. POUGH (1979)



Fig. 52. - Jaw of *Mosasaurus hoffmanni* (IRSNB R25).  $\times 1/2$ .

pointed out some of the hazards of unselective predation, for example instances are seen in snakes (with a somewhat similar mechanism of food intake) that die from choking or suffocating because of an indiscriminate swallowing of overly large prey. Large lower jaws belonging to specimens of *Mosasaurus hoffmanni* (IRSNB 1503, 1559) may illustrate the tale of over-gluttonous mosasaurs — the dentaries have pathologic deformations, what apparently are rehealed breaks of the dental rami, perhaps of mosasaurs both figuratively and literally trying to bite off more than they could chew. Other explanations for the breaks are tenable, for instance they may have occurred as an outcome of using the snout in ramming opponents, a view which might fit in with the purportedly aggressive disposition of these animals.

It is generally believed that a functional streptostylic quadrate (FRAZZETTA, 1962, 1982; RUSSELL, 1964, 1967; ROBINSON, 1966; CALLISON, 1967), which presumably was useful in retraction of the mandibles and pterygoids thereby facilitating drawing the prey into the gullet, was retained in all known mosasaurs. However in a study of *Varanus exanthematicus*, SMITH (1980, p. 779) was able to demonstrate that streptostyly was not "... primarily important for the forward movement it imparts to the lower jaw adduction during hard biting." Of significance also, was SMITH's (1980, p. 779) corroboration of THROCKMORTON's findings that "... streptostyly is independent of movement of the palato-maxillary segment (mesokinesis)." In the Mosasauridae, in contrast to *Varanus*, the derived condition, mentioned earlier, was probably increased cranial mobility (including probably a functional mesokinetic axis). This we believe was directly related to the mode of feeding in the early forms of mosasaurs. In certain later forms of mosasaurs, however, loss of mesokinesis (and possibly a firmer quadrate/squamosal joint) may have helped effect a form of hard biting analogous to that of *Varanus exanthematicus* (SMITH, 1980). This view may be supported by the condition in which the suprastapedial and infrastapedial processes of the quadrates of *Globidens* and *Prognathodon* are fused, conceivably to counteract the generation of strong vertical forces during hard biting.

As yet we have no real idea of how diverse mosasaurs were in their predatory behaviour. MASSARE's (1987) study was the first attempt to establish some of the parameters of predation among the various reptile groups, illustrated graphically in pyramids of tooth function and guild composition among Mesozoic marine reptiles. Based on tooth shape she identified five major types of tooth function (cut, pierce, smash, crunch, crush) among mosasaurs of the Coniacian to Campanian and Campanian to Maastrichtian. She found that the mosasaurs of the Coniacian-Campanian fall dominantly in the "cut" guild and that by Campanian-Maastrichtian they again fall dominantly in the "cut" guild with one exception, *Globidens* falling into the "crush" guild, "... the first occurrence of this type of predator among marine reptiles since the placodonts of the Triassic", (1987, p. 134). The overall picture though is one of a lack of diversification of predator types among mosasaurs (and marine reptiles in general) although MASSARE (1987)

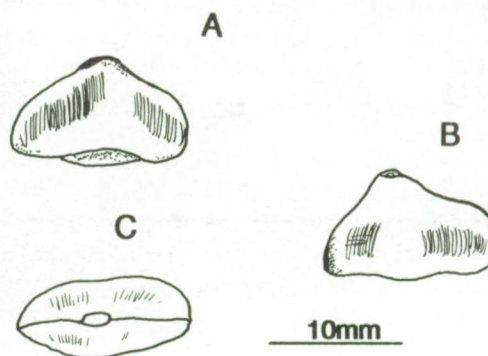
added a significant point, that the appearance of the highly specialized mosasaur *Globidens* "... may have marked the beginning of a radiation by mosasaurs. Events at the Cretaceous Tertiary boundary however ended the reign of reptiles and the large marine predators." To emphasize this point, as well as to place the feeding behaviour of *Prognathodon solvayi* and *P. giganteus* in context, a few examples of mosasaur radiation just prior to their extinction are discussed below, essentially viewed as MASSARE (1987) did through dentition and feeding. The forms discussed may at first glance not be as obviously specialized as e.g. *Globidens*. In some, for example *Goronyosaurus nigeriensis* (AZZAROLI *et al.*, 1972, 1975; SOLIAR, 1988; LINGHAM-SOLIAR, in press), the adaptations involved are of a complex of characters which probably played an even greater role in the diversification of predation in mosasaurs than any single character.

In 1924 DOLLO separated the Belgian species *Compressidens fraasi* and *C. belgicus*, (both Upper Maastrichtian) from *Globidens*, a view supported by RUSSELL (1975) but opposed by several authors (for example von HUENE, 1935; ARAMBOURG, 1952; ANTUNES, 1964 and RAAB, 1963). THURMOND (1969) replaced the preoccupied name *Compressidens* with *Carinodens*.

The slender jaws and peculiar teeth of *Carinodens fraasi* and teeth of *C. belgicus* are unique in the Mosasauridae. The teeth of *C. fraasi* are mildly inflated, somewhat laterally compressed and unicuspid. In general form and size, the tooth of *Carinodens belgicus* is similar to that of *C. fraasi* but differs in one important respect: the tooth is tricuspid, a unique condition in the Mosasauridae.

It seems fairly certain that the teeth and dentary of *Carinodens fraasi* are too delicate to have withstood the kind of crushing of heavy shelled molluscs generally attributed to the robust jaws and dentition of *Globidens* (see RUSSELL, 1975). It is clear too that the dentition of *Carinodens fraasi* did not function primarily in piercing because the tips are relatively blunt indicating a grinding role, especially evident in the multi-cusped tooth crowns of *C. belgicus*. In lizards, however, it is difficult to form a hypothesis on the type of predation based solely on tooth morphology (which manifest considerable variation in a single dental ramus). Mosasaur tooth morphology on the other hand is fairly

Fig. 53. - Tooth crowns of *Carinodens fraasi* (IRSNB 6521). A : lingual view; B : buccal view; C : dorsal view.



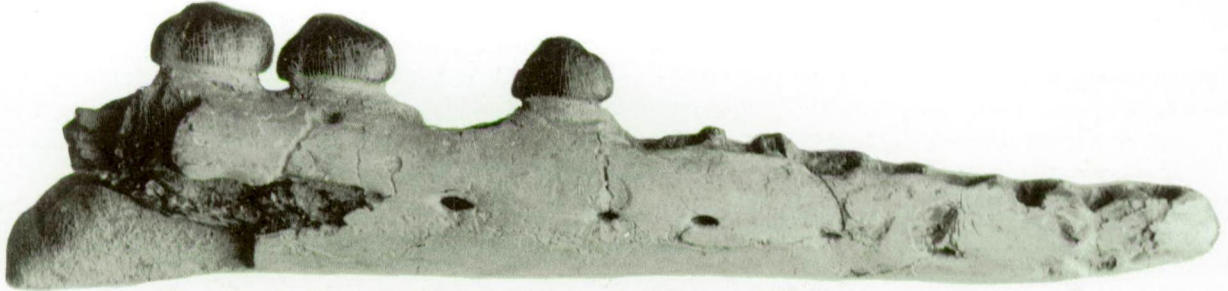


Fig. 54. - Dentary of *Carinodens fraasi* (IRSNB R43).  $\times 4/5$ .

constant along the dental row and may therefore give a reasonable idea of the type of predation.

Judging by the size of the jaws *Carinodens* was probably the smallest mosasaur known and appears to have filled a new ecological niche, that of a durophagous mosasaur specialized for feeding upon invertebrates with thin shells such as *Nautilus* and certain forms of crustaceans. The apical cusps on the teeth would presumably have been suited to crushing and shredding the thin shells and tests of such prey.

Mosasaur from Niger (LINGHAM-SOLIAR, in press) include a durophagous mosasaur based on a stout dentary and several tooth bases and the remains of teeth all poorly preserved. The teeth are large, dome shaped, lacking a constriction at the base and are covered with very fine parallel striae (approx. 65-70 per tooth). The mosasaur probably did not belong to the genus *Globidens*. Of significance, again referring to MASSARE'S (1987, p. 131) tooth guilds, is the fact that the teeth of this mosasaur appears to fit into the "crunch" guild — an entirely new guild for mosasaurs.

The unusual African mosasaur *Goronyosaurus nigeriensis* (AZZAROLI *et al.*, 1972, 1975; SOLIAR, 1988; LINGHAM-SOLIAR in press) has a remarkable series of deep lateral pits between the teeth on the exceptionally long jaws, a unique condition in mosasaurs. It is evident from this that the long straight pointed teeth of *Goronyosaurus* (probably no more than ten, the lowest number seen in mosasaurs) interdigitated by fitting into the lateral pits of the opposing rami. This together with very small eyes, probably an enhanced sense of smell, and a tactile snout leads the senior author to believe that *Goronyosaurus* may have subsisted in darker estuarine conditions feeding on the highly evasive and slippery young of other marine animals, perhaps even of mosasaurs. It seems probable that the highly specialized dentition was used in spearing the prey by rapid snapping of the very long jaws as in certain fossil marine crocodiles such as *Rhabdognathus* and *Dyrosaurus* (BUFFETAUT, 1979; HALSTEAD, 1979).

In overall terms *Plotosaurus* CAMP, 1951 (= *Kolposaurus* CAMP, 1942; non SKUPHOS, 1893) was perhaps one of the most highly evolved genera in the Mosasauridae. The distinguishing characters of the jaws and dentition are the slender and elongate skull, long jaws armed with numerous pointed, slightly posteriorly recurved teeth — 20 on each side of the upper jaw and 17 on each dentary, 15 pterygoid

teeth (in each element the highest number of teeth found in mosasaurs) and exceptionally large eyes. The battery of teeth probably served as a very efficient fish trap not dissimilar to that seen in plesiosaurs (see AUGUSTA, 1960; BROWN, 1981). The postcranial skeleton was very advanced as well and it is believed (CAMP, 1942; RUSSELL, 1967, p. 120) that *Plotosaurus* was probably among the faster swimming mosasaurs. This together with an acute sense of sight, suggested by the large eyes, may support the hypothesis that it specialized in feeding upon fast possibly surface swimming fish. The specialized fish-eating adaptations appear to be further supported by CAMP'S (1942) findings on the stomach contents of *Plotosaurus*, which reveal that fish was part of the diet.

It is of interest to note the stratigraphic position of *Plotosaurus*, which CAMP (1942, p. 26) records "may be younger than any previously recorded Maestrichtian mosasaur." Perhaps the most unusual mosasaur predators belong to the genus *Prognathodon*. It is frequently assumed that *Prognathodon* and other plioplatecarpines may have been efficient deep water diving forms, a view based on a "deep tympanic ear" and/or the presence of a calcified tympanic membrane and the assumption that such a condition served to withstand pressures at great depth (DOLLO, 1905; ABEL, 1912; CAMP, 1942; VAUGHN & DAWSON, 1956; KAUFFMAN & KESLING, 1960).

The hypothesis that *Plioplatecarpus* and *Prognathodon* were divers, based on such evidence as calcified or thick

Fig. 55. - Right quadrate of *Plioplatecarpus houzeaui* (IRSNB R36), lateral view.  $\times 2/3$ .







Fig. 56. - An ammonite with possible mosasaur tooth marks [*Placenticerus meeki*, IRSNB unregistered]; conch : 35 cm diameter; from the Bearpaw Formation (Late Campanian - Early Maastrichtian), St. Mary River, NW of McGrath, Alberta, Canada).

tympanic membranes is questionable because, at least as far as calcification of the tympanic membrane is concerned, it may have been more common in mosasaurs than previously realised. The senior author has observed it in two of the subfamilies, the Mosasaurinae (e.g. *Clidastes* sp. BMNH R2946) and the Plioplatecarpinae (e.g. *Platecarpus ictericus* BMNH R4001) in addition to our observations in the figured *Plioplatecarpus* (IRSNB R36).

The feeding behaviour of *Prognathodon* is intriguing and was first brought to attention in an interesting paper by KAUFFMAN & KESLING (1960) on an ammonite conch bitten by a mosasaur and a further paper (KAUFFMAN, KESLING & SCHMIDT, 1961). They stated that the mosasaur "was most likely a deep diver of the Platecarpinae [*Plioplatecarpinae*], a close relative of *Platecarpus brachycephalus* [nomen dubium] and *Ancylocentrum* [*Prognathodon*] *overtoni*, and a feeder on large cephalopods" KAUFFMAN & KESLING, 1960, p. 235). RUSSELL (1967) reaffirmed the view that it was a mosasaur bite judging from the tooth marks and tooth patterns, and that it was probably that of *Prognathodon overtoni*. Subsequently, similar mosasaur tooth impressions have been recorded on a hollow spined *Anapachydiscus peninsularis* specimen (SAUL, 1979).

KAUFFMAN & KESLING (1960) noted that the bones of mosasaurs, mainly Platecarpinae, have been found in the Pierre Shale adding that "In the beds of central South Dakota, the presence of high sea forms (possibly divers) suggests that the beds were off-shore outer shelf deposits. Since great numbers of large cephalopods were available on and above the mud bottoms, it is quite likely that they were included in the diet of certain mosasaurs."

An ammonite from the Bearpaw Formation (Late Campanian - Early Maastrichtian), Alberta, Canada in the collec-

tion of the IRSNB, *Placenticerus meeki* (IRSNB, unregistered), also bears tooth impressions somewhat similar to that described by KAUFFMAN & KESLING and possibly belonging to a mosasaur e.g. *Prognathodon overtoni*.

Taking into account KAUFFMAN & KESLING's extensive description of the ammonite conch bitten by a mosasaur (1960) and in particular the proposal that the mosasaur in question may have been *Prognathodon overtoni*, it is nevertheless arguable that hard shelled cephalopods such as ammonites were a regular diet of *P. overtoni*. According to RUSSELL's figure (1967, fig. 90) the most robust teeth are situated posteriorly on the dental ramus with the more slender pointed teeth anteriorly. Such dentition might imply an omnivorous diet with ammonites being probably no more than incidental prey. The general robust morphology of the jaws of *P. overtoni* (SDSM 3393) and the massive skull would be consistent with such a hypothesis. The teeth of *P. giganteus* also show certain characters, for instance somewhat pointed posteriorly recurved tips and moderately inflated tooth crowns which would seem inconsistent with specialization for a molluscivorous diet. In fact they are no more modified for such feeding behaviour than for instance the tooth crowns of *Hainosaurus* or *Tylosaurus*.

Insofar as *Prognathodon solvayi* is concerned it is all the more improbable that the dentition would have been effective in crushing heavy shelled molluscs as has been suggested for other species of *Prognathodon*. Deep striae are not a usual feature of teeth specialized for crushing (cf. placodonts, HALSTEAD, 1975; SUES, 1987). The skull of *P. solvayi* is nevertheless powerfully constructed in an animal of otherwise moderate proportions. Using figures from the length of the temporal arcade over the overall skull length

RUSSELL (1975) calculated the power of the jaw musculature in several mosasaurs. *Globidens dakotaensis* was found to have the highest ratio at 0.27 with *Prognathodon overtoni* second at 0.22. We found that *P. solvayi* has a ratio very close to that of *P. overtoni* at 0.21. What then was the function of such a massively built skull? To attempt to answer this we need to consider, at least briefly, the potential food source available to *P. solvayi*. For the purpose of this discussion the vertebrate fauna is not discussed although fish, and small forms of turtles and crocodiles may have been incidental prey types.

Certainly the contemporaneous invertebrate fauna was biologically wide despite the difficulty of quantifying certain forms which leave little trace in the fossil record. Of those of which there is a reasonable certainty of presence and here regarded as a possible food source for mosasaurs, the following may be contemplated (DHONDT, pers. comm.):

- Mollusca: large populations of soft bodied belemnites, numerous bivalves (e.g. oysters, pectinids, limids, spondylids and inoceramids), some gastropods (not often preserved because of aragonitic shells), scaphopods (perhaps too small for predation by moderately large mosasaurs);
- Brachiopoda: very numerous but small;
- Echinodermata: certain large forms of echinoids;
- Arthropoda: crustaceans are difficult to specify as to whether they are crabs or lobsters because they are only known from the burrows and a few claws.

It seems reasonable to assume that the hordes of soft bodied belemnites, sharing with mosasaurs the marine environment of the Cibly region during the Late Cretaceous, afforded a rich food source for *Prognathodon solvayi* with its well adapted powerful cranial morphology. However, it is conceivable too that invertebrates such as octopuses and other unshelled cephalopods were also utilised as a food source, although records are scanty because of their poor fossilization. It is not hard to understand that the strong jaws and powerful musculature of the massive temporal region of the skull would have been especially effective for grasping the tough bodies of such prey and it seems that the deeply striated teeth were used in piercing and gripping rather than for crushing.

There are two points about the coronoid that are noteworthy from a functional perspective. The high almost vertical posterior wall of the coronoid allows for an increased insertion area for the M. adductor mandibulae. In addition the angle of muscle insertion on a high coronoid eminence could theoretically have been closer to the horizontal axis of the skull than in a reduced flattened coronoid, thereby supplying a greater antero-posterior component to the muscle action and facilitating an increased force in this direction. This would have been particularly effective in an animal with a powerful gripping dentition (which included massive pterygoid teeth) to draw in or hold onto powerful prey.

A method of devouring prey in some marine animals involves a powerful rotational movement of the head around a central point. ALEXANDER (1967) described a similar method of feeding in sharks, whereby they grasp the prey

loosely by the teeth, chunks are then sawed off with the animal held by its own inertia, while the shark rotates around the long axis of the skull. While we do not propose such a sophisticated technique in mosasaurs it is possible that they may have seized and momentarily released prey in a rotational motion in order to repeatedly inflict puncture wounds in different regions of the prey's body.

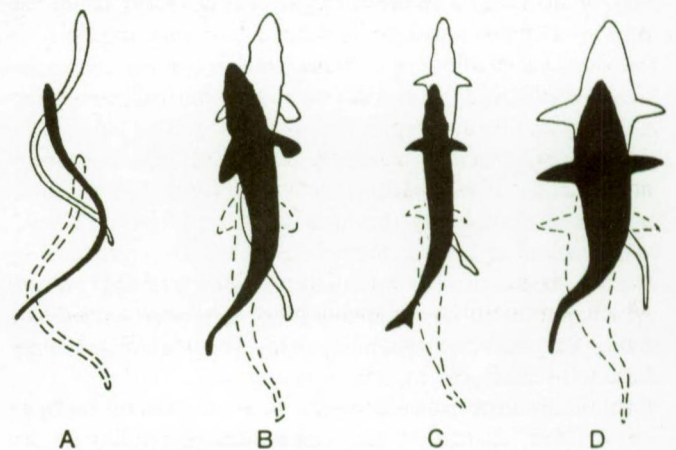
The procumbent teeth are a curiosity of *P. solvayi*. It is probable that these may have increased gape and facilitated the entry of large prey. It seems more likely, however, that *Prognathodon* foraged the shallow sea bed floor uprooting potential prey submerged in the mud or secreted under rocks and that the procumbent anterior teeth formed a primitive scoop in the nature of, but not as well developed as that of the placodonts (see AUGUSTA, 1960; HALSTEAD, 1975; SUES, 1987).

#### Swimming in mosasaurs

It is generally believed (e.g. LIGHTHILL, 1969; CARROLL, 1985; ALEXANDER, 1989) that the streamlined, spindle-shape of Jurassic and Cretaceous ichthyosaurs, together with lunate tails like those of active swimmers such as tunas and dolphins, meant that they too may have been similarly fast swimmers. Mosasaurs on the other hand possessed long relatively narrow bodies with the caudal skeletal morphology suggesting that they did not possess semilunate tails. It seems likely therefore that the mode of swimming involved lateral undulations of the body (anguilliform, RUSSELL, 1967) as in for example, marine crocodiles.

The undulatory form of locomotion has, however, been found to be a rather vague term as there are clearly very many levels of efficiency within this form of swimming (see BRAUN & REIF, 1985). More recently KÜHNKE (1982) suggested that mosasaurs swam in the axial subundulatory mode. MARSHALL (1971) defined this as subanguilliform, LINDSEY (1978) as subcarangiform and McFARLAND (1979) as carangiform. In contrast Jurassic and Cretaceous ichthyosaurs are regarded as suboscillatory swimmers, the main thrust coming from the tail (see BRAUN & REIF, 1985), a

Fig. 57. - *Swimming modes in marine vertebrates (after LINDSEY, 1978).*



form of swimming unlikely to have been achieved by the mosasaurs.

The essential difference from the undulatory mode is that in the axial subundulatory mode, the term we shall use, a significant part of the body is stiffened. With less of the body thrown into undulations it must follow that there is a reduction of induced drag and energy loss, and at least from a hydrodynamic perspective this leads to a more efficient swimming mode. Recent tetrapods using the axial subundulatory mode include crocodiles, Salamandridae, Iguanidae, Otariidae (otters) and *Castor* (beavers) and included in early reptile groups are Mesosauridae, early Ichthyosauria and Placodontia (BRAUN & REIF, 1985).

Stiffening the vertebral column in order to minimise flexion in the non propulsive region of the body in such long bodied reptiles as mosasaurs must have presented a considerable problem. Mosasaurs may have, however, achieved such stability and stiffness of the vertebral column in two evolutionarily distinct ways.

In one group of mosasaurs exemplified by *Plotosaurus*, probably one of the most advanced mosasaurs, CAMP (1942, p. 25) accounts for its advanced aquatic adaptations by such factors as "... extreme reduction of chevrons and zygapophyses... development of a more powerful swimming tail and less flexibility of the body than in varanid lizards and early mosasaurs. Related to this is the fact that the condyles in *Plotosaurus* are slightly more flattened than in *Clidastes* and *Platecarpus*." *Plotosaurus* also appears to have the most contracted paddles within the Mosasauridae (see RUSSELL, 1967; CARROLL, 1985). However, from more recent evidence it seems likely that *Plioplatecarpus marshi* possessed the most highly efficient hydrofoil shaped paddles (LINGHAM-SOLIAR, in press).

The second method of stabilizing the vertebral column, and more widespread, may have been in the provision of accessory articulations on the vertebrae such as zygosphenes and zygantra (LINGHAM-SOLIAR, in press).

The only functional reference to zygosphenes and zygantra in mosasaurs is by SWINTON (1930) who believed that the presence of such accessory articulations was probably age related, developing in older, larger mosasaurs in order to take up the excess weight load. This seems unlikely; in some of the largest mosasaurs, such as the tylosaurs and hainosaurs, zygosphenes and zygantra are either rudimentary or absent. In addition zygosphenes and zygantra are present in distinct taxa, regardless of size, such as *Clidastes* (among the smallest of mosasaurs) *Mosasaurus*, *Prognathodon solvayi*, *P. giganteus* and *Dollosaurus* (referred to *Prognathodon* in this paper).

In mosasaurs such as *Mosasaurus*, *Clidastes*, *Ectenosaurus* and *Prognathodon*, stiffness and stability of the vertebral column was probably increased by the presence of zygosphenes and zygantra. Such forms are also identified by the possession of deep articulatory surfaces of the centrum which were perhaps somewhat more spherical, a condition which may indicate swimming with powerful lateral undulations of the body.

One of the problems envisaged in strong lateral motions of the body is torsion, i.e. dorso-ventral bending of the

vertebral column and loss of efficiency, a problem also encountered in snakes. The above mentioned mosasaurs may have solved such a problem in a fundamentally similar manner to that achieved in snakes, by the presence of zygantra and zygosphenes. As noted by EDWARDS (1985, p. 165) "... snake vertebrae are replete with accessory processes that combat torsion, so that the ventral component of the muscle action would [not] be wasted energy." It is also conceivable, although more tentatively proposed, that the zygosphenes and zygantra contributed to a stiffer vertebral column. Simultaneous contraction of the intercostal muscles on both sides of the anterior part of the body would have locked the zygosphenes and zygantra into place providing strong stabilization of the vertebral joints and preventing unnecessary rotation of the spine along the long axis, and lateral flexion. The necessary lateral undulations for forward propulsion is achieved by individual movements of the vertebra in the posterior regions of the body. This type of muscle coordination is not inconceivable in reptiles, to use GASC's (1976) description in snakes "stiffness of the whole and segmentary mobility can therefore co-exist."

These functional speculations must be considered as tentative. With more data on snake morphology and musculature which EDWARDS (p. 166) points out "... is at a very primitive level..." some of the questions on mosasaur swimming may be resolved although no more than a general comparison is made.

However, not all mosasaurs used the axial subundulatory mode of swimming. From recent evidence it seems reasonably certain that one form, *Plioplatecarpus marshi*, employed a unique mode of swimming in the Mosasauridae - subaqueous flight (LINGHAM-SOLIAR in press).

Mosasaurs of the Phosphate Chalk of Ciplly and Tuffeau of Maastricht show a highly diverse morphology and with more detailed information being assembled on the other taxa we hope to get a more explicit idea of mosasaur ecotypes.

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A



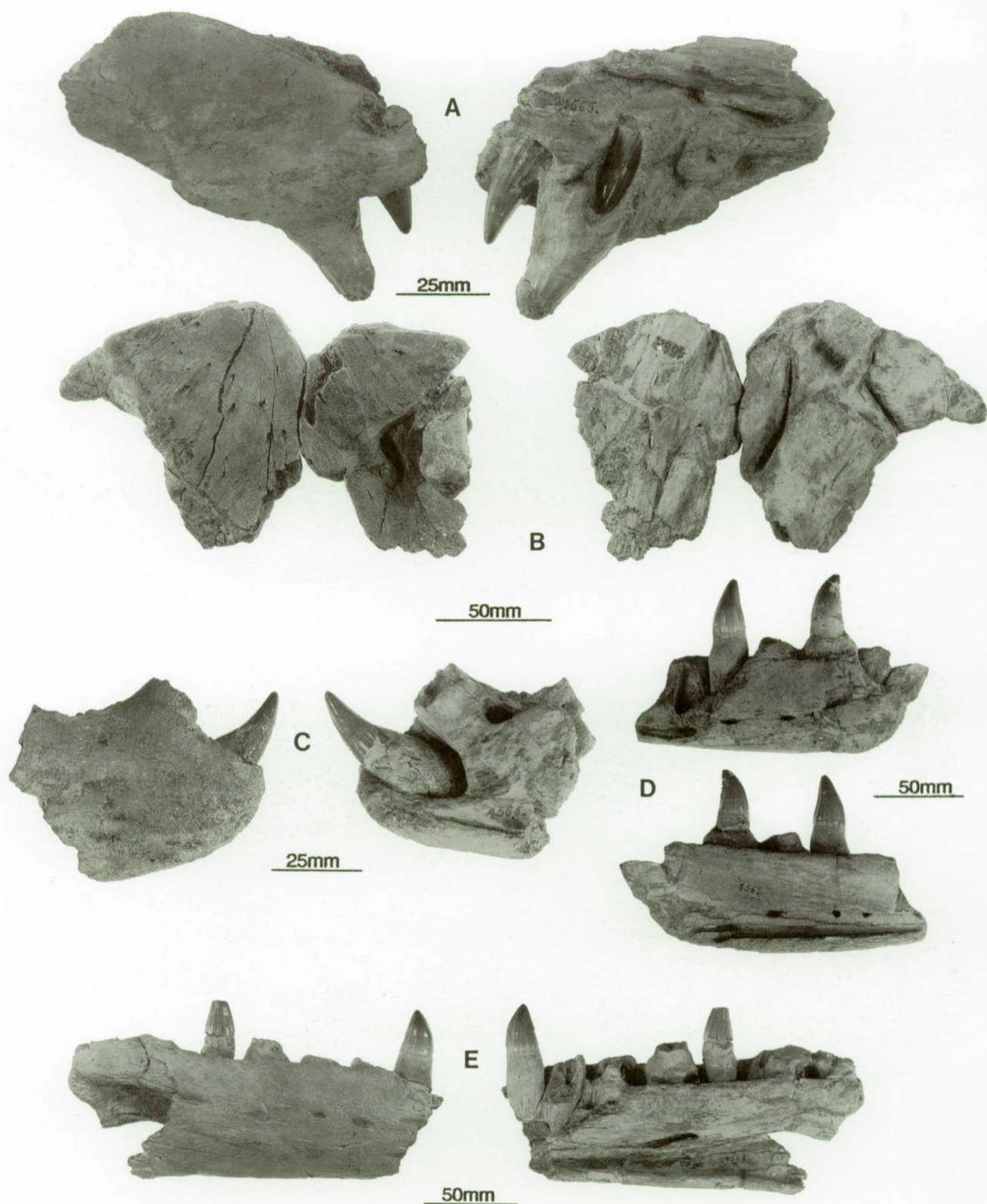
100mm

B



PLATE 1

*Prognathodon solvayi* (IRSNB R33). Skull and mandibles. A : right lateral; B : dorsal.



## PLATE 2

*Prognathodon solvayi* (IRSNB R107). A : lateral and medial views of fragmentary maxilla; B : dorsal and ventral views of fragmentary frontals; C : lateral and medial views of anterior fragment of dentary; D : lateral and medial views of fragment of left dentary; E : lateral and medial views of fragment of right dentary.



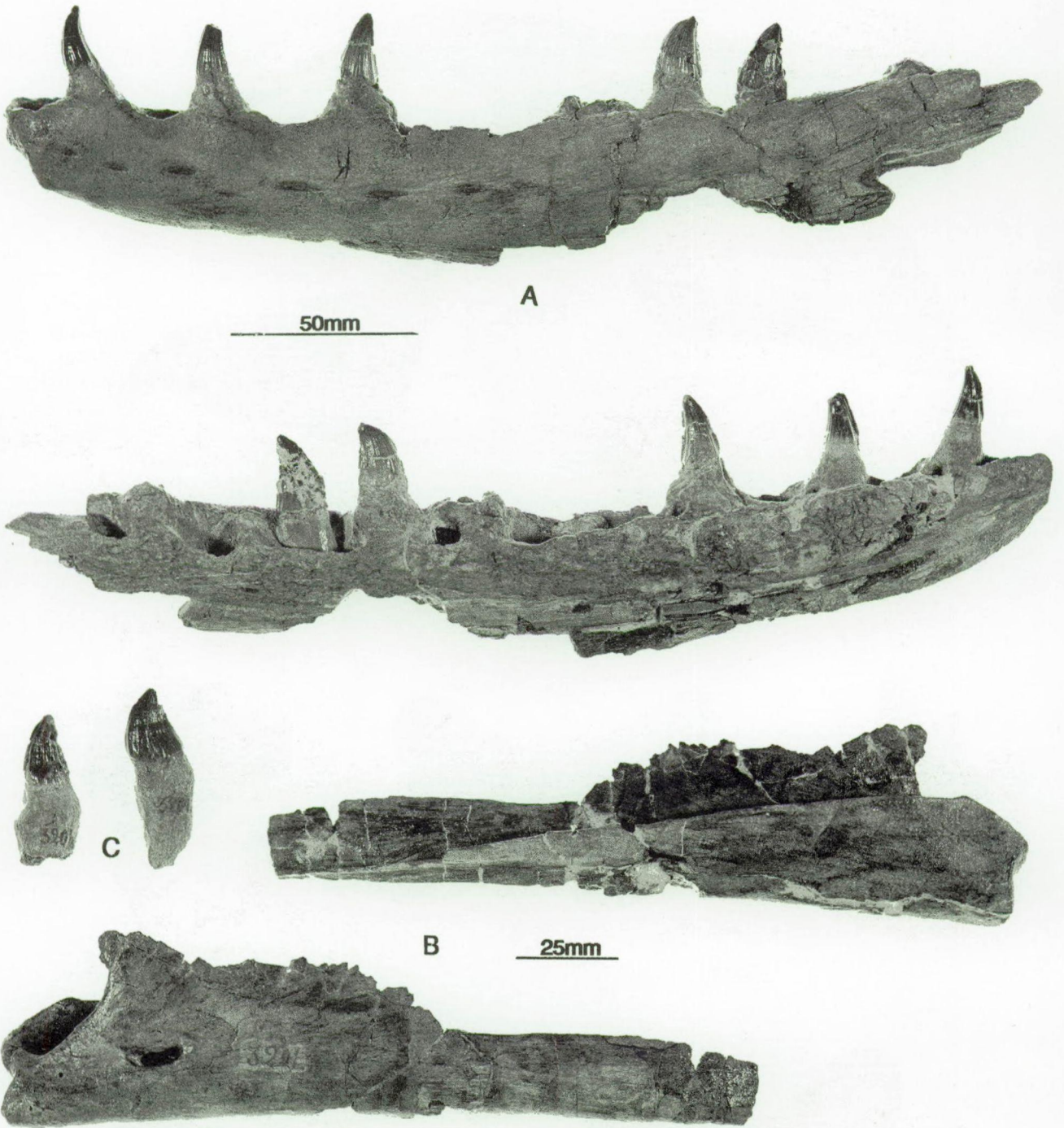
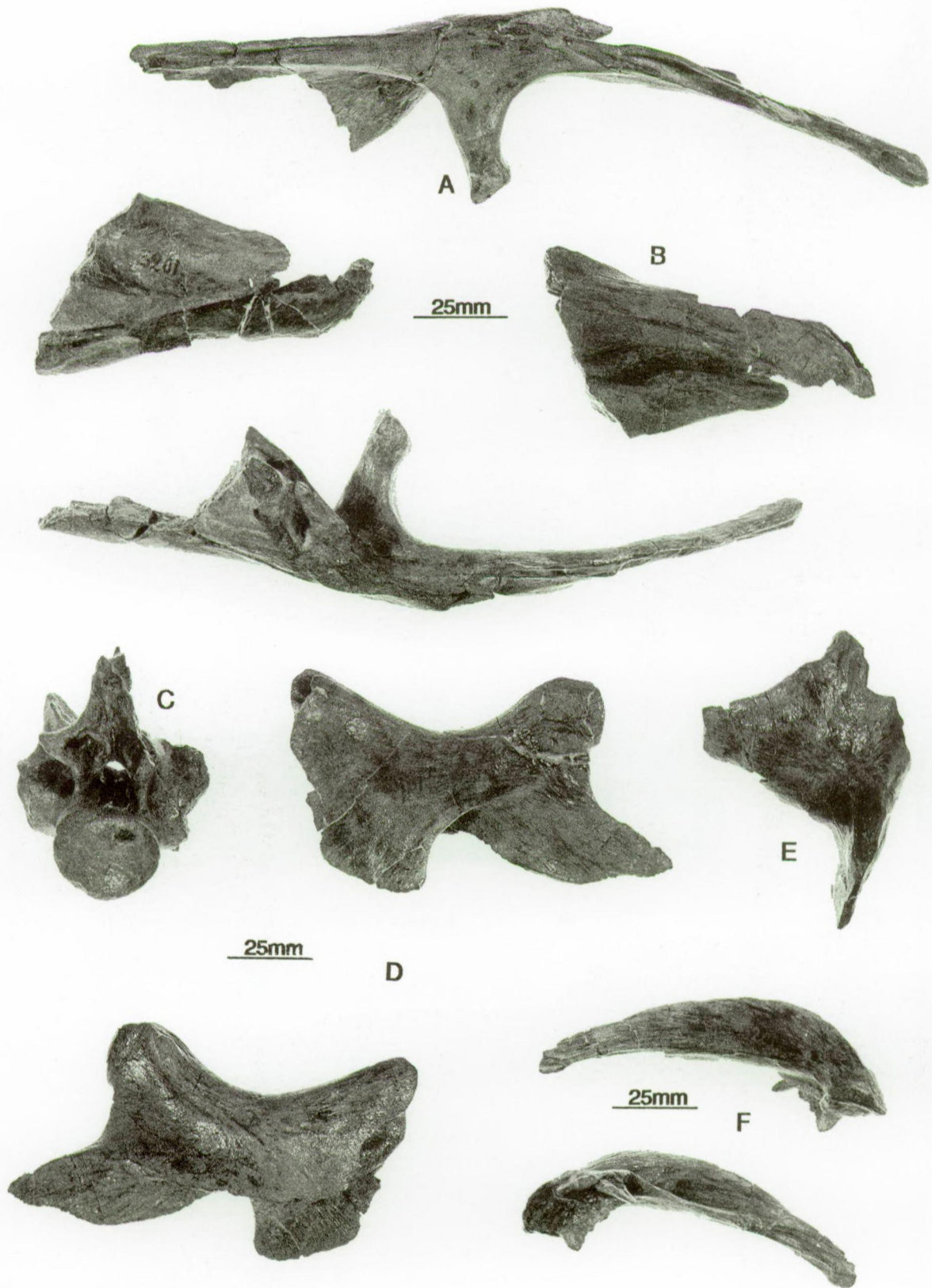


PLATE 3

*Prognathodon solvayi* (IRSNB R108). A : lateral and medial views of left dentaries; B : lateral and medial views of left splenial; C : lingual view of disassociated maxillary teeth.



## PLATE 4

*Prognathodon solvayi* (IRSNB R108). A : lateral and ventral views of pterygoid; B : lateral and medial views of prefrontal; C : posterior view of dorsal vertebra; D : lateral and medial views of coronoid; E : medial view of postorbitofrontal; F : lateral and medial views of squamosal.

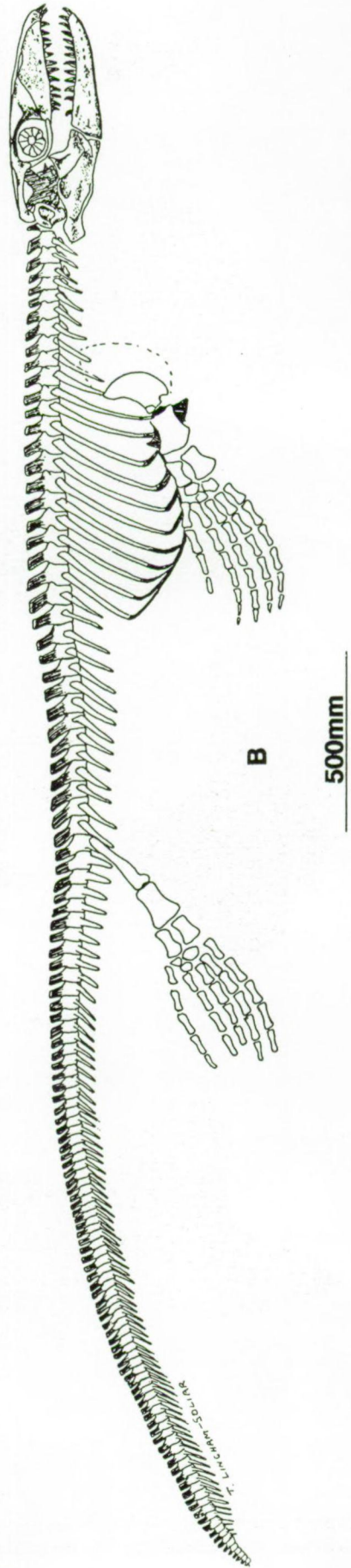
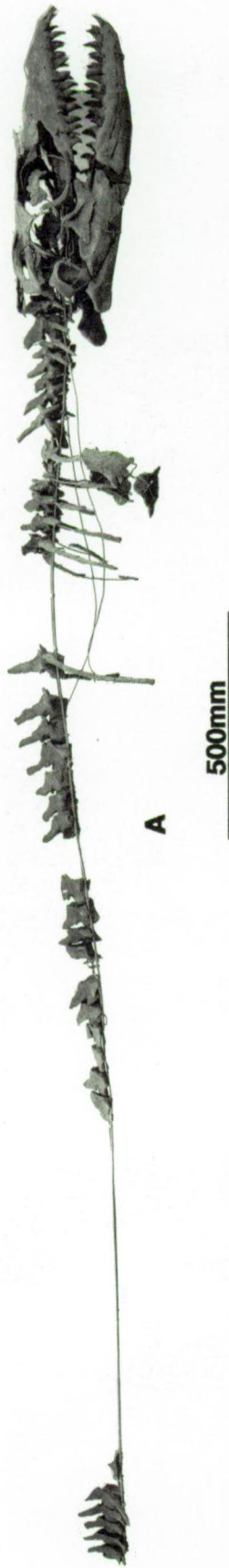
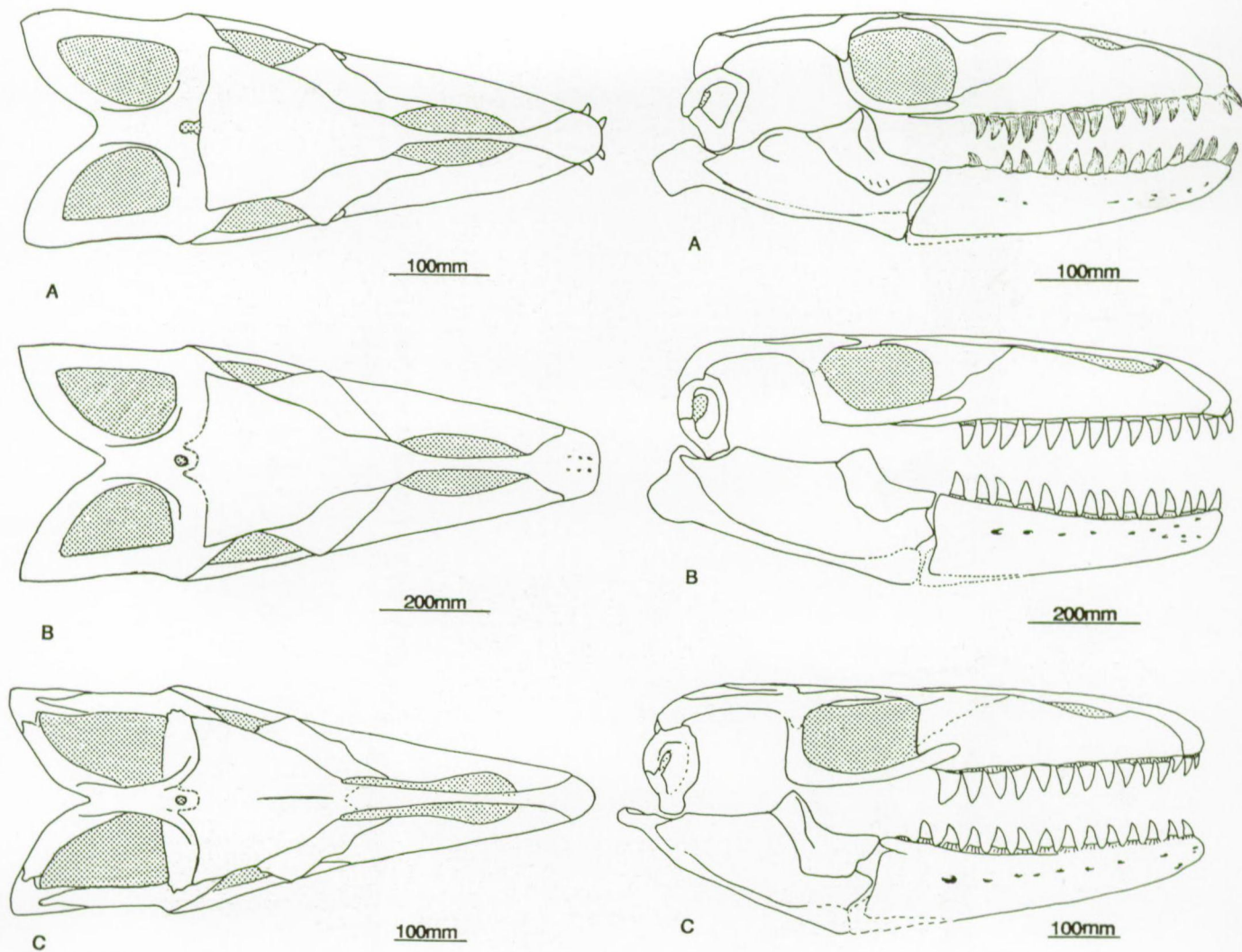


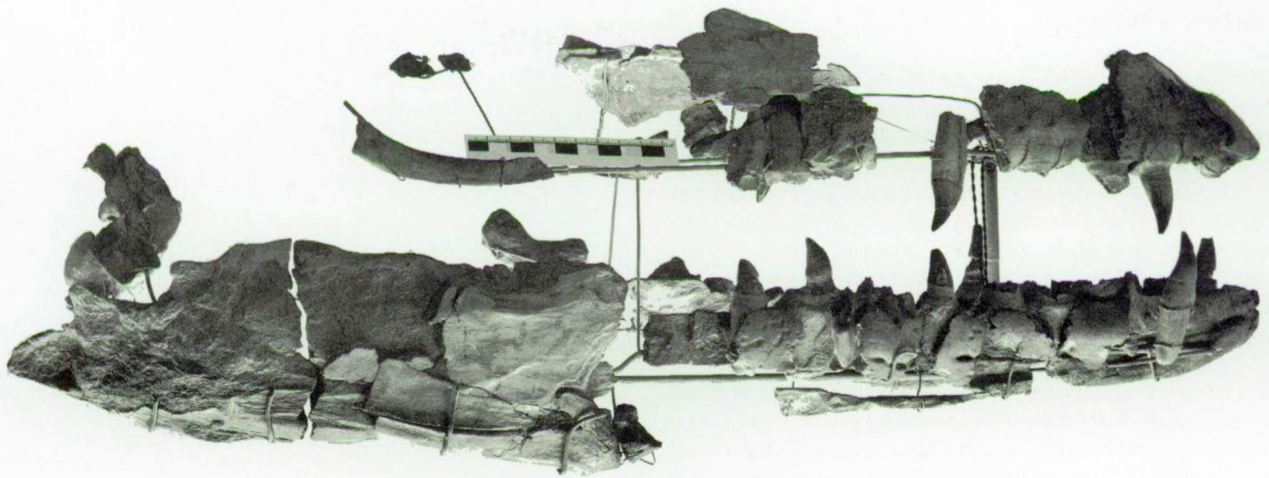
PLATE 5

*Prognathodon solvayi* (IRSNB R33). Skeleton.



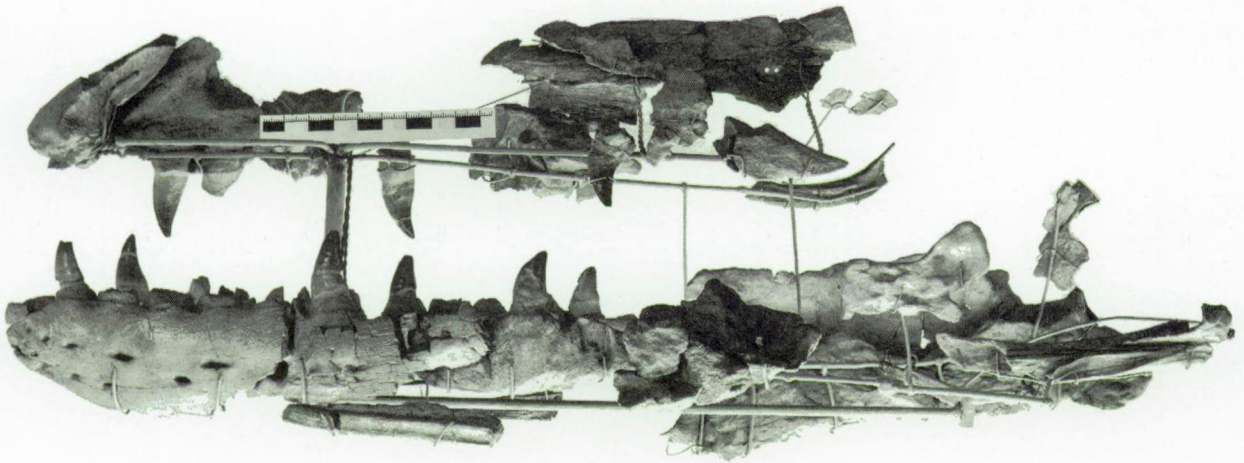
## PLATE 6

Comparison between skulls of A : *Prognathodon solvayi*; B : *P. giganteus* and C : *P. overtoni* (SDSM 3393). (i) : lateral views; (ii) : dorsal views.

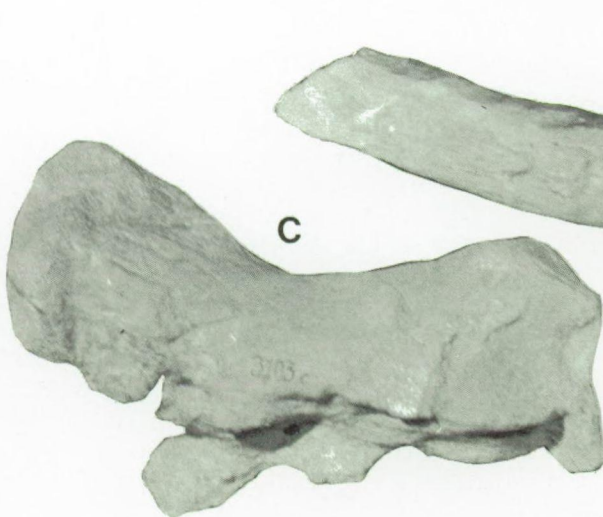


A

200mm



B



C

50mm

## PLATE 7

A : fragmentary skull and mandibles of the holotype of *Prognathodon giganteus* (IRSNB R106), right and left lateral views; B : detail of right jugal, medial view; C : detail of left coronoid, medial view.

**Note added in proof :**

Confirmation of the author's suggestion that *Prognathodon* was probably not particularly adopted to ammonite predation has come to light in a recent study by Hewitt and Westermann (in press) on the ammonite *Placenticerias* from the Upper Cretaceous of Alberta, Canada. Their results suggest that the shell wall of *Placenticerias* did not break into fragments like that of *Nautilus* (which implodes when punctured) but buckled around point loads. From this they concluded that the complexity of the ammonite septal sutures provided a strong but flexible support for the shell wall against ambient pressure and point loads.

Their findings may account for the presence, in parts of North America, of a large number of fairly intact ammonite shells with mosasaur tooth impressions (besides those of other animals e.g. sharks). Access into the shell, for consumption of the soft parts as suggested by Kaufmann and Kesling (1960), seems inconsistent with the above study.

HEWITT, R.A. & WESTERMANN, G.E.G., (in press). Mosasaur predation on the ammonite *Placenticerias* from the Upper Cretaceous Bearpaw Formation of Alberta, Canada. *Canadian Journal of Earth Sciences*.