# MOSASAURS FROM THE UPPER CRETACEOUS OF NIGER

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ABSTRACT. Fragmentary remains from the Dukamaje Formation ('*Mosasaurus* Shales'), Upper Maastrichtian, S.W. Niger, reveal a diverse mosasaur fauna of at least six genera – *Goronyosaurus*, *Igdamanosaurus* nov. gen., *Angolasaurus*, *Halisaurus*, *Plioplatecarpus*, *Mosasaurus*, and possibly *Platecarpus*. This represents an astonishingly high number of mosasaur genera from a single horizon, equalling that of the most prolific mosasaur beds of the world, the Niobrara Formation of Kansas, U.S.A. and the Craie Phosphatée de Ciply, Belgium. *Plioplatecarpus* represents the first documentation in Africa of this genus.

MOSASAURS were large marine lepidosaurian reptiles which, in a brief 25 million years, dominated the Late Cretaceous seas. Remains are found on all continents including Antarctica (Chatterjee *et al.* 1984). On the basis of skull form and, to a lesser extent, postcranial characters, they have been divided into three subfamilies, the Mosasaurinae, Tylosaurinae, and Plioplatecarpinae. Russell (1967) established, in addition, several tribal categories, for example, the Mosasaurini and Globidentini.

The majority of mosasaur remains occur in North America, in particular the Niobrara Chalk of Kansas, and the Gulf Coast, the Phosphatic Chalk of Ciply, Belgium, and the Tuffeau of Maastricht, the Netherlands (Russell 1967, charts 4, 5; Lingham-Soliar and Nolf 1989). Most other areas of the world have yielded isolated finds. However, two further areas, in Africa, are noteworthy, with perhaps the best mosasaur material known outside the North American and European sites: the '*Mosasaurus* Shales' (Upper Maastrichtian, Dukamaje Formation) of Sokoto State, N.W. Nigeria (Swinton 1930; Azzaroli *et al.* 1972, 1975; Halstead 1979; Soliar 1988) and the grey limestone coastal cliffs (Upper Turonian, 'Camadas do Tadi') of Iembe, Angola (Antunes 1964; Lingham-Soliar, in prep.).

In 1988 a joint expedition to Niger by the British Museum (Natural History), London, and Kingston Polytechnic recovered mosasaur remains, which Cyril Walker of the BMNH, the leader of the expedition, and responsible for collecting some significant specimens, placed at my disposal. The material, although fragmentary, was the first record of reptiles from the Maastrichtian of Niger. The only previous documentation of vertebrates from this horizon is of fishes (Tabaste, 1963; Cappetta 1972).

Repository abbreviations are: BMNH, British Museum (Natural History); GSN Geological Society of Nigeria; IRSNB, Institut Royal des Sciences Naturelles de Belgique; IGF, Institute of Geology and Paleontology of the University of Florence; YPM, Yale Peabody Museum. All the material described, unless otherwise stated, is housed in the BMNH.

## GEOLOGY

The following outline of the geology of Niger is my interpretation of information from David Ward and Richard Moody. The three principal localities, In Tahout, Mt Igdaman, and Kehehe, lie in the south-western corner of Niger, in an area bordering Dahomey in the south west, Nigeria in the south and Mali in the west (Text-fig. 1). This region was once part of the large West African intracontinental sedimentary basin, the Iullemmedan Basin. According to Petters (1977, 1979*a*), the subsidence of the South Central Saharan platform during Maastrichtian times created a marine embayment of the Tethys sea with its southern limits in the south-

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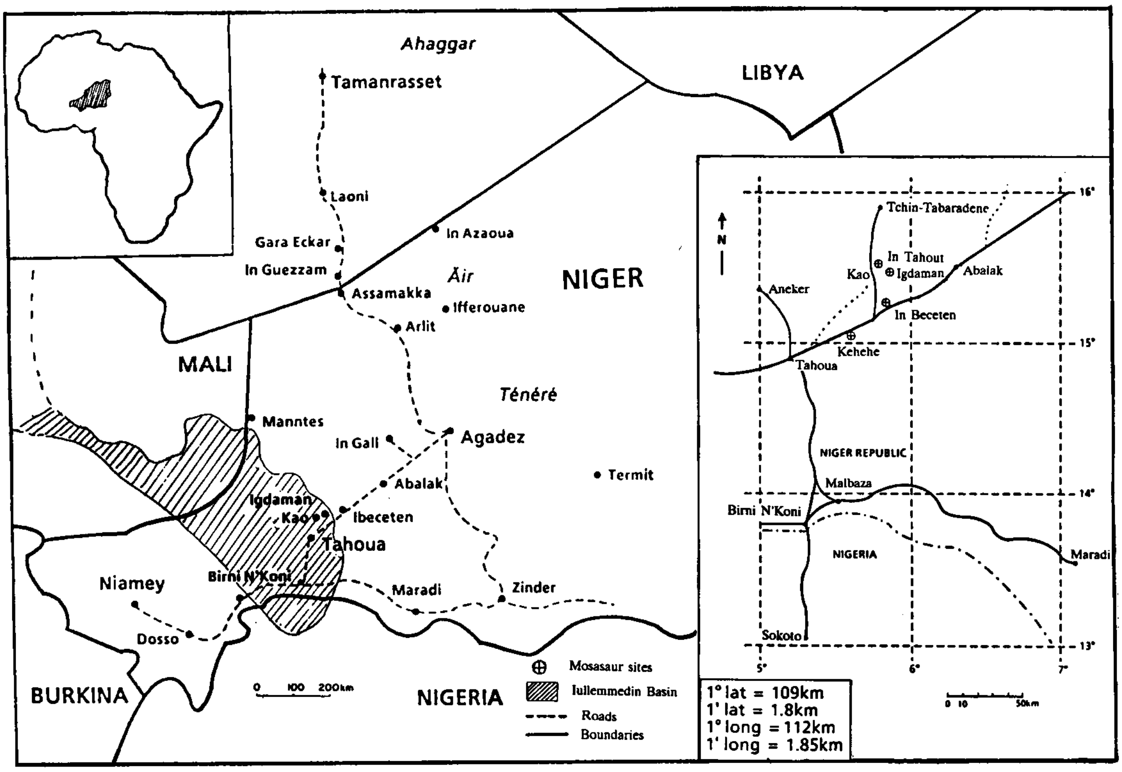


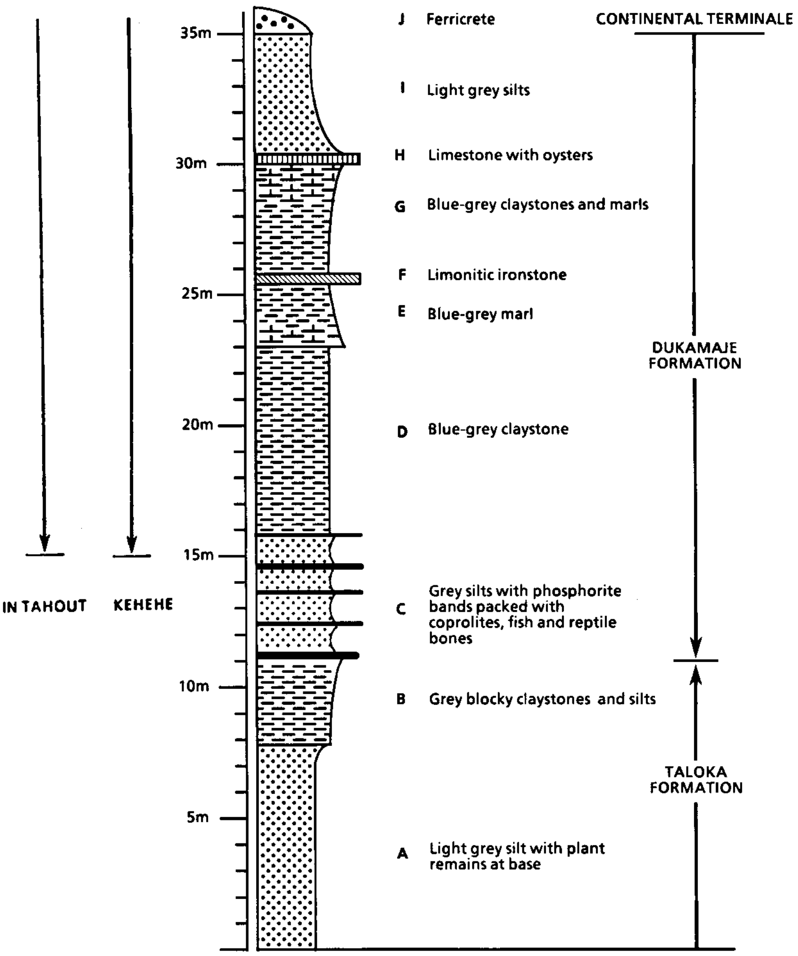
TEXT-FIG. 1 Map of Niger showing location of Igdaman, In Tahout and Kehehe (right inset, detail; David Ward pers. comm.). The Iullemmedin Basin (shaded) is figured after Petters (1977).

western part of Niger Republic and extending into the north-western tip of Nigeria. Other authors (Reyment 1965; Kogbe 1973; Adeleye 1975; Howarth 1981), in contrast, take the view that the trans-Saharan seaway was open-ended, joining the Mediterranean with the Gulf of Guinea.

The Maastrichtian horizon of N.W. Nigeria has been described in detail (reviewed Soliar 1988). Kogbe (1979) reported that '... similar fossil beds also occur in Niger Republic...' where they '... outcrop extensively'. However, there is no record, to my knowledge, of detailed stratigraphical work on this horizon in Niger besides brief mention by Greigert (1966) and Krasheninnikov and Trofimov (1969). The three localities represent exposures of the Late Cretaceous (Maastrichtian) Dukamaje Formation (David Ward, Richard Moody, pers. comm.). A detailed stratigraphic section is available for Igdaman and tentative results for the other two areas (Text-fig. 2).

In Tahout (5° 52′ 15° 22′), near Kao, a previously unrecorded locality, shows exposures of a complete series of sections of the Dukamaje Formation, with the mosasaurs coming from the lower levels on or very near the Cretaceous/Tertiary boundary. Above this lie the Palaeocene phosphate beds. Kehehe (5° 36′ 15° 2′) represents an outcrop of Late Cretaceous '*Mosasaurus* Shales', the beds resembling those described at Gilbedi and Kaffe (Reyment 1965). Of the three localities, Mt Igdaman (5° 50′ 15° 23′; Greigert 1966) yielded the largest amount of mosasaur material. Earlier work by Cappetta (1972) has shown the horizon to be abundant in inshore and marine fish remains which were apparently collected from a single thick phosphatic bed (David Ward, pers. comm.). Outcropping all the way around the hill are a series of bone beds from which the reptile and fish remains were obtained. This '*Mosasaurus* Shales', or Dukamaje Formation, is both overlain and underlain by loose sandstones equivalent to the Nigerian Wurno and Taloka Formations respectively (Text-fig. 2).

In addition to mosasaur material, the above horizons yielded the remains of a number of vertebrates, some similar to those found in the '*Mosasaurus* Shales' of Nigeria: the sea snake *Palaeophis*, pelomedusid turtles, sharks (including sawfish sharks and rays), cat fish, and the remains of the marine teleost, *Stratodus* (David Ward, pers. comm.)



TEXT-FIG. 2 Stratigraphic section at Igdaman (David Ward pers. comm.) with approximate extent of sections at In Tahout and Kehehe.

## SYSTEMATIC PALAEONTOLOGY

Order SQUAMATA
Family MOSASAURIDAE
Subfamily *Incertae Sedis*
Genus *Goronyosaurus* Azzaroli *et al.*, 1972

*Goronyosaurus* sp.

Text-figures 3, 4

*Referred material.* Premaxilla and two fragments of maxilla (R11909), probably associated. Poorly preserved dentary (R11947) with tooth sockets and remains of teeth, probably from a different individual. Mt Igdaman.

*Revised diagnosis.* Premaxilla lacking rostrum extends on to wide internarial bar; closed canal for olfactory lobes; ectopterygoid processes dorsoventrally flattened, two fork-like processes; snout approximately 55% total length of skull; maxillary teeth no more than 11, extend close to posterior border of the orbit; deep lateral interdental pits; little tapering of the dentary anteriorly; very high number of large foramina on premaxilla; elongated anterior tooth bases.

*Description.* A series of unique interdental pits on the jaw rami of specimens R11909 and R11947, and on the dental rami of the holotype of *G. nigeriensis* (IGF 14750, Azzaroli *et al.* 1975; Soliar 1988) characterise the genus *Goronyosaurus*.

*Premaxilla.* The premaxilla R11909 (Text-fig. 3A, B) is broken at a point just anterior to its union with the maxilla. No teeth are present, only four large sockets. The most striking condition of the premaxilla is the presence of a large deep interdental pit located laterally between the first and second premaxillary teeth (Text-fig. 3B). The premaxilla also shows an unusually high number of large foramina for the exits of cranial nerve V (ophthalmic branch), approximately 15 on either side, situated on the lateral and anterodorsal surfaces and extending close to the midline. The premaxilla is blunt, similar to that of *Prognathodon* (Russell 1967; Lingham-Soliar and Nolf 1989).

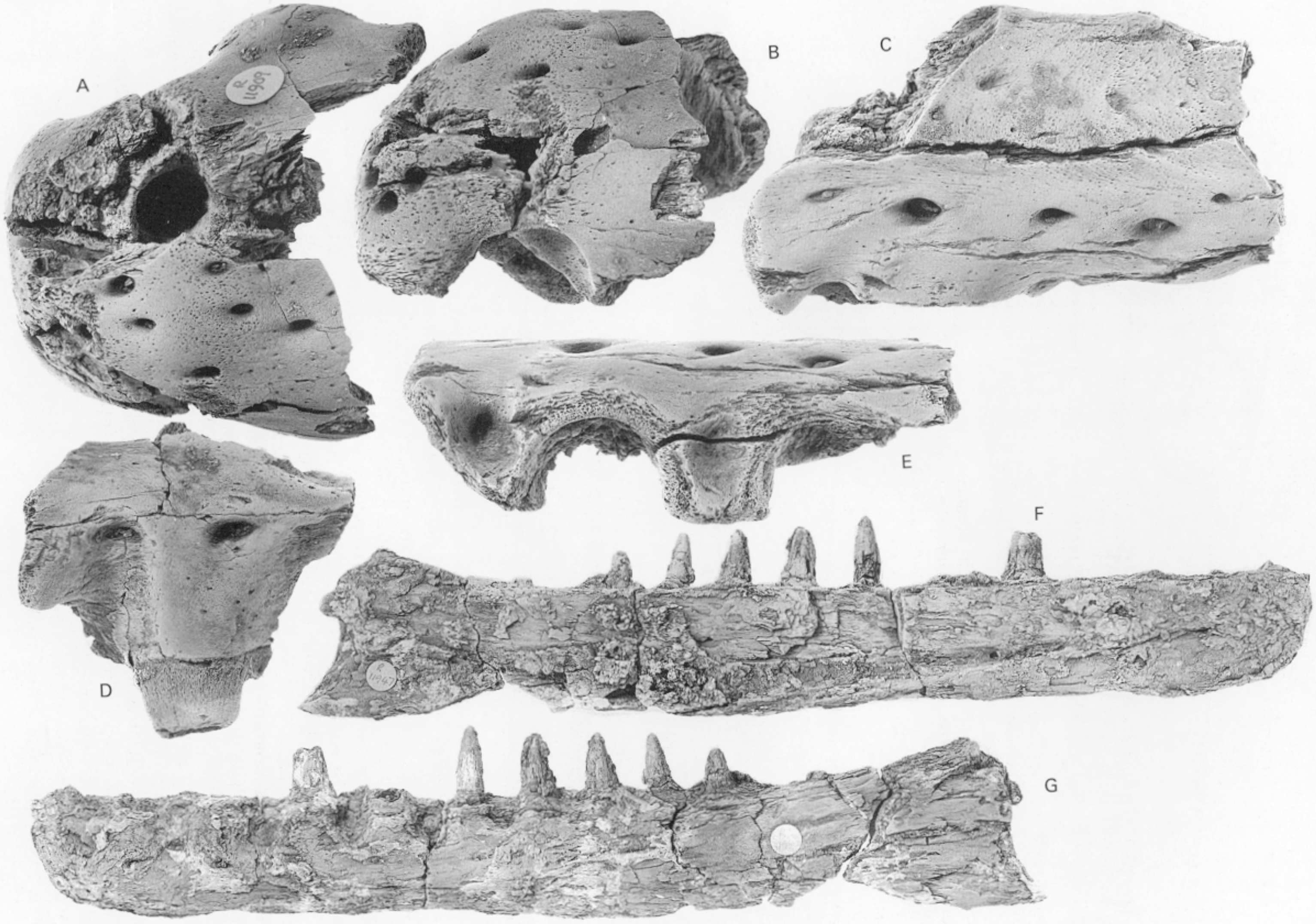
Despite poor surface preservation, the right premaxilla of *G. nigeriensis* (IGF 14750) shows approximately 10 foramina in a small area. In other mosasaurs, the number of large foramina generally does not exceed 6–7 on either side. In tylosaurs such as *Tylosaurus* (*Liodon*) *dyspelor* (Cope 1875, pl. 28), there are few large foramina, the majority being small, situated in a cluster on the lower lateral and ventral surface of the premaxilla.

*Maxilla.* Two well preserved fragments of maxilla, probably part of the same specimen R11909 (Text-fig. 3C, D), reveal the characteristic deep interdental pitting. Tooth crowns are not preserved, only an unusually long and well preserved tooth base (Text-fig. 3D) reminiscent of the one noted in the maxilla of the holotype of *Goronyosaurus* (Soliar 1988, fig. 3A; Text-fig. 10A). There are no more than eleven maxillary teeth in IGF 14750 although arguably there may be as few as nine if the two teeth at the end of the ramus are in fact displaced posterior pterygoid teeth (Text-fig. 10A).

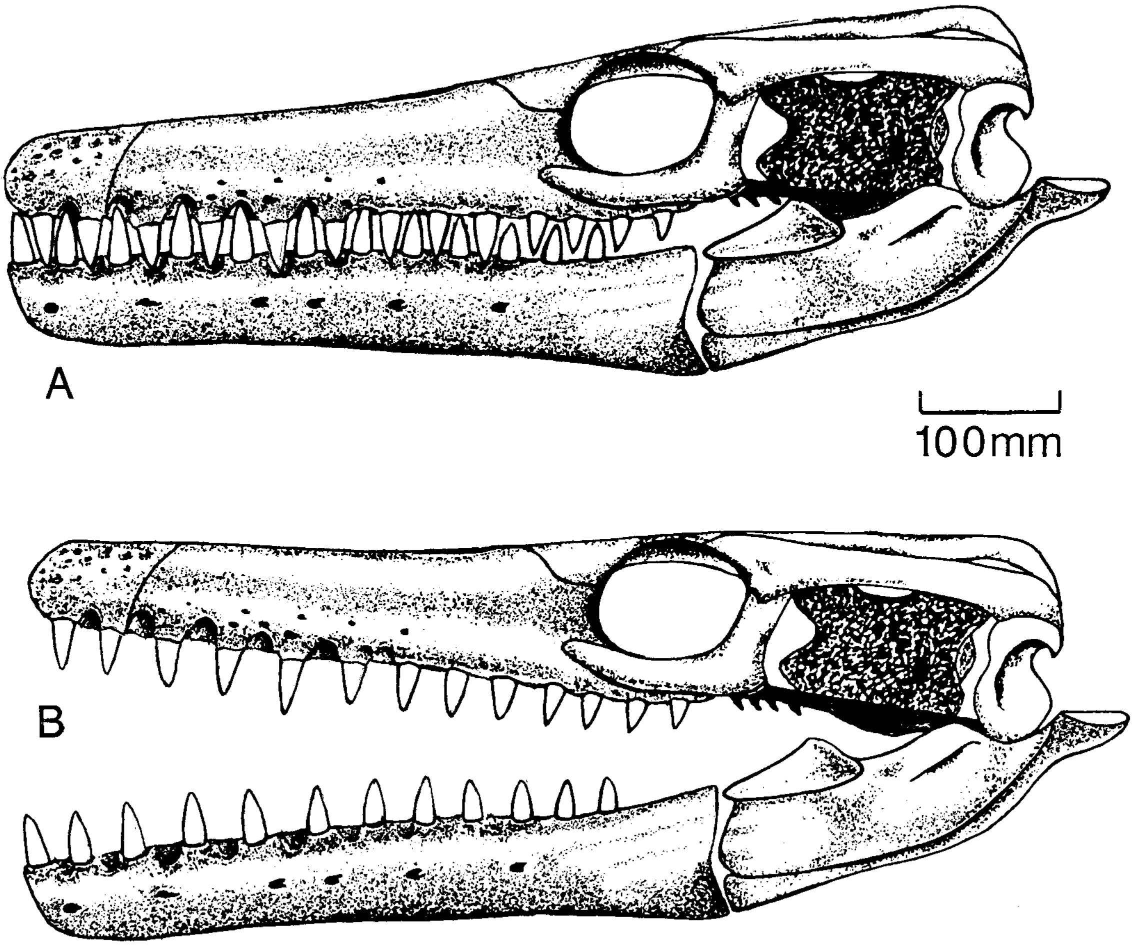
*Dentary.* The left dentary (R11947) is complete, although fractured into four separate fragments (Text-fig. 3F, G), and represents the first complete dentary of *Goronyosaurus* to be reported. It is fairly slender and scarcely tapers anteriorly, contrasting with the usual description of the element in mosasaurs: '... an anteriorly narrowing girder of bone...' (Russell 1967, p. 49). Medially, the excavation for Meckel's cartilage extends up to the second dentary tooth. All that remains of the teeth are six tooth bases and six poorly preserved relatively straight tooth crowns (Text-fig. 3F, G). The strongest indication that the dentary is referable to *Goronyosaurus* lies in the deep lateral interdental pits, extending to about the seventh tooth (Text-fig. 3G), which accords closely with those of the maxilla and the condition seen in the holotype material. Marginal teeth of R11909, R11947, and of the holotype are widely spaced.

*Discussion.* In occlusion, the jaws fitted tightly together, with the teeth overlapping their opposite numbers and fitting, uniquely for mosasaurs, into the deep interdental excavations (Text-fig. 4A). *Plotosaurus* (Camp 1942, pl. 1) shows a form of dental interdigitation, although there are no excavations for the opposing dentition – the battery of teeth (the highest number found in mosasaurs, 18 on the maxilla and 17 on the dentary) presumably formed a fish trap resembling that seen in plesiosaurs (McFarland *et al.* 1979; Brown 1981). In certain smaller specimens of *Mosasaurus hoffmanni* (e.g. IRSNB 1559, 'R12') a form of shallow interdental pitting is observed, but it is scarcely comparable with that of *Goronyosaurus*. However, Marsh (1869, p. 394) described 'the unusual depth of pits' on the outer superior edge of the lower jaw of *Mosasaurus copeanus* (synonymised *Plioplatecarpus depressus*; Russell 1967), the only record of this character in the literature, to my knowledge. Further study of this material is essential as it is probable that it belongs to a form related to *Goronyosaurus*.

The long snout of *Goronyosaurus* indicates that the adductor muscles originated relatively far back on the robust temporal arcade (Text-figs 4, 10). It is probable that static or bite forces were consequently reduced (Olson 1961; Greaves 1983), but that speed of jaw closure was conversely increased. A similar form of 'snapping' jaw mechanism was apparently prevalent in long-snouted marine crocodiles such as the Palaeocene *Rhabdognathus* and *Dyrosaurus* of the Sokoto area in N.W. Nigeria (Buffetaut 1976, 1979, p. 35). This technique of rapid impaling of prey was



TEXT-FIG. 3. *Goronyosaurus* (A–E, R11909). A, B, dorsal and lateral views of premaxilla. C, D, maxilla fragments. E, ventral view of C. ×1. F, G, R11947, medial and lateral views of left dentary. ×0·5.



TEXT-FIG. 4. Reconstruction of the skull of *Goronyosaurus nigeriensis* based on specimens IGF 14750, BMNH R11909, and R11947. A, jaws in occlusion, B, jaws open. ×0·2.

undoubtedly effective in capturing fairly evasive, moderately small, reptiles and fishes. The long pointed, relatively straight teeth in the dentary (R11903), long tooth base in the maxilla (R11909) and in the holotype (Soliar 1988; Text-fig. 10A), are consistent with such an hypothesis (Text-fig. 4).

The condition of interdental pits in *Goronyosaurus*, first figured in the holotype (Soliar 1988, fig. 3), represents an autapomorphy of the genus. The condition has also enabled a re-evaluation of previously mis-identified mosasaur material. For instance, the dentary of '*G.*' *nigeriensis*, figured by Azzaroli *et al.* (1975, pl. 1a, b), lacks interdental pits, suggesting that it is not referable to the genus, whereas a previously undescribed fragment of dentary (IGF 14751/2), revealing a series of deep external interdental pits, clearly is. Furthermore, two highly gypsiferous dentary fragments (R5682, R5683) referred to *Mosasaurus nigeriensis* (Swinton 1930), demonstrate the characteristic interdental pits of *Goronyosaurus*.

## Subfamily ?PLIOPLATECARPINAE

### *Igdamanosaurus* gen. nov.
### Type species *Igdamanosaurus aegyptiacus* Zdansky, 1935

Text-figure 5

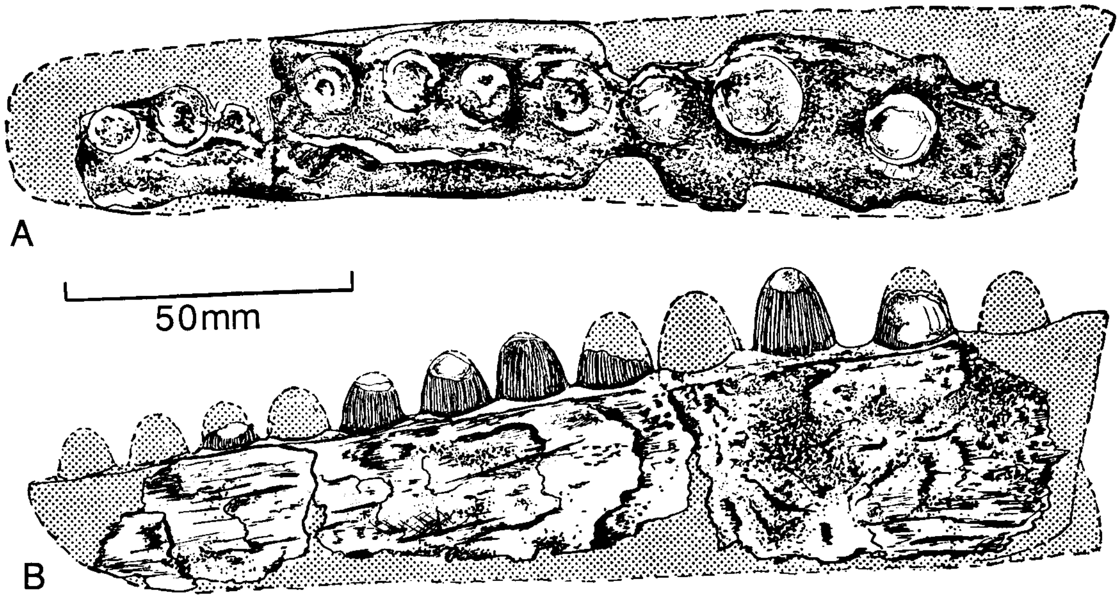
*Etymology*. Genus named after the village of Igdaman, near to which the specimen was found.

*Holotype*. BMNH R11898, consisting of three poorly preserved fragments of jaw, probably comprising a single specimen, which include two almost complete teeth and the remains of five more, and three tooth bases.

*Horizon and locality*. Mt Igdaman, near the village of Igdaman (sometimes In Dama), 5° 50′, 15° 22′.

*Diagnosis*. Massive dentary with dome-shaped unwaisted very finely striated teeth; ?anterior and posterior carina on teeth, sub-circular cross-sections.

*Description*. R11898, a right dentary, is massively proportioned (Text-fig. 5). Medially, a shallow recess indicates the groove for the splenial. There are seven teeth in various states of preservation (plus three tooth sockets) progressively increasing in size in an anteroposterior direction, except for the last, which is slightly smaller than the penultimate of the preserved teeth. The teeth are straight broad cones with rounded domed tips. The signs are that carinae are present but poor preservation makes this hard to confirm. In cross section the teeth are subcircular. Tooth crowns have unwaisted bases and are covered by fine parallel ribbing or striae, approximately 65–70 per tooth. The largest tooth is approximately 27·2 mm high and 22·5 mm wide at the base. The tooth form is clearly uniform along the entire segment of jaw (Text-fig. 5).



TEXT-FIG. 5. Right dentary of *Igdamanosaurus*. A, dorsal view. B, medial view.

*Discussion*. Two unusually small foramina for the exits of the mandibular nerve are distinguishable on the lower lateral surface of the dentary. Absence of dentary material in *Globidens* precludes any comparison, although there are similar, relatively small foramina in a maxilla of the holotype of *G. alabamaensis* (Gilmore 1912, pl. 39).

The broad domed teeth, unconstricted at the base, and parallel fine striations of R11898 are unusual for the Globidentini (cf. *G. alabamanensis* Gilmore 1912, *G. dakotaensis* Russell 1975). The teeth of R11898 on the other hand show some resemblance to those of '*G.*' *timorensis* (Huene 1935), but even more to the teeth of '*G.*' *aegyptiacus* (Zdanski 1935, pl. 2). The sharing of such an unusual tooth morphology by R11898 and '*G.*' *aegyptiacus* suggests that they should be included in the same genus. The status of '*G.*' *aegyptiacus*, however, was questioned by Russell (1975, p. 240). 'These teeth are quite unlike those in the type skull of *G. alabamaensis* and *G. dakotaensis*, and could belong to an unrecognized genus of durophagous mosasaur'. In view of this, it seems appropriate now to erect a new genus, *Igdamanosaurus*, for the reception of R11898 and '*G.*' *aegyptiacus*.

Russell (1967, p. 144) considered *Globidens* a derivative form of *Clidastes* but 'because of the highly peculiar nature of its spherical teeth', separated the genus into a new tribe of the Mosasaurinae, the Globidentini (Russell 1975). In contrast, vertical striae in *I. aegyptiacus* suggest that it represents an entirely new form of durophagous mosasaur derived from a *Platecarpus*-like ancestor and the genus is consequently assigned to the subfamily Plioplatecarpinae.

### Subfamily PLIOPLATECARPINAE
### cf. ?*Angolasaurus* Antunes, 1964

Test-figure 6

*Referred material.* Four vertebrae, BMNH R11901, R11902, R11903, R11904, of varying sizes, the smallest representing an immature individual. Mt Igdaman.

*Description.* R11901 is a well preserved almost complete cervical vertebra (Text-fig. 6A–C) which in general configuration compares with *Angolasaurus bocagei* (Antunes 1964, pl. 22). The neural spine is very narrow, with well preserved anterior and posterior zygapophyses. The lateral edges of the anterior zygapophyses extend smoothly on to the transverse processes. Distally, the synapophyses are not preserved, but the bases indicate that they were dorsoventrally compressed. Condyles and cotyles are shallow, approximately heart-shaped with the dorsal surfaces depressed slightly, as in *Platecarpus*. The lateral configuration of the hypapophyseal peduncle is similar to that of *A. bocagei* and *Platecarpus*, with the ventral surface sub-circular (Antunes 1964, pl. 22, fig. 1b, c). However, unlike *A. bocagei*, zygosphenes are not observed in R11901, although relatively poor preservation in this part of the vertebra makes identification inconclusive.

R11902 (Text-fig. 6D) is a small, fragmentary cervical vertebra probably belonging to an immature individual; it is in general similar to R11901. The main difference (which may be ontogenetic) lies in the hypapophyseal peduncle, which is not as deep as in R11901 but much broader laterally, spanning almost the entire length of the centrum. The ventral surface of the peduncle unlike that of R11901 is concave rather than convex. The cotyles seem to be fairly flat, but may be exaggerated because of weathering. Specimens R11903 and R11904 (Text-fig. 6E, F) are posterior cervical or early dorsal vertebrae. The main differences from R11901 and R11902 lie in the anteroposterior rather that dorsoventral flattening of the synapophyses. All the above vertebrae show strong cartilaginous articulations (indicated by pitting), suggesting a possible immature state of development.

*Discussion.* The vertebrae of *Angolasaurus* share broad similarities with those of *Platecarpus*, consistent with other characters that the two genera have in common: very large suprastapedial process of the quadrate, deep groove or foramen for basal artery on basioccipital, long striated teeth, and elliptical or heart-shaped articulations of centrum and free haemal spines. For the present, the above characters clearly suggest that *Angolasaurus* should be referred to the subfamily Plioplatecarpinae and not, as indicated by Antunes (1964, p. 164), to the Mosasaurinae.

### Subfamily PLIOPLATECARPINAE
### Genus *Halisaurus* Marsh, 1869

*Halisaurus* sp.

Text-figure 7A–D

*Referred material.* Vertebrae, BMNH R11983, R11906, R11951 and R11952. Mt. Igdaman.

TEXT-FIG. 6. *Angolasaurus* anterior cervical vertebrae. A, B, C, R11901, posterior, lateral, and anterior views. D R11902, small anterior cervical vertebra. E, F R11903, 11904 posterior cervical or early thoracic vertebrae. D, E, F in anterior (top) and lateral (bottom) views. × 1.

*Description*. R11923 (Text-fig. 7A–D) is an anterior dorsal, or possibly posterior cervical, vertebra. Much of the neural spine and left synapophysis are absent. The right synapophysis is stout, considerably longer than in other mosasaurs, and situated posteriorly on the centrum. The only preserved posterior zygapophysis is moderately weak. Characteristically, the neural canal is large and the condyle and cotyle nearly twice as wide as deep, nearly kidney bean-shaped with a slight emargination dorsally. There is no evidence of zygosphenes or zygantra.

TEXT-FIG. 7. A–D, *Halisaurus* vertebra (BMNH R11983). A, lateral view; B, ventral view; C, anterior view. D, posterior view. × 0·5. E–G, *Plioplatecarpus* sp. (BMNH R11984). E, anterior view; F, lateral view; G, posterior view.

*Discussion*. R11951, 11952, and 11906 are the smallest known *Halisaurus* vertebrae (cf. Bukowski 1984; table 1). They are placed in the genus *Halisaurus* on the basis of the characteristically flattened condyles and cotyles, although the problem of identification is augmented here by small size coupled with the generally primitive nature of *Halisaurus* vertebrae (Bukowski 1984). For instance, the relatively large neural canal and relatively broad span across the zygapophyses generally accord with conditions seen in less highly modified squamate families. However, a somewhat less pronounced state of these features in R11923, R11951, R11952 suggests that the vertebrae belong to *Halisaurus*.

*Halisaurus* was poorly known, being represented by isolated remains, mainly vertebrae and a few fragments of skull, until Russell (1970) assigned '*Clidastes*' *sternbergi*, a complete skeleton in the University of Uppsala) to the genus. Until it is studied in detail, '*C.*' *sternbergi* is excluded from consideration of *Halisaurus*.

In a label in the IRSNB, Russell referred the Belgian mosasaur *Phosphorosaurus ortliebi* (IRSNB R34, formerly 4671; Dollo 1889), in my view correctly, to *Halisaurus*. It seems that this assignment was based on the similarity of the frontal of IRSNB R34 to that described by Baird and Case (1966, p. 1212), which they indicated had been identified by Russell as *H. platyspondylus*. In contrast, IRSNB R34 and '*C.*' *sternbergi* differ in the size and the position of the parietal foramen. In IRSNB R34 the parietal foramen is relatively large, approximately 24 mm in diameter (Dollo 1889*b*, pl. 9, fig. 6), one of the largest in the Mosasauridae, and it is situated on the fronto-parietal suture and partly on the frontal. On the other hand, in *C. sternbergi*, 'the foramen parietale is small and lies on the boundary between the first and second third of the parietale, thus considerably further back than in *Clidastes velox* and other mosasaurians' (Wiman 1920, p. 14, fig. 3). These differences in the size and position of the parietal foramen suggest that *Halisaurus* and '*C. sternbergi* may not belong in the same genus. Estes *et al.* (1988, pp. 148–149) and Lingham-Soliar and Nolf (1989) discuss the apomorphic nature of these characters in squamates and mosasaurs respectively. Provisional assignment of *Halisaurus* to the subfamily Plioplatecarpinae, indicated in a previous cladistic analysis (Soliar 1988), is retained.

## Subfamily PLIOPLATECARPINAE

### *Plioplatecarpus* Dollo, 1882

### *Plioplatecarpus* sp.

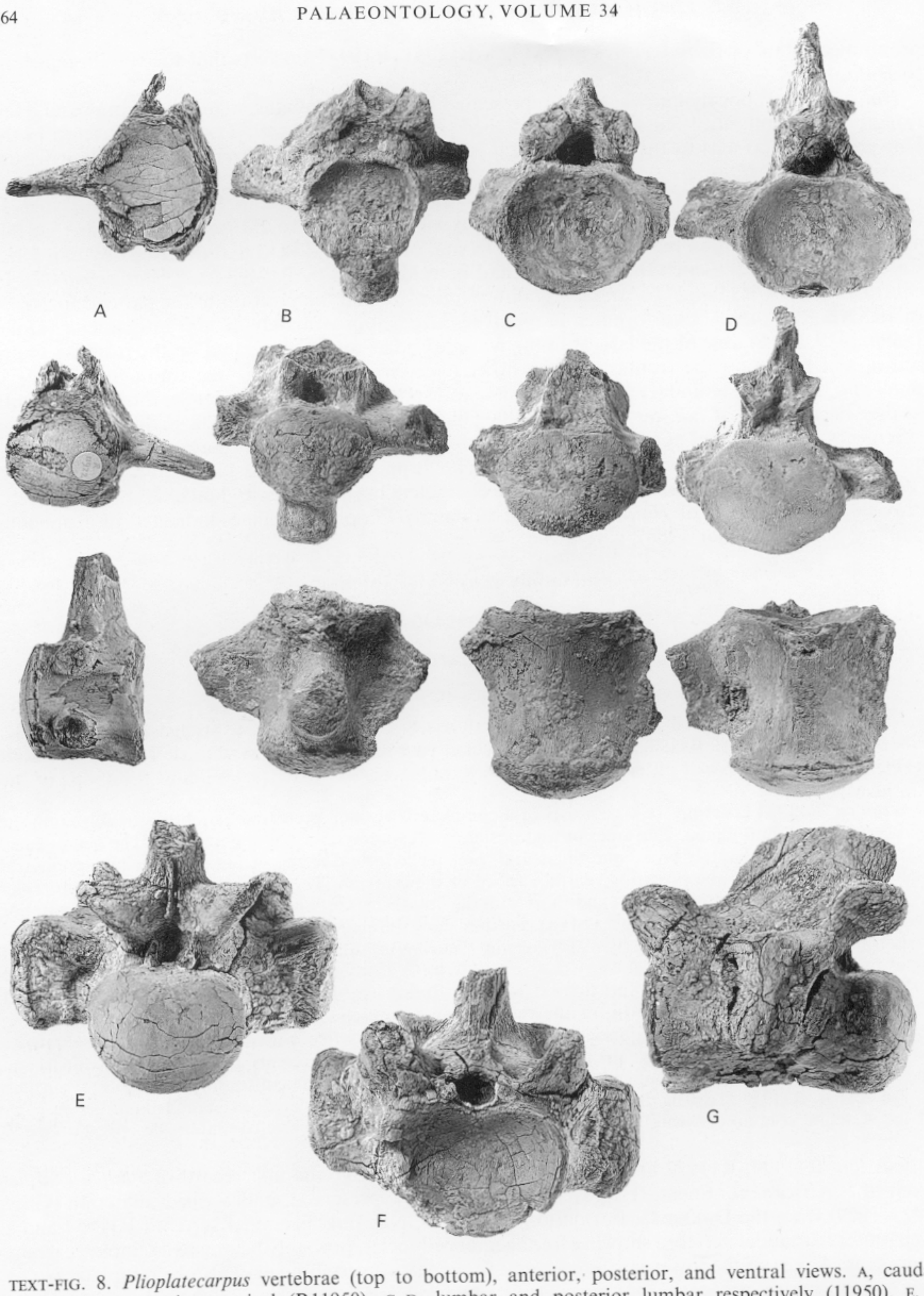
Text-figures 7E–G, 8A–D

*Referred material.* Fairly well preserved mid-cervical vertebra, BMNH R11924. Mt Igdaman. A posterior caudal vertebra, BMNH R11982. Numerous vertebrae probably belonging to a single specimen, BMNH R11950. In Tahout, top half of '*Mosasaurus* Shales'.

*Description.* R11924 (Text-fig. 7E–G) consists of a complete fairly well preserved vertebra probably from the mid-cervical vertebral region. The anterior and posterior zygapophyses are well developed. The neural canal is large, tall, and moderately broad and the neural spine posteriorly directed. A fairly slender hypapophyseal peduncle is situated on the posterior ventral surface of the centrum. The peduncle is sub-circular in cross-section. Synapophyses are quite slight and short with the dorsal surface continuing smoothly onto the anterior zygapophyses. The articulating surfaces of the centrum show the characteristic elliptical shape of cervical and early trunk vertebrae found in members of the genus *Plioplatecarpus*, the width approximately one and a half times the depth.

The caudal vertebra (R11922, Text-fig. 8A) is poorly preserved, with most of the neural spine, the left transverse process, and the distal tip of the right transverse process absent. The shape of the condyle is markedly hexagonal. Haemal peduncles indicate the presence of free haemal spines which characterise plioplatecarpines and tylosaurines. The size of the specimen (unless it represents an immature individual) and the sharply defined hexagonal configuration of the condyle, confirm assignment to *Plioplatecarpus* rather than to *Tylosaurus*. R11950 (Text-fig. 8B–D) represents a series of partly articulated vertebrae from different parts of the vertebral column (Text-fig. 8B–D). All show the characteristic vertebral conditions described above.

*Discussion.* R11924, R11922 and R11950 are to my knowledge the first record of *Plioplatecarpus* from the African continent. However, among poorly preserved undescribed material (GSN 1928–1929) from the Dukamaje Formation of Gilbedi, Nigeria), a cervical vertebra R11954 and a well preserved caudal vertebra showing free haemal peduncles, probably belong to a plioplatecarpine mosasaur. A part of the lower jaw and several fragments of vertebrae may also be plioplatecarpine but are too poorly preserved and gypsiferous to permit assignment.



TEXT-FIG. 8. *Plioplatecarpus* vertebrae (top to bottom), anterior, posterior, and ventral views. A, caudal (R11922). B, anterior cervical (R11950). C, D, lumbar and posterior lumbar respectively (11950). E, F, ?*Platecarpus* lumbar vertebra (R11899); E, posterior view; F, anterior view; G, lateral view. ×0·5.

## Subfamily PLIOPLATECARPINAE

## Genus *Platecarpus* Cope, 1869

### ? *Platecarpus* sp.

Text-figure 8E–G

*Referred material.* BMNH R11899, a fairly well preserved dorsal vertebra with most of the neural spine absent. Mt Igdaman.

*Description.* R11899 (Text-fig. 8E–G), although otherwise well preserved, lacks its neural spine from a point a few centimetres above the zygapophyses. The span and robustness of the anterior and posterior zygapophyses, suggest that the vertebra belongs to the anterior trunk series. The inflated heart-shaped condyles and cotyles, and the general configuration of the vertebra, suggest that it may be referable to *Platecarpus*.

## Subfamily MOSASAURINAE

## *Mosasaurus* Conybeare, 1822

### cf. *M. hoffmanni* Mantell, 1829

Text-figure 9E

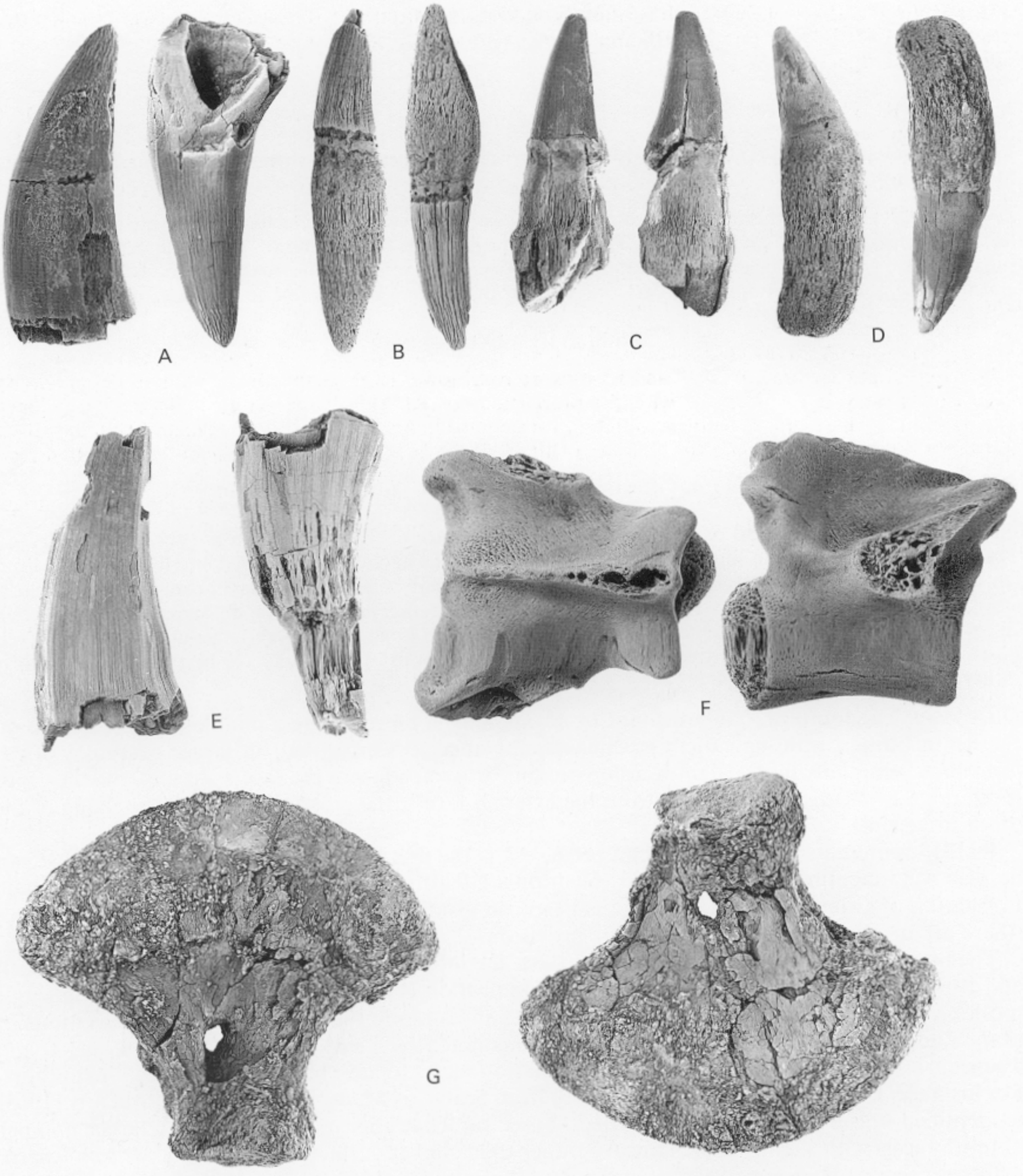
*Referred material.* BMNH R11913, a fragment of a large tooth crown. Mt Igdaman.

*Description.* The distal tip and part of the anteroventral surface of the tooth crown are absent (Text-fig. 9E). The specimen is abraded, but shows distinct signs of enamel. The buccal face is divided into five vertical prisms. On the lingual surface, however, owing to weathering, it is not possible to discern prisms with confidence, although this is difficult even in well preserved specimens of *M. hoffmanni* (i.e. the holotype skull and IRSNB 26 and 'R12'). In cross section the tooth shows a fairly deep lingual and slightly rounded buccal surface. Posterior and anterior carinae are present. The tip of the tooth appears to have been gently posteriorly recurved.

*Discussion.* The tooth probably belongs to *M. hoffmanni*, representing a middle-posterior tooth on the dental ramus, although there is some resemblance to teeth found in larger examples of *M. lemonnieri*, especially in the slight beading present between a few of the facets. At any rate the tooth is referable to *Mosasaurus* judging from the external facets, the cross section, and the shape of the tooth in general.

R11913 represents an important find because it is the first tooth from Niger or Nigeria that can be positively identified as *Mosasaurus*. Swinton's (1930) referral of a tooth from the Dukamaje Formation of Gilbedi to *M. nigeriensis*, is based on insufficient diagnostic characters for the genus (there are no descriptions of facetting or provision of cross-sections).

The literature on mosasaur dentition is sparse, the most significant papers being Edmund (1960) and Russell (1967). A problem in mosasaur classification is the erection of species based on single tooth crowns. Mosasaur teeth manifest certain changes along the tooth row, simple variations of shape and in the nature of tooth facets. This was noted by Leidy (1865, p. 56; pl. 9. fig. 3) and Thevenin (1896, fig. 3, p. 904). Despite this, variation seems to have been ignored by certain authors. For instance, Persson (1959) identified a tooth from Scania as *M. hoffmanni* and subsequently (1963) re-identified it as a new species, *M. ivoensis*, based on what appears to have been a larger number of tooth facets with slightly more concave rather than convex surfaces (conceivably *M. lemonnieri*). Another species, *M. beaugei*, was diagnosed by Arambourg (1952, p. 282–283, pl. 31) on similarly dubious grounds. His description included a variation in tooth shape in an anteroposterior direction. Following this, *M. beaugei* was identified by Price (1957) from the Gramame Formation, in Brazil.



TEXT-FIG. 9. Mosasaur teeth, buccal and lingual views. A (R11896), B (R11949), C (R11894), D (R11985), E (R11913), *Mosasaurus* cf. *hoffmanni*. ×1. F, mosasaur vertebra (R11907), dorsal and lateral views. ×2. G, mosasaur coracoid, lateral and medial views. ×0·5.

### Mosasaurinae or Tylosaurinae indet.

Text-figures 9A–D, F, G

*Referred material*. Three jaw fragments probably representing the same specimen, and including a large tooth base, BMNH R11914 (Kehehe); teeth R11986, R11949, R11894, R11895 (Igdaman); two large disassociated vertebrae, BMNH R11917 and R11918 (Kehehe); a very small vertebra R11907; a coracoid R11919 and a radius R11931 (Igdaman).

*Description.* R11914 consists of three poorly preserved fragments of jaw, probably from a maxilla, which appear to represent a single specimen. Associated with one of the fragments is a large tooth base including the jagged remains of the basal part of a tooth crown. This specimen represents the largest mosasaur jaw found in Africa. A BMNH cast of part of the maxilla of the huge holotype skull of *M. hoffmanni* (original in the Paris Museum), described by Cuvier (1834, 1836), is of almost identical proportions, and it permits an estimate of the length of the entire skull of R11914 as approximately 1·4 m.

The largest of the teeth, R11896 (Text-fig. 9A), is approximately 43 mm long and 19·7 mm wide at the base. It is posteriorly recurved with sharp anterior and posterior carinae, extending almost the entire length of the tooth. The surface is enamelled and bears no evidence of striae or facets. The size of the tooth, its general configuration, and lack of strong prisms or facets indicate that it might be tylosaurine. The rest of the teeth, R11949, R11894 and R11895 (Text-fig. 9B–D) are not as well preserved, but are probably mosasaurian.

Two very large vertebrae, R11917 and R11918 from the lower levels of the Dukamaje Formation, clearly come from a very large mosasaur with the proportions of R11914. Large vertebral material mentioned previously in the literature by various authors (Swinton 1930; Azzaroli *et al.* 1975; Soliar 1988), as well as previously undescribed material from Kaffe and Gilbedi, is similarly impregnated with a matrix of yellow marl as is R11914, possibly indicating a similar horizon for all specimens.

R11907 (Text-fig. 9F) represents probably the smallest mosasaur vertebra known, clearly belonging to an immature individual or hatchling. It belongs to the lumbar series, and the general configuration suggests that it is mosasaurian. The neural spine is absent. Articulating surfaces are heart-shaped, deeper than wide. Slight pinched depressions on the anterodorsal surfaces of the vertebra on either side of the neural spine may indicate the inception of zygosphenes in a very young individual.

R11919 (Text-fig. 9G) is a fairly well preserved coracoid, the first record of a mosasaur pectoral element in Africa. It lacks an emargination of the distal border and the coracoid foramen is moderate in size. The small size of the specimen indicates that it may belong to an immature individual or a small taxon such as *Clidastes*. R11931 is a large fragment of a radius, but no further distinction is possible.

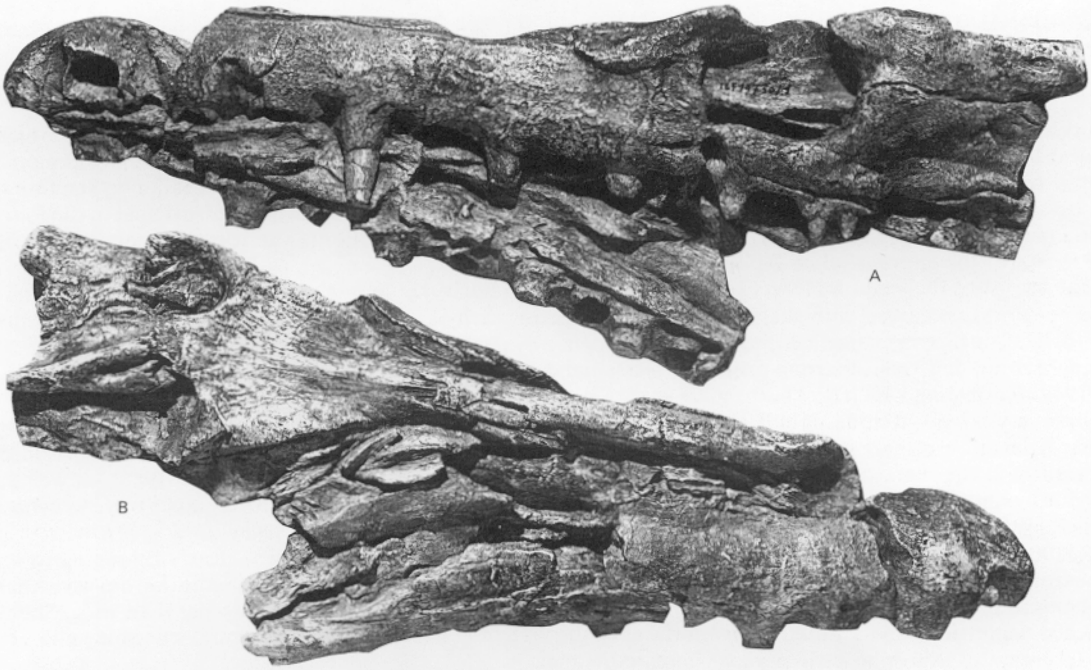
## PALAEOECOLOGY OF MOSASAURS OF THE IULLEMMEDIN BASIN OF NIGER

In the south-western part of the Iullemmedin Basin, Petters (1979*b*, p. 950) defined four marginal environments, marshes, lagoons, estuaries, and epeiric seas. These were based upon computed alpha diversity values for the Dukamaje benthic foraminiferan assemblages and on the preponderance of the arenaceous foraminifera *Miliammina*, *Haplophragmoides*, *Trochamina*, and *Ammobaculites*, which indicates adaptation to stress and marginal environments.

The environments suggested for particular mosasaurs are: *Mosasaurus* (coastal waters); ?*Platecarpus* (open sea); *Plioplatecarpus*? (deep water) (Russell 1967); *Halisaurus* (unknown); *Goronyosaurus*, *Angolasaurus*, and *Igdamanosaurus* (coastal waters and lagoons).

If Petter's interpretation of the environment of the south-western Iullemmedin Basin is correct, then the presence of suggested open-sea forms of mosasaurs such as *Platecarpus* and deep-water divers such as *Plioplatecarpus* may appear inconsistent. There is, however, very little evidence in the literature to corroborate these interpretations of the lifestyle of *Platecarpus* and *Plioplatecarpus*. Russell (1967) has shown there to be no especial significance in the tympanic membrane for example in diving. A calcified tympanic membrane in fact occurs widely in most mosasaurs, being present in members of all three subfamilies (Williston 1898; Russell 1967).

Among mosasaurs, the unique presence of enclosed olfactory lobes in *Goronyosaurus* is puzzling. The enclosed condition of the lobes in the Varanoidea (Mertens 1942) is regarded as a synapomorphy by Estes *et al.* (1988), but is not normally present in mosasaurs. The enclosed condition in *Goronyosaurus* may be associated with more highly developed olfactory lobes and sense of olfaction. This is consistent with other features of the genus that suggest an efficient detection of hidden prey; for example, the high number of large foramina on the premaxilla which suggest an array of large nerve endings to an apparently highly sensitized snout. Either condition would have been particularly useful for hunting in the quiet murky waters of sheltered bays and estuaries and



TEXT-FIG. 10. *Goronyosaurus nigeriensis* (IGF 14750). A, lateral view. B, dorsolateral view. ×0·3.

in preying upon hidden young of marine fauna including perhaps those of mosasaurs (Russell 1967, pp. 1, 65). Further, the very small eyes of *Goronyosaurus* (relatively perhaps the smallest in the Mosasauridae) suggest that *Goronyosaurus* did not rely heavily on vision.

Modern-day analogues of this kind of predation are seen in varanids which search out hidden prey by 'specialized chemoreception' followed by 'rapid, skilful capture' (Losos and Greene 1988, p. 379). These authors suggest that this is a derived condition in varanids, a view that may hold equally true for mosasaurs.

*Igdamanosaurus* is the first record in the Mosasauridae of a predator complying with Massare's (1987) tooth morphotype in the 'crunch' guild. This contrasts with the 'crush' guild in which she placed *Globidens*. From an ecological perspective, *Igdamanosaurus* probably occupied a feeding mode somewhere between *Prognathodon* (Lingham-Soliar and Nolf 1989) and *Globidens* (Russell 1967), subsisting presumably on a diet of moderately soft-shelled invertebrates.

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*Dedication*. This paper is dedicated to the memory of Beverly Halstead who made the dreams of dragons a wonderful reality for me.

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