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THE FIRST RECORD OF A NOTOSUCHIAN CROCODYLIFORM FROM ITALY

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Abstract. A serrated tooth from the Coniacian-Santonian (Upper Cretaceous) Polazzo fossil site (Karst, NE Italy) is the first record of a notosuchian crocodyliform from Italy. Although it shares synapomorphies with teeth referred to the European genus *Doratodon* and with the Gondwanan genus *Araripesuchus*, it is distinct in the unusual combination of features, suggesting the presence of a yet unreported notosuchian taxon in the Adriatic-Dinaric Carbonate Platform located in the Tethys between the Afroarabian continent and the North European landmass during Late Cretaceous times. Notosuchians were typically terrestrial crocodyliforms, supporting the presence of emergent areas on the carbonate platform.

Riassunto. Un dente munito di carene denticolate rinvenuto nel sito fossilifero di Polazzo (Carso, Italia nordorientale) e databile al Coniaciano-Santoniano (Cretacico Superiore) è la prima testimonianza di un coccodrilliforme notosuco in Italia. Sebbene condivida sinapomorfie con denti attribuiti al genere europeo *Doratodon* e con il gondwaniano *Araripesuchus*, esso si distingue per l'inusuale combinazione di caratteri, che suggerisce la presenza di una specie di notosuco non ancora identificata nella Piattaforma Carbonatica Adriatico-Dinarica, localizzata tra il continente Afroarabico e quello Nord Europeo. I notosuchi erano coccodrilliformi prettamente terrestri e questo è indicativo della presenza di aree emerse sulla piattaforma carbonatica.

Introduction

During the 1997 field work in Upper Cretaceous Polazzo fossil site (Fogliano-Redipuglia Municipality, Gorizia Province, NE Italy; Fig. 1), an unusual serrated tooth was found (Rigo 1997). The specimen was preliminarily and tentatively referred to the ziphodont crocodyliform *Doratodon* in some overviews of the Polazzo fossil assemblage (e.g., Dalla Vecchia et al. 2001b; Dalla Vecchia & Tentor 2004), but remained undescribed. The tooth is stored in the collections of the Palaeontological Section of the Museo della Rocca di Monfalcone with the specimen number MPCM 11720 (the original field number was S97/118).

The aim of this work is to describe the specimen in detail and discuss its affinity. Establishing the taxonomic status of MPCM 11720 is necessary, as there have been suggestions that the tooth could in fact belong to a theropod dinosaur (P. Currie, pers. comm.). As dinosaur evidence is rare in Italy, it would be worth of note. In the meantime, the tooth has been recently mentioned in literature as evidence of the genus *Doratodon* in the Upper Cretaceous of Italy (Delfino 2001; Rabi 2008), with potential paleogeographic implications, despite the fact that its identification in previous papers was clearly tentative and preliminary.

Terminology and methods

The odontological terminology and variables used in this paper are those of Smith & Dodson (2003) and Smith et al. (2005). The terms 'cellae' and 'caudae' are used in the sense of Abler (1992). Parameters of *Doratodon* teeth from Austria, Romania and Hungary are based on measurements taken from photographs published in Buffetaut (1979), Martin et al. (2006), and courtesy of Marton Rabi, respectively.

The averostran theropods are considered according to Ezcurra (2006) as those belonging to the least inclusive clade including neoceratosaurs and tetanurans (Fig. 2A). The crocodyliform phylogenetic framework and taxonomy followed herein is that of Sereno & Larsson (2009) and Sereno et al. (2001). Accordingly, the Crocodyliformes are the least inclusive clade including protosuchids and crown-group crocodiles (Crocodylia), the Mesoeucrocodylia is the most inclusive crocodyliform clade excluding protosuchids, and the Notosuchia is the most inclusive clade including *Notosuchus*, but excluding crown-group crocodiles (Fig. 2B).

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Fig. 1 - Location of the Polazzo site (Fogliano-Redipuglia, Italy) where MPCM 11720 was found.

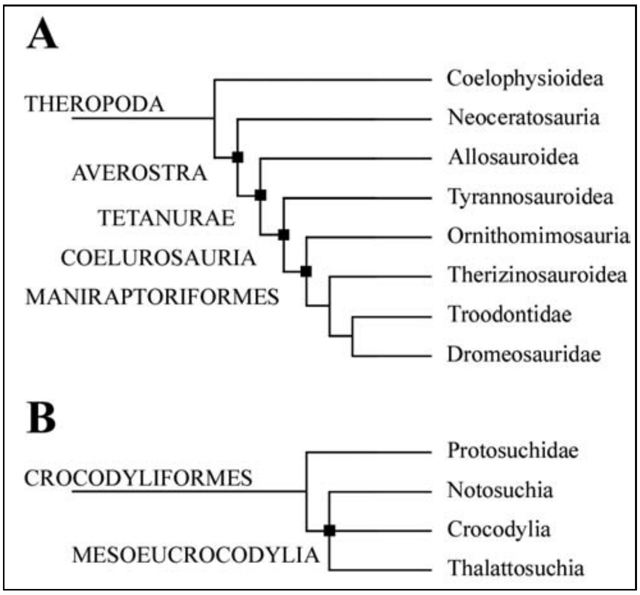

Fig. 2 - Phylogenetic relationships among the main theropod (A) and crocodyliform (B) clades mentioned in the text. Since the position of the Thalattosuchia among the Crocodyliformes is controversial, an unresolved polytomy is presented here.

Abbreviations for variables. AL, apical length; CA, crown angle; CBL, crown base length; CBW, crown base width; CBR, crown base ratio (CBW/CBL); CH, crown height; CHR, crown height ratio (CH/CBL); DA, distal apical denticles density (per mm); DB, distal basal denticles density (per mm); DC, distal mid-crown denticles density (per mm); MB, mesial basal denticles density (per mm); MC, mesial mid-crown denticles density (per mm).

Institutional abbreviations. FGGUB, Facultatea de Geologie şi Geofizica, Universitatea Bucureşti, Bucharest, Romania; MNN, Muséum National du Niger, Niamey, République de Niger; MPCM, Museo della Rocca di Monfalcone – Sezione Geopaleontologica (former Museo Paleontologico Cittadino di Monfalcone), Gorizia, Italy; UWP, Paleontological Institute, University of Vienna, Austria.

Geological and paleontological notes

The Polazzo fossil site occurs in the western portion of the Italian sector of the Karst Plateau named ‘Carso Isontino’ in Italian. It actually includes two sites, named site A and site B and probably representing two distinct, but close, stratigraphic sections (see Dalla Vecchia et al. 2001b and Dalla Vecchia & Tentor 2004 for more information).

Fieldwork at site B where MPCM 11720 was found has been undertaken systematically since 1996 by the Museo Paleontologico Cittadino of Monfalcone (now Palaeontological Section of the Museo della Rocca di Monfalcone).

Both site A and B have yielded a peculiar fossil assemblage composed mainly of perfectly articulated and well-preserved osteichthyan fishes. The ichthyofauna includes the pycnodontiform *Polazzodus coronatus* Poyato-Ariza, 2010, the alopiform *Rhynchodercetis*, small clupeomorphs, rare Chanidae, *Enchodus* sp., an anguilliform, and some small-sized beryciform acanthopterygians (Guidotti 1983; Dalla Vecchia & Tentor 2004; Poyato-Ariza 2010). Terrestrial plant remains (*Frenelopsis* sp., *Brachiphyllum* sp., *Pagiophyllum* sp., cf. *Sphenolepis*, *Cunninghamites* cf. *elegans*, some probable ginkoales and indeterminate angiosperms) are relatively common at site A, and are much rarer at site B (Dalla Vecchia & Tentor 2004). Invertebrate evidence is represented only by a few decapod crustaceans, some rudist bivalve shells and a level with trace fossils (Dalla Vecchia & Tentor 2004). Tetrapod remains were found nearly exclusively at site A and consist of disarticulated bones of non-marine chelonians and a worn tooth of a crocodyliform (Dalla Vecchia & Tentor 2004).

The fossiliferous section of site B is only 122.5 cm thick and is composed of thinly laminated, light gray-greenish limestone (Dalla Vecchia et al. 2001b; Dalla Vecchia & Tentor 2004). Microfacies analysis suggests that deposition was in a restricted lagoonal environment with intertidal episodes (Sandro Venturini, pers. comm. to F. M. D. V.). MPCM 11720 was found at the boundary between layers B and C, 200 and 190 mm thick respectively (see Dalla Vecchia & Tentor 2004, fig. 27). Both layers are composed of sets of stromatolite laminae and thin, coarser storm levels. The tooth was deposited at the base of the lamina B6 that is the lowermost storm level of layer B; other fossils found in B6 include the fish *Rhynchodercetis*. This section is part of a thicker stratigraphic section made of platy, well-bedded limestone cropping out east of the village of

Polazzo, belonging to the thick Upper Cretaceous carbonate platform sequence of the Karst. This sequence is dominated by limestone with rudist bivalves and is known in literature under the name of 'Calcari di M.te San Michele' (Martinis 1962). The lithostratigraphic unit containing the Polazzo section is called locally 'Calcari di Aurisina' (known informally also as 'calcari a Rudiste') and its age is considered Turonian-early Senonian (Tentor et al. 1994). Tintori et al. (1993) referred site A to the lower Senonian because of the presence of the foraminifer *Accordiella conica* and the algae *Sgrossoella partenopeia* above the fish levels and the foraminifer *Montcharmontia apenninica* below. *Montcharmontia* sp. was found also at site B; The foraminifers *M. apenninica*, *Pseudocyclammina sphaeroidea, Accordiella* sp., and *Scandonea samnitica*, and the algae *Sgrossoella* sp. were found in a section immediately below the fossiliferous section of site B. This assemblage suggests an early Senonian age (i.e., Coniacian-Santonian) also for site B, in agreement with the stratigraphic framework of the Karst Plateau (S. Venturini, pers. comm. to F. M. D. V.).

The Karst Plateau is formed mainly by carbonates generally supposed to have been deposited in a shallow marine environment at tropical latitudes and dominated by rudist 'reefs' during Late Cretaceous times. Following recent palaeogeographic reconstruction of western Tethys (see, for example, Eberli et al. 1993; Camoin et al. 1993; Philip et al. 2000), the Karst Plateau was situated at the northern point of a wide, isolated intraoceanic carbonate platform of Bahamian type (Adriatic-Dinaric carbonate platform) during Senonian times (Fig. 3). Emersion events affected locally or extensively this platform several times during Cretaceous times; the most important occurred during the late Campanian-Maastrichtian when a relatively large island formed (Adriatic Island: Otoničar 2007; Dalla Vecchia 2008, 2009). The emergent parts of the carbonate platform belonged to an archipelago of islands placed between the Northern European landmass and the Afroarabian continent (the European Archipelago: see Dalla Vecchia 2006; Pereda-Suberbiola et al. 2009).

Systematic Palaeontology

Archosauria Cope, 1869
Crocodylomorpha Walker, 1970
Crocodyliformes Hay, 1930
Mesoeucrocodylia Whetstone and Whybrow, 1983
Notosuchia Gasparini, 1971
Notosuchia gen. and sp. indet.
Figs 4-7A

Fig. 3 - The western Tethys during Santonian (Late Cretaceous) times, based on Eberli et al. (1993), with location of the Karst Plateau (asterisk) on the Adriatic-Dinaric Carbonate Platform. Dark gray color represents deep sea on oceanic crust, light gray epicontinental sea and marine basins on continental crust, white emergent land, and brick-pattern identifies the carbonate platforms.

Description. MPCM 11720 is a shed crown; the root was nearly completely re-adsorbed and the basal side of the crown appears concave in labiolingual view (Fig. 4A-B). Both mesial and distal cutting margins bear serrated carinae. Its AL is 12.25 mm and CH is 11.36; the CBL is 5.82 mm. The CBW is not significative because the labial side is damaged and the lingual side is slightly collapsed; width at mid-crown is 3.07 mm. The CBR cannot be calculated; however, the crown is not strongly compressed labiolingually: the width at the mid-crown is more than half the CBL (58%). The crown is relatively elongated basoapically, as the CHR equals 1.95.

The labiolingual polarity is likely indicated by the position of the mesial carina that twists on one side, presumably the lingual one.

The outline of the crown in side view is triangular, moderately curved distally (CA is 68 degrees), with a convex mesial margin that curves smoothly from the basal part to the apex, and a nearly straight and slightly inclined distal margin (Fig. 4A-B). The apical half of the crown is slightly curved lingually. The base of the crown is constricted; the constriction is well-marked

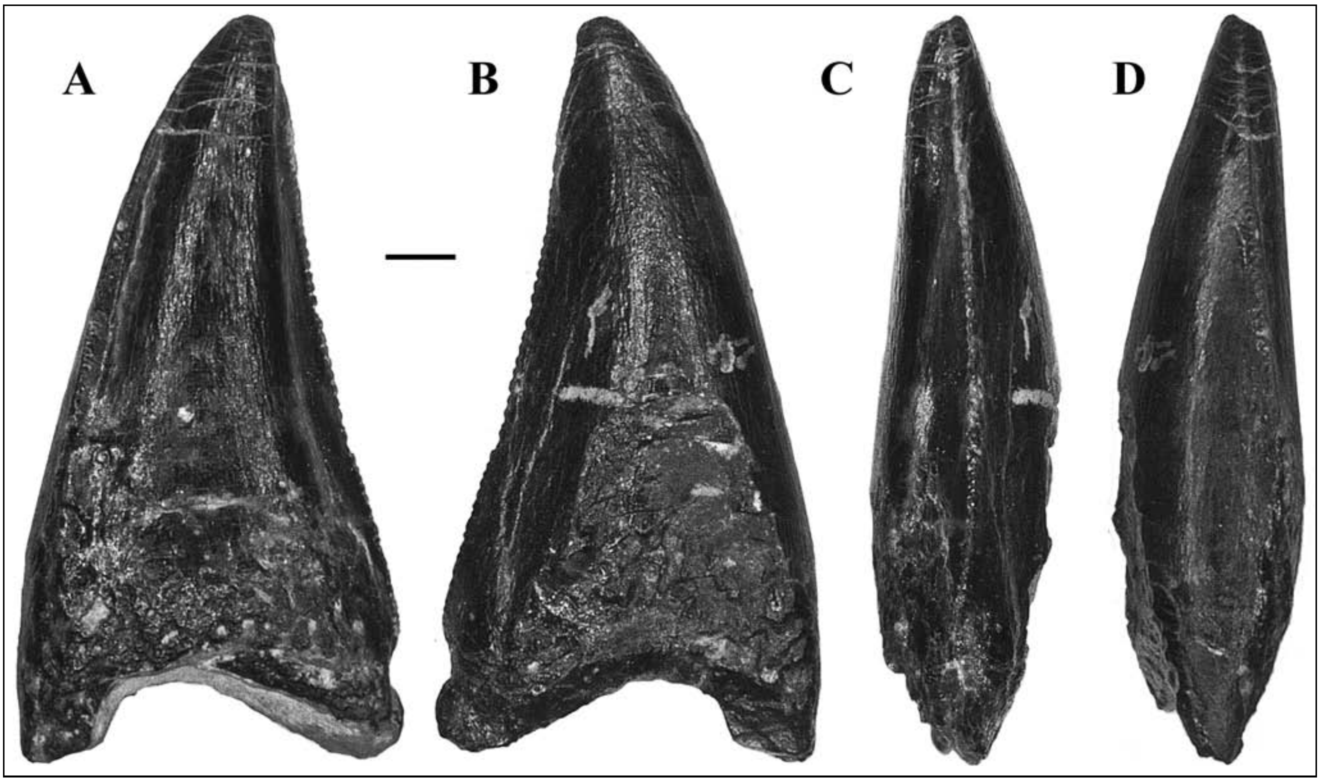

Fig. 4 - MPCM 11720, Notosuchia sp. and gen. indet. A) lingual view; B) labial view; C) distal view; D) mesial view. Scale bar equals 1 mm.

along the distal margin, where a notch is evident (Fig. 5), but it is imperceptible along the mesial margin. The distal margin presents a 'bump' just above the notch. The labial side is symmetrically convex (i.e., the apex of the convexity is central on the side; Fig. 4B); the lingual side has a central, longitudinal relief with a flat surface and step and concave mesial and distal slopes that are confluent with the serrated carinae and emphasize them (Fig. 4A, 7A).

The mid-crown cross-section is subrectangular to drop-like, with a rounded and wider mesial side, a narrower distal side with a sharp carina, a convex labial side, and a more flattened lingual side.

The apex of the crown presents a small wear facet extending slightly on the lingual surface. The crown surface is not fluted; it shows thin and irregular longitudinal wrinkles of the enamel. Small circular pits can be observed in the mid-lower part of the lingual side (Fig. 4A, 7A). The largest has a diameter of 0.43 mm, whereas the smallest has a diameter of 0.14 mm. The largest pit presents concentric lines of breakage and collapse of the tooth surface, which suggest it is a structure caused by compression by a small, conical point, possibly the tooth of a crunching fish (puncture mark).

The distal carina extends from the apex to the basal notch and is contiguously serrated (Fig. 4C). Basally, it shifts on the lingual side in correspondence of the 'bump'. A total of 45 denticles can be counted. They are slightly smaller in the basal part of the carina where the outline of the margin just above the indentation is slightly but distinctly convex ('bump') (Fig. 5); interdenticle slits in the basal part are shorter and cellae less developed than in successive denticles; DB is 8. Mid-crown denticles are more distinct, chisel-shaped, and basoapically longer than high (Fig. 6A-B); denticles are slightly inclined toward the apex of the crown, but they are symmetrical. DC is 5-5.5. Shallow caudae extend on the carina and are angled basomesially, whereas the interdenticle slits and cellae occur only in the most external part of the carina; very thin enamel ridges parallel to the caudae extend onto the lingual surface of the crown (Fig. 6A). There is an enamel ridge on the midline of each mid-distal denticle (Fig. 6B). Toward the apex, denticles become small again (DA is 7.5-8) and they are not clearly distinct in the uppermost 2.3 mm of the carina.

The mesial carina is close to the midline near the apex of the crown, but it shifts on the lingual surface just 1 mm below the apex and twists lingually (so, denticles point lingually and only slightly mesially). Thus, only a short apical segment coincides with the mesial margin of the crown (Fig. 4D). The mesial carina reaches the basal part of the crown, but the basal segment (~2.9 mm) is damaged and denticulation is only partly preserved. A total of 28 denticles can be counted in the remaining portion of the carina. MC is 6, thus the mesial denticles are slightly smaller than the corresponding distal denticles. Mid mesial denticles differ from mid distal ones in being less distinct because inter-

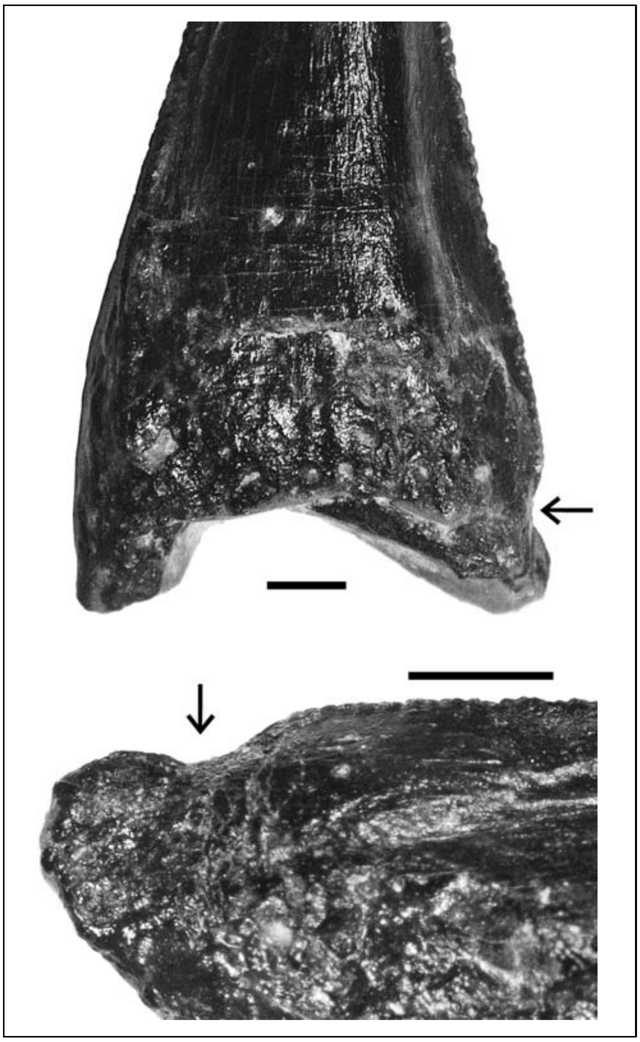

Fig. 5 - MPCM 11720, Notosuchia sp. and gen. indet. Particular of the basal constriction. The arrow points to the more marked distal constriction. Scale bar equals 1 mm.

denticle slits are very short and cut only the margin of the carina, cellae are reduced, and caudae are not developed (Fig. 6C-D). The few unworn denticles are asymmetrical (pointing apically) and longer than high. The denticles diminish in size toward the apex (~8/mm); individual denticles are not distinct in the uppermost 3.5 mm of the carina, because the interdenticle slits are very short and cut only the outer part of the carina (they look like papillae; Fig. 6C).

Discussion

The tooth obviously belongs to a carnivorous, gnathostomate vertebrate and, assuming that the shift of the mesial carina is lingual, it comes from the left upper jaw or from the right lower jaw. Serrated teeth occur in different gnathostomate groups, from chondrichthyan fishes to mammalians (e.g., Farlow et al. 1991; Abler 1992). Presence of teeth with labiolingually compressed crowns bearing finely denticulated carinae (ziphodont teeth) is considered an archosauriform synapomorphy (e.g., Benton 1999) that is secondarily lost in several derived lineages: many crocodyliforms, most pterosaurs, and ornithischian and sauropodomorph dinosaurs. Among Cretaceous archosaurs, ziphodont teeth are reported in most (but not all) theropod clades and several crocodyliforms. Therefore, the presence of ziphodont teeth is a symplesiomorphic condition that alone cannot be used for referring isolate teeth to a less inclusive archosaur clade. Although ziphodonty is probably plesiomorphic for theropods dinosaurs, isolated ziphodont teeth that are found in Cretaceous rocks originated from continental sediments – and

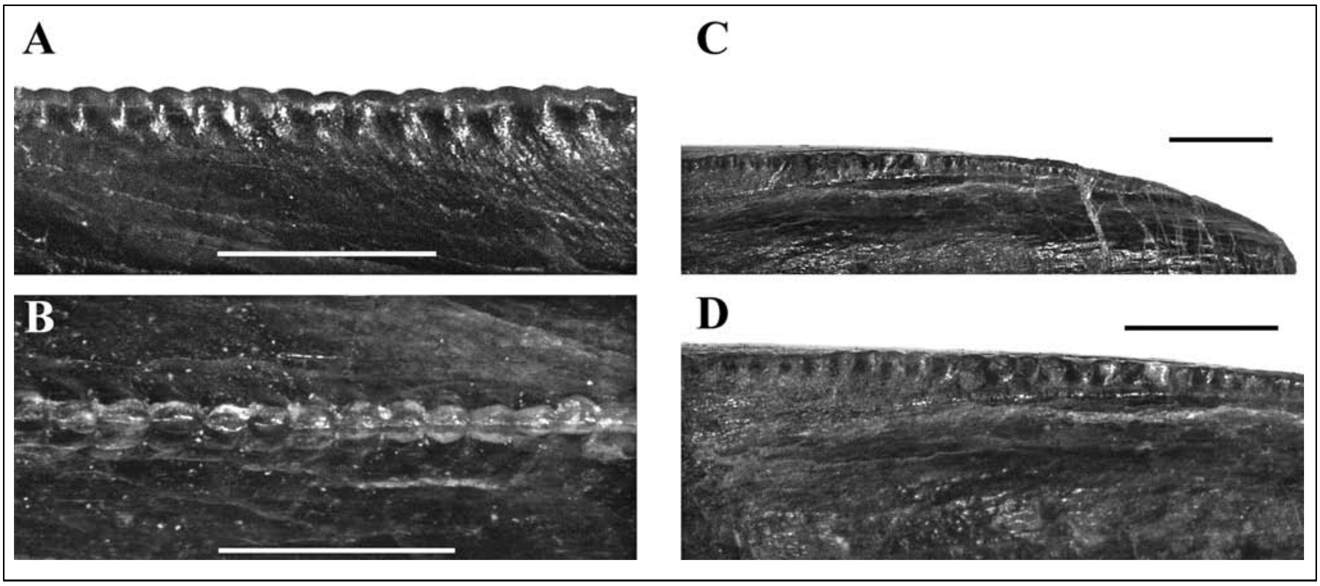

Fig. 6 - MPCM 11720, Notosuchia sp. and gen. indet. A-B) distal margin in lingual (A) and distal (B) view; C) the mid-apical part of the mesial margin in lingual view; D) mid-denticles of the mesial margin. Scale bar equals 1 mm.

sometimes also from sediments deposited in transitional/shallow marine settings – are traditionally referred to that clade (e.g., Currie et al. 1990; Fiorillo & Currie 1994; Lee 1997; Baszio 1997; Torices 2003; Torices et al. 2004; Sankey et al. 2002, 2005; Sankey 2008; Longrich 2008).

MPCM 11720 comes from a section whose sediments probably originated in an intertidal to lagoon environment containing rare marine invertebrates and foraminifers, fishes with a marine to fresh water distribution (i.e., Pycnodontiformes) and fishes with a marine distribution only (*Rhynchodercetis* and Beryciformes). However, the rare remains of terrestrial vegetation found in the tooth-bearing section, and the non-marine turtles and abundant plants collected at site A, testify to the presence of close emergent areas. Footprints of small to medium-sized bipedal dinosaurs, mostly referable to theropods with a size similar to that of the possible owner of the described tooth, are relatively common in the upper Albian and upper Cenomanian carbonate platform limestones of the nearby Istrian Peninsula, Croatia (e.g., Dalla Vecchia 1998; Dalla Vecchia & Tarlao 2000; Dalla Vecchia et al. 2001a, 2002). Small theropod teeth are reported from the Maastrichtian site of Kozina (SW Slovenia; Debeljak et al. 1999, 2002) that is about 40 km SE of the Polazzo site. Thus, the identification of MPCM 11720 as a theropod tooth would not contrast with the local and regional geological history and faunal assemblages.

Comparisons with theropod dinosaurs

Theropod teeth are considered diagnostic at low taxonomic level (e.g., Currie et al. 1990; Fiorillo & Currie 1994; Baszio 1997; Sankey et al. 2002, 2005; Smith et al. 2005; Sankey 2008; Longrich 2008). Based on the subtriangular shape of the crown and its limited curvature in labiolingual view, the relatively high labiolingual width, and the absence of apical curvature of the distal margin, MPCM 11720 differs from the lateral (maxillary and distal dentary) teeth of most theropods, the latter taxa showing labiolingually flattened, blade-like and apically recurved crowns in labiolingual view (e.g., Currie et al. 1990; Baszio 1997; Sankey et al. 2002, 2005; Brochu 2003; Sankey 2008; Longrich 2008). MPCM 11720 shares the presence of a lingually shifted mesial carina with premaxillary and mesial-most (symphysial) dentary teeth of most averostran theropods (Currie et al. 1990; Rauhut 2003; Rauhut et al. 2010). It shares some derived features with mesialmost maxillary and dentary teeth of abelisauroid neoceratosaurs: lingually shifted mesial carina (Sampson et al. 2001; Smith 2007), low but distinct basoapically elongate convex area running along the center of the lingual surface with flat to slightly concave areas adjacent to the serrated carinae (Rauhut 2004; Fanti & Therrien 2007; Smith 2007), and the presence of a straight, serrated distal margin (Smith et al. 2005). It differs from the premaxillary teeth of known abelisauroids because the crown shows a more asymmetrical cross-section profile in the latter, more markedly convex labially and flatter lingually (Smith 2007). One peculiar feature of MPCM 11720 is the presence of a slight constriction at the crown-root junction along the distal margin, marked by a low 'bump' of the serrated margin just above the indentation. Although widespread among basal dinosauriforms, ornithischians, basal sauropodomorphs, and the primitive Triassic saurischian *Eoraptor* (Langer & Benton 2006), the combination of characteristics observed in MPCM 11720 is absent in all known non-coelurosaur theropods (Rauhut 2003). Among Coelurosauria, a basal constriction of the crown is reported in the basal ornithomimosaur *Pelecanimimus* (Perez-Moreno et al. 1994), therizinosauroids (Zanno 2010), alvarezsaurids (Perle et al. 1994), troodontids (Currie 1987), the dromaeosaurid *Microraptor* (Hwang et al. 2002), toothed birds (Padian & Chiappe 1998), and in the premaxillary teeth (but not in maxillary or dentary teeth) of the basal tyrannosauroid *Proceratosaurus* (Rauhut et al. 2010). The Polazzo specimen differs from all these taxa in the presence of a serrated basal half of the mesial carina. MPCM 11720 is clearly different from the teeth of the therizinosauroids, those of the few dentate ornithomimosaurs, and those of the troodontids (including those basal taxa that bears finely denticulated carinae), because the constriction of the crown base is not marked, expecially mesially (Barrett 2009). The Polazzo tooth differs from all known theropod teeth in the incomplete serration of the mesial carina. This condition has never reported among theropods: all described specimens are either 'truly' serrated or unserrated (e.g., Currie et al. 1990; Baszio 1997; Torices 2003; Torices et al. 2003; Sankey et al. 2002, 2005; Sankey 2008; Longrich 2008). In conclusion, the combination of character conditions seen in MPCM 11720 is unreported in theropod teeth (Tab. 1). In particular, the combination of incomplete mesial serration and a basal 'bump' has never been reported in any theropod taxon. Although some single features (overall tooth morphology, denticle shape and density in the distal carina) are shared with abelisauroids, tyrannosauroids and dromaeosaurids, all alternative placements of MPCM 11720 among the Theropoda require a comparable amount of homoplasy. Pending additional evidence, it is unlikely that MPCM 11720 belongs to a yet-unreported lineage of theropods with an unusual dental morphology.

Comparisons with Crocodyliformes

Crocodyliform teeth are usually conical with unserrated carinae (Edmund 1969), but the Notosuchia

Tab. 1 - Distribution of the odontological features discussed in the text among crocodyliform and theropod taxa.

Taxon/grade	**Carinae ornamentation**	**Mid-crown cross-section**	**Basal crown constriction**	**Lingual shift of mesial carina (in non-premaxillary and non-symphysial dentary teeth)**
Crocodyliformes				
“Protosuchids”	denticles	elliptical	absent	absent
“Sphenosuchids”	denticles	elliptical	absent	absent
Non-Geosaurini thalattosuchians	absent	rounded	absent	absent
Geosaurini	denticles/ pseudo-serrations	elliptical	absent	absent
Most neosuchians	absent	rounded	absent	absent
Pristichampsus	denticles	elliptical	absent	absent
Trematochampids	denticles/ pseudo-serrations	elliptical	absent	absent
“Sebecosuchians”	denticles/absent	elliptical	absent	absent
“Notosuchids”	cusps	teardrop-shaped	marked	absent
Araripesuchus	denticles	elliptical	moderate	in *A. wegeneri*
Doratodon	denticles	elliptical	moderate	absent
Theropod dinosaurs				
Abelisauridae	denticles	elliptical or D-shaped	absent	in *Majungasaurus*
Non-maniraptoran tetanurans	denticles	elliptical or D-shaped	absent	absent
Troodontidae	denticles/absent	rounded/elliptical	present	absent
Dromaeosauridae	denticles/absent	ellitptical or D-shaped	in *Microraptor*	in *Dromaeosaurus*
MPCM 11720	Denticles, not completely individualized in the apical part of carinae	subrectangular to drop-like	moderate	present

(‘Ziphosuchia’ *sensu* Company et al. 2005), a few metriorhynchids (Andrade et al. 2010), *Pristichampsus* and the Trematochampsidae (Buffetaut 1974) are characterized by labiolingually compressed teeth with serrated cutting margins made of distinct denticles (Prasad & de Lapparent de Broin 2002; Company et al. 2005; Sereno & Larsson 2009; Turner & Sertich 2010). According to Prasad & de Lapparent de Broin (2002: 36) “true ziphodonts are those with teeth having laterally compressed crowns with posterior recurved apex, anterior and posterior carinae bearing a number of isolated festoon-like denticles” whereas ‘false ziphodont teeth’ are those where “the anterior and posterior carinae are relatively coarse and bear crenulations generally formed by anastomising, irregular ridges issued from the main body of the crown”. According to Legasa et al. (1994: 132) true ziphodont margins are those having carinae with isolated denticles, and “an ‘isolated denticle’ is a discrete morphological unit, clearly individualized by an interdenticle groove or notch”. Following this definition of ziphodonty, MPCM 11720 is not a ‘false ziphodont’ tooth and is closer to a true ziphodont condition, although the denticles of the apical half of the mesial carina and those of the the apical part of the distal carina are not clearly individualized by interdenticle slits and cellae extending on the whole carina.

According to Prasad & de Lapparent de Broin (2002), ziphodonty is highly homoplastic within Crocodyliformes (Tab. 1). For example, the marine metriorhynchids *Geosaurus giganteus* and *Dakosaurus maximus* from Upper Jurassic and lowermost Cretaceous have denticulated cutting margins, whereas their close relative *Torvoneustes* shows a ‘false’ ziphodonty (see Andrade et al. 2010).

Notosuchia is a clade that was common in South America and Africa during the Cretaceous (Gasparini et al. 1991; Sereno et al. 2003; Sereno & Larsson 2009), whereas in Europe, ziphodont taxa became more frequent during the Eocene (*Iberosuchus*, *Bergisuchus*, the ‘iberoccitanian crocodile’, and the eusuchian *Pristichampsus*; Legasa et al. 1994; Prasad & de Lapparent de Broin 2002).

The referral of MPCM 11720 to *Pristichampsus*, the Sebecosuchia (included in the Notosuchia according to Sereno et al. 2001), and the trematochampsids is dismissed because of the absence of both the basal ‘bump’ and the lingually shifted carina, and the presence of a comparatively blunter and rounded apex of the crown in those clades (Chiappe 1988; Gasparini et al. 1991; Buckley & Brochu 1999; Turner & Calvo 2005).

Comparisons with *Doratodon*

According to Company et al. (2005) and Martin et al. (2010), the notosuchian *Doratodon* is the only true ziphodont crocodyliform known in the Upper Cretaceous of Europe. Based on its small size, its scarce labiolingual compression (it is not blade-like), and modest curvature, Dalla Vecchia et al. (2001b) and Dalla Vecchia & Tentor (2004) tentatively referred MPCM 11720 to the only crocodyliform with denticulated teeth known in the Upper Cretaceous of Europe, *Doratodon*, instead of a theropod taxon. *Doratodon* is reported from the uppermost Cretaceous of Austria (Bunzel 1871; Seeley 1881; Buffetaut 1979), Spain (Company et al. 2005), Romania (Martin et al. 2006) and Hungary (Rabi 2008). Spanish, Romanian, and Hungarian specimens were found in rocks originated from fluvial and/or lacustrine sediments; the Austrian specimens come from a sequence of coal seams and freshwater/nearshore marine clastic rocks (Kvaček & Herman 2004).

Doratodon carcharidens (Bunzel, 1871) is the type species of the genus *Doratodon* Seeley (1881) and is based on almost complete mandible with poorly preserved teeth, a fragmentary maxilla and eight isolated teeth (Buffetaut 1979). All specimens excluding one tooth are from the lower Campanian Grünbach Formation of the Muthmannsdorf locality, Austria (Summesberger et al. 2007). Teeth are homodont in size (Company et al. 2005), but heterodont in shape (Buffetaut 1979). Buffetaut (1979, pl. 1) figured four isolated crowns that appear more bulbous than MPCM 11720, although Buffetaut (1979: 91) described them as "strongly compressed laterally". Furthermore, their cross-section is reported as oval and the mesial carina does not shift on the lingual side (Buffetaut 1979; Fig. 7B). The distal margin is sigmoid in labiolingual view in UWP 2349/58 and 60 (Buffetaut 1979, pl. 1, figs 6 and 7 respectively), whereas it is nearly straight in MPCM 11720. UWP 2349/59 (Buffetaut 1979, pl. 1, fig. 5) has a less sigmoid distal margin respect to the other *D. carcharidens* teeth, and a basal distal constriction (Fig. 7B). One side of UWP 2349/59 (in the caption of pl. 1, Buffetaut 1979 does not specify whether the lingual or labial is figured) seems to have a central, longitudinal relief with a flat surface (see Fig. 7B), possibly present also in UWP 2349/58. However, this would be in contrast with the description of the cross section of the *Doratodon carcharidens* teeth as oval given in Buffetaut (1979). UWP 2349/59 is only slightly less curved than MPCM 11720 (CA is 70 degrees) and less elongated basoapically (CHR equals 1.78). According to the description by Buffetaut (1979), the whole carinae are finely serrated, with 8 denticles/mm, but the crowns are somewhat smaller than MPCM 11720, the basoapical height ranging 11-7 mm. In fact, Buffetaut (1979: 91) reported that the largest tooth is 11 mm 'long' and a smaller one is "only 7 mm long [...] the anteroposterior diameter is 4 mm, the labiolingual one 2.5 mm", but he did not report the museum number of the specimens, thus we don't know to which of the figured specimens he refers.

Doratodon ibericus Company, Pereda Suberbiola, Ruiz-Omeñaca & Buscalioni, 2005 is based on an incomplete lower jaw with teeth found in the Sierra Perenchiza Formation at the Chera site (Valencia, Spain), late Campanian or early Maastrichtian in age. Teeth are heterodont in size and shape; the fourth tooth is subconical (CBR is about 0.62), whereas crowns in a more distal position are laterally compressed but straight. The fourth dentary tooth resembles MPCM 11720 in overall shape and size (Company et al. 2005, fig. 3). However, its mesial carina does not shift and twist lingually as well as that of the other teeth, including the mesial-most ones (Company et al., 2005; Julio Company, pers. comm. to F. M. D. V.). Furthermore, serrations of the carina are always formed by clearly individualized denticles in this taxon (Company et al. 2005). There are three and five denticles per mm at mid-crown in large and small teeth, respectively (Company et al. 2005). Denticles are comparatively larger, and paired denticles joined at the base are irregularly present, at least in the figured second mandibular tooth (Company et al. 2005, fig. 4). A marked basal constriction along the distal margin and the low 'bump' just apical to it, and the central, longitudinal relief with a flat surface in the lingual side are not present (Company et al. 2005; J. Company, pers. comm. to F. M. D. V.).

Several teeth from the lower Maastrichtian or possibly basal upper Maastrichtian Fântânele and Pui localities of the Hateg Basin of Transylvania (Romania) were referred by Martin et al. (2006) to *Doratodon* sp. The attribution to the genus is based on the carinae displaying a "clear plication of the enamel and the dentine, which is characteristic of the genus" (Martin et al. 2006: 32), meaning with that the presence of true denticles (Jeremy Martin, pers. comm. to A. C.). However, we note that such a feature is not autapomorphic for *Doratodon*, this being a notosuchian symplesiomorphy shared by several other taxa (Lagasa et al. 1994; Ortega et al. 2000; Sereno & Larsson 2009). The only reference to teeth in the diagnosis of *Doratodon* by Buffetaut (1979: 90-91) is "teeth strongly compressed laterally, with finely serrated edges and smooth enamel", whereas *Doratodon* is not diagnosed by any dental features in the revision by Company et al. (2005). One of the two Transylvanian morphotypes (FGGUB R.1939; Martin et al. 2006, pl. 1, fig. 1-2; Fig. 7D) resembles MPCM 11720 in the overall shape of the crown in labiolingual view, triangular and high (CHR equals 2.04, CA is 72 degrees), the slight labiolingual compression, the constriction at the base of the crown only visible distally and the presence of the 'bump' just apical to it, and the basal lingual twisting of the distal carina. However, it differs from MPCM 11720 in: the shape of the denticles, having the same denticles morphology mesially and distally, distinct denticles in the apical half of the mesial carina, the absence of lingual shift of the mesial carina, and more recurved cutting margins; furthermore, a flat central and longitudinal part on the crown in the lingual side and the relative depression between this part and the carinae are not mentioned in the description.

Rabi (2008) reports the presence of *Doratodon* in the Santonian Csehbánya Formation at Iharkút, Bakony Mts, western Hungary. One of the three Hungarian morphotypes (Marton Rabi, pers. comm. to F. M. D. V.) shares with MPCM 11720 a tall (CHR equals 2.17) and slightly distally recurved crown (CA is 70 degrees), with a basal constriction more marked distally where also a 'bump' of the carina is present, and a straight distal margin (Fig. 7D). It differs from MPCM 11720 in the absence of a lingual twist of the mesial carina, which has also well-defined, large, and chisel-shaped denticles, at least at mid-crown. From the photograph of the crown (courtesy of M. Rabi) it is impossible to state whether a central, longitudinal relief with a flat surface is present along the lingual side or not. This specimen resembles the specimen FGGUB R.1939 figured by Martin et al. (2006) (cf. Fig. 7C-D).

As shown above, the criterion used by Martin et al. (2006) to support the referral of the Romanian teeth to *Doratodon* is based on a notosuchian symplesiomorphy, not on unique diagnostic features of the genus *Doratodon*. This casts several doubts on the referral of isolated ziphodont teeth from the Upper Cretaceous of the European Archipelago to the genus *Doratodon* based only on that feature, since those serrated teeth may belong to other notosuchian genera (Sereno & Larsson 2009). Although none of the teeth referred to *Doratodon* is described in detail in the literature, the Polazzo specimen seems more similar to the type species *D. carcharidens* from the lower Campanian of Austria than those from the upper Campanian-Maastrichtian of Spain; this is not surprising because of palaeogeographic and chronostratigraphic reasons. However,

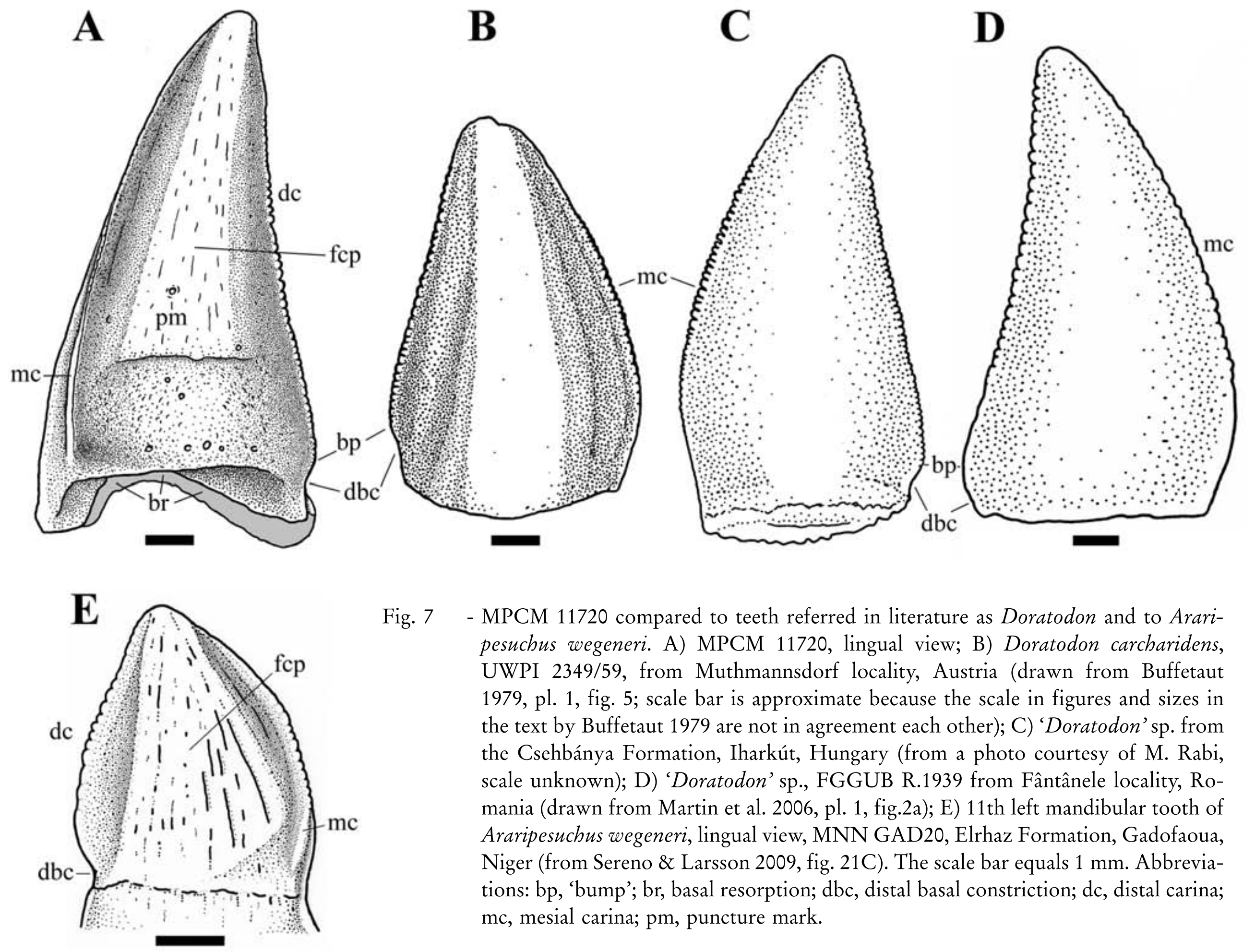

Fig. 7 - MPCM 11720 compared to teeth referred in literature as *Doratodon* and to *Araripesuchus wegeneri*. A) MPCM 11720, lingual view; B) *Doratodon carcharidens*, UWPI 2349/59, from Muthmannsdorf locality, Austria (drawn from Buffetaut 1979, pl. 1, fig. 5; scale bar is approximate because the scale in figures and sizes in the text by Buffetaut 1979 are not in agreement each other); C) '*Doratodon*' sp. from the Csehbánya Formation, Iharkút, Hungary (from a photo courtesy of M. Rabi, scale unknown); D) '*Doratodon*' sp., FGGUB R.1939 from Fântânele locality, Romania (drawn from Martin et al. 2006, pl. 1, fig.2a); E) 11th left mandibular tooth of *Araripesuchus wegeneri*, lingual view, MNN GAD20, Elrhaz Formation, Gadofaoua, Niger (from Sereno & Larsson 2009, fig. 21C). The scale bar equals 1 mm. Abbreviations: bp, 'bump'; br, basal resorption; dbc, distal basal constriction; dc, distal carina; mc, mesial carina; pm, puncture mark.

the tooth from Polazzo shows differences with all the teeth reported from Austria, Spain, and Romania. The most important of which are the presence of a lingually shifted mesial carina, and the apical part of the distal carina and apical half of the mesial carina without completely individualized denticles.

Further comparisons

Among Crocodyliformes, a straight carina running apicobasally along the mesial margin of the teeth is a plesiomorphic feature shared by most taxa, whereas a lingual shifting of the mesial carina is a poorly mentioned apomorphy with a patchy distribution (e.g., it is present in the dyrosaurid *Hyposaurus rogersii* from the Maastrichtian of New Jersey, but not in other dyrosaurids; Denton et al. 1997). A lingual shifting of the mesial carina occurs also in *Razanandrongobe sakalavae* (Simone Maganuco, pers. com. to A. C.), an enigmatic ziphodont taxon from the Middle Jurassic of Madagascar with possible crocodylomorph affinities (Maganuco et al. 2006). Recently, Sereno & Larsson (2009: 35) reported "lingually deflected mesial carina and associated trough" as an autapomorphy of the largest postcaniniform teeth of the notosuchian *Araripesuchus wegeneri* Buffetaut & Taquet, 1979, from the continental Elrhaz Formation (Aptian-Albian) of Niger. The 11th dentary tooth of *A. wegeneri* is very similar to the Polazzo tooth sharing with it a slight basal constriction, finely serrated mesial and distal carinae, and a central, longitudinal relief with a flat surface on the lingual side (Sereno & Larsson 2009, figs. 20C, 21A, 21C). It differs from MPCM 11720 mainly in the mesiodistally broader and labiolingually thicker crowns (CHR is about 1.60, CA is 63 degrees) with both mesial and distal margin markedly convex (Sereno & Larsson 2009; Fig. 7E). It is also sensibly smaller, AL being about 5 mm.

Conclusions

The serrated tooth from the Polazzo site is not a theropod tooth: the character states shared by the Polazzo specimen with some theropods are as either adaptive convergences or archosaurian symplesiomorphies (Tab. 1).

Important features distinguish it also from the known material of *Doratodon*, the only ziphodont crocodyliform genus reported to date from the European Upper Cretaceous. It is noteworthy that the Polazzo specimen shares the unusual presence of a lingual shifting of the mesial carina with one species of the notosuchian *Araripesuchus*. This genus has a pan-Gondwanan distribution; its monophyly has been questioned by Ortega et al. (2000) and Turner & Sertich (2010), but was supported by Pol & Apesteguia (2005) and Sereno & Larsson (2009). The shared presence of many characters, including an autapomorphy, suggesting a strict affinity between MPCM 11720 and a Gondwanan taxon, has evident paleobiogeographic implications. However, since the distribution of a lingually shifted mesial carina among crocodyliforms may have been overlooked in literature, the phylogenetic meaning of that character (for example, its inclusiveness among *Araripesuchus* species or notosuchians as a whole) has yet to be tested in a cladistic framework. Furthermore, the Polazzo crown has the apical part of the distal carina and apical half of the mesial carina without completely individualized denticles, a feature yet unreported in other crocodyliforms, although also probably overlooked in literature. All this suggests referring it as a yet unnamed notosuchian crocodyliform, possibly with Gondwanan affinities.

MPCM 11720 represents the first record of a notosuchian crocodyliform from Italy (Delfino 2001; Bonfiglio 2005) and from the Adriatic-Dinaric Carbonate Platform of the European archipelago as well (Steel 1973; Pereda-Suberbiola 2009). As notosuchians were typically terrestrial (O' Connor et al. 2010), MPCM 11720 is further evidence of local emergence in the northern part of the Adriatic Dinaric carbonate platform during early Senonian times.

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REFERENCES

Abler W. L. (1992) - The serrated teeth of tyrannosaurid dinosaurs, and biting structures in other animals. *Paleobiology*, 18: 161-183.

Andrade M. B., Young M. T., Desojo J. B. & Brusatte S. L. (2010) - The evolution of extreme hypercarnivory in Metriorhynchidae (Mesoeucrocodylia: Thalattosuchia) based on evidence from microscopic denticle morphology. *J. Vert. Paleont.*, 30(5): 1451-1465.

Barrett P. M. (2009) - The affinities of the enigmatic dinosaur *Eshanosaurus deguchiianus* from the Early Jurassic of Yunnan Province, People's Republic of China. *Palaeontology*, 52(4): 681-688.

Baszio S. (1997) - Systematic palaeontology of isolated dinosaur teeth from the Latest Cretaceous of South Alberta, Canada. *Cour. Forschungstinst. Senckenb.*, 196: 33-77.

Benton M. J. (1999) - *Scleromochlus taylori* and the origin of the pterosaurs. *Philos. Trans. R. Soc. Lond., Series B*, 354: 1423-1446.

Bonfiglio L. (Ed.) (2005) - Paleontologia dei Vertebrati in Italia. *Mem. Mus. Civ. St. Nat. Verona*, s. 2, Sez. Scienze della Terra, 6: 1-238.

Brochu C. R. (2003) - Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Soc. Vert. Paleont. Mems*, 7: 1-138.

Buckley G. A. & Brochu C. A. (1999) - An enigmatic new crocodile from the Upper Cretaceous of Madagascar. In: Unwin D. M. (Ed.) - Special Papers in Palaeontology: Cretaceous Fossil Vertebrates. *Palaeont. Association*, 60: 149-175.

Buffetaut E. (1974) - *Trematochampsa taqueti*, un Crocodilien nouveau du Sénonian inférieur du Niger. *C. R. Acad. Sci. (Paris)*, 279: 1749-1752.

Buffetaut E. (1979) - Revision der Crocodylia (Reptilia) aus den Gosau-Schichten (Ober-Kreide) von Österreich. *Beitr. Paläont. Österr.*, 6: 89-105.

Buffetaut E. & Taquet P. (1979) - An Early Cretaceous terrestrial crocodilian and the opening of the South Atlantic. *Nature*, 280: 486-487.

Bunzel E. (1871) - Die Reptilienfauna der Gosauformation. *Abhandl. k.k. geol. Reichsanstalt*, 5: 1-20.

Camoin G., Bellion Y., Dercourt J., Guiraud R., Lucas J., Poisson A., Ricou L. E. & Vrielynck B. (1993) - Late Maastrichtian palaeoenvironments (69.5 to 65 Ma). In: Dercourt J., Ricou L. E. & Vrielynck B. (Eds) - Atlas Tethys, Palaeoenvironmental Maps. BEICIP–FRANLAB, Rueil, Malmaison.

Chiappe L. M. (1988) - A new trematochampsid crocodile from the Early Cretaceous of North-western Patagonia (Argentina). Palaeobiogeographical and phylogenetic implications. *Cretaceous Res.*, 9: 379-389.

Company J., Pereda Suberbiola X., Ruiz-Omeñaca J. I. & Buscalioni A. D. (2005) - A new species of *Doratodon* (Crocodyliformes: Ziphosuchia) from the Late Cretaceous of Spain. *J. Vert. Paleont.*, 25(2): 343-353.

Currie P. J. (1987) - Bird-like characteristics of the jaws and teeth of troodontid theropods (Dinosauria, Saurischia). *J. Vert. Paleont.*, 7(1): 72-81.

Currie P. J., Rigby J. K. jr. & Sloan R. E. (1990) - Theropod teeth from the Judith River Formation of southern Alberta, Canada. In: Carpenter K. & Currie P. J. (Eds) - Dinosaur Systematics: Perspectives and Approaches. Cambridge University Press: 107-125, Cambridge.

Dalla Vecchia F. M. (1998) - Theropod footprints in the Cretaceous Adriatic-Dinaric carbonate platform (Italy and Croatia). In: Perez-Moreno B., Holtz T. R. Jr., Sanz J. L. & Moratalla J. J. (Eds) - Aspects of Theropod Paleobiology, *Gaia*, 15: 355-367.

Dalla Vecchia F. M. (2006) - *Telmatosaurus* and the other hadrosaurids of the Cretaceous European archipelago. An overview. *Natura Nascosta*, 32: 1-55, Monfalcone.

Dalla Vecchia F. M. (2008) - I dinosauri del Villaggio del Pescatore (Trieste): qualche aggiornamento. *Atti Mus. Civ. St. Nat. Trieste*, numero speciale: 111-129.

Dalla Vecchia F. M. (2009) - *Tethyshadros insularis*, a new hadrosauroid dinosaur (Ornithischia) from the Upper Cretaceous of Italy. *J. Vert. Paleont.*, 29(4): 1100-1116.

Dalla Vecchia F. M. & Tarlao A. (2000) - New dinosaur track sites in the Albian (Early Cretaceous) of the Istrian peninsula (Croatia). Part II - Paleontology. In: Dalla Vecchia F. M., Tarlao A., Tunis G. & Venturini S., New dinosaur track sites in the Albian (Early Cretaceous) of the Istrian peninsula (Croatia), *Mem. Sci. Geol. - Padova*, 52(2): 227-293.

Dalla Vecchia F. M. & Tentor M. (2004) - Il Carso 85 milioni di anni fa: gli straordinari fossili di Polazzo. Gruppo Speleologico Monfalconese A.d.F., 75 pp., Monfalcone.

Dalla Vecchia F. M., Tunis G., Venturini S. & Tarlao A. (2001a) - Dinosaur track sites in the upper Cenomanian (Late Cretaceous) of the Istrian peninsula (Croatia). *Boll. Soc. Paleont. Ital.*, 40(1): 25-54.

Dalla Vecchia F. M., Rigo D., Tentor M., Pacor G. & Moratto D. (2001b) - Il sito paleontologico di Polazzo (Gorizia): dati e prospettive. In: Perri M. C. (Ed.) - Giornate di Paleontologia 2001. *Giorn. Geol*, Ser. 3, 62 (2000; suppl.): 151-156.

Dalla Vecchia F. M., Vlahović I., Posocco L., Tarlao A. & Tentor M. (2002) - Late Barremian and Late Albian (Early Cretaceous) dinosaur track sites in the Main Brioni/Brijun Island (SW Istria, Croatia). *Natura Nascosta*, 25: 1-36, 3 maps, Monfalcone.

Debeljak I., Košir A. & Otoničar B. (1999) - A preliminary note on dinosaurs and non-dinosaurian reptiles from the Upper Cretaceous carbonate platform succession at Kozina (SW Slovenia). *Razprave IV. Razreda Sazu*, XL(1): 3-25.

Debeljak I., Košir A., Buffetaut E. & Otoničar B. (2002) - The Late Cretaceous dinosaurs and crocodiles of Kozina (SW Slovenia). *Mem. Soc. Geol. It.*, 57: 193-201.

Delfino M. (2001) - The fossil record of the Italian Crocodylomorpha. Abstracts of the 6th European Workshop on Vertebrate Palaeontology, Florence-Montevarchi, Italy, September 19-22, p. 28.

Denton R. K., Dobie J. L. & Parris D. C. (1997) - The marine crocodilian *Hyposaurus* in North America. In: Callaway J. M. & Nicholls E. L. (Eds) - Ancient Marine Reptiles. Academic Press: 375-397.

Eberli G. P., Bernoulli D., Sanders D. & Vecsei A. (1993) - From aggradation to progradation: the Maiella platform, Abruzzi, Italy. In: Simo T., Scott R. W. & Masse J. P. (Eds) - *A.A.P.G. Mems,* 56: 213-232.

Edmund A.G. (1969) - Dentition. In: Gans C. & Parsons T. S. (Eds) - Biology of the Reptilia, 1:117-200. Academic Press, London and New York.

Ezcurra M. D. (2006) - A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan & Lucas, 1999 from the Upper Triassic of New Mexico, USA. *Geodiversitas*, 28(4): 649-684.

Fanti F. & Therrien F. (2007) - Theropod tooth assemblages from the Late Cretaceous Maevarano Formation and the possible presence of dromaeosaurids in Madagascar. *Acta Palaeont. Pol.,* 52 (1): 155-166.

Farlow J. O., Brinkman D. L., Abler W. L. & Currie P. J. (1991) - Size, shape, and serration density of theropod dinosaur lateral teeth. *Modern Geol.*, 16: 161-198.

Fiorillo A. R. & Currie P. J. (1994) - Theropod teeth from the Judith River Formation (Upper Cretaceous) of south-central Montana. *J. Vert. Paleont.*, 14(1): 74-80.

Gasparini Z., Chiappe L. M. & Fernandez M. (1991) - A new Senonian peirosaurid (Crocodylomorpha) from Argentina and a synopsis of the South American Cretaceous crocodilians. *J. Vert. Paleont.*, 11(3): 316-333.

Guidotti G. (1983) - Studio paleontologico di due teleostei del Cretaceo superiore del Carso. Unpublished master thesis, University of Bologna, 88 pp., Bologna.

Hwang S. H., Norell M. A., Ji Q. & Gao K. (2002) - New specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from Northeastern China. *Am. Mus. Novitates*, 3381: 1-44.

Langer M. C. & Benton M. J. (2006) - Early dinosaurs: a phylogenetic study. *J. System. Palaeont.*, 4: 309-358.

Kvaček J. & Herman A. (2004) - The Campanian Grünbach Flora of Lower Austria: palaeoecological interpretations. *Ann. Naturhist. Mus. Wien*, 106A: 91-101.

Lee Y.-N. (1997) - The Archosauria from the Woodbine formation (Cenomanian) in Texas. *J. Paleont.*, 71(6): 1147-1156.

Legasa O., Buscalioni A. D. & Gasparini Z. (1994) - The serrated teeth of *Sebecus* and the Iberoccitan crocodile. A morphological and ultrastructural comparison. *Studia Geol. Salamant.*, 29: 129-144.

Longrich N. (2008) - Small Theropod Teeth from the Lance Formation of Wyoming, USA. In: Sankey J. T. & Baszio S. (Eds) - Vertebrate Microfossil Assemblages: Their role in Paleoecology and Paleobiogeography. Indiana University Press: 135-158, Bloomington & Indianapolis.

Maganuco S., Dal Sasso C. & Pasini G. (2006) - A new large predatory archosaur from the Middle Jurassic (Bathonian) of Madagascar. *Atti Soc. Ital. Sci. Nat. Mus. Civ. St. Nat. Milano*, 147(1): 19-51.

Martin J. E., Csiki Z., Grigorescu D. & Buffetau E. (2006) - Late Cretaceous crocodilian diversity in Haţeg Basin, Romania. *Hantkeniana*, 5: 31-37.

Martin J., Rabi M. & Csiki Z. (2010) - Survival of *Theriosuchus* (Mesoeucrocodylia: Atoposauridae) in a Late Cretaceous archipelago: a new species from the Maastrichtian of Romania. *Naturwissenschaften*, 97 (9): 845-854.

Martinis B. (1962) - Ricerche geologiche e paleontologiche sulla regione compresa tra il T. Iudrio e il F. Timavo. *Mem. Riv. It. Paleont. Strat.*, 8: 1-200.

O'Connor P. M., Sertich J. J. W., Stevens N. J., Roberts E. M., Gottfried M. D., Hieronymus T. L., Jinnah Z. A., Ridgely R., Ngasala S. E. & Temba J. (2010) - The evolution of mammal-like crocodyliforms in the Cretaceous of Gondwana. *Nature*, 466: 748-751.

Ortega F., Gasparini Z., Buscalioni A. D. & Calvo J. O. (2000) - A new species of *Araripesuchus* (Crocodylomorpha, Mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina). *J. Vert. Paleont.*, 20: 57-76.

Otoničar B. (2007) - Upper Cretaceous to Paleogene forebulge unconformity associated with foreland basin evolution (Kras, Matarsko Podolje and Istria; SW Slovenia and NW Croatia. *Acta Carsologica*, 36:101-120.

Padian K. & Chiappe L. M. (1998) - The origin and early evolution of birds. *Biol. Rev.*, 73: 1-42.

Pereda-Suberbiola X. (2009) - Biogeographical affinities of Late Cretaceous continental tetrapods of Europe: a review. *Bull. Soc. Geol. France*, 180: 57-71.

Pereda-Suberbiola X., Canudo J. I., Cruzado-Caballero P., Barco J. L., López-Martínez N., Oms O. & Ruiz-Omeñaca J. I. (2009) - The last hadrosaurid dinosaurs of Europe: a new lambeosaurine from the uppermost Cretaceous of Arèn (Huesca, Spain). *C. R. Palevol*, 8: 559-572.

Perez-Moreno B. P., Sanz J. L., Buscalioni A. D., Moratalla J. J., Ortega F. & Raskin-Gutman D. (1994) - A unique multitoothed ornithomimosaur from the Lower Cretaceous of Spain. *Nature*, 370: 363-367.

Perle A., Chiappe L. M., Barsbold R., Clark J. M., & Norell M. A. (1994) - Skeletal morphology of *Mononykus olecranus* (Theropoda: Avialae) from the Late Cretaceous of Mongolia. *Am. Mus. Novitates*, 3105: 1-29.

Philip J., Floquet M., Platel J. P., Bergerat F., Sandulescu M., Baraboshkin E., Amon E. O., Poisson A., Guiraud R., Vaslet D., Le Nindre Y., Ziegler M., Bouaziz S. & Guezou J. C. (2000) - Map 16. - Late Maastrichtian (69.5-65 Ma). In: Dercourt J., Gaetani M., Vrielynck B., Barrier E., Biju-Duval B., Brunet M. F., Cadet J. P., Crasquin S. & Sandulescu M. (Eds) - Atlas Peri-Tethys, Palaeogeographical Maps. CCGM/CGMW, Paris.

Pol D. & Apesteguia S. (2005) - New *Araripesuchus* Remains from the Early Late Cretaceous (Cenomanian–Turonian) or Patagonia. *Am. Mus. Novitates*, 3490: 1-38.

Poyato-Ariza F. J. (2010) *Polazzodus*, gen. nov., a new pycnodont fish from the Late Cretaceous of northeastern Italy. *J. Vert. Paleont.*, 30: 650-664.

Prasad G.V.R. & de Lapparent de Broin F. (2002) - Late Cretaceous crocodile remains from Naskal (India): comparisons and biogeographic affinities. *Ann. Paléont.*, 88: 19-71.

Rabi M. (2008) - New discovery of the Late Cretaceous ziphodont crocodyliform, *Doratodon* from the Santonian Csehbánya Formation of Hungary. Abstracts of the 6th Meeting of the European Association of Vertebrate Palaeontologists: 82, Spišská Nová.

Rauhut O. W. M. (2003) - The interrelationships and evolution of basal theropod dinosaurs. *Spec. Pap. Palaeontol. The Palaeontol. Ass.*, 69: 1-213.

Rauhut O. W. M. (2004) - Provenance and anatomy of *Genyodectes serus*, a large-toothed ceratosaur (Dinosauria: Theropoda) from Patagonia. *J. Vert. Paleont.*, 24: 894-902.

Rauhut O. W. M., Milner A. C. & Moore-Fay S. (2010) - Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. *Zool. J. Linn. Soc.*, 158 (1): 155-195.

Rigo D. (1997) - Scavo paleontologico 1997 nel Cretaceo superiore di Polazzo (Go): risultati e prospettive. *Natura Nascosta*, 15: 29-33.

Sampson S. D., Carrano M. T. & Forster C. A. (2001) - A bizarre new predatory dinosaur from Madagascar. *Nature*, 409: 504-506.

Sankey J. T. (2008) - Diversity of Latest Cretaceous (Late Maastrichtian) Small Theropods and Birds: Teeth from the Lance and Hell Creek Formations, USA. In: Sankey J. T. & Baszio S. (Eds) - Vertebrate Microfossil Assemblages: Their role in Paleoecology and Paleobiogeography. Indiana University Press: 117-134, Bloomington & Indianapolis.

Sankey J. T., Brinkman D. B., Guenther M. & Currie P. J. (2002) - Small theropod and bird teeth from the Late Cretaceous (Late Campanian) Judith River Group, Alberta. *J. Paleont.*, 76(4): 751-763.

Sankey J. T., Standhardt B. R. & Schiebout J. A. (2005) - Theropod Teeth from the Upper Cretaceous (Campanian-Maastrichtian), Big Bend National Park, Texas. In: Carpenter K. (Ed.) - The Carnivorous Dinosaurs. Indiana University Press: 127-152, Bloomington & Indianapolis.

Seeley H. G. (1881) - The reptile fauna of the Gosau Formation preserved in the Geological Museum of the University of Vienna. *Quart. J. Geol. Soc. London*, 37: 620-704.

Sereno P. C. & Larsson H. C. E. (2009) - Cretaceous Crocodyliforms from the Sahara. *ZooKeys*, 28: 1-143.

Sereno P. C., Larsson H. C. E., Sidor C. A. & Gado B. (2001) - The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science*, 294: 1516-1519.

Sereno P. C., Sidor C. A., Larsson H. C. E., Gado B. (2003) - A new notosuchian from the Early Cretaceous of Niger. *J. Vert. Paleont.*, 23(2): 477-482.

Smith J. B. (2007) - Dental morphology and variation in *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. In: Sampson S. D. & Krause D. W. (Eds), *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Soc. Vert. Paleont. Mems*, 8: 103-126.

Smith J. B. & Dodson P. (2003) - A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *J. Vert. Paleont.*, 23(1): 1-12.

Smith J. B., Vann D. R. & Dodson P. (2005) - Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. *The Anat. Rec. A,* 285A: 699-736.

Steel R. (1973) - Crocodylia. In: Kuhn O. (Ed.) - Handbuch der Palaeoherpetologie, 16: l-116, Gustav Fischer Verlag, Stuttgart-Portland.

Summesberger H., Machalski M. & Wagreich M. (2007) - First record of the late Campanian heteromorphy ammonite *Nostoceras hyatti* from the Alpine Cretaceous (Grünbach, Gosau Group, Lower Austria). *Acta Geol. Pol.*, 57(4): 443-451.

Tentor M., Tunis G. & Venturini S. (1994) - Schema stratigrafico e tettonico del Carso Isontino. *Natura Nascosta*, 9: 1-32.

Tintori A., Pugliese N. & Calligaris R. (1993) - The Polazzo locality. In: Tintori A. & Muscio G. (Eds) - Fossil fish localities of Northern Italy. Field guidebook of the Int. Symp. Mesozoic Fishes: Systematics and Paleoecology, Eichstätt, August 1993, 17-18, Eichstätt.

Torices A. (2003) - Estudio preliminar de dientes aislados de terópodos del Cretácico Superior de la Cuenca de Tremp (Pirineos Sur-Centrales, Lleida). Actas de las II Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno, 213-220, Salas de los Infantes (Burgos).

Torices A., Ruiz-Omeñaca J. I., Canudo J. I. & López-Martínez N. (2004) - Nuevos datos sobre los dinosaurios terópodos (Saurischia: Theropoda) de los Pirineos Sur-Centrales (Huesca y Lleida). *Geotemas*, 6: 71-74.

Turner A. H. & Calvo J. O. (2005) - A new sebecosuchian crocodyliform from the Late Cretaceous of Patagonia. *J. Vert. Paleont.*, 25(1): 87-98.

Turner A. H. & Sertich J. J. W. (2010) - Phylogenetic history of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *J. Vert. Paleont.*, 30(6): 177-236.

Zanno L.E. (2010) - Osteology of *Falcarius utahensis* (Dinosauria: Theropoda): characterizing the anatomy of basal therizinosaurs. *Zool. J. Linn. Soc.*, 158(1): 196-230.