

First European evidence for transcontinental dispersal of *Crocodylus* (late Neogene of southern Italy)

MASSIMO DELFINO^{1*}, MADELAINE BÖHME² and LORENZO ROOK¹

¹*Dipartimento di Scienze della Terra, Via G. La Pira 4, I-50121 Firenze, Italy*

²*Department für Geo- und Umweltwissenschaften, Richard-Wagner-Str. 10, D-80333 München, Germany*

Received March 2005; accepted for publication February 2006

It is generally assumed that the Neogene crocodylian fauna of Europe has been represented only by brevirostrine alligatoroid *Diplocynodon* and longirostrine false gharials (*Gavialosuchus* and/or *Tomistoma*), which became extinct prior to 6 Mya. Although several lines of evidence suggest that *Crocodylus* originated in Africa during the Miocene and then promptly dispersed to other continents, the occurrence of this genus in Europe has never been rigorously proven and the traditional palaeontological approach failed to identify a monophyletic group of fossil *Crocodylus* (simply leading to a proliferation of extinct taxa). The new remains reported here, from an endemic insular fauna from southern Italy, Late Messinian to earliest Pliocene in age (5–6 million years old), represent the youngest European crocodylian, and allow, for the first time in a phylogenetic context, an unambiguous demonstration that *Crocodylus* dispersed into Europe, possibly during the Tortonian. If the peculiar morphology of the medial maxillary edge is interpreted as evidence for a medial dorsal boss, the southern Italian *Crocodylus* could be related to *C. checchiai* from the late Neogene of Libya. The presence of this African immigrant in Europe confirms the role of climate change for faunal dispersal and island colonization. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, 149, 293–307.

ADDITIONAL KEYWORDS: *Crocodylus bambolii* – *Diplocynodon* – endemic faunas – late Miocene/early Pliocene – Mediterranean area – Messinian – *Microtia* fauna – *Tomistoma* – Tortonian – transmarine dispersal.

INTRODUCTION

Miocene crocodylians of Europe are currently considered to be represented by two forms only: the brevirostrine alligatoroid *Diplocynodon* (extinction around 13.5 Mya, even if doubtful remains are reported until 6.2 Mya) and the longirostrine forms (*Gavialosuchus* and/or *Tomistoma*) belonging to the tomistomine group (extinction around 10 Mya). Although the presence of *Gavialis* in Europe has been proposed on the basis of isolated teeth found in the Miocene of Portugal and France (Antunes, 1994) and family Gavialidae appears among the European Miocene herpetofauna (Rage, 1997), new tomistomine skull remains from southern Italy strongly suggest that these isolated teeth could be also referred to a slender toothed tomistomine and that gavialids should not be considered as members of the Miocene crocodylians of Europe (Delfino *et al.*, 2003).

The occurrence in the European Miocene of *Crocodylus*, as well as that of other Crocodylinae, has never been satisfactorily proven with a phylogenetic approach, and it is considered unlikely at present (Antunes, 1994; Brochu, 2000). The name *Crocodylus* (or *Crocodilus*) has been traditionally used by palaeontologists simply for the identification of crocodylians showing a ‘generalized non-alligatorid-like’ morphology, that is to say with third and fourth dentary teeth occluding not in a pit but in a notch between premaxilla and maxilla (Brochu, 1999, 2001, 2003). Therefore, even if for several decades the genus *Crocodylus* has been thought to appear in the Late Cretaceous or Palaeocene and to be a relatively common taxon in Cenozoic localities worldwide (cf. Kuhn, 1936; Steel, 1973; Carrol, 1988), the assemblage currently called ‘*Crocodylus*’ by palaeontologists may not be monophyletic (Brochu, 2000) and, in fact, all the recent revisions of European ‘*Crocodylus* remains’ allowed them to be identified as belonging to different genera and families (the claimed presence of this genus in the Pleis-

*Corresponding author. E-mail: massimo.delfino@unifi.it

tocene of Europe is not supported by the fossil record; cf. Brochu, 2001).

The origin, phylogeny and historical biogeography of *Crocodylus* have been recently discussed in detail (Brochu, 2000, 2001). Its origin should be sought in Africa but *Crocodylus* spread elsewhere very shortly thereafter. The divergence among the 12 living species has been assessed, based on protein distance data, to have occurred during the Late Miocene, between 6 and 5 Mya, while palaeontological data and sister group relationships suggest a minimum divergence age of about 19 Mya between *Crocodylus* and *Osteolaemus*. This timing is congruent with the palaeontological record of *Crocodylus* given that the oldest remains unambiguously referable to *Crocodylus* are Late Miocene in age.

The remains described here fit in the above-mentioned scenario, providing the first evidence for the occurrence of the genus *Crocodylus* in Europe and again changing the history of the crocodylian faunas of this continent.

SYSTEMATIC PALAEOLOGY

CROCODYLIA GMELIN, 1789
CROCODYLIDAE LAURENTI, 1768
CROCODYLUS LAURENTI, 1768
CROCODYLUS SP.

Locality

All crocodylian specimens were found in karstic fissure fillings exposed by quarrying activities in the Gargano pedemountain belt (41.8°N, 15.4°E, Apulia, south-eastern Italy). The name or the code of the karstic fissures are given in parentheses in the 'Referred material' section below.

Horizon

Reddish, massive or crudely stratified silty-sandy clays (Abbazzi *et al.*, 1996) yielding the so-called 'Microtia fauna', which is biochronologically dated at between 5 and 6 Myr (Upper Messinian to lowermost Pliocene; Abbazzi *et al.*, 1996; Rook, Abbazzi & Engesser, 1999).

Referred material

The material described here belongs to the following institutions: Naturalis, Nationaal Natuurhistorisch Museum (Leiden, The Netherlands; RGM), Dipartimento di Scienze della Terra dell'Università degli Studi di Firenze (Italy; DSTF), and Universitätsinstitut und Staatssammlung für Paläontologie und historische Geologie, München (Germany; BSP). It consists of: 2 premaxillae [RGM-455201 (San Giovan-

nino 1973); DSTF GH1 (F9)]; 1 maxilla (BSP 2004 I 1); 1 frontal + prefrontal [RGM 455203 (San Giovannino 1973)]; 1 jugal [RGM 455202 (San Giovannino 1973)]; 1 skull fragment [RGM 455200 (San Giovannino 1973)]; 1 lower jaw [RGM 335893 (San Giovannino 1973)]; 6 isolated teeth [RGM 453783 (Fina D), RGM 454280 (Pizzicoli 2), RGM 454950-1 (San Giovannino 1969), RGM 455205-6 (San Giovannino 1973)]; 2 coracoids [RGM 455204 (San Giovannino 1973), RGM 455327 (Pepo N)]; 1 scapula [RGM 455328 (Pepo N)]; 1 humerus [RGM 455329 (Pepo N)]; 1 ulna [RGM 455336 (Pepo N)]; 1 phalanx [RGM 455337 (Pepo N)]; 6 vertebrae [RGM 215348 (San Giovannino 1971); RGM 453472 (Gervasio 1975), RGM 455330-2 (Pepo N); DSTF GH2 (F40)]; 3 ribs [RGM 455333-5 (Pepo N)]; 19 osteoderms [RGM 335894-5 (Pepo N), RGM 451432-3 (Chiro 12 Penalba), RGM 453781-2 (Fina D), RGM 454946-9 (San Giovannino 1969), RGM 455320-6 (Pepo N); DSTF GH3-4 (F9)].

Preservation

The fossil materials come from karst fissure fillings and they are therefore represented by completely isolated skeletal remains the surface of which is usually perfectly clean and readable, only rarely being covered by thin concretionary layer. Although sometimes fragmentary, the remains are well preserved in three dimensions, and do not show any signs of deformation.

Description

Premaxilla (Fig. 1): The best preserved premaxilla (DSTF GH1) is a nearly complete left element 53 mm

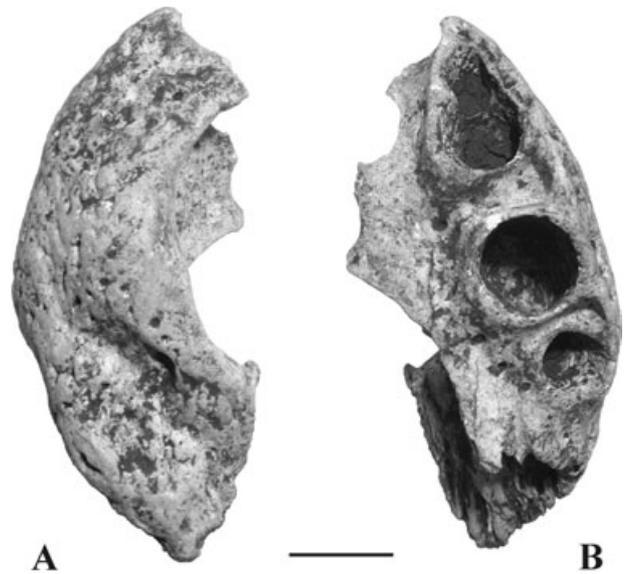


Figure 1. Left premaxilla (DSTF GH1) in dorsal and ventral views. Scale bar equals 10 mm.

long. It lacks the antero-medial region and shows the last four alveoli (the first two that are preserved are confluent). No teeth are preserved. The third preserved alveolus is the largest and is separated from the contiguous alveoli by deep mesial occlusal pits. A lateral notch at the level of the suture with the maxilla is present. Nasals contacted the premaxillae but it is not possible to establish if they bisected the naris. The postero-lateral margin of the naris is raised above the premaxilla surface and delimited by a shallow but evident 'groove'; this condition is, however, different from that shown by *Diplocynodon* (presence of a deep notch).

A second premaxilla (again a left element; RGM 455201) is smaller and rather damaged (length of the fragment: 36 mm). It partly preserves the dorsal rim of the external naris. In lateral view, the premaxilla is ventrally festooned. The last four alveoli are preserved; they do not retain teeth. As in the previous case, the third preserved alveolus is the largest, and the first two seem to be confluent (but the interalveolar space is not completely preserved here); deep occlusion pits are mesially (but close to the lateral edge) developed in the (preserved) second and third interalveolar spaces.

Maxilla (Fig. 2): The total length of the maxilla fragment (BSP 2004 I 1; Fig. 2A, B) is 37.5 mm. Teeth are not preserved. The alveoli, five in number (the last one is not complete), show an increasing size in backward direction. The dorsal, lateral and ventral surfaces of the fragment are intact; the palatal lamina is broken off nearly at its base. Each interalveolar space shows a lateral depression but the third and fourth show a true pit. The latero-ventral margin of the maxilla is not festooned. The medial edge of the maxilla, corresponding to the suture with the nasal, is elevated in a marked sagittal 'ridge', corresponding to the last preserved alveoli, medially delimited by a deep para-sagittal groove (see arrow in Fig. 2B). In the caviconchal recess, close to the palatal lamina, three depressions are visible between the first interalveolar space and the third alveolus. At the level of the fifth alveolus, fragments of the anterior and ventral wall of a blind pocket (cecal recess) are clearly preserved (Fig. 2C).

Frontal + prefrontals (Fig. 3A): The material catalogued as RGM 455203 is represented by the anterior frontal process still attached with the prefrontals, of which that on the right is nearly completely preserved and that on the left shows only a proximal fragment. The long frontal process dorsally shows a wide suture area for a firm link with nasals (not preserved). Lateral edges of the frontal and posterior edges of prefrontal are distinctly raised and rounded and constitute the medial rims of the orbits. The dorsal surface of all these elements is irregularly ornate with

roundish pits; no crest is present on the frontal surface between the orbits. The minimum interorbital distance is 21 mm. The total length of the fragment is 60 mm.

Jugal (Fig. 3B): Left jugal RGM 455202 completely lacks the region anterior to the postorbital bar; the last one is broken off nearly at the base. The posterior region medially shows an extensive area for the suture with the quadratojugal while the 'root' of the postorbital bar is characterized by an evident suture area for the junction with the ascending process of the ectopterygoid. The postero-dorsal margin of the jugal constitutes the lateral rim of the left infratemporal fenestra. On the medial surface of the element, the medial jugal foramen is rather large. The lateral jugal surface is sculpted by deep variably sized and shaped pits. Its total length is 55 mm.

Skull fragment (Fig. 4): RGM 455200 represents the postero-left region of the skull and preserves quadrate, exoccipital, squamosal and a posterior fragment of the postorbital. The dorsal surface of the squamosal and postorbital is approximately flat and ornate with several pits; the lateral edge to these elements represents the lateral edge of the skull table and does not seem to be convex; their medial edge, devoid of any particular ridge, represents the lateral rim of the left supratemporal fenestra (which does not seem to have markedly overhanging rims; the squamosal overhangs only slightly at the posterior rim of the fenestra). Although the area is not perfectly preserved, it seems that the dorsal and ventral rims of the squamosal groove for the external ear valve musculature are approximately parallel. The squamosal prongs are rather elongated.

The quadrate is relatively well preserved; its lateral edge is free and is represented by the suture surface with the missing quadratojugal; it clearly shows (Fig. 4B) a foramen aerum placed close to the medio-dorsal angle. Even if this region has been partly damaged and is still partly covered by concretionary material, SEM analysis (Fig. 4C) revealed the presence of a true foramen. Taking into consideration that its medio-dorsal surface has been abraded, the medial hemicondyle is considered to be tall (characters 112 and 113). It is not as tall as in modern comparative material of *Crocodylus* but not as small as in the *Diplocynodon ratelii* specimen used for comparison (Naturhistorisches Museum Basel, Switzerland; NHMB-MA 2275; and all the specimens from Saint Gérard-le-Puy stored in the collections of Museum national d'Histoire naturelle, Paris).

The exoccipital is fairly complete: only a small area of its lateral expansion dorsally delimiting the wide cranio-quadrate passage is missing; the medial edge shows a sector, free of suture surfaces or possible

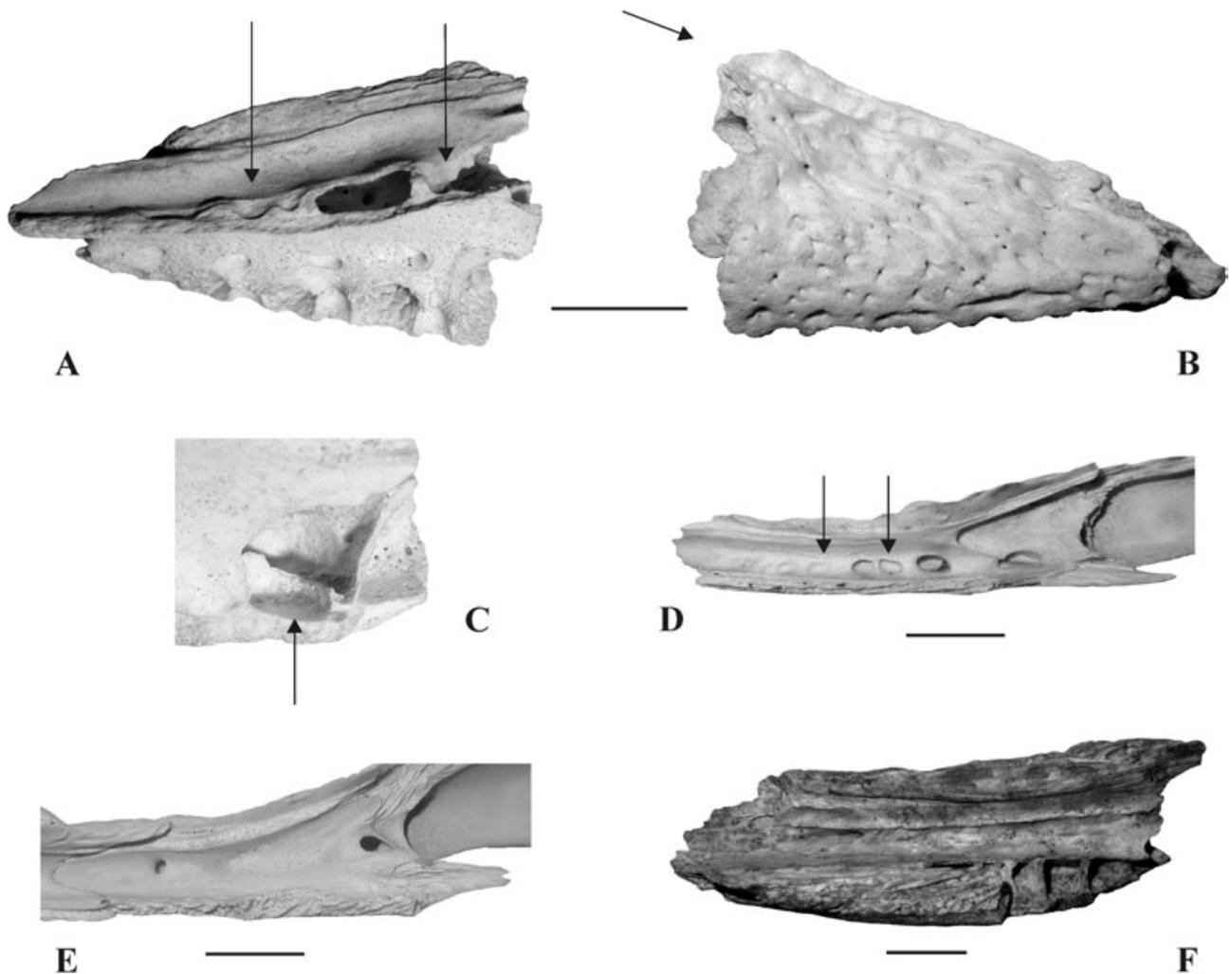


Figure 2. Blind pockets, or cecal recesses, are a synapomorphy of *Crocodylus* and absent in the only other brevirostrine crocodylian known in the European Miocene, the extinct alligatoroid genus *Diplocynodon*, and in the living African crocodylid genus *Osteolaemus*. A, B, right maxilla of *Crocodylus* sp. from Monte Gargano (BSP 2004 I 1) respectively in medial and latero-dorsal views; the arrows in A show anterior depressions and area of cecal recesses; the arrow in B shows the para-sagittal groove (see text). C, detail of a blind pocket; the arrows indicate a pocket whose lateral wall is only partly preserved. D, right maxilla in medial view of *Crocodylus niloticus*, juvenile, NMW 533; the arrows show anterior depressions and area of cecal recesses. E, right maxilla in medial view of *Osteolaemus tetraspis*, BSP 1982 X 5635. F, right maxilla in medial view of *Diplocynodon styriacus* from the Early Miocene (MN 5; BSP 1953 II 13) of Appertshofen, Germany. Teeth have been eliminated in D and F for ease of comparison. In order better to show the presence of the shallow depressions, the maxilla in A is figured in medial–ventral view; note that the palatal lamina is broken off at its base. The polygonal cavities visible on the right side of the *D. styriacus* maxilla in D are due to local breakage of the palatal lamina and are not cecal recesses. Scale bar equals 10 mm.

breakages, corresponding to the left rim of the foramen magnum; four foramina open ventro-laterally to the foramen magnum: the most evident is the foramen vagi, then, ventral to this, opens the posterior carotid foramen; two other small foramina filled with matrix are placed medially to the foramen vagi and could represent the foramina for the twelfth cranial nerve (but the smallest of them is possibly a bifurcation of the foramen vagi).

The dorso-medial margin of the exoccipital shows the suture with supraoccipital. The area corresponding to the cranio-quadrates passage is highly incomplete.

The length of the fragment is 73 mm, its maximum width is 45 mm; condyle width is nearly 23 mm.

Lower jaw (Fig. 5A, B): The fragmentary lower jaw (RGM 335893) is represented by incomplete dentaries

sutured at the level of the symphysis. The right dentary is 128 mm long and preserves 12 alveoli (plus a part of the thirteenth), while the left one is only 89.4 mm long and shows eight alveoli (plus part of the ninth). Altogether, only four teeth are preserved (for a description see 'Dentition' below): the tooth corresponding to the third right alveolus is completely out of the alveolus and it is probably fixed by the matrix on the dorsal surface of the dentary (Fig. 5B). In dorsal view, the symphysis nearly reaches the anterior border of the fifth alveolus. Several alveoli show margins distinctly 'protruded' outward (particularly developed

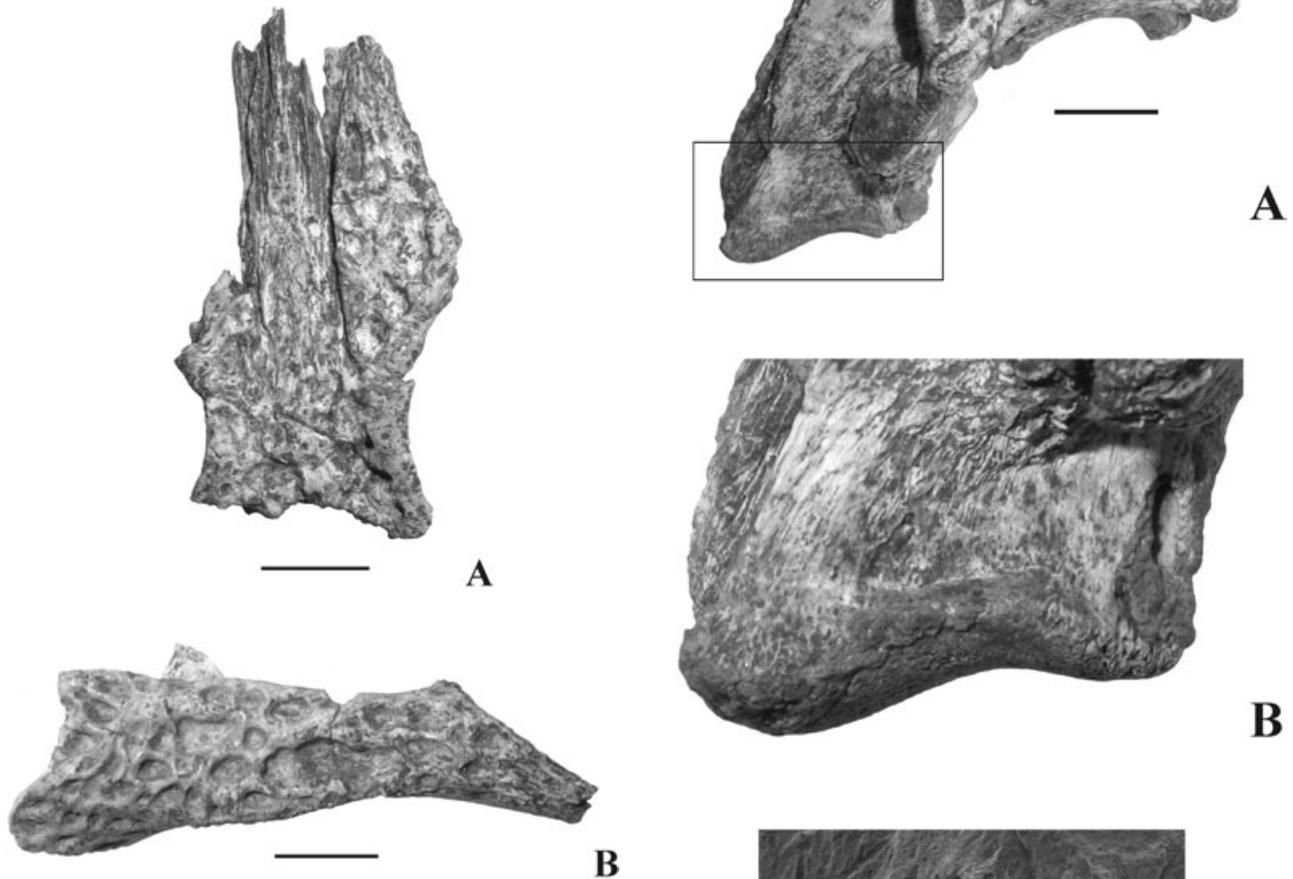
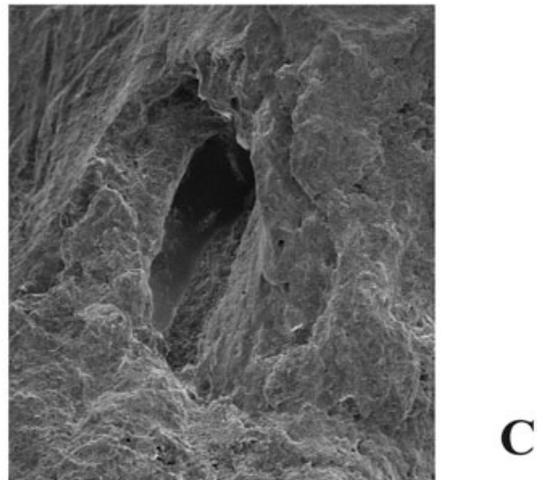


Figure 3. A, frontal and prefrontal (RGM 455203) in dorsal view; the lateral concavities represent the rims of the orbits. B, left jugal (RGM 455202) in lateral view. Scale bar equals 10 mm.

Figure 4. The quadrate reveals a foramen aerum distinctly at medio-dorsal angle. A, dorsal view of the left postero-lateral skull fragment preserving quadrate, exoccipital, squamosal and postorbital (RGM 455200). B, detail of the quadrate showing the position of the foramen aerum; SEM image of the foramen aerum opening on the quadrate. Scale bar equals 10 mm.



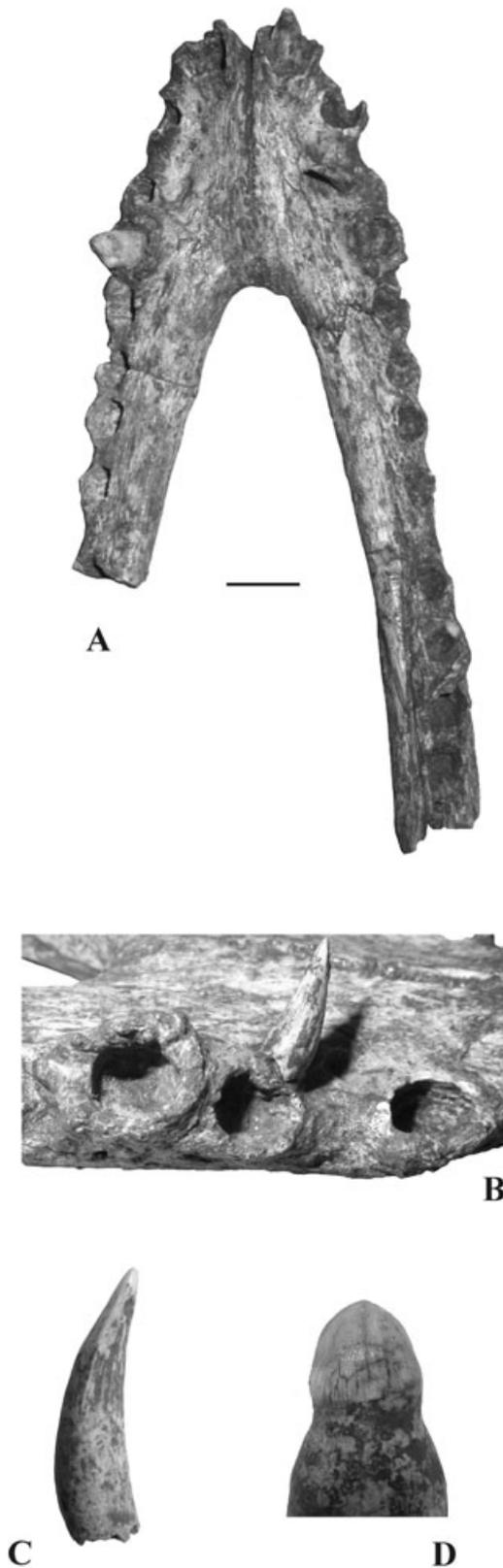


Figure 5. A, B, the lower jaw (RGM 335893) shows no sign of third and fourth confluent alveoli. A, dorsal view; B, detail of the third and fourth alveoli, on the left of the image; C, isolated tooth (RGM 454950) in mesial view; D, isolated tooth (RGM 454280) in labial view. Scale bar equals 10 mm.

in alveoli 1, 2 and 4) that confer to the dentaries a slightly festooned appearance in dorsal and lateral views. In lateral view, the dentary shows an anterior dorsal convexity centred on the fourth alveolus and a posterior one centred on the tenth interalveolar space.

The measurements of the medio-lateral diameter, mesio-distal diameter and interalveolar length are reported below (mm) for each alveolus of the right dentary (owing to the morphology and preservation of the material, all measurements are somewhat imprecise but ‘*’ indicates a genuine approximation): 6.8, 6.7, 5.5; 6.6, 6.3, 6.8; 4.7, 6.2, 2.9; 6.6, 6.5, 4.4*; 4.2, 5.9*, 5.1; 5.4, 5.3, 2.9; 5.1, 5.5, 4.5; 4.6, 5.6, 9.3; 4.9, 5.7, 3.1*; 5.7, 6.6*, 3.9; 5.4, 6.3*, 2.4; 5.0, 7.6*, 2.9; and for the left dentary: 7.4, 7.0, 6.5; 4.7, 5.7, 6.7; 5.2, 5.5, 3.0; 6.7, 6.3, 3.5*; 4.6, 5.8, 4.2; 5.1, 5.2, 2.7; 5.2, 6.0, 4.9; 4.8, 5.9, 9.1.

The third and fourth alveoli are not confluent and the fourth is slightly larger than the previous one (Fig. 5B).

On the dorsal surface of the dentaries, no occlusal pits are visible but several small depressions, filled by matrix and probably hosting a foramen at the bottom, are aligned medially to the tooth row in the anterior region and fuse together forming a groove in the posterior one.

The imprint of the splenials allows us to exclude their participation in the symphysis; their anterior tip passes ventrally to the Meckelian groove (which nearly reaches the symphysis).

The external surface of the dentaries is not particularly ornate: the pits become more frequent toward the ventral surface where they are grouped into longitudinal grooves.

Dentition (Fig. 5C, D): Ten teeth are preserved: four associated with the lower jaw and six isolated. They show a crown usually furnished by two non-denticulated mesio-distal keels corresponding to the maximal diameter and usually separating the crown surface into a labial surface that is more developed than the lingual one. The crown surface is sometimes ornate by secondary small but evident ridges longitudinally developed that do not reach the crown base (as in RGM 454950) or by an unordered but homogeneous pattern of microreliefs (as in RGM 454280). Crowns are variably shaped (from acutely conical to nearly blunt) and sized (from 12.7 to 7.2 mm). Slender and

pointed teeth such as RGM 454950 are probably anterior teeth whereas more massive teeth such as RGM 454280 probably represent the maxillary or dentary posterior region. Few teeth still preserve the root.

The dentition pattern can be defined as not homodont given that the teeth variably sized and shaped. Nothing can be said regarding the maxillary dentition but the dentary shows that the largest alveolus is the first, followed by the fourth; there is no sign of confluent third and fourth alveoli but, even if the fourth is larger than the third, they are of rather similar size. The eighth interalveolar space is by far the largest in both dentaries. Based on the presence of a notch at the boundary between premaxilla and maxilla, it seems likely that the fourth dentary tooth was occluded in a lateral notch. Nothing can be directly said about the occlusal pattern as there are no occlusal pits on the dentary.

Scapula (Fig. 6A): The right scapula (RGM 455328) lacks part of its dorsal blade but clearly preserves the proximal sector. The inferior area of its anterior edge is elevated into a high and thin deltoid crest separated from the glenoid area by a wide and deep lateral con-

cavity. The scapulocoracoid facet anterior to the glenoid fossa markedly tapers anteriorly.

Coracoids (Fig. 6C): Neither of the coracoids shows any sign of fusion with the scapula. The best preserved specimen is a right element (RGM 455327), 57 mm long, but lacking the postero-ventral tip. RGM 455204 is the result of restoration of several fragments: it is a right element that is slightly damaged, mainly in its dorsal sector where the coracoid foramen is not entirely surrounded by bone; it is similar in size to that of the previously described coracoid.

Humerus: The only preserved humerus (RGM 455329) is a fragment of a right element, 78 mm long, which lacks the proximal epiphysis; only the distal part of a relatively robust deltopectoral crest is therefore preserved.

Ulna: The fragmentary right ulna (RGM 455336) is 54 mm long and lacks its distal epiphysis. The proximal epiphysis shows a rounded olecranon process. It seems likely that this ulna, the right coracoid RGM 455327, the right scapula RGM 455328 and the right humerus RGM 455329 could have belonged to a single specimen as they come from the same locality (Pepo N) and show matching size and preservation.

Phalanx: The only available phalanx (RGM 455337) is perfectly preserved, 10 mm long, and is rather stout in general appearance.

Vertebrae (Fig. 7): All the vertebrae identified show a procoelous centrum. Two vertebrae are represented by their centra only as they were separated from their neural arch along the neurocentral suture: centrum RGM 453472 (total length 16 mm; Fig. 7A) represents a cervical vertebra as it shows evident parapophyses laterally to the condyle and a robust and long hypapophysis that is ventrally (and slightly anteriorly) directed; centrum RGM 455330 is larger (total length approximately 23 mm) and is probably one of the first dorsal vertebrae given that it shows no trace of parapophyses but a suggestion of hypapophysis; a left prezygapophysis and transverse process RGM 455331 probably belong to the centrum previously described.

DSTF GH2 (Fig. 7B) probably represents one of the last dorsal or a lumbar vertebra: its centrum is 23.2 mm long, strongly convex ventrally and it is sutured with the neural arch, which preserves prezygapophyses and postzygapophyses (the distance between the anterior edge of prezygapophyses and the posterior one of postzygapophyses is 26.1 mm) but only a proximal fragment of transverse processes and neural spine.

The caudal vertebra RGM 215348 (Fig. 7C) has a centrum 23 mm long, cotyle and condyle are weakly

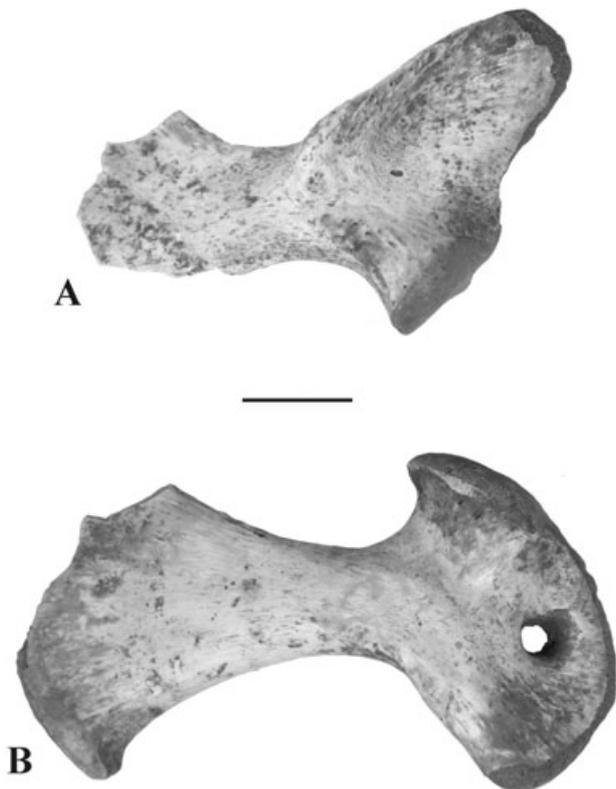


Figure 6. Pectoral girdle elements probably belonging to the same specimen: A, right scapula (RGM 455328); B, right coracoid (RGM 455327). Both in lateral view; scale bar equals 10 mm.

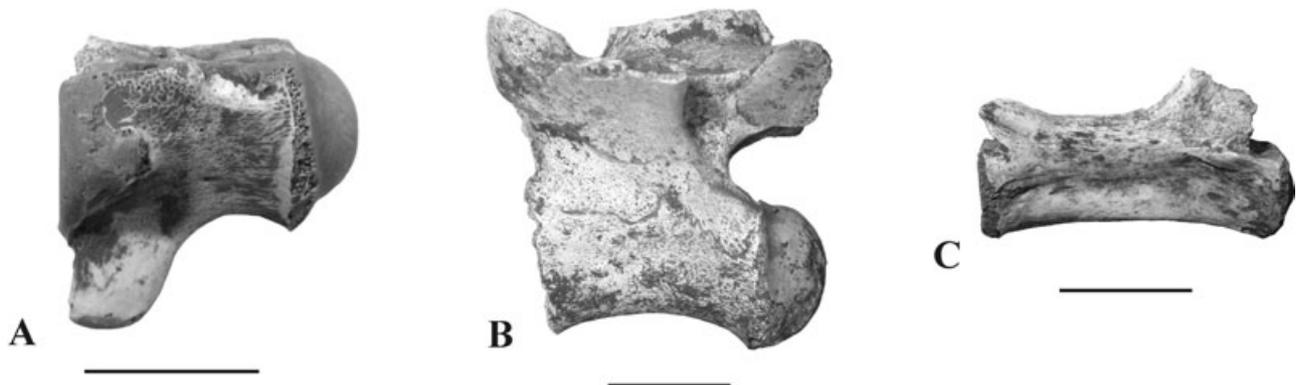


Figure 7. Vertebrae in right lateral view. A, centrum of cervical vertebra (RGM 453472) separated from the missing neural arch at the level of the open neurocentral suture and showing a long hypapophysis; B, dorsal or lumbar vertebra (DSTF GH2); C, caudal vertebra (RGM 215348). Scale bar equals 10 mm.

developed, the neurocentral suture is closed, transverse processes are absent while neural spine and postzygapophyses are broken off.

Vertebra RGM 455332 is still embedded in its matrix: it seems to be fractured and is probably not complete.

Ribs: Three ribs are preserved. Two come from the cervical region as they comprise a longitudinal shaft and two processes joining the shaft almost perpendicularly; RGM 455335 is a right rib and is the best preserved: the shaft is 21 mm long (but it is not complete) and the capitular articular surface (lower) is larger than the tubercular one (upper); it may be one of the first cervical ribs. RGM 455334 is similar in general shape, but the shaft is more elongate and entirely preserved (28 mm), and the capitulum is broken off at its base; it is a left cervical rib. RGM 455333 is fragmentary and preserves only a long capitulum and part of the shaft; it comes from a posterior area on the right side and could be the last cervical rib or one of the first dorsal ribs. These three ribs come from the same fissure (Pepo N) and could have belonged to the same individual.

Osteoderms (Fig. 8): These elements represent nearly half of the crocodylian fossil remains from the Gargano area. Their shape varies from rectangular to oval and their length from 31.8 to 14.7 mm. They are invariably characterized by a nearly flat ventral surface and a longitudinal (or nearly longitudinal) keel that in some cases is so developed that the element is triangular in cross-section (suggesting that it could be a lateral osteoderm – not caudal given the large size; RGM 454949; Fig. 8C). The rectangular osteoderms have a small anterior smooth surface; most of the osteoderms have smooth edges although some (those that are triangular in cross-section) have spiny edges. The external surface is ornate with deep roundish pits that are relatively large.

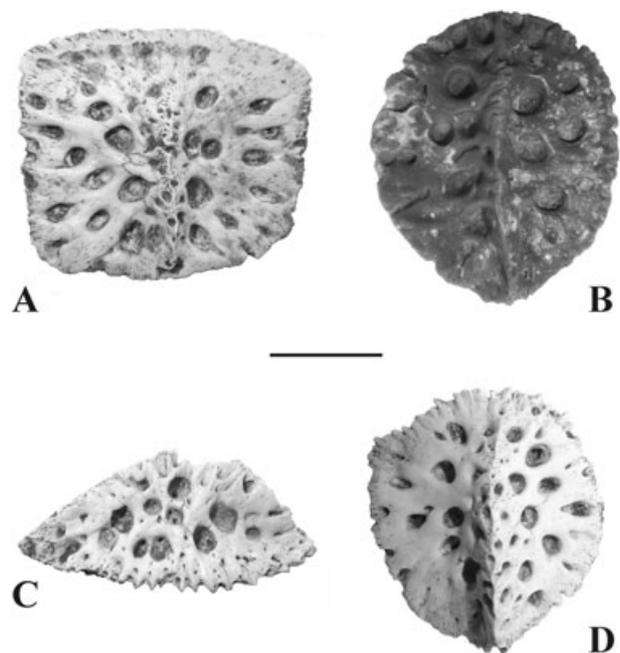


Figure 8. Osteoderms in dorsal (A, B, D) and lateral (C) views. A, RGM 454946; B, RGM 453781; C, RGM 454947; D, RGM 454948. Scale bar equals 10 mm.

On the ventral surface it is occasionally (as in RGM 453781) possible to perceive the criss-crossed pattern. There is no evidence of paired and keel-less ventral osteoderms.

Fragments RGM 451432–33 have been considered as osteoderms because of the pits that ornate the external surface but they could also represent skull fragments.

RESULTS AND PHYLOGENETIC ANALYSIS

The morphological characteristics of the Gargano crocodylian fragmentary remains can be synthesized

according to the character coding published by Brochu (1999) as follows:

???? ???? ???? ?1?? ?001 ?1?1? ???? ???? ?1?? ???? ?11??
 ???? ???? ?0?1 ???? ?0?1? ???? ?0?1? ???? ???? ?1?? ????
 ?3?? ???? 0???? ?1?? ???? ?0?1 10?? 0?1?0 ?1?? ???? 0???

Following the data matrix available in Brochu (1999) and in Gatesy, Baker & Hayashi (2004), the Gargano crocodylian does not share with *Diplocynodon* any character state that is not shared by *Crocodylus* also. The following characters states are shared with *Crocodylus* and not with *Diplocynodon*: (52-1), (77-0), (89-1), (112-3), (121-0), (128-1), (148-1). The Gargano crocodylian is therefore a brevirostrine form that does not shown any unambiguous diplocynodontine relationship. Moreover, analysis of the quadratum allows us to exclude the presence of the character that diagnoses the group of the Alligatoroidea: the foramen aerum is not located on the dorsal surface of the quadratum but close to its medio-dorsal angle as in non-alligatoroid taxa (character 121-1).

It is worth mentioning that the oval osteoderm RGM 453781 here considered as coming from the nuchal region is quite different from the nuchal osteoderms of *Diplocynodon ratelii* from Saint Gérand-le-Puy stored in the Museum national d'Histoire naturelle Paris (MNHN SG13728, i.e. they form a right angle in cross-section), while the anterior flat area of a rectangular osteoderm such as RGM 454946 is not as flat and developed as in those of the quoted *D. ratelii* specimen.

The maxilla fragment clearly shows some depressions and the remnants of a true cecal recess on the medial surface of the caviconchal recess. Such depressions lie anteriorly to the cecal recess (and can be probably considered as underdeveloped pockets) in the comparison specimen of *C. niloticus* (Naturhistorischen Museum Wien, NMW 533; Fig. 2D). According to Brochu (2000), the presence of these structures is one of the four unambiguous synapomorphies of the genus *Crocodylus* (character 148-1). As shown in Fig. 2, blind pockets are not present in the living crocodylid genus *Osteolaemus* (Fig. 2E) and in the extinct alligatoroid genus *Diplocynodon* (Fig. 2D).

A parsimony analysis of the Gargano crocodylian coding performed with PAUP 4.0b10 (Swofford, 1999) and including the taxa available in Brochu (1999) and Gatesy *et al.* (2004) confirms its allocation within the genus *Crocodylus* but causes the collapse of terminal taxa and fails to recognize any specific relationship positively matching with the available phylogenetic scheme of this genus (cf. Brochu, 2000).

However, the shape of the scapulocoracoid facet anterior to the glenoid fossa (character 25-1) weakly distinguishes this form from some of the Indopacific taxa (the clade comprising *C. johnstoni*, *C. mindorensis*, *C. novaeguineae* and *C. porosus*).

A relevant character that could offer a diagnostic element is the peculiar elevation of the medial edge of the maxilla along the maxilla–nasal suture, laterally delimited by a deep groove (Fig. 2B); such a morphology could suggest the development of a medial dorsal boss (character 101-1) that is characteristic of the living New World *Crocodylus* (Brochu, 2000) but that has been reported also for the late Neogene (Miocene–Pliocene transition?) *C. checchiai* Maccagno, 1948 from Sahabi, Libya (cf. Hecht, 1987).

As the median boss is present throughout post-hatching ontogeny in the New World *Crocodylus* (hatchling *C. acutus* already show this character; see Brochu, 2000) it should be already developed in the juvenile maxilla from Gargano.

If character 101 is scored as 1 (presence of a median boss), the Gargano *Crocodylus* clusters with the New World assemblage after a parsimony analysis. The character coding of *C. checchiai* is not available at present (but should be soon; P. Piras, work in progress), and therefore its phylogenetic relationships are unknown. Hecht (1987), discussing the presence of a dorsal median boss (= preorbital promontorium) in *C. checchiai*, considered it a synapomorphy for the New World assemblage, although a convergence could not be ruled out.

Given that the origin of *Crocodylus* seems to go back to the African Miocene, the oldest New World *Crocodylus* is Pliocene in age (Brochu, 2000, and references therein), and 'a single dispersal event from the Old World to the Americas is required' (Brochu, 2001: 22), it is tempting to consider *C. checchiai* (and possibly the Gargano *Crocodylus*) as close to the basal stock of the American clade; however, the early stages of the *Crocodylus* evolutionary history are so poorly known and the fossil remains and taxa available for study or review are so abundant that a definitive conclusion is largely premature.

As regards the specific allocation of the Gargano *Crocodylus*, the presence of a dorsal median boss could suggest relationships with *C. checchiai*, although the latter, being a continental form, is of 'normal' size. Taking into consideration the scarcity of characters codable on the material from the Gargano late Neogene, as well as the present unavailability of the codings of the contemporary crocodylian remains and '*Crocodylus*' species from the Mediterranean Basin, the fossil remains described here are simply referred to *Crocodylus* sp.

DISCUSSION

CLIMATE, ENVIRONMENT, BIOPROVINCES AND DISPERSALS

Living crocodylians show a geographical range limited to tropical and subtropical areas but one alligatoroid

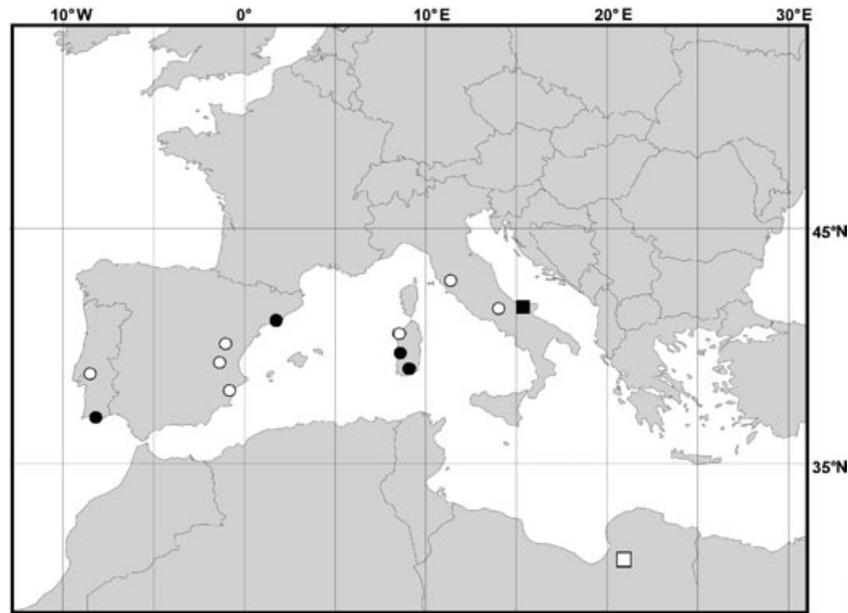


Figure 9. Late Miocene crocodylian localities in the Mediterranean area. Black dots, early Tortonian localities with tomistomine fossils; open circles, Tortonian and Messinian localities with crocodylians of unresolved phylogenetic relationships; black square, Gargano fossil locality with *Crocodylus* sp. (Miocene–Pliocene transition); open square, Sahabi fossil locality with *Crocodylus checchiai* (Late Neogene – Miocene–Pliocene transition?). Data from Böhme & Ilg (2003).

genus, *Alligator*, reaches temperate regions of the United States and China, up to 15° further north than crocodylians, and can tolerate relatively cool winters (Sill, 1968; Pough *et al.*, 2001). Fossil evidence suggests that during the Cenozoic the crocodylian range was considerably larger than at present. In the early Middle Miocene (17–14 Mya) crocodylians were widespread in western Eurasia and are now known from about 150 localities (Böhme & Ilg, 2003). The drop in temperature and changing atmospheric circulation between 14 and 13 Myr (Böhme, 2004) shifted their range south of the Alpine orogene (Böhme, 2003). During the early Late Miocene (early Tortonian) tomistomines were widely distributed in Atlantic and Mediterranean coastal marine environments (Tchernov, 1986; Antunes, 1987; Rossmann, Berg & Salisbury, 1996), whereas inland crocodylians (questionable remains of alligatoroids, cf. Antunes, 1994) were restricted to small populations in freshwater habitats of Portugal and the eastern Iberian Peninsula (Fig. 9). During the late Tortonian and Messinian crocodylians of unresolved affinities are distributed in the eastern Iberian Peninsula and in Sardinia and Italy (see below; Fig. 9).

The distribution of all crocodylians is directly linked to water as it is essential as a buffering medium against temperature extremes (Markwick, 1998). If freshwater bodies periodically dry out, long-term survival of alligatorid populations are compromised because, lacking salt-excreting glands and renal-

cloacal adaptations (cf. Brochu, 2001), they are unable to live for a prolonged period of time in brackish environments (such as estuaries or nearshore habitats), unlike *Crocodylus* and tomistomines. Therefore, increased seasonality leading to periodic absence of freshwater would theoretically affect alligatoroids more than crocodylids.

According to Brochu (2001: 18), it is not known if *Diplocynodon* was salt-tolerant or not, since it is not a member of the crown-group Alligatoridae and therefore 'seawater may not have been a significant barrier as for *Alligator*'. Regardless, the absence of modern alligatorids as well as of fossil *Diplocynodon*, or other fossil alligatoroids, from Africa seems to suggest some sort of hindrance to their dispersal. The only published 'evidence' of an alligatorid from Africa is based on very poor material from the Late Eocene of Egypt and requires confirmation (Rossmann, Müller & Forst, 2000) or is evidently based on uninformative material (D'Erasmus, 1933, 1934; see also Buffetaut, 1985; Buscalioni, Sanz & Casanovas, 1992).

Palaeoclimate studies have shown three Miocene intervals with increased North African precipitation linked to the intensification of the African monsoon: between 16.7 and 15.55 Mya (late Burdigalian to early Langhian; John, 2003; John *et al.*, 2003), between 13.8 and 12 Mya (Serravallian; John *et al.*, 2003; John, 2003) and between 7.0 and 4.6 Mya (Messinian and early Pliocene; Tiedemann, Sarnthein & Stein, 1989; Griffin, 1999, 2002). These intervals provide a rela-

tively rich crocodylian record in North Africa and Arabia (Tchernov, 1986; Hecht, 1987; Geraads, 1989; Rauhe *et al.*, 1999; Pickford, 2000; Linas-Agrasar, 2003). By contrast, the Tortonian (11.6–7.2 Mya) is characterized by an increased aridity in North Africa and Arabia (Griffin, 1999) with prevailing desert influence (Goldsmith *et al.*, 1988; Suc *et al.*, 1999) and, based on a lack of evidence so far, by the absence of crocodylians from both areas, while in the central Mediterranean Europe, a wet and subtropical climate prevailed at the same time (Andrews *et al.*, 1996; Suc *et al.*, 1999).

We argue that colonization of Mediterranean islands by *Crocodylus* during the Tortonian was triggered by increased aridity at mid-latitudes, possibly leading to an increased north–south precipitation gradient in the circum-Mediterranean.

The most parsimonious explanation for the origin of the European *Crocodylus* is active or passive dispersal from North Africa across the Mediterranean Sea. The timing of this northward dispersal, the Tortonian, fits with the age of some other crocodylian remains from the Miocene Mediterranean islands (Fig. 9; for a review of the Italian record see Delfino, 2002; Kotsakis, Delfino & Piras, 2004). They have been originally described as *Crocodylus* sp. (Scontrone, Abruzzi-Apulian palaeobioprovince; Rustioni *et al.*, 1992), *Crocodylus bambolii* Ristori, 1890 (Monte Bamboli, Tusco-Sardinian palaeobioprovince; Ristori, 1890) and undetermined crocodylians (Fiume Santo, Sassari, Tusco-Sardinian palaeobioprovince; Cordy & Ginesu, 1994). The age of the remains varies between 11–9 Mya for Scontrone (Mazza & Rustioni, 1996), 9.5–6 Mya for Monte Bamboli (levels correlate to Baccinello V1 + V2; Rook *et al.*, 2000) and 7–5.3 Mya for Fiume Santo (Rook *et al.*, 2003). These remains consist only of isolated teeth (Scontrone, Fiume Santo) or of skeletal elements poorly preserved and unsuitable for a detailed phylogenetic analysis (Monte Bamboli). If their former allocation to *Crocodylus* is confirmed by new findings or further analyses, their owners could have reached Europe with the Gargano crocodile, during the Tortonian, and therefore well before the Messinian Salinity Crisis, traditionally considered as the event that caused several trans-Mediterranean dispersals.

CROCODYLIAN EXTINCTION IN EUROPE AND THE MEDITERRANEAN AREA

The *Crocodylus* remains from the late Neogene (5–6 Mya) of what is now southern Italy are the youngest European crocodylian. Pliocene climatic worsening should have rendered Europe not warm enough for the long-term survival of crocodylians, although they could have probably temporarily survived if they had the chance to re-colonize the region

periodically from North Africa. Even allowing for the fact that crocodylians are good candidates for fossilization (teeth continuously renewed, high number of osteoderms, inhabitants of environments with high rates of sedimentation) and they have high probability of being detected in the fossil record (skeletal elements easily recognizable, large size), thus far there are no indications for recurrent dispersals, and data concerning historical times are anecdotal and not grounded on any reliable evidence or are the results of possible introductions (e.g. for Sicily; cf. Doderlein, 1872; Anderson, 1898; De Smet, 1999).

Further information about this topic may have to rely on the age reassessment and positive identification of some putative Pliocene remains from Spain that, as reported by Schleich, Kästle & Kabisch (1996: 23), could ‘either represent postmessinian invaders from Africa [...] or they were a last offshoot of the rather ubiquitous Tertiary genus *Diplocynodon*’; a thorough search of these remains in the Spanish collections provided no definitive results and their presence is considered here as anecdotal.

In the circum-Mediterranean region, *Crocodylus niloticus* was apparently present until historical times in Morocco, where it disappeared around the middle of the 20th century, in Israel, where it went extinct at the beginning of the 20th century, and in Syria (Werner, 1988; Ross, 1989; Bons & Geniez, 1996; De Smet, 1999; Spawls *et al.*, 2002). Isolated populations still survive in the gueltas of Tagant in Mauritania, in the gueltas of Tassili n’Ajjer and other localities in Algeria (extinct according to some authors) and in the Ennedi and Tibesti mountains of Chad (Bons & Geniez, 1996; Schleich *et al.*, 1996; Shine *et al.*, 2001). It seems likely that some of those populations survived after a long history of at least partial isolation since the Pliocene (isolated crocodylian teeth have been reported from the Late Pliocene of Morocco; Bailon, 2000) and then a complete isolation in the last few thousands years; however, the accumulated genetic divergence can justify a different specific allocation so that Schmitz *et al.* (2003) recently proposed the resurrection of the name *Crocodylus suchus* Geoffroy Saint-Hilaire, 1807 for some relict populations of *C. niloticus* from West Africa.

However, even if the small size of the Gargano crocodyles seems to indicate a prolonged evolution in isolation in particular ecological conditions, the available morphological characters do not seem not to justify a distinction at species rank.

SIZE

Even if it is difficult to assess the maximum size attained by the Gargano crocodyles on the basis of the available material, they were most likely relatively

small. Criteria useful to assess morphological maturity (not necessarily maximum size) of crocodylians have been discussed by Brochu (1995, 1996). Among the Gargano remains, the open scapulocoracoid contact, as well as the presence of smooth coracoid and scapula contact surfaces, could be evidence of non-maturity, but because scapulocoracoid closure has never been described in crocodylids and shows a high degree of heterochrony in alligatorid crocodylians, this character is of little help in understanding whether the *Crocodylus* remains from Gargano belonged to mature specimens. Better information may be given by the vertebrae: closure of neurocentral sutures follows a caudo-cranial sequence in modern crocodylians and therefore only cervical vertebrae with a closed neurocentral suture can be considered as reliable proxies to assess mature condition. Cervical vertebrae from the Gargano material are invariably represented by centra only, suggesting that sutures were open at death and therefore that their owners were not fully mature. A dorsal vertebra (DSTF GH2) with closed neurocentral suture and centrum length of 23.2 mm, even if not belonging to a fully mature specimen, allows us to rule out this specimen was a juvenile.

However, taking into account that the overgrown rim of the dentary alveoli could indicate old age, as well the size of the described vertebra and that of the largest skeletal element, it is possible to hypothesize that the size (total length) attained by the Gargano crocodyles should have been around 170–200 cm.

It is known that the living, or recently extinct, *C. niloticus* from the isolated Saharan/Sahelian populations did not exceed 250 cm in total length (Bons & Geniez, 1996; 150–200 cm according to Geniez *et al.*, 2004), whereas specimens from non-isolated populations of East Africa, or south of the Sahara, are usually at least twice as long as this (Ross, 1989; Spawls *et al.*, 2002). It can be concluded that *C. niloticus*, at least, had ‘dwarf’ populations in suboptimal conditions, usually related to isolation in unsuitable areas.

ISLANDS TOP PREDATOR

The recognition of the presence of *Crocodylus* in the Late Miocene insular faunas of the Abruzzi–Apulian palaeobioprovince (*Microtia–Hoplitomeryx* fauna) and possibly the Tusco-Sardinian palaeobioprovince (*Oreopithecus* fauna) again strengthens the uniqueness of these assemblages. The vertebrate assemblages of these faunal complexes display highly endemic, insular characteristics such as the lack of terrestrial mammalian carnivores and the development of gigantic (e.g. the giant insectivore *Deinogalerix*) or dwarf mammals (the bizarre ruminant *Hoplitomeryx*) and flightless birds (cf. literature in Abbazzi *et al.*, 1996). It has been argued that limited habitable areas and trophic

resources as well as the absence of terrestrial carnivores favoured endemism, especially in the case of the bipedal hominoid *Oreopithecus* (Alba *et al.*, 2001; Rook *et al.*, 1999). The crocodylian fossils from the Abruzzi–Apulian and the Tusco-Sardinian palaeobioprovinces provide the only evidence for large terrestrial predators on both these insular habitats as the largest carnivorous mammals recorded are lutrines.

CONCLUSION

The 47 crocodylian remains recovered from Neogene (Late Messinian to earliest Pliocene) fissure fillings of the Gargano area in southern Italy represent the youngest European crocodylians.

Thanks to the presence of diagnostic skeletal elements (among which a fragmentary maxilla is of particular value) it is possible to demonstrate on phylogenetic grounds that the Gargano crocodylian remains represent the first evidence of the genus *Crocodylus* in Europe. It probably dispersed from Africa, in the Central Mediterranean area, during a period of a local prevailing wet and subtropical climate and possibly during the Tortonian, and therefore before the Messinian salinity crisis that is traditionally invoked to explain trans-Mediterranean dispersals. Moreover, on the basis of the morphology of the maxilla, a phylogenetic relationship with *C. chechchiae* from the late Neogene of Libya can be advanced.

The fact that the remains come from different localities widespread in an area of several kilometres allows us to exclude the dispersal of a single individual and to interpret the sample as representing several individuals and probably a population. Given that the well-known fauna of the late Neogene Gargano archipelago does not include predators larger than lutrines, it is expected that these crocodylians had a dominant predatory role in those ecosystems.

ACKNOWLEDGEMENTS

The senior author (M.D.) would like to thank M. Freudenthal and L. Van den Hoek Ostende (Naturalis, Nationaal Natuurhistorisch Museum, Leiden) for providing access to the fossil material and profitable discussion on the Gargano fauna over many visits; C. Brochu (University of Iowa, Iowa City) for having shared unpublished information; F. Masini (Università degli Studi di Palermo) for fruitful discussions and assistance during the study of the Firenze collection; P. Arntzen, E. Gassó Miracles and R. van Zelst (Naturalis, Leiden), B. Battaille and F. de Lapparent de Broin (Museum national d’Histoire naturelle, Paris), B. Engesser (Naturhistorisches Museum, Basel), H. Grillitsch and R. Gemel (Naturhistorischen Museum, Wien), and G. Lenglet and T. Smith (Institut

royal des Sciences naturelles de Belgique, Bruxelles) for having provided modern and fossil comparative material as well as assistance during his visits; G. Malerba (Università degli Studi di Torino) for providing the SEM image; the Institut royal des Sciences naturelles de Belgique (Bruxelles) for having granted a visit under the programme 'Access to Belgian Collections' (2003). M.B. would thank U. Schmid (Augsburg) for his excellent co-operation. C. Brochu, A. D. Buscalioni (Universidad Autónoma de Madrid) and P. W. Markwick (University of Chicago) kindly commented on earlier drafts of the manuscript. This paper has developed within a wider project on Late Neogene vertebrate evolution at the University of Florence (co-ordinator L. Rook).

REFERENCES

- Abbazzi L, Benvenuti M, Boschian G, Dominici S, Masini F, Mezzabotta C, Rook L, Valleri G, Torre D. 1996.** The Neogene and Pleistocene succession and the mammal faunal assemblages of an area between Apricena and Poggio Imperiale (Foggia). *Memorie del Bollettino della Società Geologica Italiana* **51**: 383–402.
- Alba DM, Moyá Solá S, Köhler M, Rook L. 2001.** Heterochrony and the cranial anatomy of *Oreopithecus*: some cladistic fallacies and the significance of developmental constraints in phylogenetic analysis. In: de Bonis L, Andrews P, Koufos G, eds. *Phylogeny of the Neogene hominoid primates of Eurasia*. Cambridge: Cambridge University Press, 284–315.
- Anderson J. 1898.** *Zoology of Egypt. Reptilia and Batrachia, 1*. London: Bernard Quaritch.
- Andrews PA, Harrison T, Delson E, Bernor RL, Martin L. 1996.** Distribution and biochronology of European and Southwest Asian Miocene Catarrhines. In: Bernor RL, Fahlbusch V, Mittmann HW, eds. *The evolution of western Eurasian mammal faunas*. New York: Columbia University Press, 168–207.
- Antunes MT. 1987.** Affinities and taxinomial status of Miocene longirostrine crocodylians from Western Europe with remarks on phylogeny, paleoecology and distribution. *Comunicacoes dos Servicos Geológicos de Portugal* **73**: 49–58.
- Antunes MT. 1994.** On Western Europe Miocene gavials (Crocodylia): their paleogeography, migrations and climatic significance. *Comunicacoes Instituto Geológico e Mineiro* **80**: 57–69.
- Bailon S. 2000.** Amphibiens et reptiles du Pliocène terminal d'Ahl al Oughlam (Casablanca, Maroc). *Geodiversitas* **22**: 539–558.
- Böhme M. 2003.** The Miocene climatic optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* **195**: 389–401.
- Böhme M. 2004.** Migration history of air-breathing fishes reveals Neogene atmospheric circulation patterns. *Geology* **5**: 393–396.
- Böhme M, Ilg A. 2003.** fosFARbase. <http://www.wahre-staerke.com/>.
- Bons J, Geniez P. 1996.** *Amphibiens et reptiles du Maroc (Sahara occidental compris): atlas biogéographique*. Barcelona: Asociación herpetológica española.
- Brochu CA. 1995.** Heterochrony in the crocodylian scapulocoracoid. *Journal of Herpetology* **29**: 464–468.
- Brochu CA. 1996.** Closure of neurocentral sutures during crocodylian ontogeny: implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology* **16**: 49–62.
- Brochu CA. 1999.** Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. *Journal of Vertebrate Paleontology* **19**: 9–100.
- Brochu CA. 2000.** Phylogenetic relationships and divergence timing of *Crocodylus* based on morphology and the fossil record. *Copeia* **2000**: 657–673.
- Brochu CA. 2001.** Congruence between physiology, phylogenetics and the fossil record on crocodylian historical biogeography. In: Grigg GC, Seebacher F, Franklin CE, eds. *Crocodylian biology and evolution*. Chipping Norton: Surrey Betty & Sons, 9–28.
- Brochu CA. 2003.** Phylogenetic approaches toward crocodylian history. *Annual Review of Earth and Planetary Sciences* **31**: 357–397.
- Buffetaut E. 1985.** Zoogeographical history of African crocodylians since the Triassic. In: Schuchmann K-L, ed. *Proceedings International Symposium on African Vertebrates*. Bonn: Museum Alexander Koenig, 453–469.
- Buscalioni AD, Sanz JL, Casanovas ML. 1992.** A new species of the eusuchian crocodile *Diplocynodon* from the Eocene of Spain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **187**: 1–29.
- Carroll RL. 1988.** *Vertebrate paleontology and evolution*. New York: Freeman.
- Cordy JM, Ginesu S. 1994.** Fiume Santo (Sassari, Sardegna, Italia): un nuveau gisement à Oréopithèque (Oreopithecidae, Primates, Mammalia). *Comptes Rendus de l'Académie des Sciences de Paris* **318**: 697–704.
- D'Erasmus G. 1933.** Sui resti di vertebrati terziari raccolti nella Sirtica dalla missione della Reale Accademia d'Italia (1931). *Atti Reale Accademia Nazionale dei Lincei. Rendiconti Classe di Scienze Fisiche, Matematiche e Naturali* (ser. 6) **17**: 656–658.
- D'Erasmus G. 1934.** Su alcuni avanzi di vertebrati terziari della Sirtica. *Missione Scientifica della reale accademia Italiana a Cufra (1931-IX), 3 (studi paleontologici e litologici sulla Cirenaica e sulla Tripolitania orientale)*, 257–279.
- De Smet K. 1999.** Status of the Nile crocodile in the Sahara desert. *Hydrobiologia* **391**: 81–86.
- Delfino M. 2002.** *Erpetofaune Italiane del Neogene e del Quaternario*. Doctoral thesis. Modena: Modena & Reggio Emilia University.
- Delfino M, Pacini M, Varola A, Rook L. 2003.** The crocodylians of the 'Pietra Leccese' (Miocene of southern Italy). In: *Abstracts '1st Meeting of the European Association of Vertebrate Palaeontology'*, 15–20 July 2003, Basel, 18.

- Doderlein P. 1872.** Alcune generalità intorno la fauna sicula dei vertebrati. *Annuario Società Naturalisti* **6**: 1–45.
- Gatesy J, Baker RH, Hayashi C. 2004.** Inconsistencies in arguments for the supertree approach: supermatrices versus supertrees of Crocodylia. *Systematic Biology* **53**: 342–355.
- Geniez P, Mateo JA, Geniz M, Pether J. 2004.** *Amphibians and reptiles of the western Sahara: an atlas and field guide*. Frankfurt am Main: Chimaira.
- Geraads D. 1989.** Vertébrés fossiles du Miocène supérieur du Djebel Krechem el Artsouma (Tunisie Centrale), comparaisons biostratigraphiques. *Geobios* **5**: 777–801.
- Goldsmith NF, Hirsch F, Friedman GM, Tchernov E, Derin B, Gerry E, Horowitz A, Weinberger G. 1988.** Rotem mammals and Yeroham Crassostreids: stratigraphy of the Hazeva Formation (Israel) and the palaeogeography of Miocene Africa. *Newsletters on Stratigraphy* **20**: 73–90.
- Griffin DL. 1999.** The late Miocene climate of northeastern Africa: unravelling the signals in the sedimentary succession. *Journal of the Geological Society* **156**: 817–826.
- Griffin DL. 2002.** Aridity and humidity: two aspects of the late Miocene climate of North Africa and the Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology* **182**: 65–91.
- Hecht MK. 1987.** Fossil snakes and crocodylians from the Sahabi Formation of Libya. In: Boaz NT, El-Arnauti A, Wahid Gaziry A, De Heinzelin J, Dechant Boaz D, eds. *Neogene palaeontology and geology of Sahabi*. New York: Alan R. Liss Inc, 101–106.
- John CM. 2003.** *Miocene climate as recorded on slope carbonates: examples from Malta (central Mediterranean) and northeastern Australia (Marion plateau, ODP leg 194)*. Unpublished thesis, University of Potsdam.
- John CM, Mutti M, Adatte T, Laskar J. 2003.** Mediterranean proto-sapropels in the Middle Miocene: implications for the strength of the African monsoon and link to Miocene glaciations. *Geophysical Research Abstracts* **5**: 2099.
- Kotsakis T, Delfino M, Piras P. 2004.** Italian Cenozoic crocodylians: taxa, timing and biogeographic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* **210**: 67–87.
- Kuhn O. 1936.** *Fossilium Catalogus I: Animalia, Pars 75: Crocodylia*. 'S-Gravenhage: Dr W. Junk.
- Linas-Agrasar E. 2003.** New fossil crocodylians from the Middle/Upper Miocene of Tunisia. *Annales de Paléontologie* **89**: 103–110.
- Markwick PJ. 1998.** Fossil crocodylians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology* **137**: 205–271.
- Mazza P, Rustioni M. 1996.** The Turolian artiodactyls from Scontrone (Abruzzi, central Italy). *Bollettino della Società Paleontologica Italiana* **35**: 93–106.
- Pickford M. 2000.** Crocodiles from the Beglia Formation, Middle/Late Miocene boundary, Tunisia, and their significance for Saharan palaeoclimatology. *Annales de Paléontologie* **86**: 59–67.
- Pough FH, Andrews RM, Cadle JE, Crump ML, Savitzky AH, Wells KD. 2001.** *Herpetology*, 2nd edn. Upper Saddle River, NJ: Prentice Hall.
- Rage JC. 1997.** Paleobiological and paleogeographical background of the European herpetofauna. In: Gasc JP, Cabela A, Crnobrnja-Isailovic J, Dolmen D, Grossenbacher K, Haffner P, Lescure J, Martens H, Martinez Rica JP, Maurin H, Oliveira ME, Sofianidou TS, Veith M, Zuiderwijk A, eds. *Atlas of amphibians and reptiles in Europe*. Paris: SEH & MNHN, 23–28.
- Rauhe M, Frey E, Pemberton DS, Rossmann T. 1999.** Fossil crocodylians from the Late Miocene Baynunah Formation of the Emirate of Abu Dhabi, United Arab Emirates: osteology and palaeoecology. In: Whybrow PJ, Hill A, eds. *Fossil vertebrates of Arabia*. New Haven, CT: Yale University Press, 163–185.
- Ristori G. 1890.** *sopra i resti di un coccodrillo scoperti nelle ligniti Mioceniche di Montebamboli (Maremma Toscana)*. Firenze: Regio Istituto di Studi Superiori, Pratici e di Perfezionamento.
- Rook L, Abbazzi L, Delfino M, Trebini L. 2003.** The fauna from Fiume Santo (Sardinia, Italy), a faunal assemblage with a very late Miocene Ape in Europe. In: *Abstract book 'EEDEN – Environment and Ecosystems Dynamics of the Eurasian Neogene. Birth of the Modern World'*, 12–16 Stara Lesna November 2003, 73–74.
- Rook L, Abbazzi L, Engesser B. 1999.** An overview on the Italian Miocene land mammal faunas. In: Agustí J, Rook L, Andrews P, eds. *Hominoid evolution of Neogene terrestrial ecosystems in Europe*. Cambridge: University Press, 191–204.
- Rook L, Renne P, Benvenuti M, Papini M. 2000.** Geochronology of *Oreopithecus* – bearing succession at Baccinello (Italy) and the extinction pattern of European Miocene hominoids. *Journal of Human Evolution* **39**: 577–582.
- Ross CE. 1989.** *Crocodiles and alligators*. New York: Facts on File.
- Rossmann T, Berg DE, Salisbury S. 1996.** Studies on Cenozoic crocodiles: 3. *Gavialosuchus* cf. *gaudensis* (Eusuchia: Tomistomidae) from the Lower Miocene of south Germany. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **1996**: 321–330.
- Rossmann T, Müller J, Forst M. 2000.** Studies on Cenozoic crocodylians: 7. First evidence of an alligatorid from Africa and its implications for crocodylian palaeobiogeography. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **2000**: 705–714.
- Rustioni M, Mazza P, Azzaroli A, Boscagli G, Cozzini F, Di Vito E, Masseti M, Pisanò A. 1992.** Miocene vertebrate remains from Scontrone. National Park of Abruzzi, Central Italy. *Rendiconti della Accademia Nazionale dei Lincei, Classe di Scienze Fisiche Matematiche e Naturali* **3** (s. 9): 227–237.
- Schleich HH, Kästle W, Kabisch K. 1996.** *Amphibians and reptiles of North Africa*. Koenigstein: Koeltz Scientific Books.
- Schmitz A, Mausfeld P, Hekkala E, Shine T, Nickel H, Amato G, Böhme W. 2003.** Molecular evidence for species level divergence in African Nile Crocodiles *Crocodylus*

- niloticus* (Laurenti, 1786). *Comptes Rendus Palevol* **2**: 703–712.
- Shine T, Böhme W, Nickel H, Thies DF, Wilms T. 2001.** Rediscovery of relict populations of the Nile crocodile *Crocodylus niloticus* in south-eastern Mauritania, with observations on their natural history. *Oryx* **35**: 260–262.
- Sill WD. 1968.** The zoogeography of the Crocodylia. *Copeia* **1968**: 76–88.
- Spawls S, Howell K, Drewes R, Ashe JA. 2002.** *Field guide to the reptiles of East Africa*. San Diego: Academic Press.
- Steel R. 1973.** *Crocodylia*. *Encyclopedia of Paleoherpétology*. Portland: Fischer-Verlag.
- Suc JP, Fauquette S, Bessedik M, Bertini A, Zheng Z, Clauzon G, Suballyova D, Diniz F, Quezel P, Feddi N, Clet M, Bessais E, Taoufiq NB, Meon H, Combourieu-Nebout N. 1999.** Neogene vegetation changes in West European and West circum-Mediterranean areas. In: Agustí J, Rook L, Andrews P, eds. *Hominoid evolution of Neogene terrestrial ecosystems in Europe*. Cambridge: University Press, 378–388.
- Swofford DL. 1999.** *PAUP**. *Phylogenetic Analysis Using Parsimony (*and other methods)*, Version 4. Sunderland, MA: Sinauer Associates.
- Tchernov E. 1986.** Evolution of the crocodiles in East and North Africa. *Cahiers de Paléontologie Travaux de Paléontologie est-africaine*. Paris: CNRS.
- Tiedemann R, Sarnthein M, Stein R. 1989.** Climatic changes in the Western Sahara: aolo-marine sediment record of the last 8 million years (site 657–661). *Proceedings of the Ocean Drilling Program, Scientific Results* **108**: 241–277.
- Werner YL. 1988.** Herpetofaunal survey of Israel (1950–85), with comments on Sinai and Jordan and on zoogeographical heterogeneity. In: Yom-Tov Y, Tchernov E, eds. *Zoogeography of Israel, Monographiae Biologicae*, Vol. 62. Dordrecht: Junk, 355–388.