

Eocene gavialoid teeth from southern Transylvania with notes on the diversity of Paleogene crocodylians from Romania

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Abstract. Herein, we report a small collection of isolated crocodylian teeth recovered from shallow marine Eocene deposits of Turnu Roșu (Porțești), Romania. The teeth probably represent an attritional assemblage that could have belonged to several individuals of various sizes and ages, provided with heterodont dentition of at least five morphotypes (slender caniniform, triangular-lanceolate shaped, enlarged conical, slender conical, and low crowned). We assigned the isolated teeth to Gavialoidea based on a number of morphological characters shared with representatives of early gavialoids, known from the early-middle Eocene of western Europe or North Africa. The gavialoids from Turnu Roșu represent a new group for the Paleogene of Romania that probably reached the territory of southern Transylvania in the Middle Eocene. Possible scenarios for the origin of southern Transylvanian gavialoids imagine an existence of a western-eastern European route or a migration route direct from North Africa and an ancestor close to the morphology of *Marccosuchus* from the region of western Tethys.

Keywords: biogeography, early gavialoids, heterodonty, migration route, western Tethys.

Introduction

Crocodylians are a group of diapsid reptiles with a remarkably long fossil record, which extends from the Late Triassic (Carnian) of Argentina (Irmis et al. 2013) into the present. Present-day crocodylians are semiaquatic ambush hunters; however, their fossil representatives include several forms with clear signs of acquired adaptations into omnivore or even herbivory (Sues 2019). Due to their thermophilous nature, present-day crocodylians, with about 25 extant species, are largely restricted to tropical or subtropical regions. The members of Crocodyloidea and Gavialoidea share the presence of a keratinized buccal cavity and osmoregulatory pores on the tongue (Taplin et al. 1985, Taplin & Grigg 1989) that are sufficiently competent to maintain homeostasis in salt water (Grigg & Gans 1993). In contrast, lingual salt glands have not been found in any member of Alligatoroidea (Taplin 1988).

Phylogenetic analyses, based on morphological datasets, recover consistently the Crocodyloidea and Alligatoroidea on the parsimony tree as the sister taxon to each other, forming the clade of Brevirostres, whereas Gavialoidea appears as the sister taxon to Brevirostres (Brochu 1997, 2003, Rio & Mannion 2021). In this topology, the members of Tomistominae (e.g., *Tomistoma*) are recovered within the clade of Crocodylidae. The latter arrangement is in contrast with the topology resulted from molecular phylogeny, in which *Tomistoma* appears within the clade of Gavialidae (Harshman et al. 2003, Janke et al. 2005, McAliley et al. 2006, Oaks 2011, Bittencourt et al. 2019, Milián-García et al. 2020, Hekkala et al. 2021). Recent phylogenetic analyses based on combined morphological and molecular datasets recover Tomistominae within the clade of Gavialidae (Gold et al. 2014, Lee & Yates 2018, Iijima & Kobayashi 2019). Nevertheless, most taxa traditionally included in

Tomistominae appear as successive outgroups to Gavialidae (*Gavialis* + *Tomistoma*) (Rio & Mannion 2021).

Herein, we report a series of crocodylian teeth collected from the fossiliferous deposits of Turnu Roșu, recognized in the collections of the Natural History Museum, Sibiu. The isolated teeth exhibit various signs of abrasion, probably caused by water transport. The teeth may have belonged to a single taxon represented by various-sized individuals with heterodont dentition. In the present paper, we: 1) describe the identified specimens, 2) discuss the systematic position of the crocodylian taxon, and 3) outline the paleoenvironmental and paleogeographic significances of the discovered remains.

Geological setting

In the Transylvanian Depression, the widest area where the Paleogene sedimentary deposits occur is located in North-West and North-North-East. There, three distinct sedimentary areas were outlined, based mainly on the Upper Eocene-Lower Oligocene facies distribution, i.e., Gilău, Meseș, and Preluca (Rusu 1970, Popescu 1976, 1978). Further, Popescu (1984) named in these areas even some subareas: Iara and Călățele in the Gilău area, and Ileanda and Chioar in the Preluca area.

In this time span, alternances of marine and terrestrial environments are recorded as consequences of various geological events. Paleogene rocks are also cropping out in the southwestern area of the depression, in the Metaliferi sedimentary area, which mark a transgression in that region. The deposits related to the Ighiu Formation are marine (late Eocene) and brackish-marine (early Oligocene) (Codrea & Dica 2005, and references therein).

Paleogene deposits also occur on the southern margin of the Transylvanian Depression as patches overlying the metamorphic basements of the Cindrel and Făgăraș

Mountains (Fig. 1). About these deposits, the geological data are, by far, scarcer, mainly about the ones cropping out at Apoldu de Sus and Dobârca localities, both in Sibiu County (Maxim 1965, Mészáros et al. 1977, Codrea 2000, Tissier et al. 2018, and related references). Another source of data about this topic concerns the Paleogene blocks of rocks reworked in the Middle Miocene (Badenian) deposits cropping out at Râpa Roșie near Sebeș, those being mainly biogenic limestones. A microfacial study could allow at least a partial reconstruction of the former Paleogene sequences once cropping out on the southern margin of the depression, nearly completely razed by the pre-Moravian (Langhian) erosion, followed by the Moravian marine transgression (Solomon et al. 2010). The limestones analyzed from Râpa Roșie are Lower-Middle Eocene. Therefore, their source areas were not located to the northwest because in the area where the Ighiu Formation is exposed, only Upper Eocene deposits are noticed, the older ones are missing. Eocene

blocs of rocks with nummulites are also reported from the Tălmaciu conglomerates (Mészáros 1996a). We intend to have a further closer look at such rocks in the following years, in a tentative to reconstruct the Eocene paleogeography of Transylvania.

Due to this lowermost Badenian geological event, in different parts of the Transylvanian Depression, piles of conglomerates occurred, as in Ciceu-Giurgești, Bistrița-Năsăud County (Popescu 1970), Tălmaciu, Sibiu County (Mészáros 1996a), or in the close neighborhood of Cluj-Napoca city at Suceag, on Cipcheș Creek, that can be considered as members of the Dej Formation. They occurred due to the late Styrian tectonic pulse and related uplift of the Carpathian branches surrounding the Transylvanian Depression. As they are not continuous, but with local development, one may think the beginning of the Middle Miocene sedimentary basin of Transylvania hosted small grabens with strong related erosion.

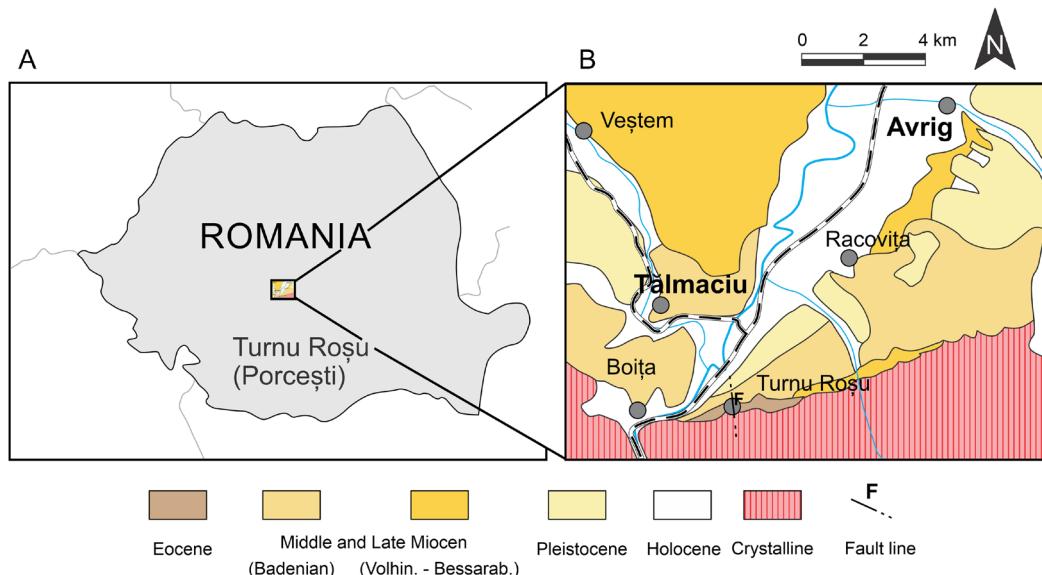


Figure 1. Location of Turnu Roșu fossil locality (A) and geologic map of the area (B) in Romania.

Nonetheless, by far, the most famous Paleogene deposits of this region are the ones from Turnu Roșu locality (former: Porcesti, Portsest, Portsesd), near Sibiu town, mainly due to the 19th mentions of the fossil shark teeth and other various invertebrate and vertebrate remains (Ackner 1850, Neugeboren 1850, 1851). These rocks are also mentioned in the monograph about the Transylvanian basin by Hauer & Stache (1863), who copied Neugeboren's list of shark taxa. These geologists considered the age of the related rocks as Middle Eocene. The Paleogene deposits from Turnu Roșu were later mentioned by Koch (1894). In his monograph, Koch also used the data published by previous geologists and paleontologists such as Neugeboren (1850, 1851), Vutskits (1883), or Primics (1884). Popescu-Voitești (1927) considered these deposits very similar to the 'lower horizon' of the 'Nummulitique' from the Getic Depression. Ilie (1958) copied Neugeboren's shark list, but in an inadequate manner: incomplete, with mistaken orthography of some taxa. In several other works (e.g., Bombiță 1963, Tătărim-Vlaicu 1967, Şuraru et al. 1967, Bucur & Ianoliu 1987), two

viewpoints can be noticed about the local stratigraphy: part of these geologists considered the deposits older than the Priabonian, while others agreed with the Priabonian age of the upper limestones of this succession.

A basic contribution about the stratigraphy of this locality was published by Mészáros (1960). He divided the sedimentary succession into five 'horizons': i. of mollusk molds with five levels, with: '*Ampullospira*, *Cardium*, *Vulsella*, *Lucina*, *Corbis*'; ii. nummulites; iii. conglomerates; iv. coarse limestone; v. sandstones. The stratigraphy is completed by a list of 83 taxa of mollusks. This succession remained unchanged in other subsequent works as the ones of Mészáros & Ianoliu (1971, 1972, 1973) or Bucur & Ianoliu (1987). Concerning the geological age, Mészáros (1960) considered these rocks as Ypresian-Lutetian, but later contributions (Mészáros & Ianoliu 1971, 1972, 1973; Mészáros 1996b) also agreed with the presence of a Priabonian sequence, as well as the possible Oligocene age of the uppermost sandstones. Mészáros (1996a) also sketched a stratigraphic chart and coined a group he named Turnu-

Roșu - Porcești, with three formations: Valea Satului Formation (Cuisian, with lowermost clay with foraminifers, followed by sandstones, conglomerates, marls with *Nummulites planulatus*, *N. aquitanicus*, *N. globulus*, conglomerates with *Ampullinopsis porcensis* and limy sandstone); Strada Muntelui Formation (Lutetian-Priabonian, with microconglomerates, followed by limestones with *N. laevigatus*, *N. distans*, *N. gallensis*, *N. murchisoni*, *Assilina exponens* and finally, limestone with *N. millecaput*, *N. distans*, *N. pratti*, *Assilina praespira*, *Operculina alpina*, *Discocyclina nummulitica*, *Asterocydina stella*) and Valea Satului Formation (Priabonian - lowermost Oligocene; basal conglomerates with *N. fabianii*, *N. chavanesi*, and *Chlamys biarritzensis*, followed by sandstones, limy sandstones with mollusks and shark teeth). However, this stratigraphic chart may be considered a sketch rather than a final work: it is issued in a poorly known review, in Romanian, with a very brief German abstract devoid of lithologic logs. Neither in the text nor the provided figure (i.e., fig. 1) are the disconformities not mentioned at all, whereas the thicknesses of the formations are missing. Probably it was just a preliminary signal of a more extended work that the author intended to complete, but it was never achieved due to his unexpected and sudden death. Despite all these weaknesses, this stratigraphy is in use, *faute de mieux*.

Mészáros (1960: abb. 2) interpreted the Paleogene sedimentary rocks as patches lying over a metamorphic basement belonging to the Făgăraș Mountains, resulted from the erosion that razed the majority of the Paleogene lithologic evidence of the sedimentary basin from southern Transylvania. He mapped the largest outcrops on the left and right banks of Satului Valley. Another smaller patch is crossed by Nișului Valley, and the other three restricted patches occur eastward. Later, a more complex tectonic pattern was sketched, with at least one of the Paleogene patches, cropping out in Valea Caselor (Mészáros & Ianoliu 1971), as bounded by faults. Unfortunately, the illustrated cross-section is not completed by a geological map, and on the drawn panorama of the locality, only the Nișului and Satului valleys are marked (we may think that Valea Caselor Valley could be nothing than a synonym of Valea Satului Valley). As the previous geologists noticed, the Paleogene deposits from the southern Transylvanian margin expose different facies than the ones from the north-western side of the Transylvanian basin. Former geologists such as Popescu-Voitești (1936) observed these differences and presumed different paleogeographic provinces on one side or the other of the Carpathians. Later, Bombiță (1963) rejected this pattern and mentioned the existence of trans-Carpathian Paleogene seaways. Their paleogeography is difficult to reconstruct due to subsequent erosion that razed these rocks, but their former existence can hardly be denied.

Material and methods

The material analyzed in the present work is part of the paleontological collection hosted by the Natural History Museum in Sibiu. The fossil teeth (including sharks and crocodilians) from the actual Natural Sciences section of the Brukenthal Museum had a long and convoluted history. The collections of the former

Transylvanian Society of Natural Sciences (Siebenbürgischer Verein für Naturwissenschaften), established in 1848 by the German ethnics from Sibiu (= Hermannstadt) led by Michael Bielz, moved very many times from one place to another until a specially intended building designed by C. W. Fr. Maetz was erected (Petranu 1922). In 1866, the Society bought the Michael Ackner collection of minerals and fossils. In this collection, it is known that fossil shark teeth were present, all originating from Turnu Roșu ("Portsesd") (Ackner 1850). In the list of fish taxa, he wrongly inserted the sirenian "*Halyanassa* von Meyer. Rippenstücke" but also the Triassic "*Placodus Andriani. Münst.*", "*Nothosaurus Bronnii. Münst.*" as well as "*N. mirabilis*". Obviously, these are wrong systematic allocations as long as Triassic deposits are missing from Turnu Roșu locality. One can presume that crocodile teeth could have been present among the remains he considered to belong to "*Megalosaurus* Bucklandi. Mant. daselbst. (Zähne)", to "*Mastodonsaurus* Jaegeri. v. Meyer. daselbst. (Zähne)" or to "*Ichthyosaurus communis* Bronn. daselbst." (Ackner 1850: 174). The list is poor in details: the author just mentioned the taxa, the locality of origin, and if there were teeth or bones.

Other sources for the vertebrate teeth from Turnu Roșu were Samuel von Brukenthal, M. Bielz, and L. J. Neugeboren's collections. Neugeboren used some of these fossils for his work on the fossil sharks issued in 1850 and 1851 but already prepared in 1848 (Neugeboren 1850, 1851, Ciobanu 1996). He described 63 species of eight genera, of which 19 were new to science (Ciobanu 2002).

The crocodilian specimens under inventory numbers 8418-8420, 9287, 9344, 9345, and 31708 are part of the old core collection of the museum (Fig. 2O), the Society Collection (gathered by the founders of the museum, mostly before the year 1900). The other specimens, under the inventory numbers 35124-35137, 35141, and 35149 are part of the Richard Brekner collection. As far as we know, this collection was gathered around 1934. No details are known regarding the collection outcrop of any specimens other than that they were gathered in the Turnu Roșu locality.

The teeth were photographed using a Nikon D5300 camera equipped with a Sigma 105 mm lens. The details of the teeth were photographed using a Nikon 7000 camera mounted on a Nikon SMZ 1000 binocular microscope. To achieve maximum clarity, a focus stacking technique was used with the help of the CombineZP software.

Results

Systematic paleontology

Class Reptilia LAURENTI, 1768

Eusuchia HUXLEY, 1875 sensu BROCHU 2003

Crocodylia GMELIN, 1789 sensu BENTON & CLARK 1988

Gavialoidea (HAY, 1930)

Gavialoidea includes *Gavialis gangeticus*, and all crocodilians more closely related to it than to *Alligator mississippiensis* and *Crocodylus niloticus* (Norell et al. 1994, Brochu 2003, Sues 2019, Rio & Mannion 2021).

Gavialoidea indet.

Referred material: 21 isolated teeth that may have belonged to individuals provided with heterodont dentition of at least five different morphotypes (see below).

The isolated teeth may have belonged to individuals of different sizes and ages. In all the specimens, the tooth root is not preserved. The tooth crown displays various degrees of abrasion marks, probably as a consequence of water transport; frequently, various parts of the crown enamel are missing. Nevertheless, in most of the specimens, the tooth crown still preserves important details of the tooth

morphology, as follows: the mesiodistal carinae are well-defined without denticles and extensive, usually reaching the base of the tooth crown; the margins of the carinae are smooth and more or less sharp, due to presence of wide and deep crenulations extending parallel to the margins of carinae. However, the carinae are enforced at their base by wrinkles derived from the apicobasal ridges that extend close to the tooth margins resulting in a superficially ziphodont or pseudoziphodont appearance; both the lingual and labial surfaces of the crown bear numerous apicobasal ridges (at least ten or higher) that are of much lower height than the mesiodistal carinae; the apicobasal ridges, if preserved, never extend onto the apical region; instead, a network of irregular and anastomosing short ridges is exposed there.

Variations in the tooth morphology allow differentiations of the following morphotypes: A) includes slender caniniform teeth that are slightly curved lingually and compressed labiolingually; B) includes triangular lanceolate teeth that are compressed labiolingually; C) includes enlarged conical teeth that are slightly compressed labiolingually; D) includes slender conical teeth that are pointed apically, recurved posteriorly and with subcircular crown base; E) includes low crowned teeth with their base wider than the crown height and compressed slightly

labiolingually.

Morphotype A (Fig. 2). The crown of this morphotype is slender and about 2.5 higher than the widest point of its mesiodistal width (Fig. 2A-C). Apparently, there is no constriction present at the crown base. The stem is gently curved posteriorly and lingually and widening basally; the lingual surface is more flattened than the labial side resulting in an asymmetrical placement of the mesiodistal carinae (Fig. 2E, L). The latter structures are sharp, prominent, and smooth; in some specimens, rare wrinkles are present on both sides of the carinae (Fig. 2G, J). On both sides of the crown surface, about ten apicobasal ridges are exposed. As none of the specimens preserve the apical margin, we could only state that the ridges extend up to the close vicinity of the apical region (Fig. 2A-C). The ridges possess more or less smooth margins and are bordered by shallow crenulations. The pulp cavity is relatively large at the base of the crown (Fig. 2D, E); however, it becomes constricted on the upper half of the stem, being reduced to a small foramen (Fig. 2L, M). The transversal or longitudinal cracks present in some of the specimens (Fig. 2L, M) display a large number of growing lines. Nevertheless, some blackish lines (e.g., Fig. 2L) may correspond to lines of arrested growths, suggesting that the tooth-growing process was not perfectly continuous.

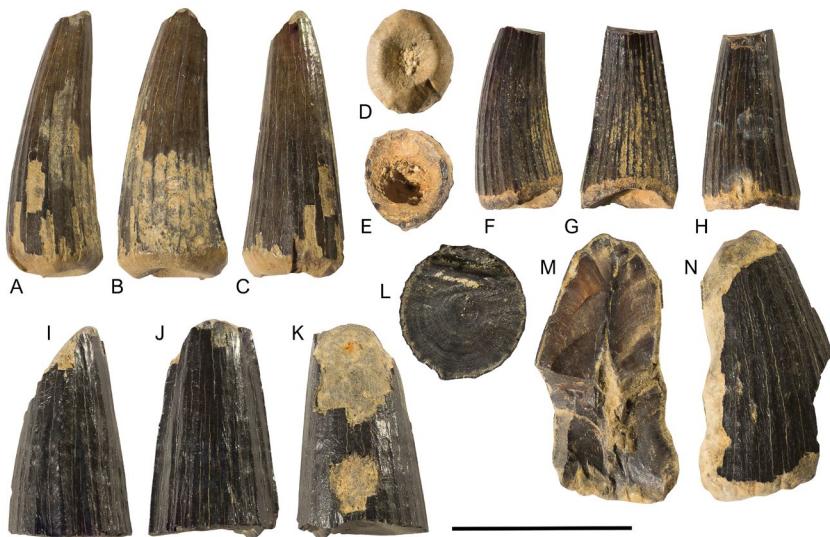


Figure 2. Gavialoid teeth (morphotype A) from Turnu Roșu fossil locality. Isolated specimens no. 8420 (A-D), no. 35134 (E-H), no. 35128 (I-L) and no. 35133 (M, N).
 A, F, I - mesial,
 B, G, J - lingual,
 C - distal,
 D, E, L - ventral,
 H, K, N - labial,
 M - longitudinal section views.
 Scale bar = 5 mm.

Morphotype B (Figs. 3, 4). The crown of this morphotype has an elongated triangle or lanceolate shape and labiolingually compressed (Fig. 3A-B); its height is distinctly higher than the mesiodistal width at the crown base. The mesiodistal carinae are long, prominent, and with numerous denticle-like wrinkles that reinforce the edge of the carinae (Fig. 3B-H, 4A-B, 4D-E). The apicobasal ridges extend on the lower two-thirds of the crown surfaces, delimited by crenulations, whereas on the upper third, the labial and lingual surfaces are covered by a network of low, anastomosing ridges reaching the top of the apical region. In some of the specimens (e.g., Fig. 3I, K, L; 4G, I), the enamel-free surfaces of the dentin still preserve the imprints of the apicobasal ridges. In ventral view, similarly to morphotype A, the labiolingual compression appears asymmetrical (Fig.

3G, J; 4F, J).

Morphotype C (Fig. 5). A single specimen is available for study. It is about three to four times larger than the other specimens from the collection. The crown is distinctly higher than the width of its base; both the lingual and labial surfaces are strongly convex; a considerable part is devoid of enamel covering. The mesiodistal carinae are present; however, these are comparably of lower height than those seen in morphotypes A and B (Fig. 5A-C). The apicobasal ridges are also less prominent, the crenulations are rather shallow, and there is a network of longitudinal striations that cover both the labial and lingual surfaces where the enamel is still conserved (Fig. 5D). In ventral view, the shape of the tooth-crown is subcircular; however, it is somewhat wider mesiodistally than labiolingually (Fig. 5E).

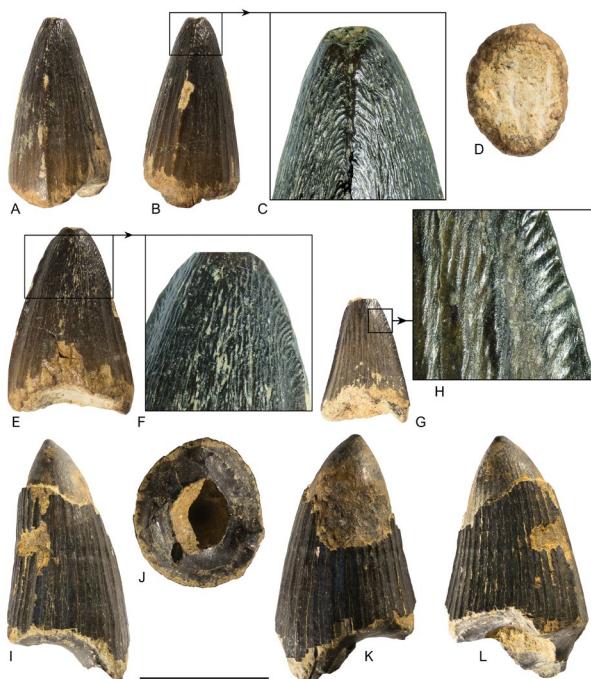


Figure 3. Gavialoid teeth (morphotype B) from Turnu Roșu fossil locality. Isolated specimens no. 8418 (A-F), no. 35140 (G, H), and no. 35126 (I-L). A, K - mesial, B, I - distal, E, G, L - lingual, D, J - ventral views; C, F, and H details (magnification not to scale). Scale bar = 5 mm.

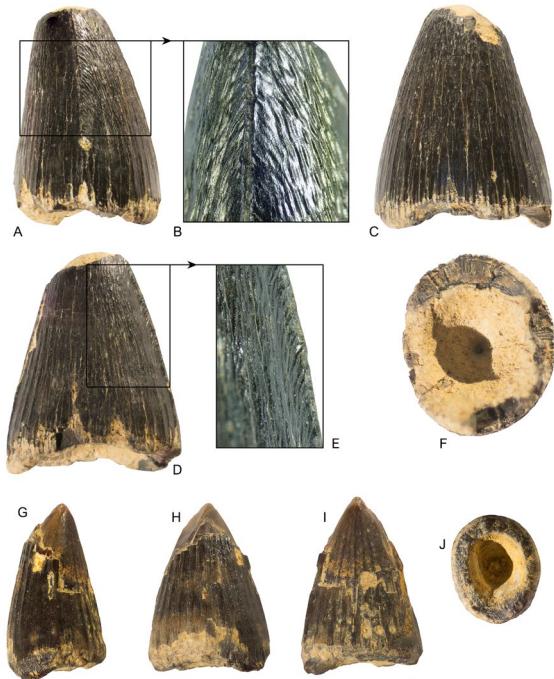


Figure 4. Gavialoid teeth (morphotype B) from Turnu Roșu fossil locality. Isolated specimens no. 35125 (A-F) and no. 8419 (G-J). A - mesial, G - distal, D and I - lingual, C and H labial, F and J - ventral views; B and E details (magnification not to scale). Scale bar = 5 mm.

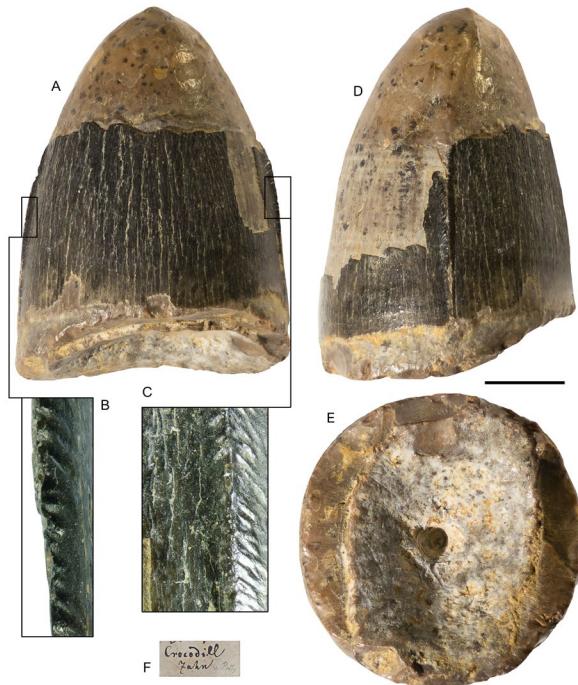


Figure 5. Gavialoid tooth (morphotype C) from Turnu Roșu fossil locality (no. 31708) (A-E); F - original ticket of specimen no. 31708. A - lingual, D - ?mesial, E - ventral views; B and C details (magnification not to scale). Scale bar = 5 mm.

Morphotype D (Figs. 6, 7). This morphotype includes slender conical, apically pointed, and strongly curved tooth crowns. The available specimens are devoid of enamel, except their apical region, that still preserves a striated cap with enamel cover. The dentin still preserves the circular growing lines, which are sometimes of different colour (Fig. 6A, B, E; 7A, B). Some longitudinal lines seen on the dentine

surface (Fig. 7C) may represent the imprints of the apicobasal ridges. In ventral view, the base of the crown is more or less circular (6D, 7D).

Morphotype E (Fig. 8). A single specimen of this morphotype has been identified in the collection. The tooth-crown base is distinctly wider than its height. The mesiodistal carinae are present; these are of relatively low

height and strengthened by numerous denticle-like structures (Fig. 8A-C, E-G). The apicobasal ridges are well-defined and numerous (about 18-20 ridges on both the lingual and labial sides), delimited by deep and narrow crenulations; the upper side of the crown is devoid of enamel. In ventral view, the labiolingual compression appears asymmetrical; the labial side is more convex than the lingual side (Fig. 8D).

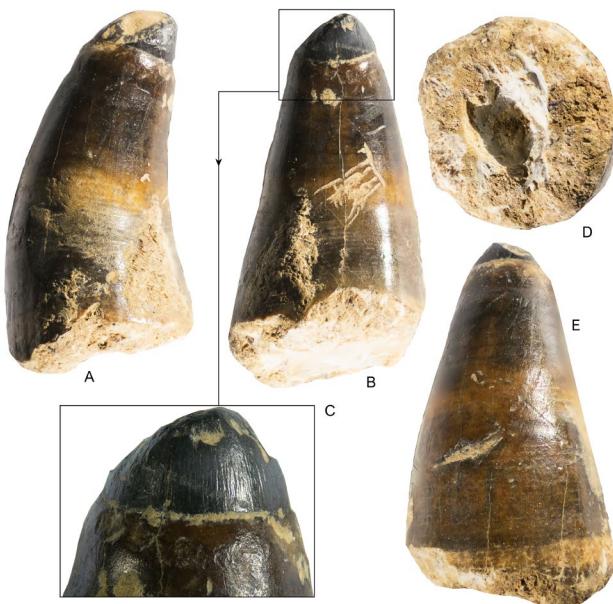


Figure 6. Gavialoid tooth (morphotype D) from Turnu Roșu fossil locality (no. 9344). A – lateral, B – distal, C – mesial, D – ventral, E – detail (magnification not to scale). Scale bar = 5 mm.



Figure 7. Gavialoid tooth (morphotype D) from Turnu Roșu fossil locality (no. 9345). A – lateral, B – distal, C – mesial, D – ventral views; C detail (magnification not to scale). Scale bar = 5 mm.

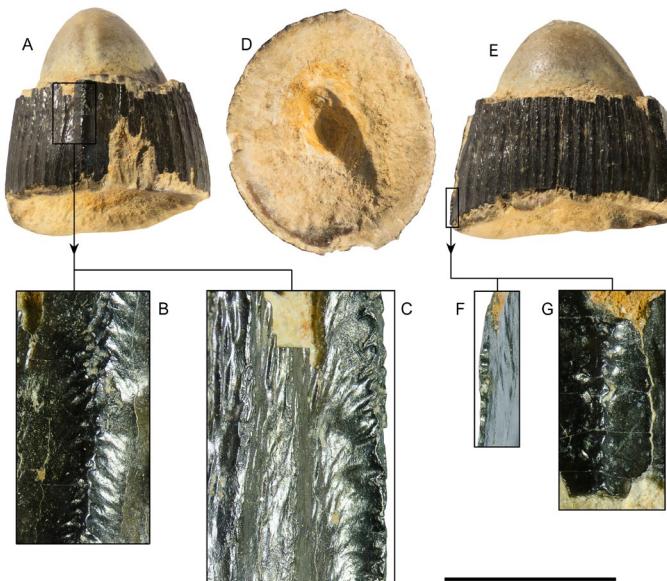


Figure 8. Gavialoid tooth (morphotype E) from Turnu Roșu fossil locality (no. 35124). A – mesial, B – ventral, C – lingual views; D, E, F and G details (magnification not to scale). Scale bar = 5 mm.

Discussion

The teeth recovered from the Eocene of Turnu Roșu (Porțești), Romania, may have belonged to several individuals of different sizes and ages, provided with heterodont dentition. The specimens of the identified morphotypes are comparable to those of various gavialoid crocodilians (including 'Tomistominae') known from the Paleogene of Europe, North America, North Africa, and Asia (e.g., Brochu 2006, 2007, Piras et al. 2007, Zvonok & Skutskas 2011, Jouve et al. 2014, 2019, Martin et al. 2019, Zoboli et al. 2019, Kuzmin & Zvonok 2021, Massonne et al. 2021).

Morphotype A, that includes slender caniniform teeth (Fig. 2), is reminiscent of the anterior maxillary and mandibular teeth of *Dollosuchoides* from the early-middle Eocene Bracklesham Group of southern England (Brochu 2007: text. figs 3-5), that are also slender, slightly recurved, provided with mesiodistal carinae and longitudinal ridges. These characters are best seen in the right dentary of the BMNH 26125 specimen, formerly part of the type and referred material of *Dollosuchus dixoni* Owen, 1849 (Brochu 2007: text. fig. 5B), currently a synonym of *Dollosuchoides densmorei* (Brochu 2007). The caniniform teeth from Turnu Roșu further resemble those of *Megadontosuchus arduini* (de Zigno, 1880), known from the middle Eocene of Italy (Piras et al. 2007) and those of *Marccosuchus zennaroii* Jonet & Wouters, 1977, from the early Eocene (Ypresian) of Ouled Abdoun Basin, Morocco (Jouve et al. 2014), in having posteriorly curved tooth-crowns with longitudinal ridges and crenulations; however, in these latter forms, the caniniform teeth appears more robust and significantly larger. *Eosuchus lerichei* Dollo, 1907, is known from the late Paleocene of northern France, whereas *E. minor* (Marsh, 1870) was recorded from the late Paleocene or early Eocene of New Jersey, North America, both collected from deposits representing marginal marine settings (Brochu 2006). Several anterior teeth in the maxilla and dentary (e.g., see Brochu 2006: fig. 10: 1 and 2 from *E. minor* and fig. 13 for *E. lerichei*) of the above forms share a number of characters with those of the morphotype A from Turnu Roșu, as it follows: the tooth-crown is slender, curved posteriorly, pointed apically, and bearing mesiodistal carinae and apicobasally extending ridges; the base of the tooth-crown is not constricted. A gavialoid crocodilian, reported as 'Tomistominae indet.' from the middle Eocene of Ikovo, Ukraine (Zvonok & Skutskas 2011, Kuzmin & Zvonok 2021), consists of a partial mandible (right dentary with four preserved teeth) and an isolated second mandibular tooth. Similarly to morphotype A from Turnu Roșu, the Ikovo gavialoid also possesses gently curved tooth-crowns with dorsoventrally extending ridges and crenulations. The latter character is also shared with *Maomingosuchus acutirostris*, known from the late Eocene (late Bartonian-Priabonian) of the Na Duong coal mine in northern Vietnam (Massonne et al. 2021).

The elongated triangle - lanceolate shaped tooth-crowns of morphotype B specimens from Turnu Roșu are also recognizable in some of the above Eocene taxa, like those of *Marccosuchus zennaroii* in having well-defined apicobasally aligned ridges that reach up to the two-thirds of the crown height, whereas the apex is heavily ornamented with coarse, dense and irregular wrinkles (Jouve et al. 2014). In some

teeth of *M. zennaroii*, similar to morphotype B, the mesiodistal carinae are ornamented with wrinkles perpendicular to the carinae and bear false serrations, producing the false-ziphodont appearance (Jouve et al. 2014). A somewhat similar morphology is preserved on the isolated tooth of the Crocodylia indet. from the early Eocene (Ypresian) of Escalaplano, southern Sardinia, Italy (Zoboli et al. 2019: fig. 2A), on that of *Maomingosuchus* sp. from the late Eocene-early Oligocene of Krabi, Thailand (Martin et al. 2019: fig. 3A), and possibly on the posterior mandibular teeth of *Dollosuchoides densmorei* (Brochu 2007: fig. 4).

The only specimen of morphotype C may correspond in size and morphology to those preserved in some of the gavialoids with enlarged teeth, like *Megadontosuchus arduini* (de Zigno, 1880) (Piras et al. 2007), *Marccosuchus zennaroii*, in which the 5th maxillary and the 11th mandibular teeth are enlarged (Jouve 2014), or *Maomingosuchus acutirostris*, in which the 5th maxillary and the 11th and 12th mandibular teeth are enlarged (Massonne et al. 2021).

Morphotype D may correspond to one of the posteriormost maxillary tooth positions, whereas morphotype E, displaying a strongly backward curved apical region and subcircular shape, is reminiscent of the 4th dentary tooth seen in *Maomingosuchus acutirostris* (Massonne et al. 2021: fig. 2).

Compared to the isolated teeth of other crocodilian groups recorded from the Paleogene of Romania (i.e., Diplocynodontidae and Planocraniidae), the gavialoid teeth may be differentiated from those of the other groups by possession of two or three diagnostic characters, as follows: the tooth-crown of Diplocynodontidae is provided with smooth apicobasal carinae and with faint striations on the labiolingual surfaces, and it possesses a small constriction separating the tooth-crown and the root (Rio et al. 2019); the isolated teeth of Planocraniidae, recorded from the late Palaeocene (Thanetian) of Jibou, possess labiolingually compressed tooth crowns bearing finely serrated crests and small constrictions at the base of tooth-crowns (Venczel et al. 2021). The teeth of Sebecosuchia, another crocodilian group present in the Paleogene of Europe, should be excluded from the potential components of Turnu Roșu crocodilian fauna because the mesiodistal carinae of that group display the true ziphodont condition (e.g., see Dalla Vecchia & Cau 2011: fig. 7).

The fossil record of gavialoids from Turnu Roșu represents a new group of crocodilians for the Paleogene fauna of Romania; however, apparently, the group did not reach the Paleogene sedimentary areas from northern Transylvania (i.e., Gilău, Meseș or Preluca sedimentary basins) and probably disappeared from southern Transylvania shortly after the middle Eocene (see below). A challenging argument to answer this question is linked to the fact that the source of origin of the gavialoid specimens in the Turnu Roșu area is still unknown. We may only presume that the fossil record of gavialoids from Turnu Roșu could represent the northernmost point of distribution in Romania for this thermophilous group of reptiles, and the stratigraphic extent of their distribution possibly did not reach the level of the Bartonian. It is known that during the Bartonian - Priabonian interval, the fossil record of gavialoids (other representatives than 'tomistomine') was

limited to North Africa (Agrasar 2004, Jouve et al. 2019), while that of 'tomistomine' was restricted during the Bartonian to southern Europe (Italy and France) (Piras et al. 2007, Jouve 2016). Nevertheless, the late Eocene (Priabonian) shallow marine deposits from the Gilău sedimentary area (Cluj-Mănăstur and Leghia localities) have yielded a number of diplocynodontid remains (Sabău et al. 2021, Venczel & Codrea 2022), representing the only crocodilian group that has survived successfully the Eocene-Oligocene transition (Codrea & Venczel 2020, Massonne & Böhme 2022), supposedly because of its increased cold tolerance (Martin 2010, Jouve et al. 2019).

Considering that western Tethys may have played an important role in the early evolutionary history of gavialoids (Jouve et al. 2014, Jouve 2016), the potential origin of the Turnu Roșu gavialoids is from Western European territories or directly from North Africa. The first possibility could have been linked to the geographic distribution of the early diverging clade of gavialoids outside Gavialidae that included *Maroccosuchus*, *Dollosuchoides*, and *Kentisuchus* (see Rio & Mannion 2021: figs. 22, 23). As we have discussed above, the isolated gavialoid teeth from Turnu Roșu share a number of features reminiscent to both *Maroccosuchus* and *Dollosuchoides*. Therefore, we may presume that a closely related representative of that clade may have extended its range of distribution from western Europe into the southern Transylvanian territory and further into more eastern European territories, as that of Ikovo locality from Ukraine (Zvonok & Skutskas 2011, Kuzmin & Zvonok 2021). The second scenario may have also started from North Africa from a *Maroccosuchus*-like ancestor that could have migrated directly into southern Transylvania, along the intervening dry lands, and across the remnants of the Tethys Ocean. Nevertheless, to sustain consistently, in geologic time and space, one of these scenarios, further details of stratigraphic data and a series of better-preserved fossils are needed.

Conclusions

We assigned the collection of isolated crocodilian teeth from Turnu Roșu to Gavialoidea, a group recorded for the first time from the Paleogene of Romania. The isolated teeth were recovered from shallow marine deposits that may be correlated with the middle Eocene. The identified morphotypes share a number of morphological characters with representatives of early gavialoids (e.g., *Dollosuchoides*, *Megadontosuchus*, *Maroccosuchus*), known from the early-middle Eocene of western Europe or North Africa. Two possible scenarios for the origin of the southern Transylvanian gavialoids were the existence of a western-eastern European route or a migration route direct from North Africa. The starting point for both scenarios probably was represented by the western Tethys that could have played an important role in the early evolutionary history of early gavialoids.

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