

The Mosasaur *Plioplatecarpus* (Reptilia, Mosasauridae) from the Upper Cretaceous of Europe

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Abstract

This study represents the first extensive description of the genus *Plioplatecarpus* DOLLO 1882, from the Maastrichtian of Belgium and The Netherlands. It is based primarily on holotype and previously undescribed material. Unusual characters of the skull roof, the basioccipital and the jaws and dentition are examined and the character states assessed where possible. A reliable formula for the vertebral column is provided, based on perhaps the most complete *Plioplatecarpus* known, a specimen of *P. houzeaui*. Taxonomy, feeding, as well as the alleged behaviour of deep diving, are discussed, contrasting frequently with previous views. The ecology of *Plioplatecarpus* is mentioned in the light of recent material discovered in Africa and on documentation of the North American *P. primaevus*. It also takes account of recent information on the use of underwater-flight in *P. marshi*

Key-words: *Plioplatecarpus*, taxonomy, feeding, ecology, diving, underwater-flight

Résumé

Cette étude est la première description approfondie des représentants du genre *Plioplatecarpus* DOLLO, 1882, provenant des dépôts maastrichtiens de Belgique et des Pays-Bas. Elle se base principalement sur le matériel-type et sur des spécimens non-décrits antérieurement. Des particularités de la voûte crânienne, le basioccipital, les mâchoires et la dentition sont examinés et la valeur de ces caractères est discutée dans la mesure du possible. Une formule fiable est établie pour la colonne vertébrale sur base du spécimen sans doute le plus complet de *Plioplatecarpus*, appartenant à l'espèce *P. houzeaui*. La systématique, l'alimentation ainsi que le prétendu comportement de plongeur en eau profonde sont discutés; les conclusions contrastent, dans de nombreux cas, avec les vues antérieures. L'écologie de *Plioplatecarpus* est abordée la lumière du matériel nouvellement découvert en Afrique et de la documentation concernant *P. primaevus* d'Amérique du Nord. L'information récente concernant la pratique du "vol sous-marin" chez *P. marshi* est également pris en considération.

Mots-clefs: *Plioplatecarpus*, taxinomie, alimentation, écologie, plongée, "vol sous-marin".

Introduction

In the early days of research on the Mosasauridae, mosasaur material was invariably "lumped" together in a single genus, *Mosasaurus*. But even earlier than this, when the first mosasaur was simply referred to as the "Grand animal de Maestricht", FAUJAS-ST-FOND (1799), in his beautifully illustrated work, figures, as miscella-

neous shark teeth, the first specimen, a tooth crown, referable to *Plioplatecarpus*. This remarkable plate also shows the teeth of two mosasaurs, *Leiodon* and *Carinodens*, unknown at the time (LINGHAM-SOLIAR, 1992).

During MARSH's visit to the IRSNB, he recommended that a specimen of *Mosasaurus hoffmanni* should be assigned to *M. gracilis* on the basis of the slender, posteriorly recurved teeth (DOLLO, 1882), since it clearly did not belong to any of the known species of mosasaurs. However, OWEN's (1851-1864) *Mosasaurus gracilis*, from the chalk of Offham, Sussex, on the other hand, was later regarded by LYDEKKER (1888) as the predaceous fish, *Pachyrhizodus* [a view, according to WOODWARD (1906), endorsed by O. C. MARSH]. Although WOODWARD (1889) initially agreed with LYDEKKER he subsequently (WOODWARD, 1906) endorsed OWEN's opinion. My observation of the relevant material favours LYDEKKER's (1888) opinion that it belongs to a fish. It is therefore curious that MARSH should have used this name if he regarded *Mosasaurus gracilis* a fish, as alleged by WOODWARD.

The Belgian specimen, including material described by UBAGHS (1879) is, however, undoubtedly mosasaurian and DOLLO (1882) soon after renamed it *Plioplatecarpus marshi*, in honour of Professor MARSH.

DOLLO's descriptions of *Plioplatecarpus marshi* are exceedingly brief: "teeth are long slender and recurved; crowns faceted and striated and subcircular in cross-section; cervical hypapophyses articulated; zygosphenes absent; chevrons free; coracoid emarginated; humerus massive and phalanges subcylindrical; two posterior lumbar vertebrae fused to form a sacrum" (DOLLO, 1882, p. 64).

BAUR (1892) later criticized DOLLO's (1890) erection of a new family, the Plioplatecarpidae, to accommodate the single genus *Plioplatecarpus*, being satisfied instead of its affiliations with *Mosasaurus*. He particularly criticized the "sacrum", the basioccipital canal, and the interclavicle characters. Subsequently, DOLLO (1894) recanted and synonymised the Plioplatecarpidae with the Mosasauridae. However, there is no doubt today that DOLLO was right in his original judgement, even if some of the characters he used are incorrect.

Abbreviations

BMNH: British Museum (Natural History). Department of Palaeontology. Cromwell Road, London SW7 5BD. U.K.

IRSNB: Institut Royal des Sciences Naturelles de Belgique, rue Vautier 29, B-1040 Brussels, Belgium.

NHMM: Natuurhistorisch Museum Maastricht, de Bosquetplein 7, Maastricht, The Netherlands.

TSMHN: Teylers (Stichting) Museum, Haarlem, The Netherlands.

Cranial abbreviations used in the text:

Cranial morphology: a, angular; ar, articular; bo, basioccipital; bs, basisphenoid; bt, basiptyergoid process; che, cerebral hemispheres; cor, coronoid; d, dentary; ec, ectopterygoid; en, external naris; f, frontal or frontal suture; gl, intermandibular articulation; IAM, internal auditory meatus; j, jugal; l, lacrymal; m, maxilla or maxillary suture; op, opisthotic; of, olfactory lobe; p, parietal or suture for parietal; paf, parietal foramen, pmx, premaxilla; pof, postorbitofrontal or suture for postorbital frontal; popr, paroccipital process of opisthotic; pr, prootic;

pra, prearticular; prf, prefrontal or suture for prefrontal; pt, pterygoid; q, quadrate; sa, surangular; sp, splenial; sq, squamosal; st, supratemporal; sta, stapes; tym, tympanum; vc, vidian canal Cranial nerves: V, trigeminal nerve; VI, abducens nerve; VII, facial nerve; VIII, acoustic nerve, a, anterior branch, p, posterior branch; IX, glossopharyngeal nerve; X, vagus nerve; XI, accessory nerve; XII, hypoglossal nerve.

Stratigraphic position of the material from The Netherlands and Belgium

Most specimens of *Plioplatecarpus* came from the St. Pietersberg and from the townships Sibbe, Eben-Emael, and Zichem near Maastricht (Fig. 1). The greater part of this material was discovered in the "Tuffeau de Maastricht" (type Maastrichtian = Maastricht Formation of Felder, 1975), specifically in the Nekum Chalk (Fig. 2). The only exceptions are the mosasaur material described

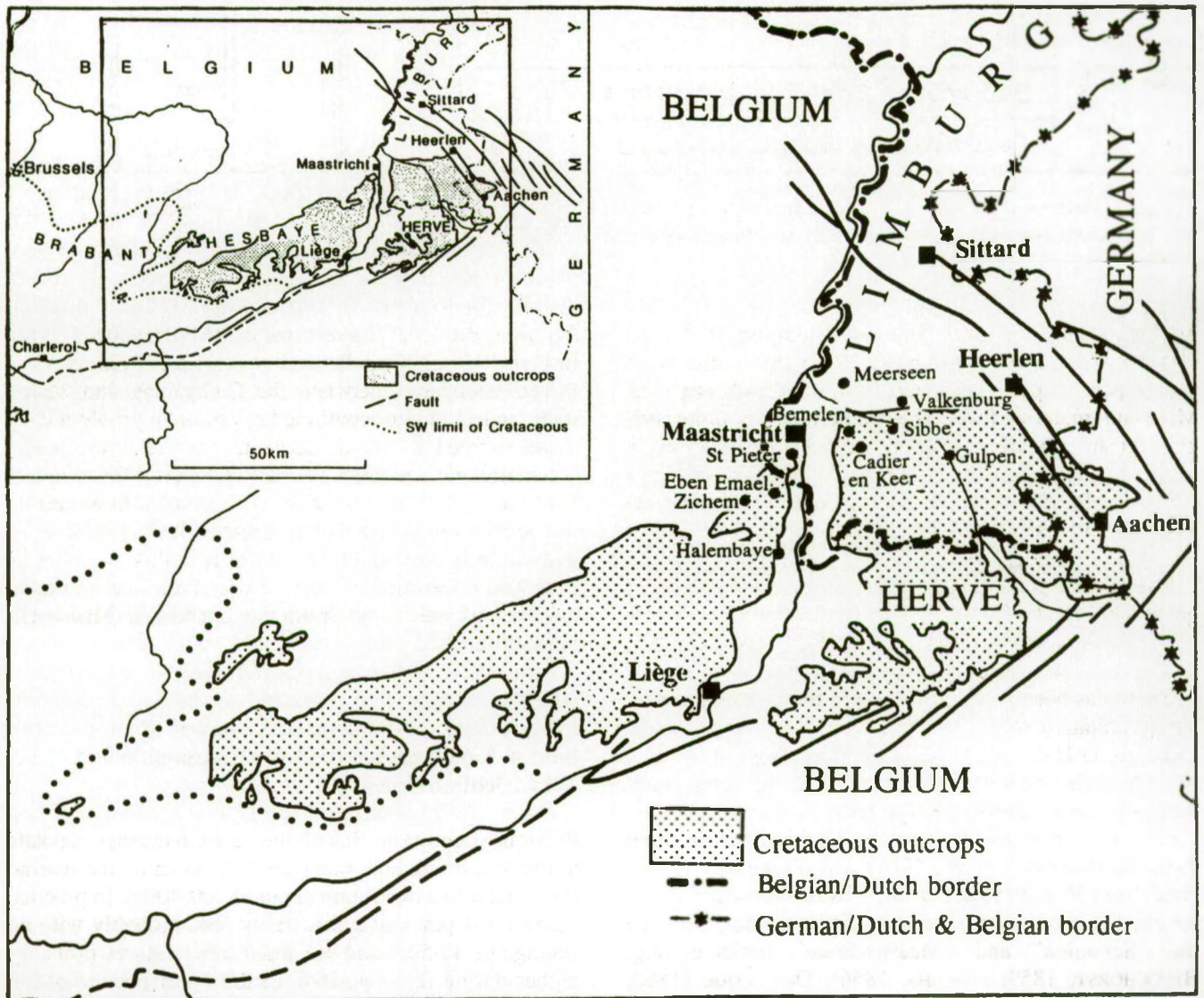


Fig. 1 — Geological and locality map of the Cretaceous Chalk of Belgium and The Netherlands showing some of the most important localities connected with this study. Inset after KENNEDY, 1987.

				PALAEOGEOGRAPHY				
				WATER DEPTH	DISTANCE TO SHORE	TEMPERATURE	WATER ENERGY	
Maastricht Fmn.	Upper	Meerssen Chalk	casimirovensis Zone	shallow	nearshore	warm	high	
		Nekum Chalk						
	Lower	Emael Chalk	junior Zone					
		Schiepersberg Chalk						
		Gronsveld Chalk						
		Valkenburg Chalk						
Gulpen Fmn.	Upper	Lanaye Chalk		cimbrica Zone	deep	offshore	temperate	low
		Lixhe Chalk 3						
		Lixhe Chalk 2						
		Lixhe Chalk 1						
	Lower	Vijlen Chalk						
		Beutenaken Chalk	obtusa Zone					
		Zeven Wegen Chalk	mucronata Zone					

Fig. 2 — Belemnite zonation of the uppermost Campanian and Maastrichtian (separated by wavy line) in South Limburg (after KENNEDY, 1987) and main variations in palaeoecological conditions based on ROBASYNSKI *et al.*, 1985.

by UBAGHS (1879) and material belonging to Mr R. GARCET (CASE, 1976; GARCET, 1982) that came from the Upper Gulpen Formation, Lanaye Chalk (Fig. 2). Mosasaur material from The Netherlands is quite striking in its remarkably good surface preservation in contrast to material from the Phosphatic Chalk of Ciply (Hainaut, Belgium) which shows considerable surface abrasion and distortion. Unfortunately most of the Dutch material is fragmentary and disarticulated.

The Maastrichtian type section occurs in the E.N.C.I quarry, below the Lichtenberg farm, at the Sint Pietersberg near Maastricht (Figs. 1 & 2) (ROBASZYNSKI *et al.*, 1985).

There has been some confusion in the past concerning the delimitation of the Maastrichtian in the Netherlands. OMALIUS D'HALLOY (1808, cited from ROBASYNSKI *et al.*, 1985) first reported the presence of the calcarenite, named by him "Tuffeau". The term "calcaire de Maestricht" was subsequently used by DUMONT (1832, cited from ROBASYNSKI *et al.*, 1985) and d'ORBIGNY (1840, cited from ROBASYNSKI *et al.*, 1985). Historically, however, the problem has been in distinguishing between the "Senonien" and "Maastrichtian" horizons (e.g. BINCKHORST, 1859; UBAGHS, 1866). DEWALQUE (1868, cited from ROBASYNSKI *et al.*, 1985) on the other hand was the first to clearly distinguish between the "Senonien" and "Maestrichtien" and RUTOT (1894) used for

the first time the correct form "Maastrichtian" (for further discussion see ROBASYNSKI *et al.*, 1985, p. 9).

The boundaries between the Campanian and Maastrichtian in Limburg continued to present a problem until it was agreed at the Symposium on Cretaceous stage boundaries held at Copenhagen (October, 1983) to keep the base of the Maastrichtian close to the appearance of *Belemnella lanceolata* (ROBASZYNSKI *et al.*, 1985).

As far as this study is concerned, this problem is essentially academic because most of the mosasaurs in the Netherlands came from the uppermost Maastricht Formation.

Palaeoecology and palaeoenvironment of the Limburg area during Late Campanian and Maastrichtian times.

Previous suggestions that all the Late Cretaceous deposits in the Maastricht area had been laid down on the marine shelf, point to a maximum depth of 200-400m. In practice the water depth was considerably less, probably with an average of 40-50m and sea water temperatures probably higher during the deposition of the upper portion of the Maastricht Formation when the main Tethyan currents reached the Maastricht area. A representation of the variations in palaeoecological conditions in the Campa-

nian-Maastrichtian of South Limburg, based on ROBASYNSKI *et al.* (1985), is presented in Figure 2.

According to JELETZKY (1955), representatives of the genus *Belemnitella* are generally associated with a warm-water environment and representatives of the genus *Belemnella* with a cold-water environment. ROBASYNSKI *et al.*, (1985) have suggested that this could be an explanation for the disappearance of the genus *Belemnitella* and the appearance of *Belemnella* at the transition of the Campanian/Maastrichtian and the reappearance of *Belemnitella* and disappearance of *Belemnella* at the end of the Lower Maastrichtian. It seems from this that the Campanian and Maastrichtian deposits in the Limburg area were laid down in a nearshore water depositional regime with changing temperatures (ROBASYNSKI *et al.*, 1985, p. 18). Furthermore, the shallow waters and high energy level in the Upper Maastricht Formation (Fig. 2) presents a taphonomic picture that may partly account for the generally disarticulated and broken nature of European *Plioplatecarpus* material.

For the geological setting and palaeoecology of the material from the Ciply Phosphatic Chalk of Belgium, see LINGHAM-SOLIAR & NOLF (1989).

Systematic Palaeontology

Order SQUAMATA OPPEL, 1811

Family MOSASAURIDAE GERVAIS, 1853

Subfamily PLIOPATECARPINAЕ (WILLISTON), 1897

1884 *Plioplatecarpidae* DOLLO: 653.

1890 "mosasauriens microrhynques" DOLLO: 163.

1897 *Platecarpinae* WILLISTON: 177.

1967 *Plioplatecarpinae* RUSSELL: 148.

EMENDED DIAGNOSIS. Short skull. No rostrum anterior to premaxillary teeth. Maximum twelve teeth on maxilla. External nares large. Moderate to large-size quadrate; large suprastapedial process with parallel sides, may be fused to infrastapedial process or almost touching. Cranial nerves X, XI and XII leave lateral wall of opisthotic through single foramen; canal in floor of basioccipital for basilar artery; maximum 14 teeth in dentary.

Length of presacral region less than postsacral. Caudal chevrons free. Appendicular elements heavily cartilaginous.

Tribe PLIOPATECARPINI (RUSSELL, 1967)

DIAGNOSIS. Highly pointed to moderately pointed skull; delicately proportioned jaws. Delicate teeth, strongly and abruptly posteriorly recurved, subcircular in cross-section. Huge parietal foramen.

Plioplatecarpus DOLLO, 1882

1882 *Plioplatecarpus* DOLLO: 62.

1889b *Oterognathus* (DOLLO); DOLLO: 272, pl. 9, fig. 10.

1894 *Oterognathus* (DOLLO); DOLLO: 221.

Generic type. *Plioplatecarpus marshi* DOLLO, 1882.

EMENDED GENERIC DIAGNOSIS. Long antero-median extension of frontal forming large part of postero-medial border of the external nares; smaller lateral extension forms postero-lateral border of external nares. Margins of dorsal parietal surface meet in front of diverging parietal rami forming triangular table anteriorly. Exit for cranial nerve VII on prootic opens directly on lateral surface of prootic; basioccipital canal has one or two ventral exits. Suprastapedial process not fused to very large infrastapedial process on quadrate, almost touch; tympanic ala thick, laterally cup shaped. Dentary teeth reduced in number.

Vertebral formula (based on *Plioplatecarpus houzeaui* IRSNB R37: 7 cervicals, 15 dorsals, 16 pygals, 24 intercaudals and 58 terminals.

Articulating surfaces of cervical and anterior lumbar vertebral centra wider than deep (width 1.5 x depth), smoothly elliptical in outline. Neural spines of caudal centra, vertical on postsacrals 54-72, decrease uniformly in length from base to end of tail (DOLLO, 1894, pp. 235-236). Very large scapula, larger than coracoid. Glenoid articulating surface flat to slightly convex on both elements, do not form smoothly continuous surface. Superior border of scapula gently convex, deeply pitted. Coracoid expands medially to point behind glenoid articulation. Distal and proximal ends of humerus moderately expanded, shaft of humerus short and broad; pectoral crest large to enormous; pectoral crest and glenoid condyle not separated by a deep groove. Distal end of radius expanded. Shaft of radius very wide with only slight emargination. Humero-radial articulation subcircular.

Plioplatecarpus marshi DOLLO, 1882

(Figs. 3-15, Pls. 2-4)

1869 *Mosasaurus gracilis* COPE: 261-262.

1879 *Mosasaurus gracilis* UBAGHS: 245, pls 3-5.

1882 *Plioplatecarpus marshi* DOLLO: 64-65, pl. 6.

1885a *Plioplatecarpus marshi* DOLLO; DOLLO: 319-335, figs (on pages 320, 323, 333) and fig. 1.

1885b *Plioplatecarpus marshi* DOLLO; DOLLO: 34.

1886 *Mosasaurus gracilis* SWANSTON: 134.

1888 *Plioplatecarpus marshi* DOLLO; DOLLO: 6, figs 4-8.

1889b *Plioplatecarpus marshi* DOLLO; DOLLO: 303, pl. 10, figs 6, 7.

1890 *Plioplatecarpus marshi* DOLLO; DOLLO: 153, pl. 2, figs 2, 4, 7, 8.

1904 *Plioplatecarpus marshi* DOLLO; DOLLO: 207-213, pl. 6, figs 1-5.

1909 *Plioplatecarpus marshi* DOLLO; DOLLO: 105.

1913 *Plioplatecarpus marshi* DOLLO; DOLLO: 617, pl. 25, fig. 2.

1924 *Plioplatecarpus marshi* DOLLO; DOLLO: 172.
 1967 *Plioplatecarpus marshi* DOLLO; RUSSELL: 123.

HOLOTYPE: IRSNB R38, fragmentary skull and incomplete postcranial skeleton, comprising scapula and coracoid, portion of interclavicle, humerus, radius, ulna, phalanx, ribs, cervical, thoracic and lumbar vertebrae.

HORIZON AND LOCALITY OF HOLOTYPE: Upper Maastrichtian, Maastricht Formation, Craie "grisâtre à silex gris" (DOLLO, 1882, p. 64), near Zichen, Limburg, Belgium (Figs. 1 & 2).

REFERRED SPECIMENS: BMNH 42940, IRSNB R39, R40, 3673, 1622, 1675, NHMM 198349, 1989104, 1989124, 1989126, 1423, 003900, TSMHN 11291, 11276, 11209.

HORIZON AND LOCALITY OF REFERRED SPECIMENS: Specimen IRSNB R39 comes from the Upper Maastrichtian, Upper Gulpen Formation, Lanaye Chalk, near Eben-Emael, Liège, Belgium (Figs. 1 & 2). Specimen BMNH 5868 is from the Upper Campanian, Marlbrook Marl of Arkansas, U. S. A.

All the other specimens are from the Maastrichtian stratotypical area and from the same horizon as the holotype.

DIAGNOSIS: Reduced lateral walls of premaxilla; suture along part of midline of premaxilla; delicate, though relatively broad, internarial bar. Three large foramina on the postero-ventral surface of the frontal on either side of the cranial midline. Very slender dentary; inner occlusal border deeper than outer; large mandibular foramen anteriorly. Small coronoid. Pear-shaped or double articulation processes on splenio-angular joint.

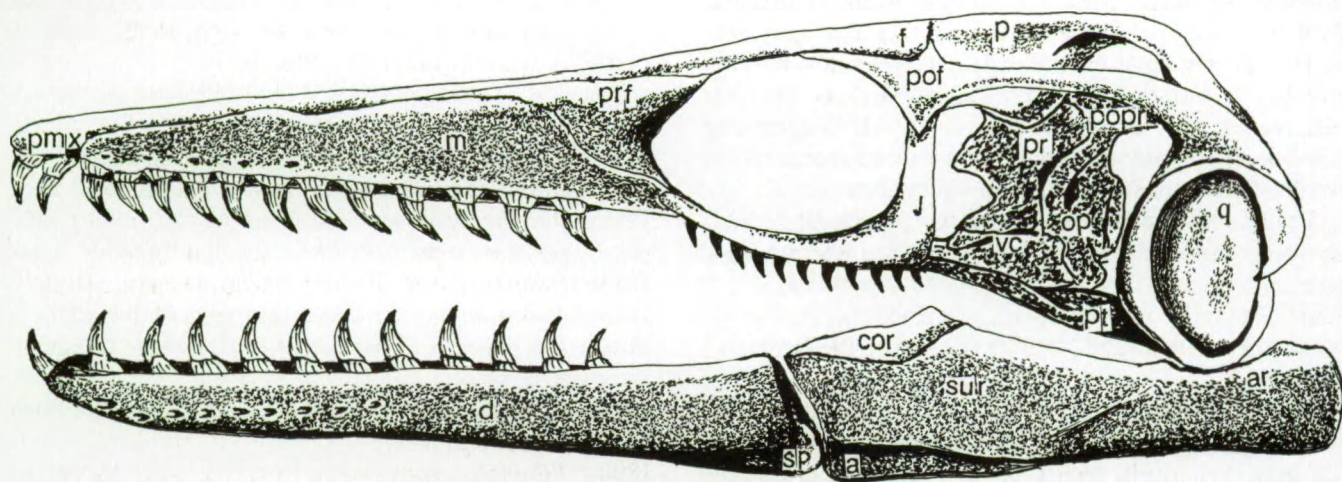
Vertebral formula based on IRSNB R40 & 3673: 7 (excluding atlas), 15 dorsals, 13 or 15 pygals, 30 intercaudals, about 40 terminals. Specimen IRSNB 3673 has 13 pygals and 29 caudals (Fig. 14) Laterally broad and deeply pitted dorsal surfaces of neural spines on cervical vertebrae. Deep pitting on dorsal surface of neural spines of terminal caudal vertebrae. Massive scapula, extends anteriorly and posteriorly. Large emarginated coracoid; very large coracoid foramen. Very stout humerus with huge pectoral crest. Radius broader than long; little emargination; circular proximal articulation. Broad posterior wing on ulna. Articulation of phalanges deeply pitted. Ribs sturdy with broad articulation head. Broad, robust interclavicle.

DESCRIPTIONS AND COMPARISONS

Descriptions are based essentially on the fragmentary holotype material IRSNB R38, R39, 1622, 3673, NHMM 1989124, 198349, TSMHN 11276, 11291. Restorations of *Plioplatecarpus marshi* are based primarily on IRSNB R38. Comparisons are made with the North American species *P. primaevus* (RUSSELL, 1967), *P. depressus* (COPE, 1869), *P. crassartus* (LINGHAM-SOLIAR & NOLF, 1989, p. 171, fig. 50) and *Plioplatecarpus* sp. BMNH 5868 (Pl. 1), from the Upper Campanian, Marlbrook Marl of Arkansas, U.S.A.

SKULL. Despite the highly fragmentary nature of the cranial material of *P. marshi*, it is clear from the slender premaxilla, maxilla, dentary and partial frontals that the skull was exceedingly narrow and sharply pointed anteriorly (Fig. 3).

PREMAXILLA. The premaxilla is relatively well preserved in IRSNB R38. It is rather narrow dorsally and truncated along the ventro-lateral surfaces. A row of probably no more than four large foramina is arranged



100mm

Fig. 3 — Composite restoration of the skull of *Plioplatecarpus marshi* based on IRSNB R38, 1622, R39 (extensive restoration).

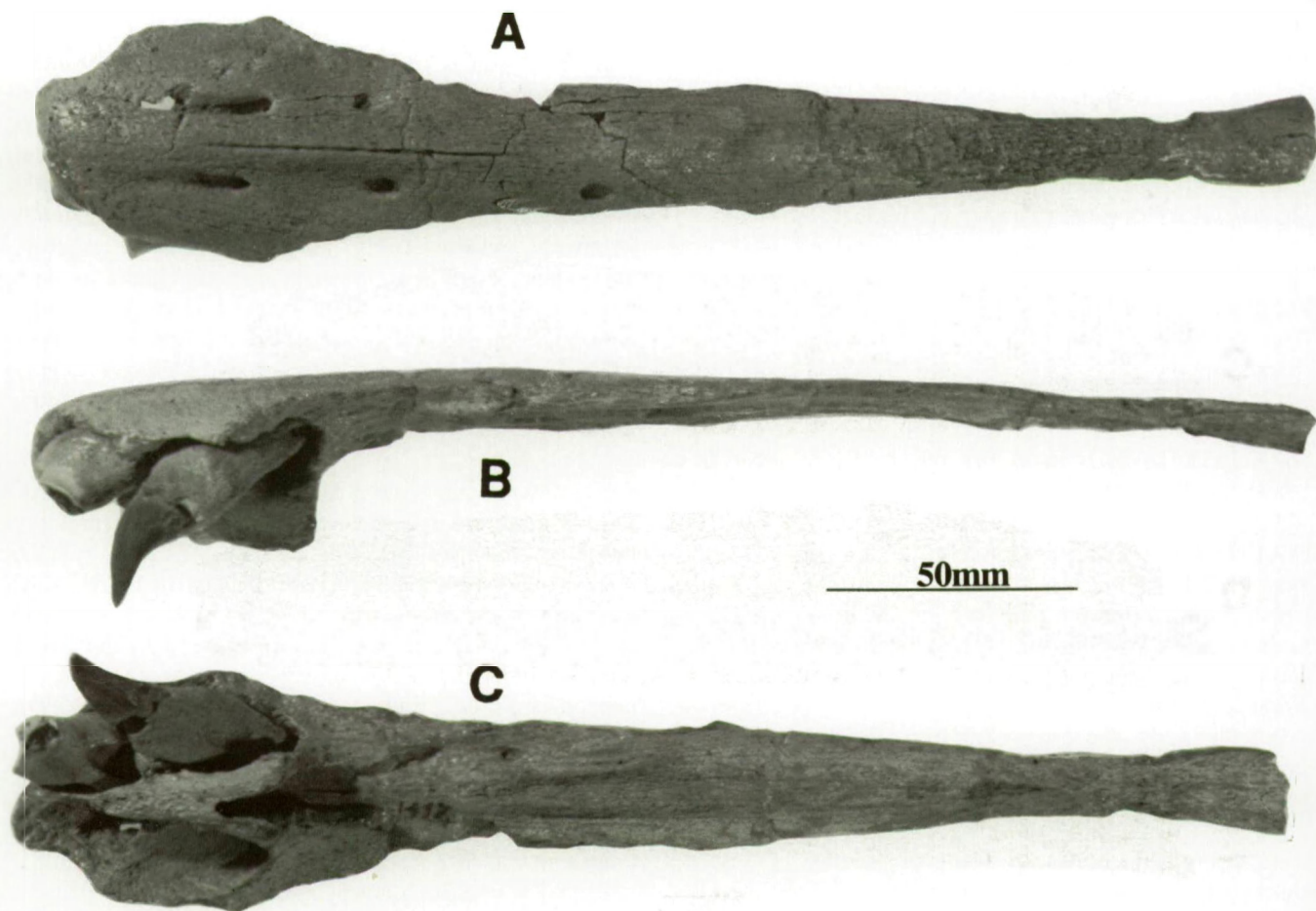


Fig. 4 — *Plioplatecarpus marshi* (IRSNB R38). Premaxilla. A, dorsal view, B, lateral view; C, ventral view.

in a relatively straight line on either side of the dorsal midline. Tooth bases are orientated at a very steep angle anteriorly with the crowns sharply recurved posteriorly [(cf. e.g. in *Prognathodon solvayi*, (LINGHAM-SOLIAR & NOLF, 1989, pl. 2)]. For a slender skull, the internarial bar is particularly broad (cf. *Mosasaurus hoffmanni* DOLLO, 1882, 1889b) although vertically flattened. It constricts slightly just past the midpoint. Along the longitudinal midline a split in the bone penetrates through to the ventral surface (Fig. 4A, C). This may represent a vestigial suture not previously noted in mosasaurs. The perfect symmetry on either side of this split, as well as good preservation of this element suggests that this is a real condition and not an artifact. A fragment of the premaxilla, specimen BMNH 42940 (from The Netherlands), belonging to *Plioplatecarpus* is also split along the longitudinal axis.

MAXILLA. There are only three fragments of the maxilla preserved, specimens IRSNB R38, R39 and a large portion, IRSNB 1622 (Fig. 5A-E). In the holotype fragment, the foramina situated above the gum line are small, all but for one near the midpoint of the bone. Specimen IRSNB 1622 is well preserved and represents about two thirds of the bone (Fig. 5C-E). Teeth are absent but there are eleven tooth sockets. Twelve or thirteen teeth were

probably present in life. The tooth bases are strongly inclined anteriorly. Foramina are relatively large and extend no further than the midpoint of the length of the bone. A notch on the dorsal margin adjacent to the third/fourth maxillary tooth presumably marks the anterior border of the external nares (Fig. 6).

FRONTAL. Two fragments of the frontal are preserved, specimens IRSNB R38 and NHMM 1983 (Fig. 5F, G respectively). The latter specimen represents approximately half the frontal split along the longitudinal axis. Posteriorly the bone was sliced during the mining process. However, both specimens together provide a reliable restoration (Fig. 7). The orbital margin is slightly convex and smoothly bevelled. The posterior boundary is absent. On the ventral surface of the holotype fragment, three fairly large foramina lie adjacent to the anterior termination of the excavation for the parietal foramen (Fig. 5F). Unfortunately specimen NHMM 1989104 is broken off at this point although a missing thin plate of bone (the whole plate is probably missing in the holotype) reveals narrow furrows that may have led to similar foramina as in the holotype (Fig. 5G).

POSTORBITOFRONTAL. The only known specimen of the postorbitofrontal in *Plioplatecarpus marshi*, to my knowledge, belongs to poorly preserved material (unregistered

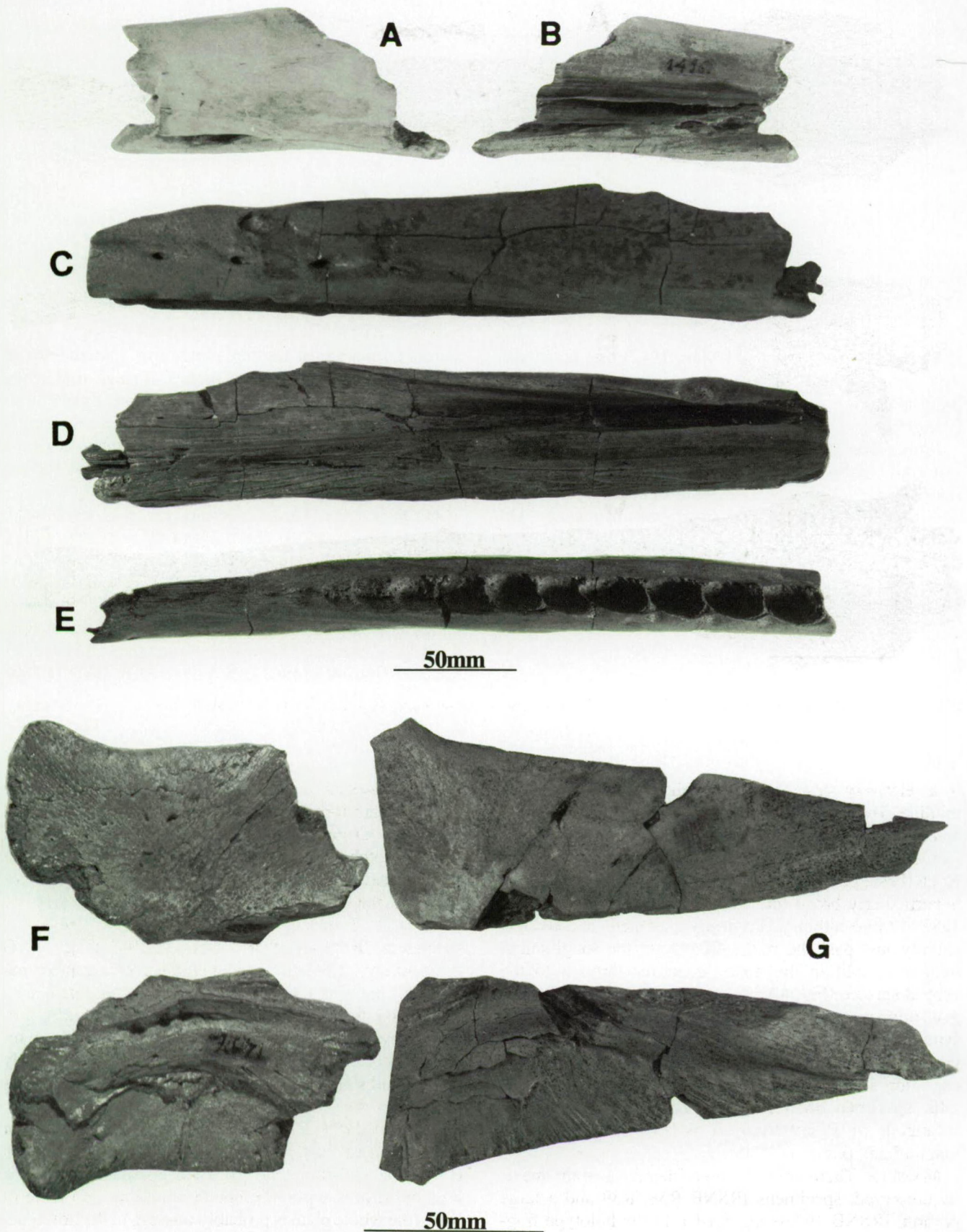


Fig. 5 — *Plioplatecarpus marshi*. Maxilla. (IRSNB R38). A, lateral view; B, medial view. (IRSNB 1622). C, lateral view; D, medial view; E, occlusal view. Frontal (IRSNB R38). F, dorsal and ventral views (top to bottom). (NHMM 1983). G, dorsal and ventral views (top to bottom).

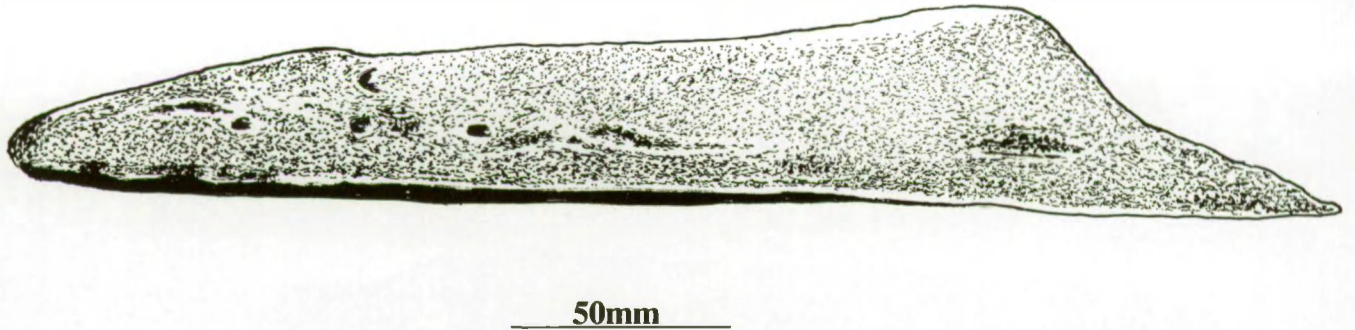


Fig. 6 — *Plioplatecarpus marshi*. Restoration of the maxilla based on IRSNB 1622 and R39. Lateral view.

IRSNB specimens, dated 1st May, 1912) that is tentatively assigned to *P. marshi*. It is noteworthy that the prefrontal wing is extensive and broadly underlaps the frontal bone.

JUGAL. The jugal is also only known from the above material. It is broadly similar to the element in *Mosasaurus hoffmanni*, although it is more delicately proportioned. Medially there are two significant differences. On

the dorsal margin of the horizontal arm, just anterior to the junction of the two axes, there is a small roughened nubbin that presumably provided for ligamentous connections in life. A shallow roughened excavation on the anterior medial tip of the jugal also indicates a ligamentous connection with the postero-lateral surface of the maxilla.

THE BRAINCASE. The basioccipital unit was described in some detail by DOLLO (1885a) and DE VILLERS (1943). The description here is essentially new but may overlap on certain points. The holotype IRSNB R38 and NHMM 003900 (Figs 8A, B respectively) present the best preserved and almost complete braincase. In addition, relatively good braincase is present in specimen IRSNB R39. Material from Arkansas, U.S.A., specimen BMNH 5868

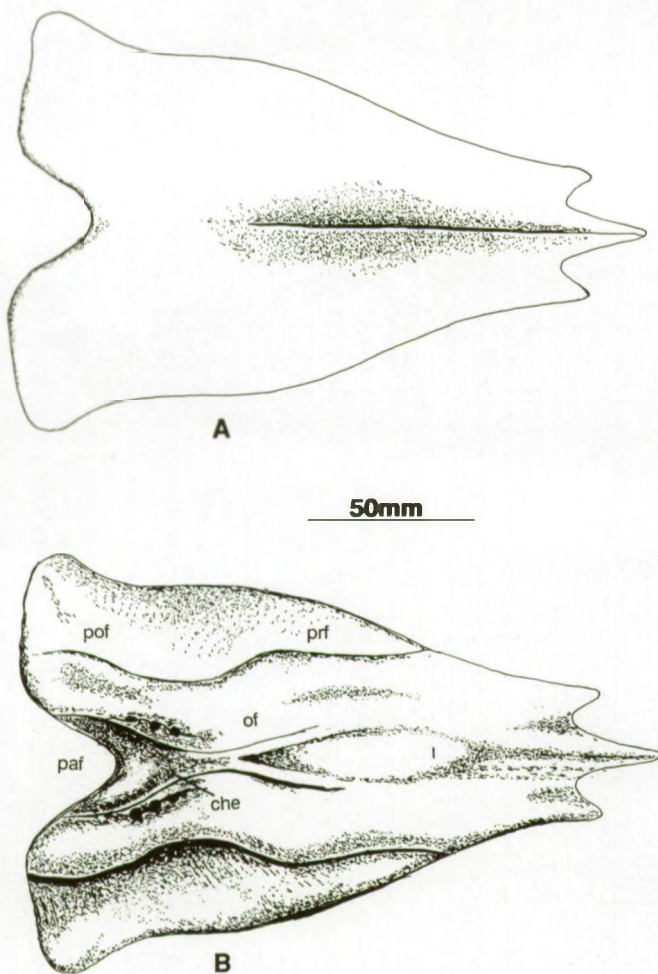


Fig. 7 — *Plioplatecarpus marshi* (IRSNB R38). Restored frontal. A, dorsal view; B, ventral view.

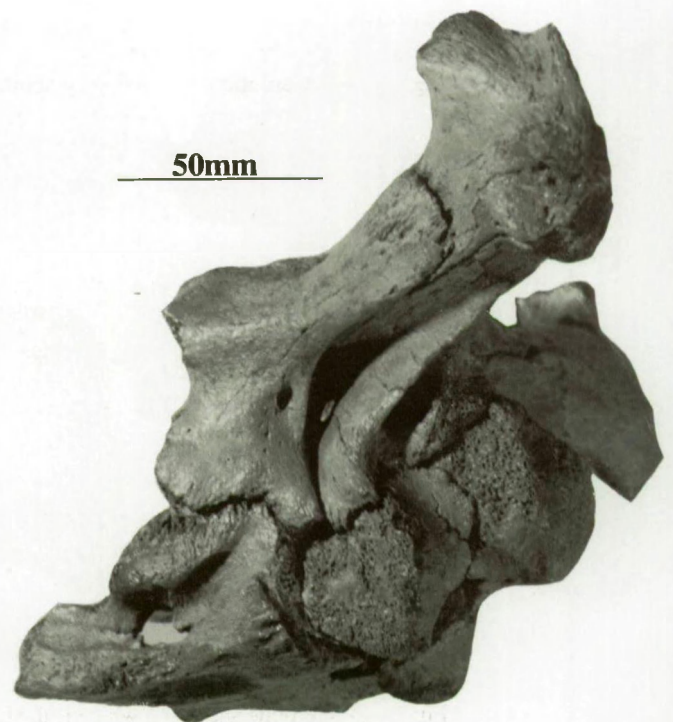


Fig. 8 — *Plioplatecarpus marshi*. Braincase. Lateral view. A, IRSNB R38; B, NHMM 003900.

(Pl. 1) may represent a closely related form. The exit for cranial nerve VII opens directly onto the lateral surface of the prootic, lacking an otosphenoidal crest. However, in IRSNB R39, cranial nerve VII leaves via two foramina. The exit for cranial nerve VIII (IAM) is similar to that of

Clidastes (RUSSELL, 1967). Cranial nerve IX leaves the braincase from virtually beneath the posterior border of the prootic. The lateral wall for the vidian canal is absent in all four *Plioplatecarpus* specimens examined. Whether it is eroded or represents a real lack of development is

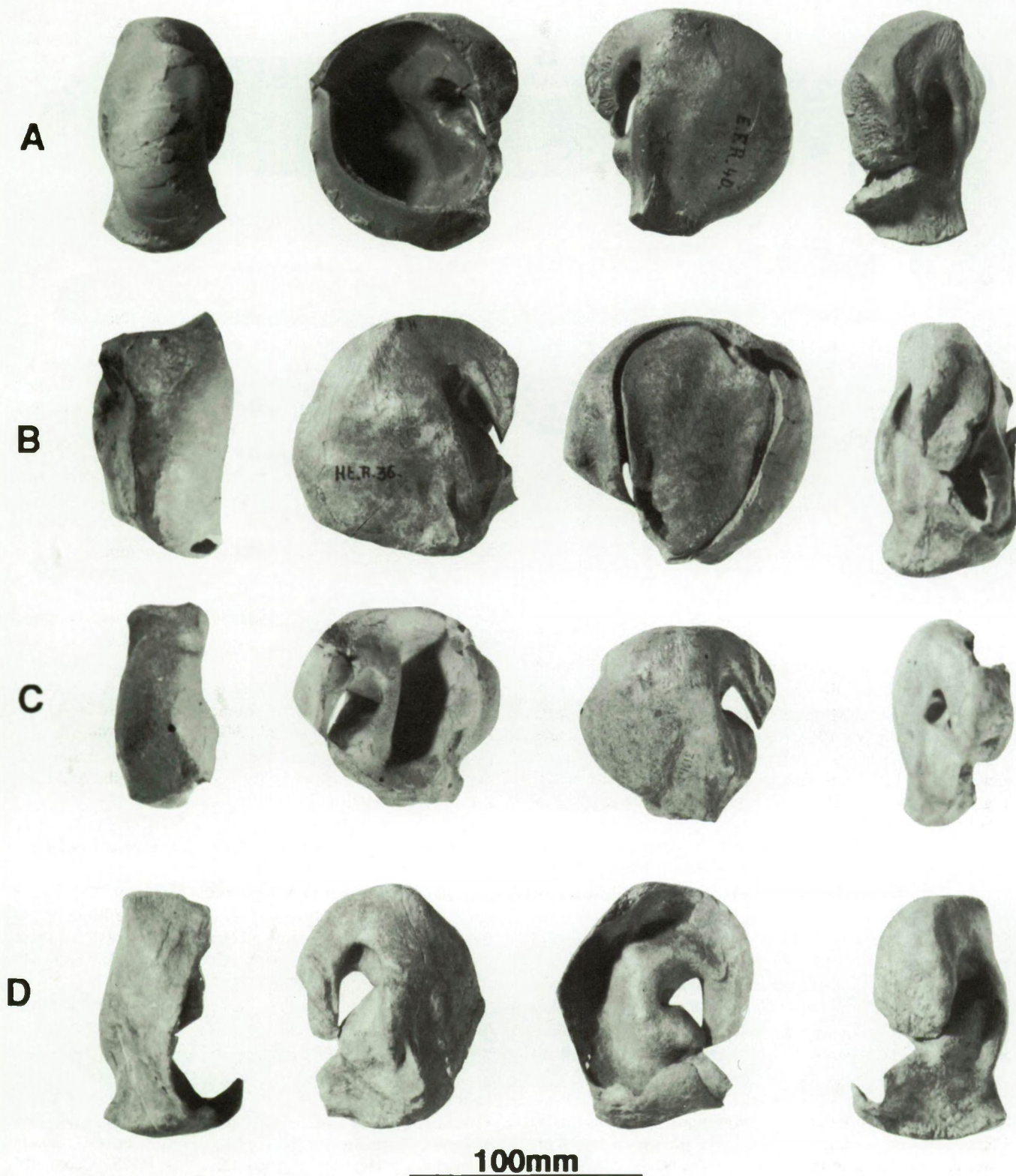
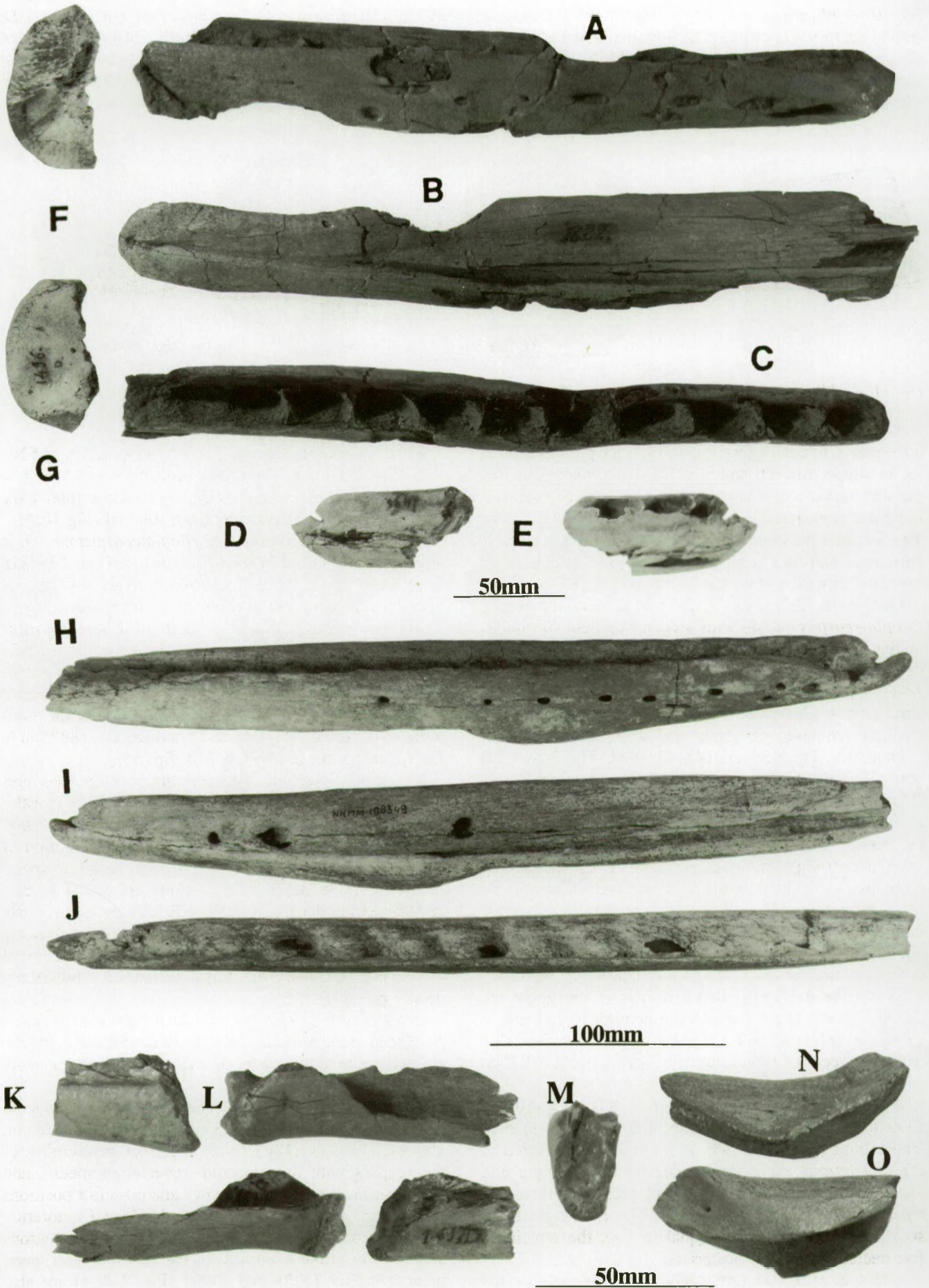


Fig. 9 — *Plioplatecarpus quadrates* (left to right, anterior, lateral, medial & posterior). A, *Plioplatecarpus marshi* (IRSNB R40); B, *P. houzeaui* (IRSNB R36); C, *P. houzeaui* (IRSNB 3101); D, *P. houzeaui* (IRSNB 3108).



← Fig. 10 — *Plioplatecarpus marshi* (IRSNB 1622). Dentary. A, lateral view; B, medial view; C, occlusal view. (IRSNB R39). D, medial view; E, lateral view. Fragment of articular. F, medial view; G, lateral view. (NHMM 198349). Dentary of immature specimen. H, lateral view; I, medial view; J, occlusal view. (IRSNB R38). Splenial & angular. Lateral & medial views (top to bottom). K, splenial; L, angular; M, posterior view of splenial. Coronoid. N, lateral view; O, medial view.

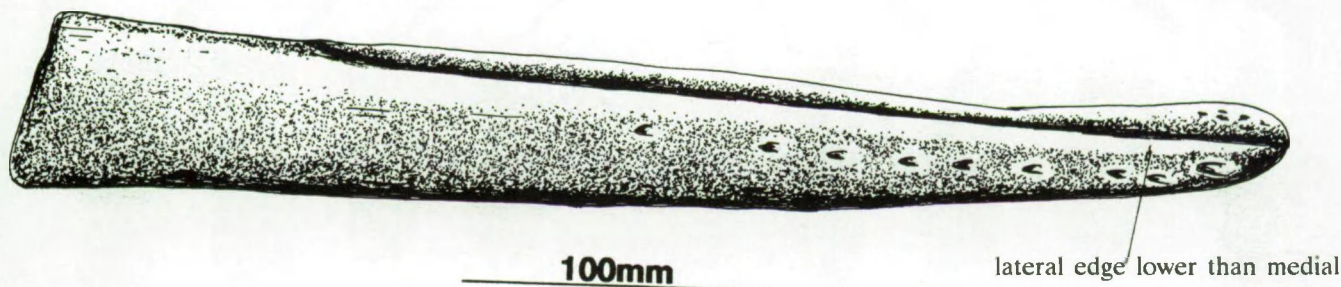


Fig. 11 — *Plioplatecarpus marshi*. Restoration of dentary based on IRSNB 1622.

uncertain although generally good surface preservation in the holotype material and NHMM 003900 suggests that the wall was either absent in life or that it was exceptionally thin (discussed in LINGHAM-SOLIAR & NOLF, 1989). The foramen for the basilar artery in the basioccipital is enormous and has a single ventral exit, unlike in *P. houzeaui* in which there are two exits.

QUADRATE. This is one of the best preserved bones of *Plioplatecarpus marshi* with several excellent specimens in the collection e.g. IRSNB R40 (Fig. 9A). Detailed descriptions of the element are given by DOLLO (1885b, 1888, 1890, 1904) and will consequently not be repeated here (see *P. houzeaui* for discussion concerning the calcified tympanic membrane and diving in mosasaurs).

DENTARY. The dentary, IRSNB 1622 (Fig. 10A-C) is very slender with just a small posterior segment absent. Teeth are not preserved although there are eleven tooth sockets with presumably a further one or two located on the missing posterior segment. As in the maxilla the tooth bases are strongly inclined anteriorly. They occupy virtually the whole depth of the dental ramus. A row of large foramina extends along the midline of the bone decreasing in size posteriorly. The first foramen is enormous although it may be somewhat exaggerated by weathering. A few isolated foramina are present below the main row. Medially the meckelian fossa extends to the tip of the dentary. A striking feature of the dentary is the significantly lower lateral wall compared with the dorso-medial wall, also seen in the anterior dentary fragment of IRSNB R39 (Fig. 10D, E).

A slender dental element, NHMM 198349 (Fig. 10H-J) from the Maastrichtian horizon at Sibbe (Fig. 1) near Valkenburg (MEIJER, 1983), is provisionally referred to *Plioplatecarpus marshi*. The dentary is complete and although the tooth crowns are not preserved there are clearly sockets for thirteen teeth. The first eight tooth sockets are approximately equal in size, the remaining five decreasing in size posteriorly.

SPLENIAL AND ANGULAR. Only two fragments of the

splenial and one of the angular are preserved in IRSNB R38 (Fig. 10K, L). The articulation between these two bones forms a pear-shaped tuberosity on the angular and a similarly shaped excavation on the splenial (Fig. 10M).

CORONOID. The coronoid in *Plioplatecarpus marshi* is amongst the smallest in the Mosasauridae (Fig. 10N, O), smaller only in *P. houzeaui*. The coronoid eminence is low and the lateral and medial wings abbreviated.

MARGINAL DENTITION. The teeth in *Plioplatecarpus marshi* are weakly implanted and the crowns are finely striated. They are readily distinguished from those of Platecarpus species in being more delicate, more pointed and abruptly posteriorly recurved from about the mid-point of the crown (Figs 12 & 13 and DOLLO, 1882, pl. 6, fig. 6.; cf. RUSSELL, 1967, p. 154, fig. 85).

VERTEBRAL COLUMN. The vertebral column was previously described in a functional analysis of underwater flight in *Plioplatecarpus marshi* (LINGHAM-SOLIAR, 1992b). However, included here is a new restoration of the posterior vertebral column (Fig. 14) based on specimen IRSNB 3673. The articulation surfaces of several vertebrae from the holotype IRSNB R38 are seen in Plate 2. Of interest is a series of posterior caudals showing relatively short neural spines compared with the height of the centra. Unusually the dorsal surfaces are broad and deeply pitted (Pl. 3A).

INTERCLAVICLE. This is the most robust interclavicle I have seen in the Mosasauridae (DOLLO, 1885a and Pl. 2G, H) and quite unlike that of *Plioplatecarpus houzeaui* IRSNB R37 (Fig. 25).

SCAPULA AND CORACOID. The scapula and coracoid have been described previously (LINGHAM-SOLIAR, 1992b). DOLLO's (1882, pl.6) incorrect positioning of the scapula with the coracoid, reversal of medial and lateral surfaces as well as anterior and posterior positions of the scapula is noted. I have included here a restoration of the type scapula (Fig. 15) and for comparative reasons and because of the scantiness of the material, new specimens TSMHN 11276 and 11291 (Pls. 3 & 4) are also

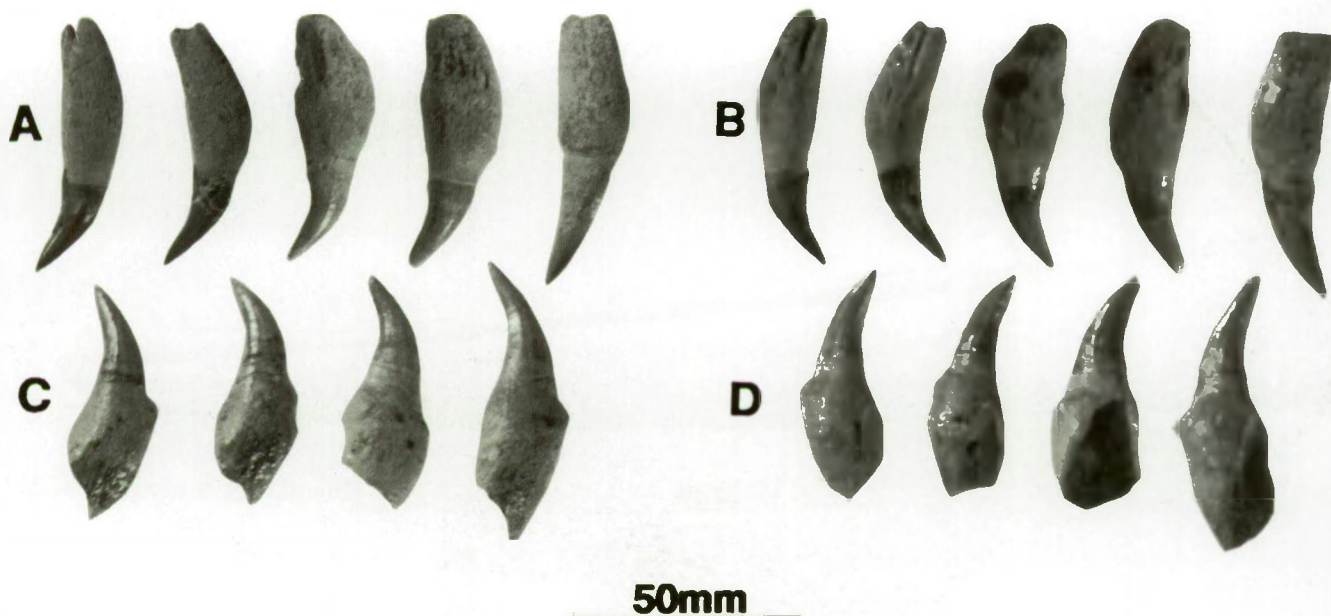


Fig. 12 — *Plioplatecarpus marshi* (IRSNB R39). Disassociated teeth. Maxilla. A, buccal view; B, lingual view. Dentary. A, buccal view; B, lingual view.

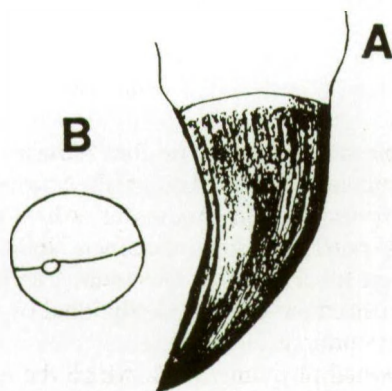


Fig. 13 — *Plioplatecarpus marshi* (IRSNB R39). Tooth restoration. A, buccal view; B, transverse section taken at the base.

figured although it is not certain that the scapula and coracoid are related. For instance specimen TSMHN 11276 reveals the extraordinarily deep pitting of the articulation surface (see LINGHAM-SOLIAR, 1992b for a functional analysis). A fragment of specimen BMNH 5868 (Pl. 1L, M), the North American species also

indicates a broad blade and a pitted dorsal edge for the cartilaginous suprascapula. The coracoid foramen may be located posteriorly although this is not certain at present.

DISCUSSION

THE SKULL ROOF. Two cranial elements, the premaxilla and the frontal, show certain unusual conditions. The premaxilla is normally completely fused in mosasaurs. Hence the dorsal suture along part of the premaxilla perhaps reflects the ancestral condition of lizards in which the premaxillae are separate bones. For instance, separate premaxillae are found in gekkonids, scincids and in fossil ardeosaurids (ESTES *et al.*, 1988, p. 142) and bavarisaurids (ESTES, 1983; MATEER, 1983). In all other lepidosauromorphs in which the condition can be determined, the premaxillae are separate (ESTES *et al.*, 1988, p. 142). In most squamates, the premaxilla is usually fused, a condition ESTES *et al.* (1988, p. 142) interpreted as a synapomorphy of squamates. For the present the apparent longitudinal suture of the premaxilla of *Plioplatecarpus marshi* (IRSNB R38) is interpreted as a character reversal. The foramina on the ventral surface of the frontal probably represent exits for blood vessels or cranial nerves, although the condition has not, to my

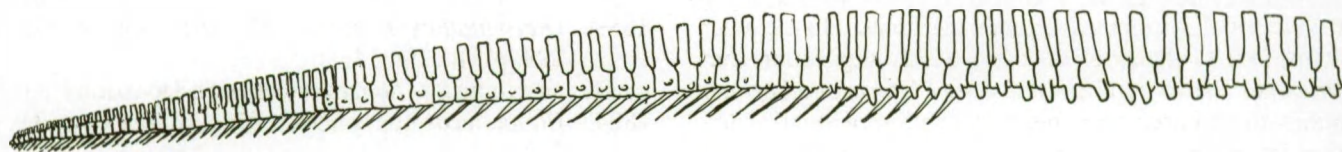


Fig. 14 — *Plioplatecarpus marshi* (IRSNB 3673). Restoration of posterior vertebral column.



Fig. 15 — *Plioplatecarpus marshi* (IRSNB R38). Restoration of scapula.

knowledge, been observed in mosasaurs before. It may, however, be somewhat comparable to the condition in *Sphenosuchus acutus* (WALKER, 1990, p. 90) in which similar foramina mark the exits for cranial nerves. Part of a large excavation along the midline of the frontal indicates two conditions:

- (i) that the forebrain was large and
- (ii) the presence of a very large parietal foramen (also indicated by the cleft on the posterior margin of the frontal). Both conditions occur in the closely related *Plioplatecarpus houzeau*. Anterior to this is part of a second excavation that presumably housed the olfactory lobes. A relatively deep excavation along the ventrolateral margin indicates a fairly broad invasion by the anterior wing of the postorbitofrontal. Although only about half the frontal length is preserved in IRSNB R38, it clearly matches closely with the large fragment of specimen NHMM 1983.

BASIOCCIPITAL FORAMINA AND RELATED SYSTEMATICS. The presence of one or two exits for the basilar artery seems to have no obvious significance (LINGHAM-SOLIAR & NOLF, 1989, p. 151) and the reason it enters the basioccipital at all has not been established. On the other hand TELLES-ANTUNES' (1964, p. 236) suggestion that there are four ventral foramina in *Platecarpus bocagei* seems to be based on a misinterpretation of small nutritive foramina. Such foramina are seen on the ventral surface of the basioccipital in most mosasaurs (e.g. *Platecarpus* sp. BMNH 4001).

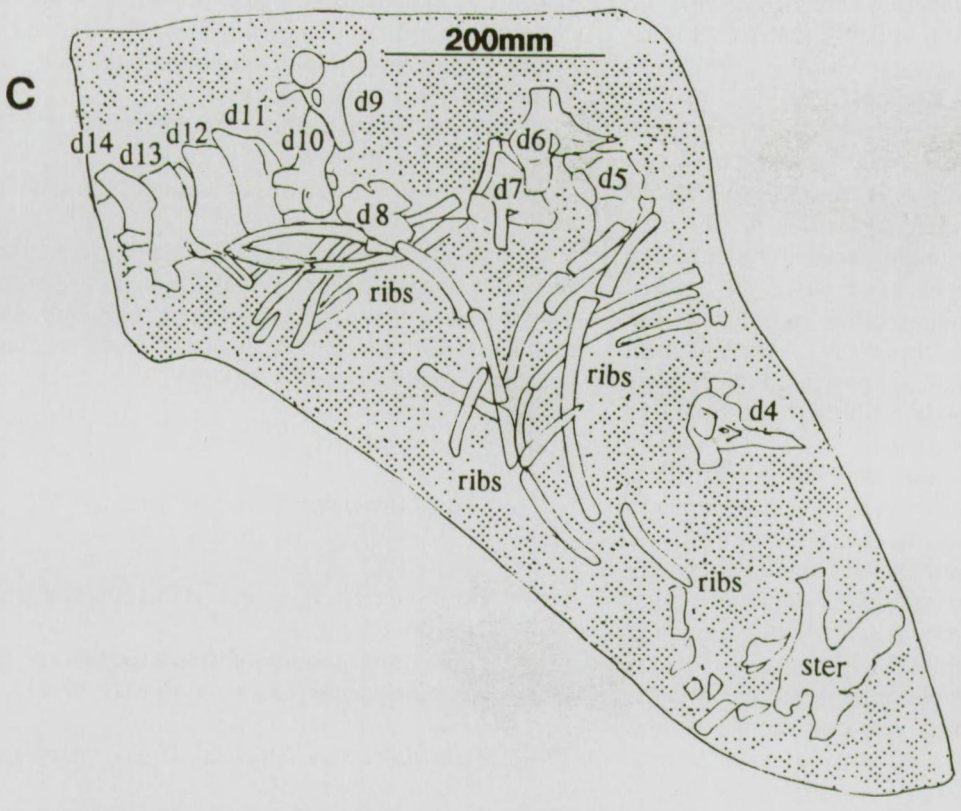
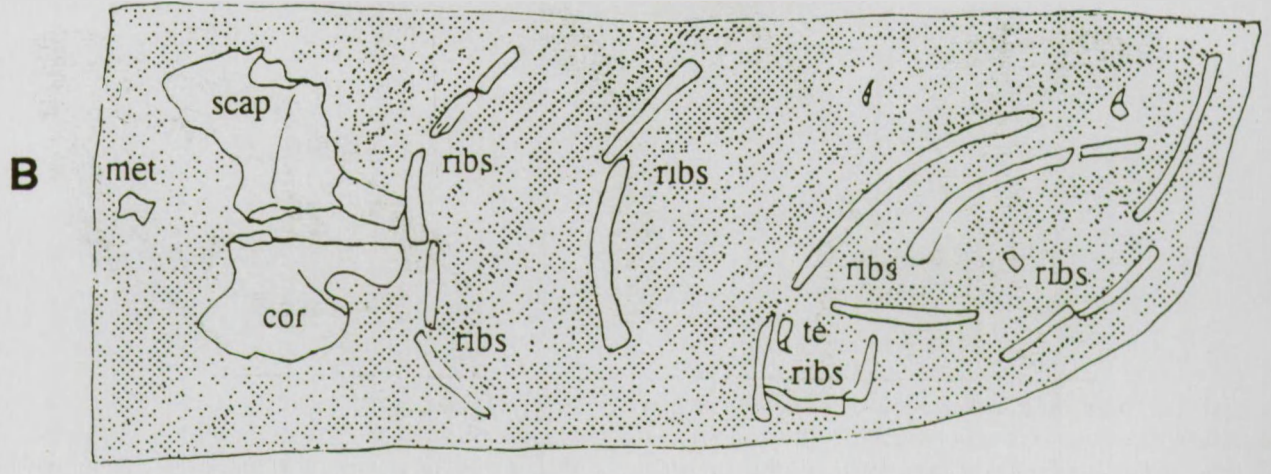
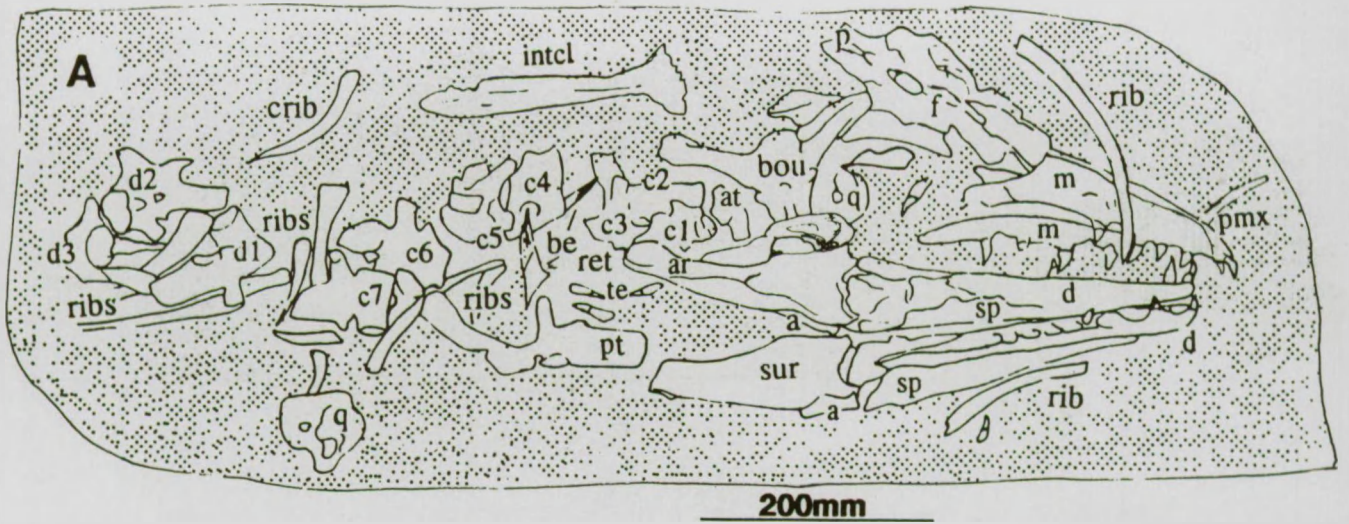
LOWER JAW. The dentary in *Plioplatecarpus marshi* is

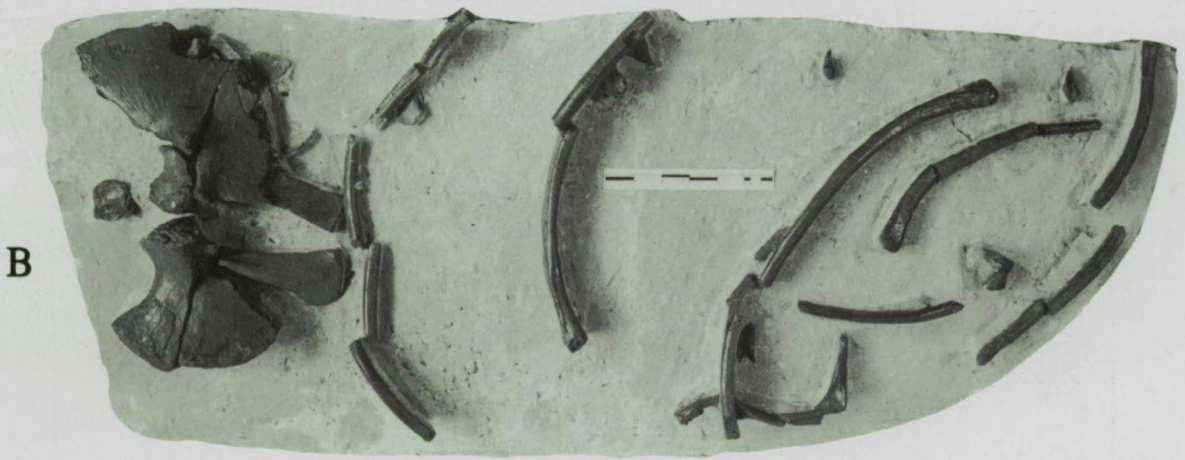
relatively the most slender in the Mosasauridae and readily distinguished from that of *P. houzeau*, or for that matter from any other mosasaur. Although MEIJER (1983, fig. 1) considered that specimen NHMM 198349 did not belong to any known mosasaur, I am convinced that it comes from an immature individual of *P. marshi*. Three features prompt this view:

- (i) the unusual phenomenon in which the lateral wall of the dentary is lower than the medial;
- (ii) very strong anterior inclination of the tooth bases, and;
- (iii) the mandibular exits for cranial nerve V extend no further than approximately half the length of the bone. Furthermore a complete loss of teeth, although circumstantial, reflects the peculiarly weak tooth implantation seen in *Plioplatecarpus* (DOLLO, 1913).

***Plioplatecarpus houzeau* DOLLO, 1889**
(Figs. 16-26, Pls. 5-8)

- 1889b *Oterognathus houzeau* (DOLLO); DOLLO: 272-293, pl. 10, fig. 14.
- 1889c *Oterognathus houzeau* (DOLLO); DOLLO: 69.
- 1894 *Plioplatecarpus houzeau* DOLLO; DOLLO: 233-237.
- 1904 *Plioplatecarpus houzeau* DOLLO; DOLLO: 207-213, pl. 6, figs 6-10.
- 1967 *Plioplatecarpus houzeau* DOLLO; RUSSELL: 159.





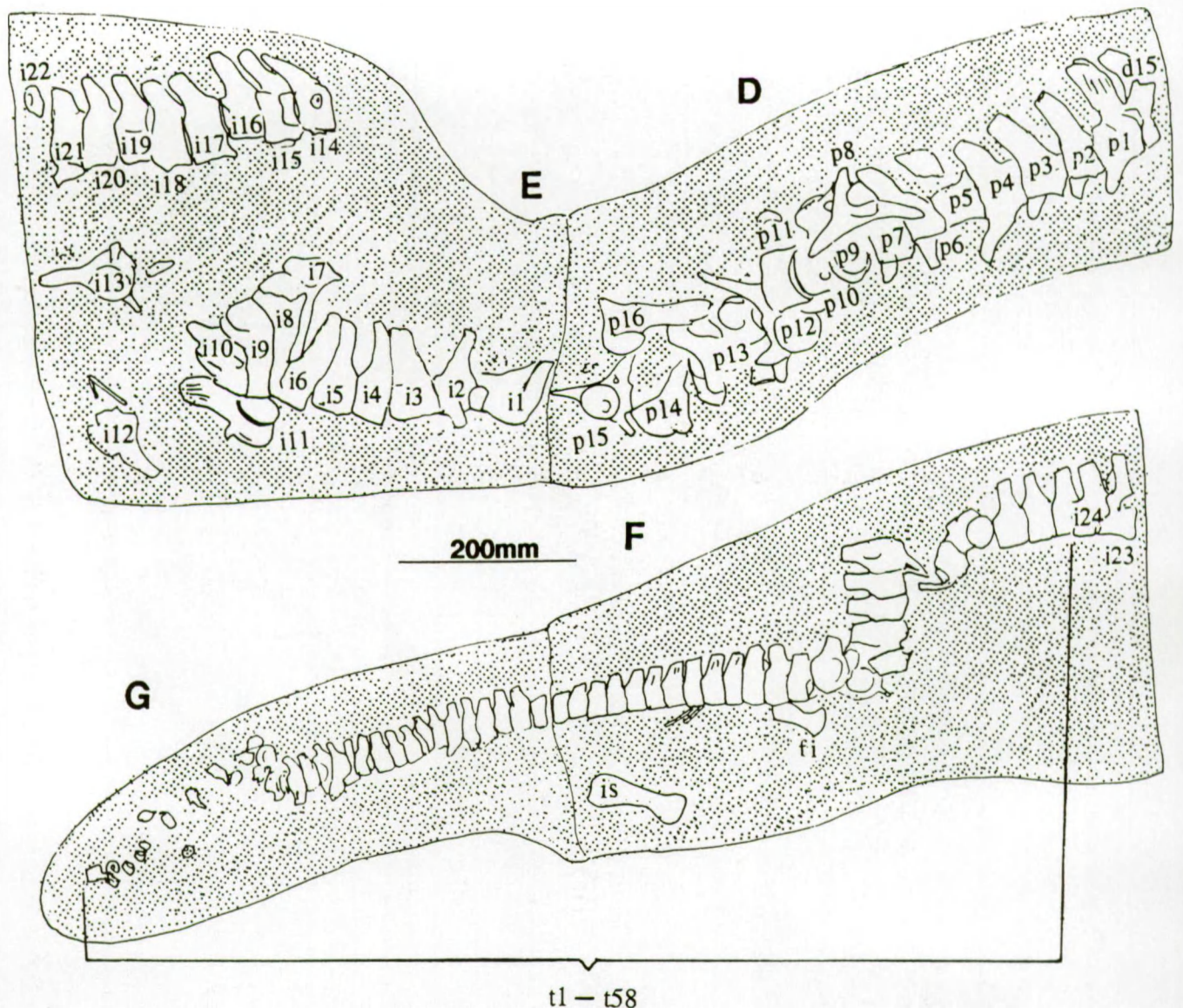


Fig. 16 — *Plioplatecarpus houzeaui* (IRSNB R37). Almost complete skeleton preserved in matrix (7 blocks). Abbreviations not included in previous list. Bou, basioccipital unit; be, belimnites; c1, cervical vertebra 1; cor, coracoid; crib, cervical rib; d1, dorsal vertebra 1; fi, fibula; ic1, intercaudal vertebra; is, ischium; intcl, interclavicle; met, metacarpal; p1, pygal vertebra; pmx, premaxilla; ret, retroarticular; scap, scapula; ster, sternum; sur, surangular; t1, terminal vertebra; te, tooth/teeth.

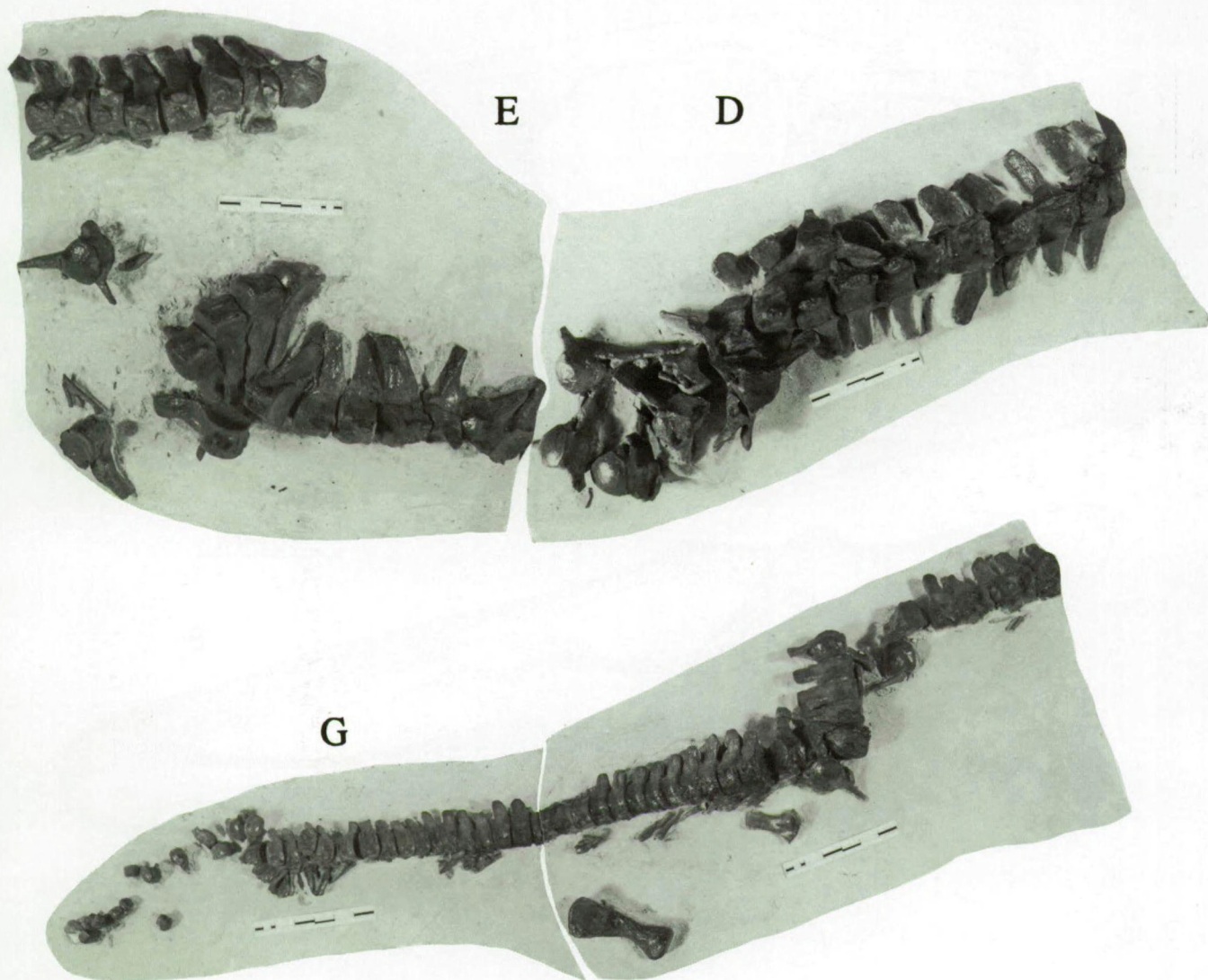
HOLOTYPE: IRSNB R35 (IRSNB 3111), fragmentary skull. Specimen includes left and right dentary, angular, surangular, coronoid, articular, prefrontal, right pterygoid, vertebrae.

HORIZON AND LOCALITY OF HOLOTYPE: Maastrichtian, Brown Phosphatic Chalk at Ciply, Hainaut, Belgium (LINGHAM-SOLIAR & NOLF, 1989).

REFERRED SPECIMENS: IRSNB 3099, 3101, R36 (3100), 3107, 3108, 3155, 3160, 3859, 3154, 3152 3130, 3122, R37.

HORIZON AND LOCALITY OF REFERRED SPECIMENS: As for holotype.

DIAGNOSIS: Premaxilla short, blunt anterior to premaxillary teeth. Short maxilla; last four teeth on maxilla greatly reduced in size. Incomplete longitudinal fusion of frontals along anterior half of the bone. Parietal is short; strongly constricted along longitudinal midpoint; parietal foramen is enormous, oval shaped. The horizontal and vertical arms of the jugal meet in a large ala-like process; distal tip of vertical arm of jugal fits into a deep socket-like excavation in the postorbitofrontal. Postorbitofrontal wing to the squamosal extends to the end of the latter element; ventral, anteriorly directed ala-like process on the squamosal, single dorsal entrance and double ventral exit for the basilar artery on the basioccipital. Dentary short; very large posterior edentulous region on the dentary; teeth set in deep grooves in dental rami. Very



small coronoid. Massive anterior prearticular process. Highly kinetic elements of the lower jaw. *Plioplatecarpus houzeaui* is smaller than *P. marshi*.

DESCRIPTIONS AND COMPARISONS

SKULL. Descriptions are based primarily on the referred specimens because of the fragmentary nature of the holotype material. The skull (Fig. 17) is delicately constructed and somewhat blunter than in *P. marshi* (Fig. 3). Fig. 16

PREMAXILLA. The premaxilla is quite broad dorsally and lacks a rostrum anterior to the teeth. Because of poor preservation it is not possible to comment on the foramina for the fifth cranial nerve. The internarial bar is relatively broad, narrowing at the midpoint between the external nares.

MAXILLA. The maxilla is relatively small, giving the teeth a somewhat exaggeratedly large appearance (Fig. 18A-D). Teeth are fairly long, exceptionally pointed and posteriorly recurved. The tooth bases virtually take up the whole of the depth of the maxilla. The narial emargina-

tion commences at about the mid-point of the second maxillary tooth. The teeth are subequal in size up to the seventh and then rapidly decrease in size, the last four teeth occupying the slender posterior segment of the dental ramus. Along the longitudinal mid-point of the dentary a row of large foramina extends from about the first maxillary tooth to about the sixth.

FRONTAL. The general shape of the frontal is distinctive (Fig. 19 & Pl. 6). It is a relatively narrow, delicately constructed bone, somewhat emarginate at the orbits becoming convex anteriorly, then curving out slightly to form a short slender prong that makes up a small part of the lateral border of the external nares on either side of the skull. A long antero-medial process of the frontal forms the posterior part of the internarial bar. Posteriorly the frontal extends into two broad flanges, on either side of the enormous parietal foramen, and meets the post-orbitofrontals and anterior segment of the parietal. A ridge, bounded on either side by a shallow excavation, extends along the longitudinal midline from the anterior wing to over half the length of the frontal. Ventro-

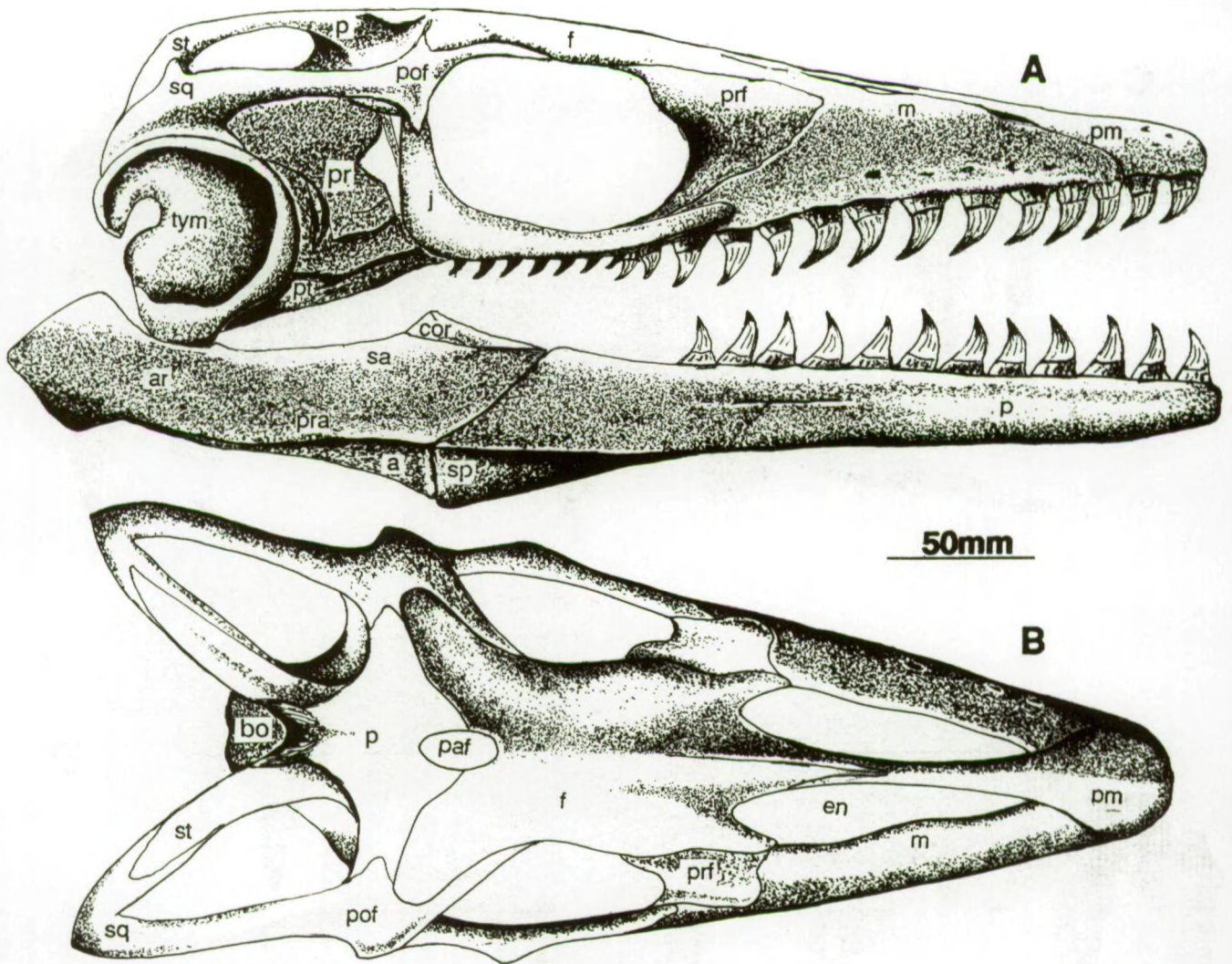


Fig. 17 — *Plioplatecarpus houzeau* (IRSNB 3101, 3130 & R35). Skull restoration (extensive). A, lateral view; B, dorsal view.

laterally a deep continuous excavation indicates that the prefrontal and postorbitofrontal were in contact but that they were overlapped by the frontal along the orbital margins. The ventral excavation surrounding the parietal foramen is enormous, manifestly larger than in any other known mosasaur with the implication of a particularly well developed forebrain. Anteriorly a narrow excavation represents the dorsal roof of the olfactory lobes. (Pl. 5B)

LACHRYMAL. The lachrymal is well preserved in IRSNB 3101. It is relatively large for the size of the skull but has the characteristic arrow-head shape (Fig. 18E, F).

PREFRONTAL. A part of the prefrontal is preserved (Fig. 7A, B). The supraorbital ala is poorly developed and in place of a nubbin on the ala there is a small ridge (Pl. 7A).

POSTORBITOFRONTAL. A fairly well preserved postorbitofrontal is present in IRSNB R36. The frontal wing is large and underlies the posterior wings of the frontal. The parietal wing is short and is united in a suture with the parietal. The posterior wing is long and extends to the

extreme posterior corner of the squamosal. The ventral wing of the postorbital unusually forms a deep, posteriorly directed excavation that articulates with the vertical arm of the jugal.

JUGAL. The jugal in *Plioplatecarpus houzeau* is delicate and with a rather characteristic shape (Pl. 7C, D), particularly in the broadly expanded ala-like process at the junction of the horizontal and vertical arms. The horizontal arm is narrow and virtually tubular but becoming somewhat dorsoventrally compressed anteriorly, at the same time curving steeply upward to the margin of the prefrontal bone. The vertical arm terminates in a slender point that was clearly received by a deep excavation in the ventral surface of the postorbitofrontal.

SQUAMOSAL. The squamosal in specimen IRSNB R36 is a rather delicate, markedly arrow-head shaped bone with an unusually long ala or tongue extending anterolaterally (Pl. 7E). The postorbitofrontal wing to the squamosal extends virtually to the posterior border of the squamosal, ending in a rather broad spatulate process.

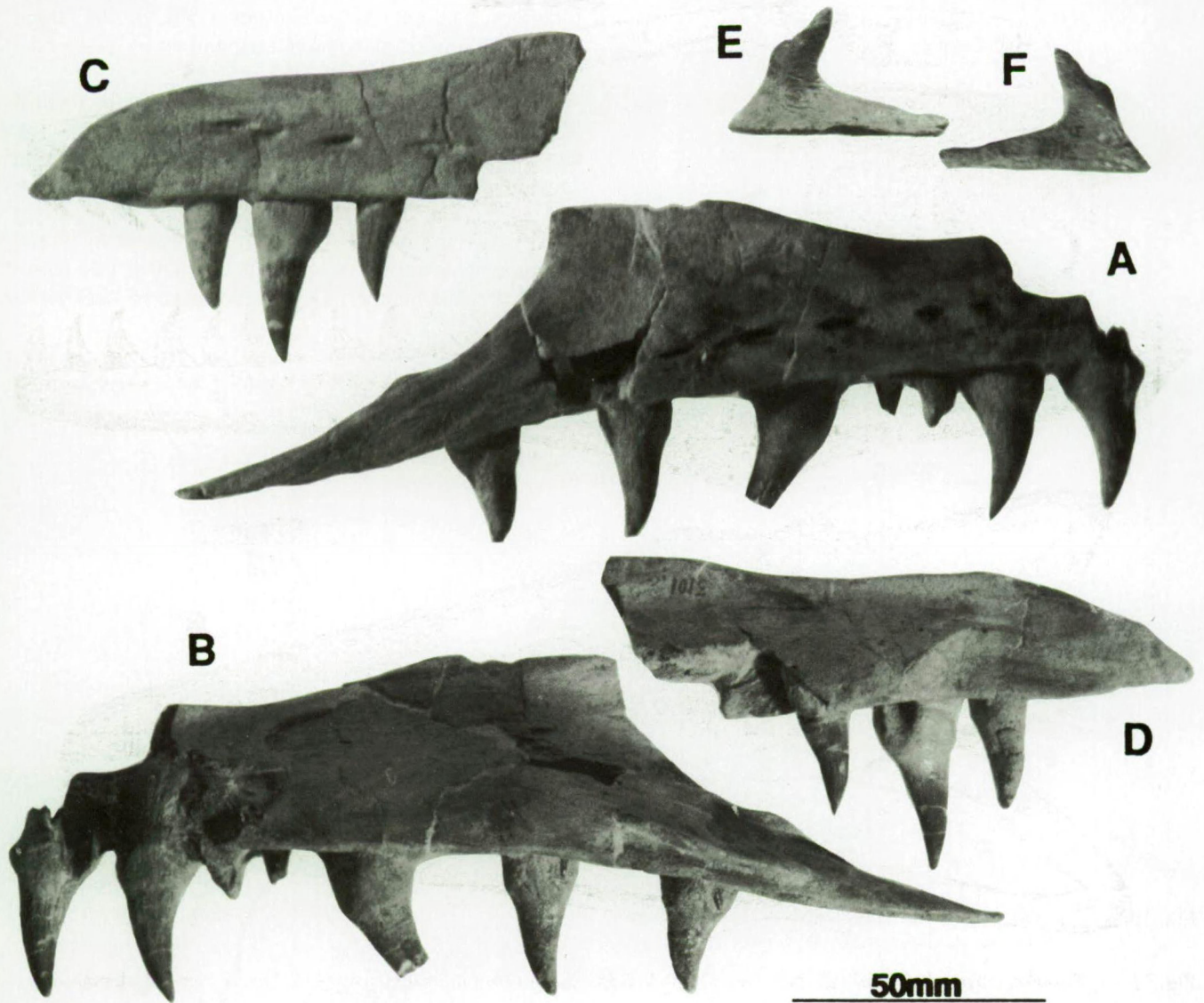


Fig. 18. — *Plioplatecarpus houzeai* (IRSNB 3101). Right maxilla. A, lateral view; B, medial view. Left maxilla. C, lateral view; D, medial view. Lachrymal. E, lateral view; F, medial view.

PALATINE. The palatine is preserved in just one specimen of *Plioplatecarpus houzeai*, IRSNB 3130. It is fused to the pterygoid posteriorly and a portion of the prefrontal dorsally. In most respects it is very similar to the palatine of *Prognathodon solvayi* (LINGHAM-SOLIAR & NOLF, 1989, fig. 13).

PARIETAL. The parietal is complete in only one specimen, *Plioplatecarpus houzeai* IRSNB 3130 (Fig. 20), but is poorly preserved. Several important characters are, however, established. The parietal foramen is enormous and lies approximately equally between the frontal and parietal bones. The fronto-parietal suture is irregular, with the parietal meeting the frontal on a narrow boundary. The main body of the parietal is short and somewhat constricted at the dorsal mid-point. The diverging suspensorial rami are relatively straight and deeply striated

on the ventral extremities where they were sutured to the squamosals in life (Pl. 6F). At the junction of the diverging processes the parietal is deeply notched, presumably for the attachment of the cervico-mandibularis musculature. An unusually large descending process or ala is present on the ventral surface of the parietal (Pl. 6A, B). Striae on the ventromedial surface suggest the presence of ligaments for attachment to the prootic of the basioccipital unit.

Fig. 20

BASIOCCIPITAL UNIT. The basioccipital unit is disarticulated and incomplete (Fig. 21). The exoccipitals are absent. The basioccipital condyle is highly dorsoventrally compressed and relatively broad, spanning almost the complete width of the basioccipital. Dorsally, a single large foramen is present while the exit ventrally is

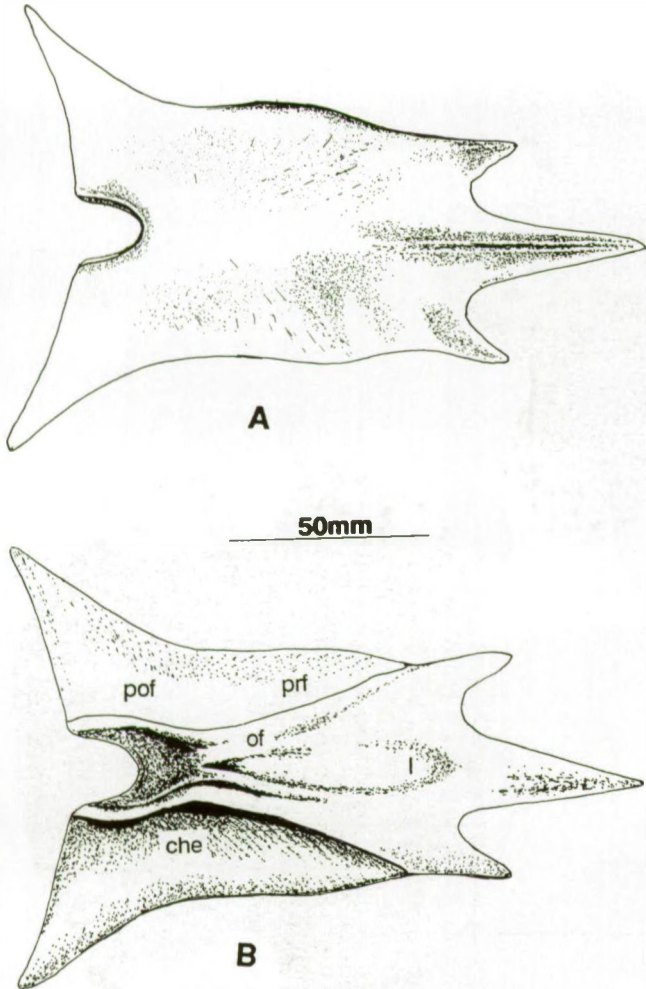


Fig. 19 — *Plioplatecarpus houzeau*. (IRSNB 3108). Frontal Restoration. A, dorsal view; B, ventral view.

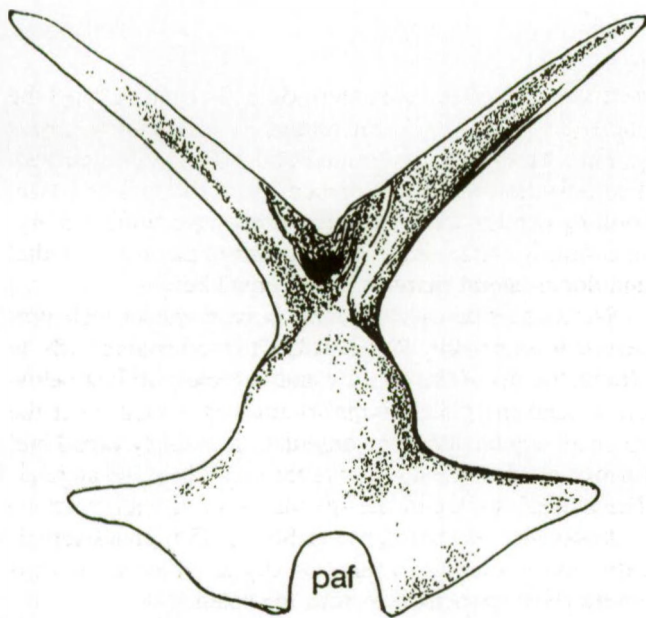


Fig. 20 — *Plioplatecarpus houzeau*. (IRSNB 3108). Parietal Restoration. Dorsal view.

biramous. The exit for cranial nerve VII, on the lateral face of the prootic, is without a trace of an otosphenoidal crest.

PTERYGOID. The pterygoids are preserved in IRSNB R3108, R3101 (Pl. 8A, B), 3130 and R35 (Pl.8C, D). The element is a delicate bone although it is clear from specimen IRSNB 35 that the quadratic process was quite expansive. The tooth row forms a slight curve. Eight tooth bases and one broken tooth are present in R3108 but poor preservation makes it hard to tell if this represented the full number. Despite presence of only tooth

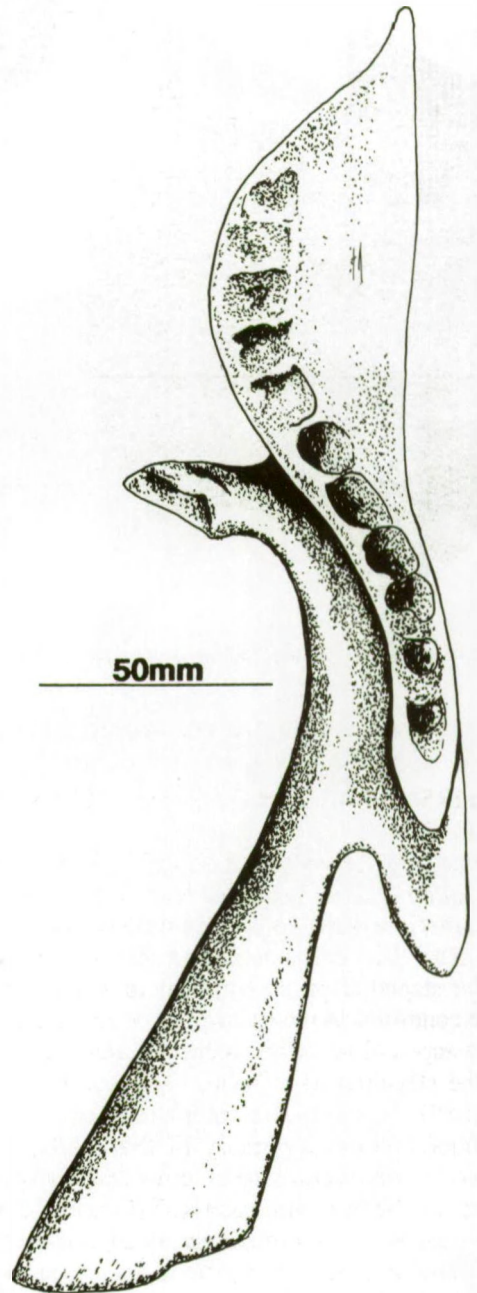


Fig. 22 — *Plioplatecarpus houzeau*. Reconstruction of the pterygoid based on IRSNB 3101 & 3130. Ventral view.

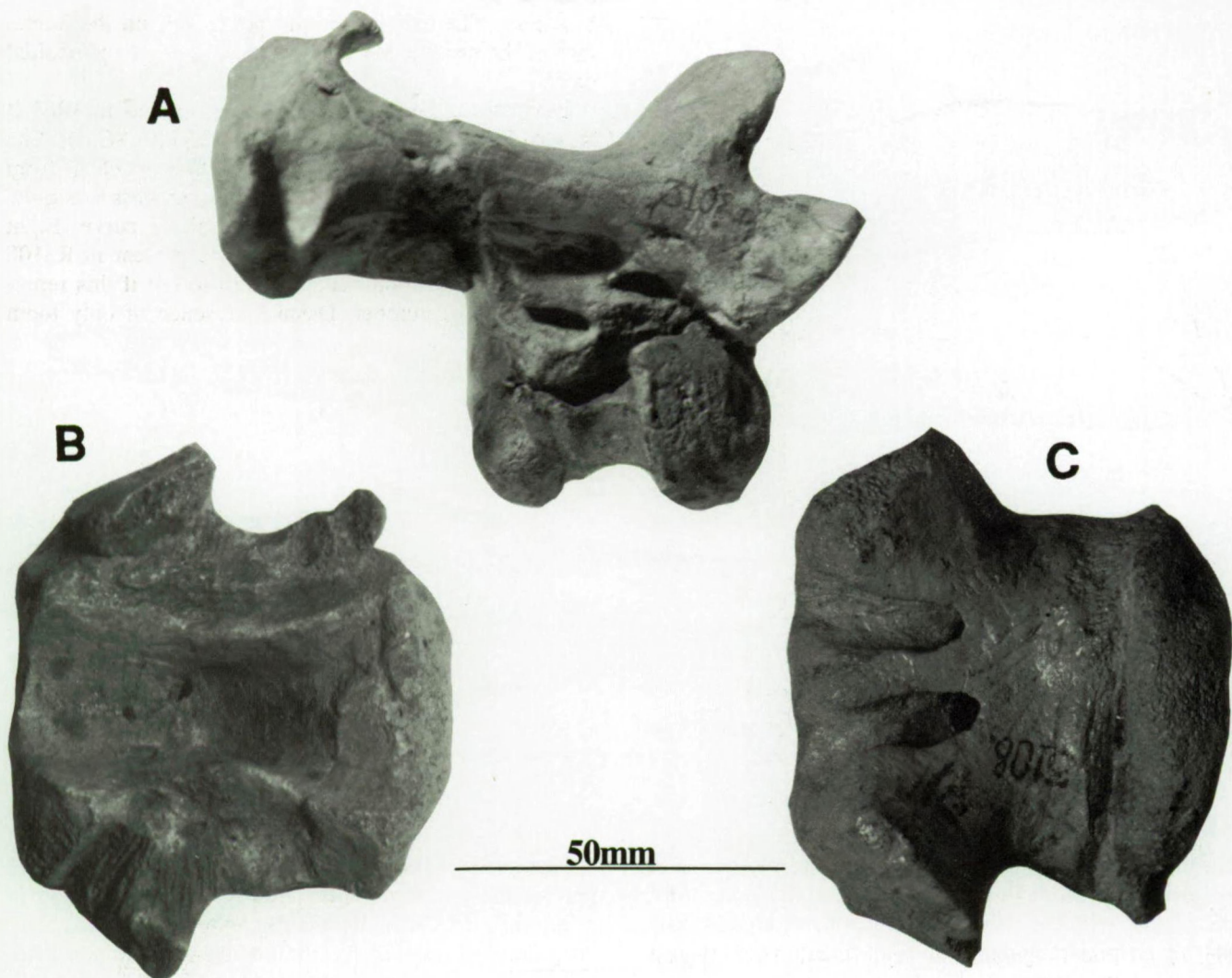


Fig. 21 — *Plioplatecarpus houzeau*. (IRSNB 3108). Basioccipital unit. A, lateral view; B, dorsal view; C, ventral view.

bases in IRSNB 3101 there were clearly 11 teeth in each pterygoid (Fig. 22).

QUADRATE. The quadrate in *Plioplatecarpus houzeau*, as in *P. marshi*, is the best preserved element (Pl. 8E-G). The quadratic tympanum is enormous and specimen IRSNB R36 (Fig. 9B) shows that it was clearly calcified. The stapedia pit is elliptical in shape. The most variable condition in the species is the shape and size of the infrastapedial process which in certain cases almost closes the stapedia meatus (also see RUSSELL, 1967, p. 160, fig. 87).

DENTARY. The right dentary of the holotype is well preserved but for the missing anterior tip (DOLLO, 1889b; Figs 23 & 24) but is complete in R37 (Fig. 16A & Pl. 5C). The bone tapers from a relatively broad contact with the postmandibular unit, rapidly to a very slender dental ramus, the postero-ventral surface is rather concave although the ventral margin of the dentary itself is relatively straight. The teeth are quite unusually set in a deep groove along the dental ramus. The tooth bases are

very strongly orientated anteriorly and occupy almost the entire depth of the dental ramus, as in *Plioplatecarpus marshi*. The teeth are pointed and posteriorly recurved. The posterior edentulous process is striking in its size, forming perhaps a third of the entire length of the dentary. In contrast to the condition in *P. marshi* the dorso-medial and dorso-lateral margins are of equal height.

SPLENIAL. The right splenial is particularly well preserved in specimen IRSNB R35. It extends anteriorly to almost the tip of the dentary and vertically to just below the medial margin. A large foramen is present near the splenial articulation. The articulation is fairly broad and forms a shallow cup to receive the condyle of the angular. The medial surface of the splenial is somewhat concave.

ANGULAR. The angular in IRSNB R35 is characteristically mosasauroid, forming a slight tuberos process anteriorly for articulation with the splenial.

SURANGULAR. The surangular in IRSNB R35 is a small bone compared with that of other mosasaurs. A large foramen is present on the lateral surface just below the

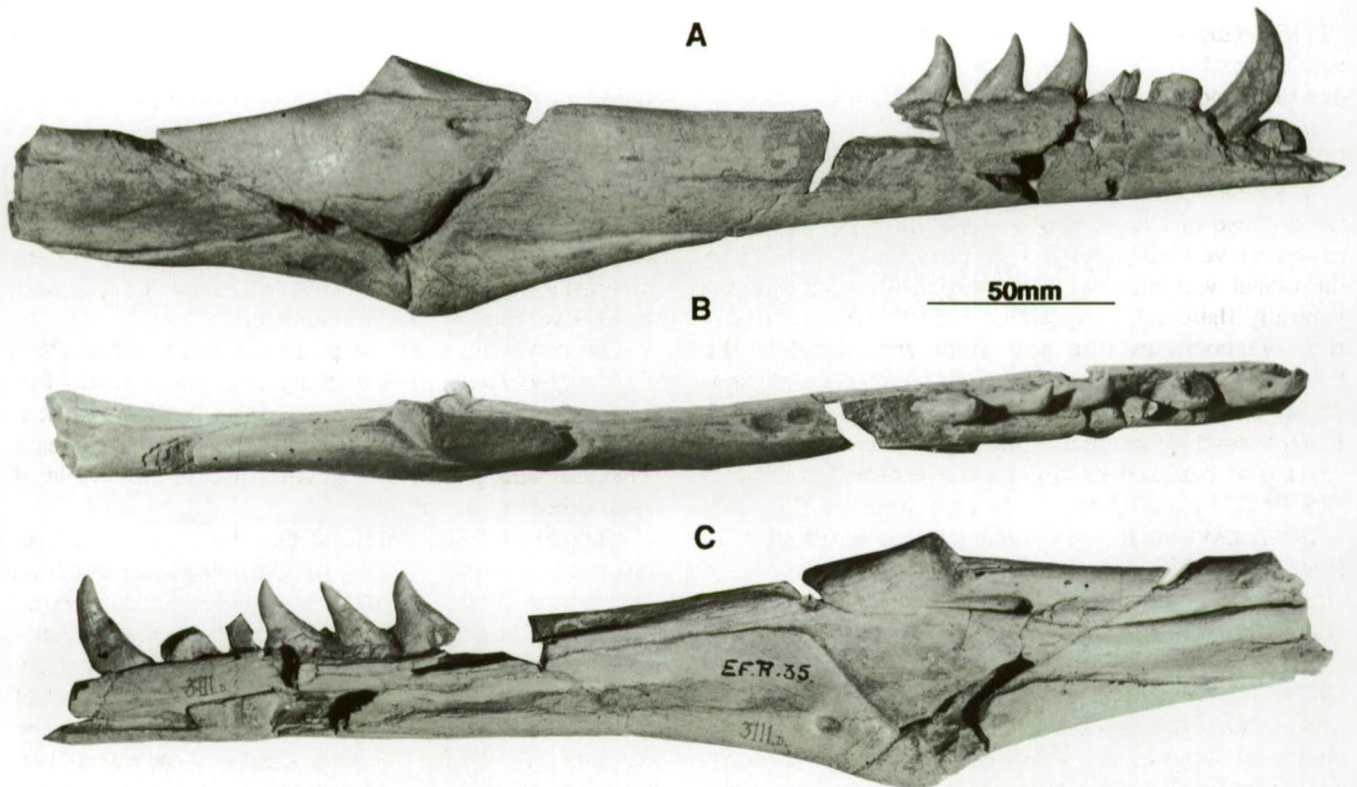


Fig. 23 — *Plioplatecarpus houzeau*. (IRSNB R35). Lower Jaw. A, lateral view; B, occlusal view; C, medial view.

coronoid. The surangular is somewhat abruptly truncated posteriorly (cf. for example *Platecarpus*, RUSSELL, 1967, pp. 66, 67) with the articular forming a considerable part of the post mandibular unit. This condition is highly unusual in mosasaurs.

CORONOID. The coronoid in IRSNB R35 is smaller than in any other known mosasaur (Fig. 23). Laterally it is just barely noticeable, seated on the crest of the surangular. The medial surface of the coronoid is somewhat deeper than the lateral surface but nevertheless does not reach the rather pinched mandibular fossa of the surangular. A broad expanse of the surangular separates the medial wing of the coronoid from the angular.

ARTICULAR. The prearticular contributes the largest part of the postmandibular unit, a unique condition in mosasaurs (Fig. 23). Its anterior extension is strikingly deep and extends far into the presplenial foramen anteriorly.

RETROARTICULAR PROCESS. The retroarticular process in *Plioplatecarpus houzeau* is preserved only in IRSNB 3108. It is more or less rectangular, in lateral aspect, the ventral margin inclined at approximately 45 degrees to the horizontal. On the medial surface the foramen for the chorda tympani lies in a slight excavation formed by the articular and the retroarticular process.

MARGINAL DENTITION. Teeth are similar to those of

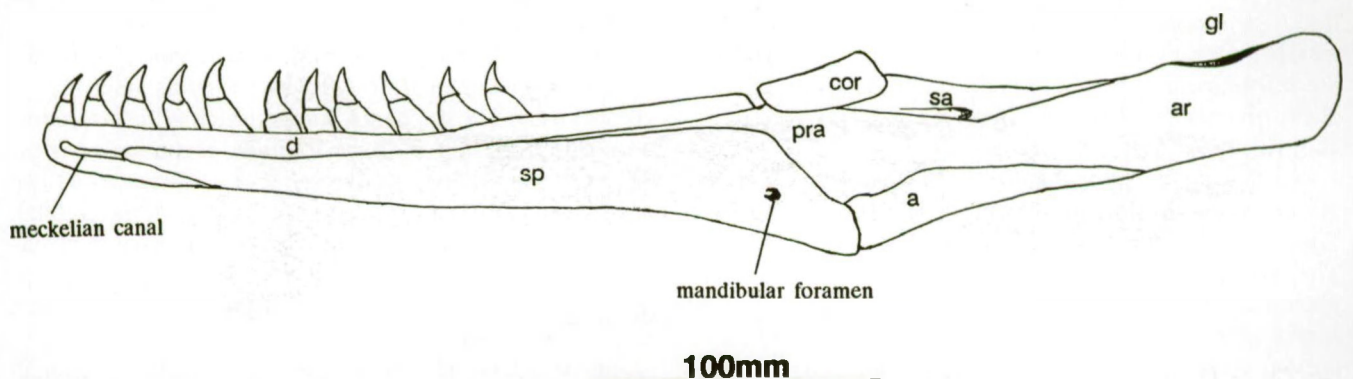


Fig. 24 — *Plioplatecarpus houzeau*. Reconstruction of the lower jaw based on the holotype (IRSNB R35). Medial view.

Plioplatecarpus marshi although striae and carinae appear somewhat less distinct. Whether or not this may be due to the poorer preservation is not certain at present.

POSTCRANIAL SKELETON.

VERTEBRAL COLUMN. The vertebrae are generally similar to those of *Plioplatecarpus marshi*. Transverse processes are vertically compressed. Articulation surfaces in the dorsal vertebrae are heart-shaped if slightly dorsoventrally flattened. In specimen IRSNB 3108 the posterior zygapophyses disappear from approximately the third to fourth thoracic vertebra and the anterior zygapophyses from approximately the sixth thoracic vertebra (cf. *P. depressus*). Zygosphenes and zygantara are absent (Fig. 25A). The best and most complete vertebral column is IRSNB R37 although it is embedded in matrix (Fig. 16).

INTERCLAVICLE. It is preserved in matrix in IRSNB R37 (Figs 16A & 25B). The bone is eroded anteriorly but it is clear that generally it is more delicate than in *Plioplatecarpus marshi*.

STERNUM. A rarely preserved sternum is present in IRSNB R37 (Fig. 16C) and was clearly quite large in size.

SCAPULA AND CORACOID. These elements are relatively almost as large as in *Plioplatecarpus marshi* although somewhat lacking the extensive antero-posterior component in *P. marshi* (Figs 16B & 26).

DISCUSSION

JAWS AND FEEDING. Two possible reasons are proposed for

the strong anterior inclination of the tooth bases: either to accommodate tooth bases in relatively shallow dental rami, or to counteract the pressures exerted by struggling prey, preventing teeth being pulled out of their sockets as prey was swallowed or as the lower jaw was disengaged and moved forwards. The latter interpretation seems to be supported by the fact that the teeth of durophagous mosasaurs such as *Globidens* and *Carinodens* are in contrast set in vertical sockets, where the main movement was up and down for crushing.

The construction of the postmandibular unit of *Plioplatecarpus houzeaui* is striking. The most obvious feature is the absence of strong overlapping bones particularly noticeable in the coronoid, surangular and angular. This jaw was particularly kinetic in contrast to that of most other mosasaurs.

GREGORY (1951) postulated that the jaws of the Cretaceous toothed bird *Hesperornis* and those of mosasaurs and in particular *Clidastes* sp. demonstrate convergent evolution. While some resemblances are noted, his subsequent comment (GREGORY, 1952) that a skull of *Ichthyornis* in the AMNH (MARSH, 1880) was in fact that of an immature mosasaur, is incorrect as pointed out by RUSSELL (1967, p. 121). One similarity, however, between the lower jaw of *Hesperornis* and *Plioplatecarpus houzeaui* is noted here, that of an oblique articulation between the angular and splenial bones (Figs 23 & 24). This presumably facilitated a greater spring levering of the anterior and posterior units of the lower jaw. In view

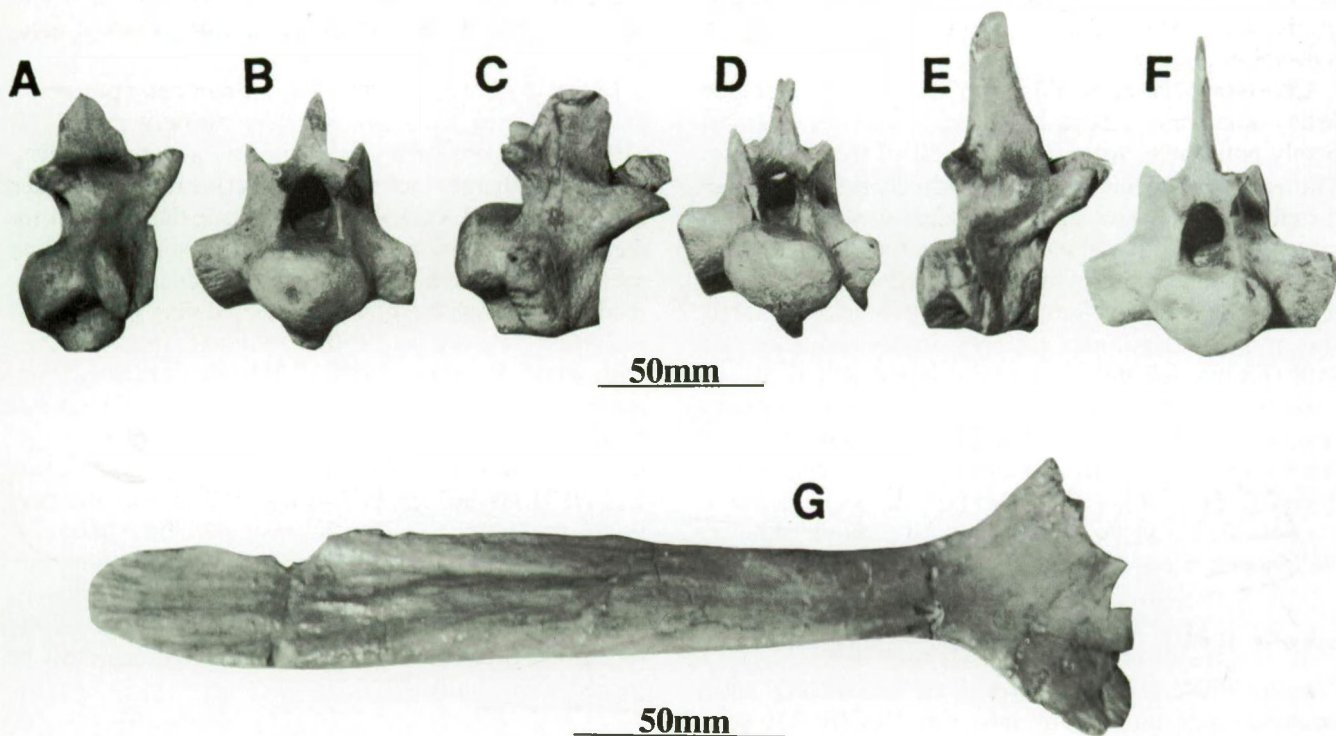


Fig. 25 — *Plioplatecarpus houzeaui*. (IRSNB 3108). Vertebrae. Atlas. A, lateral view; B, posterior view; Cervical vertebra. C, lateral view; D, posterior view. Thoracic vertebra. E, lateral view; F, posterior view. (IRSNB R37). Interclavicle. G, dorsal view.

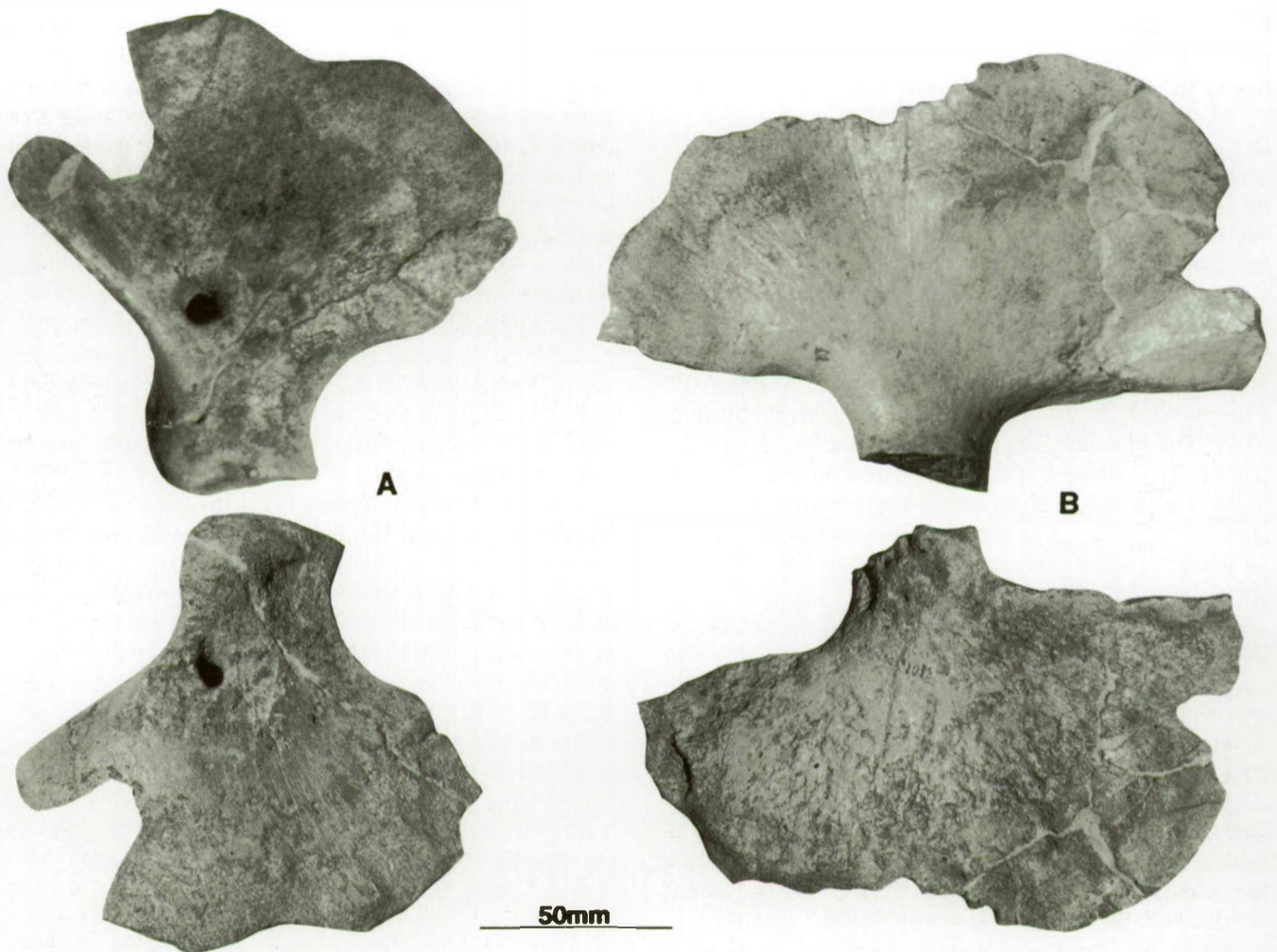


Fig. 26 — *Plioplatecarpus houzeaui*. (IRSNB 3101). Coracoid. A, lateral and medial views (top to bottom). Scapula. B, lateral and medial views (top to bottom).

of this, it is probable that the exceedingly broad articular, interleaving between the splenial and dentary provided stability for the whole lower jaw, and in particular, may have functioned to prevent disarticulation at the slender splenio-angular joint as the dentary pivoted slightly downwards when it engaged prey. In contrast, GREGORY (1951) supposed that a similarly broad prearticular in *Hesperornis* served to restore the jaw to the original position after lateral distortion. The unusual deep groove for the tooth row in the dentaries of *P. houzeaui* is also seen in *Hesperornis* (GREGORY, 1951, p. 347) and is presumed here to be a homoplastic condition although its function is not clear at present.

RELATIONSHIP OF THE QUADRATE WITH DEEP-DIVING AND WITH THE SYSTEMATICS OF PLIOPATECARPUS

DOLLO (1904, 1905) interpreted the remarkably intact calcified tympanic ear in specimen IRSNB R36 as a specialization for deep diving. This view was later supported by VAUGHN & DAWSON (1953). RUSSELL (1967, p. 49), however, observed a calcified tympanic membrane in members of three subfamilies of the Mosasauridae.

Most recently, MARTIN & ROTHSCHILD (1989) presented the condition of a calcified tympanic membrane in *Platecarpus* and "absence" in *Clidastes* (this is incorrect as seen in LINGHAM-SOLIAR & NOLF, 1989) as supportive evidence for their hypothesis of deep diving in *Platecarpus* (LINGHAM-SOLIAR, 1992a). Among the characters with which RUSSELL (1967, p. 160) distinguished *Plioplatecarpus primaevus* from *P. marshi* was the larger size of the posterior prominence beneath the stapedial pit, somewhat similar to the condition seen in *P. houzeaui* IRSNB 3108 (Fig. 33). In *P. houzeaui* it is clear that there is a considerable variation in this condition. Other characters, however, are constant in the species *P. houzeaui*. Indeed it is virtually impossible to distinguish between the quadrates of *P. houzeaui* and *P. marshi*, hence the separation of species based on such variations must be treated with caution.

PALEOBIOLOGY OF PLIOPATECARPUS

Plioplatecarpus houzeaui is quite distinct from *P. marshi* and significantly smaller. *P. marshi* is somewhat more evolved, demonstrated by the conditions of the pectoral

girdle in particular. However, *P. houzeaui* is in turn more advanced than the species in the Pierre Shale of the Western Interior of the U.S.A. (RUSSELL, pers. comm.). Because of the fragmentary nature of the North American material of *Plioplatecarpus*, it is very difficult to decide whether or not certain features of the quadrates and vertebrae are sufficient to have warranted RUSSELL'S (1967) species distinctions or whether they could simply be interpreted as intraspecific differences similar to those seen in both *P. marshi* and *P. houzeaui*. Further examination of the North American material is necessary. In my opinion, European and North American forms of *Plioplatecarpus* may prove to be more closely related. Recent material from the Upper Demopolis Formation of Sumter County, Alabama (Campanian/Maastrichtian boundary) of an almost complete mosasaur, *Plioplatecarpus* "gandyi" (BURNHAM, 1990, abstract; unpublished Masters thesis, 1991 and pers. comm.) in my opinion shows striking similarities to *P. houzeaui* material and specimen BMNH 5868 shows considerable resemblance to *P. marshi*.

It seems that underwater flight in *Plioplatecarpus marshi* was an adaptation to a complex environment of, for instance, weed beds or coral reefs, consistent with my recent proposal that *Plioplatecarpus* was confined to estuarine and lagoonal conditions. Sustained caudal swimming was replaced by pectoral propulsion (LINGHAM-SOLIAR, 1992b) as has previously been observed in fishes in confined areas (WEBB, 1982, p.339). In such a confined environment, axial undulation with a large lashing tail can be seen as a distinct disadvantage. Pectoral propulsion presumably allowed greater manoeuvrability and perhaps even facilitated in *Plioplatecarpus*, the invasion of the plesiosaur niche.

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PLATES

Pl. 1 — *Plioplatecarpus* sp. (BMNH 5868). Basioccipital unit. A, posterior view; B, lateral view; C, dorsal view. Quadrate. D, lateral view; E, medial view; F, posterior view. Splenial. G, lateral view. Retroarticular. H, lateral view. Atlas neural spine. I, lateral view; J, medial view. Atlas intercentrum. K, posterior view. Scapula. L, lateral view of portion of blade; M, dorsal view. Phalanges. N, lateral view. Intermedium. O, lateral view, P, articulation surface. Q, articulation surface of phalanges.

Pl. 2 — *Plioplatecarpus marshi* (IRSNB R38). Posterior views. A, B, cervical vertebrae; C, anterior thoracic; D, posterior lumbar; E, ?pygal; F, atlas neural spine (left to right) lateral, medial and posterior views. Interclavicle. G, ventral view; H, dorsal view.

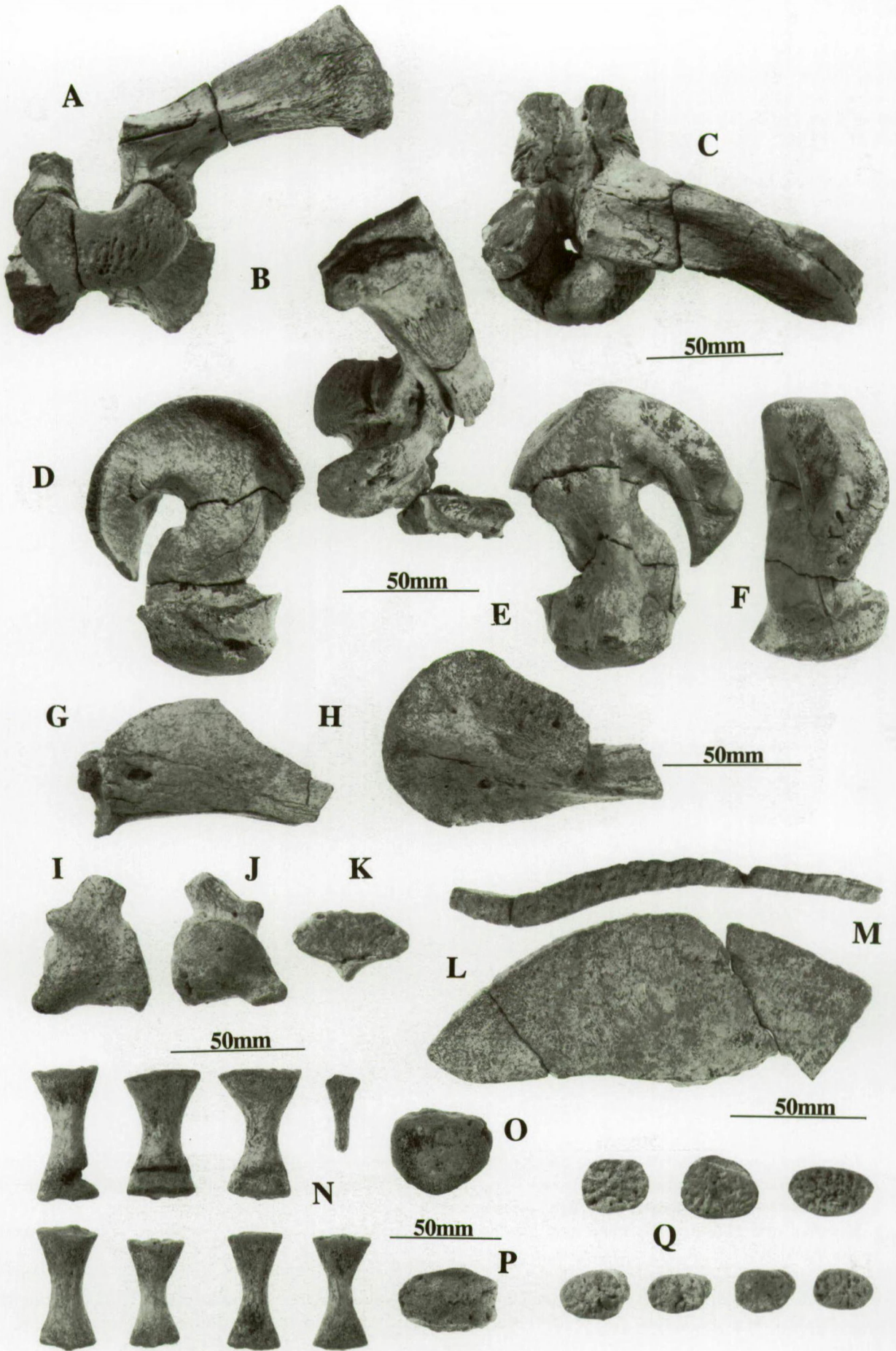


Plate 1.

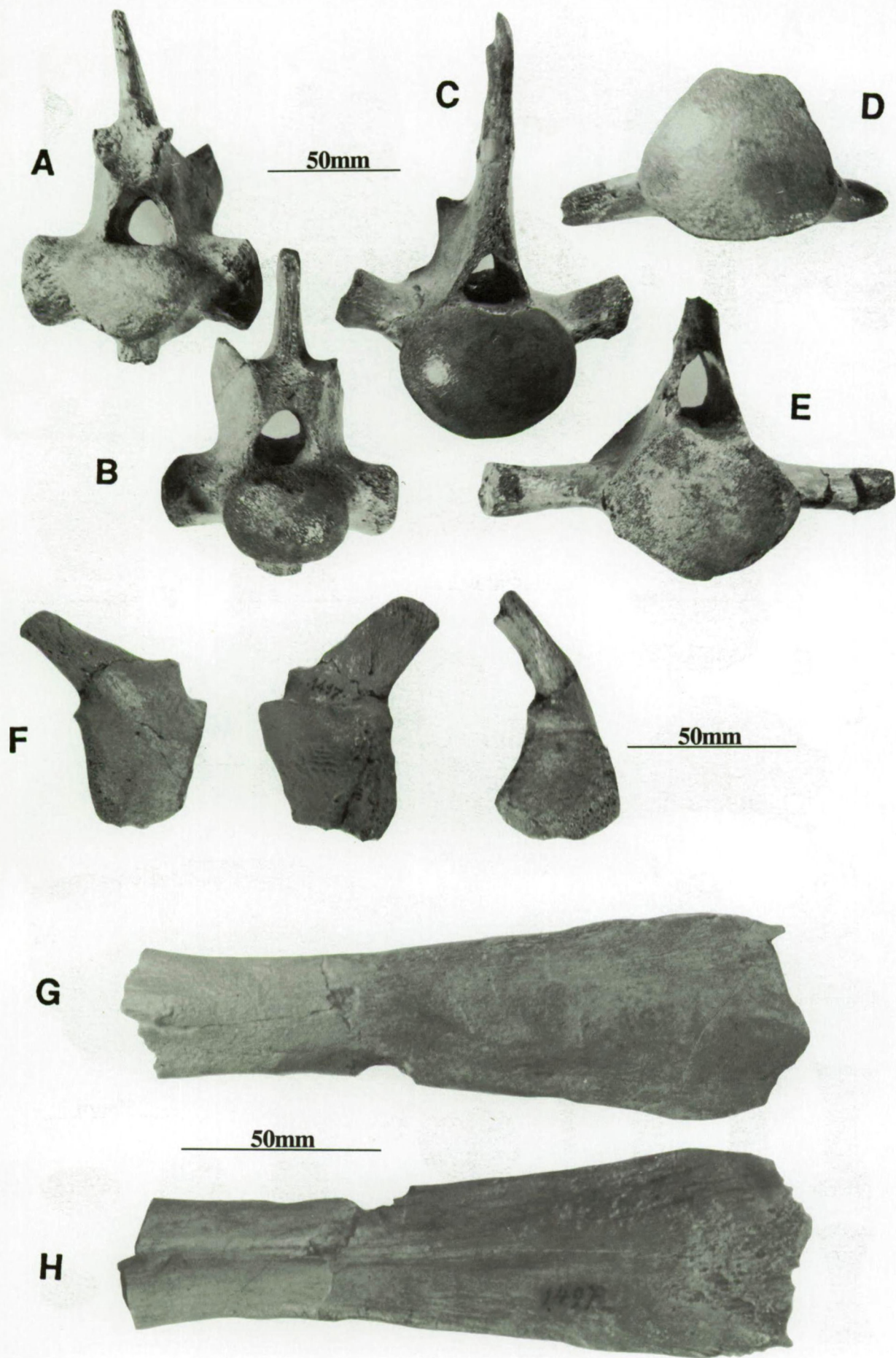
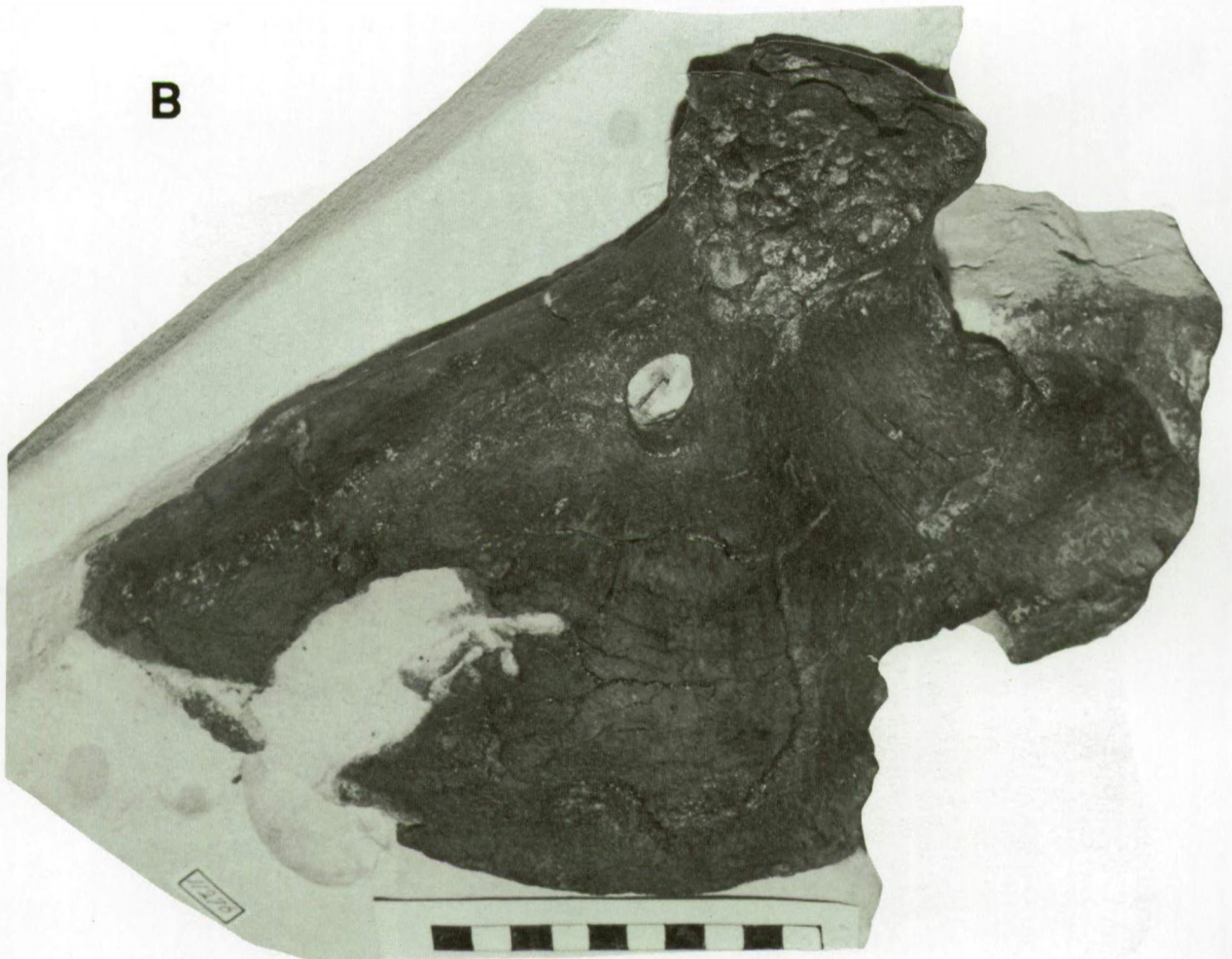


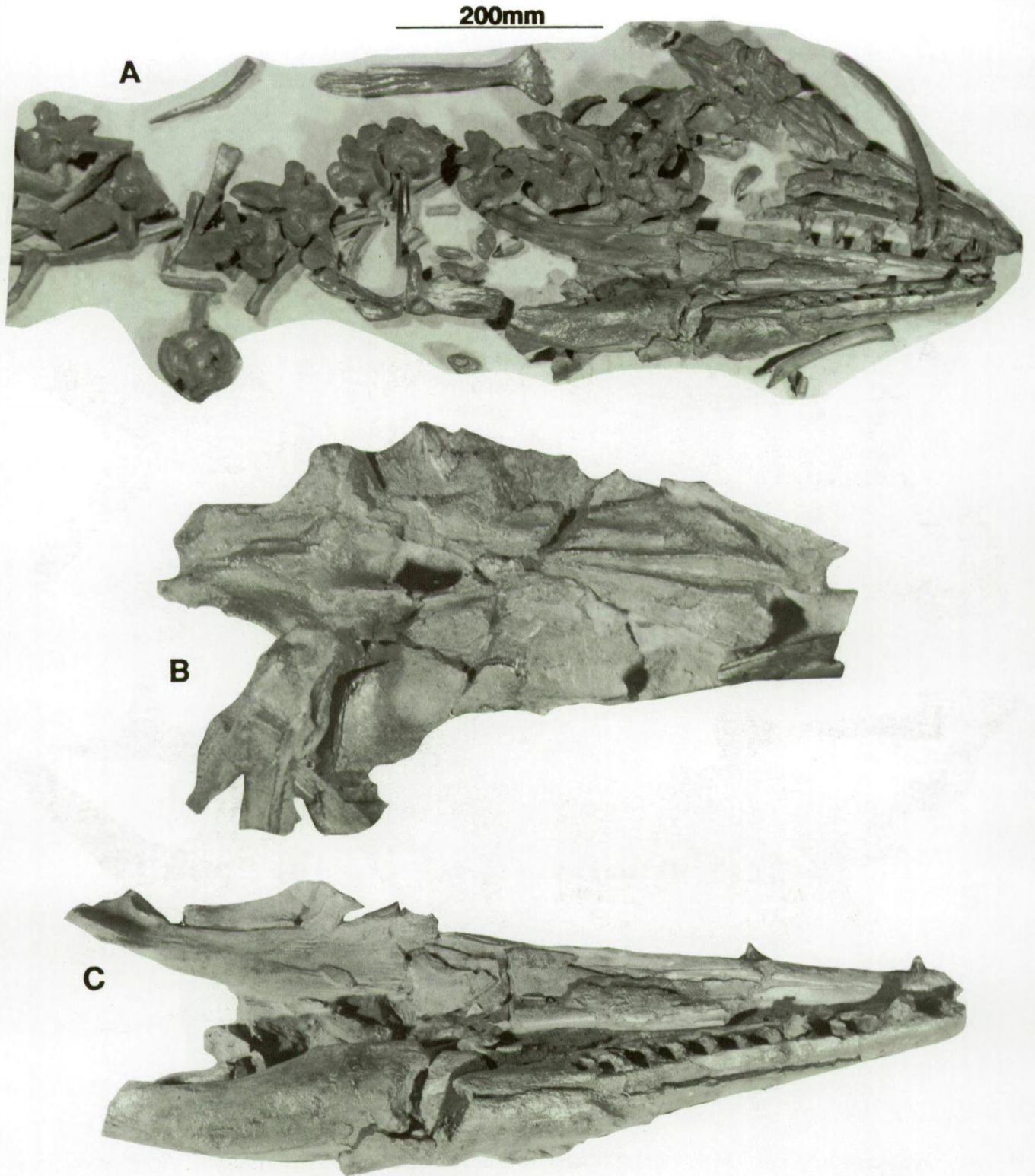
Plate 2.



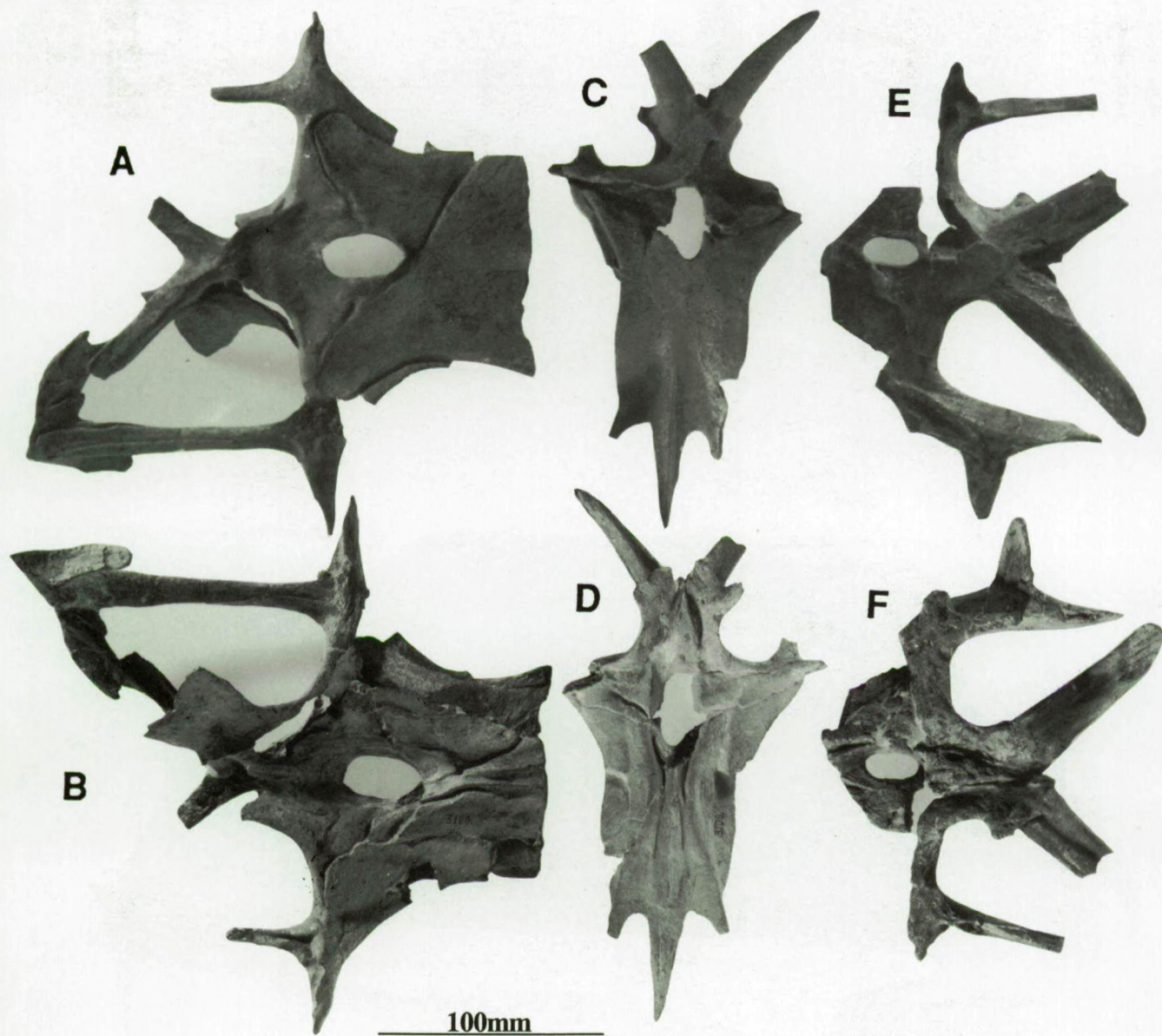
Pl. 3 — *Plioplatecarpus marshi* (TSMHN un-numbered specimen). A, posterior caudal vertebrae. (TSMHN 11276). B, coracoid.



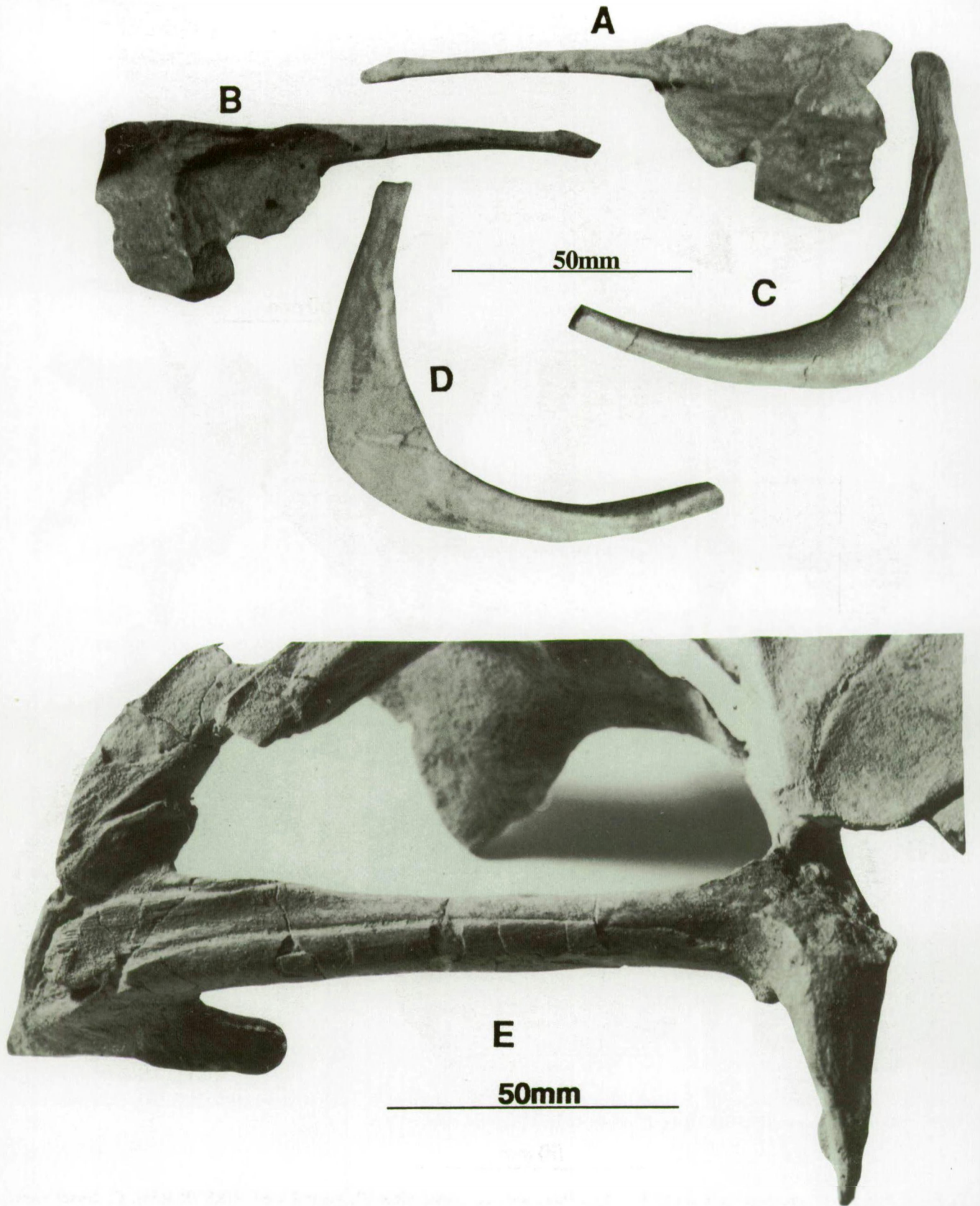
Pl. 4 — *Plioplatecarpus marshi* (TSMHN 11291). A, scapula; B, coracoid. lateral views.



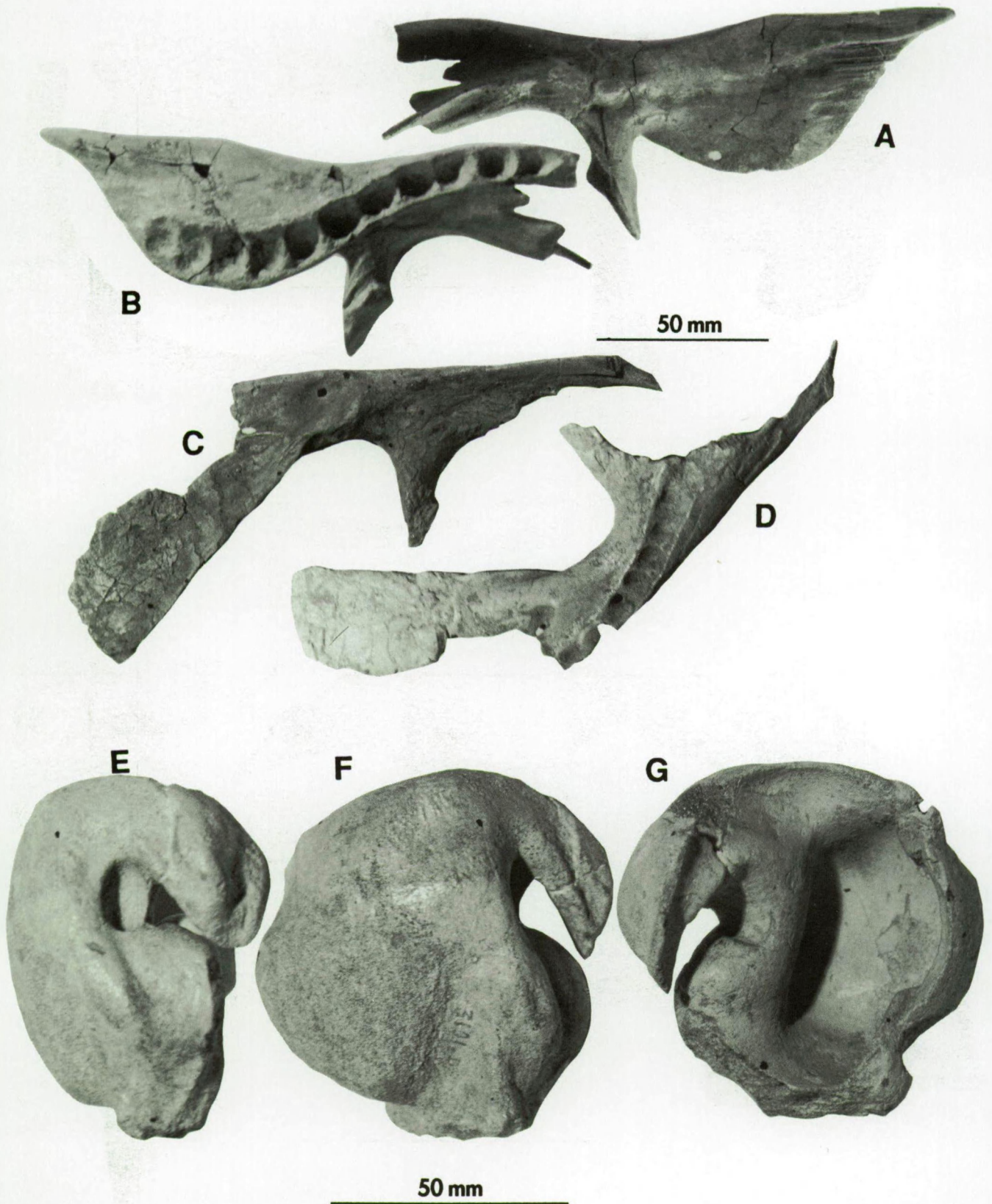
Pl. 5 — *Plioplatecarpus houzeau* (IRSNB R37). A, anterior skeleton of *Plioplatecarpus houzeau* (Fig. 16) in matrix. B, ventral view of frontal and partial parietal; C, dorso-lateral view of lower jaws (B & C, detail).



Pl. 6 — *Plioplatecarpus houzeaui*. Frontals. (IRSNB R36). A, dorsal view; B, ventral view. (IRSNB 3108). C, dorsal view; D, ventral view. (IRSNB 3101). E, dorsal view; F, ventral view.



Pl. 7 — *Plioplatecarpus houzeau* (IRSNB 3101). Prefrontal. A, dorsal view; B, ventral view. Jugal. C, lateral view; D, medial view. (IRSNB R36). Squamosal with large antero-lateral tongue.



Pl. 8 — *Plioplatecarpus houzeau*. (IRSNB 3101). Pterygoid. A, dorsal view; B, ventral view. (IRSNB R35). C, dorsal view; D, ventral view. (IRSNB R3101). Quadrate. E, postero-medial view; F, medial view; G, lateral view.

