Phylogenetic position of the crocodylian *Megadontosuchus arduini* and tomistomine palaeobiogeography

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A cladistic analysis of *Megadontosuchus arduini* from the middle Eocene of Monte Duello (NE Italy) confirms its tomistomine relationships, but the low number of scorable characters determines a low resolution within the tomistomine clade. However, *Megadontosuchus* is clearly distinct from the other Eocene European or North African tomistomines, in having a moderate elongated but robust rostrum, massive maxillary and dentary teeth and large supratemporal fenestrae. The rostrum and teeth characteristics could indicate that *M. arduini* had a degree of feeding specialization intermediate between *Maroccosuchus zennaroi* and the Eocene European tomistomines. A summary of tomistomine palaeobiogeography suggests that despite only one species with a rather restricted range survives at present, such a clade had a glorious past with a world wide distribution documented by a conspicuous fossil record that starts at least in the early Eocene. At present, a detailed knowledge of tomistomine palaeobiogeography is hindered by the lack of modern taxonomic revisions of some fossil remains and therefore by the poor understanding of phylogenetic relationships.

Key words: Crocodylidae, Tomistominae, *Tomistoma schlegelii*, palaeobiogeography, Eocene, Italy.

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Introduction

De Zigno (1880) described longirostrine crocodylian remains from the middle Eocene of Monte Duello (Verona, Italy) and formally erected a new species upon this material, *Crocodylus arduini* (originally written as *Crocodilus*). Since then, many authors (Kuhn 1938; Brochu 1997, 2001; Kotsakis et al. 2004) declined to include this taxon in the genus *Crocodylus*, placing it instead among tomistomines. Mook (1955) proposed a new genus for this species, *Megadontosuchus*, and in the same paper erected another new tomistomine genus, *Kentisuchus*, for "*Crocodylus*" *spenceri* Buckland, 1836. A number of papers describe or mention *M. arduini*, accepting its specific validity (Nicolis 1882; Lydekker 1886; Uzielli 1886; Fabiani 1915; Del Vecchio 1921; Mook 1955; Steel 1973; Altichieri 1980; Pinna 1989; Roccaforte et al. 1994; Brochu 2001). Kotsakis et al. (2004, 2005) quoted this species as a basal tomistomine. Brochu (1997, 2001) hypothesized that *Kentisuchus spenceri*, *Megadontosuchus arduini*, and *Dollosuchus dixoni* (Owen, 1850) are closely related and underlined that in case of congeneric attribution the genus *Dollosuchus* should have priority. Direct observation of the type specimens (*D. dixoni*—IRScNB 482—currently preserved in the Gand Museum, Belgium, *K. spenceri*—BMNH 19633, and *M. arduini*—MGPD 1Z) evidenced that the three forms represent probably three different species. Recent phylogenetic analyses (Jouve 2004; Delfino et al. 2005; Brochu 2006, in press) showed that *Dollosuchus dixoni* is a basal tomistomine close to *Kentisuchus spenceri*. Recently, Brochu (in press) expressed doubts about the generic and specific identity for the Belgian specimen of *Dollosuchus dixoni*. No modern description or phylogenetic analysis have been published until now for *Megadontosuchus arduini*. We present here a complete list of the remains attributed to *M. arduini* to date (Appendix 1), a redescription of all known material referred to this species and a cladistic analysis primarily based on Gatesy et al.'s (2004) dataset. As the holotype has never been designated by de Zigno (1880) nor a lectotype by Mook (1955), we choose the specimen MGPD 1Z as the lectotype (figured in de Zigno 1880: pls. 1, 2, and here as Figs. 1–3).

Institutional abbreviations.—BMNH, The Natural History Museum, London, United Kingdom; IRScNB, Institut Royal des Sciences Naturelles, Bruxelles, Belgium; MGPD, Museo di Geologia e Paleontologia, Università degli Studi di Padova, Italy.

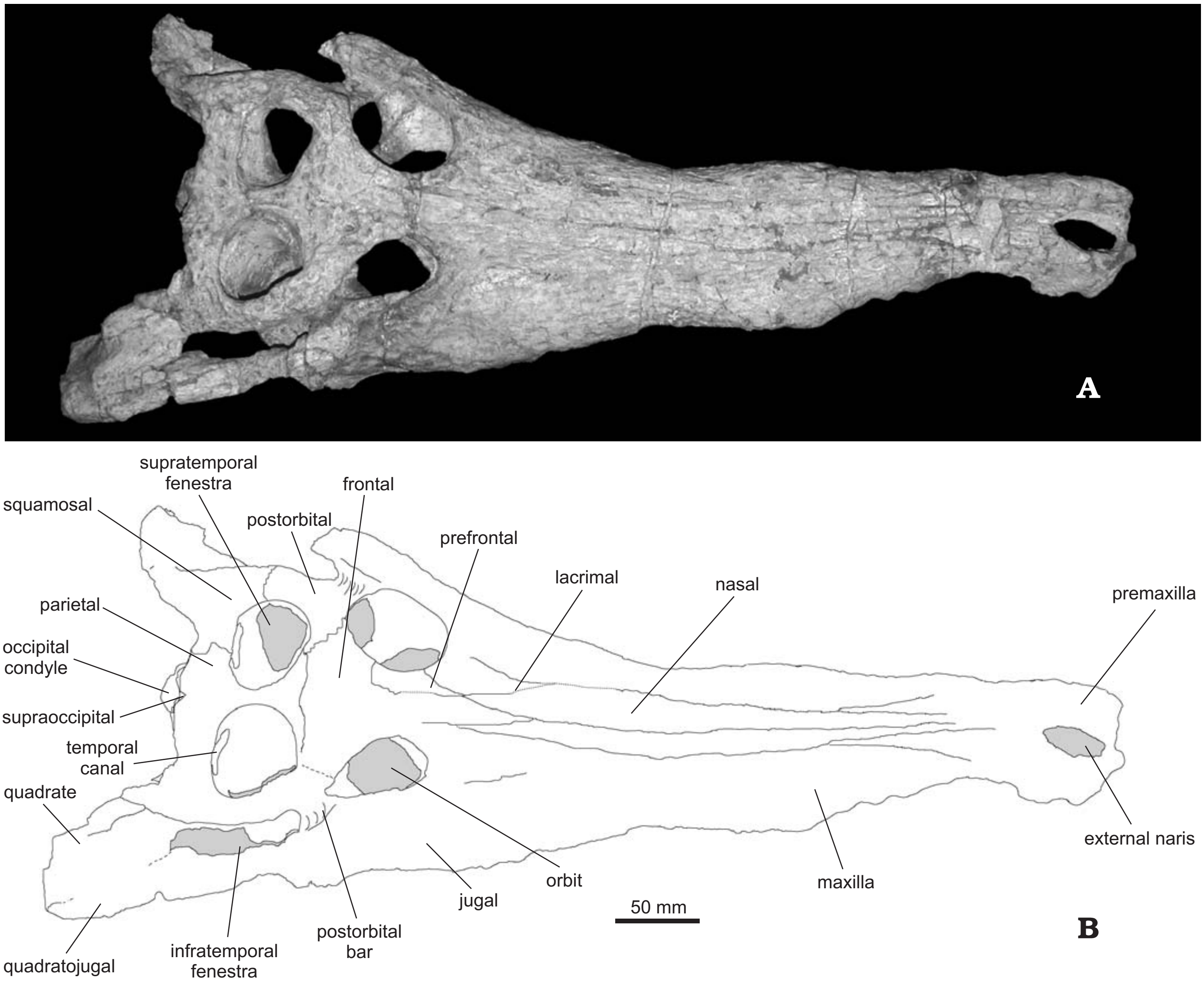

Fig. 1.Tomistomine crocodile *Megadontosuchus arduini* (de Zigno, 1880), MGPD 1Z, lectotype from Monte Duello (Roncà, Province of Verona, NE Italy); middle Eocene. Skull in dorsal view. Photograph (**A**) and explanatory drawing of the same (**B**).

Systematic palaeontology

Eusuchia Huxley, 1875

Crocodylia Gmelin, 1789 (*sensu* Benton and Clark 1988)

Crocodyloidea Fitzinger, 1826 (*sensu* Brochu 2003)

Crocodylidae Cuvier, 1807 (*sensu* Brochu 2003)

Tomistominae Kälin, 1955 (*sensu* Brochu 2003)

Genus *Megadontosuchus* Mook, 1955

Type species: *Crocodilus arduini* de Zigno, 1880; see below.

Megadontosuchus arduini (de Zigno, 1880)

Lectotype: MGPD 1Z, a nearly complete skull (Figs. 1–3) with lower jaw (de Zigno 1880: pl. 1: 1–3 and pl. 2: 1–3).

Type locality and age: Monte Duello (Roncà, Province of Verona, NE Italy); middle Eocene.

Referred material.—MGPD 5Z, skull lacking the anterior part of the rostrum; MGPD 4Z, anterior part of the rostrum belonging to the specimen MGPD 5Z; MGPD 6Z, fragment of a right mandibular ramus, lacking retroarticular process; MGPD 8Z, nearly complete mandibular ramus; probably these remains belong to the original type series. Two vertebrae MGPD 24Z (cervical) and MGPD 25Z (dorsal; de Zigno 1880: pl. 2: 6 and 4, 5, respectively).

Emended diagnosis.—*Megadontosuchus arduini* is a tomistomine differing from all other members of the clade because of this combination of features: the robust rostrum, the massive maxillary and dentary teeth and large supratemporal fenestrae. Approximately 14–16 maxillary teeth, and approximately 14–17 dentary teeth. Small occipital condyle. Large narial aperture and foramen incisivum. Nasals in contact with external naris without bisecting it. Large mandibular fenestra. Elongated squamosal prongs reaching nearly the half of quadrate ramus.

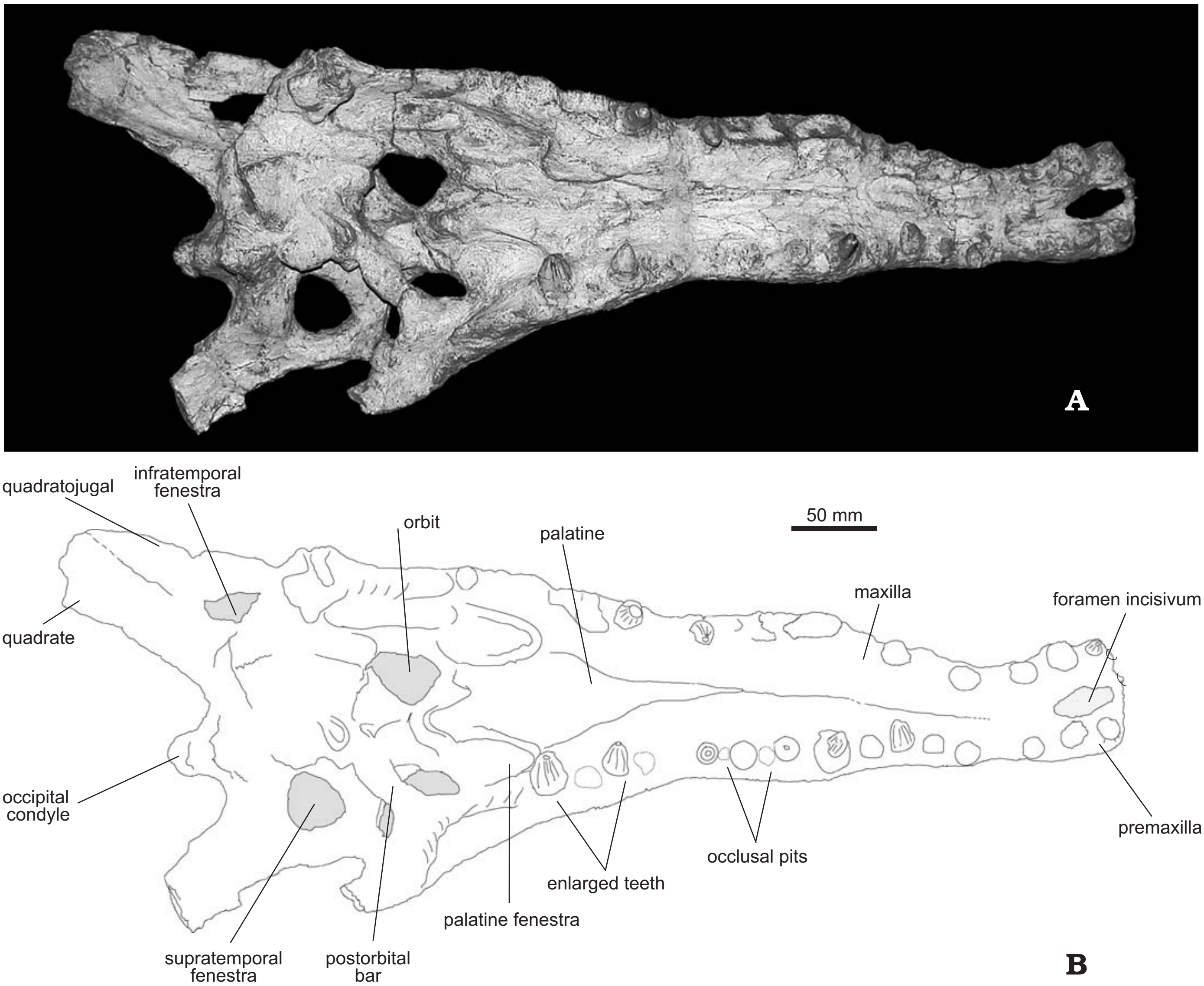

Fig. 2. Tomistomine crocodile *Megadontosuchus arduini* (de Zigno, 1880), MGPD 1Z, lectotype from Monte Duello (Roncà, Province of Verona, NE Italy); middle Eocene. Skull in ventral view. Photograph (**A**) and explanatory drawing of the same (**B**).

Description

Skull

Preservation, form, and general features.—The lectotype (Figs. 1–3) is an almost complete skull that, although dorsoventrally flattened, retains the undulatory outline ("festooning") of the maxillary and dentary visible in dorsal and, despite the deformation, lateral view. It is very difficult to recognize cranial and mandibular sutures due to the preservation and historical museum preparation that focused on the maintenance of the general external shape and not of the fine morphology. The minimal distance between supratemporal fenestrae is approximately 10 mm. Only the right infratemporal fenestra is visible due to the absence of the left jugal bar. The jugal border of the right orbit is medially displaced. The right orbit appears longer, due to post-mortem deformation. Posteriorly, the quadrate ramus is very expanded medio-laterally (in occipital view it is nearly the half of semi cranial width at maximum quadrate lateral expansion). The skull morphology in ventral view (Fig. 2) is difficult to reconstruct precisely due to the collapse of secondary palate posteriorly to the maxillo-palatine suture; such suture is wedge-like shaped. Palatines are antero-posteriorly elongated. Pterygoids and ectopterygoids are totally crushed down. Choanae are not visible. Despite a marked erosion, basioccipital seems to be medio-distally short. In occipital view (Fig. 3) only the sutures between squamosals and exoccipitals are slightly visible. The general profile is flattened and compressed.

Dorsal view.—In dorsal view, the lectotype shows an evident festooning despite the post-mortem deformation. External nares are wide but antero-posteriorly elongated, with maximum width at their anterior border. It is difficult to evaluate the position of the anterior nasal tip; however, the nasals

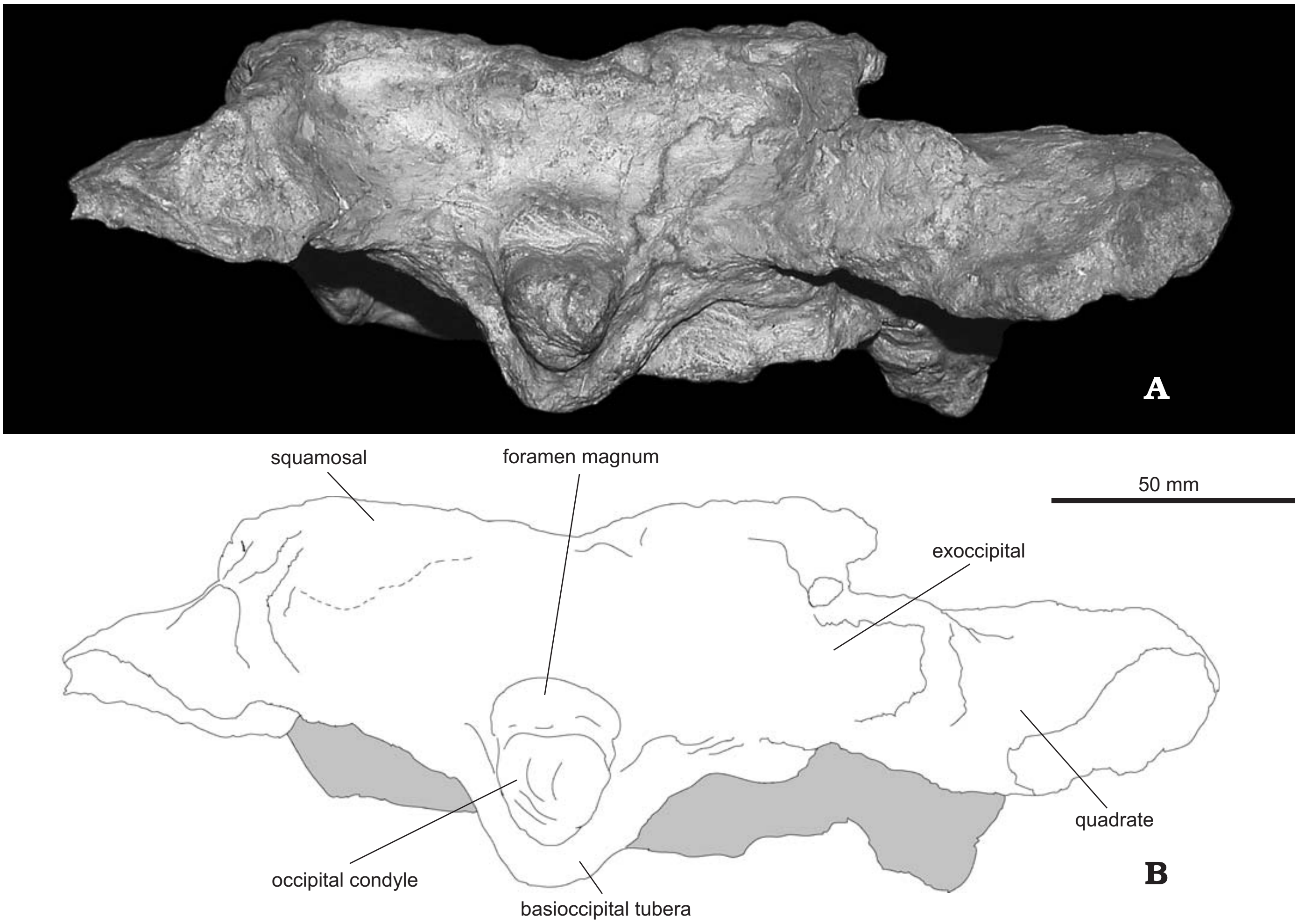

Fig. 3. Tomistomine crocodile *Megadontosuchus arduini* (de Zigno, 1880), MGPD 1Z, lectotype from Monte Duello (Roncà, Province of Verona, NE Italy); middle Eocene. Skull in occipital view. Photograph (**A**) and explanatory drawing of the same (**B**).

profile suggests a contact between nasals and external nares (Fig. 1B). De Zigno (1880) also quoted this character in his original description. In the skull MGPD 4Z it is impossible to evaluate nasal sutures. The maxilla presents, both in dorsal and lateral view, an evident festoon in correspondence of the fifth maxillary tooth, whose alveolus is the largest. This character is usually always present in tomistomines (but not in gavialoids) despite rostral elongation (Brochu 1997, and references therein): an exception is represented by *Toyotamaphimeia machikanensis* (Kamei and Matsumoto, 1965) from Japan, where the largest maxillary alveoli are the twelfth and thirteenth (Kobayashi and Tomida 2005; Kobayashi et al. 2006).

The lacrimal-prefrontal suture is difficult to trace: only a small part is visible posterior to the naso-lacrimal suture. The maxilla is slightly curved in medial direction posterior to the sixth alveolus. Orbits are sub-oval and their longer axes converge antero-medially, forming an angle of about 30°. The orbital rim is upturned, especially along its medial margin. The frontal is concave between orbits, possibly reflecting relatively advanced maturity. The anterior frontal spine reaches the level of the eleventh or twelfth maxillary alveolus. The frontoparietal suture is linear and entirely developed on skull table. This is evident on the left side while on the right this detail is not visible. The postorbital bar is slender like in all tomistomines and does not flush with jugal. The scoring of this character can be, however, affected by the allometric effect in hyperadult morphologies and by the subjective interpretation during the coding (i.e., the postorbital bar in "*Tomistoma*" *cairense* and *Gavialosuchus americanus* is more massive than in other tomistomines). The lateral sides of the cranial roof are gently convex. The parieto-squamosal suture enters supratemporal fenestra approximately at the middle of its posterior rim. The medial walls of supratemporal fossae are differently inclined in lateral direction because of the compression. Assuming that the left side is not significantly affected by deformation and thus it better represents the original morphology, it can be stated that the skull table surface slightly overhangs the supratemporal fossa. The supratemporal fenestrae are relatively large in comparison with *Tomistoma schlegelii* J. Müller, 1838, as in most primitive tomistomines (i.e., *K. spenceri* and "*Gavialosuchus*" *americanus* [Sellards, 1915]) and they are wider than long (ratio = 1.2; see Discussion). Squamosal prongs are unusually elongated along paraoccipital process.

Ventral view.—In ventral view, most sutures are not visible with confidence. It is evident that the palatine process is wedge-like shaped and reaches the ninth maxillary tooth. The palatine fenestrae reach anteriorly the eleventh maxillary tooth. They are irregularly oval and rather close to each other. No other details are shown in that region because of the collapse of secondary palate. The premaxillo-maxillary suture is not visible due to the 19th century preparation (when a sort of cement has been added) that masks the fine morphology of this area. However, the lateral constriction corresponding to such suture is evident. The foramen incisivum is particularly long (~30 mm) in comparison with premaxillary length. On the right side of the premaxilla five alveoli are present; *M. arduini* retained the second alveolus that usually disappears during ontogeny (i.e., in *Tomistoma*; Brochu 1997, and references therein). The pterygoids and ectopterygoids are totally crushed. The basisphenoid region is poorly preserved but the exposure of basisphenoid ventral to basioccipital was probably very short.

Occipital view.—In occipital view it is nearly impossible to distinguish any suture. The left quadrate ramus is broken at the end of squamosal prong. The right quadrate is better preserved: it is dorso-ventrally flat, but this could be partly due to dorso-ventral compression. The basioccipital tubera appear rather narrow and not developed medio-laterally as in *Tomistoma schlegelii*, but also in this case we cannot exclude that post-mortem deformation partly contributed to such morphology. The foramen magnum is nearly as large as the width of occipital condyle (it is narrower in *Gavialosuchus eggenburgensis* Toula and Kail, 1885 and *T. schlegelii*, but larger in *D. dixoni* and *Maroccosuchus zennaroi* Jonet and Wouters, 1977). The well developed crest formed by squamosal and paraoccipital process of exoccipital is evident. The skull table profile is concave in the area corresponding to the supraoccipital. The exposure (in occipital view) of the basisphenoid ventral to the basioccipital tubera cannot be evaluated.

Lower jaw

On the left ramus all bones are preserved with the exception of the coronoid. However, their sutures are nearly invisible due to fossilization and historical preparation. Coronoid and retroarticular process are missing in the right ramus. The two mandibular rami are differently deformed: the left one maintains its curvature along the dentary margin while the compression completely straightened the right mandibular ramus. Interalveolar spaces are equal or larger than alveolar width. The splenial sutures are not visible. However, on the basis of geometric relationships of lower jaw elements, it can be inferred that the splenial participates in the symphysis but it is impossible to evaluate the length of the splenial symphysis (i.e., if it was longer than five alveoli; therefore states 1–3 can be excluded and for this reason the character 43 is scored as “0/4”).

Postcranial elements

Dermal armour.—The available osteoderms are isolated and for this reason it is impossible to evaluate the morphology of midline and lateral rows elements. They are squared and profusely ornamented with few circular and large pits widely separated from each other. A sagittal crest is present; when laterally viewed, such a crest is not abruptly but gradually emerging from the external surface.

Vertebral series.—The two procoelous vertebrae MGPD 24Z and MGPD 25Z are poorly preserved and consist only of the centra. De Zigno (1880) quoted these vertebrae as cervical and dorsal respectively. MGPD 24Z is approximately 35 mm long. A block of sediment partially hides the dorsal part of centrum. Neural arch is missing but the neurocentral suture is not visible due to the presence of sediment. Ventrally is visible the broken hypapophysis whose basis is 13 mm long. Laterally the parapophysis occupies a rather low position relatively to dorsal margin. MGPD 25Z is 37 mm long. The neurocentral suture is visibly open. Ventrally, the hypapohysis is broken and positioned fairly close to the anterior margin of centrum. The parapohysis is nearly completely abraded but its scar suggests a more dorsal position than in MGPD 24Z: probably this vertebra was one of the anterior dorsal vertebrae.

Nine vertebral centra (again with open neurocentral sutures) attributed in schaedis in the museum label to “*Gavialis*” *dixoni* by de Zigno, might be referable to *M. arduini*.

Appendicular skeleton.—The available forelimb and hind limb elements are not informative because they consist only of unrecognisable small fragments.

Phylogenetic analysis

To reduce computational time we selected 47 taxa from the morphological dataset of Gatesy et al. (2004; actually based on Brochu’s [1999] matrix) together with the coding of *Megadontosuchus arduini* (specified in Appendix 2), *Toyotamaphimeia machikanensis* (coding from Kobayashi et al. 2006), and *Tomistoma petrolicum* (unpublished coding kindly provided by Chris Brochu). Three additional characters were added according to the same dataset of Delfino et al. (2005). Alligatoroidea was pruned to include only *Leidyosuchus canadensis* Lambe, 1907, *Diplocynodon hantoniensis* (Wood, 1846), *Brachychampsa montana* Gilmore, 1911, *Alligator mississippiensis* (Daudin, 1801), and *Caiman latirostris* (Daudin, 1801). *Bernissartia fagesii* Dollo, 1883 and *Hylaeochampsa vectiana* Owen, 1874 were treated as sequential outgroups. The matrix, comprehensive of 47 taxa and 167 characters, was processed with PAUP 4.0b10* (Swofford 2002). Both ACCTRAN and DELTRAN optimizations were performed with TBR in effect and 100 replicates of random addition sequence. Characters where treated as unordered. The analysis returned 8638 trees 413 steps long. Strict consensus tree and consensus indices is shown in Fig. 4A. To explore phylogenetic signal among tomistomines without the noise produced by the high number of uncertainties due to the poor preservation of *M arduini*, we repeated the analysis without the latter. This last analysis produced 4344 trees of 409 steps. The strict consensus topology for tomistomines is shown in Fig. 4B. This phylogenetic sketch will be taken in to account to support the palaeobiogeographical considerations expressed below. Together with these two trees, an Adams consensus tree, presented in Fig. 4C, has been calculated to verify the non-strict relationships between *Megadontosuchus* and other tomistomines. Its topology is completely congruent with that of Fig. 4B.

Discussion

The large amount of missing characters for *Megadontosuchus arduini*, due to the scanty preservation of the remains, is probably the main cause for node collapse among tomistomines more derived than *Kentisuchus spenceri* in the strict consensus tree (Fig. 4A). The three unambiguous synapomorphies supporting Tomistominae in the strict consensus tree of our analysis regard a deep splenial symphysis, longer than five dentary alveoli and splenial constricted within symphysis and forming narrow "V" (43-4), a suborbital fenestra without posterior notch (88-0), and a palatine process generally in form of thin wedge (118-1). The three unambiguous synapomorphies supporting the polytomic clade containing all other tomistomines concern the presence of a sulcus between articular and surangular (60-0), the squamosal groove that flares anteriorly (84-1), and the exclusion of nasals, at least externally, from naris but with nasals and premaxillae still in contact (95-2). Not all known tomistomine species are considered in this analysis nor in previous studies (Brochu 1997, 1999, 2003, 2006, in press; Brochu and Gingerich 2000; Jouve 2004; Kobayashi et al. 2006). The inclusion of these species (mainly *Tomistoma coppensi* Pickford, 1994, but see palaeobiogeography section for a complete list) will help in understanding tomistomine evolu-

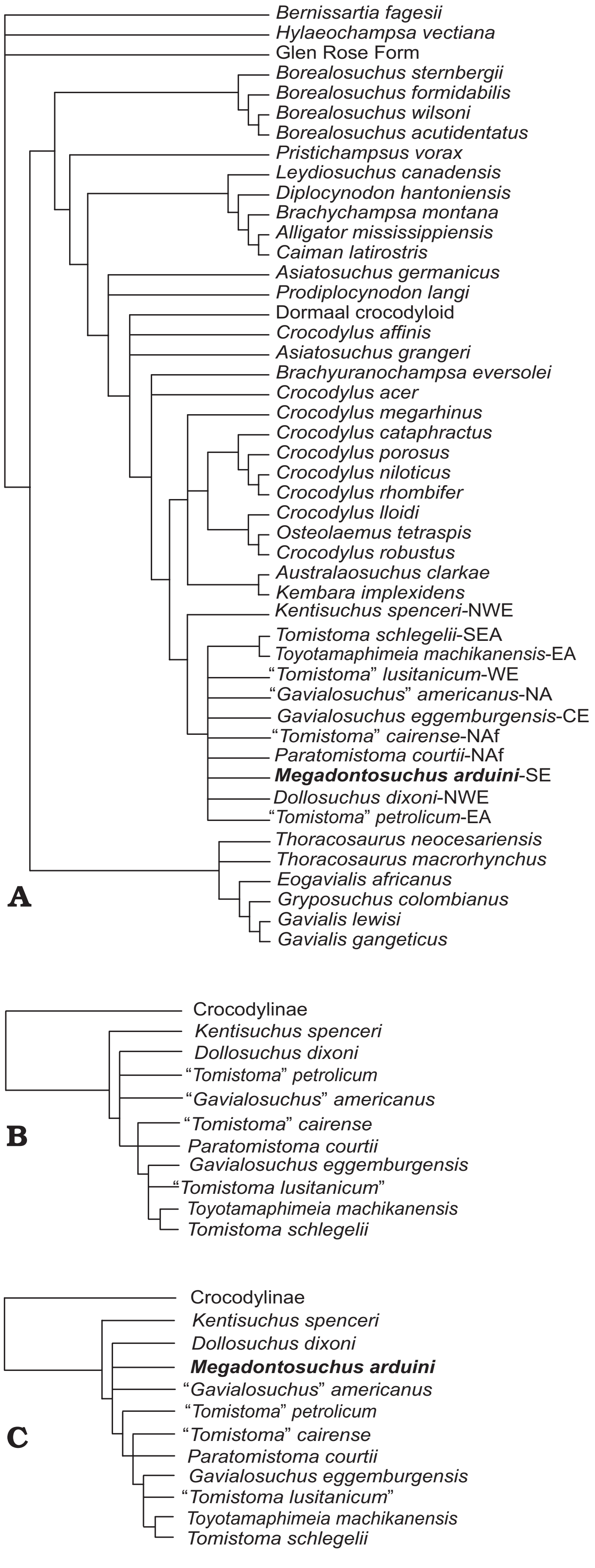

Fig. 4. **A**. Strict consensus trees for 8638 trees 413 steps long derived from the analysis including *Megadontosuchus arduini*. The geographic range of tomistomines is abbreviated as follows: CE, Central Europe; EA, Eastern Asia; NA, North America; NAf, Northern Africa; SEA, South Eastern Asia; WE, Western Europe; NWE, North Western Europe. Consensus statistics: tree length (L) = 430; consistency index (CI) = 0.4581; homoplasy index (HI) = 0.5419; CI excluding uninformative characters = 0.4261; HI excluding uninformative characters = 0.5739; retention index (RI) = 0.7272; rescaled consistency index (RC) = 0.3331. **B**. Strict consensus topology for 4344 trees 409 steps long derived from the analysis excluding *M. arduini*. Consensus statisics: L = 416; CI = 0.4712; HI = 0.5288; CI excluding uninformative characters = 0.4388; HI excluding uninformative characters = 0.5612; RI = 0.7406; RC = 0.3489. **C**. Adams consensus tree derived from the 47 taxa matrix.

tionary history and possibly change the topology here presented. Recently, Kobayashi et al. (2006) and Brochu (in press) incorporated in their analyses *Toyotamaphimeia machikanensis* and *Tomistoma petrolicum* (as "*T. petrolica*") respectively. In their analyses *Toyotamaphimeia machikanensis* results as sister taxon of *Tomistoma schlegelii*, while *Tomistoma petrolicum* as polytomic with *Tomistoma schlegelii* and *Gavialosuchus eggemburgensis*. Our results place *T. petrolicum* in a more congruent position with stratigraphic data (Fig. 4B and C).

The *Tomistoma* genus name (note that the Latin words with a component of the Greek word "stoma", like peristoma, are neutral; consequently the species name of members of the genus *Tomistoma* must be neutral; International Commission on Zoological Nomenclature 1999: Article 34.2) is undoubtedly abused in the historical literature and some species (i.e., "*Tomistoma*" *taiwanicum* Shikama, 1972, "*Tomistoma*" *glareae* [Astre, 1931], "*Tomistoma*" *borisovi* Efimov, 1988) are represented by scanty material that does not permit a specific or even generic identification. Despite the unresolved clade containing *Megadontosuchus arduini*, some additional morphological considerations can be expressed. Undoubtedly, the closest forms are *Dollosuchus dixoni* and *Kentisuchus spenceri*. The dentition of *M. arduini* is distinct from that of *K. spenceri* and *D. dixoni*: teeth are notably larger in *M. arduini* relatively to rostrum proportions. The rostra of *D. dixoni* and *K. spenceri* are more slender than in *M. arduini*. For these reasons we consider *Megadontosuchus* a valid genus. *Kentisuchus* and *Dollosuchus* are more similar to each other and could be assigned to the same genus (in this case *Dollosuchus* should have priority) but a more specific work is needed to support such conclusion.

Megadontosuchus arduini shows relatively large supratemporal fenestrae, comparable in dimension to the orbits, while in *Tomistoma schlegelii* the supratemporal fenestrae are much smaller than orbits. This feature is subjected to a marked ontogenetic change: in fact, orbits show a significant relative reduction in size during growth. Anyway the type of *Megadontosuchus* is to be regarded as an adult-subadult individual: the concavity and ornamentation of fronto-parietal region, as well total skull length, exclude a juvenile growth stage. The open neurocentral suture in cervical (MGPD 24Z) and dorsal (MGPD 25Z) vertebrae does not conflict with the adult morphology suggested by the skull. Cervical vertebrae, and sometimes those of anterior trunk, remain unfused until fairly late (Brochu 1996). For that reason the allometric change of orbits does not affect their comparison with supratemporal fenestrae in *M. arduini*.

Recently, Endo et al. (2002) correlated the dimension of supratemporal fenestrae with the functional role of M. pseudotemporalis in *Gavialis*, *Tomistoma*, *Mecistops*, and *Toyotamaphimeia*. This muscle has a more important functional role, during feeding acquisition, manipulation, and mastication, in species with large supratemporal fenestrae. This trait has probably an adaptive nature and is differently distributed among tomistomine species. *Maroccosuchus*, the oldest tomistomine after *Dollosuchus dixoni*, shows supratemporal fenestrae visibly smaller than orbits albeit this ratio is not the same as in *Tomistoma schlegelii*. Other basal tomistomines have large supratemporal fenestrae in comparison to orbits: it can be seen in *Dollosuchus dixoni*, *Kentisuchus spenceri*, and *Thecachampsa* spp. Conversely, "*Tomistoma*" *cairense* L. Müller, 1927 has orbits larger than supratemporal fenestrae. In *Paratomistoma courti* Brochu and Gingerich, 2000 it is difficult to recognize the orbital contour due to the fragmented material but it seems (Fig. 2; Brochu and Gingerich 2000) that supratemporal fenestrae were relatively larger than in "*Tomistoma*" *cairense*. *Gavialosuchus eggenburgensis* has relatively small supratemporal fenestrae.

The snout of *M. arduini*, *K. spenceri, M. zennaroi*, and *D. dixoni* is not as long as in more derived tomistomines: in fact *G. eggenburgensis*, *T. schlegelii*, "*T.*" *cairense*, and *T. coppensi* show a longer and more slender snout. This feature is related to feeding ecology and probably to the percentage of fish items in the diet (Cleuren and De Vree 2000). From early Eocene, tomistomines experienced an increase in diet specialization similar to that of Gavialoidea (with different timing; Brochu 2004). Actually the earliest forms have a less specialized snout morphology than that of most Miocene forms. However it is difficult to assess on the basis of fossil record if the common ancestor of tomistomines and other crocodylines was medium-slender or a short snouted form, like the majority of crocodylines. More material from Palaeocene outcrops is needed to understand this issue.

The paraoccipital processes are very developed in *Megadontosuchus arduini*: they constitute nearly a crest together with squamosal prongs, dorsally to quadrate ramus. This feature is absent among other tomistomines. *Tomistoma lusitanicum* Vianna and Moraes, 1945 possesses well-developed paraoccipital process but not as evident as in *Megadontosuchus*.

Tomistomine distribution and palaeobiogeography

Palaeogene European and North African tomistomines.—According to the present knowledge of crocodylian evolutionary history, the oldest members of Tomistominae can be traced back to the early Eocene or possibly to the Palaeocene if the tomistomine nature of a skull from Spanish Pyrenees will be confirmed (Costa et al. 1995; Jouve 2004). Early Eocene tomistomines have been described in Europe and northern Africa (Brochu 2003): *Kentisuchus spenceri* from England, *Maroccosuchus zennaroi* from Morocco, and, slightly younger, *Dollosuchus dixoni* from Belgium (Buckland 1836; Owen 1850; Swinton 1937; Jonet and Wouters 1977). An early Eocene tomistomine referred to ?*Kentisuchus* sp. could be possibly present in Ukraine (Efimov 1993). The presence of tomistomine crocodylians in this area is further testified in the middle Eocene, both in Europe and in North Africa; relevant findings come from France, "*Tomistoma*" *glareae* (Astre, 1931; see discussion in Steel 1973; Vasse 1993; Jouve 2004), Germany, Tomistomidae indet. (Rossmann 2002), Italy, *Megadontosuchus arduini* (de Zigno 1880; this work) and Egypt, "*Tomistoma*" *cairense* and, slightly younger, *Paratomistoma courti* (see Müller 1927; Brochu and Gingerich 2000).

Such trans-Tethyan distribution is reasonable because, contrary to the fresh water environment of the sole extant tomistomine, *Tomistoma schlegelii*, several tomistomine fossil remains come from estuarine or marine coastal settings, suggesting the possibility of dispersion across marine barriers (Brochu 2003) and not only along river systems. Contacts at the Palaeocene/Eocene limit between the faunas of opposite sides of the Tethys are also shown by other vertebrate taxa, reptiles, and mammals (Broin 1988; Rage 1996; Gheerbrant et al. 2001).

The northern African *Tomistoma* species described by Andrews (1901, 1905) from Egypt (late Eocene and early Oligocene), *T. africanum* Andrews, 1901, *T. gavialoides* Andrews, 1905, and *T. kerunense* Andrews, 1905 could be, according to Buffetaut (1982) and Brochu (2001), synonyms and should be ascribed to the gavialoid *Eogavialis*, as *E. africanus* (Andrews, 1901); on the contrary, according to Tchernov (1986) and Rauhe et al. (1999), they should be referred to the African endemic crocodyline *Euthecodon*.

During the early Eocene, *Kentisuchus* and *Dollosuchus* inhabited Europe. The origin of *M. arduini* and its presence in the Tethyan Eocene islands of North Italy, could be related to the dispersal across small marine straits of a member of the northern stock (Kotsakis et al. 2004), but a vicariant event cannot be excluded categorically.

Palaeogene Asian tomistomines.—Efimov (1988, 1993, and references therein), described several tomistomines from Eocene and early Oligocene sediments of Asia (Kazakhstan and Kyrgyzstan): *Dollosuchus zajsanicus* Efimov, 1988 (early–middle Eocene), *Ferganosuchus planus* Efimov, 1982 (middle Eocene), "*Tomistoma*" *borisovi* Efimov, 1988 (late Eocene) and an unidentified tomistomine from the early Oligocene. With the exception of *Ferganosuchus*, all the remains on which these taxa and identifications have been based, are rather fragmentary and therefore poorly diagnostic (Jouve 2004 even suggested that *Ferganosuchus* might be a gavialoid) but this material might indicate the presence of tomistomines in central Asia. In the late Eocene, tomistomines were present in eastern Asia (Yeh 1958; Li 1975) as shown by "*Tomistoma*" *petrolicum* from south China. Moreover, a tomistomine, "*Tomistoma*" *tandoni* Sahni and Mishra, 1975 was described on the basis of remains coming from the middle Eocene of the Indian subcontinent (Sahni and Mishra 1975).

It seems therefore that during the late Eocene and early Oligocene, tomistomines inhabited an area larger than before but, apparently, not Europe.

Despite the presence of a persisting obstacle to dispersal represented by the Obik sea, the chance of spreading from Europe to Asia and vice-versa during different stages of the Eocene was rather high at least for some salt tolerant taxa. Moreover, a possible pre-collision dispersal route from Asia to the Indian subcontinent has been invoked for the crocodylian *Pristichampsus* (see Kotsakis et al. 2004, and references therein).

Nonetheless, before developing any firm hypothesis about the palaeobiogeography of such Asian Palaeogene taxa, taxonomic revision and reassessment of phylogenetic relationships is needed.

North and South American tomistomines.—A single Palaeogene datum is available for the Neotropics: ?*Charactosuchus kugleri* Berg, 1969 was described on the basis of material coming from the middle Eocene of Jamaica (Berg 1969) that later on was linked to the Belgian *Dollosuchus* (see Domning and Clark 1993; James M. Clark, personal communication in Langston and Gasparini 1997). Tomistomine remains have been reported in the early Miocene of Venezuela (Sánchez-Villagra et al. 2000, 2001), but successively attributed to the gavialoid *Siquisiquesuchus venezuelensis* by Brochu and Rincón (2004). Three species belonging to the genus *Charactosuchus* are reported from South America: *Charactosuchus fieldsi* Langston, 1965 in the middle Miocene of Colombia, *C. mendesi* (Souza Filho and Bocquentin, 1989) and the so far not fully described *C. sansoai* Souza Filho, 1991 (Langston 1965; Souza Filho and Bocquentin 1989; Souza Filho 1991; Souza Filho et al. 1993; Gasparini 1996; Langston and Gasparini 1997) in the late Miocene–early Pliocene of Brazil. According to Estes and Báez (1985), an opinion not accepted by Langston and Gasparini (1997), *Charactosuchus* could have entered South America from North America during the Miocene. Webb and Tessman (1967), on the basis of isolated teeth, report the presence of this genus in the early Pliocene of Florida and South Carolina. Since the relationships of *Charactosuchus* are still to be understood (Brochu 2003), its biogeographic history is still questionable. If the affinities of ?*C. kugleri* with *Dollosuchus* will be confirmed, a European origin could not be ruled out and then it could be theorised a dispersal toward North America at some stage in the early Eocene through the De Geer or Thule bridges (Agustí and Antón 2002), followed by a vicariant event when the link between the two northern continents disappeared. A combination of dispersion and vivariance can be claimed also for the South American *Charactosuchus*.

In North America, remains of tomistomines are known at least from the late Oligocene (Erickson and Sawyer 1996) to the Pliocene (Auffenberg 1954). Such remains have been traditionally referred to *Gavialosuchus*, a genus erected for the European taxon *G. eggenburgensis* by Toula and Kail (1885) (see Steel 1973; see below), but recently returned to genus *Thecachampsa* (see Myrick 2001). Three species have been described: *Thecachampsa carolinensis* (Erickson and Sawyer, 1996), *Thecachampsa antiqua* (Leidy, 1852) and *Thecachampsa americana*. The last species could be synonymous with *T. antiqua* (Sellards 1915, 1916; Mook 1924; Auffenberg 1954; Erickson and Sawyer 1996; Brochu 1997; Myrick 2001). However *T. antiqua* is represented only by isolated

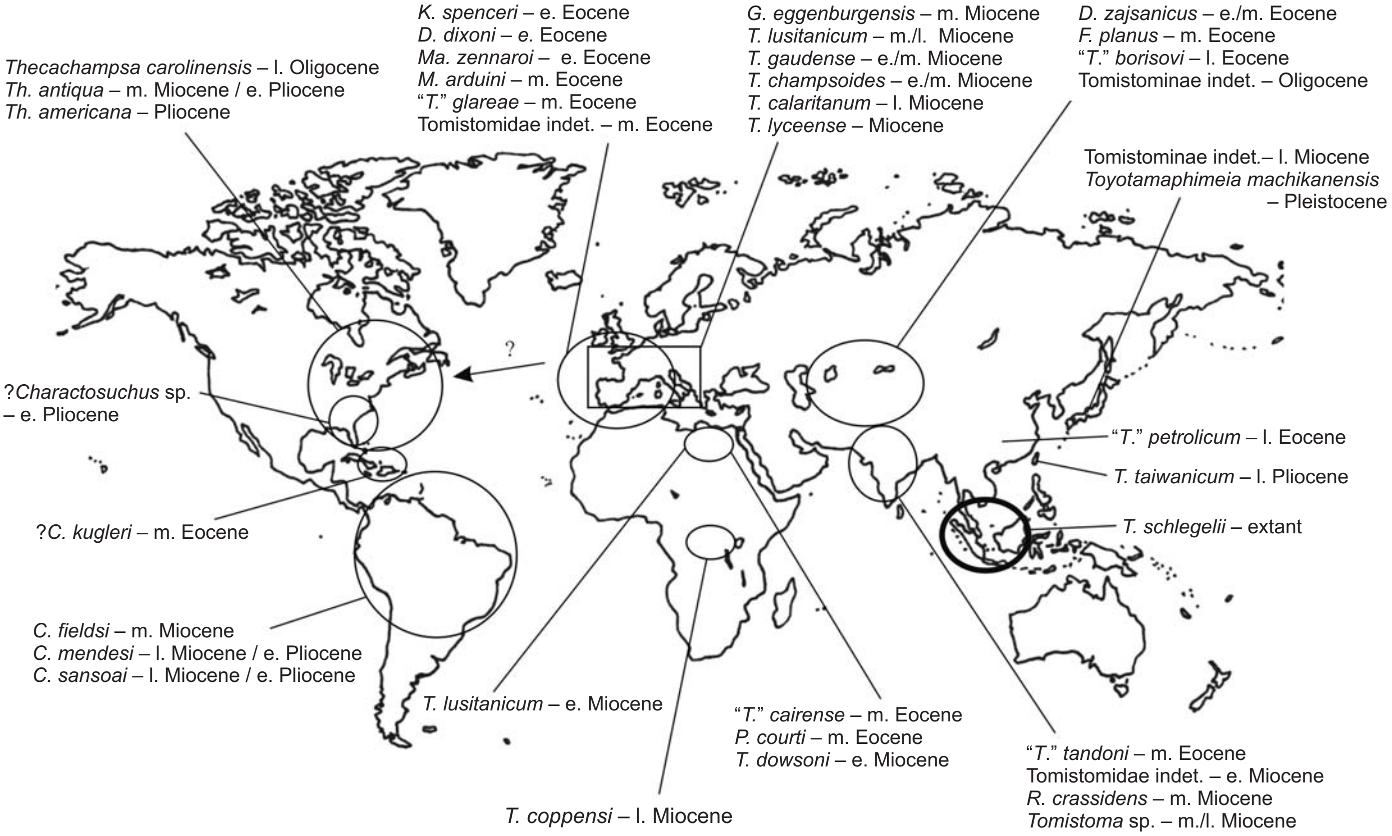

Fig. 5. Schematic global distribution of tomistomine fossil record and approximate present range (in thick circle) of the only extant species *Tomistoma schlegelii*. Taxa are reported from the literature without taxonomic changes. Abbreviations: *C.*, *Charactosuchus*; *D.*, *Dollosuchus*; *F.*, *Ferganosuchus*; *G.*, *Gavialosuchus*; *K.*, *Kentisuchus*; *M.*, *Megadontosuchus*; *Ma.*, *Maroccosuchus*; *P.*, *Paratomistoma*; *R.*, *Ramphosuchus*; *T.*, *Tomistoma*; *Th.*, *Thecachampsa*; e., early; m., middle; l., late.

teeth and for that it is non-diagnosable (Chris Brochu personal communication 2006).

Wide divergences can be underlined in the opinions expressed by different authors about the affinities of such taxa. Myrick (2001) considered the American taxa and the Portuguese remains referred to *Tomistoma lusitanicum* as co-specific. It is worth noting that according to Vianna and Moraes (1945), authors of the later taxon, the Portuguese form was a subspecies of the American species *Tomistoma americanum* (= *Thecachampsa americana*), and that only later on Antunes (1961), elevated the subspecific name to species rank. On the contrary, Brochu (2003) and Brochu and Gingerich (2000) consider the North American "*Gavialosuchus*" clearly distinct from the group represented by "*Tomistoma*" *cairense–Paratomistoma* and all European Miocene tomistomines. Our phylogenetic analysis supports this view (Fig. 4).

According to this hypothesis, a dispersal during the Eocene climatic optimum (Prothero 1994), early Eocene or even (thanks to the salt water tolerance) during the middle Eocene, from Europe to North America can be advanced. A vicariant event also could be invoked to justify the presence of *Thecachampsa* in North America due to the North Atlantic opening during the latest early Eocene. Such an interpretation implies a widespread distribution of *Kentisuchus–Dollosuchus* stock in North America and North Europe. Moreover, if *Charactosuchus* and *Thecachampsa* would eventually show direct phylogenetic relationships, their derivation from a common form close to *Kentisuchus–Dollosuchus* could be suggested. A direct derivation of *Thecachampsa* from *Charactosuchus* cannot be ruled out. However, this relationship should be validated by a stronger phylogenetic support (possibly thanks to new fossil material).

Neogene European and African tomistomines.—In the "Mediterranean" area, after an apparent absence during the late Eocene and the early Oligocene, tomistomines reappear in Europe (France) in the late Oligocene (Antunes and Cahuzac 1999) and their remains are rather common in the early Miocene and, above all, middle Miocene. Their remains have been collected in Portugal, France, Italy, Malta, Germany, Austria, former Yugoslavia, and Poland (see literature in Steel 1973; Buffetaut et al. 1984; Młynarski 1984; Antunes 1987, 1994; Antunes and Ginsburg 1989; Kotsakis et al. 2004). Six species have been described for the European Miocene remains: *Tomistoma lyceense* (Costa, 1848), *Tomistoma gaudense* (Hulke, 1871), *Gavialosuchus eggenburgensis*, *Tomistoma champsoides* Lydekker, 1886, *Tomistoma calaritanum* Capellini, 1890 (actually described in two papers published in the same year: Capellini 1890a, b) and *Tomistoma lusitanicum*. North Africa hosted tomistomines during the early Miocene as testified by *Tomistoma* *dowsoni* Fourtau, 1920 in Egypt and, possibly, the above-mentioned *T. lusitanicum* in Libya (Fourtau 1920; Arambourg and Magnier 1961; Llinas-Agrasar 2004). The generic and specific status as well as the relationships among all these species are rather controversial. According to some authors (Antunes 1994; Brochu 2003; Kotsakis et al. 2004; this paper) *G. eggenburgensis*, *T. lusitanicum* (and possibly *T. calaritanum*) could be valid species but according to others (Rossmann et al. 1999) they belong to a single species whose name, for priority reasons, should be *Gavialosuchus gaudensis*. Actually, if all these remains belong to the same species the specific name *T. lyceensis* should have priority (Costa 1848; Aldinio 1896; Capellini 1897), but the species *T. lyceensis* could be a *nomen vanum* (Delfino et al. 2003).

Whichever name should be used, it is common opinion that all the European Miocene tomistomines are (if not conspecific) strictly linked to each other and that they reached Europe before the end of the Oligocene from Asia (Antunes 1994) or Africa (Kotsakis et al. 2004). After the closure of the Turgai Strait and the emergence of the Paratethys, the ancient barriers between Asia and the European Archipelago no longer existed. From the beginning of Oligocene the possibilities for Asian species to reach Europe greatly increased (Agustí and Antón 2002). On the other hand comunications and faunal exchanges between Europe and Africa are not testified for this time span (Turner and Antón 2004) but a salt water tolerance makes possible a colonization of Europe from North Africa.

Tomistomines (*T. calaritanum* and *Tomistoma* sp. from Sardinia) survived in southern Europe up to the latest Miocene as evidenced by the Italian fossil record in particular (Antunes and Cahuzac 1999; Kotsakis et al. 2004), but, surprisingly, have never been reliably reported in the late Miocene sites of northern Africa despite their presence in Uganda, *Tomistoma coppensi* Pickford, 1994 and possibly in Congo (former Zaire; Aoki 1992; Pickford 1994; Delfino in press).

Neogene and Quaternary Asian tomistomines.—Tomistomine remains are also reported in some Neogene sites of the Indian subcontinent: Tomistomidae indet. in the early Miocene (Vijayasarathi and Sabale 1985), *Tomistoma* sp. in the middle–late Miocene from Nepal (West et al. 1991) and the large *Ramphosuchus crassidens* (Falconer and Cautley, 1840) in the middle Miocene (Head 2001). The affinities of the latter still have not been analysed with a modern approach and therefore it is not possible to state if it directly descended from the Asian Palaeogene taxa or if it dispersed eastward from Africa after the collision of the Afro-Arabian plate with Eurasia in the early Miocene.

In Eastern Asia tomistomines are reported from the late Miocene of Japan (Taruno 1999) and late Pliocene–Pleistocene of Japan and Taiwan: Tomistominae indet., *Toyotamaphimeia machikanensis*, and “*Tomistoma*” *taiwanicum* respectively (Kobatake et al. 1965; Kobatake and Kamei 1966; Shikama 1972; Aoki 1983; Sun et al. 1992; Taruno 1999; Katsura 2004; Kobayashi and Tomida 2005; Kobayashi et al. 2006). Taruno (1999) attributed the fossil tomistomines coming from late Miocene outcrop in Osaka group (Japan) to *Toyotamaphimeia machikanensis*. Later on, however, Kobayashi et al. (2006) refuted this attribution on the basis of several morphological differences (among others: slenderer snout, broader skull table, circular supratemporal fenestra). For that reason the Kishiwada tomistomine will be considered here as Tomistominae indet.

Following Aoki (1983), who erected the new genus *Toyotamaphimeia* for the Japanese species, also the remains from Taiwan should be included in the same genus, but for Jouve (2004) the morphology of the toothrow of “*T.*” *taiwanicum* suggests gavialoid and not tomistomine relationships. A significant chronological gap separates the above-mentioned remains and the extant species *T. schlegelii*, of which, curiously, no fossil remains are known at present. Due to such gap, it is impossible to express any well-grounded biogeographic hypothesis.

Although it seems probable that tomistomines inhabited the area presently corresponding to the range of *T. schlegelii*, the incompleteness of the fossil record does not support any palaeobiogeographic consideration.

Palaeobiogeographic conclusions.—A peculiar problem emerging from the study of tomistomine distribution is the attribution of a large number of species of Asia, Europe and Africa to the living genus. Besides the similarities of many species from Miocene sites of peri-Mediterranean area to the living *T. schlegelii*, it is very difficult to accept a congeneric attribution for a stock of species (*T. calaritanum*, *T. lusitanicum*, *T. dawsoni*, and *T. schlegelii*) spanning from Portugal to Borneo and from late Oligocene to Recent. It seems more parsimonious to ascribe the European and African Miocene taxa to the genus *Gavialosuchus* and consider the genus *Tomistoma* restricted to the Oriental biogeographical region.

Clearly, the phylogenetic context should drive taxonomy but it is worth noting that Jouve’s (2004) results suggest a close relationship between *T. schlegelii* and *T. lusitanicum*, while our results show a polytomy with them and *G. eggemburgensis* as already suggested by Brochu (2000). New fossils could resolve such ambiguity.

The morphological predisposition for salt tolerance reported for extant *T. schlegelii* (Leslie and Taplin 2001) and the marine (or brackish) coastal settings from which most fossil tomistomines come, support the idea that tomistomine biogeography, as testified by a world wide distributed fossil record, is best explained with a series of dispersal events across salt water barriers, responsible for the origin of single species or genera. Even if in few cases a vicariant event cannot be ruled out (the origin of *Megadontosuchus*, *Charactosuchus*, and the distribution of *Thecachampsa*, as specified above), the timing of tomistomine evolution as taxonomic unit indicates that vicariance cannot be considered the leading mechanism for the distribution of their fossil record. In fact, in this case an Early Jurassic divergence for all tomistomines should be invoked, a solution in contradiction with the known phylogeny of Eusuchia.

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References

Agustí, J. and Antón, B. 2002. *Mammoths, Sabretooths and Hominids: 65 Million Years of Mammalian Evolution in Europe*. 313 pp. Columbia Univ. Press, New York.

Aldinio, P. 1896. Sul *Tomistoma* (*Gavialosuchus*) *lyceensis* del calcare miocenico di Lecce. *Atti dell'Accademia Gioenia di Scienze Naturali in Catania (Serie 4)* 9: 1–11.

Altichieri, L. 1980. Il giacimento di Monte Duello (Verona). *In*: *I vertebrati fossili italiani. Catalogo delle Mostra. Verona 1980*, 159–160. Museo Civico di Storia Naturale, Verona.

Andrews, C.W. 1901. Preliminary note on some recently discovered extinct vertebrates from Egypt. *Geological Magazine*, *Decade 4* 8: 436–444.

Andrews, C.W. 1905. Notes on some new Crocodilia from the Eocene of Egypt. *Geological Magazine*, *Decade 5* 2: 481–484.

Antunes, M.T. 1961. *Tomistoma lusitanica*, crocodilien du Miocène du Portugal. *Revista da Facultade de Ciências Universidad de Lisbõa*, *Serie IIc* 9: 3–88.

Antunes, M.T. 1987. Affinities and taxonomical status of Miocene longirostrine crocodilians from Western Europe with remarks on phylogeny, paleoecology and distribution. *Comunicaçoes dos Serviços Geológicos de Portugal* 73: 49–58.

Antunes, M.T. 1994. On Western Europe Miocene gavials (Crocodylia) their paleogeography, migrations and climatic significance. *Comunicaçoes dos Serviços Geológicos de Portugal* 80: 57–69.

Antunes, M.T. and Cahuzac, B. 1999. Crocodilian faunal renewal in the Upper Oligocene of Western Europe. *Comptes Rendus de l'Académie des Sciences de Paris, Série 2* 328: 67–63.

Antunes, M.T. and Ginsburg, L. 1989. Les crocodiliens des faluns miocènes de l'Anjou. *Bulletin du Musée Nationale d'Histoire naturelle de Paris*, *Section C* 11: 79–99.

Aoki, R. 1983. A new generic allocation of *Tomistoma machikanense*, a fossil crocodilian from the Pleistocene of Japan. *Copeia* 1983: 89–95.

Aoki, R. 1992. Fossil crocodilians from the Late Tertiary strata in the Sinda Basin, Eastern Zaire. *African Study Monographs*, *Supplement* 17: 67–85.

Arambourg, C. and Magnier, P. 1961. Gisements de vertébrés dans le bassin tertiaire de Syrte (Libye). *Comptes Rendus de l'Académie des Sciences de Paris, Série D* 252: 1181–1183.

Astre, G. 1931. Les crocodiliens fossiles des terrains tertiaires sous-Pyrénéens. *Bulletin de la Société d'Histoire naturelle de Toulouse* 61: 25–71.

Auffenberg, W. 1954. Additional specimens of *Gavialosuchus americana* (Sellards) from a new locality in Florida. *Quarterly Journal of Florida Academy of Sciences* 17: 185–209.

Benton, M.J. and Clark, J.M. 1988. Archosaur phylogeny and the relationships of the Crocodilia. *In*: M.J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods. Vol. 1*, 295–338, Clarendon Press, Oxford.

Berg, D.E. 1969. *Charactosuchus kugleri*, von Jamaica. *Eclogae Geologicae Helvetiae* 62: 731–735.

Brochu, C.A. 1996. Closure of neurocentral sutures during crocodilian ontogeny: implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology* 16: 49–62.

Brochu, C.A. 1997. *Phylogenetic Systematics and Taxonomy of Crocodylia*. Unpublished Ph.D. thesis. 467 pp. University of Texas, Austin.

Brochu, C.A. 1999. Phylogeny, systematics, and historical biogeography of Alligatoroidea. *Society of Vertebrate Paleontology Memoirs* 6: 9–100.

Brochu, C.A. 2001. Congruence between physiology, phylogenetics, and the fossil record on crocodylian historical biogeography. *In*: G. Grigg, F. Seebacher, and C.E. Franklin (eds.), *Crocodilian Biology and Evolution*, 9–28. Surrey Beatty and Sons, Sydney.

Brochu, C.A. 2003. Phylogenetic approaches toward crocodylian history. *Annual Review of Earth and Planetary Science* 31: 357–397.

Brochu, C.A. 2004. A new Late Cretaceous gavialoid crocodylian from eastern North America and the phylogenetic relationships of Thoracosaurs. *Journal of Vertebrate Paleontology* 24: 610–633.

Brochu, C.A. 2006. Osteology and phylogenetic significance of *Eosuchus minor* (Marsh 1870), new combination, a longirostrine crocodylian from the Late Paleocene of North America. *Journal of Paleontology* 80: 162–186.

Brochu, C.A. (in press). Systematics and taxonomy of Eocene tomistomine crocodylians from Britain and Northern Europe. *Palaeontology*.

Brochu, C.A. and Gingerich, P.D. 2000. New tomistomine crocodylian from the middle Eocene (Bartonian) of Wadi Hitan, Fayum Province, Egypt. *Contributions of Museum of Paleontology of University of Michigan* 30: 251–268.

Brochu, C.A. and Rincón, A.D. 2004. A gavialoid crocodylian from the Lower Miocene of Venezuela. *In*: M. Sánchez-Villagra and J. Clack (eds.), Fossils of the Castillo Formation, Venezuela: Contributions in Neotropical Palaeontology. *Special Papers in Palaeontology* 71: 61–79.

Broin, F. de 1988. Les tortues de Gondwana. *Studia Palaeocheloniologica* 2: 103–142.

Buckland, W. 1836. *Geology and Mineralogy Considered with Reference to Natural Theology*. 618 pp. Pickering, London.

Buffetaut, E. 1982. Systématique, origine et évolution des Gavialidae sud-américains. *Geobios, Mémoire spéciale* 6: 127–140.

Buffetaut, E., Crouzel, F., Juillard, F., and Stigliani, F. 1984. Le crocodilien longirostre *Gavialosuchus* dans le Miocène moyen de Polastron (Gers, France). *Geobios* 17: 113–117.

Buscalioni, A.D., Ortega, F., Weishampel, D.B., and Jianu, C.M. 2001. A revision of the crocodyliform *Allodaposuchus precedens* from the Upper Cretaceous of the Hateg Basin, Romania. Its relevance in the phylogeny of Eusuchia. *Journal of Vertebrate Paleontology* 21: 74–86.

Capellini, G. 1890a. Sul coccodrilliano garialoide (*Tomistoma calaritanus*) scoperto nella collina di Cagliari nel 1868. *Rendiconti della Reale Accademia dei Lincei, serie 4* 6 (I semestre): 149–151.

Capellini, G. 1890b. Sul coccodrilliano garialoide (*Tomistoma calaritanus*) scoperto nella collina di Cagliari nel MDCCCLXVIII. *Atti della Reale Accademia Lincei, Memorie della Classe di Scienze Fisiche, Matematiche e Naturali, serie 4* 6: 507–533.

Capellini, G. 1897. A proposito di *Tomistoma lyceensis*. *Rivista Italiana di Paleontologia* 3: 18–20.

Cleuren, J. and De Vree, F. 2000. Feeding in crocodiles. *In*: K. Schwenk (ed.), *Feeding, Form, Function, and Evolution in Tetrapod Vertebrates*, 337–358. Academic Press, New York.

Costa, M., Galobart, A., Roger, E., and Schleich, H. 1995. Primer hallazgo de resto fosiles de cocodrilo en el Parque National de Ordesa y Monte Perdido (Pirineo Central, Huesca). *XI Jornadas de Paleontologia*, Huesca, 63–64.

Costa, O.G. 1848. *Paleontologia del regno di Napoli. Parte I. Stable Tip.* 203 pp. Tramater, Napoli.

Cuvier, B. 1807. Sur les différentes espèces de crocodiles vivants et sur leurs caractères distinctifs. *Annales du Muséum d'Histoire Naturelle* 10: 8–66.

Daudin, F.M. 1801–1803. *Histoire naturelle, generale et particuliere des reptiles. Vol. 1*. 384 pp. F. Dufart, Paris.

Del Vecchio, C. 1921. Su alcuni denti di *Tomistoma* (Crocodilia) dell'Oligocene di Visone presso Acqui. *Atti della Società Italiana di Scienze Naturali* 60: 419–431.

Delfino, M. (in press). Late Neogene crocodylian faunas from Libya and the Mediterranean area. *In*: *Geology of East Libya, Proceedings, 3rd Symposium Geology of East Libya, Sedimentary Basins of Libya, 21–23 November 2004*. 5 pp. Bingazi, Libya.

Delfino, M., Pacini, M., Varola, A., and Rook, L. 2003. The crocodiles of the "Pietra Leccese" (Miocene of southern Italy). *Abstracts of 1st Meeting European Association of Vertebrate Palaeontology*, 18. Basel.

Delfino, M., Piras, P., and Smith, T. 2005. Anatomy and phylogeny of the gavialoid crocodylian *Eosuchus lerichei* from the Paleocene of Europe. *Acta Palaeontologica Polonica* 50: 565–580.

Dollo, L. 1883. Première note sur les crocodiliens de Bernissart. *Bulletin de Musée Royal d'Histoire Naturelles de Belgique* 2: 309–340.

Domning, D.P. and Clark, J.M. 1993. Jamaican Tertiary marine Vertebrata. *In*: R.M. Wright and E. Robinson (eds.), Biostratigraphy of Jamaica. *Geological Society of America Memoir* 182: 413–415.

Efimov, M.B. 1982. New fossil crocodiles from the USSR [in Russian]. *Paleontologičeskij žurnal* 1982 (2): 146–150.

Efimov, M.B. 1988. The fossil crocodiles and champsosaurids of Mongolia and USSR [in Russian]. *Trudy, Sovmestnaâ Sovetcko-Mongol'skaâ Paleontologičeskaâ Èkspediciâ* 36: 1–108.

Efimov, M.B. 1993. The Eocene crocodiles of the GUS—a history of development. *Kaupia* 3: 23–25.

Endo, H., Aoki, R., Taru, H., Kimura, J., Sasaki, M., Yamamoto, M., Arishima K., and Hayashi Y. 2002. Comparative functional morphology of the masticatory apparatus in the long-snouted Crocodiles. *Anatomia, Histologia, Embryologia* 31: 206–213.

Erickson, B.R and Sawyer, G.T. 1996. The estuarine crocodile *Gavialosuchus carolinensis* n. sp. (Crocodylia: Eusuchia) from the Late Oligocene of South Carolina, North America. *Science Museum of Minnesota Monographs (Paleontology)* 3: 1–47.

Estes, R. and Báez, A. 1985. Herpetofaunas of North and South America during the Late Cretaceous and Cenozoic: evidence for interchange? *In*: F.G. Stehli and S.D. Webb (eds.), *The Great American Biotic Interchange*, 139–197. Plenum Press, New York.

Fabiani, R. 1915. Il Paleogene del Veneto. *Memorie del'Istituto di Geologia della Regia Università di Padova* 3: 1–336.

Falconer, H. and Cautley, P.T. 1840. Notice on the remains of a fossil monkey from the Tertiary strata of the Sewalik Hills in the North of Hindoostan. *Transactions of Geological Society of London* 2: 499–504.

Fitzinger, L.J. 1826. *Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften. Nebst einer Verwandtschaftstafel und einem Verzeichnisse der Reptiliensammlung des K.K. zoologischen Museum's zu Wien*. vi + 66 pp. Vienna.

Fourtau, R. 1920. Un nouveau genre de gavialidés. Suppl. II. *In*: *Contribution à l'étude des vertébrés miocènes de l'Égypte*, 116–121. Egypt Survey Department, Cairo.

Gasparini, Z. 1996. Biogeographic evolution of the South American crocodilians. *Münchner Geowissenshaftliche Abhandlungen* 30: 159–84.

Gatesy, J., Baker, R.H., and Hayashi, C. 2004. Inconsistencies in arguments for the supertree approach: supermatrices *versus* supertrees of Crocodylia. *Systematic Biology* 53: 342–355.

Geoffroy Saint-Hilaire, E. 1807. Description de deux crocodiles qui existent dans le Nil, compares au crocodile de Saint-Domingue. *Annales du Muséum d'Histoire naturelle* 10: 67–86.

Gheerbrant, E., Sudre, J., Iarochene, M., and Moumni, A. 2001. First ascertained African "condylarth" mammals (primitive ungulates: cf. *Bulbulodentata* and cf. *Phenacodonta*) from the earliest Ypresian of the Ouled Abdoun Basin, Marocco. *Journal of Vertebrate Paleontology* 21: 107–118.

Gilmore, C.W. 1911. A new fossil alligator from the Hell Creek beds of Montana. *Proceedings of the United States National Museum* 41: 297–302.

Gmelin, J.F. 1789. Regnum animale. *In*: *Caroli a Linne Systema Naturae per regna tri naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Volume 1 (3)*, 1033–1516. G.E. Beer, Leipzig.

Head, J.J. 2001. Systematics and body size of the gigantic, enigmatic crocodyloid *Ramphosuchus crassidens*, and the faunal history of Siwalik group (Miocene) crocodilians. *Journal of Vertebrate Paleontology* 21(Supplement to No. 3): 59A.

Hulke, J.W. 1871. Note on some reptilian fossils from Gozo. *Quarterly Journal of Geological Society of London* 27: 29–33.

Huxley, T.H. 1875. On *Stagonolepis robertsoni*, and on the evolution of the Crocodilia. *Quarterly Journal of the Geological Society of London* 31: 423–438.

International Commission on Zoological Nomenclature 1999. *International Code of Zoological Nomenclature, Fourth Edition, Adopted by the International Union of Biological Sciences*. 306 pp. International Trust for Zoological Nomenclature, London.

Jonet, S. and Wouters, G. 1977. *Maroccosuchus zennaroi*, crocodilien eusuchien nouveau des phosphates du Maroc. *Notes et Mémoires du Service Géologique du Maroc* 38: 177–202.

Jouve, S. 2004. *Etude des crocodyliformes fini Crétace-Paléogène du Bassin de Oulad Abdoun (Maroc) et comparaison avec les faunes africaines contemporaines: systématique, phylogénie et paléobiogéographie*. Ph.D. thesis. 652 pp. Muséum National d'Histoire Naturelle de Paris, Paris.

Kälin, J.A. 1955. Zur Stammesgeschichte der Crocodilia. *Revue Suisse de Zoologie* 62: 347–56.

Kamei, T. and Matsumoto, E. 1965. *In*: N. Kobatake, M. Chiji, N. Ikebe, S. Ishida, T. Kamei, K. Nakaseko, and E. Matsumoto (eds.), *Discovery of a Crocodile Fossil from the Osaka Group* [in Japanese]. *Quaternary Research* [= *Daiyonki Kenkyu*] 4 (2): 47–58.

Katsura, Y. 2004. Paleopathology of *Toyotomaphimeia machikanensis* (Diapsida, Crocodylia) from the Middle Pleistocene of Central Japan. *Historical Biology* 16: 93–97.

Kobatake, N. and Kamei, T. 1966. The first discovery of fossil crocodile from Central Honshu Japan. *Proceedings of Japanese Academy* 42: 264–269.

Kobatake, N., Chiji, M., Ikebe, N., Ishida, S, Kamei, T., Nakaseko, K., and Matsumoto, E. 1965. Discovery of a crocodile fossil from the Osaka Group [in Japanese]. *Quaternary Research* [= *Daiyonki Kenkyu*] 4 (2): 47–58.

Kobayashi, Y. and Tomida, Y. 2005. Anatomy of *Toyotomaphimeia machikanensis* (Crocodylia) from the Pleistocene of Japan and reassessment of its phylogenetic status. *Journal of Vertebrate Paleontology* 25 (Supplement to No. 3): 78A–79A.

Kobayashi, Y., Tomida, Y., Kamei, T., and Eguchi, T. 2006. Anatomy of a Japanese tomistomine crocodylian, *Toyotamaphimeia machikanensis* (Kamei et Matsumoto, 1965) from the Middle Pleistocene of Osaka prefecture: the reassessment of its phylogenetic status within Crocodylia. *National Science Museum Monograph* 35: 121.

Kotsakis, T., Argenti, P., Barisone, G., Delfino, M., Palombo, M.R., Pavia, M., and Piras, P. 2005. Il Paleogene: i vertebrati continentali. *In*: L. Bonfiglio (ed.), Paleontologia dei Vertebrati in Italia. *Memorie del Museo Civico di Storia Naturale di Verona, Serie 2, Scienze della Terra* 6: 131–139.

Kotsakis, T., Delfino, M., and Piras, P. 2004. Italian Cenozoic crocodilians: taxa, timing and biogeographic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 210: 67–87.

Kuhn, O. 1938. Die Crocodilier aus dem Eozän des Geiseltales bei Halle. *Nova Acta Leopoldina, Nova Serie* 6: 313–329.

Lambe, L.M. 1907. On a new crocodilian genus and species from Judith River formation of Alberta. *Transactions of the Royal Society of Canada* 3: 219–244.

Langston, W. 1965. Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America. *University of California Publications in Geological Sciences* 52: 1–152.

Langston, W. and Gasparini, Z. 1997. Crocodilians, *Gryposuchus* and the South American gavials. *In*: R.F. Kay, R.H. Madden, R.L. Cifelli, and J. Flynn (eds.), *Vertebrate Paleontology in the Neotropics. The Miocene fauna of La Venta, Colombia*, 113–154. Smithsonian Institution Press, Washington.

Leidy, J. 1852. Description of a new species of crocodile from the Miocene of Virginia. *Journal of Academy of Natural Sciences of Philadelphia* 2: 135–138.

Leslie, A.J. and Taplin, L.E. 2001. Recent development in osmoregulation of crocodilians. *In*: G. Grigg, F. Seebacher, and C.E. Franklin (eds.), *Crocodilian Biology and Evolution*, 265–279. Surrey Beatty and Sons, Sydney.

Li, J.-L. 1975. New material on *Tomistoma petrolica* of Maoming, Kwantung [in Chinese]. *Vertebrata Palasiatica* 13: 190–191.

Llinas-Agrasar, E. 2004. Crocodile remains from the Burdigalian (Lower Miocene) of Gebel Zelten (Libya). *Geodiversitas* 26: 309–321.

Lydekker, R. 1886. On the occurrence of the crocodilian genus *Tomistoma* in the Miocene of the Maltese islands. *Quarterly Journal of Geological Society of London* 42: 20–22.

Młynarski, M. 1984 Notes on the amphibian and reptilian faunas of the Polish Miocene. *Acta Zoologica Cracoviensia* 27: 127–148.

Mook, C.C. 1924. Further notes on the skull characters of *Gavialosuchus americana* (Sellards). *American Museum Novitates* 155: 1–2.

Mook, C.C. 1955. Two new genera of Eocene crocodilians. *American Museum Novitates* 1727: 1–4.

Müller, J. 1838. Waarnemingen over de Indische krokodillen en Beschrijving van eene nieuwe soort. *Tydschrift voor Natuurlijke Geschiedenis en Physiologie* 5: 67–87.

Müller, L. 1927. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. V. Tertiäre Wirbeltiere: 1. Beiträge zur Kenntnis der Krokodilier des ägyptischen Tertiärs. *Abhandlungen der Bayerischen Akademie der Wissenschaften* 31 (2): 1–97.

Myrick, A.C. 2001. *Thecachampsa antiqua* (Leidy, 1852) (Crocodylidae, Thoracosaurinae) from fossil marine deposits at Lee Creek Mine, Aurora, North Carolina, USA. *Smithsonian Contributions in Paleobiology* 90: 219–225.

Nicolis, E. 1882. *Note illustrative alla carta geologica della provincia di Verona*. 150 pp. H.I. Münster, Verona.

Owen, R. 1850. Monograph on the fossil Reptilia of the London Clay and of the Bracklesham and other Tertiary beds. Part II. Crocodilia. *Palaeontographical Society Monographs* 3: 5–50.

Owen, R. 1874. Monograph on the fossil Reptilia of the Wealden and Purbeck Formations. Supplement no. VI. (*Hylaeochampsa*.). *Palaeontographical Society Monographs* 27: 1–7.

Pickford, M. 1994. Late Cenozoic crocodiles (Reptilia: Crocodylidae) from the Western Rift, Uganda. *In*: B. Senut and M. Pickford (eds.), *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire, Vol. II—Palaeobiology*, 137–155. CIFEG, Publication Occasionnelle, Orléans.

Pinna, G. 1989. *Il grande libro dei fossili*. 383 pp. Rizzoli, Milano.

Prothero, D. 1994. *The Eocene–Oligocene Transition*. 291 pp. Columbia University Press, New York.

Rage, J.-C. 1996. Terrestrial trans-Tethyan dispersals: an overview. *In*: *Expanded Abstracts of First European Workshop on Vertebrate Palaeontology, 1st–4th May 1996, Copenhagen*, 4 pp.

Rauhe, M., Frey, E., Pemberton, D.S., and Rossmann, T. 1999. Fossil crocodilians from the Late Miocene Baynunah Formation of the Emirate of Abu Dhabi, United Arab Emirates: osteology and palaeoecology. *In*: J. Whybrow and A. Hill (eds.), *Fossil Vertebrates of Arabia*, 163–185. Yale University Press, New Haven.

Roccaforte, P., Sorbini, L., and Piccoli, G. 1994. The fossiliferous sites with Tertiary vertebrates in Northeastern Italy. *Memorie di Scienze Geologiche* 46: 373–400.

Rossmann, T. 2002. Studies on Cenozoic crocodiles: 10. First evidence of a tomistomid crocodilian (Eusuchia: Tomistomidae) from the Middle Eocene (Geiseltalian, MP 11) of Grube Messel, Germany. *Neues Jahrbuch.für Geologie und Paläontologie, Monatshefte* 2002: 129–146.

Rossmann, T., Berg, D.E., and Salisbury, S.W. 1999. Studies on Cenozoic crocodiles: 3. *Gavialosuchus* cf. *gaudensis* (Eusuchia: Tomistomidae) from the Lower Miocene of south Germany. *Neues Jahrbuch für Geologie und Paläontologie, Montatshefte* 1999: 321–330.

Sahni, A. and Mishra, V.P. 1975. Lower Tertiary vertebrates from western India. *Monographs of the Palaeontological Society of India* 3: 1–48.

Sánchez-Villagra, M.R., Burnham, R.J., Campbell, D.C., Feldmann, R.M., Gaffney, E.S., Kay, R.F., Lozsán, R., Purdy, R., and Thewissen, J.G.M. 2000. A new near-shore marine fauna and flora from the early Neogene of northwestern Venezuela. *Journal of Paleontology* 74: 957–968.

Sánchez-Villagra, M.R., Gasparini, Z., Lozsan, R., Moody, J.M. Jr., and Uhen, M.D. 2001. New discoveries of vertebrates from a near-shore marine fauna from the Early Miocene of northwestern Venezuela. *Paläontologische Zeitschrift* 75: 227–232.

Scortegagna, F.O. 1836. *Sulla formazione geologica della Collina detta la Favorita presso Lonigo*. 25 pp. Poligrafica G. Antonelli, Verona.

Scortegagna, F.O. 1838. Sopra il teschio di un coccodrillo fossile rinvenuto nel Monticello di Lonigo. *Atti dell'Ateneo Veneto* 2: 139–149.

Sellards, E.H. 1915. A new gavial from the Late Tertiary of Florida. *American Journal of Science* 40: 135–138.

Sellards, E.H. 1916. A new tortoise and a supplementary note on the gavial, *Tomistoma americana*. *American Journal of Science* 42: 235–240.

Shikama, T. 1972. Fossil Crocodilia from Tsochin, south-western Taiwan. *Yokohama National University, Science Report, Section II* 19: 125–132.

Souza Filho, J.P. 1991. *Charactosuchus sansaoi*, uma nova espécie de Crocodilidae (Crocodylia) do Neógeno do Estado o Acre, Brasil. *Actas do XII Congreso Brasileiro de Paleontologia*, 36. São Paulo.

Souza Filho, J.P. and Bocquentin, J. 1989. *Brasilosuchus mendensi* n.g., n.sp., um novo representante da familia Gavialidae do Neógeno do Estado do Acre, Brasil. *Anais do XI Congreso Brasiliero de Paleontologia* 1: 457–463. Curitiba.

Souza Filho, J.P., Bocquentin, J., and Silva, E. 1993. Novas interpretaçoes do genero *Brasilosuchus* (Crocodylia) do Neógeno do Estado do Acre, Brasil. *Resumos do XIII Congreso Brasileiro de Paleontologia e do I Simposio de Paleontologia Cone Sul*, 130. São Leopoldo.

Steel, R. 1973. *Handbuch der Paläoherpetologie, Vol. 16: Crocodylia*. 116 pp. Fischer-Verlag, Stuttgart.

Sun, A., Li, J., Ye, X., Dong, Z., and Hou, L. 1992. *The Chinese Fossil Reptiles and Their Kins*. 260 pp. Science Press, Beijing.

Swinton, W.E. 1937. The crocodile of Maransart (*Dollosuchus dixoni* [Owen]). *Mémoires du Musée d'Histoire Naturelle de Belgique* 80: 1–44.

Swofford, D.L. 2002. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4*. Sinauer Associates, Sunderland.

Taruno, H. 1999. A fossil crocodile from Nagareki Town, Kishiwada City. *In*: Kishiwada City Board of Education (ed.), *Excavation Report on a Fossil Crocodile from Nagareki Town, Kishiwada City*, 1–36. Natural History Museum of Kishiwada City, Kishiwada, Osaka.

Tchernov, E. 1986. Evolution of the crocodiles in East and North Africa. *Cahier de Paléontologie. Travaux de Paléontologie est-africaine*. 65 pp. Editions CNRS, Paris.

Toula, F. and Kail, J.A. 1885. Über einen Krokodil-Schädel aus den Tertiärablagerungen von Eggenburg in Niederösterreich: eine paläontologische Studie. *Denkschriften der Keiserlichen Akademie der Wissenschaften von Wien, Mathematisch-naturwissenschaftliche Klasse* 50: 299–355.

Turner, A. and Antón, M. 2004. *Evolving Eden*. 269 pp. Columbia University Press, New York.

Uzielli, G. 1886. Sopra un cranio di coccodrillo trovato nel Modenese. *Bollettino della Società Geologica Italiana* 5: 355–364.

Vasse, D. 1993. *Systématique de crocodiles du Crétacé supérieur et du Paléogène d'Europe. Aspects paléobiogéographiques et paléoécologiques*. Unpublished Ph.D. thesis. 224 pp. Université Paris VI, Paris.

Vianna, A. and Moraes, A. 1945. Sur un crâne de crocodile fossile decouvert dans le Miocène de Lisbonne. *Boletim de la Sociedade Geológica de Portugal* 4: 161–170.

Vijayasarathi, G. and Sabale, A.B. 1985. Miocene crocodilian (Tomistomidae) fossil from southwestern Kutch, Gujarat. *Current Science* 54: 1071–1073.

Webb, S.D. and Tessman, N. 1967. Vertebrate evidence of a low sea level in the middle Pliocene. *Science* 156: 379.

West, R.M., Hutchinson, J.H., and Munthe, J. 1991. Miocene vertebrates from the Siwalik Group, Western Nepal. *Journal of Vertebrate Paleontology* 11: 108–129.

Wood, S.V. 1846. On the discovery of an alligator and of several new Mammalia in the Hordwell Cliff; with observations upon the geological phenomena of that locality. *London Geological Journal* 1: 117–122.

Yeh, H.-K. 1958. A new crocodile from Maoming, Kwangtung [in Chinese]. *Vertebrata Palasiatica* 2: 237–242.

Zigno, A. de 1880. Sopra un cranio di coccodrillo scoperto nel terreno eoceno del Veronese. *Atti della Reale Accademia Lincei*, *Memorie della Classe di Scienze Fisiche, Matematiche e Naturali, Serie 3* 5: 65–72.

Appendix 1

A list of the material examined attributed to *Megadontosuchus arduini* arranged according to its original identification.

Megadontosuchus arduini (Monte Duello): MGPD 1z, skull and mandible (original figured syntype; proposed lectotype); MGPD 4z, incomplete skull lacking part of the rostrum (probably a syntype); MGPD 5z, anterior part of the rostrum (probably a syntype; same specimen of MGPD 4z); MGPD 6z, fragment of right mandibular branch (probably a syntype); MGPD 8z; fragment of right mandibular branch (probably a syntype); MGPD 24z, vertebral centrum (figured syntype, probably the same individual of MGPD 1z); MGPD 25z, vertebral centrum (figured syntype, probably the same individual of MGPD 1z); MGPD 7030z, MGPD 7031z, MGPD 7032z, tooth; MGPD 7033z, MGPD 7063z, MGPD 7064z, fragment of mandibular branch; MGPD 7065z, tooth.

?*Megadontosuchus arduini* (Monte Duello): MGPD 7023z, MGPD 7024z, MGPD 7025z, tooth; MGPD 7026z, 5 teeth; MGPD 7027z, MGPD 7028z, MGPD 7029z, tooth; MGPD 7073z, MGPD 7075z, MGPD 7079z, indet. fr.

Gavialis dixoni (Monte Duello): MGPD 7037z, MGPD 7038z, tooth; MGPD 7039z, 6 teeth; MGPD 7040z, tooth; MGPD 7042z, indet.; MGPD 7044z, MGPD 7045z, MGPD 7046z, MGPD 7047z, MGPD 7048z, MGPD 7049z, MGPD 7056z, MGPD 7057z, MGPD 7058z, vertebral centrum; MGPD 7060z, fragment of right mandibular branch; MGPD 7061z, tooth; MGPD 7062z, fragment of right mandibular branch.

Crocodylus champsoides (Monte Duello): MGPD 7466z, fragment of left mandibular branch; "*Crocodylus*" (Monte Duello): MGPD 7067z, MGPD 7068z, MGPD 7069z, MGPD 7070z, MGPD 7071z, osteoderm.

Crocodylus spenceri (Colle La Favorita): MGPD 7438C, fragment of left mandibular ramus. These remains were described by Scortegagna (1836, 1838), who attributed them to *Crocodylus acutus* Geoffroy Saint-Hilaire, 1807. Fabiani (1915) referred this material possibly to *C. spenceri.*

Crocodylia indet. (Monte Duello): MGPD 7041z, tooth and vertebral centrum; MGPD 7050z, MGPD 7051z, MGPD 7052z, MGPD 7053z, MGPD 7054z, MGPD 7055z, vertebral centrum.

Appendix 2

Character coding of *Megadontosuchus arduini*. Characters 1–164 are defined in Brochu (1999). Characters 165 and 166 are defined in Buscalioni et al. (2001). Character 167 corresponds to character 165 of Brochu (2006).

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?????????? ???????1?? ?????????? ????1????? ??(04)???1?0? ?11??????0 ?1?10??0?1 ????0?021?
20?0?10?1? ?1??1????0 0?1??????? ???????10? ??10??????    ?0??0??201 1000?1???? ??1???????
0??????
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