

THE MOSASAUR *GORONYOSAURUS* FROM THE UPPER CRETACEOUS OF SOKOTO STATE, NIGERIA

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ABSTRACT. New mosasaur material from the Upper Cretaceous of Sokoto State, Nigeria, was described in detail by Azzaroli *et al.* (1972, 1975). Largely on the basis of what they interpreted as a highly unusual jugal bone in the skull, they erected in 1972, the new genus *Goronyosaurus*, and subsequently (1975) placed it in a new subfamily, the Goronyosaurinae, representing a totally unique development of a squamate skull.

A reassessment of the material suggests that the description of the jugal by Azzaroli *et al.* (1972, 1975) is incorrect. However, other characters described by them, plus new information added here, vindicates the erection of a new genus, which can be tentatively assigned to the Tylosaurinae.

MOSASAURS, large marine varanid lizards, were widely distributed in the Upper Cretaceous in both the Old and New Worlds. The first mosasaur specimen was found in 1780 by Dr Hoffmann in the district of Maastricht, Holland, in rocks of Upper Cretaceous age. Over fifty years elapsed before the fossil was named *Mosasaurus* by Conybeare (in Parkinson 1822). Dollo (1890) divided the family Mosasauridae into three groups based on the degree of development of the rostrum—microrhynchous, mesorhynchous, and megarhynchous.

Williston (1897) placed Dollo's groups in the subfamilies Mosasaurinae, Platecarpinae, and Tylosaurinae. In Camp and Allison's (1961) classification the Platecarpinae is replaced by the Plioplatecarpinae.

MOSASAURS FROM WEST AFRICA

Mesozoic vertebrate remains in West Africa are relatively rare. In contrast Sokoto State, in north-west Nigeria, yields quantities of marine vertebrates from the uppermost Cretaceous, Maastrichtian Dukamaje Formation (Swinton 1930; Jones 1948; Reyment 1965; Kogbe 1973; Petters 1979*a, b*; Halstead 1979*c*).

Vertebrate remains from the Sokoto region were first described by Nopcsa (1925) as including dinosaurs from the Tertiary. Swinton (1930) subsequently demonstrated them to be crocodylian and of Palaeocene age (see Halstead and Middleton 1976). However, Swinton (1930) described further material from a Cretaceous horizon, the 'Mosasaurus shales'. On the basis of postcranials and jaw fragments Swinton (1930) erected the new species, *M. nigeriensis*. A new crocodylian from the Cretaceous was described under the name *Sokotosuchus* (Halstead 1973, 1975; Buffetaut 1976, 1979) and a new turtle genus *Sokotochelys* (Walker 1979; Halstead 1979*a, b*) from the same horizon.

Until 1970, the only work on African mosasaurs, besides Swinton's in 1930, was on rather isolated finds. Broom (1912) described *Tylosaurus capensis* from South Africa; Deperet and Russo (1925) described *Leiodon anceps* from Morocco and Arambourg (1952) described further mosasaur remains; Antunes (1964) described a species of mosasaur from Angola. Further mosasaur material has been recorded from Libya (Quass 1902) and Egypt (Strømer and Weiler 1930; Zdansky 1935; Leonardi and Malaroda 1946).

In December 1969 to January 1970 and February and March 1971 expeditions were mounted by Professor A. Azzaroli of Florence University, Italy, to collect fossil vertebrates in Sokoto State, Nigeria. New mosasaur material from the Goronyo district of Sokoto State was discovered by de

Guili *et al.* (1970) and described in detail by Azzaroli *et al.* (1972, 1975). The remains comprised a large number of vertebrae, two right humeri, a fragment of a premaxilla, eight fragments of mandibles, a fragment of a pterygoid of a small size, and an almost complete skull, albeit badly crushed.

The first mosasaur remains recognized from Nigeria were described by Swinton (1930). The two associated dorsal vertebrae (BMNH R5674) were selected as the lectotype of *M. nigeriensis*, by Halstead and Middleton (1982). The new materials discovered by the Italian expeditions and figured by de Guili *et al.* (1970), Azzaroli *et al.* (1972, 1975), and Halstead and Middleton (1982), were assigned to the same species.

A number of unusual features were described by Azzaroli *et al.* (1972, 1975) including the following:

- the maxillaries extended beyond the posterior margin of the orbits;
- the jugal had a broad ascending ramus;
- the inner surface of the frontal bore a fully closed canal housing the olfactory lobes;
- in the pterygoids the roots of the ectopterygoidal processes and of the quadratic rami were widely spaced and the ectopterygoids articulated with the posterior margins of the ectopterygoidal processes.

On the basis of these characters Azzaroli *et al.* (1972) established the new genus *Goronyosaurus*. However, as they did not consider it possible to place it in any of the existing subfamilies of mosasaurs, Azzaroli *et al.* (1975) subsequently erected the new subfamily, the Goronyosaurinae for its reception.

A key character and also by far the most contentious related to the features of the jugal. In the normal squamate skull the lower temporal bar is missing and the jugal which forms the anterior border of the infratemporal vacuity is greatly reduced. According to Azzaroli *et al.* (1975) in *Goronyosaurus* the jugal was enormously expanded into a deep elongated sheet covering a large proportion of the infratemporal vacuity. This would make it a unique feature in the squamate reptile skull.

GEOLOGY

An early note by Raeburn and Tattam (1930) on the geology of the Sokoto region was later followed by a more detailed account by Jones (1948).

The Cretaceous Dukamaje Formation and the Palaeocene Dange Formation yield abundant vertebrate remains. Vertebrates of the Dukamaje Formation are concentrated in a bone bed about 40 cm thick and belong to the Maastrichtian period (Swinton 1930; White 1934; Jones 1948; Reyment 1965; Kogbe 1973; Petters 1979*a, b*; Halstead 1979*c*, 1980). See text-fig. 1.

The type localities listed by Reyment (1965) were simply the villages which gave their names to the formations. Kogbe (1973) published detailed sections which were subsequently revised by Petters (1979*a, b*) and Halstead (1979*c*, 1980). See text-fig. 2.

SYSTEMATIC PALAEONTOLOGY

Order SQUAMATA

Suborder SAURIA

Superfamily VARANOIDEA

Family MOSASAURIDAE

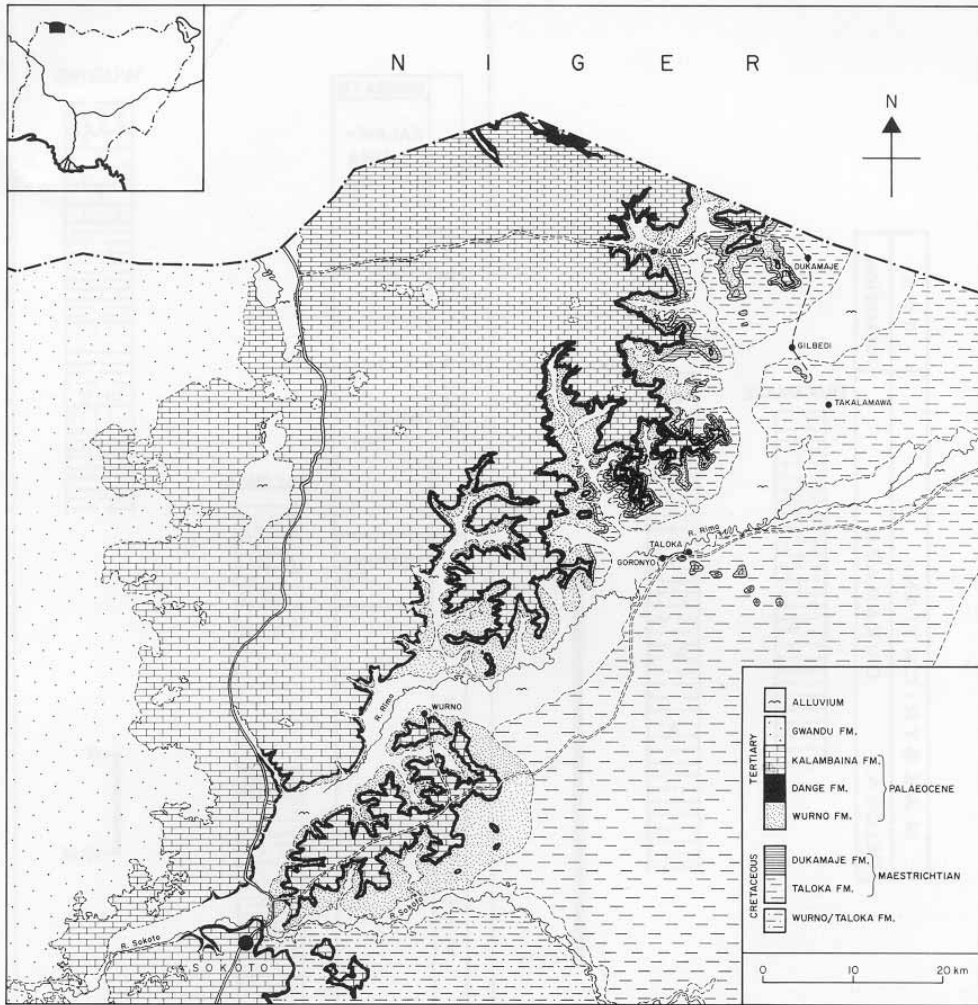
Subfamily TYLOSAURINAE

Genus GORONYOSAURUS Azzaroli *et al.*, 1972

Goronyosaurus nigeriensis (Swinton, 1930)

Text-figs. 3-6, 7C-F

Type species. Goronyosaurus nigeriensis.

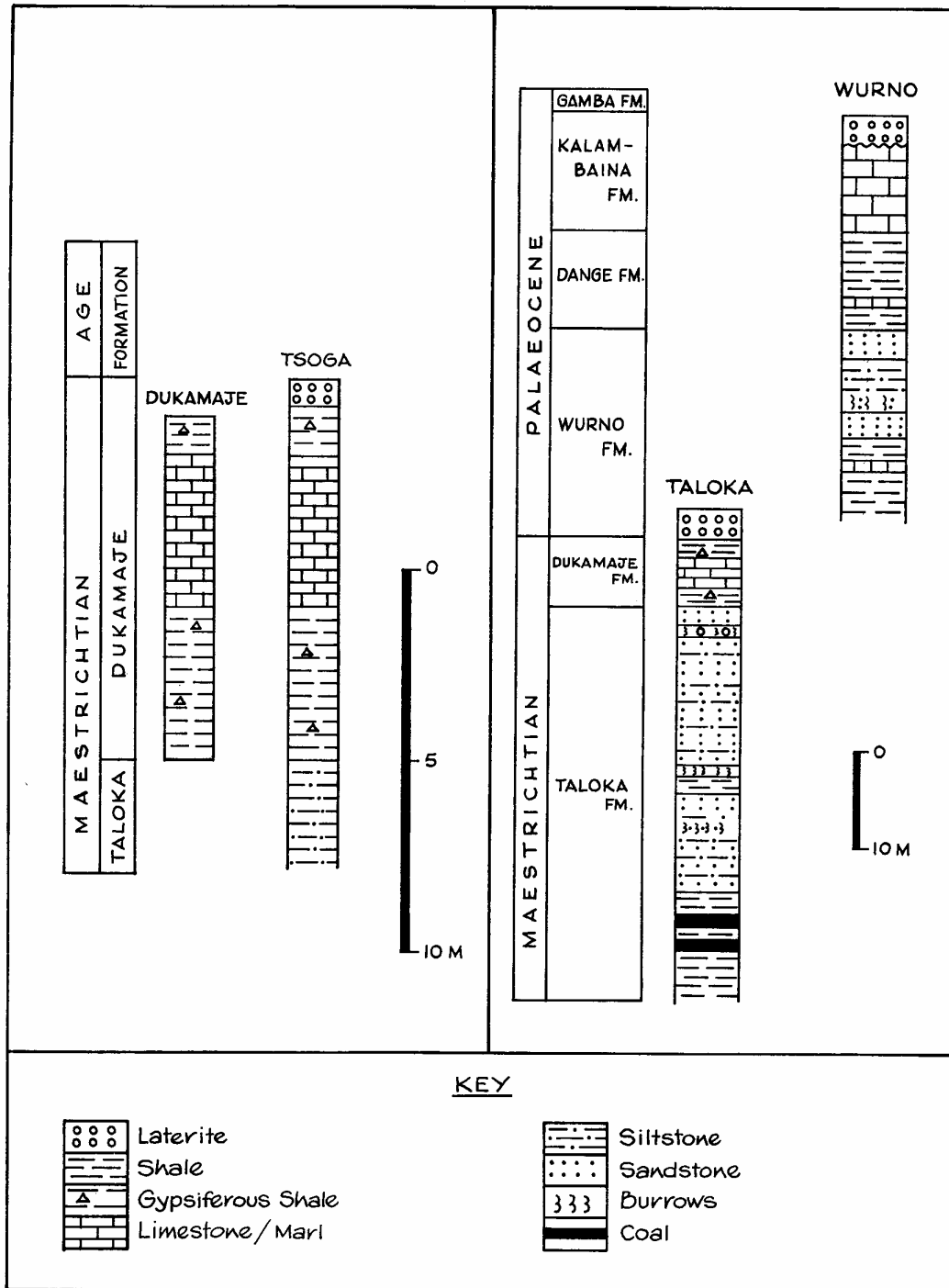


TEXT-FIG. 1. Geological map of Sokoto region (after Parker and Carter 1965).

Lectotype. Two associated dorsal vertebrae, R5674, housed in the British Museum (Natural History), London, figured Swinton 1930, pl. 10, fig. 2a-c.

Type horizon and locality. Gypsiferous shale member, Dukamaje Formation, Maastrichtian, Cretaceous; Benbow Hill, south-east of village of Gilbedi, Sokoto State, Nigeria.

Diagnosis. Small premaxillary rostrum, with wide internarial bar; closed canal on undersurface of frontals; ectopterygoid process dorsoventrally flattened forming two fork-like processes; postorbital maxillary teeth.



TEXT-FIG. 2. Geological sections (after Petters 1979a, b).

Associated material. Skull and associated postcranial remains, housed in Museum of Geological Survey of Nigeria, Kaduna South, Nigeria, IGF 14750, figured Azzaroli *et al.* 1975, pls. I-XI; complete set of casts housed in Museum of Geology and Palaeontology, University of Florence, Italy; cast of skull in Cole Museum, Department of Zoology, University of Reading.

Horizon and locality of associated material (IGF 14750). Gypsiferous shale member, Dukamaje Formation, Maastrichtian, Cretaceous; summit of hill overlooking village of Taloka, Sokoto State, Nigeria.

DESCRIPTION OF MATERIAL

Skull

The largest fragment of the skull is crushed with considerably distorted parts. The crushing appears to have taken place with the right and dorsal surfaces coming to lie uppermost and the left side underneath (text-fig. 3).

The skull appears to be unusually long and narrow. The length of the skull is 655 mm (estimated reconstructed length 710 mm) and the width of the widest part of the frontals between the orbits is 112 mm. Table 1 gives a comparison of length/width of skull for several groups of mosasaurs (data from Russell 1967).

TABLE 1

Species	Skull length in mm	Skull width in mm	Ratio of skull length : skull width
<i>Platecarpus ictericus</i>	431	97	4.4 : 1
<i>Plotosaurus tuckeri</i>	588	148	4 : 1
<i>Prognathodon overtoni</i>	702	188	3.73 : 1
<i>Tylosaurus nepaeolicus</i>	717	116	6.18 : 1
<i>T. proriger</i>	585	118	5 : 1
<i>T. proriger</i>	600	113	5.3 : 1
<i>Mosasaurus missouriensis</i>	614	142	4.3 : 1
<i>M. maximus</i>	1091	262	4.16 : 1
<i>Plesiotylosaurus crassidens</i>	880	156	5.64 : 1
<i>Goronyosaurus nigeriensis</i>	710	112	6.31 : 1

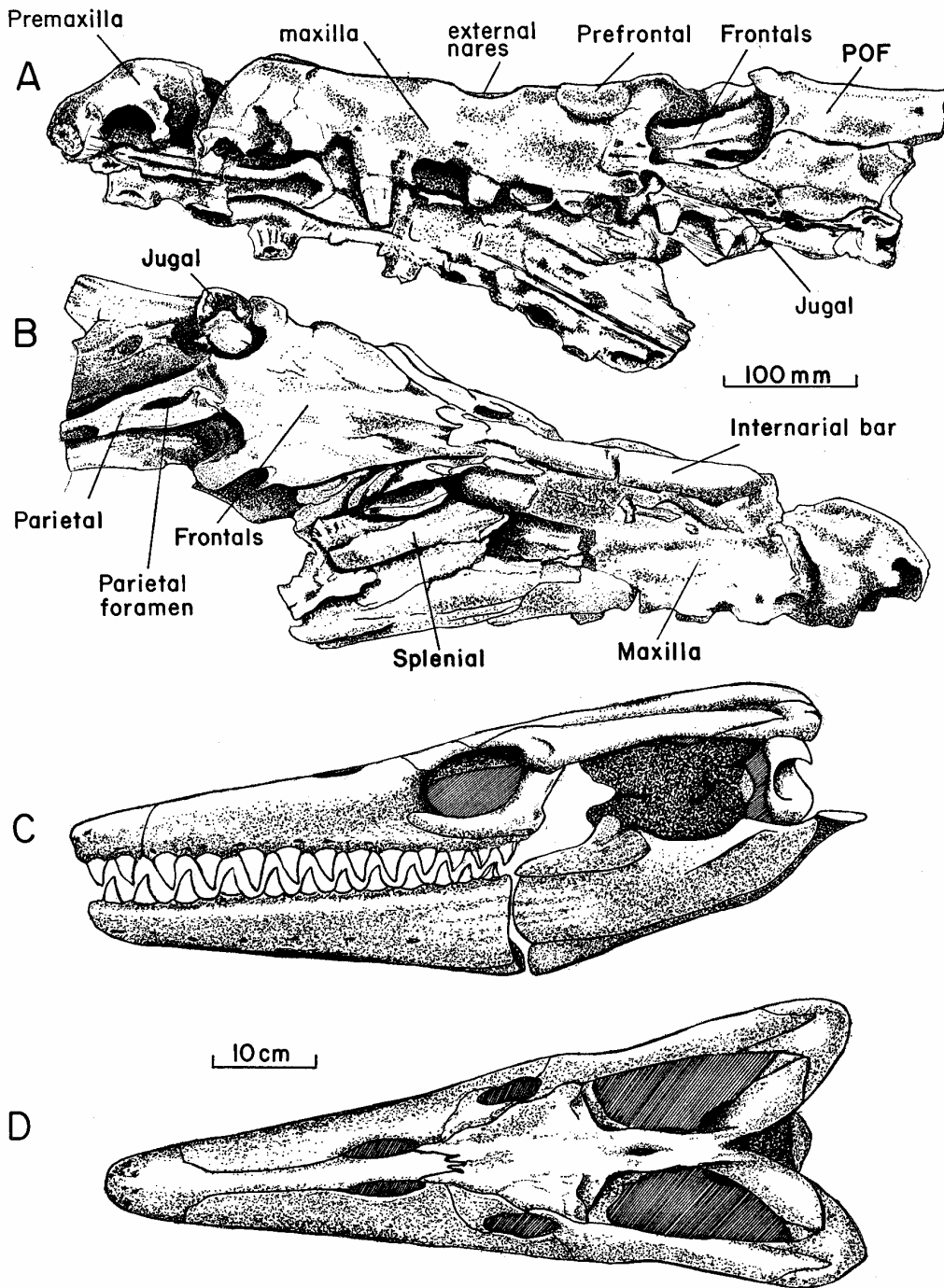
Jugal. Because of the extreme crushing in this region particularly, the boundaries of the left jugal (ventrally positioned *in situ*) are difficult to ascertain (see text-fig. 4A). The interpretation of a large postorbital lamina of the jugal (Azzaroli *et al.* 1975) would make it a unique feature among mosasaurs and all diapsid reptiles.

In their discussion Azzaroli *et al.* (1972, 1975) suggest that these broad postorbital rami of the jugals are superposed to similarly descending rami of the postorbitofrontals and that these two bones were possibly united by ligamentary tissue making a certain movement possible. There is, however, no precedent for such a function among mosasaurs (see Callison 1967).

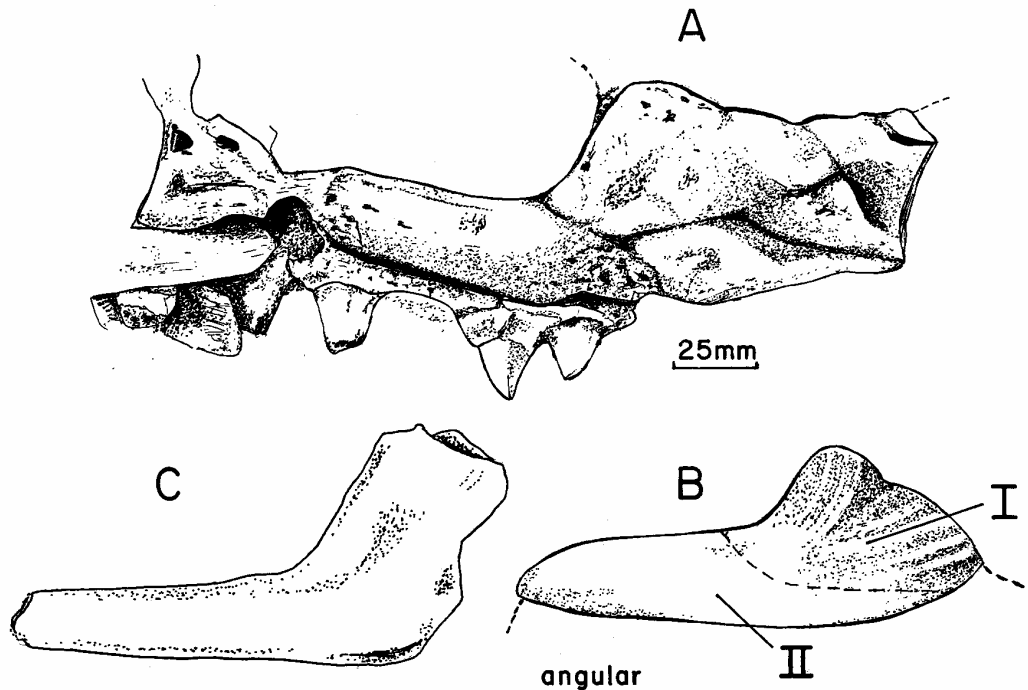
Halstead and Middleton (1982) viewed the description of the jugals by Azzaroli *et al.* (1975) as doubtful. I am of the opinion that the broad postorbital laminae of the jugals described by Azzaroli *et al.* (1975) is an artefact of crushing. Careful examination reveals that the supposed ascending ramus of the jugal is composed of at least three separate parts, with the actual ascending ramus of the jugal having been broken off at a point just above its posteroventral process and displaced. A bone protruding from the left supratemporal vacuity may represent a portion of the true ascending ramus of the jugal.

The upper part of the 'lamina' adjacent to the orbit is composed of a fragment of bone approximately 5 mm thick. The thickness is observed readily along the orbital and postorbitofrontal margins. The ventral part of the lamina is made up of another thicker tongue-shaped bone approximately 10 mm thick anteriorly, and flattening out posteriorly to approximately 5 mm. Dorsoposteriorly to this is a thin flange of bone which has fused to the preceding two fragments of bone.

The horizontal axis of the jugal itself, is on average 19 mm thick and the great and abrupt difference in thickness with the lamina makes it clear that the horizontal axis of the jugal is unrelated to the ascending



TEXT-FIG. 3. *Goronyosaurus nigeriensis* skull, IGF 14750-1, lacking occipital unit. A, left view. B, right and dorsal view. Reconstruction of skull. C, left view. D, dorsal view. Abbreviation: POF = postorbitofrontal.



TEXT-FIG. 4. A, detail of jugal and surrounding area. B, I and II represent fragments of the coronoid making up the 'lamina' of the jugal. C, jugal of *Leiodon perlatus* (BMNH R35637-9).

'lamina'. Despite the absence, in the main, of discernible seams separating the three bones making up the 'lamina', demarcation is made clear by abrupt changes in thickness and in surface consistency, and including seams along the anterior and dorsal boundaries.

With reasonable confidence it is possible to identify part of the lamina adjacent to the orbit as a portion of the coronoid from the lower jaw. The thin posteriormost wall of the coronoid is in life buttressed ventromedially to the surangular (see Russell 1967, p. 53). It is at this weak point that the coronoid would have been likely to have broken off. Following which the fragment of the coronoid (text-fig. 4BI) could have been displaced to lie postorbitally at a slight angle forming a part of the 'lamina' adjacent to the orbit. The fragment of bone forming the posteroventral part of the 'lamina' is identified with equal confidence as the remaining part of the coronoid (text-fig. 4BII). The dimensions of this part of the 'lamina' are compatible with this interpretation. It can, therefore, be assumed that the jugal is of typical mosasauroid dimensions, perhaps comparing more closely with the more robust jugal of *L. perlatus* (BMNH R35637-9) possessing a strong posteroventral process (text-fig. 4C). A similar large posteroventral process is also found in *T. nepaeolicus* (BMNH R3627).

Premaxillae. The premaxilla has suffered considerable lateral compression. The tooth sockets and tooth bases are large suggesting that the premaxilla possessed strong teeth. The foramina which mark the exits of the ophthalmic ramus of the fifth cranial nerve appears to be situated in a cluster either on or very close to the dorsal mid-line. In *Clidastes*, *Mosasaurus*, *Plotosaurus*, *Platecarpus*, and *Prognathodon*, Russell (1967, p. 16) states that the foramina are located on either side of the dorsal mid-line while in *Tylosaurus* they are distributed randomly on the sides of the rostrum. Although in a giant premaxilla of the genus *Prognathodon* sp. indet. (BMNH 49939) the foramina appears to be nearer the mid-line as in *Goronyosaurus*. The premaxilla in *Goronyosaurus* ends abruptly in front of the anterior teeth as in *Platecarpus*, *Plioplatecarpus*, *Prognathodon*, and *Plesiotylosaurus* (Dollo 1889, p. 275 and Russell 1967, p. 16).

Maxillae. The maxillae are highly unusual as they extend beyond the posterior margin of the orbits and are also toothed postorbitally (see text-fig. 3). There does, however, appear to be a slight exaggeration in the length of the postorbital part of the maxillae due to a severe break in the left maxilla at a point just anterior to the last four maxillary teeth. Consequently, during the crushing of the skull, the maxilla, from the point of the break, apparently was forced slightly posteriorly along the horizontal axis of the jugal. It is probable that the gap caused by this break may have been mistaken for a tooth socket by Azzaroli *et al.* (1972, 1975). While it is possible that there is room for another tooth in this area, it nevertheless remains uncertain and the number of maxillary teeth is more probably eleven.

Internarial Bar. This is a very robust bone with a maximum width of 29 mm and minimum width of 135 mm. There is very little narrowing of the internarial bar along most of its length including especially the area between the external nares. The narrowest point being where the internarial bar joins the premaxillary rostrum (see text-figs. 3 and 7). The ruggedness of the internarial bar, its wide and almost unconstricted form, and its penetration of the frontals to a point far behind the posterior termination of the external narial opening, resembles that of members of the Tylosaurinae subfamily, in particular *T. proriger*. In, for example, *Clidastes*, *Mosasaurus*, *Plotosaurus*, *Platecarpus*, *Ectenosaurus*, and *Plesiotylosaurus* (Russell 1967, p. 17) the internarial bar is constricted between the external nares and is a much more slender body. However, the point of origin of the internarial bar is more triangularly shaped unlike in *Tylosaurus* where it is rectangular. The nares themselves in *Goronyosaurus* appear unusually small and rather posteriorly situated. Both the ruggedness of the internarial bar and the posterior position and smallness of the nares are unusual among mosasaurs and the nearest comparison may be made among members of the subfamily Tylosaurinae, in particular *T. proriger*.

Splennial. On the right side of the skull, embedded with the upper jaw material, there is a fragment of the right splenial which had become displaced during the crushing of the skull. This bone is laterally compressed and it is possible to locate, at its posterior end, the surface which articulated with the angular bone of the lower jaw. In posterior outline the articulating surface is laterally compressed as in *Prognathodon*. A small portion of the thin ala which is normally expanded to enclose the medial surface of the dentary, can be seen.

Frontal. The frontal is a triangularly shaped bone and links with the internarial process from the premaxilla. The internarial process penetrates deeply into the anterior end of the frontal and at some distance from the external nares as in *Tylosaurus*. Dorsally there is an anteromedian ridge present.

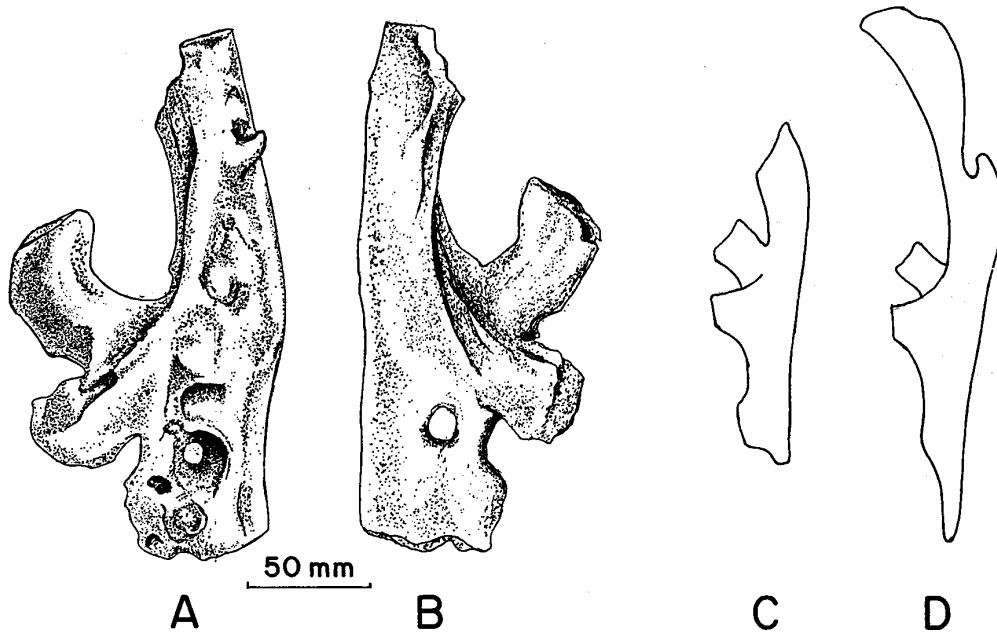
Prefrontal. Crushing and distortion have resulted in the left prefrontal being displaced slightly anteriorly and ventrally. Azzaroli *et al.* (1975) have stated that the prefrontals emarginate with the external nares. A re-examination demonstrates that this is not the case, even when disregarding the slight displacement. The position of the prefrontals is similar to that found in *Tylosaurus*. The indications are that the slender prominences from the prefrontals where they border the orbits, and the anterior tips of the postorbitofrontals originally linked these two bones, thereby completing the emargination of the orbits. The frontals themselves do not appear to emarginate with the orbits.

Parietal. The parietal, although a strong unit, is particularly narrow in *G. nigeriensis*. Because of a severe break anteriorly, it is difficult to distinguish exactly the point of contact with the frontal bone, but the indications are that the groove separating the frontal from the parietal was fine, indicating that mesokinetic movement was consequently limited. The parietal foramen is long and narrow. It is widely separated from the frontal suture as in *T. nepaeolicus*.

Pterygoid. Azzaroli *et al.* (1972, 1975) represented the pterygoid as a greatly shortened bone lacking basisphenoid and palatine processes, quite unlike the pterygoids of other known mosasaurs. A re-examination, however, indicates that there is no reason to assume that the main body of the pterygoid is different from that of a typical mosasaur. A distinct break can be observed along the posterior margin of the left pterygoid, at a point which marks the origin of the basisphenoid process (text-fig. 5). Anteriorly, too, the indications are that the process leading to the palatine has broken off.

Breaks in these regions of the palatine are not uncommon in mosasaurs as both the basisphenoid and palatine processes are frequently quite flattened and slender. The palatine processes especially are invariably lost during fossilization. Russell (1967, p. 43) mentions that anteriorly the pterygoid in mosasaurs must have been firmly buttressed against the palatine but the contact is rarely preserved.

The ectopterygoid process is, however, unusual. It is a dorsoventrally flattened structure consisting of two fork-like processes, the longer of which ends in a broad expanded termination, similar to *Tylosaurus*



TEXT-FIG. 5. A, occlusal view of the left pterygoid. B, dorsal view of the left pterygoid. C, reconstruction of the left pterygoid by Azzaroli *et al.*; D, by Soliar.

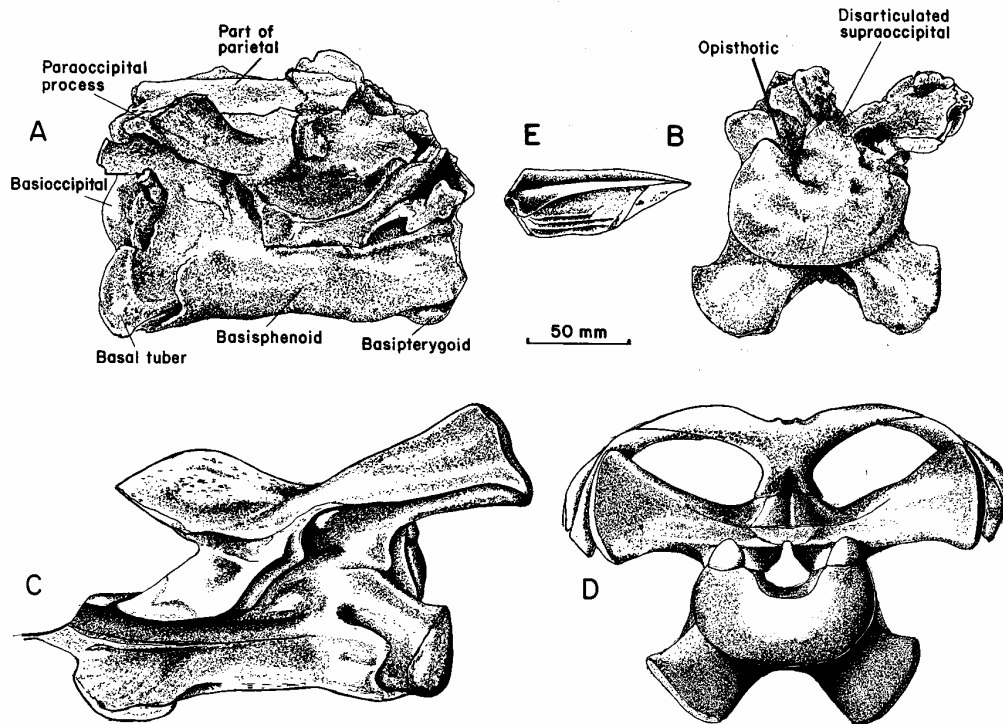
(Russell 1967), which made contact with the ectopterygoid probably by means of a fibrous joint. The shorter process may have served to prevent the pterygoid from slipping too far backwards by apposing with the ectopterygoid and may have served also as a point of origin of the *M. pterygoideus profundus* or *M. pterygoideus superficialis* muscles. A groove on the dorsal side of the quadratic ramus probably marked the insertion point of the *M. protractor pterygoid* muscle.

Occipital Unit. Although the occipital unit is in a poor state of preservation some important features can be observed. In general, the occipital unit is narrow and bears certain tylosaurine characteristics in addition to an unusual supraoccipital bone (see text-fig. 6E).

During fossilization the supraoccipital must have been dislodged, and at present lies in a semi-vertical position, but appears fairly undistorted. The bone is unusual when compared with descriptions of the supraoccipital in other mosasaurs. Instead of the roof-shaped element described by Russell (1967, p. 40), the dorsal surface of the supraoccipital has a deep groove along its mid-line with gently convex surfaces on either side to the lateral edges. The ventral surfaces of the supraoccipital slopes inwards and fits over the paroccipital process. As in other mosasaurs the supraoccipital is strongly grooved and ridged longitudinally along the ventral surfaces. The ventral extremity was probably hollowed to fit over the posterior part of the brain stem.

The lateral wall of the basisphenoid is unusually steeply sulcate inwardly from the ventral edge. The vidian canal which carries the internal carotid artery and the palatine branch of the seventh cranial nerve into the basisphenoid, is uncovered. However, it is possible that the lateral wall of the vidian canal, usually a thin sheet of bone, is lost. Russell (1967, p. 33) makes a similar observation in the basisphenoid of a specimen of *Plioplatecarpus*. Features that compare with those of *Tylosaurus* are the elongate basisphenoid and slender basiptyergoid process together with a narrow alar process of the prootic bone. The basal tuber of the basioccipital appears to be intermediate in size as in the tylosaurs.

Teeth. Remains of the teeth can be seen on both the left and right maxillae (see text-fig. 3A). Besides four small complete postorbital teeth and one partial tooth crown at the anterior end of the left maxilla, all the remains are of tooth bases only.



TEXT-FIG. 6. *Goronyosaurus nigeriensis* occipital unit, IGF 14750-2. A, right view. B, posterior view. C, reconstruction, view of left side. D, reconstruction, posterior view. E, reconstruction, left view of supraoccipital.

The posterior maxillary teeth are small, bicarinate, with recurved tips. The teeth appear to be smooth and enamelled. The tooth bases in the remaining part of the maxillae are large, indicating strong teeth.

The partial tooth crown is covered at the base by extraneous material. Despite this and the tip being broken off much of the tooth can still be seen. The tooth is elongated and particularly straight with slight lateral compression. Fore and aft carinae are present. The surface appears to have been smooth but it is damaged and it is hard to tell with any certainty whether vertical striations may have been present. In cross-section the lingual and buccal surfaces appear to be similar. This tooth appears to bear some similarity with the badly worn, highly gypsiferous material described by Swinton (1930) in which he states that 'the teeth remains are closely similar to those of *Leiodon anceps* but probably the crowns were more elongated and slender'.

Postcranial elements. A straightforward description of the postcranial elements of *M. nigeriensis* will not be repeated here as they have been described at length by Swinton (1930) and Azzaroli *et al.* (1975).

Caution must, however, be exercised when trying to establish mosasaur relationships on vertebral characters alone as significant variations exist even within genera. Swinton (1930) points out that whereas *M. nigeriensis* has no zygosphenes on the dorsals, a specimen of undoubted *M. camperi* (*M. hoffmannii*) in the BMNH certainly has zygosphenes. A similar variation exists in the chevron attachment of the caudals with the chevrons being either fused or free. Taking such factors into account, I find that there is insufficient evidence other than to state that the vertebrae of *G. nigeriensis* show definite mosasauroid characters—for many of the characters discussed are shared at least among the Mosasaurinae and Tylosaurinae.

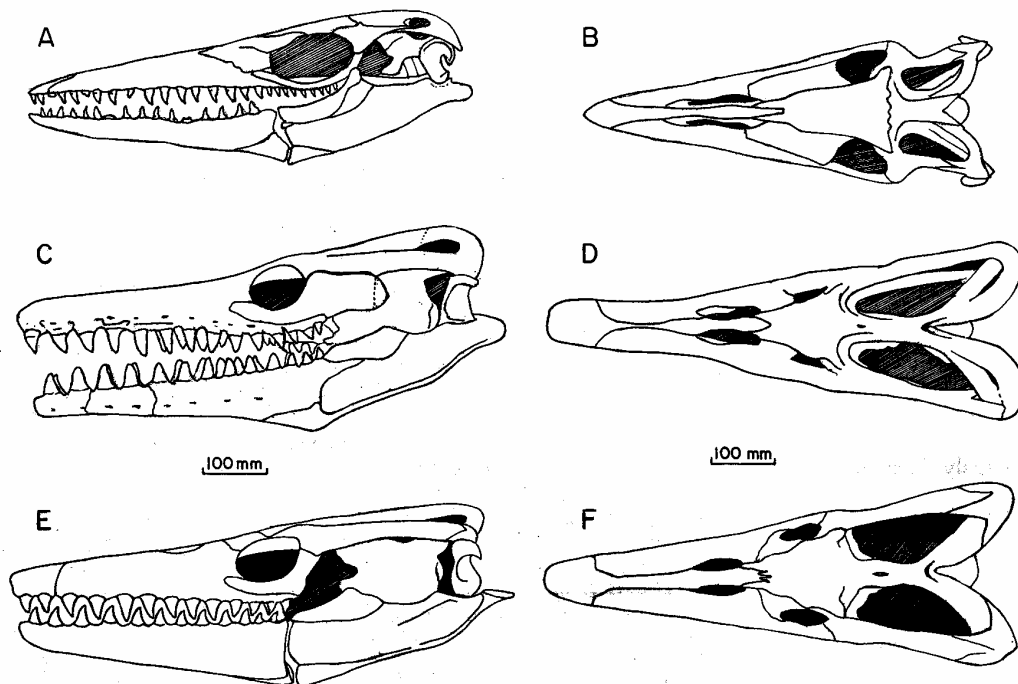
Crushing and Distortion. Because of the critical importance of the jugal in Azzaroli *et al.*'s (1975) erection of a new subfamily the Goronyosaurinae, I would like to further clarify certain points which are relevant to their misinterpretation.

The individual bones which make up the jugal consist of what I believe to be at least three distinct fragments of bone but appear to lack very definite seams or joins. This I believe is not unusual and may be accounted for by the fossilization process during which fusion of the fragments occurred. Instances are seen where during extreme crushing and poor fossilization, e.g. *Platecarpus coryphaeus* (BMNH R.2947) fusion of the bones in certain areas show little or no trace of joins between identifiably separate bones. Specifically in *G. nigeriensis* there are areas where similar fusion has taken place. For example, on the left side of the skull below maxillary teeth 7/8 there is evidence of complete fusion between fragments (unidentified bones, possibly parts of the lower jaw or palatine) and the medial side of the right maxilla. A further area of complete fusion involves a part of the splenial with a fragment (possibly part of the lower jaw). There also appears to be fusion between the lower part of the right premaxilla with the maxilla.

It seems most unlikely that the distinct grooves between the 'lamina' and postorbitofrontals mark suture points as Azzaroli *et al.* (1975) state. These bones in life would have been in close contact and the severe compression suffered by the skull would have in all probability caused fusion of the bones as witnessed in other parts of the skull where the bones were even more remote.

CONCLUSIONS

Re-examination of the specimens of *Goronyosaurus* leads to the view that the interpretation of some of the key characters by Azzaroli *et al.* (1972, 1975), especially with regard to the jugal, was based on a misinterpretation of the crushed elements. The functional significance of the broad ascending ramus of the jugal and its kinetic movement, as described by Azzaroli *et al.* (1975) appears doubtful. However, an unusual feature of *G. nigeriensis*, the wide and robust internarial bar, appears to be misrepresented in the reconstruction by Azzaroli *et al.* (1975) as a considerably narrower and more delicate bone.



TEXT-FIG. 7. Comparative reconstructions of skull of *Goronyosaurus nigeriensis*. A, lateral view. B, dorsal view of generalized mosasaur skull (not to scale). C, D, Azzaroli *et al.* reconstruction. E, F, Soliar reconstruction.

G. nigeriensis presents a curious mixture of characters (text-fig. 6). The jugal is like that of *Leiodon anceps* (Deperet and Russo, 1925, p. 340), the internarial bar is like that of a tylosaurin somewhat resembling that of *T. proriger*; the maxillaries including maxillary teeth extend postorbitally unlike any other mosasaur. Table 2 indicates that *G. nigeriensis* had a uniquely narrow skull among the larger mosasaurs comparing more closely with members of the plesiotylosaurs and tylosaurs and closest to *T. nepaeolicus*. Such evidence does point to the possibility that *G. nigeriensis* may be more closely related to the members of the subfamily Tylosaurinae.

A major character that distinguishes members of the subfamily Tylosaurinae, is the large premaxillary rostrum although it may vary among members of the genus *Hainosaurus*. There is not much material available on the hainosaurs although Dollo (1904) does remark on the variation including that of the rostrum in a new species *H. lonzeensis* with that of *H. bernardi*—'par sa Rostre plus conique et a face superieure plus arrondie, et par ses Dimensions moindres,—indiquant egalement, une espece differente du *Hainosaurus bernardi*, Dollo, 1885, du Senonien superieur de Hainaut' (1904, p. 213).

A tentative suggestion is made that *G. nigeriensis* may even be a juvenile of a very much larger tylosaur such as *H. bernardi* which may grow up to 17 m (56 ft.) (see Russell 1967, p. 210). As very little is known of juvenile stages of mosasaurs it may prove to be that certain aberrant features such as the postorbital maxillaries may simply be present only in the juvenile stages. Swinton (1930) mentions that the presence or absence of zygosphenes and zyganchra in the vertebral column may in some instances be related to the age of the individuals (zygosphenes and zyganchra may be present only in older individuals in order to take up the extra load).

However, the presence of the small premaxillary rostrum together with a wide internarial bar, a closed canal on the undersurface of the frontal for the reception of the olfactory lobes, the unusual ectopterygoidal processes of the pterygoid, plus a tentative acceptance of the postorbital maxillary teeth necessitate at least the erection of a new genus within the subfamily Tylosaurinae.

Reconstruction

In their reconstruction Azzaroli *et al.* calculated the body length based on skull to body ratio being 'approximately the same as in other mosasaurs' (1975, p. 28). This is, however, quite confusing as the head to body proportions vary considerably among mosasaurs and can produce considerable discrepancies in body lengths. Table 2 gives an idea of the head and body proportions in a few selected mosasaurs.

Working on Azzaroli *et al.*'s (1975) derived body length of 7.80 m it would appear that the ratio of head to body they used was 9.1:100. Taking into account that it is a rough estimate, it still nevertheless appears particularly low when compared with the figures in Table 2. For instance, we find an appreciable difference in body length if we increase head length from 9.1% to just 10%. The length of *G. nigeriensis* goes down from 7.8 m (25 ft.) to 7.1 m (23 ft.). Using the tylosaur figure of 13.8% head, then the overall length of *Goronyosaurus* is dramatically reduced to 5.14 m (16.85 ft.). This, coincidentally, would not be incongruous with the tentative suggestion that *G. nigeriensis* might be a juvenile of a larger tylosaur.

The skull of *Goronyosaurus* gives us some clues as to its way of life. *Goronyosaurus* had a uniquely elongated muzzle provided with straight, long, strong teeth. Added to this we can, from

TABLE 2

Genera	Head length	Body length
<i>Platecarpus</i> (from von Huene, 1911)	9.8 %	5.60 m (18½ ft.)
<i>Platecarpus</i> (from Lambe, 1914)	10.4 %	6.25 m (20½ ft.)
<i>Tylosaurus</i> (from Williston, 1896)	13.0 %	6.34 m (20¾ ft.)
<i>Tylosaurus</i> (from Osborn, 1899)	13.8 %	8.83 m (29 ft.)

the ruggedness of the postorbitofrontals, and associated bones, assume that the processes from the parietal to the supratemporals were of equally large dimensions and would have provided large areas for the points of origin of massive jaw muscles, the depressor mandibulae, the major muscles for closing the jaws. Such powerful, strongly toothed jaws indicate that *Goronyosaurus* was certainly capable of attacking large prey.

White's (1934) study of fossil fishes of the Sokoto region indicates the presence of several families of fishes in the Upper Cretaceous deposits, including members of the families Lamnidae, Pycnodontidae, and Eotrigonodontidae as well as the remains of indeterminable bony fishes. This in itself would have provided rich feeding grounds for *Goronyosaurus*. However, in addition to the prolific fish life discoveries of marine turtle and crocodile remains in the Dukamaje Formation (see Halstead 1979a, b) indicate that the waters were probably rich in such fauna. *Goronyosaurus* could have been capable of seizing the smaller members of these families but in addition it is quite probable that *Goronyosaurus* may have preyed upon the juveniles of, for example, the giant pelomedusid turtles (Halstead 1979a, b) and the young of dyrosaurid crocodiles such as *Sokotosuchus ianwilsoni* (Halstead 1975; Buffetaut 1976, 1979). Dollo (1897, p. 520) refers to the discovery of turtle bones in the body cavity of the Belgian *Hainosaurus*.

Although *Goronyosaurus* was in all probability more pelagic in behaviour than the crocodiles and turtles, it is more than likely that the members of the genus *Goronyosaurus* converged in numbers in the rich littoral waters in which the Dukamaje Formation was deposited (see Petters 1977; Buffetaut 1979) with their only real rivals being the giant mosasaurs such as *Tylosaurus*.

From the streamlined skull we can ascertain that *Goronyosaurus* probably possessed hydrodynamic qualities superior to other mosasaurs except perhaps the much smaller *Clidastes*.

Evolution of African Mosasaurs

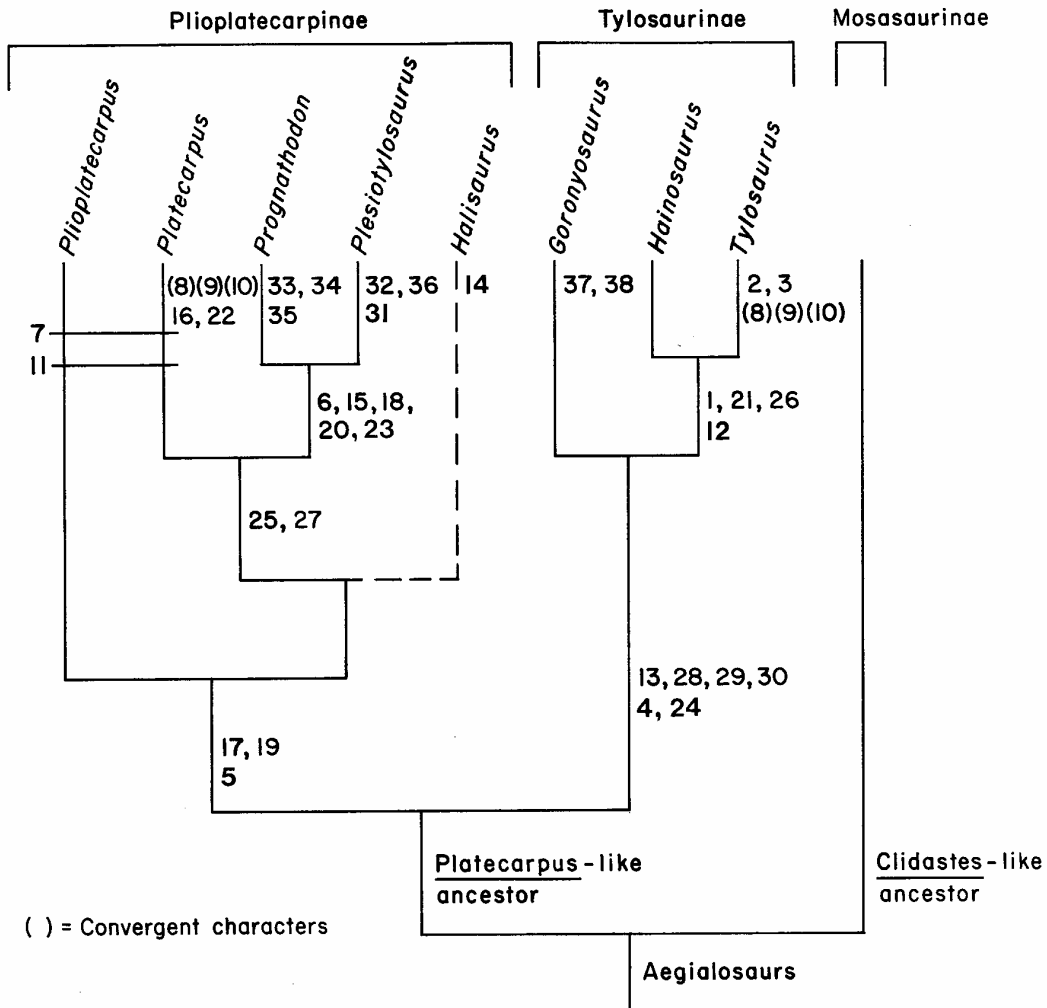
It is possible that the evolution of *Goronyosaurus* continued through a period when the larger mosasaurs such as *Tylosaurus* had disappeared elsewhere. Certainly the latest tylosaurs in other parts of the world belong to no later than the Campanian period. Azzaroli *et al.* (1975) commented on and figured three very large vertebrae found at Tunga which they believed belonged to some representative of the subfamily Tylosaurinae, with which I am in agreement. If this is so it would make it a very interesting find for tylosaurs as the geological age of Tunga is Maastrichtian. Nevertheless because of the incompleteness of the material this identification can only be accepted tentatively. Azzaroli *et al.* (1975, p. 30) also describe three vertebrae, one collected at Taloka and two at Tunga which they refer to the genus *Halisaurus* on the basis of the characteristic flattened centra. This is as they stated 'noteworthy insofar as it is the first record of this genus outside North America' (1975).

It would appear that large mosasaurs such as the tylosaurs or hainosaurs continued to flourish in the Sokoto region after they had disappeared from other parts of the world by the Senonian (see Russell 1967, charts 1-7 and Dollo 1904). It is, therefore, not unreasonable to surmise that conditions too may have been conducive to the evolution of a more dynamic streamlined and smaller tylosaur such as *G. nigeriensis*.

Systematic position of Goronyosaurus

Using cranial characters alone it is possible to draw up a cladogram of generic relationships among the members of the subfamilies Plioplatecarpinae and Tylosaurinae. The subfamily Mosasaurinae (not represented) was considered as the outgroup. The following list of apomorphic characters was used:

1. Premaxilla with large rostrum.
2. Dorsal mid-line of premaxilla smooth.
3. Internarial bar arises from rectangular base.
4. Internarial bar unconstricted between external narial opening.
5. Canal or deep groove on floor of basioccipital and basisphenoid for basilar artery.
6. Broad triangular alar from supraorbital process on prefrontal.



TEXT-FIG. 8. Cladogram of affinities among some of the more important genera of mosasaurs including *Goronyosaurus*, in the subfamilies Plioplatecarpinae and Tylosaurinae. The subfamily Mosasaurinae is used as the outgroup.

7. Ala on supraorbital process is a small nubbin.
8. First two processes of POF connected under frontal by thin sheet of bone, separated by a groove.
9. POF process to the jugal is large.
10. Face of POF beneath the posterolateral corner of the frontal is smooth.
11. Parietal foramen is large.
12. Parietal invades the posterodorsal surfaces of the frontal medially by firm suture providing little mesokinetic movement.
13. Penetration of the basisphenoid posteriorly by bilobate tunnel.
14. Small flattened quadrate with very reduced tympanic ala.
15. Pterygoid teeth increases anteriorly from very small diameter to equal mandibular teeth.

16. Ectopterygoidal process projects from main body of the pterygoid at an acute angle.
17. Suprastapedial process very large.
18. Supra and infrastapedial process fused.
19. Tympanic ala highly developed.
20. Very blunt termination of premaxilla.
21. Jaws long.
22. Keel on quadrate shaft for origination of the M. depressor mandibulae.
23. Pterygoid teeth: large.
24. Prefrontal excluded from external narial border.
25. Frontal does not emarginate with orbits.
26. Broad dentary projection.
27. Quadrate-medial surface flat. In front of this a heavy ridge descends vertically.
28. Wide robust internarial bar.
29. Small orbits.
30. Skull narrow and long.
31. Massive quadrate.
32. Dentary teeth: sixteen to seventeen.
33. Massive jaws.
34. Heavy dentition.
35. Elliptical teeth.
36. Long narrow jaws.
37. Maxillaries extend beyond the posterior margin of the orbits.
38. The inner surface of the frontal bears a fully closed canal housing the olfactory lobes.

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Note added in proof: A new plioplatecarpine mosasaur, *Selmasaurus russelli* (Wright and Shannon, 1988) from the Upper Cretaceous of Alabama shares a number of features with *Goronyosaurus*; the similarity of the two genera, however, is increased in the light of the present reinterpretation of *Goronyosaurus* and the elimination of its 'bizarre' characters.

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