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Late Cretaceous neosuchian crocodiles from the Sultanate of Oman

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Abstract

Two apparently new crocodilian taxa from the Late Cretaceous (Late Campanian–Maastrichtian) Al-Khod Conglomerate of the Sultanate of Oman are described. The fragmentary state of preservation precludes formal naming, yet enables comparisons to be made with other taxa. One is a short-snouted terrestrial species showing affinities to Trematochampsidae based on similarities shared with *Trematochampsa oblita*; the other, an aquatic neosuchian, is related to longirostrine crocodiles with rather short splenials at the symphysis. The material supplies more evidence of similarities between the crocodilian faunas of Afro-Arabia and Madagascar. Currently, the Al-Khod fauna represents one of the better known, albeit otherwise poorly documented, Mesozoic vertebrate faunas from the Middle East.

Keywords: Crocodyliformes; Neosuchia; Trematochampsidae; Sultanate of Oman; Late Cretaceous; Late Campanian–Maastrichtian

1. Introduction

Vertebrate remains from the Upper Cretaceous of the Al-Khod area, Sultanate of Oman, were first recorded by Nolan et al. (1990). A reconnaissance trip in 1997 by ASS and AFH confirmed the potential of the Al-Khod Conglomerate for vertebrate palaeontological research (e.g., Schulp et al., 2000). Subsequent fieldwork by four of us (ASS, JWMJ, SSH and AFH) in 1998 yielded much additional material, including dinosaur, turtle and crocodile remains. Here we describe a crocodilian assemblage from Al-Khod, consisting of both terrestrial and aquatic species. These specimens constitute the first record of Late Cretaceous neosuchians from the Arabian Peninsula. The only other report of Mesozoic neosuchians we know of is that of isolated vertebrae from the Jurassic Hanifa Limestone south-east of Jizan, Saudi Arabia (Whitmore in Madden et al., 1995). Lower Palaeocene strata (Umm Himar Formation) along the western edge of the Arabian Peninsula have yielded abundant crocodilians of a diverse assemblage of long-snouted dyrosaurs reported on by Langston (1995). Mesozoic crocodiles from Africa, Madagascar and India are much better known, although the Early Cretaceous record is far better than that for the Late Cretaceous. The majority of this material is rather fragmentary (Buffetaut, 1985), with the exception of the bizarre Cenomanian fauna of Baharîya, Egypt (Stromer, 1925, 1933), and the Campanian assemblage from Maevarano, Madagascar (Buckley et al., 1997; Krause et al., 1999). Interpretation of these assemblages has revealed a peculiar palaeobiogeographic scenario for Gondwana, suggesting a greater similarity between the Late Cretaceous biota of South America and Indo-Madagascar (via Antarctica), and increasing endemism on the Afro-Arabian plate (Sampson et al., 1998). Crocodiles

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from the Sultanate of Oman fill a gap in the Afro-Arabian Cretaceous fossil record, and provide an opportunity to test this palaeobiogeographic hypothesis.

2. Locality

The specimens are from the type area of the Al-Khod Conglomerate (Nolan et al., 1990), located some 30 km west of Muscat, Sultanate of Oman (Fig. 1). Although additional outcrops exposing the Al-Khod Conglomerate Formation as well as the Simsima, Qahlah and Samhan formations (Nolan et al., 1990; Robertson and Searle, 1990) were surveyed during the 1998 fieldwork, the type area of the Al-Khod Conglomerate Formation was the only one to yield crocodilian remains.

3. Geological setting and stratigraphy

During the Late Cretaceous, Tethyan oceanic crust was obducted onto the Arabian platform, which resulted in the formation of the proto-Oman Mountains (Robertson and Searle, 1990; Hanna, 1995; Alsharhan and Nasir, 1996). Associated with the formation of the Oman Mountains, eroded material was deposited in fluvial and deltaic environments on the foothills of the ophiolite, forming among other units the Al-Khod and Qahlah formations. Both of these formations are predominantly clastic in character. Prospecting efforts mainly focused on these two units. The coeval Simsima and Samhan formations (Nolan et al., 1990) consist mainly of carbonates, but because the lower parts of these formations also show terrigenous influence at some outcrops, some prospecting effort was also directed to these outcrops.

The Al-Khod Conglomerate Formation was defined by Nolan et al. (1990). The formation disconformably overlies the Semail Ophiolite. The lithology in a number of outcrops was logged and sampled in more detail by ASS and JWMJ in February–March, 1998 (Schulp et al., 2000).

The formation consists of a series of conglomerates interbedded with sandstones and shales. The clast-supported conglomerates are composed of ophiolite or chert pebbles, derived from the Semail Ophiolite or Hawasina Imbricates. The succession starts with a chert- and ophiolite-clast-dominated base, followed by Mesozoic carbonate debris, and is topped by pre-Permian quartzite clast-dominated conglomerates, representing the source area of the clastics in reverse stratigraphic order.

The sandstones and shales, rarely exposed, vary in colour from red to green and grey. The invertebrate fauna, which comprises various bivalves (including oysters) as well as freshwater gastropods, is indicative of a palaeoenvironment of varying salinity; driftwood and shell hash are common in some beds. Nolan et al.

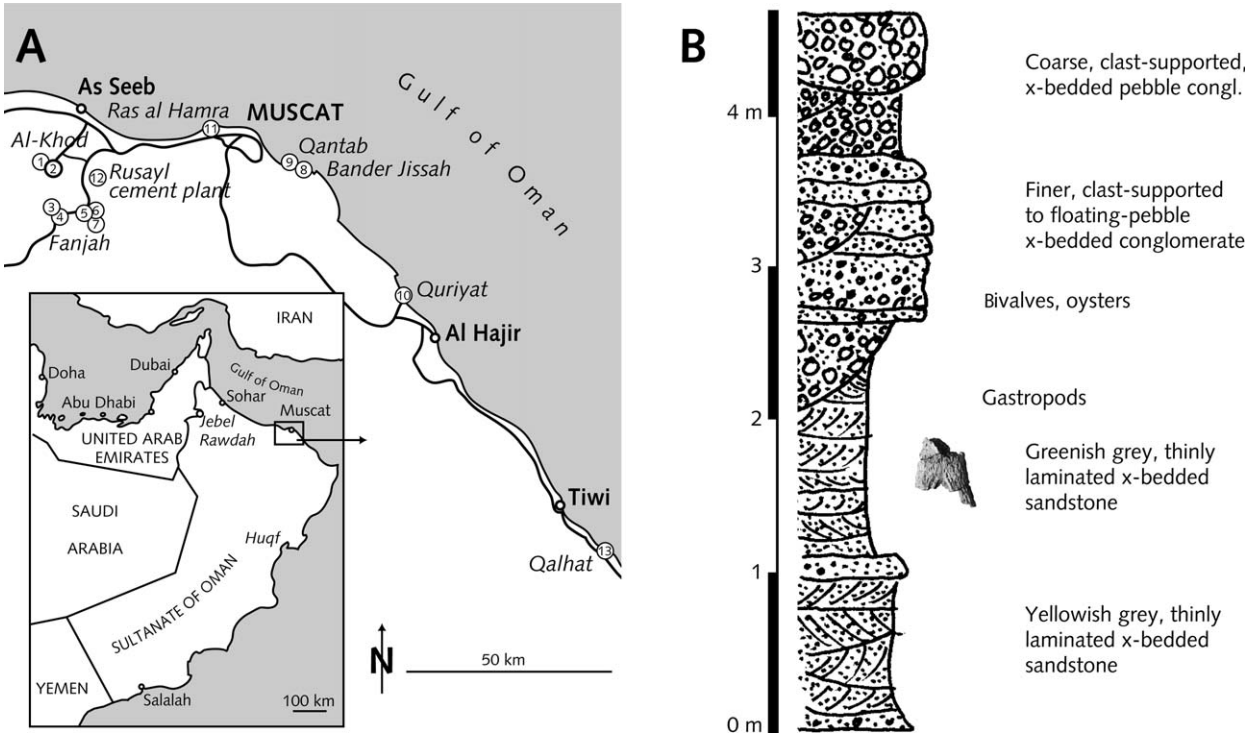

Fig. 1. Sketch map (A) showing the Al-Khod-2 locality and other localities (numbered) visited during fieldwork in 1998. Log of the escarpment (B) from which SQU-2-1998-69 was collected; see also fig. 1 in Schulp et al. (2000).

(1990) considered the Al-Khod Conglomerate to have formed in a fan deltaic setting.

The crocodilian remains were collected by JWMJ as surface float from the fine-grained layers of the Al-Khod Formation, in between the escarpments of the type section (Fig. 1). No radiometric or detailed biostratigraphic dates are available for the Al-Khod Conglomerate Formation, but its age is constrained by the source of the conglomerates, the age of the overlying formation and the presence of presumed in situ dinosaur remains (Schulp et al., 2000). As the formation disconformably overlies the Semail Ophiolite, which was obducted onto the Oman continental margin during the Late Campanian–Maastrichtian (Robertson and Searle, 1990), and as it contains clasts of the same ophiolite, it must be younger than Late Campanian. The disconformably overlying Jafnayn Formation is of Late Palaeocene age (Nolan et al., 1990). If the dinosaur remains reported in Schulp et al. (2000) are considered not to have been reworked, a latest Campanian to Maastrichtian age may therefore be assumed.

4. Systematic palaeontology

All material described here is housed in the collections of the Earth Sciences Department of the Sultan Qaboos University, Al-Khod, Sultanate of Oman. Casts of SQU-2-1998-57 and SQU-2-1998-69 are in the collections of the Natuurhistorisch Museum Maastricht (NHMM2003190 and NHMM2003191, respectively) and the Universidad Autonóma de Madrid (UPUAM-OM1 and UPUAM-OM2, respectively). Although the majority of the vertebrate remains from the Al-Khod Conglomerate are highly abraded and mostly fragmentary, the presence of a few well-preserved bones suggests that extensive pre-fossilisation and reworking may be excluded for at least part of the material.

Crocodyliformes (sensu Benton and Clark, 1988)
Neosuchia (Benton and Clark, 1988)

cf. *Trematochampsa* (Buffetaut, 1974) indet.

Dentary: SQU-2-1998-57 (NHMM2003190/UPUAM-OM1)
Fig. 2A–C

Description. This is a fragmentary right dentary of a robust, short-snouted crocodile. Its anterior orientation is delimited by the scar of the splenial that tapers under a rather acute angle. The lateral wall is thick and convex. Four complete and neat alveoli are preserved. The preserved part of the tooth row contains the hypertrophied tooth and a series of two or three and one-half successive alveoli. The first alveolus is twice the diameter of the other alveoli (31 mm and no more than 15 mm in labio-lingual diameter, respectively). This hypertrophied tooth pushes the dentary wall outward, making the lateral profile of the preserved part slightly concave. The dentary hardly increases in height posteriorly. With a height of 40 mm anteriorly and 55 mm posteriorly, the dentary is rather low. Its dorsal outline does not form a wave or festooning, and the tooth row is rectilinearly aligned. The three alveoli behind the first enlarged alveolus are almost the same. Occlusal pits for maxillary teeth are observed at the posteriormost interalveolar space, although the poor preservation makes them difficult to discern. The preserved part of the dentary is sparsely sculptured with only a few widely spaced oval grooves. The external surface below the tooth row does not show any depressed or smooth areas. Nutritional foramina are limited to the anteriormost two alveoli.

In medial view, the dentary shows a narrow sloping expansion medial to the tooth row that probably was covered by the splenial lamina. A thick splenial lamina is expected anteriorly, in the area where the splenial scar becomes thicker. Whether the splenial participated in the symphysis or not cannot be determined. The Meckelian groove begins between the third and the fourth preserved alveolus and continues as a canal up to the first preserved alveolus. The combination of the set of characters mentioned above indicates that the fragment should be placed in the median portion of the dentary.

Discussion. We assign this fragment to the Neosuchia based on the strongly convex profile of the dentary and the presence of a conspicuous heterodont dentition. Consequently, the position of the fragment in the mandible should correspond to the mid-posterior half of the ramus. If the hypertrophied tooth would correspond to an anterior fourth, the symphyseal area would have been extremely short, and the front of the mandible would have been curved, probably forming a rounded mandibular tip.

The fragment preserves the transition from the Meckelian canal to the Meckelian vein, which occurs in the area that comprises the alveolar interval beginning at the ninth or tenth tooth position. This feature is in agreement with other observations such as: (1) the slight decrease in the cranial height with respect to its rear portion; (2) the rectilinear margin of the dentary without any deep festooning; (3) the scarce and uniform ornament of the lateral surface; and (4) the reduced number of teeth. The first enlarged alveolus of the specimen should correspond to a ninth, tenth or eleventh position. The increase in the alveolar diameter at that position is frequent in neosuchians (e.g., *Goniopholis*, *Bernissartia*, *Tadzhikosuchus*) as well as in modern crocodiles. Thick and wide interalveolar walls, as seen in the Al-Khod mandible, are more frequent in crocodyloids than in alligatoroids.

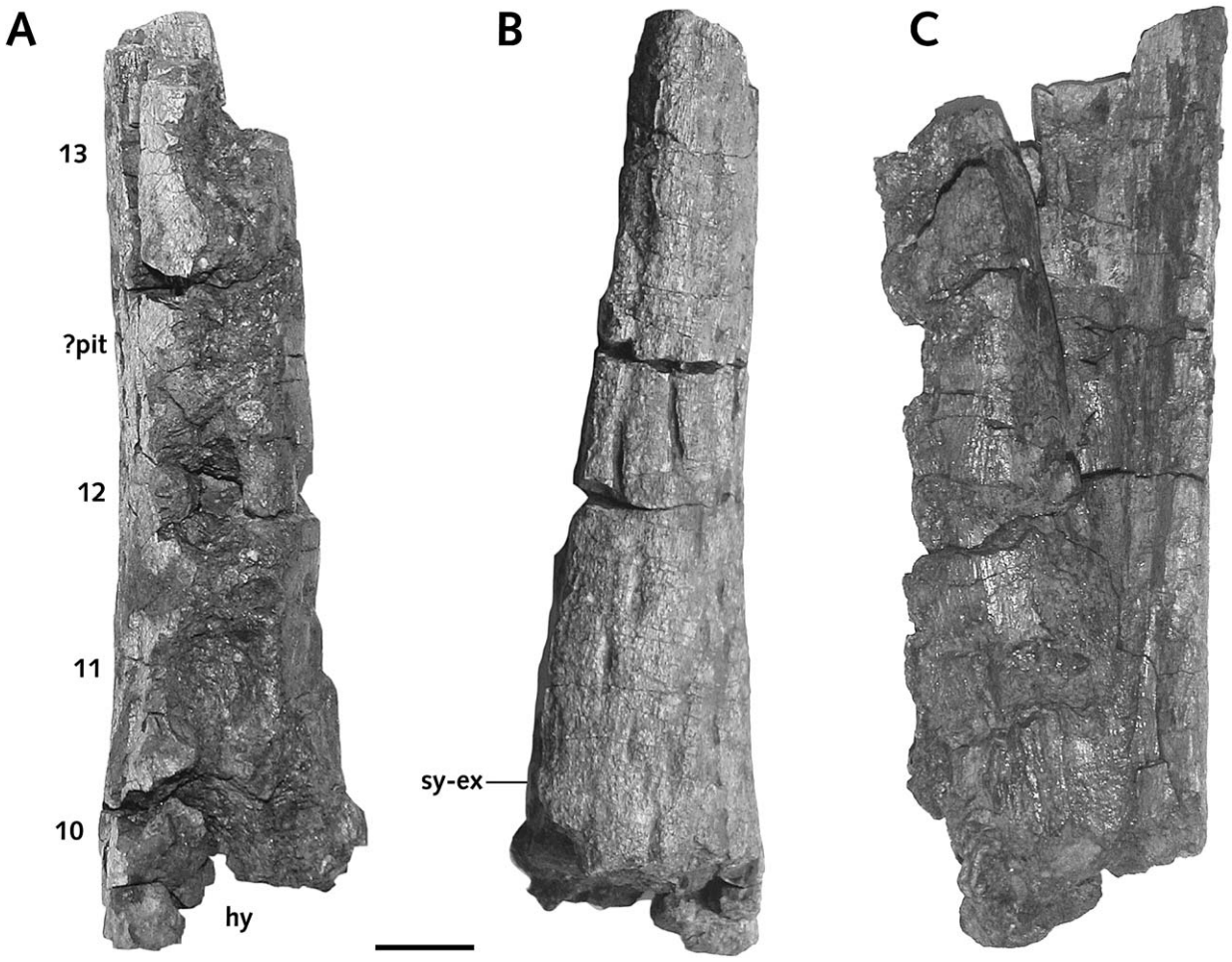

Fig. 2. Short-snouted neosuchian (SQU-2-1998-57) related to trematochampsids; Late Cretaceous Al-Khod Conglomerate of Al-Khod, Sultanate of Oman. A, dorsal view; B, ventral view; C, medial view. Abbreviations: hy, hypertrophied tooth; sy-ex, symphyseal anterior extension, tooth alveoli (tenth to thirteenth). Scale bar represents 15 mm.

Although not many features can be recognised in this specimen, we attribute it here to the Trematochampsidae based on similarities shared with *Trematochampsa oblita* from the Campanian of northwest Madagascar (Buffetaut and Taquet, 1979). That species was described on the basis of a more complete mandible than the specimen described here. The holotype is half the size of the Oman specimen; *T. oblita* is characterised by an extremely long (involving nine teeth) and wide mandibular symphysis, and by the presence of a hypertrophied tenth tooth. The Al-Khod crocodile and *T. oblita* share the presence of a hypertrophied tooth, which is twice the diameter of the successive posterior teeth. Generally, the ventral surface of the dentary in crocodiles becomes wide and low in the symphyseal area. In brevi- and mesorostral crocodiles the mandibular symphysis extends from the first tooth up to the fourth to seventh position. It is unusual in short-snouted species that the symphyseal area extends to almost the tenth position. In such a case, the ventral dentary ramus should widen at that level, as seen in the Al-Khod specimen and in *Trematochampsa oblita*, that is, in front of the tenth hypertrophied tooth. Both traits, the tenth enlarged tooth and the long and wide symphysis, may be considered as apomorphies shared by *Trematochampsa* and the Al-Khod specimen.

Unfortunately, the other African species attributed to *Trematochampsa* (*T. taqueti*) lacks the posterior part of the dentary (Buffetaut, 1976), although *T. taqueti* has a shorter mandibular symphysis. Some differences can be mentioned concerning the attribution of the Al-Khod crocodile to *Trematochampsa oblita*. The heavy ornamentation of the dentary in the latter is one of them. The Al-Khod specimen corresponds to a posterior mandibular part where the ornamentation is less pronounced. However, in the Al-Khod specimen, the sculpture pattern resembles that of *Peirosaurus* from the Upper Cretaceous of South America (Gasparini, 1982). The other difference involves the presence of an external occlusion pit for the maxillary tooth at the rear dental series as in alligatorids (Buffetaut and Taquet, 1979). Neither in *T. oblita* nor in the Al-Khod crocodile is the occlusal pit at the end of the mandible well enough preserved. The fragmentary nature of the

Trematochampsa material described so far, together with the small dental portion of the Al-Khod specimen, does not permit a more detailed comparison. Thus, we refer to the fragment described here as cf. *Trematochampsa*, keeping in mind that, although it has putative synapomorphies with *T. oblita*, the discovery of additional material of this taxon from Al-Khod could probably lead to the definition of a new genus of these robust, short-snouted African crocodiles.

Neosuchia (Benton and Clark, 1988) indet.

Mandible: SQU-2-1998-69 (NHMM2003191/UPUAM-OM2)
Fig. 3A–C

Description. The second specimen from Al-Khod described here is a mandible fragment of a longirostrine crocodile. The most significant character of this specimen is the short splenial symphysis. SQU-2-1998-69 is about 100 mm long, and contains six alveoli as well as the cranial and caudal edges of the splenial symphysis. The mandibular rami diverge caudally, being 100 mm wide at the posteriormost preserved part. Rostrally, the mandible narrows to 65 mm. The lateral wall of the dentary is rather low (maximum height 30 mm), and decreases further to 15 mm in height anteriorly. At that level, the first preserved alveolus is very low and the alveolar collar is outwardly directed. The dorsal surface of the dentary symphyseal area has a convex transverse section. The dentary surface is ornamented with pits laterally and ventrally. The ventral surface of the splenial symphysis is also sculptured. The alveolar diameters vary from 12 mm at the three anteriormost alveoli to 20 mm in the largest, and 15 mm in last two that are preserved. Alveolar size ranges from small to medium, subcircular diameters. Caudal alveoli face dorsally in the tooth row, while cranial ones turn to deflect outwards. This transition also involves the reduction in height of the alveolar margin. Alveolar collars are not elevated but separated by shallow notches; the first and second alveoli are widely spaced. The splenial symphysis extends between the second and fifth preserved alveoli.

Discussion. The crocodyliform SQU-2-1998-69 from Al-Khod is interpreted to be a member of the

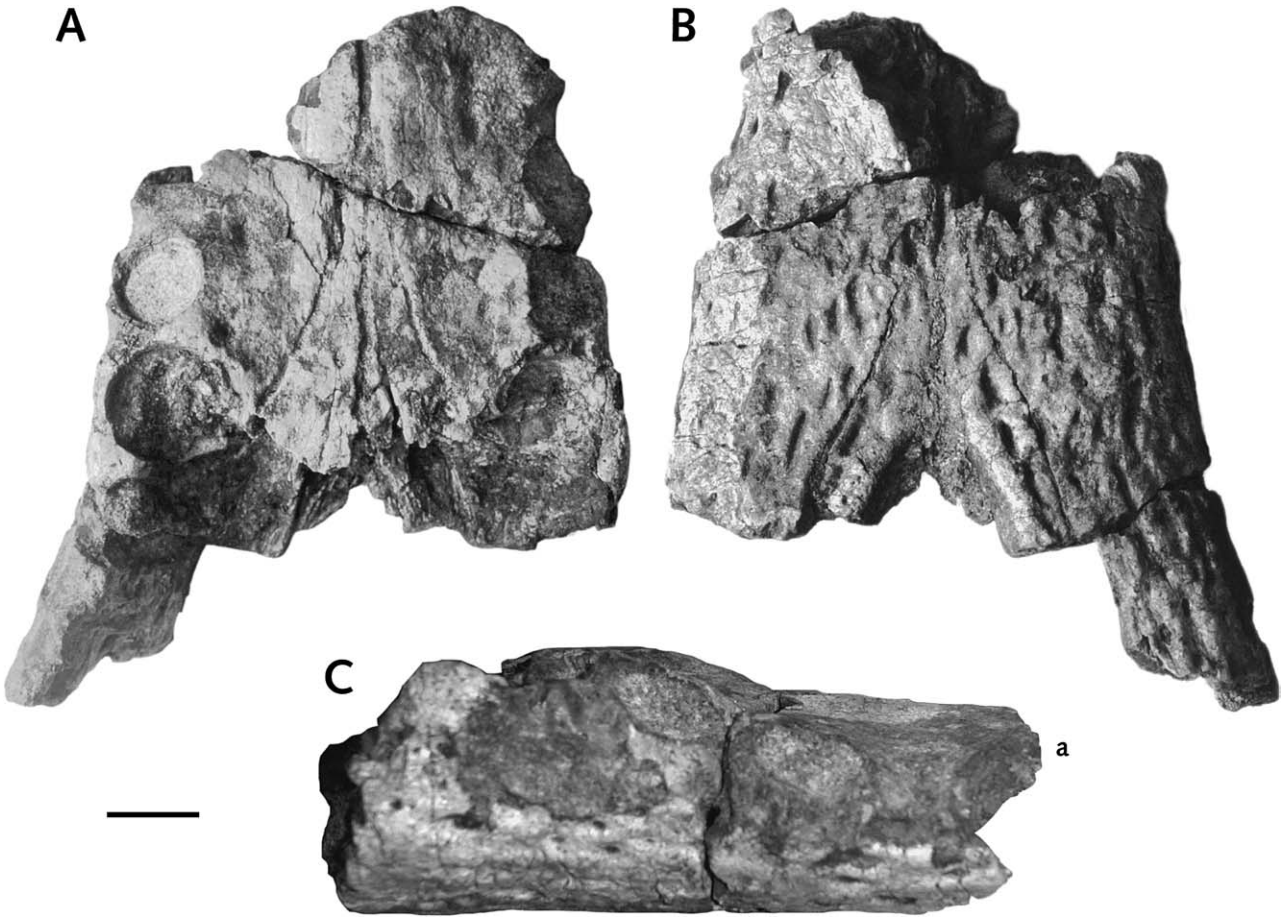

Fig. 3. Longirostrine neosuchian (SQU-2-1998-69) from the Late Cretaceous Al-Khod Conglomerate of Al-Khod, Sultanate of Oman. A, dorsal view; B, ventral view; C, lateral view. Abbreviation: a, anterior. Scale bar represents 15 mm.

neosuchian clade based on the presence of a rather long snout, and a long symphyseal area. This could either be a dyrosaurid, or pertain to other longirostrine genera of uncertain affinities such as *Elosuchus* or *Maroccosuchus*. A short splenial symphysis is not usual within longirostrine crocodiles (character 43 in Brochu, 1999, in which splenial symphysis involves more than five dentary teeth in longirostrine modern eusuchians). Splenials which profoundly participate in the symphysis have been proposed as a derived character state shared convergently by most longirostrine neosuchians: Metriorhynchidae, *Dyrosaurus*, *Gavialis*, *Hyposaurus*, *Pholidosaurus* and *Terminonaris* (Wu et al., 2001). Most of these slender-snouted dyrosaurids (*Dyrosaurus*, *Congosaurus*, *Hyposaurus* and *Rhabdognathus*) do possess long and acute splenials at the symphysis. However, a wide range of variation exists among dyrosaurids, especially regarding robust genera such as *Phosphatosaurus* and *Sokotosaurus* (Swinton, 1930, 1950; Buffetaut, 1978; Langston, 1995). Attribution of the fragment to *Phosphatosaurus* cannot be ruled out. The specimen shows externally projecting alveoli and notches between the alveolar collars, as frequently seen in dyrosaurids. Isolated teeth from the Maastrichtian of Egypt were attributed to *Phosphatosaurus* (Gemmellaro, 1921). Generally, isolated crocodilian teeth are of limited taxonomic use, although the teeth figured in Gemmellaro (1921) resemble SQU-2-5 (Fig. 4; collected separately from the same locality).

Only a few longirostrine crocodiles seem to have developed rather short splenials at the symphysis. One is the recently erected genus *Elosuchus* from the uppermost Lower Cretaceous of North Africa in which the splenial symphysis involves six dentary teeth (Lapparent de Broin, 2002). However, mandibular alveoli in *Elosuchus* seem to face dorsally all along the symphysis. The other is the Ypresian (Eocene) form discovered in the phosphates of Morocco, *Maroccosuchus zennaroi*. In this species either the symphyseal length or the splenial symphysis is short in comparison with different species of *Tomistoma* (Jonet and Wouters, 1977), and some of the teeth involved in the symphyseal area are procumbent and separated by notches as in the Al-Khod specimen.

Fig. 4. Isolated tooth (SQU-2-5) from the Late Cretaceous Al-Khod Conglomerate of Al-Khod, Sultanate of Oman. Scale bar represents 10 mm.

5. Discussion

Africa and Madagascar both had singular Gondwanan crocodilian assemblages during the Late Cretaceous. The faunal profile of Africa and Madagascar was shaped by the presence of terrestrial and aquatic mesosuchian genera (non-eusuchian crocodiles), and by the significant absence of modern crocodylians (Buscalioni et al., 2003). In Africa, Late Cretaceous crocodyliforms have been recorded from Nigeria, Egypt, Niger, Sudan, and Morocco (Table 1). These fossils can be phylogenetically placed within Ziphosuchia (i.e., *Libycosuchus* and *Hamadasuchus*) or as members of Neosuchia (*Dyrosaurus*, *Sokotosuchus* and *Trematochampsa*) (see revisions carried out by Ortega et al., 1995, 2000 concerning all of the above-mentioned taxa).

Aegyptosuchus and *Stomatosuchus*, both with a set of autapomorphic features, have complex evolutionary histories, and their phylogenetic affinities are not yet clear. The Maevarano Formation of Madagascar has yielded an extremely diverse assemblage of crocodilians: *Araripesuchus*, a long-snouted crocodilian of uncertain affinity, material referred to *Trematochampsa oblita*, a possible eusuchian, and a plethora of bizarre animals such as the pug-nosed form with mitten-shaped teeth, *Simosuchus clarki* (Buckley et al., 2000), and the large crocodile *Mahajangasuchus insignis* (Buckley et al., 1997; Krause et al., 1999). Madagascar contains elements of a Gondwanan stock; the relationships of the striking crocodile *Simosuchus* with the South American genus *Uruguaysuchus* and African *Malawisuchus* (Buckley et al., 2000) imply the dominance of an ancient Gondwanan common ancestor (South America + Madagascar). Regarding the closest allies (*Baurusuchus*, *Libycosuchus*, *Malawisuchus*, *Notosuchus*, *Sebecus*, *Uruguaysuchus*), *Simosuchus* may be a member of the clade Ziphosuchia (Ortega et al., 2000). A temporal calibration of Ziphosuchia (Fig. 5) suggests that the Gondwanan common stock should have been there since the Jurassic (Buscalioni et al., 2003). Therefore, Madagascar could also be viewed as a relict area that kept members of an ancient southern fauna yet still poorly known in Africa. Of course it should be noted that this does not rule out further dispersals from Africa to Madagascar.

Table 1
Crocodylomorph genera from the Late Cretaceous of Africa and Madagascar

Africa		
Dyrosaurus sp.	Cenomanian	North Sudan and Egypt
Sokotosuchus ianwilsoni	Maastrichtian (Sokoto)	Nigeria, Egypt, Morocco
Libycosuchus brevirostris	Cenomanian (Baharîya)	Egypt
Aegyptosuchus peyeri	Cenomanian (Baharîya)	Egypt
Trematochampsa taqueti	Cenomanian (Baharîya)	Egypt
Hamadasuchus rebouli	Cenomanian (Hamada)	Morocco
Stomatosuchus inermis	Santonian	Niger
Madagascar		
Trematochampsa oblita	Campanian (Maevarano Fm)	Madagascar
Mahajangasuchus insignis	Campanian (Maevarano Fm)	Madagascar
Simosuchus clarki	Campanian (Maevarano Fm)	Madagascar
Araripesuchus sp.	Campanian (Maevarano Fm)	Madagascar

It has been suggested that the Afro-Arabian dinosaur faunas were intrinsically endemic, different from those of Madagascar, India and South America, since these latter landmasses were still interconnected through the Kerguelen Plateau during the Late Cretaceous (Krause et al., 1999). If the taxonomic attribution of the crocodilian remains of the Al-Khod Formation in the Sultanate of Oman is correct, this hypothesis is falsified; the crocodilian assemblage shows that Madagascar and the Arabian Peninsula share the presence of *Trematochampsa* or allied species, while Madagascar and Africa share the presence of *Trematochampsa* and allied species

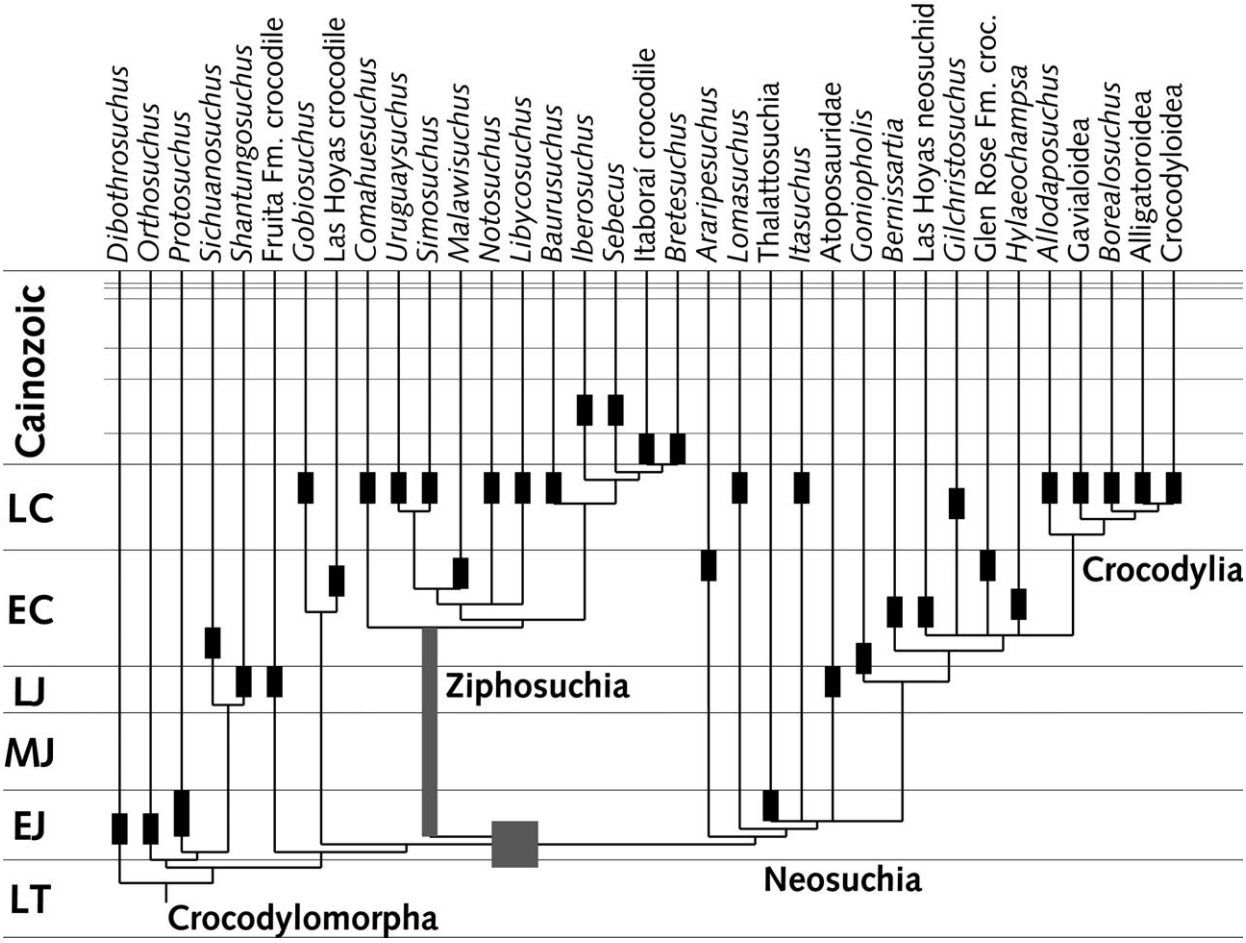

Fig. 5. Calibrated dendrogram of Crocodylomorpha based on congruent cladograms describing the interrelationships of members of the Ziphosuchia (Buckley et al., 2000; Ortega et al., 2000). Note the gap (in grey) in the fossil record of the Ziphosuchia. A ghost lineage can be predicted based on the stratigraphic range of its sister group, Neosuchia. The common ancestor of both major clades is placed in the Early Jurassic (grey square), thus the gap in the Ziphosuchia fossil record is evaluated to be around 66 million years (modified from Buscalioni et al., 2003).

of *Araripesuchus* (i.e., "*Araripesuchus*" *wegneri* from Niger).

Very few Mesozoic terrestrial or estuarine vertebrate fossils have been recorded so far from the Middle East. This is surprising, as the Arabian Peninsula offers enormous exposures of easily accessible Mesozoic rocks. Of course it should be taken into account that an important part of the Mesozoic sequences on the Arabian Peninsula consists of shelf carbonates, not the most appropriate depositional environment for the preservation of terrestrial or estuarine vertebrate fossils. Nevertheless, a number of formations on the peninsula might be expected to yield terrestrial vertebrates (Martill et al., 1996; Jacobs et al., 1999; Whybrow and Hill, 1999). The lack of fossils is explained by Jacobs et al. (1999, p. 454) "…[by] the relatively few vertebrate palaeontologists actually working [on the Arabian Peninsula, but]…there is also a possibility that some discoveries go overlooked in unpublished proprietary reports generated in the extensive exploration for oil in Arabia". For example this could be the case with the reported titanosaur bones from Saudi Arabia which are briefly mentioned in Lambert (1990), but have never been described. Account should also be taken of the fact that most palaeontological research in the region is carried out in the context of oil exploration, which mainly focuses on micropalaeontology (e.g., Elliott, 1983). Further work on the Cretaceous rocks of the Arabian Peninsula is needed to establish the degree of isolation or connection between Afro-Arabia and Madagascar.

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