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1 Fossil crocodylid remains from Scontrone (Tortonian, Southern Italy) and the late
2 Neogene Mediterranean biogeography of crocodylians

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16
17 **Abstract**

18 New fossil remains from the Tortonian of Scontrone (Abruzzo, Southern Italy) provide further
19 information on the crocodylids with a generalized rostral morphology that inhabited the
20 Mediterranean area during the late Miocene. Particularly informative is the nearly complete right
21 dentary SCT 276. Thanks to the fact that the third and fourth alveoli are clearly separated by a bony
22 septum and are markedly different in size, being the fourth much larger than the third, it is possible
23 to exclude that SCT 276 belonged to the alligatoroid *Diplocynodon* and to tentatively refer it to cf.
24 *Crocodylus* sp. This genus has been previously identified on a phylogenetic basis in the same
25 palaeobioprovince, the Apulo-Abruzzi bioprovince (Gargano Terre Rosse; Messinian-Zanclean;

1 *Crocodylus* sp.), and it is likely present also in the Tusco-Sardinian palaeobioprovince (Monte
2 Bamboli, Tortonian, cf. *Crocodylus* sp.). SCT 276 currently represents the oldest possible evidence
3 of the presence of *Crocodylus* and it proves that this taxon could have already reached Europe
4 during the Tortonian, well before the Messinian Salinity Crisis that is traditionally considered as the
5 event that caused several trans-Mediterranean dispersals. Furthermore, it is tempting to associate the
6 absence of alligatoroids and the presence of crocodylids in these palaeobioprovinces (actually
7 systems of islands) to the different behavioural, morphological and physiological traits of extant
8 alligatorids and crocodylids, which render rather salt intolerant the former and salt tolerant the
9 latter.

10

11 *Keywords: Crocodylus, Diplocynodon, Euthecodon, Tomistoma/Gavialosuchus, salt tolerance,*
12 *intercontinental dispersal*

13

14

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1 **1. Introduction**

2

3 The Mediterranean region does not host any crocodylian at present, but *Crocodylus* was apparently
4 present in historical times in Syria, Egypt, Morocco, where it disappeared around the middle of the
5 XX century, and Israel, where it went extinct at the beginning of the same century (Anderson,
6 1898; Werner, 1988; Ross, 1989; Bons and Geniez, 1996).

7 Fossil evidence shows that crocodylians inhabited Europe up to the late Miocene and possibly
8 earliest Pliocene (Delfino et al., 2007). During the late Neogene, the crocodylian faunas of the
9 Mediterranean area was represented by four taxa (Fig. 1): two slender-snouted crocodylids, the
10 osteolaemine *Euthecodon* Fourtau, 1920 and tomistomines whose allocation to *Tomistoma* Müller,
11 1846 and/or *Gavialosuchus* Toulou and Kail, 1885 has still to be defined (Rossmann et al., 1999;
12 Piras et al., 2007), and two taxa with a generalized rostrum, the alligatoroid *Diplocynodon* Pomel,
13 1847 and the crocodylid *Crocodylus* Laurenti, 1768.

14 The origin of *Crocodylus* and its early biogeographic history is still unclear. With 12 species
15 currently recognized, it is the most speciose and widely distributed crocodylian genus: from
16 Australia to Asia, Africa and America (Uetz et al., 2011). According to both palaeontological and
17 molecular data (Brochu, 2000; Oaks, 2011), the genus arose in the Miocene, but it is not clear if its
18 origin has to be sought in Asia or in Africa. The recent analysis by Oaks (2011), based on the
19 mitochondrial and nuclear genome, concluded that the ‘out-of-Africa’ hypothesis has to be rejected
20 because *Crocodylus* originated in the Indo-Pacific area, however, Brochu and Storrs (2012)
21 remarked that an African origin of crocodylines is strongly supported by phylogenetic analyses
22 including fossils.

23 Growing evidence, mostly molecular (Schmitz et al., 2003; Hekkala et al., 2011; Meredith et al.,
24 2011; Oaks, 2011) but also morphological (Nestler, 2011), suggests that the extant Nile crocodile,
25 *Crocodylus niloticus* (Laurenti, 1768) is actually a cryptic complex of paraphyletic species. At least
26 one further species, *Crocodylus suchus* Geoffroy Saint-Hilaire, 1807, could be considered valid.

1 The African fossil record of *Crocodylus*, including remains of putative *Crocodylus*, is rather
2 abundant and it is still being revised (Storrs, 2003; Brochu, 2007; Brochu et al., 2010; Brochu and
3 Storrs, 2012) so that an updated taxonomic identification of a large part of the remains, as well as
4 the proper phylogenetic position of some taxa, is still pending. So far, some fossils previously
5 referred to *Crocodylus* have been ascribed to extinct genera, *Rimasuchus* Storrs, 2003 and *Voay*
6 Brochu, 2007.

7 The knowledge of the European *Crocodylus* has been significantly improved by the recent revision
8 of historical collections, as well as by the analysis of recently collected or prepared remains. The
9 only European crocodylian remains that have been referred to *Crocodylus* on a phylogenetic basis
10 come from the late Miocene-early Pliocene of the Gargano region (Apulia), at the western edge of
11 the Apulo-Abruzzi palaeobioprovince (Delfino et al., 2007). On the eastern side of the same
12 palaeobioprovince, at Scontrone (Tortonian, late Miocene; Mazza and Rustioni, 2008), crocodylian
13 remains are represented by isolated teeth that were originally referred to genus *Crocodylus* sp. by
14 Rustioni et al. (1992). Due to the fact that isolated teeth are nearly uninformative for crocodylian
15 taxonomy, the identification of this material has been questioned (Kotsakis et al., 2004; Delfino et
16 al., 2007) or cautiously accepted (Delfino and Rook, 2008) by crocodylian scholars.

17 Recently prepared material from Scontrone significantly improves the knowledge of the
18 crocodylians of this locality by supporting the original identification by Rustioni et al. (1992). Here
19 we will present these remains and discuss their importance in the context of the biogeography of the
20 late Neogene Mediterranean crocodylians.

21

22 **2. Systematic palaeontology**

23

24 **Abbreviations:** BSP, Universitätsinstitut und Staatssammlung für Paläontologie und historische
25 Geologie, München, Germany; MGUV, Museo de Geología Universitat de Valencia, Spain; RGM,
26 Naturalis, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; SCT, Scontrone

1 collection at Soprintendenza per i Beni Archeologici dell’Abruzzo, Chieti, Italy (partly exhibited at
2 “Centro di Documentazione Paleontologico *Hoplitomeryx*, Scontrone).

3

4 CROCODYLIA Gmelin 1789

5 CROCODYLIDAE Cuvier, 1807

6 *CROCODYLUS* Laurenti, 1768

7 cf. *Crocodylus* sp.

8 **Locality and age:** Scontrone (Abruzzo, Central Italy), late Miocene, Tortonian, 9 Ma (Patacca et
9 al., this volume).

10 **Referred material:** SCT 6: 1 tooth; SCT 14a: 13 teeth; SCT14b: 12 teeth; SCT 24: fragmentary
11 left articular; SCT 25: 1 tooth; SCT 98: 2 teeth; SCT 108a: 1 osteoderm (?); SCT 110: 2 teeth; SCT
12 118: 2 teeth; SCT 135: 1 tooth; SCT 139: 1 tooth; SCT 158: 1 tooth; SCT 187: 1 right prefrontal;
13 SCT 188: 2 teeth; SCT 200: 5 teeth; SCT 212: 1 tooth; SCT 223: 1 tooth; SCT 241: 1 tooth; SCT
14 244: 1 tooth; SCT 245: 1 tooth; SCT 267: 1 tooth; SCT 268: 1 tooth; SCT 276: 1 dentary; SCT
15 284a: 1 tooth; SCT 284b: 1 tooth; SCT 284c: 1 tooth; SCT 323: 1 tooth; SCT 341: 1 tooth; SCT
16 405: 1 tooth; SCT 409: 1 tooth; SCT 415: 1 nasal (?) fragment associated with fragmentary bones
17 and 1 tooth; SCT 435: skull fragment.

18 **Description:** SCT 276 (Fig. 2) is a nearly complete right dentary, 21 cm long, preserving 13
19 alveoli, none of which hosts a complete tooth. The dentary is festooned. When seen in lateral view,
20 the first, fourth, and eleventh alveoli correspond to the major convexities, whereas the second (or
21 better the second interalveolar space) and the eighth alveoli are located at the bottom of the
22 concavities. In dorsal view, the moderate festooning corresponds to the alternance between alveoli
23 (convexities) and interalveolar spaces (concavities). The approximate mesiodistal width of the first
24 9 alveoli and of the corresponding interalveolar space is as follows (the first number indicates the
25 position of the alveolus and of the interalveolar space; the following numbers indicate their width):
26 1: 11.0 - 9.1; 2: 8.1 - 8.4; 3: 6.1 - 2.1; 4: 11.9 - 2.8; 5: 6.2 - 3.7; 6: 7.1 - 3.8; 7: 7.5 - 6.0; 8: 7.9 - 9.5;

1 9: 9.0 - 4.0. The third and fourth alveoli are clearly separated by a bony septum (approximately 2.1
2 mm wide) and are markedly different in size, being the fourth (11.9 mm) much larger than the third
3 (6.1 mm). The eighth interalveolar space is the largest and corresponds to a wide and deep lateral
4 concavity. Despite some erosion of the rim of the alveoli, it is clear that it was not distinctly
5 protruding as in the case of the alveoli of the lower jaw RGM 335893 of *Crocodylus* sp. from
6 Gargano (Delfino et al., 2007: fig. 5B). Small foramina are aligned medially to the alveoli. Occlusal
7 pits are scarcely visible: possible pits are located slightly laterally to the twelfth and the thirteen
8 interalveolar spaces. The dentary symphysis reaches the posterior half of the fifth alveolus. The scar
9 of the splenial has a ventral tip longer than the dorsal one.

10 Associated to the dentary there is an isolated tooth without apex. It is 11 mm long, 6,9 mm wide at
11 the base (maximum diameter), and provided by evident mesiodistal carinae and ridged medial and
12 lateral surfaces.

13 The slab SCT 415 (Fig. 3A) hosts a possible nasal bone, exposed in medial view, which is slightly
14 arched (dorsally?).

15 The incomplete right prefrontal (Fig. 3B) is characterized by a moderately raised orbital rim and by
16 the apparent absence of any relevant transversal ridge on the pitted dorsal surface.

17 Several dozens of isolated teeth do not significantly differ from the one described above (SCT 276),
18 being only slightly different in terms of size, shape (from slender and pointed to relatively massive
19 and blunt), and in terms of the expression of the carinae and ridges, which are related to their former
20 position within the buccal cavity (Fig. 3C). A few teeth (as SCT 241) preserve their root.

21

22 **3. Discussion**

23

24 *3.1. The Scontrone crocodylian remains and their relevance*

25

1 The characters described above match with the morphology of *Crocodylus*, already identified in
2 Apulo-Abruzzi palaeobioprovince, and allow us to exclude the presence of the alligatoroid
3 *Diplocynodon*, the only other crocodylian with a generalized rostral morphology that, according to
4 the present knowledge of crocodylian biogeography, was present in Europe during the late
5 Miocene. The dentary of *Diplocynodon* is characterized, among others, by subequal and confluent
6 third and fourth alveoli, and, usually by a large seventh interalveolar space (Brochu, 1999; Martin,
7 2010; Delfino, pers. obs.). Even if the material so far known from Scontrone does not allow to
8 detect the autapomorphies of *Crocodylus* (see Brochu, 2000, but consider that in that paper
9 *Mecistops cataphractus* (Cuvier, 1825) was still considered to belong to *Crocodylus*), for both
10 morphological and biogeographic reasons the dentary from Scontrone can be referred to cf.
11 *Crocodylus* sp., therefore confirming the original identification by Rustioni et al. (1992).
12 At the moment, the only European fossils referable to *Crocodylus* are those coming from the late
13 Miocene-early Pliocene of the Gargano region (*Crocodylus* sp.; Delfino et al., 2007), from the
14 Tortonian of Monte Bamboli (cf. *Crocodylus* sp.; note that *Crocodylus bambolii* Ristori, 1890 is a
15 *nomen dubium*; Delfino and Rook, 2008), and from the Tortonian of Scontrone (cf. *Crocodylus* sp.;
16 Rustioni et al., 1992; this paper). The crocodylian remains so far discovered in the Tortonian of
17 Fiume Santo (a Sardinian locality belonging to the same palaeobioprovince of Monte Bamboli)
18 have not been identified at genus level, being represented by isolated teeth only (Abbazzi et al.,
19 2008). Remarkably, according to Böhme and Ilg (2003) the collections of the University of
20 Valencia host material referable to *Crocodylus* sp. (MGUV 14437, 14451, 14452, 14457, 14461,
21 14463-14467, 14469 - 14472, 14474, 14475, 14490, 14816) from the Messinian (MN13) locality
22 Venta del Moro (Cabriel Basin, Spain); the highly desirable full description of this material is still
23 pending.
24 Even if the identification of the crocodylian remains from Scontrone is partly based on
25 biogeography and therefore there is the risk of introducing in the discussion some sort of circular
26 reasoning, it is tempting to place them in a Mediterranean picture. The remains from Scontrone,

1 being at least 9 Ma old (Patacca et al., this volume; 10 Ma according to Mazza and Rustioni, 2008;
2 not older than 10.56 Ma according to Patacca et al., 2008), currently represent the possible oldest
3 European evidence of the presence of *Crocodylus* and broadly predate the oldest remains so far
4 referred to this genus, which are from Africa and date back to about 7 Ma (Brochu and Storrs,
5 2012). They prove that this taxon could have reached Europe “during the Tortonian and therefore
6 well before the Messinian Salinity Crisis, traditionally considered as the event that caused several
7 trans-Mediterranean dispersals” (Delfino et al., 2007: 303).

8 As for the origin of the *Crocodylus* that inhabited the two Italian palaeobioprovinces, Kotsakis et al.
9 (2004) discussed the possible ways of dispersal from Africa, which was considered as the centre of
10 origin of the genus (Brochu, 2000, 2001). The dispersal may have taken place once or twice with
11 independent colonisation of each area. *Crocodylus* is well known for being able to survive in
12 saltwater because of its morphological, physiological and behavioural properties (among others
13 Taplin and Grigg, 1981; Taplin et al., 1982; Grigg et al., 2001; Cramp et al., 2008, 2010) and its
14 current distribution is best explained assuming significant transoceanic dispersals (Brochu, 2001,
15 2003). Being the late Neogene Mediterranean Sea a relatively small basin with a complex
16 physiography characterized by considerable peninsulas and gulfs, and scattered by several islands
17 (see maps in Meulenkamp and Sissingh, 2003), one can assume that it could have been easily
18 crossed by *Crocodylus*. Such assumption is strongly supported by the recent advances on the
19 knowledge of the behavioural strategies of a crocodile species, the estuarine crocodile *Crocodylus*
20 *porosus* Schneider 1801, which is able to voluntarily migrate taking advantage of water surface
21 currents as well as to quickly disperse over considerable distances (a minimum of 590 km in 25
22 days; Campbell et al., 2010). Even if it is not known if such characteristics were shared by the
23 *Crocodylus* populations that formerly inhabited the Mediterranean area, the presence of this genus
24 in several different late Miocene localities could indicate that it routinely crossed the basin, or that
25 at least it was able to disperse for considerable distances along the coasts (see the case of the Nile
26 soft-shelled turtle that nowadays reaches the eastern Greek islands, Taskavak et al., 1999).

1 Crucial is therefore the specific identification of the late Miocene *Crocodylus* remains of the
2 Mediterranean area. So far, only the remains from As Sahabi (Libya) have been identified at species
3 level, with the description of the species *Crocodylus checchiai* Maccagno, 1947, characterized,
4 among others, by a distinctly raised midrostral boss (Maccagno, 1947, 1952; Delfino, 2008b).
5 According to the recent results by Brochu and Storrs (2012), this species had a large range reaching
6 the Turkana Basin (Nawata Formation, latest Miocene to earliest Pliocene) and its presence in the
7 northern sector of the Tethys, even if requires an overwater dispersal, could be likely. Up to now,
8 the European remains referred to *Crocodylus* (with a different degree of precision) have not been
9 identified at species level. The fact that the possible nasal SCT 415 (Fig. 3A) from Scontrone is
10 apparently slightly convex (presumably in dorsal direction) could be either an evidence for the
11 presence of midrostral boss or related to its fragmentation and possible deformation, an issue that
12 will be solved after the full preparation of the material. It is worth pointing out that the juvenile
13 maxilla BSP 2004 I 1 from the Gargano Terre Rosse referred to *Crocodylus* sp. has a peculiar para-
14 sagittal groove delimiting a markedly raised medial edge that could be related to the presence of a
15 boss (Delfino et al., 2007: fig. 2B), supporting its phylogenetic relationship with *C. checchiai*, if not
16 their conspecificity. However, all the skeletal elements from Gargano indicate that this *Crocodylus*
17 was smaller than *C. checchiai*, and the lower jaw RGM 335893 is characterized by several alveoli
18 showing margins distinctly ‘protruded’ outward (Delfino et al., 2007: fig. 5) that could indicate, if
19 not pathologic, a late ontogenetic stage. Comparative material of juvenile maxillae of extant
20 *Crocodylus* species with a midrostral boss, as well as further fossil remains, should be examined to
21 solve this issue.

22 23 3.2 The late Neogene crocodylians of Europe and of the Mediterranean area

24 The *Crocodylus* remains so far described or mentioned are not the only late Neogene crocodylians
25 of Europe and of the Mediterranean area (Fig. 1). Besides this genus, remains of another

1 generalized crocodylian, *Diplocynodon*, and of two slender-snouted taxa, *Euthecodon* and
2 *Tomistoma/Gavialosuchus* have been reported.

3 According to Böhme and Ilg (2003), the European endemism *Diplocynodon* is present in four
4 Tortonian localities: Subpiatră 2/1R (Romania; MN6; cf. *Diplocynodon* sp.), Crevillente 4 (Spain;
5 MN12; *Diplocynodon* sp.), Masia de la Roma 4B (Spain, MN10, *Diplocynodon* sp.), and Ribatejo
6 (Portugal; MN9; *Diplocynodon* sp.). Other *Diplocynodon* data, from Bulgaria and Libya, are
7 actually better considered as undetermined crocodylians. The age and validity of *Diplocynodon*
8 *levantinum* Huene and Nikoloff, 1963 from Bulgaria, formerly considered as Pliocene in age but
9 later on as late Miocene (Huene and Nikoloff, 1963, Rauhe and Rossmann, 1995; Ginsburg and
10 Bulot, 1997), should be reassessed. D'Erasmus (1933, 1934) referred a few cranial and postcranial
11 remains from the Libyan locality of As Sahabi to *Diplocynodon* sp., but also wrote that it was not
12 possible to identify with confidence this genus on the basis of the material at his disposal.

13 Maccagno (1952) underlined that this *Diplocynodon* has a character in common (shape of
14 squamosal) with *C. checchiai* but differs for another (interorbital area). By the analysis of the
15 available descriptions and figures, it is possible to suggest that these remains should not be
16 identified at genus rank, in agreement with Buffetaut (1985) and Buscalioni et al. (1992) who
17 considered the presence of *Diplocynodon* at As Sahabi as poorly documented and questionable.

18 According to the present knowledge of the fossil record, alligatoroids never reached Africa
19 (Brochu, 2001), and the first evidence of an alligatoroid in Africa (Rossmann et al., 2000) actually
20 requires further confirmation being represented by fragmentary remains.

21 So far, the slender-snouted osteolaemine crocodylid *Euthecodon* has been identified only in African
22 localities (only late Neogene localities are listed here): Beglia (Tunisia; middle-late Miocene,
23 *Euthecodon* sp.; Pickford, 2000; Llinas Agrasar, 2003), Djebel Krechem el Artsouma (Tunisia;
24 Tortonian; *Euthecodon* cf. *E. nitriae* Fourtau, 1920; Geraads, 1989; see Pickford, 2000, for doubts
25 on this identification), As Sahabi (Libya; Messinian-Zanclean; *Euthecodon* sp.; Hect, 1987), and
26 Wadi el Natrun (Egypt; Piacentian-Gelasian; *Euthecodon nitriae*; the age of this site is Pliocene

1 according to Böhme and Ilg, 2003, but late Miocene according to Pickford, 2000). Due to the
2 extremely peculiar morphology of this taxon, the misidentification of its remains is rather unlikely,
3 therefore its absence from the European fossil record could likely reflect the fact that it never
4 dispersed outside Africa.

5 The Neogene fossil record of the other slender-snouted crocodylid, *Tomistoma* (but see Rossmann
6 et al., 1999, for a discussion on the possible referral of these materials to *Gavialosuchus*), indicated
7 that it inhabited both the African and the European sides of the Mediterranean Basin (for a
8 summary of tomistomine global distribution see Piras et al., 2007), even if its presence in the late
9 Miocene of Africa seems to be doubtful. Robinson and Black (1969) listed *Tomistoma* in the fauna
10 of the middle-late Miocene Beglia Formation of Tunisia, but Pickford (2000) did not find any
11 *Tomistoma* remains while revising their collection. Nevertheless, the Neogene presence of
12 *Tomistoma* in Northern Africa is testified by *Tomistoma dowsoni* Fourtau, 1920 (Wadi Moghara;
13 Egypt; early Miocene; Fourtau, 1920) and it still inhabited Africa in the late Miocene (Pickford,
14 2000). On the European side of the Mediterranean, *Tomistoma* was identified in a few late Miocene
15 localities: Olhos de Agua (Portugal; Tortonian; MN9; *Tomistoma* cf. *T. lusitanica* Vianna and
16 Moraes, 1945; Böhme and Ilg, 2003), Sant Pere de Ribes (Spain; Tortonian; MN9; *Tomistoma* cf.
17 *T. lusitanica* Böhme and Ilg, 2003), Is Miriones (= Is Mirrionis; Italy; Tortonian-Messinian;
18 *Tomistoma calaritanus* Capellini, 1890; Capellini, 1890).

19 A similar pan-Mediterranean distribution is shown by *Crocodylus*, which, besides the above
20 mentioned Italian and Spanish localities, has been identified in the Tortonian of Tunisia (Djebel
21 Krechem el Artsouma; *Crocodylus* cf. *C. checchiae*; Geraads, 1989; see Pickford, 2000, for doubts
22 on this identification) and in the Messinian-Zanclean of Libya (As Sahabi; *Crocodylus checchiae*
23 Maccagno, 1947; Maccagno, 1947, 1952; Delfino, 2008b). Pickford (2000) reported a crocodylid
24 fragmentary dentary from the middle-late Miocene of Bled Douarah (Beglia Formation, Tunisia) that
25 he referred to as *Crocodylus lloydi* Fourtau, 1920. This species is now ascribed to the osteolaemine

1 genus *Rimasuchus*, but its proper identification should be revised with the addition of more
2 complete, diagnostic skeletal elements.

3 The material from As Sahabi is particularly relevant because it represents the most complete late
4 Miocene *Crocodylus* remains of the whole Mediterranean area. Crocodylian remains have been
5 collected at As Sahabi since 1931 and reported since 1933 on (D'Erasmus, 1933, 1934; Petrocchi,
6 1941), even though the first thorough descriptions were published in 1947 and 1952 by Maccagno
7 who carefully described a new species, *Crocodylus checchiai*. Further remains of *C. checchiai* from
8 this locality have been recently described by Delfino (2008b). Leakey et al. (1996) considered *C.*
9 *checchiai* as synonym of *C. niloticus*. Hect (1987) accepted the validity of *C. checchiai* and
10 underlined morphological affinities (mainly the development of a preorbital promontorium) with
11 some American species. Brochu and Storrs (2012) recently described new remains of this taxon
12 from the Turkana Basin, and cladistically analyzed its relationships for the first time confirming its
13 referral to *Crocodylus*.

14 *Crocodylus* inhabited the African Mediterranean countries until historical times (with very few
15 fossils testifying its presence during the Pleistocene; as an example, see Bailon, 2000, who reported
16 material from Morocco) and seems to be the last crocodylian that inhabited Europe (Messinian-
17 Zanclean; Delfino et al., 2007). Rage (1997) stated that European crocodylians went extinct in
18 France during the early Pliocene without mentioning any precise locality. These remains could be
19 represented by few fragments coming from "Sables de Montpellier", but so far they have not been
20 identified in detail (Delfino, 2008a).

21

22 **4. Conclusions**

23

24 The Scontrone crocodylian remains, referred to cf. *Crocodylus*, could represent the oldest fossil
25 evidence of *Crocodylus*, being at least 2 Ma younger than the earliest evidence of this genus
26 published so far (Africa; Brochu and Storrs, 2012). Such a little difference does not allow us to state

1 that *Crocodylus* originated in Europe (further findings will hopefully clarify this issue), but
2 underlines that dispersal across saltwater barriers has been a key factor for the distribution and
3 evolution of this genus since its earliest steps documented by the fossil record. Rather striking is the
4 difference in the distribution pattern of the crocodylians that inhabited the Mediterranean area
5 during the Neogene (see Fig. 1). The difference in the distribution of the two slender-snouted
6 crocodyloids *Tomistoma/Gavialosuchus* and *Euthecodon*, pan Mediterranean for the first, but
7 exclusively African for the second, could be somehow related to the extreme specialization of
8 *Euthecodon* (considered a freshwater piscivore as the living Indian Gharial, *Gavialis gangeticus*
9 (Gmelin, 1789); Ginsburg and Buffetaut, 1978; Pickford, 2000) that possibly imposed significant
10 ecological constraints to its dispersal across the sea.

11 The two generalized crocodylians have also a different distribution: *Crocodylus* has been identified,
12 as *Crocodylus checchiai*, *Crocodylus* sp. or cf. *Crocodylus* sp., in several circum-Mediterranean
13 localities, both in continental areas and in islands, whereas the alligatoroid *Diplocynodon* is present
14 only in continental settings in the northern side of the basin (it is absent in the systems of islands
15 belonging to the above mentioned palaeobioprovinces). The different tolerance to saltwater shown
16 by extant crocodylids and alligatorids could have influenced their former ranges and the timing of
17 their extinction in Europe. Assuming an African origin of *Crocodylus*, the saltwater tolerance
18 allowed it to disperse across the Mediterranean Sea and to colonize the large central Mediterranean
19 islands (at least the Apulo-Abruzzi and Tusco-Sardinian palaeobioprovinces) and Europe. It is also
20 possible that *Crocodylus* took advantage of brackish environments (as estuaries or nearshore
21 habitats) as buffering media against temperature extremes in periods of increased seasonality
22 leading to periodic absence of freshwater, as those of the latest Miocene, and that therefore its
23 extinction in Europe was delayed in comparison to other taxa, the European endemism
24 *Diplocynodon* included (Markwick, 1998; Delfino et al., 2007). If the properties of extant alligators
25 are extended to extinct alligatoroids, it could be tentatively stated that *Diplocynodon* was relatively
26 cold tolerant (see Martin, 2010) but its presumed salt intolerance limited the possibility of its

1 temporary colonization of brackish environments and hindered its dispersal from continental
2 Europe to the Mediterranean islands and Africa.

3

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5

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18

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20 **Figure captions**

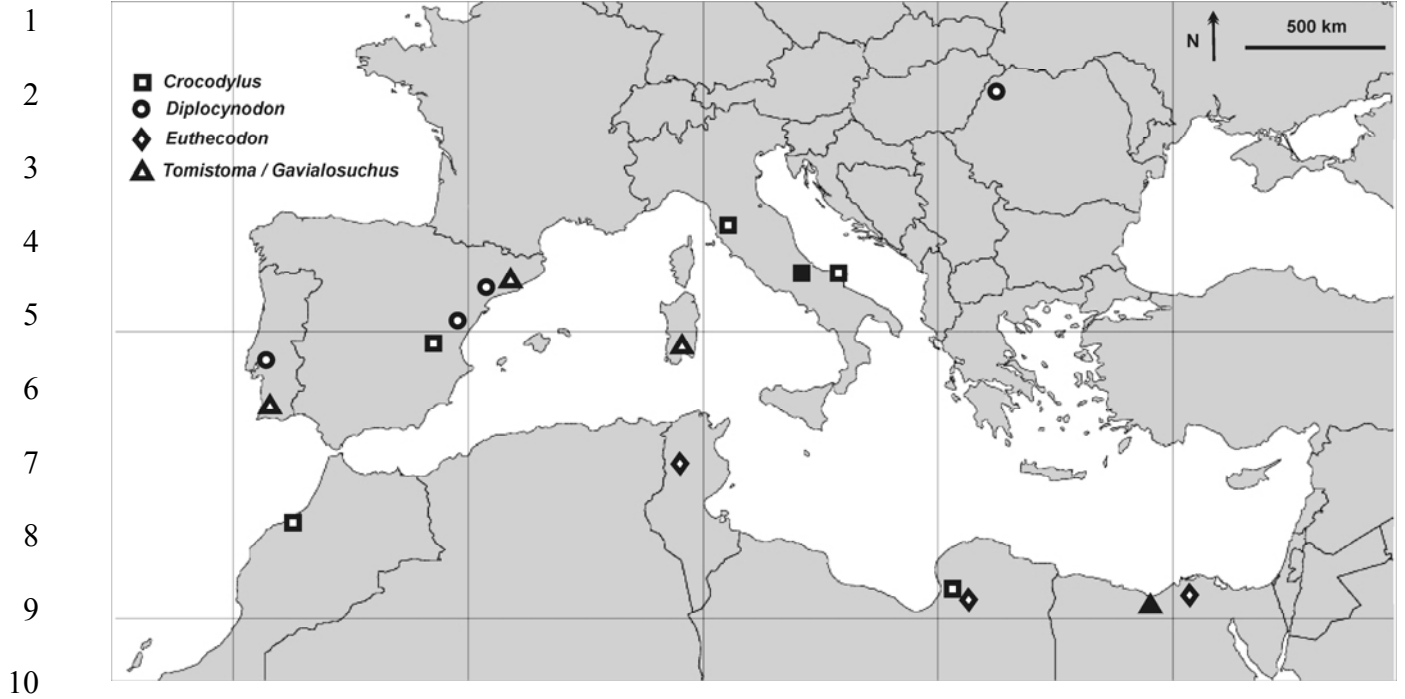
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22 Fig. 1: Late Neogene European and Mediterranean localities with fossil crocodylians identified at
23 least at genus level. The solid square indicates Scontrone, where the remains of cf. *Crocodylus* sp.
24 described in this paper come from. The early Miocene locality of Wadi Moghara, Egypt (solid
25 triangle) is included just to indicate that tomistomines were previously present in the Mediterranean
26 area, although their presence in the late Neogene is doubtful. The localities are not shown on a

1 paleogeographic as they cover a wide time span presenting different palaeogeographic
2 arrangements.
3
4 Fig. 2: **A**, **B**, cf. *Crocodylus* sp. from Scontrone (Italy), right dentary in right lateral and dorsal
5 views (SCT 276). **C**, *Diplocynodon* sp., unnumbered specimen in the collections of
6 Naturhistorisches Museum, Basel (Switzerland), early Miocene, Montaignu (France); dorsal view of
7 the anterior region of a left dentary showing that alveoli IV and V are confluent and subequal in
8 size. **D**, detail of **B** clearly showing that alveoli IV and V are well separated and different in size. **E**,
9 detail of the right dentary SCT 276 in medial view (anterior to the top) with arrows showing the
10 anterior tips of the splenial scar. Scale bar equals 10 mm, but **C-E** not to scale.

11
12 Fig. 3: cf. *Crocodylus* sp. from Scontrone (Italy). **A**, slab with a possible nasal in medial view,
13 unidentified bones and tooth (SCT 415). **B**, incomplete right prefrontal in dorsal view (SCT 187).
14 **C**, isolated tooth (SCT 25) showing the slender morphology characterizing anterior teeth.
15 Abbreviations: **om**, orbital margin; **n**, nasal. Scale bars equal 10 mm.

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11 **Fig. 1**

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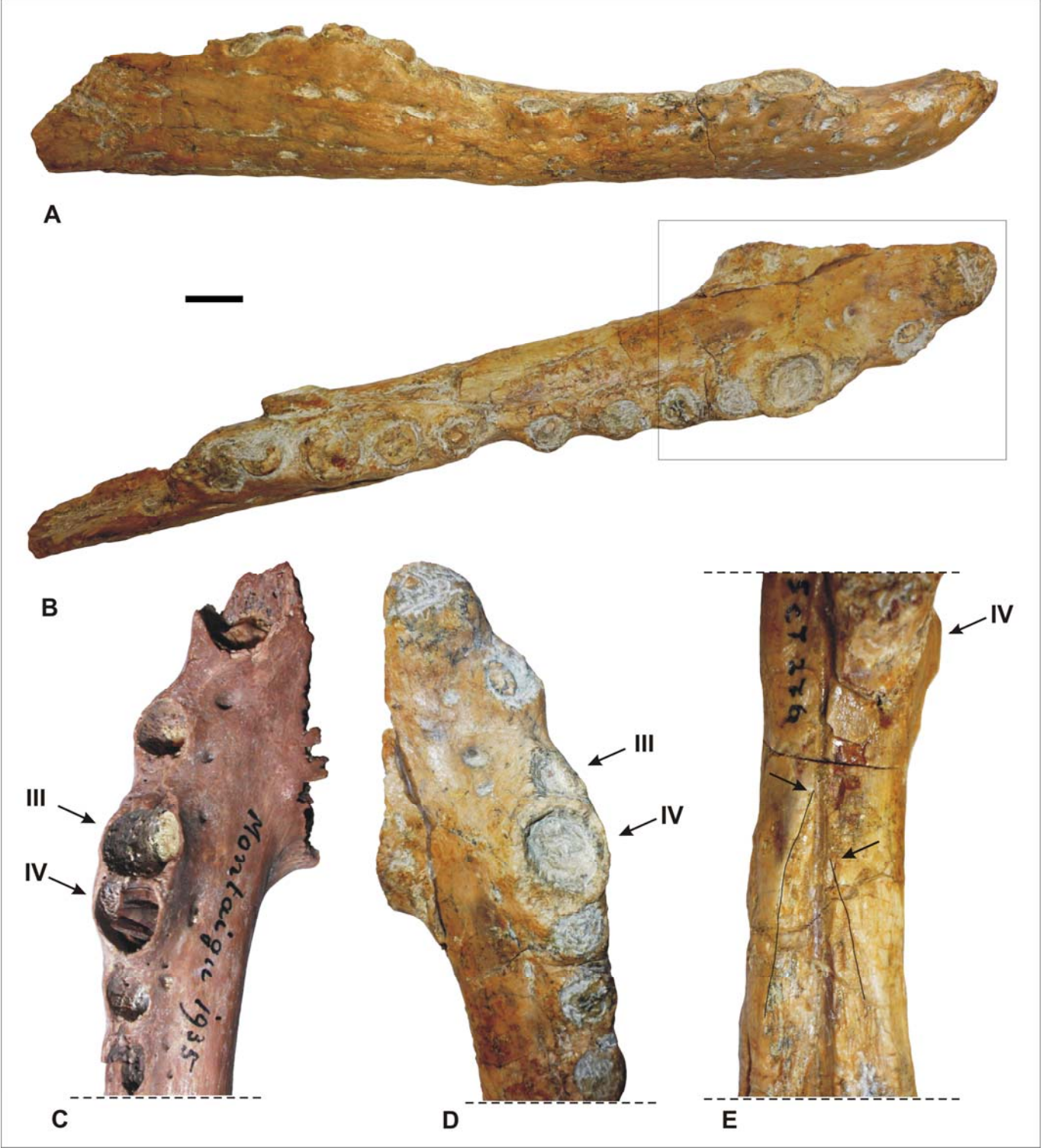


Fig. 2

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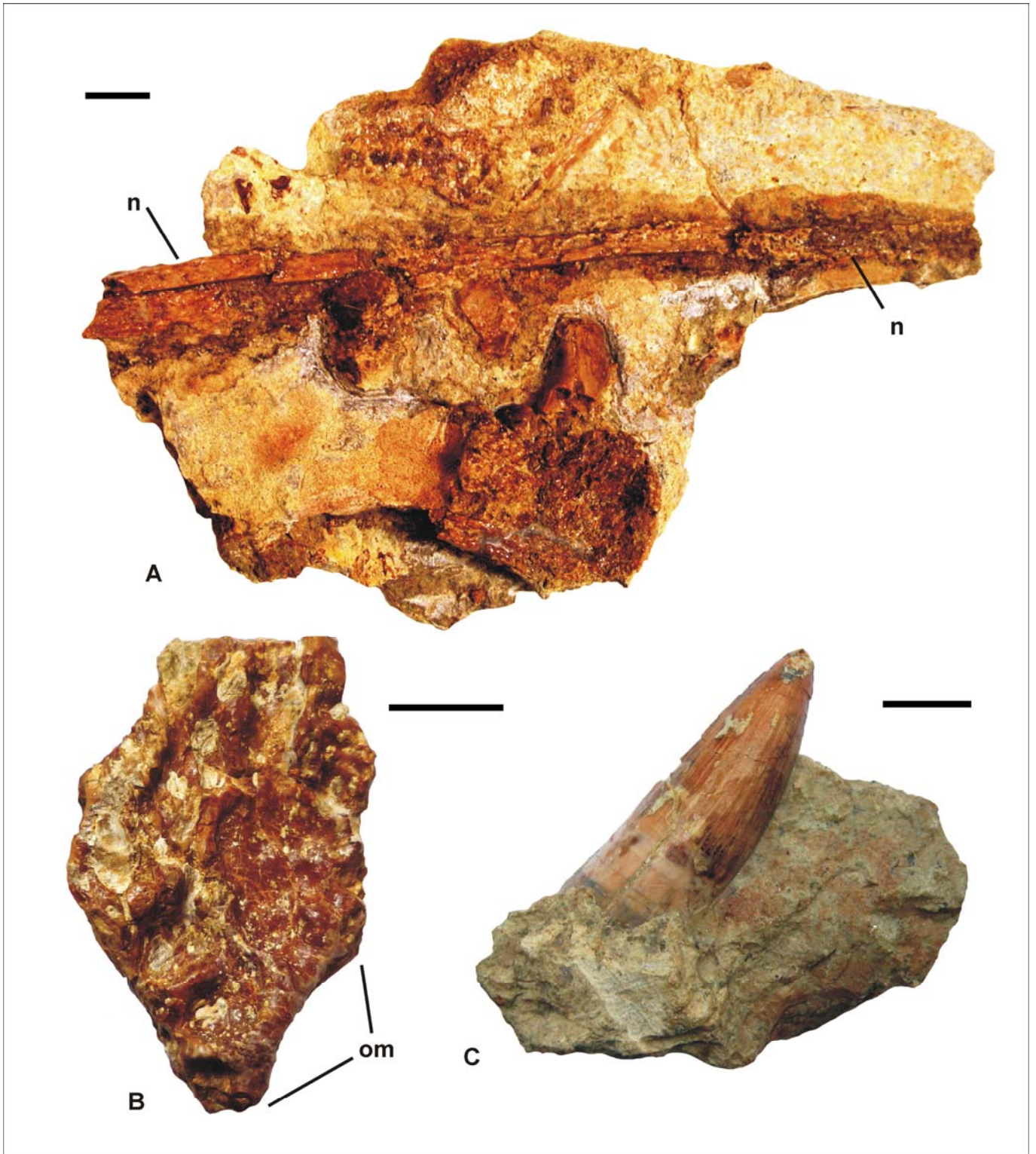


Fig. 3