# Italian Cenozoic crocodilians: taxa, timing and palaeobiogeographic implications

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## Abstract

Crocodylian remains are collected in 39 fossil-bearing localities but only in seven localities specimens with reliable taxonomic attributions, at least to genus level have been collected. Three species have been reported from the early Lutetian Purga di Bolca site: *Pristichampsus* cf. *Pristichampsus rollinati*, *Asiatosuchus* sp., *Hassiacosuchus* sp. (= *Allognathosuchus* sp.). The three crocodilians discovered at Purga di Bolca have been reported also from Geiseltal and Messel (Middle Eocene, Germany). Bolca at that time was part of a Tethysian archipelago and no mammals have been found there till now. Crocodilians and turtles clearly arrived from the European mainland across a marine water barrier. Among the other fossiliferous localities of Veneto, very interesting is the Monte Zuello site, of late Middle Eocene age, yielding a longirostrine crocodilian, *Megadontosuchus arduini*, a tomistomine species. Tomistomines are known in contemporaneous sediments of both Europe and Africa, but the European forms *Dollosuchus* and *Kentisuchus* seem the closest taxa. Remains of Oligocene age have been collected in Veneto and Liguria, but the fossils discovered in the second region are teeth or fragmented bones. The fossil crocodilians of Monteviale (Veneto), of Early Oligocene age, have been assigned to two species but they have been recently all identified as *Diplocynodon ratelii*, known from several European sites of Late Eocene, Oligocene and Miocene age. This species arrived in the Monteviale area from the European mainland across a narrow sea. Several crocodilian fossils of Miocene age are very fragmentary or represented by isolated teeth. In the Middle and Late Miocene of Sardinia, a well-established species, *Tomistoma calaritanum* is present. Remains of *Tomistoma* of the same age have been reported in some localities in Tuscany, Apulia, Sicily and Malta. In the Mediterranean area, the genus is known from European and African sites (of older age). The colonisation of Europe by this genus is the result of a dispersion from Africa (or less probably from Asia). During Late Miocene Sardinia and Tuscany belong to the same palaeobioprovince characterized by the *Oreopithecus–Maremmia* fauna. In Tuscany, a crocodilian identified as *Crocodylus bambolii* is present in the late Miocene site of Monte Bamboli. If the generic attribution of this form is correct, its ancestors must have arrived from Africa. Another fossil assemblage of Late Miocene age characterizes the Apulia–Abruzzi palaeobioprovince (*Hoplitomeryx–Microtia* fauna) and testifies complete isolation between the two palaeobioprovinces. In this last area, remains of *Crocodylus* sp. have been collected in coastal sandstones at Scontrone (Abruzzi) and in several fissure fillings of Gargano of slightly younger age. The ancestors of this species arrived from Africa while no African elements are present among the mammalian fauna. The dispersion of the genus *Crocodylus* in the Italian palaeoislands may

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have taken place once, with allopatric differentiation of the two populations (Tuscany–Sardinia and Apulia–Abruzzi) or twice with independent colonisation of each area.

## 1. Introduction

The fossil remains of the Cenozoic Italian crocodilians are frequent (Fig. 1) though, unfortunately, the majority of these remains are represented by bone fragments, osteoderms or, more habitually, by isolated teeth. Short summaries of the crocodilian Italian faunas have been recently published (Delfino, 2001a,b) revealing that all the crocodilian taxa belong to the crown-group Crocodylia, but a profound phylogenetic revision is still missing. Herein, we go over the last generic allocation recently revised of data concerning the crocodilian remains from Italy and Malta. Both, from a geographic point of view, belong to the "Italian Region" (Lanza and Corti, 1996). The taxonomic data provided represent an updated version
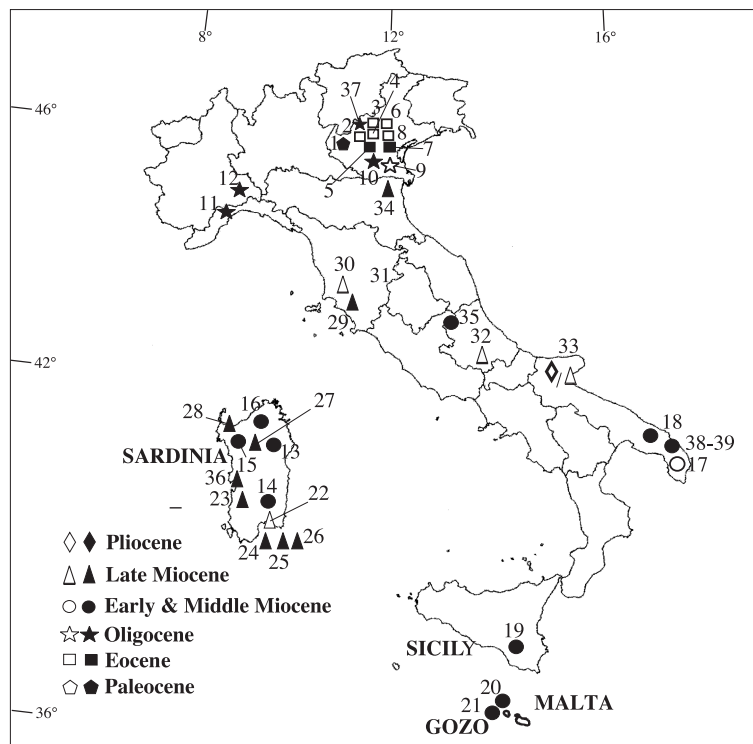


Fig. 1. Italian Cenozoic crocodile-bearing localities. White symbols represent localities with systematically meaningful remains. Black symbols represent all other localities. (1) Spilecco, (2) Monte Bolca, (3) Monte Zuello, (4) Roncà, (5) Montecchia di Crosara, (6) Colle La Favorita near Lonigo, (7) Monticello di Fara, (8) Cornedo, (9) Monteviale, (10) Faedo, (11) Santa Giustina, (12) Visone, (13) Strintu de Melonis near Nurri, (14) Fangario and Bingia Fargeri, (15) Florinas, (16) La Crucca, (17) Iola, (18) Cannole, (19) Donnalucata, (20/21) Gozo Island, (22) Is Miriones, (23) Tres Nuraghes, (24/25/26) neighbours of Cagliari (Piazza d'armi di Cagliari, Cimitero di Cagliari and Bonaria), (27) Monte Oria, (28) Fiume Santo, (29) Casteani, (30) Montebamboli, (31) Radicondoli, (32) Scontrone, (33) Gargano (between Apricena and Poggio Imperiale), (34) Monticino, (35) Lettomanoppello, (36) Capo della Frasca, (37) Chiuppano, (38–39) Melpignano and Melpignano–Cursi.

of a working taxon–locality database originally created for Neogene–Quaternary and extended to the entire Cenozoic (Italian Paleoherpetofaunas Database; Delfino, 1997, 2002, 2003). Although teeth morphology has been widely used in the past for taxonomical purposes, its value seems to be, with few exceptions (i.e., ziphodont crocodilians), rather weak or useless at present (Brochu, 2000). This represents a constraint in the number of findings that can be reasonably allocated at lower taxonomic units and therefore ineffective for palaeobiogeographic considerations. In some cases, the quality of data is influenced by the uncertain taxonomic allocation implying, obviously, different hierarchical level for palaeobiogeographic interpretations. Nevertheless, the fossil record is sufficient enough to allow for some general palaeobiogeographic considerations, and to depict an evolutionary scenario of the crocodilian Cenozoic assemblages by combining palaeogeographic, palaeobiologic and phylogenetic interpretations.

The palaeogeographic maps are simplified versions of those published by Rögl (1998, 1999) and Scotese (2002). The Italian region consisted of archipelagos during the Cenozoic, at least up to the end of the Messinian. After, it developed into peninsular conditions, with a high content of nonmarine organisms. This palaeogeographic shifting is founded in the mammalian fossil record testifying first, the presence of many endemic assemblages, and the subsequent colonisation of these islands due to dispersion through filter bridges (from Balkan peninsula and/or Central–Western Europe) or sweepstakes routes (from Africa) or by vicariance events (i.e., Corso-Sardinian block) (Kotsakis et al., 1997). We use here crocodilian fossil record as further evidence to contrast former palaeobiogeographic hypotheses, and to elaborate a complex but complete scenario on the evolutionary faunas of the Italian region within a broader Eurasiatic framework.

## 2. The Cenozoic crocodilian fossil record

All fossil crocodilians collected in Italy and Malta have been reported in Table 1. We specified the age, the taxonomic allocation (where possible), the fossil material, the localities, the palaeoenvironment suggested by sedimentology and fossil assemblages and the supposed origin.

### 2.1. Palaeocene

*Spilecco* (Fig. 1; no. 1)—The Italian Palaeocene has yielded only a single crocodilian tooth collected from coastal deposits in the Spileccian stratotype (Spilecco, Verona, Veneto). This remain was originally referred to a mosasaur (Nicolis, 1907; Medizza, 1980a). Due to the fact that the Spilecco succession belongs partially to the Thanetian (Late Palaeocene) and partially to the Ypresian (Early Eocene), and that the precise origin of the specimen is unknown, the age of this crocodilian could be even younger (Medizza, 1980a).

#### 2.1.1. Palaeobiogeographic implications

Because of the paucity of Spilecco's material, and because of the poorly known and patchy Palaeocene European fossil record (Ginsburg and Bulot, 1997; Brochu, 2003), it is hard to draw any palaeobiogeographic implication. Due to the width of the Tethys, it is possible that this form comes from the Northern Tethysian margin, Spilecco being closer to this margin.

### 2.2. Eocene

*Bolca* (Fig. 1; no. 2)—All the Eocene crocodilians of Italy were discovered at the Veneto region (Fig. 1) with the majority of the specimens found in the locality of Vestenanova di Bolca (Verona), internationally known for its rich icthyofauna. Several complete crocodilian skeletons, invariably deformed by the lithostatic weight, come from the early Lutetian of the Monte Purga area, where sediments of fresh or brackish water outcrop (Sorbini, 1972, 1999). The Monte Purga crocodilians have been described (or mentioned) by several workers (Lioy, 1865a,b,c,d, 1866, 1896, 1906; Nicolis, 1882, 1884; Sacco, 1895; Fabiani, 1912, 1914, 1915; Del Vecchio, 1921; Berg, 1966; Sorbini, 1972; Steel, 1973; Medizza, 1980b; Pinna, 1989; Vasse, 1992; Roccaforte et al., 1994; Rauhe and Rossmann, 1995; Del Favero, 1999). Traditionally, these remains have been allocated to two species: *Crocodylus vicetinus* Lioy 1865 and *Crocodylus bolcensis* Sacco 1895. The last hallmark revision of the European crocodilian assemblages was carried out by Berg (1966, 1969). He summarized the presence of four genera at Monte

Table 1
Summary of taxa, localities (for numbers refer to map in Fig. 1), referred materials (Mat.), age, palaeoenvironment (Palaeoe.) and supposed origin

| Age | Taxon | Mat. | Locality | Palaeoe. | Supposed origin |
|---|---|---|---|---|---|
| L Palaeocene (?) | Crocodylia indet. | i to | Spilecco (loc. no. 1) | co w | N Thethysian margin? |
| M Eocene | *Hassiacosuchus* sp. (=? *Allognathosuchus* sp.) | c, p | Bolca–Monte Purga (loc. no. 2) | fr/br w | NAm–>NEu–>It |
| M Eocene | *Asiatosuchus* sp. (including original holotype of *C. vicetinus*) | c, p | Bolca–Monte Purga (loc. no. 2) | fr/br w | As–>Eu–>It |
| M Eocene | *Pristichampsus* cf. *P. rollinati* (including original holotype of *C. bolcensis*) | c, p | Bolca–Monte Purga (loc. no. 2) | fr/br w | As–>Eu–>It |
| M Eocene | *Megadontosuchus arduini* (holotype) | c, p | Monte Zuello (loc. no. 3) | co/br w | NEu–>It |
| M Eocene | Crocodylia indet. (=? *Megadontosuchus arduini*) | c | Roncà (loc. no. 4) | fr w | ?NEu–>It |
| M Eocene | Crocodylia indet. (=? "*Crocodylus vicetinus*") | f | Roncà (loc. no. 4) | fr w | |
| Eocene | Crocodylia indet. (=? *Megadontosuchus arduini*) | c f | Montecchia di Crosara (loc. no. 5) | fr w | ?NEu–>It |
| L Eocene | Crocodylia indet. (=? *Megadontosuchus arduini*) | f, i te | Colle La Favorita (loc. no. 6) | fr w | ?NEu–>It |
| L Eocene | Crocodylia indet. (=? *Megadontosuchus arduini*) | c f | Monticello di Fara (loc. no. 7) | fr w | ?NEu–>It |
| M–L Eocene | Crocodylia indet. (=? "*Crocodylus vicetinus*") | c, p | Cornedo (loc. no. 8) | no info | |
| E Oligocene | *Diplocynodon* cf. *D. rateli* | c, p | Monteviale (loc. no. 9) | fr w | NEu–>It |
| E Oligocene | ?*Diplocynodon rateli* (=*D. dalpiazi*) (including original holotype of *C. dalpiazi*) | c, p | Monteviale (loc. no. 9) | fr w | NEu–>It |
| E Oligocene | ?*Diplocynodon rateli* (=*A. monsvialensis*) (including original holotype of *C. monsvialensis*) | c, p | Monteviale (loc. no. 9) | fr w | NEu–>It |
| E Oligocene | Crocodylia indet. (=*D. dalpiazi*) | i te | Faedo (loc. no. 10) | no info | ?NEu–>It |
| L Oligocene | Crocodylia indet. | c f | Chiuppano (loc. no. 37) | fr w | |
| L Oligocene | Crocodylia indet. | i te | Santa Giustina (loc. no. 11) | fr w | |
| L Oligocene | Crocodylia indet. (=*Tomistoma* sp.) | i te | Visone (loc. no. 12) | co w? | ?Af–>It |
| E Miocene | Crocodylia indet. | i to | Lettomanoppello (loc. no. 35) | co w | |
| E Miocene | Crocodylia indet. (=*Tomistoma* sp.) | i te | Strintu de Melonis (loc. no. 13) | co w | ?Af–>It |
| M Miocene | Crocodylia indet. (=*Tomistoma* cf. *T. calaritanum*) | i te | Fangario (loc. no. 14) | co w | ?Af–>It |
| M Miocene | Crocodylia indet. (=*Tomistoma* cf. *T. calaritanum*) | i te | Bingia Fargeri (loc. no. 14) | co w | ?Af–>It |
| M Miocene | Crocodylia indet. (=*Tomistoma* cf. *T. lusitanicum*) | i te | Florinas (loc. no. 15) | co w | ?Af–>It |
| M Miocene | Crocodylia indet. (=*Tomistoma* cf. *T. calaritanum*) | p | La Crucca (loc. no. 16) | co w | ?Af–>It |
| Miocene | Tomistominae indet. (original holotype of *Tomistoma lyceense*) | c, p | Iola (loc. no. 17) | co w | |

Table 1 (*continued*)

| Age | Taxon | Mat. | Locality | Palaeoe. | Supposed origin |
|---|---|---|---|---|---|
| Miocene | Tomistominae indet. | c, p | Melpignano (loc. no. 38) | co w | ?Af–>It |
| Miocene | Crocodylia indet. | c | Melpignano–Cursi (loc. no. 39) | co w | |
| Miocene | Crocodylia indet. | i te | Cannole (loc. no. 18) | co w | |
| Miocene | Crocodylia indet. | i to | Donnalucata (loc. no. 19) | co w | |
| E–M Miocene | "*Tomistoma gaudense*" (holotype) | c | Gozo Island (loc. no. 20) | o s | Af–>It |
| E–M Miocene | "*Tomistoma champsoides*" (holotype) | c, p | Gozo Island (loc. no. 21) | o s | Af–>It |
| L Miocene | *Tomistoma calaritanum* (holotype) | c, p | Is Miriones (loc. no. 22) | co w | Af–>It |
| L Miocene | Crocodylia indet. (=*Tomistoma* cf. *T. calaritanum*) | i te | Tres Nuraghes (loc. no. 23) | co w | ?Af–>It |
| L Miocene | Crocodylia indet. | i to | Cimitero di Cagliari (loc. no. 24) | co w | |
| L Miocene | Crocodylia indet. | i te | Piazza D'armi di Cagliari (loc. no. 25) | co w | |
| L Miocene | Crocodylia indet. (=*Tomistoma* cf. *T. calaritanum*) | i to | Bonaria (loc. no. 26) | co w | ?Af–>It |
| L Miocene | Crocodylia indet. | i to | Monte Oria (loc. no. 27) | no info | |
| L Miocene | Crocodylia indet. | i te | Fiume Santo (loc. no. 28) | d e | |
| L Miocene | Crocodylia indet. | i to | Casteani (loc. no. 29) | fr w | |
| L Miocene | "*Crocodylus bambolii*" (holotype) | c, p | Montebamboli (loc. no. 30) | fr w | Af–>It |
| L Miocene | Crocodylia indet. | i to | Radicondoli (loc. no. 31) | br w | |
| L Miocene | Crocodylia indet. (=*Crocodylus* sp.) | i te | Scontrone (loc. no. 32) | co l | Af–>It |
| L Miocene (? E Pliocene) | *Crocodylus* sp. | c, p | Gargano (loc. no. 33) | f f | Af–>It |
| L Miocene | Crocodylia indet. | i te | Monticino (loc. no. 34) | f f | |
| L Miocene | Crocodylia indet. | i to | Capo della Frasca (loc. no. 36) | no info | |

The reported taxonomic allocation of some specimens is tentative; all the identifications made on isolated teeth have been considered as Crocodylia indet.; the traditional taxonomic allocation is reported within parentheses (see the text for a comprehensive summary of the opinion expressed by different authors). Early (E), Middle (M), Late (L); North (N), Africa (Af), America (Am), Asia (As), Europe (Eu), Italy (It); cranial remains (c), fragment (f), isolated teeth (i te), isolated tooth (i to), postcranial (p); brackish waters (br w), coastal lagoon (co l), coastal waters (co w), deltaic environment (d e), fissure filling (f f), fresh waters (fr w), open shelf (o s).

Bolca: *Diplocynodon* sp. (= *C. vicetinus*, partim), *Asiatosuchus* sp. (= *C. vicetinus*, partim), *Allognathosuchus* sp. (= *C. vicetinus*, partim), *Pristichampsus* cf. *Pristichampsus rollinati* (Gray 1831) (= *C. bolcensis*).

Recent revisions partially refine these allocations. In the case of *Asiatosuchus*, Vasse (1992), and Rauhe and Rossmann (1995) refer to *Asiatosuchus depressifrons* (Blainville, 1955) the Monte Bolca remains formerly considered by Berg as *Asiatosuchus* sp., while the remains identified by Berg (1966) as *Diplocynodon* sp. have been assigned by Del Favero (1999) to *Diplocynodon* cf. *Diplocynodon ratelii* Pomel, 1847. However, Vasse (1992) identifies the fossils of Monte Bolca as *A. depressifrons* because considers all the European remains of *Asiatosuchus* as belonging to a single species. On the

contrary, Brochu (2003) clearly distinguish two forms: *Asiatosuchus germanicus* Berg 1966, and *Crocodylus depressifrons*. Lacking recent revision of the Monte Bolca material, we prefer to identify this material as *Asiatosuchus* sp.

*Diplocynodon* (from the Purga di Bolca site) has an equivocal age. The matrix embedding this crocodile contains nannofossils indicating a late Eocene or early Oligocene age, which sharply contrasts with the early Lutetian age of Bolca (Del Favero, 1999). It is likely that the crocodilians, as happened with some mammal remains (the rhinoceros *Epiaceratherium bolcense* Abel 1910 = *Trigonias ombonii* G.B. dal Piaz 1930, cf. Kotsakis, 1984a) had been discovered in the Early Oligocene of Monteviale and then referred by mistake to Monte Bolca. Therefore, *Diplocynodon* cf. *Diplo-*

*cynodon ratelii* has been tentatively listed under the locality of Monteviale in Table 1.

*Monte Zuello* (Fig. 1; no. 3)—From another Venetian locality, Monte Zuello (Verona), whose age is Bartonian (late Middle Eocene), comes a complete skull and other remains of a longirostrine crocodilian referred by de Zigno (1880) to *Crocodylus arduini* de Zigno 1880 and then by Mook (1955) to a new genus, *Megadontosuchus*. Several authors quoted subsequently these remains (Nicolis, 1882; Lydekker, 1886a; Uzielli, 1886; Fabiani, 1915; Del Vecchio, 1921; Mook, 1955; Steel, 1973; Altichieri, 1980a; Pinna, 1989; Roccaforte et al., 1994; Brochu, 2001).

*Megadontosuchus arduini* is a longirostrine crocodilian included in the genus *Tomistoma* by Kuhn (1938). Recently, Brochu (2001) has partially confirmed this attribution considering the Monte Zuello remain as a tomistomine close to *Dollosuchus dixoni* (Owen 1850) (Middle Eocene of Maransart, Belgium) and to *Kentisuchus spenceri* (Buckland 1837) (Early Eocene of London Clay of the Isle of Sheppey, Southern England) (see Fig. 5). Following the priority rule of zoological nomenclature, if these three forms belong to the same genus, the generic name *Dollosuchus* should have prevalence (Brochu, 2001). Personal observations (Piras et al., in preparation) suggest that probably the three forms represent at least two different species, as *M. (= Dollosuchus) arduini* is distinct from *D. dixoni*.

*Roncà* (Fig. 1; no. 4) and *Montecchia di Crosara* (Fig. 1; no. 5)—Kuhn (1938) for Roncà (Verona, Veneto) and Lioy (1896) for Montecchia di Crosara (Verona, Veneto) referred the crocodilian material to *Crocodylus arduini*. From Bartonian levels of Roncà did Fabiani (1915), and latter Bergounioux (1954), note *Crocodylus vicetinus*, but it still need of revision to verify if these remains can be ascribed to *C. arduini*.

*Colle La Favorita* (Fig. 1; no. 6) and *Monticello di Fara* (Fig. 1; no. 7)—Remains of a longirostrine species have been also found at Colle La Favorita near Lonigo (Vicenza, Veneto) and nearby Monticello di Fara (Vicenza, Veneto) (Arduino, 1765; Fortis, 1802; Brocchi, 1814; Scortegagna, 1825, 1836, 1838; Lioy, 1896; Del Vecchio, 1921; Roccaforte et al., 1994). Referred to *Crocodylus spenceri* Buckland 1837, these remains (whose age is presumably Late Eocene–Priabonian), never revised up to now, could

possibly belong to *Megadontosuchus arduini*. It is worth noting that following Lydekker (1888) *Crocodylus arduini* is a synonym of *Crocodylus spenceri*, this hypothesis should be tested in a revision of the original material (Piras et al., in preparation).

Steel (1973) refers that remains coming from the Modena surroundings had been ascribed by Uzielli (1886) to the taxon *Megadontosuchus arduini*; in fact, Uzielli, after having compared the San Valentino (Modena, Emilia) specimen of Cretaceous age with *Crocodylus arduini*, states that this fossil definitely represents a new species. The same specimen has been referred by Simonelli (1896) to a new genus and species of metriorhynchid (*Capelliniosuchus mutinensis* Simonelli 1896). After Gortani (1926–1927), this specimen belongs to Dinosauria indet., but later on Sirotti (1989) identified it as a mosasaur.

*Cornedo* (Fig. 1; no. 8)—A partial skeleton of *Crocodylus vicetinus* comes from the late Middle Eocene or Late Eocene of Cornedo (Vicenza, Veneto) (Squinabol, 1902; Fabiani, 1915; Roccaforte et al., 1994). The specimen lacks of a recent taxonomic revision.

### 2.2.1. Palaeobiogeographic implications

Italian Eocene crocodilians belong at least to the following taxa: *Hassiacosuchus* sp. (= *Allognathosuchus* sp.; see discussion), *Asiatosuchus* sp., *Megadontosuchus arduini* and *Pristichampsus* cf. *Pristichampsus rollinati*.

The three crocodilian genera of Bolca are also recorded in the deposits of Messel (Germany, early Lutetian, MP 11; cf. Aguilar et al., 1997) and Geiseltal (Germany, same age): *Hassiacosuchus* sp. (= *Allognathosuchus* sp.; see discussion), *Asiatosuchus* sp. (if *Asiatosuchus germanicus* and *Asiatosuchus depressifrons* belong really to the same genus—see Brochu, 2003) and *Pristichampsus*. This last genus is present with the same species, *Pristichampsus rollinati*, in the three sites. On the other hand, *Megadontosuchus* belongs to the tomistomine group, recorded in a broad area from the Early Eocene of Europe and from the Middle Eocene of Africa (Tchernov, 1986; Brochu and Gingerich, 2000; Brochu, 2001; Rossmann, 2002).

The continental strata of the Lutetian of Monte Bolca resulted from the deposition of sediments in

an insular environment inside an archipelago of the Tethys. Mammals are totally unknown, and reptiles are represented either by crocodilians or by turtles. The island has been populated by crocodilians that were able to cross at least relatively short distances of salty waters, as already suggested by Angielc- zyck and Gingerich (1998). Following Rauhe (1995), the skeletal structure of *Hassiacosuchus* (= *Allognathosuchus*) seems to indicate predomi- nantly terrestrial habits and this could hinder mi- gration across open seas. Nevertheless, the distance between this Tethysian archipelago and the northern edge of the Tethys should have been relatively small. In addition, the Bolca chelonians belonging to the genera *Neochelys* and *Trionyx* (*s.l.*.) show a north Tethysian origin (Broin, 1977; Kotsakis, 1977, 1978).

The diet of all the crocodilian genera living in the "Bolca archipelago" could not include mammals that, on the contrary, are present and highly diversified at Messel and Geiseltal; in these last two sites the trophic niche of mammal predators could have been occupied by *Bergisuchus* and, at least partially, by *Asiatosuchus* (cf. Keller and Schaal, 1992).

In accord with the evolutionary history and phylo- genetic relationships of these Eocene genera, it is strongly suggested that the Italian crocodilians colon- ised the Bolca islands from the northern edge of the Tethys. However, for most cases, it is needed a detailed systematic work on the interrelationships of

the European crocodilian species to get a better understanding on their origin and dispersion/vicari- ance paleobiogegraphic patterns.

Two hypotheses have been advanced about the systematics of the genus *Allognathosuchus*. After Rossmann et al. (2000), all the species ascribed to this genus by Steel (1973), as well as other species more recently erected, are monophyletic and belong to the genus *Allognathosuchus*. After Brochu (1999), the genus is nonmonophyletic and must be split in at least three genera: *Allognathosuchus*, *Navajosuchus* and *Hassiacosuchus*. Both hypotheses have a palaeobio- geographical implication and two models can be proposed: Fig. 2

(1) If the monophyly of *Allognathosuchus* is correct, a "dispersive hypothesis" can be invoked for this genus. According to monophyletic view, remains of *Allognathosuchus* are known from the Palae- ocene of New Mexico (USA) and Bolivia and have been reported from the Early and Middle Eocene and, possibly, Early Oligocene of North America as well as in the Eocene of Europe and in the Late Eocene of Egypt (Rossmann et al., 2000). The European remains are extremely interesting because of their age (Early Eocene) and prove- nance (Dormaal, Belgium). It might be argued that *Allognathosuchus* entered Europe (Fig. 2) at the beginning of the Eocene (as already suggested by Buffetaut, 1985), when the European and
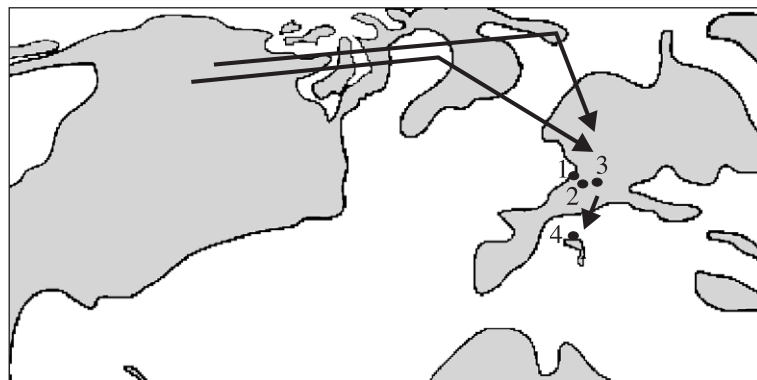


Fig. 2. "Dispersive hypothesis" for *Allognathosuchus*. Dispersal way through the De Geer (north) and/or Thule (south) land bridges (not shown) from North America to Europe during Ypresian (Paleocene). Palaeogeographical reconstruction modified from Scotese's Early Lutetian map (2002). (1) Dormaal, (2) Messel, (3) Geiseltal, (4) Monte Bolca. If *Hassiacosuchus* is different from *Allognathosuchus*, a vicariant event must be invoked for the presence of the former genus in Europe. The dispersion from mainland Europe to Bolca archipelago is the same in both cases.

North American bioprovinces were in contact through Greenland and northwestern Europe as testified by the immigration in Europe of several mammal taxa (Savage and Russell, 1983; Agustí and Anton, 2002). Remains of *Allognathosuchus* sp. of Early Eocene age, possibly similar to *Allognathosuchus woutersi* (cf. Buffetaut, 1985), are signalled at Ellesmere Island (Canadian Arctic archipelago; Estes and Hutchinson, 1980). Since in the Palaeocene, Europe and North America did not exchange terrestrial faunas because of the presence of an epicontinental North Atlantic sea, the Belgian taxon *A. woutersi* Buffetaut 1985 can be considered as the first species that entered Europe during the Early Eocene and, if *Allognathosuchus* is monophyletic, the Belgian species could be the ancestor of the German and Italian forms. Rossmann et al. (2000) propose two different ways for the dispersal of *Allognathosuchus* in Europe: the already mentioned way and a South American one via Africa, supported by the discovery of a mandibular fragment found in the Late Eocene of El Fayum (Egypt). The available palaeontological data seem to better agree with the former one. However, the systematic status of *A. woutersi* is rather weak because based on very scanty material (personal observations by M. Delfino and P. Piras in Bruxelles); consequently, this scenario is a little weakened.

(2) On the other hand, if *Allognathosuchus* is nonmonophyletic, the European forms must be assigned to the genus *Hassiacosuchus* (see Brochu, 1999). The Middle Eocene fossils from Messel and Geiseltal (Germany) must be assigned to *Hassiacosuchus haupti* Weitzel 1935 (or to two very closely related species, *H. haupti* from Messel, and *Hassiacosuchus brevirostris* (Kuhn 1938) (new combination) from Geiseltal (Rauhe, 1995; Brochu, 1999) and the Italian remains from Monte Bolca must be considered as *Hassiacosuchus* sp. closely related to the German forms. Although this scenario better suggests a vicariant event for the insular Monte Bolca *Hassiacosuchus* species, it is more difficult to unravel because it is still need to demonstrate how occurred the dynamics of the two radiations of alligatoroids in Europe from North America (Buscalioni et al., 1997; Brochu, 1999, 2003). This problem can be resolved with a clarification of relationships of European alligatoroids (*Musturzabalsuchus*, *Acynodon*, *Hassiacosuchus*, *Arambourgia*, *Hispanochampsa*; Piras and Buscalioni, in preparation) with the North American members of this group. However, even if the Middle Eocene European forms don't belong to *Allognathosuchus* but to *Hassiacosuchus* their ancestors could be arrived from North America during Early Eocene (see the first hypothesis). After the most recent phylogenetic analyses (Brochu, 1999, 2003) the origin of *Hassiacosuchus* from Cretaceous European primitive alligatoroids seems unlikely.

The genera *Pristichampsus* and *Asiatosuchus* identified at Bolca seem to be Asiatic immigrants. The rich mammalian fauna of Messel does not include species of Asiatic origin with the exception of pangolins (Storch and Schaarschmidt, 1992). The Ob Sea and the Turgai strait could have acted as a much more efficient barrier for mammals than for crocodilians that could possibly cross relatively narrow saltwater bodies. At least some crocodylids can disperse across saltwater barriers.

According to the recent revision of the genus *Pristichampsus* (Rossmann, 1998; see also Keller and Schaal, 1992), only two species can be considered as valid: *Pristichampsus hengdongensis* (Li, 1984) known from the Palaeocene to Middle Eocene of China and the Middle Eocene of India, and *Pristichampsus rollinati* (Gray 1831) known from the Late Palaeocene of China, the Early and Middle Eocene of Wyoming, the Middle Eocene of Germany and Italy and the Middle and Late Eocene of France (the palaeobiogeographic considerations are not changed by the different opinion expressed by Brochu, 2001 for the genera *Pristichampsus*, *Planocrania* and *Quinkana*). After Brochu (2001), the genus *Pristichampsus* includes more than two species, while some taxa assigned by Rossmann (1998) to the genus *Pristichampsus* must be ascribed to *Planocrania*. Such a distribution is not in contradiction with the presence of *Pristichampsus* cf. *P. rollinati* in Italy; it is likely that this species spread out from Asia to Europe at the beginning of the Middle Eocene (Fig. 3). However, an alternative hypothesis of colonisation of Europe from Asia through North America during the Early Eocene, cannot be ruled out.
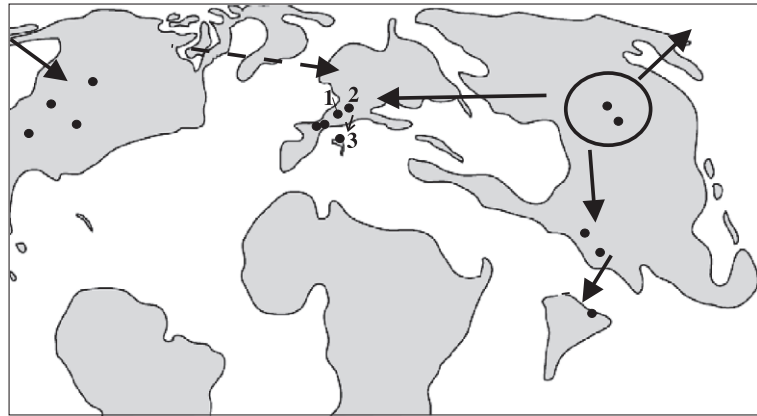
Fig. 3. "Dispersive hypothesis" for *Pristichampsus* from Central Asia to North America, Europe and India during Early Lutetian. Palaeogeographical reconstruction modified from Scotese's Early Lutetian map (2002). (1) Messel, (2) Geiseltal, (3) Monte Bolca. Dotted line represents an alternative dispersive hypothesis from Asia to Europe through North America during Early Eocene.

The genus *Asiatosuchus* shows a marked Eurasiatic distribution with a stratigraphic range going from the Palaeocene of Russia and China to the Oligocene of Monteviale in Italy, if the allocation of the Monteviale remains to *Asiatosuchus monsvialensis* is accepted (Franco and Piccoli, 1993). If this allocation is not accepted, the last occurrence of the genus is recorded in the Late Eocene of Mongolia and Europe (Vasse, 1992). The ancestor of *Asiatosuchus* could have reached Europe from Asia at the beginning of the Eocene (Fig. 4) if *Asiatosuchus germanicus* and *Asiatosuchus depressifrons* belong really to the same genus (see Brochu, 2003).

Finally, the affinity (but not specific identity) of *Megadontosuchus arduini* with the European taxa *Kentisuchus spenceri* and *Dollosuchus dixoni* seems to show a probable Western European origin for the Italian species (Fig. 5).

## 2.3. Oligocene

*Monteviale* (Fig. 1; no. 9)—Monteviale (Early Oligocene) is the site that has furnished the highest number of fossil Oligocene crocodilians, both in terms of specimens and species number. The associated mammal assemblage suggests an age of MP 21,
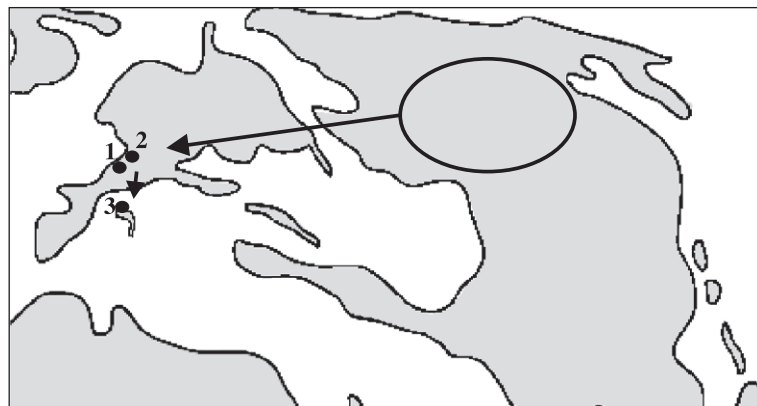


Fig. 4. Possible dispersal ways of *Asiatosuchus* at the beginning of the Early Eocene from Asia to Europe. Palaeogeographical reconstruction modified from Scotese's Early Lutetian map (2002). (1) Messel, (2) Geiseltal, (3) Monte Bolca.
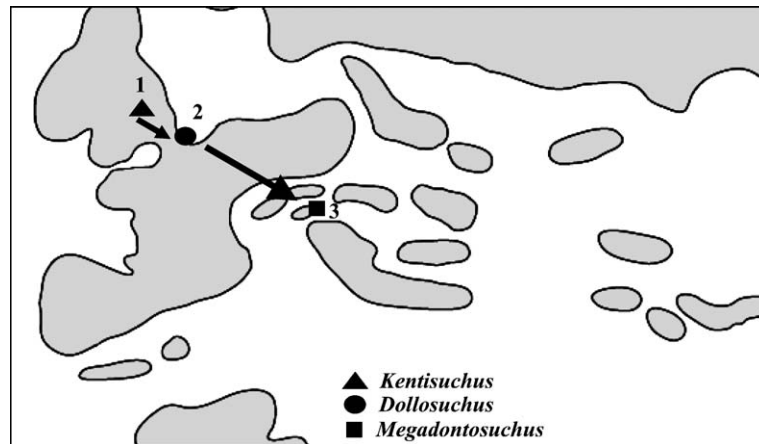
Fig. 5. Palaeogeographic distribution of the Eocene Tomistominae *Kentisuchus*, *Dollosuchus* and *Megadontosuchus* in Western Europe; these genera seem to be closely related. Palaeogeographical reconstruction modified from Rögle's Priabonian map (1998). (1) Isle of Sheppey, (2) Maransart, (3) Monte Zuello.

although a younger age cannot be excluded (MP 22; Kotsakis et al., 1997). The Monteviale crocodilians were quoted by Lioy (1865b), but only after nearly 50 years Fabiani (1914) mentioned the presence of two species and created (as a page footnote!), the species *Crocodylus monsvialensis*. One year later, the same author (Fabiani, 1915) proposed the establishment of a second species, *Crocodylus dalpiazi*, without furnishing any details. Berg (1966) put forward the hypothesis that *C. monsvialensis* was a descendant of *Crocodylus vicetinus* of the early Middle Eocene of Monte Bolca, maybe even a synonym. It was not until the end of the 20th century that the remains of *C. monsvialensis* and *C. dalpiazi* were the target of detailed studies (Franco and Piccoli, 1993; Franco et al., 1992; Rauhe and Rossmann, 1995; Franco, 1995; cf. also Altichieri, 1980b; Pinna, 1989; Roccaforte et al., 1994). According to Franco et al. (1992), Franco and Piccoli (1993) and Franco (1995), the remains referred by Fabiani (1914, 1915) to the genus *Crocodylus* should be ascribed to *Diplocynodon dalpiazi* (Fabiani, 1915) and *Asiatosuchus monsvialensis* (Fabiani, 1914). Rauhe and Rossmann (1995) consider the remains of both species as representatives of the genus *Diplocynodon*.

Del Favero (1997, 1999), examining some remains of crocodilians coming, according to the historical information, from Monte Bolca, discovered that they were indeed from Monteviale (see previous discussion about Eocene). These remains have been referred to *Diplocynodon* cf. *Diplocynodon ratelii*. Following Brinkman and Rauhe (1998), *Diplocynodon dalpiazi* and *Asiatosuchus monsvialensis* are synonymous with *D. ratelii*. Del Favero (1997, 1999) agrees with the specific identity of *D. dalpiazi* with *D. ratelii*, and considers highly probable the attribution of *Crocodylus monsvialensis* to the same species.

To summarize the opinions of the different authors, it can be affirmed that Monteviale crocodilians belong to *Diplocynodon* (with a single species, *Diplocynodon ratelii*), while the presence of *Asiatosuchus* is quite improbable.

*Faedo* (Fig. 1; no. 10), *Chiuppano* (Fig. 1; no. 37), *Santa Giustina* (Fig. 1; no. 11) and *Visone* (Fig. 1; no. 12)—The presence of *Diplocynodon dalpiazi* has been reported also for the Early Oligocene of Faedo (Vicenza, Veneto; Roccaforte et al., 1994). A fragment of a crocodilian skull has been collected in the Chiuppano outcrop of early Late Oligocene age (Vicenza, Veneto); this fossil has never been studied and/or figured (Accordi, 1951). Capellini (1890b) reported the presence of crocodilian remains in the small basin of Santa Giustina (Savona, Liguria); remains that Issel (1892) described as belonging to the genus *Crocodylus*. The tooth remains described and figured by Issel (1892) belong to a very young specimen and do not allow any taxonomic allocation. The age of the basin should be, according to Lorenz (1968), ''middle

Stampian" and therefore corresponding to the middle part of the Late Oligocene. From sandy marls of Late Oligocene age, outcropping in the surroundings of Visone near Acqui (Alessandria, Piedmont), Del Vecchio (1921) described some crocodilian teeth that he referred to *Tomistoma*.

### 2.3.1. Palaeobiogeographic implications

The Oligocene crocodilians of Italy have been ascribed to the following taxa: *Asiatosuchus monsvialensis*, *Diplocynodon dalpiazi* and *Diplocynodon* cf. *Diplocynodon ratelii*. The first two are very problematic: both are very probably synonymous with *D. ratelii* (however, a systematic revision would be necessary, in particular for *A. monsvialensis*—see below).

The genus *Diplocynodon* is by far the best known Oligocene crocodilian from Italy. Three recent publications concerning the systematic arrangement of the genus *Diplocynodon* reach rather different conclusions: Rauhe and Rossmann (1995) refer this genus to the family Leidyosuchidae, while Ginsburg and Bulot (1997) ascribe it to the subfamily Crocodylinae of the family Crocodylidae. Brochu (2001) using cladistics places this genus in the Diplocynodontinae, a basal member of Alligatoroidea. Whichever the systematic position of *Diplocynodon*, its earliest record in Europe is during the Late Palaeocene and is relatively common in the Eocene, Oligocene and Miocene, disappearing during the last phase of the Miocene, not bearing the climatic deterioration oc-

curred at the beginning of Late Miocene (Zachos et al., 2001; Böhme, 2003). *Diplocynodon* was a common genus during the Early Oligocene either in West Europe (Vignaud et al., 1996; Brinkman and Rauhe, 1998) or in Eastern Europe (Gramann, 1958) and from there should have reached the Venetian–Balkan–Anatolian area that at the time was a nearly continuous belt of emerged land (Rögl, 1998, 1999). *Diplocynodon* has been also reported in more recent sites of this region (Croatia, Paunovich, 1992; Turkish Thracia, Schleich, 1994) (Fig. 6).

Because the genus *Diplocynodon* is geographically widespread and span temporally from the early Paleocene to the Miocene, it is rather complex to address a detailed paleogeographic pattern for the Italian region. However, the mammal assemblage of Monteviale is quite peculiar and indicates that there were no common elements at a specific level between the Venetian area and Western Europe. Some similarities can be noted with the faunas of Möhren 13 (Bavaria, Germany) and Detan (NW Bohemia, Czech Republic) or with those of the Karakaya and Çavaşlu (Turkish Thracia) (Kotsakis, 1984a; Kotsakis et al., 1997). It is by far significant a future revision of the putative species *Diplocynodon dalpiazi* and *Diplocynodon* cf. *Diplocynodon ratelii* from Monteviale to get insight whether they came from the east or the northern areas (Fig. 6), or whether they conform a local isolated faunal assemblage like the peculiar *Diplocynodon* from the Miocene of Southern Germany described by Scherer (1978, 1979, 1981).
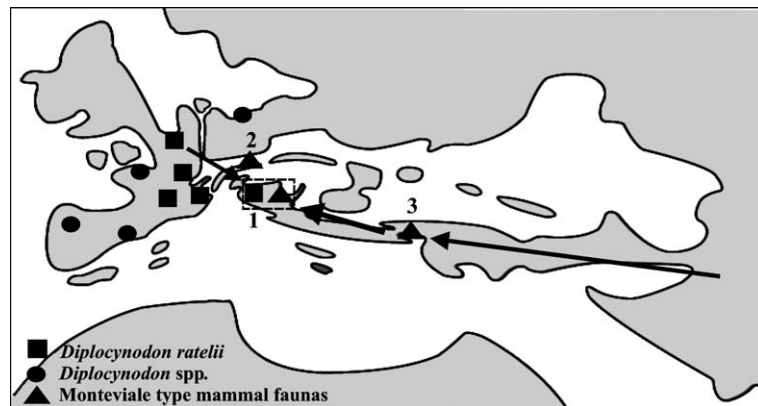


Fig. 6. Possible dispersal ways of *Diplocynodon ratelii* from Western Europe to Monteviale and of Monteviale mammal association from Western Asia to Monteviale during Early Oligocene. Palaeogeographical reconstruction modified from Rögle's Middle Kiscellian–Solenovian map (1998). (1) Monteviale, (2) Möhren 13, (3) Karakaya and Çavaşlu.

The presence of the genus *Tomistoma* in the site of Visone near Acqui seems to be rather weak since teeth are not diagnostic at a family level. Nevertheless, it should be underlined that Antunes and Cauhzac (1999) mentioned, on the basis of two isolated teeth, the presence of *Tomistoma* sp. in the Chattian levels of Saint-Geours-de-Maremne (France), arguing that their size is much larger than that of the *Diplocynodon* teeth, the only other genus that could be reasonably present in the same area and age. This line of evidence cannot be overlooked for the proper allocation of the Visone remains even if the size of teeth of Geours-de-Maremne is even greater than that of those described by Del Vecchio (1921). It does not seem appropriate to express any palaeobiogeographic consideration because of the weakness of the evidence for a proper allocation.

## 2.4. Early and Middle Miocene

Although usually fragmentary, crocodilian fossils are relatively frequent in the Italian sites of Miocene age. The following remains come from Early and Middle Miocene sites.

*Strintu de Melonis near Nurri* (Fig. 1; no. 13), *Fangario and Bingia Fargeri* (Fig. 1; no. 14), *Florinas* (Fig. 1; no. 15) and *La Crucca* (Fig. 1; no. 16)— From Strintu de Melonis, Nurri (Nuoro, Sardinia) (=Comidanu "da Strintu Argiolu alla Stazione di Nurri" in Del Vecchio, 1921) come some teeth allocated by Lovisato (1892) to *Tomistoma* sp. The age of the layer from which the teeth have been unearthed is Aquitanian (Esu and Kotsakis, 1983). Isolated teeth, Langhian in age (Esu and Kotsakis, 1983) and referred to *Tomistoma* cf. *Tomistoma calaritanum* Capellini 1890 (cf. Capellini, 1890b; Lovisato, 1892), have been found near Fangario and Bingia Fargeri (Cagliari, Sardinia). To the taxon *T. calaritanum* have been referred some postcranial remains coming from the locality La Crucca (Sassari, Sardinia) (Spano, 1985) while isolated teeth coming from Florinas (Sassari, Sardinia) have been identified as *Tomistoma* cf. *Tomistoma lusitanicum* (Vianna and Moraes 1945) by Marras and Ventura (1985). These remains coming from the Sassari area can be considered Serravalian in age.

*Iola* (Fig. 1; no. 17), *Cannole* (Fig. 1; no. 18), *Melpignano* and *Melpignano−Cursi* (Fig. 1; nos. 38–39)—Some crocodilian remains come from the "Pietra Leccese", a marine calcarenite whose precise age is unknown but possibly lies between the Late Burdigalian and the Early Tortonian (Bossio et al., 1987a,b). At Iola (Lecce, Apulia), remains have been found that Costa (1848, 1854, 1864a,b) referred at first to *Streptospondylus lyceensis* Costa 1848 and then to *Steneosaurus lyceensis* (Costa 1848). Capellini (1890b) disputed that they could belong to these genera and stated that a nontomistomine form should have been taken into account. A revision carried out by Aldinio (1896) referred the remains to *Tomistoma lyceense* (Costa 1848) but, once again, Capellini (1897) criticized this allocation. New remains coming from the Lecce area (Melpignano), allow to strongly support a tomistomine relationships of the "Pietra Leccese" crocodilians (Pacini, 2003; Delfino et al., 2003) even if, in the absence of a general review they are of little help for palaeobiogeographic reconstructions. Fossils of an undetermined crocodilian come from Cannole (Lecce, Apulia; Costa, 1850) and Melpignano−Cursi (Pacini, 2003; Delfino et al., 2003).

*Donnalucata* (Fig. 1; no. 19), *Gozo Island* (Fig. 1; nos. 20/21) and *Lettomanoppello* (Fig. 1; no. 35)—In the Sicilian−Maltese area, fossils of crocodilian are known in the layers with phosphate nodules of the "*Globigerina* limestone" of the Aquitanian−Serravalian (Giannelli and Salvatorini, 1972) of the Gozo Island (Malta) (Hulke, 1871; Adams, 1879; Lydekker, 1886b, 1888). Such fossils have been allocated to two different species: *Crocodylus gaudense* Hulke 1871 and *Melitosaurus champsoides* Owen 1850 *in schaedis* in Hulke 1871. Lydekker (1886b) assigned both species to the genus *Tomistoma*: *Tomistoma gaudense* (Hulke 1871) and *Tomistoma champsoides* Lydekker 1886. A single isolated tooth has been reported from a horizon with phosphate nodules outcropping near Donnalucata (Ragusa, Sicily; Ruggieri, 1961).

Another area, that after some authors, yielded crocodilian remains, is the Belluno area (Libàno, Bolzano Bellunese and other localities; Belluno, Veneto) (Catullo, 1856; Taramelli, 1871), but the several isolated teeth discovered in the Burdigalian sandstones and identified as crocodilian, could very probably be remains of odontocetes (Dal Piaz, 1908). From Lettomanoppello (Pescara, Abruzzo) one single tooth has been collected in sediments of Burdigalian age (Carnevale pers. com.).

### 2.4.1. Palaeobiogeographic implications

During the Early and Middle Miocene, the crocodilians living in the Italian and Maltese area could exclusively belong to the genus *Tomistoma*. An increase of temperature marked the Chattian (Late Oligocene) (Zachos et al., 2001) but it was followed by climatic worsening around the Oligocene–Miocene boundary and by a new, more marked, amelioration during the Early Miocene (Prothero, 1994). Following Antunes and Cauhzac (1999), the Early Oligocene climatic changes lead to the extinction of several Palaeogene genera of European crocodilians allowing the survival of *Diplocynodon* only (*Diplocynodon* survived in Europe up to the beginning of Late Miocene–early Pliocene but has never been reported in Italy for this period). This decrease in crocodilian biodiversity does not uniquely concern Europe but is identifiable on a global scale (Markwick, 1994, 1998a,b).

According to Antunes and Cauhzac (1999), *Tomistoma* appeared in Europe during the Late Oligocene coming in the Mediterranean area from Asia. A different approach were expressed by Tchernov (1986), who proposed that *Tomistoma* originated in Africa and then spread to Asia and (directly) to the Mediterranean area (Fig. 7). The species *Tomistoma africanum* Andrews 1905 and *Tomistoma gavialoides* Andrews 1905 of the Late Eocene–Early Oligocene of Egypt, are not assigned to this genus at present. Some authors (Buffetaut, 1982; Brochu, 2001) put the latter species in synonymy with the former and ascribe all the remains to *Eogavialis africanus* (Andrews 1905). According to others (Tchernov, 1986; Rauhe

et al., 1999), such species should be assigned to the exclusively African genus *Euthecodon*. However, if the oldest unequivocal representative of the genus *Tomistoma* is *Tomistoma cairense* Müller 1927 of the Middle Eocene of Egypt, then a dispersal event from Africa should better explain the Mediterranean distribution of *Tomistoma* (Fig. 7). Brochu (1997) don't exclude that all the Mediterranean forms belong to the same species; in this case allopatric speciation in different European regions must be rejected.

In the Early and Middle Miocene, the following taxa should have been present in the Mediterranean area: *Tomistoma dowsoni* Fourtau 1920 in Egypt and Libya (Arambourg and Magnier, 1961), *Tomistoma eggenburgense* (Toula and Kail 1885) in Austria, *Tomistoma gaudense* and *Tomistoma champsoides* in Malta, *Tomistoma calaritanum* in Sardinia, *Tomistoma lusitanicum* in Portugal (Antunes, 1961, 1987). *Tomistoma* remains have also been reported for Spain, France, former Yugoslavia and Poland (Antunes, 1994 and quoted references). The species *T. eggenburgense*, *T. calaritanum* and *T. lusitanicum* seem to be valid (Antunes, 1961; Steel, 1973) while the others are in need of modern revision. The Sardinian species is very probably related to *T. lusitanicum* of late Middle Miocene of Portugal. Isolated teeth from Portugal have been identified as *T. calaritanum* by Zbyszewski (1949) but the same and new materials have been referred to *Gavialis* by Antunes (1994). Marras and Ventura (1985) mentioned the presence of *T. lusitanicum* in Sardinia but this allocation seems to be uncertain since it is based on isolated teeth. Since mostly the presence of *tomistoma* in the Italian region
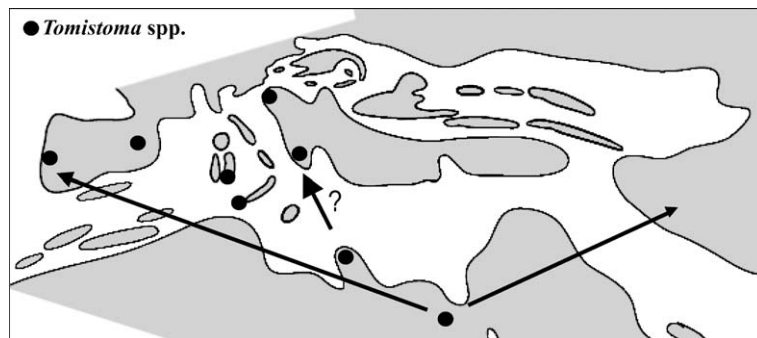


Fig. 7. Dispersion of *Tomistoma* from Africa to Asia and Europe during Early–Middle Miocene. Palaeogeographical reconstruction modified from Rögle's Langhian map (1998).

rests on isolated material (teeh and postcraneal) it does not introduce any light whether they may belong or not to the same species.

## 2.5. Late Miocene

According to mammals, the palaeobiogeography of the Italian Late Miocene has been divided into four areas: (a) the Tusco–Sardinian area; (b) the Apulo–Abruzzi area, (c) the Calabro–Sicilian area, and (d) the Alpine area, hosted a nonendemic fauna with European affinities. Crocodilian remains have been collected only in the first two palaeobioprovinces.

## 2.6. Tusco–Sardinian area

*Is Miriones* (Fig. 1; no. 22), *Tres Nuraghes* (Fig. 1; no. 23), *surroundings of Cagliari* (Fig. 1; nos. 24/25/26), *Monte Oria* (Fig. 1; no. 27), and *Capo della Frasca* (Fig. 1; no. 36)—The bulk of the crocodilian remains of the Italian Late Miocene come from the Tusco–Sardinian area. The discovery of crocodilians was first mentioned by Gennari (1869), and after by Capellini (1890a,b), Lovisato (1892, 1902), Del Vecchio (1921), Gortani (1922), Repossi (1922), and recently by Cordy and Ginesu (1994). With the exception of the "holotype" of *Tomistoma calaritanum* (a skull severely damaged by bombs during the II World War), all the Sardinian rests are isolated teeth. Usually, these remains have been allocated, on the basis of their morphology, to two different taxa: *Tomistoma* sp. and a "true crocodile", that is to say a brevirostrine form. *Tomistoma* comes from Late Miocene localities of Is Miriones (Cagliari; type locality of *T. calaritanum*), Tres Nuraghes (Oristano) and Bonaria (Cagliari) (Capellini, 1890b; Lovisato, 1892, 1902; Del Vecchio, 1921).

Following Lovisato (1892), a tooth from Monte San Giovanni or Monte della Pace should belong to a "true crocodile". Del Vecchio (1921) refers isolated teeth from "Piazza d'armi di Cagliari (Cagliari), "Cimitero di Cagliari" (Cagliari), "Cava Timon a Montixedu di Bonaria" (Cagliari), "Capo della Frasca" (Oristano) and "Monte Oria" (Sassari) to the same unnamed form.

For nearly all those remains, it is not possible to ascertain a more precise age than a generic "Late Miocene" (or even Middle–Late Miocene).

*Fiume Santo* (Fig. 1; no. 28)—The last Sardinian crocodilians, conservatively referred as Crocodylia indet., were recorded from Fiume Santo (Sassari) by Cordy and Ginesu (1994) for the endemic fauna with *Oreopithecus* and *Maremmia* corresponding, most likely, to the level V2 of Baccinello (Tuscany) that is referable to the Turolian (MN 12 or basal MN 13) (Kotsakis et al., 1997; Rook et al., 1999, 2003).

*Casteani* (Fig. 1; no. 29), *Montebamboli* (Fig. 1; no. 30) and *Radicondoli* (Fig. 1; no. 31)—In the Tuscany side of the Tusco–Sardinian palaeobioprovince, remains of crocodilians come from horizons (with the endemic association that also hosts *Oreopithecus* and *Maremmia*) of the Casteani and Montebamboli areas (Grosseto).

From Casteani (Turolian fauna corresponding to the V1 level of Baccinello, therefore to the Late MN 11 or to MN 12; cf. Rook et al., 1999) comes a single tooth ascribed to *Crocodylus* sp. by Weithofer (1888), while from Montebamboli (again a Turolian fauna but corresponding to the V2 level of Baccinello, therefore to MN 12 or the base of MN 13; cf. Rook et al., 1999) comes the cranial, dental and postcranial remains that Ristori (1890) used for the institution of the species *Crocodylus bambolii* Ristori 1890. Antunes (1994) suggests that the Montebamboli material could belong to *Diplocynodon*, while Franco (1991) implicitly considers them as belonging to *Crocodylus*.

Brochu (2001, Fig. 4), tentatively places *Crocodylus bambolii*, within the genus *Crocodylus* along the African species *Crocodylus pigotti* Tchernov and Van Couvering 1978, *Crocodylus ndokoensis* Pickford 1994 and *Crocodylus checchiai* Maccagno 1947.

To a different genus, *Tomistoma*, has been ascribed a single tooth, found in 1981 in the Late Miocene of Radicondoli (Siena, Tuscany), that should be better considered as an undetermined Crocodylia (Bossio et al., 1981; unpublished data).

## 2.7. Apulo–Abruzzi area

*Scontrone* (Fig. 1; no. 32), *Gargano* (Fig. 1; no. 33)—In the Apulo–Abruzzi palaeobioprovince, crocodilian remains have been collected in two different localities. From beach deposits of Scontrone (L'Aquila, Abruzzi, early Tortonian in age), come some crocodilian teeth associated with mammal

remains belonging to the endemic fauna with *Hoplitomeryx* (Early Vallesian in terms of mammal ages). Rustioni et al. (1992) and Rustioni and Mazza (1993) considered these remains as *Crocodylus* sp. From the ''terre rosse'' karst fissures of the Gargano area (between Apricena and Poggio Imperiale; Foggia, Apulia), in association with an endemic fauna that hosts *Hoplitomeryx* and *Microtia*, Freudenthal (1971, 1985) reported crocodilian rests. A Late Miocene and/or Early Pliocene (Turolian or Early Ruscinian) age has been proposed for these fauna (cf. discussion in Abbazzi et al., 1996 and Kotsakis, 2003). The remains have been studied by Delfino (2002) who identified the material as *Crocodylus* sp.

*Monticino* (Fig. 1; no. 34)—From this locality (Brisighella, Emilia–Romagna, late Turolian, MN 13) come two isolated teeth referred to Crocodylia indet. (Delfino, 2002) The mammalian assemblage collected in this site belongs to a ''normal'' European fauna without endemic characters.

### 2.7.1. Palaeobiogeographic implications

According to the palaeobiogeography of the Italian Late Miocene mammals, it is possible to recognize three major bioprovinces (Torre et al., 2000). The Tusco–Sardinian area and the Apulo–Abruzzi are characterized by the presence of mammalian endemic assemblage that comprises the genera *Oreopithecus* and *Maremmia* and *Hoplitomeryx* and *Microtia* respectively. The Calabro–Sicilian area shows a nonendemic fauna with African affinities while a fourth area, the Alpine area, hosted a nonendemic fauna with European affinities. The entire peninsula (with the possible exception of the Apulia–Gargano area) was invaded by faunas of European origin after the evaporitic Messinian (Fig. 8).

*Tomistoma* and *Crocodylus* are the only Late Miocene crocodilians from Italy.

Following Antunes and Cauhzac (1999), the last occurrence (LO) of *Tomistoma* in the Tago area (Portugal) is $10.95 \pm 0.25$ Ma BP. Although the age of the Sardinian sediments from which occur the last *Tomistoma* cannot be precisely dated (Cherchi, pers. comm.), it seems that *Tomistoma* survived in Italy a little longer than in Portugal.

The origin of the genus *Crocodylus* is unanimously placed in Africa even if some of the Palaeogene species of Egypt, referred to the genus *Crocodylus* (*Crocodylus megarhinus* Andrews 1905 and *Crocodylus articeps* Andrews 1905—the last species synonym of the first one after Brochu, 2000) are not considered to belong to this genus (Brochu, 2000).

*Crocodylus pigotti* comes from the Early Miocene of Kenya (Tchernov and Van Couvering, 1978) and *Crocodylus lloydi* Fourtau 1920, is found in several northern and eastern African localities, but whose range could be extended, following Rauhe et al. (1999), from the Late Oligocene or basal Miocene to the Late Pleistocene or even the beginning of the Holocene. On the contrary, Brochu (2001) considers *C. lloydi* as limited to the Early Miocene.

The ancestor of the European *Crocodylus* should be sought after the Middle and Late Miocene African members of the genus, that is to say: *Crocodylus lloydi*, *Crocodylus checchiai* and *Crocodylus ndokoensis*. Since the latter could be the forerunner of
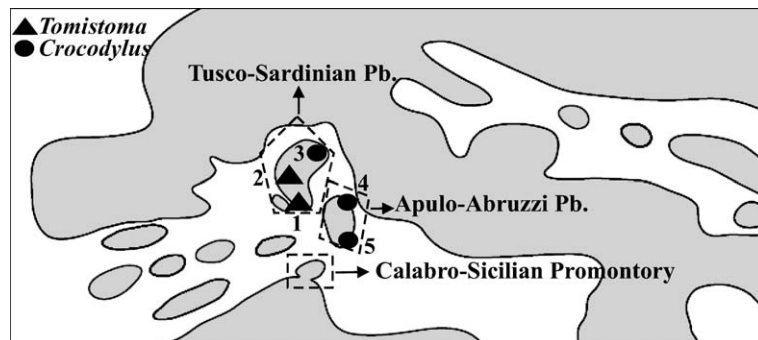


Fig. 8. Late Miocene Italian palaeobioprovinces and fossil crocodile-bearing localities. Palaeogeographical reconstruction modified from Jones's Late Serravalian–Tortonian map (1999). (1) Is Miriones, (2) Several localities of Sardinia, (3) Montebamboli, (4) Scontrone, (5) Gargano (between Apricena and Poggio Imperiale).

the highly specialized living species *C. cataphractus* Cuvier 1824 (Brochu, 2000), the candidates could be the first two.

In Italy, *Crocodylus* is reported with confidence in the Turolian of the Apulo–Abruzzi palaeobioprovince and it is possibly present in the Tusco–Sardinian palaeobioprovince in horizons of the same age (if the generic allocation of the Montebamboli crocodylians will be confirmed). Not so well grounded is the presence of *Crocodylus* in the Vallesian of Scontrone.

The possible scenarios concerning the colonisation of the Italian insular palaeobioprovinces by African representatives of *Crocodylus* are at least two. The first could imply a contemporaneous dispersal in both the palaeobioprovinces through an eastern way (Middle East–Anatolia–Balkans) or a more direct way through the Calabro–Sicilian promontory of Africa. An allopatric speciation would have as result the origin of two different species in the two areas: *Crocodylus bambolii* in the Tusco–Sardinian palaeobioprovince and *Crocodylus* sp. in the Apulo–Abruzzi. Otherwise, only *C. bambolii* would be present in both areas.

A second scenario could be that the two areas were colonised independently in different times and in different ways or, alternatively, that the stock that reached one of the two areas dispersed into the other. Only a general revision of all the material originally referred to *Crocodylus* could shed light on this topic.

In the faunal assemblage of the Apulo–Abruzzi palaeobioprovince with *Hoplitomeryx* and *Microtia*, there are no African elements while an African origin has been suggested for some of the elements of the assemblage with *Oreopithecus* and *Maremmia* found in the Tusco–Sardinian palaeobioprovince (*Oreopithecus*, *Maremmia*, *Tyrrhenotragus*; see discussion in Kotsakis, 1984b); the African origin of these elements has been criticized and is considered unlikely (Benvenuti et al., 2001).

Therefore, the presence of *Crocodylus*, which has a clear African origin, represents a peculiarity of these faunas and the dispersal of this reptile probably followed a route precluded to mammals; maybe across the sea. This way of dispersion seems to be the most parsimonious as fossils belonging to the genus *Crocodylus* do not have been discovered in European mainland close to Apulia. The well-known salt tolerance of the living *Crocodylus* suggests a direct arrival from Africa through the Mediterranean Sea.

## 2.8. Pliocene

With the exception of the Gargano archipelago, in which the genus *Crocodylus* could have survived during the Early Ruscinian (MN 14; for a discussion of the chronological allocation cf. Abbazzi et al., 1996; Kotsakis, 2003), Pliocene crocodilians are not known in Italy (nor in Europe).

## 3. Conclusions

Table 1 summarized the available updated information on Cenozoic crocodilian assemblages from Italy and Malta. It has been recorded 39 fossil bearing localities, most are old known localities that bring together complete specimens and mostly isolated bones and teeth. Only seven of these localities have reliable significant remains at least to generic taxonomic level (i.e., Vestenanova di Bolca, Monte Zuello, Monteviale, Gozo Island, Is Miriones, Montebamboli, Gargano between Apricena and Poggio Imperiale). The Italian early Cenonozoic (Eocene and Oligocene) record shares with Europe the following genera: *Asiatosuchus*, *Pristichampsus*, *Diplocynodon*, and *Hassiacosuchus* (=*Allognathosuchus*). On the contrary, African immigrants (i.e., *Tomistoma* and *Crocodylus*) compose crocodilian assemblage during late Cenozoic (Miocene). Three endemic species has been recognised: *Megadontosuchus arduini*, *Tomistoma calaritanum*, and *Crocodylus bambolii*.

Below we summarize the preferred paleobiogeographic hypotheses that involve basically dispersal events:

(1) During the early Lutetian (probably corresponding to MP 11), Bolca archipelago (Veneto) was inhabited by: *Pristichampsus* cf. *Pristichampsus rollinati*, *Hassiacosuchus* sp. (=*Allognathosuchus* sp.) and *Asiatosuchus* sp. These genera also occurred in the coeval German deposits of Messel and Geiseltal. The Bolca crocodilians should have dispersed from the northern edge of the Tethys.

(2) From the Priabonian of Monte Zuello (Veneto) and from other Venetian localities, come remains of a longirostrine crocodilian, *Megadontosuchus arduini*, whose affinities with the Western Europe

tomistomine forms *Dollosuchus* e *Kentisuchus* seem to be clear and indicate a European origin for this taxon also.

(3) During the Oligocene of Monteviale (Veneto), in lignite deposits of the Early Rupelian (MP 21), several crocodilian remains referable to the genus *Diplocynodon* and probably to one single species, *Diplocynodon ratelii*, have been collected. This species has been found in coeval localities across the entire Western and Central Europe and suggest that the Monteviale crocodilians come from that area. This Western and Central European affinity of the Monteviale crocodilians is apparently contrasting with the associated mammals that uniquely show affinities with some faunas of the Bavarian, Bohemian and Western Thracia area.

(4) Early and Middle Miocene coastal deposits of Sardinia and Gozo (Malta) is represented by the genus *Tomistoma*. This genus could have dispersed from Africa into the entire Mediterranean area during the Late Oligocene where it underwent a speciation process;

(5) During the Tortonian, *Tomistoma* survives in Sardinia with the species *Tomistoma calaritanum* that was found in several coastal deposits. During the Turolian (or even Vallesian), the Apulo–Abruzzi and the Tusco–Sardinian palaeobioprovinces were inhabited by the genus *Crocodylus* whose ancestor presumably came from Africa where remains belonging to the same genus were already found at the beginning of the Neogene. It is not possible to hypothesize if it dispersed once or twice, because the identification at genus level of the Tuscan material has to be confirmed and the Apulian material has not been allocated at species level. The associated mammal fauna does not host any African elements, and the crocodilians represent therefore an exception; they probably dispersed across the sea, a way precluded to many mammals.

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