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An enigmatic crocodyliform tooth from the bauxites of western Hungary suggests hidden mesoeucrocodylian diversity in the Early Cretaceous European archipelago

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ABSTRACT

Background. The Cretaceous of southern Europe was characterized by an archipelago setting with faunas of mixed composition of endemic, Laurasian and Gondwanan elements. However, little is known about the relative timing of these faunal influences. The Lower Cretaceous of East-Central Europe holds a great promise for understanding the biogeographic history of Cretaceous European biotas because of the former proximity of the area to Gondwana (as part of the Apulian microcontinent). However, East-Central European vertebrates are typically poorly known from this time period. Here, we report on a ziphodont crocodyliform tooth discovered in the Lower Cretaceous (Albian) Alsópere Bauxite Formation of Olaszfalu, western Hungary.

Methods. The morphology of the tooth is described and compared with that of other similar Cretaceous crocodyliforms.

Results. Based on the triangular, slightly distally curved, constricted and labiolingually flattened crown, the small, subequal-sized true serrations on the carinae mesially and distally, the longitudinal fluting labially, and the extended shelves along the carinae lingually the tooth is most similar to some peirosaurid, non-baurusuchian sebecosuchian, and uruguaysuchid notosuchians. In addition, the paralligatorid Wannchampsus also possesses similar anterior teeth, thus the Hungarian tooth is referred here to Mesoeucrocodylia indet.

Discussion. Supposing a notosuchian affinity, this tooth is the earliest occurrence of the group in Europe and one of the earliest in Laurasia. In case of a paralligatorid relationship the Hungarian tooth would represent their first European record, further expanding their cosmopolitan distribution. In any case, the ziphodont tooth from the Albian bauxite deposit of western Hungary belongs to a group still unknown from the Early Cretaceous European archipelago and therefore implies a hidden diversity of crocodyliforms in the area.

Subjects Paleontology

Keywords Notosuchia, Paralligatoridae, Early Cretaceous, Alsópere Bauxite Formation, Albian, Hungary

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INTRODUCTION

During the mineral explorations in the Transdanubian Range of Hungary, Central-East Europe, various bauxite deposits have been discovered and studied in the Bakony Mountains, among others, by Jenö Noszky Jr. and colleagues (*Noszky, 1951; Mindszenty, Szöts & Horváth, 1989*). In 1950, during fieldwork at the Boszorkány Hill close to the village Olaszfalu, Noszky found a tooth and an unidentified bone fragment in a piece of bauxitic clay. *Kretzoi & Noszky (1951)* briefly described (but did not figure) the tooth and identified it as crocodilian.

Although Kretzoi & Noszky (1951) did not assign accession number to the specimen in their description, it has been presumed that it was deposited in the collection of the Hungarian Geological Museum of the Hungarian Geological Institute (MAFI; now Geological and Geophysical Institute of Hungary [MFGI], Department of Geological and Geophysical Collections). The wherabouts of the tooth were unknown until late 2014, when one of us (LM) located it among uncatalogued vertebrate specimens of the collection. The tooth was found in a small box without an inventory number but with a label indicating its identity. Next to it was a walnut-sized piece (and smaller fragments) of bauxite still embedding presumably the same indeterminate bone fragment that was mentioned by Kretzoi & Noszky (1951). The bauxite pieces exhibit cut marks and fit to a fist-sized piece of bauxite housed in the mineralogical collection (inv. no.: MFGI ÁT 5868). This fist-sized rock in turn lacks the cut out portions but has an inventory card that indicates that the "Saurius tooth" was found in it. Thus, it is clear that Noszky found the tooth and the bone fragment in this fist-sized bauxitic clay (MFGI ÁT 5868), and cut out the fossil-containing portions. The remaining piece of rock was catalogued and placed in the mineralogical collection as a bauxite sample, whereas the tooth and the bone were put into the vertebrate collection, where they remained uncatalogued even after the publication of Kretzoi & Noszky (1951). The specimens were catalogued properly only while preparing the present paper under the inventory numbers MFGI V 2015.90.2.1. (tooth) and MFGI V 2015.90.2.2. (bone fragment).

In this paper, we give a new and comparative description of this isolated tooth briefly mentioned by *Kretzoi & Noszky (1951)* and discuss its taxonomic affinity and paleobiogeographic significance in light of the currently available crocodyliform record.

LOCALITY, GEOLOGICAL SETTING AND AGE

The piece of bauxitic clay that contained the tooth together with the small chunk of unidentified bone was collected in a small pit-like depression at the Boszorkány Hill, south of the village of Olaszfalu (Fig. 1), Bakony Mountains, western Hungary (*Kretzoi & Noszky*, 1951). The specimen came from a fault zone containing the Lower Cretaceous Alsópere Bauxite Formation. The embedding bauxitic rock, "according to thermic analyses, is not bauxite, but a clay consisting of caolinites, but stratigraphically it is equivalent to the Alsópere Bauxite" (*Kretzoi & Noszky*, 1951). The Alsópere Bauxite Formation occurs in small lenses with a maximum thickness of 5–7 m and was deposited on the karstic surface of the Upper Triassic Dachstein Limestone and in some places on the eroded surface of Liassic limestones. Its lithological features are best represented by the stratigraphic



Figure 1 Location map (red circle) of the Mesoeucrocodylia indet. tooth (MFGI V 2015.90.2.1.), found between the villages of Olaszfalu and Eplény in the Bakony Mountains, western Hungary. (A) Hungary in Central Europe. (B) Location of the Olaszfalu area in Hungary. (C) The locality close to the villages of Olaszfalu and Eplény.

column of the Ot-84 borehole at Olaszfalu (*Császár et al., 1993*: Fig. 5). The Alsópere Bauxite Formation is a terrestrial deposit mainly built up of allite and kaolinite. It is quite heterogenous containing reddish bauxitic clay and brownish-reddish clayey bauxite.

As is usual with bauxites, the age of the Alsópere Bauxite Formation can only be indirectly established from the age of the underlying and overlying deposits. Although not observable directly at the locality, the youngest underlaying beds are members of the Uppermost Aptian Tata Limestone Formation indicating a younger age for the Alsópere Bauxite. In the surrounding area of the locality, the Alsópere Bauxite Formation is covered by the Tés Clay Formation, representing a transitional unit from terrestrial, paludal to marine sedimentary environments. Based on sporomorphs (*Juhász, 1979; Juhász, 1983*), foraminifers and ostracods (*Császár, 1986*), the age of the Tés Clay Formation is Middle–Upper Albian. The stratigraphic record therefore indicates a Lower Albian age for the Alsópere Bauxite Formation (*Császár, 1986; Császár et al., 1993; Császár, Fözy & Mizák, 2008*).

RESULTS AND DISCUSSION

Description

Orientation

A common characteristic of conical crocodyliform teeth is that they curve somewhat lingually and/or distally. When these teeth are longer than wide (in the horizontal plane) then the greater dimension corresponds to the mesiodistal length and the shorter one to the labiolingual width. Based on these general features, we interpret the slightly concave surface between the two carinae as the lingual and the more convex surface as the mesial side of the crown.

Morphology

The tooth (MFGI V 2015.90.2.1.) has a whitish color most probably as a result of oxidation. The central part of the crown missing, but having a pulp cavity completely filled with sediment (Fig. 2). It has a high, apically pointed, triangular, and slightly distally and lingually curved crown. The apicobasal length of the crown is 16 mm, the mesiodistal width is 5 mm and the labiolingual thickness is 3 mm; thus, the crown is slightly labiolingually flattened. The mesial and distal carinae of the crown are preserved only on the apical third and are denticulated (Figs. 2A, 2B and 2H). Following the definitions of Legasa, Buscalioni & Gasparini (1994) and Prasad & Lapparent de Broin (2002), in the case of true ziphodonts the carina is composed of isolated denticles separated by interdenticle grooves. The serration of MFGI V 2015.90.2.1. (Fig. 2G) is closer to the true ziphodont type in having individual denticles on the carinae. The interdenticle grooves of the serrated carinae are quite shallow and slightly curve ventrally towards the central region of crown (at least along the preserved apical part; Fig. 2J). Nevertheless, these denticles are clearly not the marginal prolongation of the enamel ridges as would be expected in a pseudoziphodont tooth. The outer keel of the denticles is rounded (Figs. 2G–2J). Based on the incomplete, preserved part of the carinae the average serration density on both the mesial and distal carinae is 6 denticles per mm. The lingual side of the crown bears a central convexity bordered by a pair of grooves mesially and distally, which in turn support the denticulated carinae. The distal groove is slightly wider mesiodistally than the mesial one (Figs. 2A and 2B). Similar grooves cannot be observed on the labial side of the crown. Labially, at least six shallow, longitudinal flutes occur in the basal part and terminate at the mid-length of the crown (Fig. 2C). The base of the crown is poorly preserved but on the distal side a slight constriction can be observed (Figs. 2A and 2B). The tooth base is still embedded in a piece of bauxitic matrix, but the root is visible both on the lingual and labial sides.



Figure 2 Mesoeucrocodylia indet. crocodyliform tooth (MFGI V 2015.90.2.1.) from the Lower Cretaceous (Lower Albian) Alsópere Bauxite Formation. (A) Reconstruction of the tooth in lingual view. (B) The tooth in lingual; (C) labial; (D) distal; (E) mesial; (F) apical view. (G)–(J), Details of the serrated distal carina. (K) Details of the flutings on the labial side of the tooth. Abbreviations: co, constriction between the crown and root; dg, distal groove; fl, fluting on the enamel surface; mg, mesial groove; sdc, serrated distal carina; smc, serrated mesial carina; r, root.

Comparison and taxonomic assignment

Thecodont teeth with serrated carinae are known in a variety of Mesozoic amniotes including plesiosaurians (e.g., *Massare*, 1987), basal archosauriforms (e.g., *Abler*, 1992; *Senter*, 2003; *Beatty & Heckert*, 2009), basal pterosaurs (e.g., *Ősi*, 2011), theropod dinosaurs (e.g., *Smith*, *Vann & Dodson*, 2005), and crocodyliforms (e.g., *Prasad & Lapparent de Broin*, 2002; *Andrade et al.*, 2010; *Marinho et al.*, 2013; *Rabi & Sebők, in press; Martin, in press*).

Plesiosaurs

Among plesiosaurs, some pliosaurs have teeth with ziphodont carinae and slightly flattened crown, but the longitudinal fluting or the lingual grooves along the carinae do not appear in these forms. Their teeth are usually conical and elongated frequently with coarse striations and without constrictions between the crown and the root (e.g., *Massare*, 1987; *Sasson*, *Noè & Benton*, 2012).

Spinosaurid theropods

The subcircular cross-section and longitudinal fluting along the crown of spinosaurids are comparable to the tooth from Hungary in some aspects. Spinosaurid teeth, however, have no constriction between the crown and the root, and teeth are usually much larger and more robust (see e.g., *Canudo et al., 2008*). The enamel of spinosaurids is distinctly fluted by relatively wide grooves extending the along the entire height of the crown both labially and lingually in most species (but see *Baryonyx, Charig & Milner, 1986; Charig & Milner, 1997; Buffetaut, 2007*). These flutes are much wider (the ridges between the flutes are essentially crest-like, e.g., see *Kellner, 1996; Buffetaut, 2008; Buffetaut, 2013*) than those seen in the Hungarian tooth. No spinosaurid teeth have the shelf-like, lingual grooves along the carinae mesially and distally as seen in MFGI V 2015.90.2.1.

Protosuchians

Protosuchian crocodyliforms show a great variety of dentition including some ziphodont forms. Among the two species of the Early Cretaceous *Sichuanosuchus (Peng, 1996; Wu, Sues & Dong, 1997)*, only *S. huidongensis* possesses teeth with serrated carinae. Here, both the premaxillary and maxillary (including the posterior ones) teeth are finely serrated, and the latter teeth are compressed labiolingually. Neither the longitudinal flutes, nor the lingual grooves along the mesial and distal carina are present in this basal form (*Peng, 1996*). Dental features similar to those of *S. huidongensis* have been described for the Upper Jurassic *Hsisosuchus chungkingensis (Young & Chow, 1953)*.

Metriorhynchids

Among metriorhynchid thalattosuchians, the cosmopolitan *Dakosaurus (Mason, 1869; Gasparini, Pol & Spalletti, 2006*), and *Geosaurus (Andrade et al., 2010)* possess tooth morphology broadly similar to that seen in MFGI V 2015.90.2.1. Posterior maxillary and dentary teeth of *Dakosaurus* are robust, conical, labiolingually compressed, and mesiodistally serrated, but lack the grooves mesially and distally along the lingual side of the carinae (*Gasparini, Pol & Spalletti, 2006*). The teeth of *Geosaurus* from the Late Jurassic of Germany are more compressed labiolingually and they are much more like an isosceles triangle with almost straight mesiodistal carinae (*Andrade et al., 2010*) in contrast with the slightly curved carinae of MFGI V 2015.90.2.1. Besides morphological differences, a further suggestive argument is that the stratigraphic position of the specimen in the unambiguously terrestrial Alsópere Bauxite Formation (*Császár, 1986*) makes a marine crocodyliform identity highly unlikely.

Baurusuchids

In Baurusuchus (MPMA-62-0001-02; Carvalho, Campos & Nobre, 2005; Vasconcellos & Carvalho, 2007; Riff & Kellner, 2001, Ösi A. pers. obs.) and Campinasuchus (Carvalho et al., 2011), the hypertrophied teeth are robust, subcircular in cross-section, and the carinae on the mesial and distal edges are serrated with marked denticles. Tooth crowns lack the

longitudinal grooves mesially and distally on the lingual side and the longitudinal fluting labially, and the crowns are not or very slightly constricted. The two poorly preserved teeth of Wargosuchus (Martinelli & Pais, 2008) show similar morphology as well. The teeth of *Pissarrachampsa* are generally similar to those of other baurusuchids, but the maxillary and posterior dentary tooth crowns are laterally strongly compressed. However, neither mesiodistally positioned longitudinal grooves mesially and distally on the lingual side, nor labial longitudinal fluting are present (Montefeltro, Larsson & Langer, 2011). In Pabwehshi, the anterior teeth are similar to those of other baurusuchids, but all the teeth bear longitudinal striae (Wilson, Malkani & Gingerich, 2001) making them different from MFGI V 2015.90.2.1. The teeth of Gondwanasuchus (Marinho et al., 2013) are similar to the Hungarian specimen in having labiolingually compressed, serrated crowns. They bear five or six deep and wide longitudinal flutes that converge apically and are separated by ridges. Similar longitudinal fluting is present on MFGI V 2015.90.2.1. as well, though these flutes are more shallow and are not present in the apical half of the crown. As in many baurusuchids, the distal carina of the strongly curved teeth of Gondwanasuchus is concave in contrast to the slightly convex carina present in the Hungarian specimen. In conclusion, the teeth of baurusuchids are generally similar to MFGI V 2015.90.2.1. but the latter shows a combination of morphological characters that clearly distinguishes it from the teeth of these genera.

Peirosaurids

Peirosaurids show more diverse tooth crown morphology than baurusuchids. The premaxillary, the hypertrophied maxillary, and the dentary teeth of Montealtosuchus(MPMA-16-0007-04; Carvalho, Vasconcellos & Tavares, 2007) are basically similar to the Hungarian specimen in having an oval cross-section, slightly convex, finely serrated carinae and slightly constricted crown, but they lack the grooves mesially and distally on the lingual side and the longitudinal fluting labially. Pepesuchus (Campos et al., 2011) differs from MFGI V 2015.90.2.1. in having triangular teeth with striated external surfaces and well-marked longitudinal lines on the crowns, as well as in the carinae lacking serrations. The teeth of Uberabasuchus (Carvalho, Ribeiro & Avilla, 2004) are much more like those of baurusuchids in having massive conical teeth, with serrations posteriorly only. Barcinosuchus possesses teeth on which the serrations are quite similar to those on the Hungarian tooth (Leardi & Pol, 2009: Fig. 3G), though the presence or absence of serration on the carinae varies among the teeth. In Lomasuchus (Gasparini, Chiappe & Fernandez, 1991), the anterior, more pointed teeth are serrated but on the other hand they exhibit a flat lingual and convex labial surface without fluting or lingual grooves mesially and distally, in contrast to MFGI V 2015.90.2.1. The pointed, hypertrophied and serrated teeth of Hamadasuchus rebouli from the Albian-Cenomanian Kem Kem beds (Larsson & Sues, 2007: Fig. 3) are similar to MFGI V 2015.90.2.1. in having similar longitudinal fluting labially, but these teeth are not as compressed labiolingually and lack the lingually developed grooves mesially and distally along the serrated cutting margin.

Mahajangasuchids

This clade, defined by *Sereno & Larsson (2009)*, comprises two Late Cretaceous bizarre forms, *Mahajangasuchus insignis* and *Kaprosuchus saharicus*, of which the former species has labiolingually compressed tooth crowns with serrated carinae. These teeth differ from the Hungarian tooth in being extremly robust in cross-section and without fluting or lingual grooves along the carinae (*Turner & Buckley, 2008*). *Kaprosuchus* possesses labiolingually compressed teeth with smooth mesial and distal carinae (*Sereno & Larsson, 2009*).

Trematochampsids

Regarding trematochampsids, the teeth of *Trematochampsa* from the Lower Senonian of Niger (*Buffetaut, 1976*) are comparable with the tooth from Olaszfalu. Teeth of this genus are massive but some of them are labiolingually compressed (*Buffetaut, 1976*: pl. 6, Fig. 3). However, these differ from the Hungarian specimen in having longitudinal enamel striae and in the absence of the lingually developed grooves mesially and distally along the serrated cutting margin.

Non-baurusuchid sebecosuchians

Among these forms the teeth of Doratodon carcharidens from the Santonian of Hungary (Rabi & Sebők, in press: Fig. 4) and Doratodon ibericus from the Campanian of Spain (Company et al., 2005) are most similar to MFGI V 2015.90.2.1. The teeth of these species also possess slightly concave grooves towards the mesial and distal carinae, and in D. *ibericus* the longitudinal flutes occur labially as well. Serration of the carinae of both species is, however, more pronounced, and the crown of D. carcharidens is more constricted basally than that seen in the Olaszfalu specimen. Among sebecids, the teeth of Sebecus are similar in having flattened, pointed, triangular tooth crowns with serrations (*Colbert, 1946*: Fig. 21) but the labial fluting and the lingual grooves along the carinae are not present on the teeth. The same features can be observed in the teeth of Iberosuchus (Ortega, Buscalioni & Gasparini, 1996), though they are more distally curved than the Hungarian specimen. Ilchunaia (Gasparini, 1972) differs from MFGI V 2015.90.2.1. in having two additional carinae on the crown. Besides these forms, Sahitisuchus possesses ziphodont, straight or posteriorly curved teeth with pointed and labiolingually compressed crowns (see e.g., the 4th, left mandibular tooth in Kellner, Pinheiro & Campos, 2014: Fig. 6), but labial fluting is not present in the teeth.

Uruguaysuchids

Among uruguaysuchids the teeth of *Araripesuchus wegeneri* show features similar to the tooth from Olaszfalu. Enlarged teeth, though proportionally not as high as the Hungarian tooth, are present in this species in the anterior parts of the dentary and maxilla. The teeth are labiolingually flattened and pointed, and have lingual grooves ("trough" of *Sereno & Larsson, 2009*: 51) along the carinae mesiodistally. Dentary teeth have finely denticulate margins and fluting occurs on the lingual surface of the enlarged, fourth premaxillary tooth. These flutes, however, appear to be more dense in the teeth of *A. wegeneriSereno & Larsson, 2009*: Fig. 19A) than in the Hungarian specimen.

Planocraniids

Among neosuchians some planocraniids possess ziphodont dentition (*Brochu, 2013*) but similar to the condition in most notosuchians they also lack the labial fluting and lingual grooves along the carinae.

Paralligatorids

This recently revised clade of non-eusuchian neosuchian (*Montefeltro et al., 2013*) or possibly eusuchian (*Turner, 2015*) crocodilians contains at least one species with a tooth morphology similar to the Hungarian specimen. *Wannchampsus kirpachi* from the Early Cretaceous of North America (*Adams, 2014*) also possesses labiolingually slightly flattened, ziphodont teeth with narrow, longitudinal fluting on the labial side, constricted crown, and lingual grooves along the carinae mesiodistally. These teeth (isolated but associated with the type material) of *W. kirpachi* differ from the Hungarian tooth in having only modestly compressed crowns labiolingually and strong carinae with denticles (*Adams, 2014*: Fig. 9). In other paralligatorids, this tooth morphology is not present. Only the oldest member of the group, *Batrachomimus pastosbonensis* (*Montefeltro et al., 2013*) is comparable. It possesses non-ziphodont teeth with longitudinal fluting along the whole upper tooth row, but these flutes are much finer and more abundant than in the Hungarian specimen (F Montefeltro, pers. comm., 2015).

Other mesoeucrocodylians

Some other crocodyliforms possess teeth with generally similar morphology as well. An isolated tooth referred to Notosuchia indet. from Coniacian–Santonian beds of Italy (*Dalla Vecchia & Cau, 2011*) is similar to the Hungarian specimen in having labiolingually flattened, pointed, triangular crown with ziphodont carinae. However, the slightly concave distal carina, the lingually shifting mesial carina, the lack of fluting on the crown surface and the marked constriction below the distal carina clearly distinguish these two types of teeth from each other. Hypertrophied teeth of the atoposaurid *Theriosuchus*, for example, have striae on the sides that are inclined and terminate in the carinae resulting in pseudoziphodont morphology (*Martin et al., 2014*).

To sum up, we can conclude that the tooth from the Albian Alsópere Bauxite Formation, western Hungary does not bear diagnostic features unambiguously referring it to any certain clade of crocodyliforms, but is most similar to the ziphodont teeth of some peirosaurid, non-baurusuchian sebecosuchian, and uruguaysuchid notosuchians (sensu *Sereno et al., 2001; Pol et al., 2014*). Among peirosaurids, the hypertrophied, labiolingually slightly flattened teeth of the North African Albian *Hamadasuchus* are the most similar to the specimen described here in having labial fluting and serrated carinae. Among sebecosuchians, the European Late Cretaceous *Doratodon ibericus* shows the greatest similarity with the Early Cretaceous Hungarian tooth. The enlarged teeth of *Araripesuchus wegeneri* are also similar in various aspects.

Besides notosuchians, it closely resembles the teeth of the paralligatorid *Wannchampsus kirpachi*. On the basis of these comparative results, we refer the tooth

from Olaszfalu to Mesoeucrocodylia indet., until more complete material helps to clarify its precise taxonomic assignment.

PALEOBIOGEOGRAPHIC INFERENCES

Since the tooth from Olaszfalu either represents a notosuchian (sensu *Sereno et al., 2001*; *Pol et al., 2014*) or a paralligatorid (*Adams, 2014*; *Turner, 2015*) neosuchian crocodyliform, two paleobiogeographic scenarios can be outlined.

In case of a notosuchian affinity, this tooth represents the earliest indication of notosuchian crocodyliforms on European landmasses. Previously, the remains of this clade were known only from Cenomanian to Eocene deposits in different regions of the European archipelago: Hamadasuchus-like teeth from the Cenomanian of France (Vullo et al., 2005; Vullo & Néraudeau, 2008), a Coniacian–Santonian aged isolated tooth referred to Notosuchia from Italy (Dalla Vecchia & Cau, 2011), remains of the notosuchian Doratodon carcharidens from the Santonian of Iharkút, Hungary (Rabi & Sebők, in press) and from the Lower Campanian of Muthmannsdorf, Austria (Buffetaut, 1979), and Doratodonibericus from the Campanian of Spain (Company et al., 2005). Doratodon has been reported from the Lower Maastrichitian of Romania as well (Grigorescu et al., 1999). Finally, a number of fragmentary remains from the Paleogene of Europe are referred mainly to sebecosuchians (Buffetaut, 1980; Buffetaut, 1986; Ortega, Buscalioni & Gasparini, 1996; *Martin, in press*, and references therein). With a notosuchian affinity, the Hungarian tooth would date back the European occurrence of the otherwise primarily Gondwanan group to the Early Cretaceous (Early Albian). The other non-Gondwanan notosuchian is Chimaerasuchus paradoxus from Aptian–Albian deposits of China (Wu, Sues & Sun, 1995). Though the material is fragmentary, bearing numerous highly apomorphic features, most phylogenetic analyses have found Chimaerasuchus being nested well within Notosuchia (Pol et al., 2014). The phylogeny of Pol et al. (2014) dates the origin of basal notosuchians to the Early Jurassic and infers an almost 60 My long ghost lineage (i.e., the first half of notosuchian evolution; Pol et al., 2014: Fig. 47). The hypothesis of Pol et al. (2014) argues for a more complex biogeographic history of the group, and therefore their Laurasian temporal distribution is perhaps well underestimated. The Hungarian specimen may suggest that notosuchian crocodyliforms existed already in the Early Albian in the southern part of the European archipelago. If the tooth from Olaszfalu is from a notosuchian, then, along with Santonian neobatrachian anurans (Szentesi & Venczel, 2010), Coniacian–Santonian notosuchians (Dalla Vecchia & Cau, 2011; Rabi & Sebők, in press), Santonian bothremydid turtles (Rabi, Tong & Botfalvai, 2012; Rabi, Vremir & Tong, 2013), and Albian and Santonian abelisaurids (Accarie et al., 1995; Ősi & Buffetaut, 2011), all clades of Gondwanan origin, it would suggest that faunal links between the European archipelago and Africa might have existed during most of the Cretaceous (Csiki-Sava et al., 2015; Rabi & Sebők, in press); contra (Ezcurra & Agnolín, 2012).

Based on the similar dental characters seen in the North American *Wannchampsus kirpachi*, a paralligatorid affinity is also plausible, though the exact tooth morphology of *W. kirpachi* is actually not present in other paralligatorid forms. In case of a paralligatorid

affinity, the Hungarian tooth would represent the first European record of the group further expanding their cosmopolitan distribution.

Either a notosuchian, or a paralligatorid, the tooth from the Albian bauxite deposit of western Hungary represents a group still unknown from the Early Cretaceous European archipelago, and therefore implies a hidden diversity of crocodyliforms in the area. The currently known record of late Early Cretaceous (Barremian–Albian) European crocodyliforms includes goniopholidids (*Andrade et al., 2011*), possible hylaeochampsids (*Buscalioni et al., 2011*), atoposaurids (*Brinkmann, 1992; Schwarz & Salisbury, 2005*), and bernissartiids (*Buffetaut & Ford, 1979; Buscalioni & Sanz, 1990; Sweetman, Pedreira-Segade Vidovic, 2015*), none of them having ziphodont teeth. The ziphodont tooth from Olaszfalu from a certainly terrestrial deposit of the Transdanubian Range (Apulian microplate, *Csontos & Vörös, 2004*) may suggest the existence of terrestrial crocodyliforms in the European archipelago. Hopefully, future discoveries will reveal the affinities of this peculiar taxon, and help to specify the composition of European Early Cretaceous crocodyliform diversity.

CONCLUSIONS

Rabi & Sebők (in press) recently noted that there is no sign of true ziphodont crocodyliforms in the Early Cretaceous of Europe. The tooth (MFGI V 2015.90.2.1.) from the Albian Alsópere Bauxite Formation, western Hungary, however, is ziphodont and closely resembles that of some peirosaurid, non-baurusuchian sebecosuchian, and uruguaysuchid crocodyliforms—all of which have been united into a single clade, Notosuchia (*Sereno et al., 2001; Pol et al., 2014*). In case of notosuchian affinity this tooth would represent the earliest indication of the clade in Europe. Besides notosuchians, the paralligatorid *Wannchampsus kirpachi* possesses similar dental features to the tooh presented here. If the Hungarian specimen is from a paralligatorid, then it would be the first occurrence of the group in the European archipelago. On the basis of these comparative results, we refer the tooth from Olaszfalu to Mesoeucrocodylia indet., until more complete material helps to clarify its precise taxonomic assignment. The tooth from the Albian of western Hungary certainly represents a group still unknown from the European Lower Cretaceous, and therefore adds to the diversity of Early Cretaceous crocodyliforms in the area.

Institutional abbreviations

MFGI	Magyar Földtani és Geofizikai Intézet, Budapest, Hungary
MGUV	Museo del Departamento de Geología, Universidad de Valencia, Burjassot,
	Spain
MPMA	Museu de Paleontologia de Monte Alto, Monte Alto, Brazil

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Attila Ősi analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Márton Rabi and László Makádi analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper.

REFERENCES

- Abler WL. 1992. The serrated teeth of tyrannosaurid dinosaurs, and biting structures in other animals. *Paleobiology* 18:161–183.
- Accarie H, Beaudoin B, Dejax J, Friès G, Michard J-G, Taquet P. 1995. Découverte d'un Dinosaure Théropode nouveau (*Genusaurus sisteronis* n. g., n. sp.) dans l'Albien marin de Sisteron (Alpes de Haute-Provence, France) et extension au Crétacé inférieur de la lignée cératosaurienne. *Comptes Rendus de l'Académie des Sciences Série IIa. Sciences de la Terre et des Planétes* 320(4):327–334.
- Adams TL. 2014. Small crocodyliform from the Lower Cretaceous (late Aptian) of central Texas and its systematic relationship to the evolution of Eusuchia. *Journal of Paleontology* **88(5)**:1031–1049 DOI 10.1666/12-089.

- Andrade MB, Young MT, Desojo JB, Brusatte SL. 2010. The evolution of extreme hypercarnivory in Metriorhynchidae (Mesoeucrocodylia: Thalattosuchia) based on evidence from microscopic denticle morphology. *Journal of Vertebrate Paleontology* 30(5):1451–1465 DOI 10.1080/02724634.2010.501442.
- Andrade MB, Edmonds R, Benton MJ, Schouten R. 2011. A new Berriasian species of Goniopholis (Mesoeucrocodylia, Neosuchia) from England, and a review of the genus. Zoological Journal of the Linnean Society 163:S66–S108 DOI 10.1111/j.1096-3642.2011.00709.x.
- **Beatty BL, Heckert AB. 2009.** A large archosauriform tooth with multiple supernumerary carinae from the Upper Triassic of New Mexico (USA), with comments on carina development and anomalies in the Archosauria. *Historical Biology* **21**:57–65 DOI 10.1080/08912960903154511.
- Brinkmann W. 1992. Die Krokodilier-Fauna aus der Unter-Kreide (Ober-Barremium von Uña (Provinz Cuenca, Spanien). *Berliner Geowissenschaftliche Abhandlungen (E)* 5:1–123.
- **Brochu CA. 2013.** Phylogenetic relationships of Palaeogene ziphodont eusuchians and the status of *Pristichampsus* Gervais, 1853. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **103**:521–550 DOI 10.1017/S1755691013000200.
- **Buffetaut E. 1976.** Ostéologie et affinités de *Trematochampsataqueti* (Crocodylia, Mesosuchia) du Sénonien inférieur d'In Beceten (République du Niger). *Géobios* **9**:143–198.
- **Buffetaut E. 1979.** Revision der Crocodylia (Reptilia) aus den Gosau-Schichten (Ober-Kreide) von Österreich. *Beiträge zur Paläontologie von Österreich* **6**:89–105.
- **Buffetaut E. 1980.** Histoire biogéographique des Sebecosuchia (Crocodylia, Mesosuchia): un essai d'interprétation. *Annales de Paléontologie* **66**(1):1–18.
- Buffetaut E. 1986. Un Mésosuchien ziphodonte dans l'Éocène supérieurde La Livinière (Hérault, France). *Geobios* 19(1):101–113 DOI 10.1016/S0016-6995(86)80038-9.
- Buffetaut E. 2007. The spinosaurid dinosaur Baryonyx (Saurischia, Theropoda) in the Early Cretaceous of Portugal. Geological Magazine 144(6):1021–1025 DOI 10.1017/S0016756807003883.
- **Buffetaut E. 2008.** Spinosaurid teeth from the Late Jurassic of Tendaguru, Tanzania, with remarks on the evolutionary and biogeographical history of the Spinosauridae. In: Mazin J-M, Pouech J, Hantzpergue P, Lacombe V, eds. *Mid-mesozoic life and environments. Documents des Laboratoires de Géologie de Lyon*, vol. 164. 26–28.
- **Buffetaut E. 2013.** An early spinosaurid dinosaur from the Late Jurassic of Tendaguru (Tanzania) and the evolution of the spinosaurid dentition. *Oryctos* **10**:1–8.
- Buffetaut E, Ford RLE. 1979. The crocodilian *Bernissartia* in the Wealden of the Isle of Wight. *Palaeontology* 22(4):905–912.
- **Buscalioni AD, Sanz JL. 1990.** The small crocodile *Bernissartia fagesii* from the Lower Cretaceous of Galve (Teruel, Spain). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* **60**:129–150.
- Buscalioni A, Piras P, Vullo R, Signore M, Barbera C. 2011. Early eusuchia crocodylomorpha from the vertebrate-rich Plattenkalk of Pietraroia (Lower Albian, southern Apennines, Italy). *Zoological Journal of the Linnean Society* 163:199–227 DOI 10.1111/j.1096-3642.2011.00718.x.
- Campos DA, Oliveira GR, Figueiredo RG, Riff D, Azevedo SAK, Carvalho LB, Kellner AWA. 2011. On a new peirosaurid crocodyliform from the Upper Cretaceous, Bauru Group, southeastern Brazil. Anais da Academia Brasileira de Ciências 83:317–327 DOI 10.1590/S0001-37652011000100020.

- **Canudo JI, Gasulla JM, Gomez-Fernandez D, Ortega F, Sanz JL, Yagüe P. 2008.** Primera evidencia de dientes aislados atribuidos a Spinosauridae (Theropoda) en el Aptiano inferior (Cretácico Inferior) de Europa: Formación Arcillas de Morella (España). [First evidence of isolated teeth referred to Spinosauridae (Theropoda) from the lower Aptian (Lower Cretaceous) of Europe: Arcillas de Morella Formation (Spain)]. *Ameghiniana* **45**:649–662.
- **Carvalho IS, Ribeiro LCB, Avilla LS. 2004.** *Uberabasuchus terrificus* sp. nov., a new Crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil. *Gondwana Research* **7**:975–1002 DOI 10.1016/S1342-937X(05)71079-0.
- **Carvalho IS, Campos ACA, Nobre PH. 2005.** *Baurusuchus salgadoensis*, a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. *Gondwana Research* **8**:11–30 DOI 10.1016/S1342-937X(05)70259-8.
- **Carvalho IS, Vasconcellos FM, Tavares SAS. 2007.** *Montealtosuchus arrudacamposi*, a new peirosaurid crocodile (Mesoeucrocodylia) from the Late Cretaceous Adamantina Formation of Brazil. *Zootaxa* **1607**:35–46.
- Carvalho IS, Teixeira VPA, Ferraz MLF, Ribeiro LCB, Martinelli AG, Neto FM, Sertich JJW, Cunha GC, Cunha IC, Ferraz PF. 2011. *Campinasuchus dinizi* gen. et sp. nov., a new Late Cretaceous baurusuchid (Crocodyliformes) from the Bauru Basin, Brazil. *Zootaxa* 2871:19–42.
- Charig AJ, Milner AC. 1986. *Baryonyx*, a remarkable new theropod dinosaur. *Nature* 324(6095):359–361 DOI 10.1038/324359a0.
- Charig AJ, Milner AC. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum of London* 53:11–70.
- **Colbert EH. 1946.** *Sebecus*, representative of a peculiar suborder of fossil Crocodilia from Patagonia. *Bulletin of the American Museum of Natural History* **87**(**4**):217–270.
- **Company J, Suberbiola XP, Ruiz-Omenaca JI, Buscalioni AD. 2005.** A new species of *Doratodon* (Crocodyliformes: Ziphosuchia) from the Late Cretaceous of Spain. *Journal of Vertebrate Paleontology* **25**(2):343–353 DOI 10.1671/0272-4634(2005)025[0343:ANSODC]2.0.CO;2.
- **Császár G. 1986.** Dunántúli-középhegységi középsö-kréta képzödmények rétegtana és kapcsolata a bauxitképzödéssel. [Middle Cretaceous formations of the Transdanubian Central Range: stratigraphy and connection with bauxite genesis]. *Geologica Hungarica series Geologica* **23**:1–295.
- Császár G, Fözy I, Mizák J. 2008. Az olaszfalui Eperjes földtani felépítése és fejlődéstörténete. *Földtani Közlöny* 138(1):21–48.
- Császár G, Jocha-Edelényi E, Knauer J, Szentgyörgyi K. 1993. Terrestrial and shallow marine Cretaceous clastics of Hungary. *Cretaceous Research* 14:307–335 DOI 10.1006/cres.1993.1023.
- Csiki-Sava Z, Buffetaut E, Ősi A, Pereda-Suberbiola X, Brusatte SL. 2015. Island life in the Cretaceous—faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. *ZooKeys* **469**:1–161 DOI 10.3897/zookeys.469.8439.
- **Csontos L, Vörös A. 2004.** Mesozoic plate tectonic reconstruction of the Carpathian region. *Palaeogeography, Palaeoclimatology, Palaeoecology* **210**:1–56 DOI 10.1016/j.palaeo.2004.02.033.
- Dalla Vecchia FM, Cau A. 2011. The first record of a notosuchian crocodyliform from Italy. *Rivista Italiana di Paleontologia e Stratigrafia* 117(2):309–321.
- **Ezcurra MD, Agnolín FL. 2012.** A new global palaeobiogeographical model for the Late Mesozoic and Early Tertiary. *Systematic Biology* **61**(4):553–566 DOI 10.1093/sysbio/syr115.

- Gasparini Z. 1972. Los Sebecosuchia (Crocodilia) del territorio argentino. Consideraciones sobre su status taxonómico. Ameghiniana 9:23–34.
- Gasparini Z, Pol D, Spalletti LA. 2006. An unusual marine crocodyliform from the Jurassic-Cretaceous boundary of Patagonia. *Science* 311:70–73 DOI 10.1126/science.1120803.
- Gasparini Z, Chiappe LM, Fernandez M. 1991. A new Senonian peirosaurid (Crocodylomorpha) from Argentina and a synopsis of the South American Cretaceous crocodilians. *Journal of Vertebrate Paleontology* 11:316–333 DOI 10.1080/02724634.1991.10011401.
- Grigorescu D, Venczel M, Csiki Z, Limberea R. 1999. New Latest Cretaceous microvertebrate fossil assemblage from the Hateg Basin (Romania). *Geologie en Mijnbouw* 78:301–314 DOI 10.1023/A:1003890913328.
- **Juhász M. 1979.** A dunántúli alsó-és középsőkréta palinológiája. (Palynology of the Transdanubian Lower and Middle Cretaceous). PhD diss., JATE, Szeged. Manuscript, 124p.
- Juhász M. 1983. Palynostratigraphic zonation of the transdanubian middle creataceous. *Acta Geologica Hungarica* 26:41–68.
- Kellner AWA. 1996. Remarks on brazilian dinosaurs. *Memoirs of the Queensland Museum* 39(3):611–626.
- Kellner AWA, Pinheiro AEP, Campos DA. 2014. A new sebecid from the Paleogene of Brazil and the crocodyliform radiation after the K–Pg boundary. *PLoS ONE* 9(1):e81386 DOI 10.1371/journal.pone.0081386.
- Kretzoi M, Noszky J. 1951. Saurius-fog a bakonyi bauxitképződményből. Földtani Közlöny 81:333.
- Larsson HCE, Sues H-D. 2007. Cranial osteology and phylogenetic relationships of Hamadasuchus rebouli (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of Morocco. Zoological Journal of the Linnean Society 149(4):533–567 DOI 10.1111/j.1096-3642.2007.00271.x.
- Leardi JM, Pol D. 2009. The first crocodyliform from the Chubut Group (Chubut Province, Argentina) and its phylogenetic position within basal Mesoeucrocodylia. *Cretaceous Research* 30:1376–1386 DOI 10.1016/j.cretres.2009.08.002.
- Legasa O, Buscalioni AD, Gasparini Z. 1994. The serrated teeth of *Sebecus* and the Iberoccitanian crocodile, a morphological and ultrastructural comparison. *Studia Geologica Salmanticensia* 24:123–144.
- Marinho TS, Iori FV, Carvalho IS, Vasconcellos FM. 2013. *Gondwanasuchusscabrosus* gen. et sp. nov., a new terrestrial predatory crocodyliform (Mesoeucrocodylia: Baurusuchidae) from the Late Cretaceous Bauru Basin of Brazil. *Cretaceous Research* 44:104–111 DOI 10.1016/j.cretres.2013.03.010.
- Martin JE. A sebecosuchian in a middle Eocene karst with comments on the dorsal shield in Crocodylomorpha. *Acta Palaeontologica Polonica* In Press.
- Martin JE, Rabi M, Csiki-Sava Z, Vasile Ş. 2014. Cranial morphology of *Theriosuchus sympiestodon* (Mesoeucrocodylia, Atoposauridae) and the widespread occurrence of *Theriosuchus* in the Late Cretaceous of Europe. *Journal of Paleontology* **88(3)**:444–456 DOI 10.1666/13-106.
- Martinelli AG, Pais DF. 2008. A new baurusuchid crocodyliform (Archosauria) from the Late Cretaceous of Patagonia (Argentina). *Comptes Rendus Palevol* 7:371–381 DOI 10.1016/j.crpv.2008.05.002.
- Mason JW. 1869. On *Dakosaurus* from the kimmeridge clay of shotover hill. *The Quarterly Journal* of the Geological Society of London 25:218–220 DOI 10.1144/GSL.JGS.1869.025.01-02.36.
- Massare JA. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology* 7(2):121–131 DOI 10.1080/02724634.1987.10011647.

- Mindszenty A, Szöts A, Horváth A. 1989. Excursion A3: karstbauxites in the Transdanubian Midmountains. In: Császár G, ed. *Excursion guidebook IAS 10th regional meeting*, Budapest. Gent: IAS, 11–48.
- Montefeltro FC, Larsson HCE, Langer MC. 2011. A new baurusuchid (Crocodyliformes, Mesoeucrocodylia) from the Late Cretaceous of Brazil and the phylogeny of Baurusuchidae. *PLoS ONE* **6**(7):e21916 DOI 10.1371/journal.pone.0021916.
- Montefeltro FC, Larsson HCE, De França MAG, Langer MC. 2013. A new neosuchian with Asian affinities from the Jurassic of northeastern Brazil. *Naturwissenschaften* 100(9):835–841 DOI 10.1007/s00114-013-1083-9.
- Noszky J. 1951. Jelentés az 1950: évben Magyarországon az É-i Bakony középső és Ny-i részén Alsópere-Zirc-Bakonybél-Ugod és Bakonyjákó térségében végzett bauxitkutató munkálatokról. Manuscript. Budapest: Geological Institute of Hungary, 1–297.
- Ortega F, Buscalioni AD, Gasparini Z. 1996. Reinterpretation and new denomination of *Atacisauruscrassiproratus* (Middle Eocene; Issel, France) as cf. *Iberosuchus* (Crocodylomorpha, Metasuchia). *Geobios* 29(3):353–364 DOI 10.1016/S0016-6995(96)80037-4.
- Ősi A. 2011. Feeding-related characters in basal pterosaurs: implications from jaw mechanism, dental function and diet. *Lethaia* 44:136–152 DOI 10.1111/j.1502-3931.2010.00230.x.
- Ősi A, Buffetaut E. 2011. Additional non-avian theropod and bird remains from the early Late Cretaceous (Santonian) of Hungary and a review of the European abelisauroid record. *Annales de Paleontologie* 97(1–2):35–49 DOI 10.1016/j.annpal.2011.07.001.
- **Peng G. 1996.** A Late Jurassic Protosuchian *Sichuanosuchus huidongensis* from Zigong, Sichuan Province. *Vertebrata PalAsiatica* **34(4)**:269–278.
- **Pol D, Nascimento PM, Carvalho AB, Riccomini C, Pires-Domingues RA, Zaher H. 2014.** A new notosuchian from the Late Cretaceous of Brazil and the phylogeny of advanced notosuchians. *PLoS ONE* **9(4)**:e93105 DOI 10.1371/journal.pone.0093105.
- **Prasad GVR, Lapparent de Broin F de. 2002.** Late Cretaceous crocodile remains from Naskal (India): comparisons and biogeographic affinities. *Annales de Paléontologie* **88**:19–71.
- **Rabi M, Sebők N. 2015.** A revised Eurogondwana model: Late Cretaceous notosuchian crocodyliforms and other vertebrate taxa suggest the retention of episodic faunal links between Europe and Gondwana during most of the Cretaceous. *Gondwana Research* In Press DOI 10.1016/j.gr.2014.09.015.
- Rabi M, Tong H, Botfalvai G. 2012. A new species of the side-necked turtle *Foxemys* (Pelomedusoides: Bothremydidae) from the Late Cretaceous of Hungary and the historical biogeography of the Bothremydini. *Geological Magazine* 149(4):662–674 DOI 10.1017/S0016756811000756.
- **Rabi M, Vremir M, Tong H. 2013.** Preliminary overview of Late Cretaceous turtle diversity in Eastern Central Europe (Austria, Hungary, and Romania). In: Brinkman DB, Holroyd PA, Gardner JD, eds. *Morphology and evolution of turtles: origin and early diversification*. Dordrecht: Springer, 307–336.
- Riff D, Kellner AWA. 2001. On the dentition of *Baurusuchus pachecoi* Price (Crocodyliformes, Metasuchia) from the Upper Cretaceous of Brazil. *Boletim do Museu Nacional, Nova Série, Geologia* 59:1–15.
- Sasson J, Noè LF, Benton MJ. 2012. Cranial anatomy, taxonomic implications and palaeopathology of an Upper Jurassic Pliosaur (Reptilia: Sauropterygia) from Westbury, Wiltshire, UK. *Paleontology* 55(4):743–773 DOI 10.1111/j.1475-4983.2012.01151.x.

- Schwarz D, Salisbury SW. 2005. A new species of *Theriosuchus* (Atoposauridae, Crocodylomorpha) from the Late Jurassic (Kimmeridgian) of Guimarota, Portugal. *Geobios* 38:779–802 DOI 10.1016/j.geobios.2004.04.005.
- Senter P. 2003. New information on cranial and dental features of the Triassic Archosauriform reptile *Euparkeriacapensis*. *Palaeontology* **46**:613–621 DOI 10.1111/1475-4983.00311.
- Sereno PC, Larsson HC, Sidor CA, Gado B. 2001. The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science* 294(5546):1516–1519 DOI 10.1126/science.1066521.
- Sereno PC, Larsson HCE. 2009. Cretaceous crocodyliforms from the Sahara. *ZooKeys* 28:1–143 DOI 10.3897/zookeys.28.325.
- Smith JB, Vann DR, Dodson P. 2005. Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. *The Anatomical Record* 285A:699–736 DOI 10.1002/ar.a.20206.
- Sweetman SC, Pedreira-Segade U, Vidovic SU. 2015. A new bernissartiid crocodyliform from the Lower Cretaceous Wessex Formation (Wealden Group, Barremian) of the Isle of Wight, southern England. *Acta Palaeontologica Polonica* **60**(2):257–268 DOI 10.4202/app.00038.2013.
- Szentesi Z, Venczel M. 2010. An advanced anuran from the Late Cretaceous (Santonian) of Hungary. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 256(3):291–302 DOI 10.1127/0077-7749/2010/0054.
- Turner AH. 2015. A Review of *Shamosuchus* and *Paralligator* (Crocodyliformes, Neosuchia) from the Cretaceous of Asia. *PLoS ONE* 10(2):e0118116 DOI 10.1371/journal.pone.0118116.
- Turner AH, Buckley GA. 2008. Mahajangasuchus insignis (Crocodyliformes: Mesoeucrocodylia) cranial anatomy and new data on the eusuchian-style palate. Journal of Vertebrate Paleontology 28:382–408 DOI 10.1671/0272-4634(2008)28[382:MICMCA]2.0.CO;2.
- Vasconcellos FM, Carvalho IS. 2007. Cranial features of *Baurusuchus salgadoensis* Carvalho, Campos and Nobre 2005, a Baurusuchidae (Mesoeucrocodylia) from the Adamantina Formation, Bauru Basin, Brazil: paleoichnological, taxonomic and systematic implications. In: Carvalho IS, Tardin Cassab RC, Schwanke C, Caravalho MA, Fernandes ACS, Rodrigues MAC, Carvalho MSS, Arai M, Oliveira MEQ, eds. Rio de Janeiro: Interciência, 327–340. *Available at http://www.igeo.ufrj.br/~ismar/1/1_33.pdf*.
- Vullo R, Néraudeau D. 2008. Cenomanian vertebrate assemblages from southwestern France: a new insight into the European mid-Cretaceous continental fauna. *Cretaceous Research* 29(5–6):930–935 DOI 10.1016/j.cretres.2008.05.010.
- Vullo R, Néraudeau D, Allain R, Cappetta H. 2005. Un nouveau gisement àmicrorestes de vertébrés continentaux et littoraux dans le Cénomanien inférieur de Fouras (Charente-Maritime, Sud-Ouest de la France). Comptes Rendus Palevol 4(1–2):95–107 DOI 10.1016/j.crpv.2004.11.006.
- Wilson JA, Malkani MS, Gingerich PD. 2001. New crocodyliform (Reptilia, Mesoeucrocodylia) from the Upper Cretaceous Pab Formation of Vitakri, Balochistan (Pakistan). *Contributions from the Museum of Paleontology, University of Michigan* **30**(12):321–336.
- Wu XC, Sues HD, Sun A. 1995. A plant-eating crocodyliform from the Cretaceous of China. *Nature* 376:678–680 DOI 10.1038/376678a0.
- Wu XC, Sues HD, Dong Z. 1997. Sichuanosuchus shuhanensis, a new? Early Cretaceous Protosuchian (Archosauria: Crocodyliformes) from Sichuan (China), and the monophyly of Protosuchia. Journal of Vertebrate Paleontology 17(1):89–103 DOI 10.1080/02724634.1997.10010956.
- Young CC, Chow MC. 1953. New fossil reptiles from Szechuan China. *Acta Paleontologica Sinica* 1:87–109.