Crocodile remains from the Burdigalian (lower Miocene) of Gebel Zelten (Libya)

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ABSTRACT

The Gebel Zelten locality in Cirenaica, North Central Libya (Burdigalian, lower Miocene) has yielded numerous fossil remains of crocodilians. Although fragmentary in nature, several forms can be distinguished, among them the longirostrines *Euthecodon arambourgi* Ginsburg & Buffetaut, 1978 and *Tomistoma lusitanica* Antunes, 1967 and the brevirostrine *Rimasuchus lloydi* Fourtau, 1918. There are also other remains present in the collections from this locality that cannot be assigned with confidence to any known crocodilian species due to their fragmentary condition. Nevertheless, these remains indicate the presence of at least one additional taxon, a previously unidentified brevirostrine form differing from *Rimasuchus lloydi* in the morphology of its lower jaw. The crocodilian fauna from this locality shows similarities with that from the Burdigalian of Wadi Moghara (Egypt), pointing to the existence of a crocodilian assemblage in North Africa during the early Miocene, showing both forms endemic to the African continent (*Euthecodon arambourgi*, *Rimasuchus lloydi*) and forms that were also present at that time all around the Mediterranean basin and Asia (Tomistominae and Gavialoidea). The presence of crocodilians in North Africa at that time also indicates the existence of a tropical, warm and humid climate, before the onset of more arid conditions in the region that led to the disappearance of the crocodilians and the development and expansion of the Sahara desert.

KEY WORDS
Reptilia,
Crocodylia,
Crocodylidae,
Tomistomina,
Burdigalian,
Gebel Zelten,
Libya,
North Africa,
climate.

RÉSUMÉ

Les restes de crocodiles provenant du Burdigalien (Miocène inférieur) de Gebel Zelten (Libye).

Le gisement de Gebel Zelten, en Cyrénaïque, Libye nord-centrale (Burdigalien, Miocène inférieur) a produit de nombreux restes de crocodiliens. Même fragmentaires, quelques formes peuvent être distinguées, parmi celles-ci les longirostrines *Euthecodon arambourgi* Ginsburg & Buffetaut, 1978 et *Tomistoma lusitanica* Antunes, 1967 et le brevirostrine *Rimasuchus lloydi* Fourtau, 1918. Il y a aussi d'autres restes dans les collections provenant de ce gisement qui ne peuvent être identifiées avec confiance parce qu'ils sont très fragmentaires. Néanmoins, ces restes indiquent la présence d'au moins un autre taxon, un brevirostrine pas encore identifié qui diffère de *Rimasuchus lloydi* dans la morphologie de sa mâchoire. La faune de crocodiliens provenant de ce gisement montre les ressemblances avec celle du Burdigalien du Wadi Moghara (Egypte), indiquant l'existence d'un assemblage de crocodiliens en l'Afrique du Nord durant le Miocène inférieur et montrant les deux formes endémiques d'Afrique (*Euthecodon arambourgi*, *Rimasuchus lloydi*) et les formes qui étaient présentes aussi à l'époque autour du bassin méditerranéen et de l'Asie (Tomistominae et Gavialoidea). La présence de crocodiliens en Afrique du Nord à cette époque indique également l'existence d'un climat tropical, chaud et humide, antérieur à des conditions plus arides dans la région qui ont mené à la disparition des crocodiliens et au dévelopement et à l'augmentation du désert du Sahara.

INTRODUCTION

The Gebel Zelten locality of Sirte Basin (Cirenaica, Libya) (Fig. 1) consists of outcrops of the Marada Formation. This formation shows a series of facies ranging from continental to fluviatile sediments in the south to marine (littoral and offshore) deposits in the north, which indicate the existence of large rivers flowing northward into the Tethyan basin (Savage & Hamilton 1973). This locality has yield abundant vertebrate remains, especially those of a rich mammalian fauna including diverse groups such as sirenians, proboscideans, hyracoids, perissodactyls, artiodactyls, creodonts and carnivorans (Savage & Hamilton 1973). Besides the mammals, this locality has also yielded other vertebrates such as fish, birds, chelonians and crocodilians, including both long-snouted taxa and taxa of a more generalized cranial morphology. They are represented mainly by fragmentary cranial elements, although there are also many isolated postcranial bones, especially vertebrae, which cannot be assigned to any of the forms represented by cranial material. Previous accounts of the crocodilians present at this locality reported the existence of at least four different taxa: *Euthecodon arambourgi* Ginsburg & Buffetaut, 1978 (Ginsburg & Buffetaut 1978; Tchernov 1986), *Rimasuchus lloydi* Fourtau, 1918 (Tchernov 1976, 1986; Storrs 2003), *Tomistoma dowsoni* Fourtau, 1918 (Savage & Hamilton 1973; Tchernov 1986), and an undetermined "gavialid" (Ginsburg & Buffetaut 1978; Buffetaut 1982).

In the present paper, additional material from the same locality is reported and described. Fossils are housed at the Department of Earth Sciences, University of Bristol (BRSUG) and the Muséum national d'Histoire naturelle, Paris (MNHN). The evidence indicates the existence of a tomistomine (*Tomistoma lusitanica*) together with a previously undescribed brevirostrine form. All these elements point to the existence of a diverse

crocodilian fauna in a tropical climatic regime during the Burdigalian of North Africa.

MATERIALS

MATERIAL HOUSED IN BRSUG
Crocodylidae indet. 1: BRSUG 27360: partial skull table accompanied by fragmentary occipital and quadrate regions and braincase.

MATERIALS HOUSED IN MNHN
Tomistoma lusitanica: MNHN.LBE.300: anterior portion of snout; MNHN.LBE.301: posterior portion of snout; MNHN.LBE.302: fragment of anterior part of snout.
Crocodylidae indet. 1: MNHN.LBE.311: complete skull table accompanied by almost complete occipital region and braincase and fragmentary right quadrate region.
Crocodylidae indet. 2: MNHN.LBE.306: almost complete skull table (lacking part of the right postorbital and squamosal) accompanied by the right quadrate region and a fragmentary occipital region lacking the basioccipital; MNHN.LBE.307: anterior part of right dentary; MNHN.LBE.308: posterior part of a right lower jaw. All these specimens were found in association, possibly coming from a single individual.

SYSTEMATICS

CROCODYLIFORMES
Clark *in* Benton & Clark, 1988
MESOEUCROCODYLIA
Whetstone & Whybrow, 1983
NEOSUCHIA Clark *in* Benton & Clark, 1988
EUSUCHIA Huxley, 1875
CROCODYLIA Gmelin, 1789
Family CROCODYLIDAE Cuvier, 1807
Subfamily TOMISTOMINAE Kälin, 1955
Genus *Tomistoma* Müller, 1846

***Tomistoma lusitanica* Antunes, 1961**

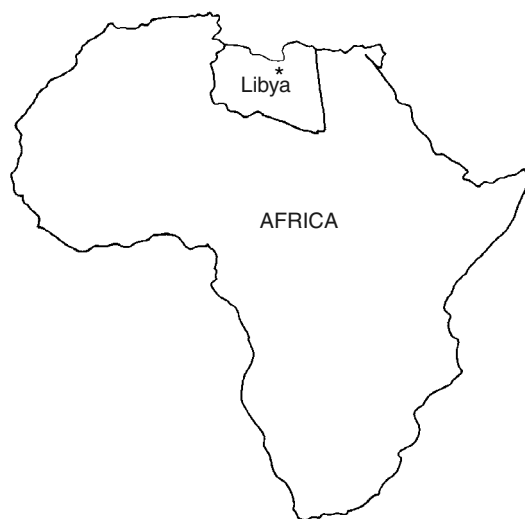MATERIAL EXAMINED. — MNHN.LBE.300, MNHN.LBE.301 and MNHN.LBE.302.

FIG. 1. — Map of Africa showing location of the Gebel Zelten locality (*) in Northern Libya.

DESCRIPTION
Snout (Fig. 2)
The snout is represented by three fragments: MNHN.LBE.300, representing the anterior part of the snout; MNHN.LBE.301, representing its posterior part; and MNHN.LBE.302, which includes only a small fragment of the anterior portion of the snout. The premaxillae are almost completely preserved, lacking only their anteriormost portion, including the anterior border of the external naris. This is heart-shaped and its lateral borders converge backward. The posterodorsal processes of the premaxillae reach backward to the level of the posterior border of the third maxillary alveolus. The premaxillae are not expanded on its anterior part and there is not notch behind the first maxillary alveolus, unlike the condition seen in gavialoids. The foramen incisivum is not preserved. Only the last three pairs of premaxillary alveoli are preserved. Of this, the anteriormost is the largest, the following one is slightly smaller and the posteriormost one is the smallest, being clearly smaller than the two other. The premaxillary alveoli are well apart from each other, being the lateral margin of the premaxillae indented.
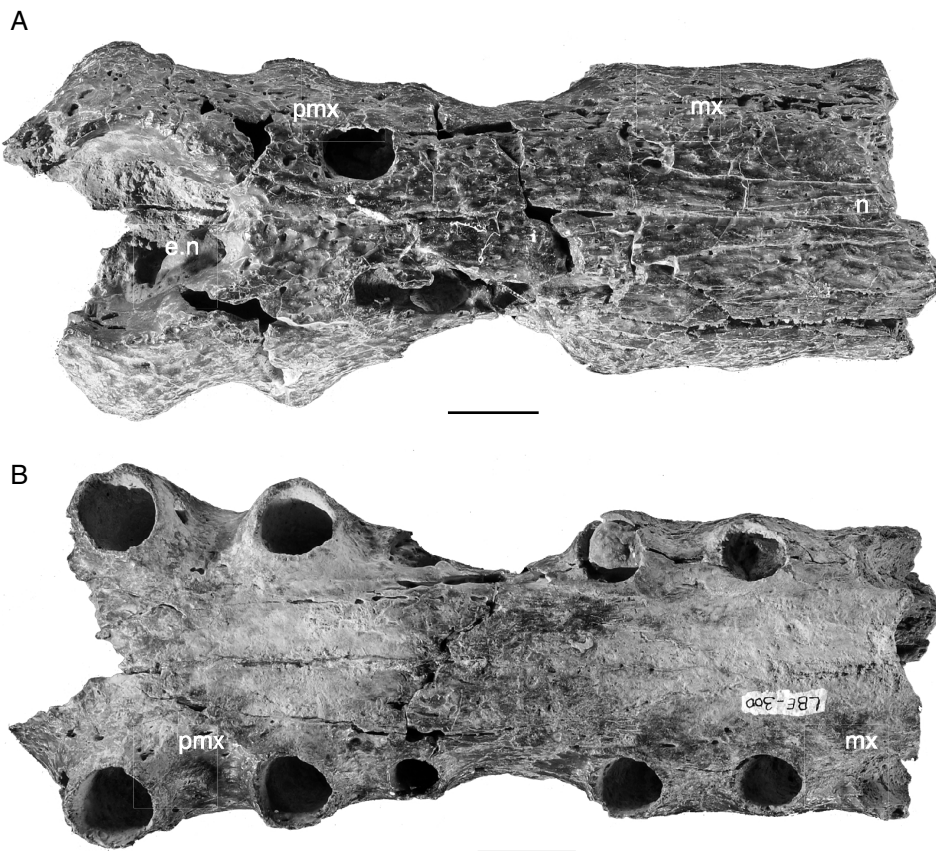
A

B

FIG. 2. — *Tomistoma lusitanica* Antunes, 1967 (MNHN.LBE.300), anterior portion of the snout; **A**, dorsal view; **B**, ventral view. Abbreviations: **e.n**, external naris; **n**, nasals; **mx**, maxillae; **pmx**, premaxillae. Scale bars: 2 cm.

In ventral aspect, the premaxillo-maxillary suture is V-shaped and reaches backward to the level of the second maxillary alveolus. There is a marked lateral constriction and diastema between the premaxillae and the maxillae. Unfortunately, the total maxillary tooth count cannot be established. The palate has a convex section and the tooth row is dorsally placed. The maxillary alveoli are subcircular to slightly oval in shape. The alveolar collars are higher at their distal margins. The diameter of the alveoli decreases toward the rear part of the snout. The lateral borders of the maxillae remain parallel through much of the length of the snout and diverge gradually toward its posterior part.

The palatines are partially preserved, including only the anterior intermaxillary process and the anterior portion of the interfenestral part. Only the anterior border of the right palatine fenestra is preserved. The sutures between palatines and maxillae are not very clear, although an obscure palatine anterior process seems to extend up to the level of the third posteriormost alveolus. The palatines are smooth anteriorly, without sending lateral processes into the lateral fenestrae.

The nasals are in contact with the premaxillae, preventing the contact of both maxillae in the dorsal surface of the snout, as in *Tomistoma* and unlike *Gavialis* (although there is nasal-premaxillary contact in some gavialoids such as *Eogavialis*). The nasal-premaxillary suture is W-shaped, and its anteriormost edge reaches the level of the second maxillary alveolus (in speci-

men MNHM.LBE.302, it reaches the level of the first one). The nasals are isolated from the posterior border of the external naris by the premaxillae. The nasals remain moderately narrow and parallel through much of the length of the snout before becoming gradually broader and divergent toward the rear part. The dorsal surface of the snout is slightly sculptured by numerous small shallow pits.

There are certain features (nasal-premaxillary contact, enlarged anterior maxillary alveoli, absence of a neat expansion of the premaxillae forming a notch behind the first premaxillary alveolus) that are reminiscent of a tomistomine crocodylid. The material is very similar to that of *T. dowsoni* Fourtau, 1918 from the Burdigalian of Wadi Moghara, Egypt, and seems to confirm previous reports of this form at Gebel Zelten (Savage & Hamilton 1973; Tchernov 1986). However, Brochu (Brochu & Gingerich 2000) synonymized all the early Miocene forms of the Mediterranean basin previously referred to as *Tomistoma* (including *T. dowsoni*) under the name *T. lusitanica* Antunes, 1961. Therefore, I refer the present material to *T. lusitanica* Antunes, 1961.

Family CROCODYLIDAE Cuvier, 1807

CROCODYLIDAE indet. 1

MATERIAL EXAMINED. — BRSUG 27360 and MNHN.LBE.311.

DESCRIPTION
Skull table (Fig. 3)
The skull table is rectangular in shape, wider than long. Its surface is transversely concave and its ornamentation consists of small irregular pits. The posterior margin of the skull table is almost linear and horizontal. Its lateral margins are parallel to subparallel, their anterior (postorbital) margins deflect medially toward the orbits. The bars formed by the postorbitals and squamosals are narrow. The plate between the supratemporal fossae is so narrow that the ornamentation on its

surface is formed by a low longitudinal ridge. This ridge runs backward to the posterior margin of the skull table over the dorsal surface of the parietal and supraoccipital. The dermal bones of the skull table do not overhang the borders of the supratemporal fossae.

The supratemporal fenestrae are wide and subrectangular in shape. The orbito-temporal foramen, situated in the posterior wall of the supratemporal fenestra, is large and is bordered by the squamosal, quadrate and parietal.

The postorbital constitutes about half the length of the lateral border of the supratemporal fenestra, and extends posteriorly about half the length of the lateral borders of the skull table. Its anterolateral corner is rounded and overhangs the base of the postorbital bar. The postorbital bar is partially preserved. There is a large nutrient foramen on its base.

The squamosal is also large. Its dorsal surface has a depression on its posterolateral corner separating it from the large posterolateral squamosal projection. On its lateral aspect, the squamosal forms the dorsal wall of the otic meatus. It has a shallow longitudinal groove for the attachment of the external ear valve musculature whose borders remain parallel before flaring anteriorly toward the postorbital. In lateral view, the postorbital-squamosal suture is oriented ventrally and it does not pass medially ventral to the skull table. The squamosal-quadrate suture extends dorsally along the posterior margin of the external auditory meatus.

The parietal is posteriorly wide. It narrows at the interfenestral space and its anteriormost portion has a short length. Only the posterior part of the frontal is preserved. It is excluded from the anterior border of the supratemporal fossa by the parietal and the postorbitals. The fronto-parietal suture is concavo-convex, with the convex side toward the parietal. The dorsal surface of the posterior part of the frontal is concave, especially in the interorbital plate, which is wider than the interfenestral plate. Only the posterior and posteromedial borders of the orbits are preserved. They were larger than the supratemporal fenestrae and directed upward and slightly outward.
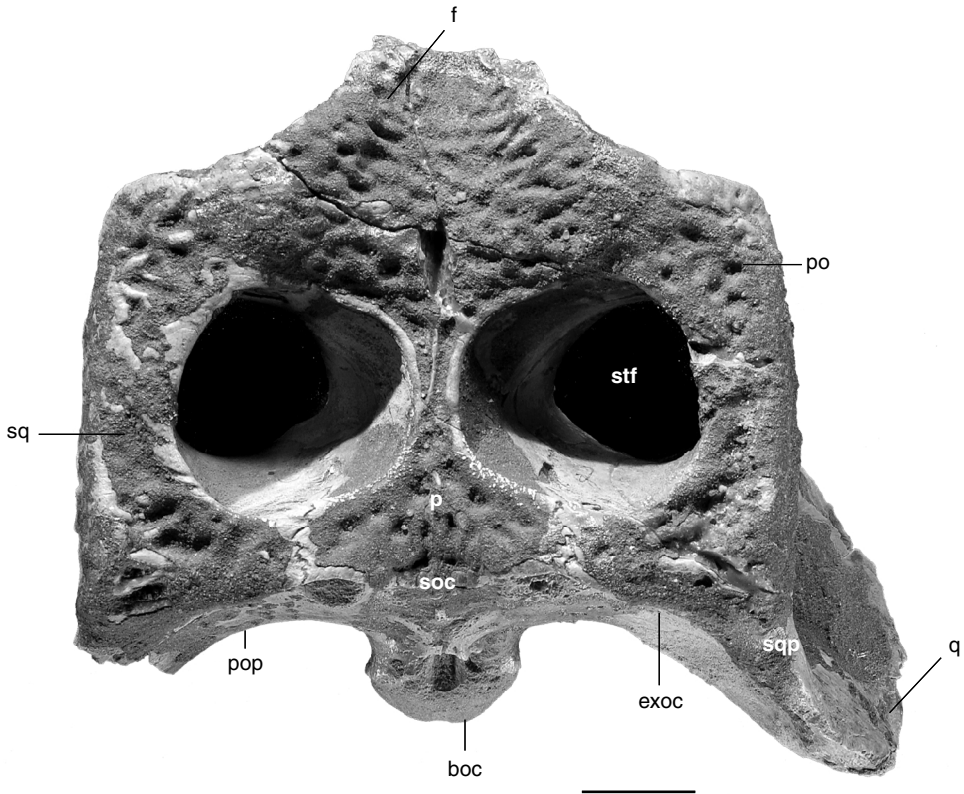
FIG. 3. — Crocodylidae indet. 1 (MNHN.LBE.311), skull table in dorsal view. Abbreviations: **boc**, basioccipital condyle; **exoc**, exoccipital; **f**, frontal; **p**, parietal; **po**, postorbital; **pop**, paraoccipital process; **q**, quadrate; **soc**, supraoccipital; **sq**, squamosal; **sqp**, squamosal projection; **stf**, supratemporal fenestra. Scale bar: 2 cm.

Quadrate region (Figs 4; 6)
The articular surface of the quadrate is badly eroded but it seems to have been divided in two hemicondyles (medial and lateral). The quadrate forms the floor and much of the anterior and posterior walls of the external auditory meatus, where it contacts the squamosal. The posterior margin of the otic aperture is invaginate. There is a foramen preoticum just in front of the external otic aperture. The distal end of the quadratojugal is also preserved. It abuts the lateral border of the quadrate and reaches backward just to the level of the lateral articular hemicondyle. Its lateral surface seems to have been sparsely sculptured.

The quadratojugal did not extend dorsally to contact the squamosal and the quadrate that formed the dorsocaudal border of the infratemporal fenestra. The quadrate contacted the postorbital at the medial aspect of the base of the postorbital bar. The foramen aereum cannot be observed; however, a shallow groove is visible on its usual position on the dorsomedial surface of the quadrate. On its ventral surface, the quadrate presents a longitudinal crest running for about three fourths of its length and reaching its distal end, near which it thickens. The quadrate abuts the lateral wall of the braincase and shows a sharp ridge near the basisphenoid.

Occipital region (Fig. 5)
The occipital surface is slightly inclined backward, but not to the degree seen in gavialids. Dorsal to the foramen magnum, its posterior surface is vertical. The exoccipital borders of the
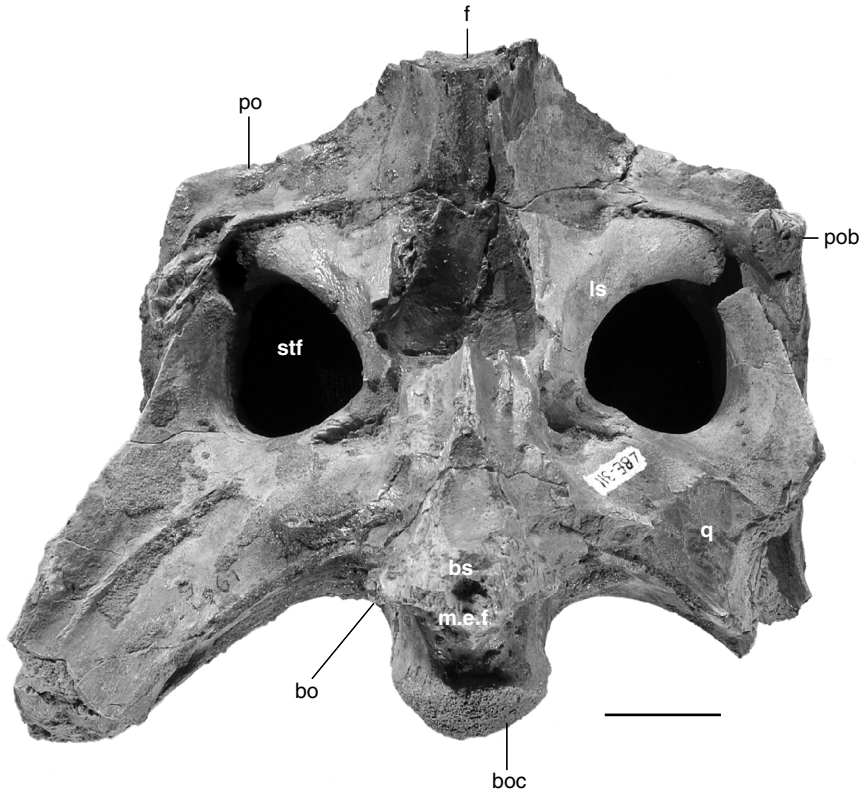
Fɪɢ. 4. — Crocodylidae indet. 1 (MNHN.LBE.311), skull table and braincase in ventral view. Abbreviations: **bo**, basioccipital; **boc**, basioccipital condyle; **bs**, basisphenoid; **f**, frontal; **ls**, laterosphenoid; **m.e.f**, median eustachian foramen; **po**, postorbital; **pob**, postorbital bar; **q**, quadrate; **stf**, supratemporal fenestra. Scale bar: 2 cm.

foramen magnum and the basioccipital are visible in dorsal view.

The supraoccipital is large and subtriangular in shape, being far wider than high. Its dorsal border is clearly concave. The supraoccipital extends downward to about two thirds the distance to the dorsal border of the foramen magnum, from which it is excluded by the exoccipitals. The supraoccipital has a low median vertical crest accompanied by a shallow depression on each side of it. Toward both of its dorsolateral ends, the supraoccipital shows the two large tuberosities of the ventromedial borders of the postemporal fenestrae. The postemporal fenestrae are bordered by the squamosals, the supraoccipital, the exoccipitals and the parietal bone. In dorsal view, the supraoccipital is triangular in outline, being approximately as long as wide, and it occupies the central quarter of the posterior margin of the skull table.

The squamosals also participate in the occiput. The squamosals form the posterolateral projections over the paraoccipital processes of the exoccipitals, although these projections do not reach their distal extremities. The occipital view of the squamosal extends along its contact with the exoccipital to the ventrolateral corner of the supratemporal fenestra.

The exoccipitals have long paraoccipital processes that are devoid of sculpture on their surface and extend for a long distance lateral to the entrance of the cranio-quadrate passage. The foramen magnum is elliptical in shape, wider than tall. The exoccipitals form the dorsal and lateral borders of
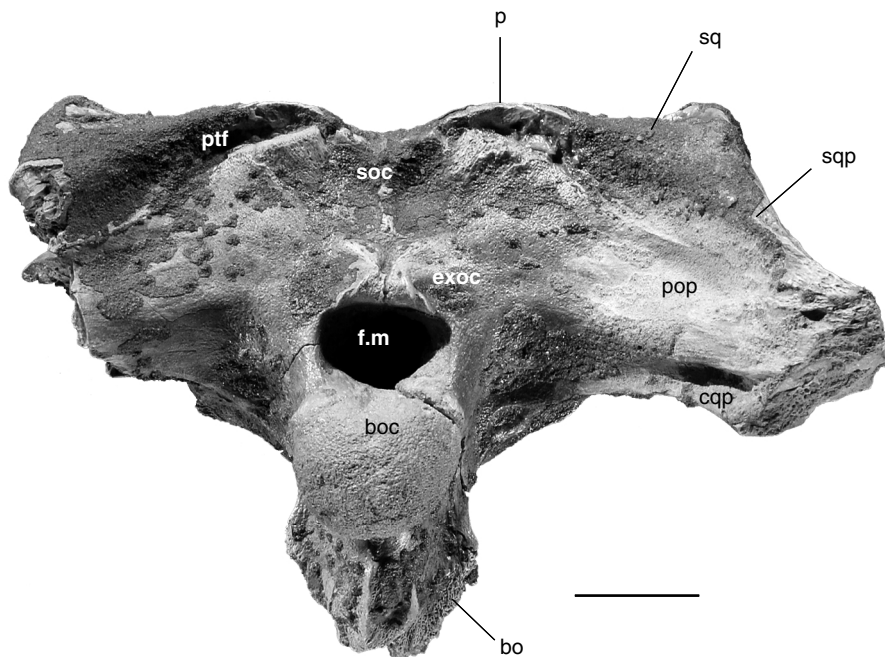
FIG. 5. — Crocodylidae indet. 1 (MNHN.LBE.311), occipital region. Abbreviations: **bo**, basioccipital; **boc**, basioccipital condyle; **cqp**, cranio-quadrate passage; **exoc**, exoccipital; **f.m**, foramen magnum; **p**, parietal; **pop**, paraoccipital process; **ptf**, postemporal fenestra; **soc**, supraoccipital; **sq**, squamosal; **sqp**, squamosal projection. Scale bar: 2 cm.

that foramen. The ventral processes of the exoccipitals are short and cover only the dorsalmost part of the lateral borders of the exoccipital. The hypoglossal foramen is small and is placed dorsomedially to the foramen vagus. It is oval-shaped with acute ends and very deep. The foramen caroticum posterious is also oval-shaped and deep and it is situated immediately ventral to the former and over the suture with the quadrate.

The basioccipital forms the basioccipital condyle and the ventral border of the foramen magnum. The basioccipital condyle is subcircular in outline. The basioccipital shelf is tall and does not form the prominent tuberosities seen in gavialoids. It presents a prominent vertical median crest. The lateral eustachian canals opened dorsolaterally to the medial one. They are placed at the level of the lowest point of the ventral process of each exoccipital. The median eustachian canal opened in the ventral aspect of the basisphenoid, just anterior to the suture with the basioccipital.

Braincase (Figs 4; 6)

Its walls are formed by the parietal, the laterosphenoids, the quadrates, the exoccipitals, the prootics, the basisphenoid and the basioccipital. The foramen ovale is wide and its dorsal and posterior borders extend posterodorsally as a shallow recess over the posterior margin of the laterosphenoid and the anterior margin of the quadrate. The laterosphenoids are relatively well preserved. They form the anterior border of the foramina ovale. Their capitate processes are oriented anteroposteriorly toward the middline and they do not seem to have been very long. The lateral wing-like process of the laterosphenoid contacts the base of the postorbital bar medially and its anterior border is slightly constricted.

The basisphenoid is incompletely preserved, lacking the basisphenoid rostrum. Only a very small part of the pterygoids is preserved, covering the lateral surfaces of the basisphenoid. The caudal part of the basisphenoid placed between the
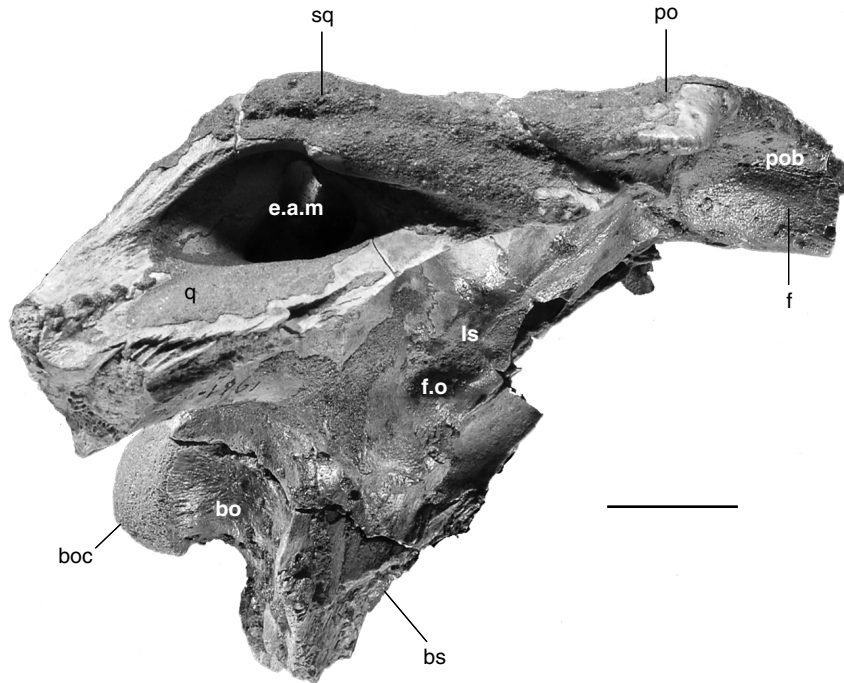
F<small>IG</small>. 6. — Crocodylidae indet. 1 (MNHN.LBE.311), skull table and braincase in right lateral view. Abbreviations: **bo**, basioccipital; **boc**, basioccipital condyle; **bs**, basisphenoid; **e.a.m**, external auditory meatus; **f**, frontal; **f.o**, foramen ovale; **ls**, laterosphenoid; **po**, postorbital; **pob**, postorbital bar; **q**, quadrate; **sq**, squamosal. Scale bar: 2 cm.

posterior border of the pterygoids and the anterior border of the basioccipital is thick and not reduced to a thin lamina, but it is not extensively exposed on the braincase wall anterior to the median eustachian foramen. The basisphenoid is not broadly exposed ventral to the basioccipital. The quadrate-pterygoid suture is linear from the basisphenoid to the foramen ovale and there is not significant ventral quadrate process on the lateral wall of the braincase.

CROCODYLIDAE indet. 2

M<small>ATERIAL</small> <small>EXAMINED</small>. — MNHN.LBE.306, MNHN.LBE.307 and MNHN.LBE.308.

D<small>ESCRIPTION</small>
Skull table and associated regions (Fig. 7A)
The skull table is almost as wide as long. Its lateral borders converge anteriorly. The surface of the skull table is nearly flat and sculptured by numerous wide but shallow pits that are ovate in shape. The supratemporal fenestrae are small and suboval. Their lateral margins are clearly longer than the medial ones. The interfenestral plate and the lateral borders of the skull table are broad. The squamosals form about two thirds of the length of the lateral borders of the skull table, the postorbitals making up the other third. The anterolateral margin of the postorbital is broadly rounded. The frontal is excluded from the anterior border of the supratemporal fenestrae by the parietal and the postorbitals. The fronto-parietal suture is concavo-convex, with the convexity facing toward the parietal. The frontal is slightly depressed with respect to the postorbitals.
The posterior margin of the skull table is slightly concave. The parietal and the supraoccipital make up its central half and the squamosals make up the other. The posterior part of the parietal is
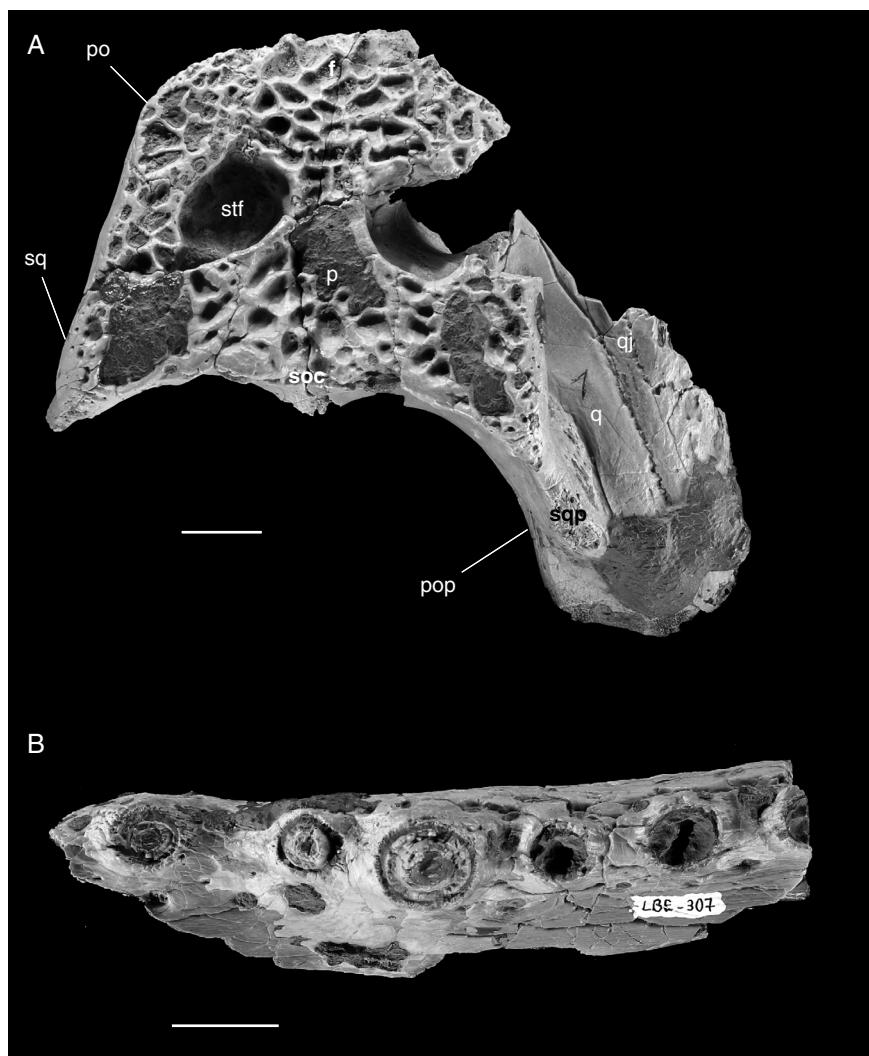
Fig. 7. — Crocodylidae indet. 2; **A**, fragmentary skull table in dorsal view (MNHN.LBE.306); **B**, anterior portion of right dentary in dorsal view (MNHN.LBE.307). Abbreviations: **f**, frontal; **p**, parietal; **po**, postorbital; **pop**, paraoccipital process; **q**, quadrate; **qj**, quadratojugal; **soc**, supraoccipital process; **sq**, squamosal; **sqp**, squamosal projection; **stf**, supratemporal fenestra. Scale bars: 2 cm.

broad and almost quadrangular in outline. The exposure of the supraoccipital on the dorsal surface of the skull table is reduced. In occipital view, the supraoccipital is large and subtriangular in outline. The occipital surface is planar and fully verticalized. Only the right quadrate region is preserved. The articular surface of the quadrate is differentiated into a medial and a lateral hemi-condyle. The foramen aereum is close to the median margin of the quadrate. The posterior margin of the external otic meatus is invaginate. There is a foramen preoticum in front of the external auditory aperture. The posterior part of the quadratojugal is also preserved. It reaches backward to the level of the articular surface of the quadrate but it does not participate in that

surface. Its lateral surface is ornamented with large and shallow pits, although the ornamentation has somewhat been eroded.

Lower jaw (Fig. 7B)
Only the right dentary and splenial are fragmentary preserved. The mandibular ramus is robust. The total dentary tooth count cannot be determined with certainty. The dentary symphysis is short and its rear part is damaged, so its exact posterior extent cannot be determined, although it probably extended backward to the level of the fourth or fifth dentary tooth. It is unclear whether the splenial participated in the symphysis, although this seems unlikely. Although short, the dentary symphysis is clearly more elongated than that of *R. lloydi* or *C. niloticus*. The ventral border of the symphysis is nearly flat and horizontal, resembling that of *R. lloydi*. The anterior fragment of the lower jaw preserves six alveoli (second-seventh), all of which are subcircular in outline. The second alveolus was apart from the first one, which is not preserved. It is also clearly apart from the third, this being the greatest interalveolar distance. From the third alveolus backward, all the alveoli are clearly apart from each other and regularly spaced, including those from the fourth to the seventh. This is in sharp contrast with the condition observed in *R. lloydi* or *C. niloticus*, in which these alveoli are close together (in some individuals of *C. niloticus* these alveoli are slightly apart and there are pits for the reception of the first maxillary teeth slightly labially to them; there are no such pits in the present specimen).

The posterior fragment of the lower jaw preserves seven alveoli, most probably those from the ninth to the 15th. All are apart from each other but the distance is not too great in any case. They are circular to subcircular in outline and there are no great differences in size among them. The splenial forms the medial border of the last three alveoli, unlike in *R. lloydi* or *C. niloticus*. The lateral border of the lower jaw is strongly festooned. The fourth dentary alveolus occupies the highest point in the first convexity, whereas the 11th occupies that of the second. The ventrolateral

surface of the dentary is sculptured with longitudinal grooves and small pits.

DISCUSSION

Despite its fragmentary nature, the crocodilian fauna at Gebel Zelten seems to have been diverse. Other crocodilian faunas from the Burdigalian of North Africa, such as that at Wadi Mogahara (Egypt), were also diverse, with at least four different taxa, including both longirostrine and brevirostrine forms (Fourtau 1918).

Euthecodon arambourgi Ginsburg & Buffetaut, 1978 is the oldest species of its genus, dating from the Burdigalian of Libya. It may be represented by fragmentary remains of the same age from other North African localities such as Wadi Moghara in Egypt (Fourtau 1918). It is replaced in the Pliocene by *E. nitriae* Fourtau, 1920, present at Wadi Natrum (Fourtau 1920; Tchernov 1986) (this form could be also present in the Pliocene of Sahabi, Libya; however the material referred from this locality is too fragmentary to permit an identification at species level; Hecht 1987). Between both forms there is a considerable time gap spanning the middle and late Miocene, although the genus is represented by fragmentary jaw material from some localities scattered across North Africa, such as Beglia (Tunisia) (Pickford 2000; Llinás Agrasar 2003). In East Africa, the genus is already present in the early Miocene of Kenya, although the fragmentary nature of its remains renders an identification at specific level impossible (Tchernov & Van Couvering 1978; Buffetaut 1979). In the Plio-Pleistocene it is represented by the species *E. brumpti* Joleaud, 1920 (Joleaud 1920; Tchernov 1976, 1986; Storrs 2003) which becomes extinct in the middle Pleistocene (Tchernov 1986; Storrs 2003).

Rimasuchus lloydi Fourtau, 1918 was first found at Wadi Moghara, Egypt and described under the name *Crocodylus lloydi* Fourtau, 1918. It is also present in Gebel Zelten (Savage & Hamilton 1973; Tchernov 1976, 1986; Storrs 2003) and at a slightly later date in the early Miocene of

Namibia and South Africa (Pickford 1996). The name *C. lloydi* was also applied to materials collected in younger beds (Plio-Pleistocene) in East Africa (Tchernov 1976, 1986; Pickford 1994; Leakey *et al.* 1996), but some authors regarded the tangibility of some of these identifications as questionable (Brochu 1997, 2000). However, they are not so different from the early Miocene form, the only differences being their larger size and greater robustness, an even more brevirostrine snout (and a more bulldog-like aspect), an external naris with lateral borders converging more clearly backward and a wider and more laterally open premaxillo-maxillary notch. All these differences could well be the result of intraspecific variability due to the broad geographic range (and presumably habitat diversity) of this species. Recent cladistic analysis (Brochu 1997, 2000; Brochu & Gingerich 2000) show that this form does not belong to the genus *Crocodylus* and in his review of this form, Storrs (2003) erected a new genus, *Rimasuchus* Storrs, 2003 to refer to it. Besides *Rimasuchus lloydi*, there seems to be another brevirostrine crocodile at Gebel Zelten (MNHN.LBE.306, 307 and 308; see above). This seems to differ from the former in the morphology of its lower jaw, having a more elongated symphyseal region, alveoli fourth to seventh clearly set apart from each other and a splenial that forms the medial border of the last three alveoli. However, due to its fragmentary condition, very little can be said about its affinities.

Tomistomine remains are known from early Miocene deposits all around the Mediterranean. Although they were given many names depending on their place of origin, all these forms seem to have been the same animal and they were synonymized by Brochu (Brochu & Gingerich 2000) under the name *Tomistoma lusitanica* Antunes, 1961. In North Africa, they are found at Wadi Moghara, Egypt (Fourtau 1918), and Gebel Zelten (Savage & Hamilton 1973). The only other record from a putative African tomistomine from a later date is that of *Tomistoma coppensi* Pickford, 1994 from the late Miocene-early Pliocene of Uganda and Zaire (Pickford 1994).

The presence of this crocodilian fauna points to the existence of tropical climatic conditions in the Early Miocene of North Africa (Markwick 1998; Pickford 2000) before the onset of more arid climatic conditions and the early stages of the development of the Sahara desert (Pickford 2000).

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