Late Cretaceous crocodilian diversity in Haţeg Basin, Romania

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Abstract — The rich and diverse Maastrichtian continental vertebrate fauna from the Haţeg Basin, Romania, included until recently only one crocodilian taxon (*Allodaposuchus precedens*), along which other taxa were also cited in the last decade (*Doratodon*, *Acynodon*, *Musturzabalsuchus*). This assemblage is noteworthy since it includes taxa with a wide European distribution, unlike the mainly endemic dinosaurs and mammals. In the past few years a large number of crocodilian remains were recovered from the Haţeg Basin. The preliminary survey of this material suggests the crocodilian assemblage includes, besides *Allodaposuchus*, ziphosuchians (*Doratodon* and a new heterodont taxon) and eusuchians (cf. *Acynodon* and an indeterminate eusuchian), demonstrating widely divergent ecological adaptations within the group. The new taxa seem to confirm the largely endemic character of the Haţeg fauna.

Keywords — Late Cretaceous, Haţeg Basin, Crocodylomorpha, diversity

Introduction

Crocodilians are common components of the Late Mesozoic continental faunas, their local diversity usually surpassing that seen in Modern ecosystems. Although less well known than those from North America, South America and Africa, a relatively diverse crocodilian assemblage is also documented in the Late Cretaceous Western European faunas (see Buscalioni et al, 1999), several different taxa being reported to co-occur at different localities (e.g. Buscalioni et al., 1999; Company et al., 2005; Martin & Buffetaut, 2005).

The Late Cretaceous (Maastrichtian) vertebrate assemblage from the Haţeg Basin was, on the contrary, rather unusual in that it was for a long time known to include just one crocodilian taxon, described by Nopcsa (1915) as *Crocodylus affuvelensis*, later referred to as *Allodaposuchus precedens* (Nopcsa, 1928). *Allodaposuchus* was recently revised by Buscalioni et al. (2001); their phylogenetic analysis proposed this taxon as the sister group of the Crocodylia.

Only recently the presence of another taxon (cf. *Doratodon*) was suggested based on isolated teeth (Grigorescu et al., 1999). Two further taxa (*Acynodon* sp. and *Musturzabalsuchus* sp.) were listed by Jianu & Boekschoten (1999), but these authors did not substantiated their claim, and no further reference was made of the presence of these taxa, nor was any material explicitely referred to them.

The largest part of southern and central Europe was an archipelago during the Late Cretaceous, leading to development of local endemic faunas, as evidenced in Haţeg by the dinosaurian and mammal assemblages. Interestingly, the above-mentioned crocodylian assemblage appears rather unusual in that it includes taxa known also from other Late Cretaceous European sites, while all other vertebrates described at a lower taxonomic level (frogs, chelonians, pterosaurs, dinosaurs, mammals) seem to be endemic to the Transylvanian area to which Haţeg belonged. *Allodaposuchus* was present in the Campanian-Maastrichtian of France and Spain (Buscalioni et al., 2001, Martin & Buffetaut, 2005). *Doratodon* was first described from the Lower Campanian of Austria (Bunzel, 1871, Buffetaut, 1979), and was recently also cited from the Campanian of Spain (Company et al., 2005). Finally, both *Acynodon* and *Musturzabalsuchus* are reported from different Campano-Maastrichtian localities of Spain and southern France (Buscalioni et al., 1997, 1999; Company et al., 2005; Martin & Buffetaut, 2005).

Recent fieldwork across the Haţeg Basin, employing especially microvertebrate fossil extraction through screenwashing, has yielded a wealth of new material referable to crocodilians. These are often represented by fragmentary isolated remains (especially teeth) and since teeth alone are not diagnostic, it is difficult to appreciate the diversity. However, the material at hand seems to document a larger diversity than previously thought, also revealing that crocodilians occupied a wide range of ecological niches.

The following report is a preliminary attempt to identify fragmentary remains representative of the known crocodilian diversity from the Haţeg Basin. Next, a comparison will be made with other crocodilians from Late Cretaceous localities in northern Spain and southern France.

The discovery of new European taxa can challenge established hypotheses concerning distri-

bution or origins of crocodilian groups such as Eusuchia (Brochu, 1999) or Mesosuchia (Pol, 2003), also contributing to a better understanding of paleobiogeographical relationships and dispersal dynamics between Laurasia and Gondwana during the Cretaceous (Rage, 2002).

Geological setting

The Late Cretaceous continental deposits of the Haţeg Basin consist of a thick pile of siliciclastic molasse-type deposits accumulated following the main thrusting phase and nappe emplacement of the Laramian orogenetic phase (Willingshofer et al., 2001). They consist of alternating sequences of conglomerates, sandstones and mudstones, outcropping in the northwestern and central part of the basin, and representing dominantly fluvial deposits formed in both channel belts and floodplains, the latter being places of recurrent episodes of pedogenesis. Although the age of the deposits is poorly constrained, available data suggest they are Maastrichtian in age (Grigorescu & Csiki, 2002). Sedimentological, geochemical and clay mineralogy studies suggest a seasonally dry, subhumid warm climate (Therrien, 2005; Bojar et al., 2005).

A rich fossil assemblage, including plants, invertebrates and vertebrates was recovered from the Maastrichtian continental deposits (see Grigorescu, 2005, for a review); vertebrates are represented by fishes, frogs, albanerpetontids, turtles, lizards, snakes, crocodilians, diverse dinosaurs (including birds) and mammals. Crocodilian remains are abundant and widespread in these deposits, being recovered from channel, floodplain and pond deposits, but are represented mainly by isolated teeth or dermal scutes.

Institutional abbreviations — FGGUB: Paleontology Collection, Faculty of Geology and Geophysics, University of Bucharest

Crocodylomorpha Walker, 1970 (sensu Benton and Clark, 1988)
Ziphosuchia Ortega et al., 2000
Doratodon sp.

Described material — isolated teeth (FGGUB R.1937, R.1939, several uncatalogued specimens from Fântânele, FGGUB R.1990, R.1991, several uncatalogued specimens, Pui microvertebrate fossil site, see Grigorescu et al., 1985) (Pl. 1, figs. 1-4).

Description — The isolated teeth were recovered by sieving and preserve only the crown. The teeth are small to moderate in size; two types are present. The first one is more robust with a short, symmetrical triangular crown, whereas the second one shows a more elongate, asymmetrical crown, with the mesial margin more curved than the distal one and the apex pointing distally. The teeth are slightly labiolingually compressed with relatively large serrations on the mesial and distal edges. The base of the crown on the distal edge is depressed. The base of the mesial edge seems to have been continuous with the root. From a distal view, the serrations are not straight at the base of the crown but they are shifted either lingually or labially. Each denticle is well defined, but not symmetrical; the apex of each denticle points toward the apex of the tooth.

Discussion — The labiolingually compressed teeth with large serrations are reminiscent of the morphology described for Sebecosuchia (Company et al., 2005). While *Doratodon* does not belong to Sebecosuchia, it is considered basal to this group and lies within a larger group, the Ziphosuchia. These isolated ziphodont teeth confirm the presence of *Doratodon* in the Late Cretaceous of Romania, as previously suggested by Grigorescu et al. (1999). Here, the carinae are well preserved and display clear plication of the enamel and the dentine, which is characteristic of the genus. The variation of crown height may represent morphological variation along the tooth row. *Doratodon* is cosmopolitan within the Late Cretaceous European archipelago with occurrences in Spain (dentary; Company et al., 2005) and Austria (various skull and mandibular elements; Buffetaut, 1979) and now also from Romania.

Crocodylomorpha Walker, 1970 (sensu Benton and Clark, 1988)
Ziphosuchia Ortega et al., 2000
Gen et sp. indet.

Described material — A right maxilla (FGGUB R.1945) and one isolated tooth (FGGUB R.1987), both from the Fântânele microvertebrate fossil site (see Grigorescu et al., 1999) (Pl. 1, fig. 8).

Description — The anteriormost part is missing. The anteromedial border of the bone seems to preserve the sutural contact with the nasal. On the other hand, the remaining edges of the maxilla are all broken and cannot provide information on the sutural relationships with other bones. The dorsal surface of the bone is ornamented with fine pits less than 0.5 mm in diameter, densely covering the surface of the bone. Nine alveoli are preserved; there is possibly a tenth one, which seems broken. The

dorsal surface of the maxilla has a peculiar shape. The main body and the lateral border are almost flat. However, the most medial part of the bone, which contacts the nasal, extends vertically, giving a convex shape to the dorsal surface. The dorsal surface of the posterior maxillary ramus shows a smooth and slightly concave surface that seems to correspond to the margin of the antorbital fenestra. The ventral border of the maxilla is not even.

Four teeth are preserved in the specimen, documenting a clearly heterodont dentition. All the teeth are single-rooted and labiolingually compressed. Two major types of teeth are present. In the mesial portion of the maxilla, the teeth bear a cingulum at the base of the crown and terminate with a single pointed asymmetrical cusp. In the distal portion of the maxilla, the teeth have a platform-like morphology with a very short and concave crown. The single cusp is extremely reduced and is located in the centre of the cingulum. The transition from a single cusped morphology to a concave morphology is rapid and occurs abruptly between the sixth and seventh teeth position.

Some teeth recovered from the same site by screenwashing can tentatively be assigned to this crocodilian. Their shape recalls that of the apical part of the mesial maxillary teeth: they are labiolingually compressed and the distal edge is shorter than the mesial one. However, the cingulum is absent and instead, from this level, the outline of the tooth shows a depression in its distal part. The root is deflected mesially.

Discussion — The presence of an antorbital fenestra implies that the specimen is not eusuchian. Among crocodilians, teeth are not considered reliable characters because they are often similar in shape and no comprehensive study has been performed to underline the differences between taxa (Brochu, 1999). This is especially the case among eusuchians and other crocodyliforms with classical pointed teeth. However, notosuchians are unique in their heterodont dentition (although recently a heterodont eusuchian was also described from the Santonian of Hungary; Ősi, 2004). Pol (2003) emphasized that notosuchians have a diverse and bizarre dental morphology, strikingly different from all other known crocodyliforms, with clove-shaped and multicusped teeth in a single longitudinal row in *Simosuchus clarki* (Buckley et al., 2000), multicusped teeth with a high central cusp and small cusps on a cingulum in *Malawisuchus mwakasyungutiensis* (Clark et al., 1989; Gomani, 1997) or molariform maxillary teeth with three longitudinal rows in *Chimaerasuchus paradoxus* (Wu and Sues, 1996), respectively with short compressed maxillary tooth crowns disposed like reversed triangles in *Sphagesaurus huenei* (Pol, 2003). Moreover, recent cladistic analyses show that Notosuchia is a monophyletic group (Sereno et al., 2001, 2003; Pol, 2003), which is also referred to Ziphosuchia (Ortega et al., 2000). Therefore, based on dental morphology, it is suggested that FGGUB R.1945 belongs to the Ziphosuchia. Finally, The morphology of the teeth and their position along the tooth row are definitively unique to that specimen.

Crocodylomorpha Walker, 1970 (sensu Benton and Clark, 1988)
?Eusuchia indet.

Described material — A skull fragment including the occiput and partial skull table (FGGUB R.1781) and a right maxilla (FGGUB R.1782), found associated in the Tuştea nesting site (Pl. 1, fig. 9).

Description — The complete skull is rather small with an estimated length of 80 mm; of this, only the right maxilla will be described briefly here. It is 36 mm long as preserved. The anterior border is incomplete, but enough is preserved to visualize the connection with the premaxilla. The mesioventral margin of the maxilla slopes dorsally toward the mesial end of the bone and the size of the teeth decreases in the same direction, suggesting the presence of a deep notch between the premaxilla and maxilla. In dorso-lingual view the palatal wall of the maxilla shows two small foramina and the anterior border of the suborbital fenestra. The suture for the reception of the palatal wall of the left maxilla is present. It is thin and its orientation in a perpendicular plane permits to properly orient the maxilla. The mesial dorsal surface of the maxilla is not especially flat, but somehow elevated from the tooth row. Small pits cover completely the surface of the bone. The posterior ramus of the maxilla is straight and follows the lateral edge of the suborbital fenestra; the dorsal surface of the ramus is flat, medially sloping, corresponding to the surface for the jugal/lacrimal, The rostral margin of the suborbital fenestra reaches the level of the seventh or sixth maxillary tooth. The dentition is very peculiar. 11 alveoli are present; some others may have been present distally. The first three alveoli are rather small with a diameter of 1.6 mm; the third preserves a small conical tooth. The 5th maxillary tooth is the largest and is of the type described for *A. precedens*, but apparently somewhat more slender. The base of the crown is constricted, the crown is quite elongate with carinae occurring

lingual to the mesiodistal plane. One of the most striking features of the dentition concerns the morphological transition between the 5th, conical maxillary tooth (the 6th is not preserved) and the posterior series. These teeth (preserved in the 7th, 8th and 10th alveoli) are labiolingually compressed with a short, leaf-shaped, pointed crown and constriction between the crown and the root.

Discussion — None of these characters match the revised diagnosis of *Allodaposuchus* (Buscalioni et al., 2001). The suborbital fenestra does not reach the fourth maxillary tooth, the distal wall of the maxilla is not vertical, no smooth surface is present dorsal to the tooth row, the intra-alveolar wall is rather thin, and instead of gradual decrease in alveolar diameter there is an abrupt change behind the 5th or 6th alveolus. The mesial end of the maxilla is not especially flattened.

The small size of the specimen makes its attribution to a juvenile highly probable. The distal dentition is very similar to some small isolated teeth from Cruzy attributed to an unidentified alligatoroid (Martin & Buffetaut, 2005).

Crocodylomorpha Walker, 1970 (sensu Benton and Clark, 1988)
cf. Alligatoroidea
cf. *Acynodon*

Described material — isolated teeth (FGGUB R. 1935, R.1936, R.1988, 1989), from the Fântânele microvertebrate fossil site (see Grigorescu et al., 1999) (Pl.1, figs. 5-7).

Description — Only isolated teeth recovered by sieving are known. The root is missing. The base of the crown is slightly constricted. The overall morphology reminds that of premaxillary and anterior maxillary teeth of *Acynodon*. The crown is short, the tooth is somewhat globular in occlusal view, the lingual base is bulbous and is demarcated from the spatulate apex whereas the labial edge is continuous from the base to the tip. The size is also comparable to that of *Acynodon* teeth. The major difference occurs on the labial surface, which displays two pronounced apicobasal grooves. These constrict the surface in three portions, the middle one being the largest. Secondly, a vertical and flat flange marks the mesial or distal edge of the tooth. This flange is straight from the base to the largely rounded end, which occurs between one-third and two-thirds of the crown height. In some higher and more pointed specimens (R.1989), the labial grooves are almost indistinct, and the flange is short, weakly developed; these probably represent more anterior tooth positions. Two shallow grooves are also present on the lingual surface. Wear facets occur on the spatulate tip, but also on the lingual edge of the vertical flange.

Discussion — The isolated teeth compare quite well with those of *Acynodon*. However, the pronounced labial grooves and the vertical flange are observed in several isolated teeth and probably do not represent an artefact of preservation. This morphology is unique. These teeth provide evidence of a specialized and maybe short-snouted alligatoroid in the Haţeg ecosystem. The presence of wear facets on the flange suggests an even more extreme feeding specialization than in *Acynodon* known from southwestern Europe.

Two species of *Acynodon* were originally reported from Spain: *A. iberoccitanicus*, now recognized from various skull material and *A. lopezi*, based only on isolated teeth. None of the reported species corresponds to the Romanian teeth. *A. lopezi* is unique in displaying longitudinal grooves on the lingual surface (Buscalioni et al., 1997). The ornamentation on *A. iberoccitanicus* is very light, with a set of very shallow grooves on the labial surface.

Paleobiogeographic affinities

Eusuchian crocodilians appear to be widespread throughout the European continental Late Cretaceous. The genus *Allodaposuchus* is mentioned from Romania, northern Spain and southern France (Buscalioni et al., 2001). Eusuchia of uncertain affinities are also present at various localities and are exemplified in Haţeg by a maxilla and a skull fragment. Labiolingually compressed rear dentition is found among derived alligatorids such as *Alligator* or the Caimaninae (Brochu, 2004), but relying on this character alone is not sufficient to diagnose an alligatorid. Moreover, the earliest recognized alligatorids are from the Paleocene of North America, and they are present in Europe in the Eocene. More derived members such as the Caimaninae are restricted to the Tertiary of South America; the first occurrence of the genus *Alligator* is from the Late Eocene of North America (Brochu, 2003). *Musturzabalsuchus*, a genus reported from northern Spain (Buscalioni et al., 1997) does not seem to be present in Romania, despite previous claims. *Acynodon* is known from various localities in northern Spain and southern France (Buscalioni et al., 1997; 1999). The *Acynodon*-like teeth from Haţeg may provide evidence for a separate evolutionary line of European alligatoroids, but more complete material is needed to test this hypothesis. Based on their presence in Romania, it is not excluded that

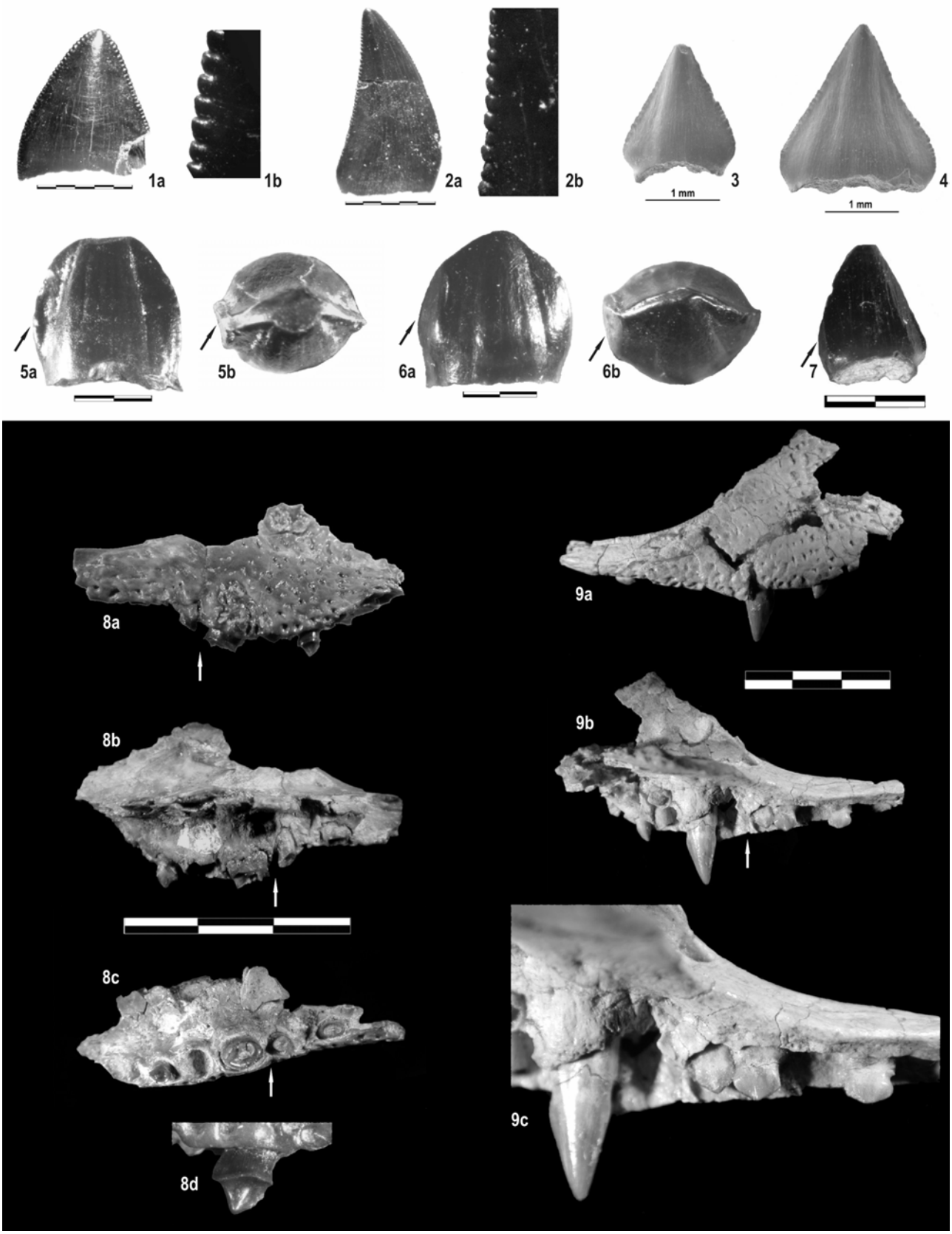

Plate 1 — Crocodilian remains from the Haţeg Basin. **1 – 4**. ***Doratodon* sp.**, isolated teeth. **1**. FGGUB R.1937 in **a** – labial view and **b** – close-up (x5) of distal denticles; **2**. FGGUB R.1939 in **a** – labial view and **b** – close-up (x7) of distal denticles; **3**. FGGUB R. 1991, lingual view; **4**. FGGUB R.1990, lingual view. **5 – 7. cf. *Acynodon***, isolated teeth. **5**. FGGUB R.1936 in **a** – lingual and **b** – occlusal view; **6** – FGGUB R.1935 in **a** – labial and **b** – occlusal view; **7** – FGGUB R.1989 in lingual view; arrows point to the lateral flange. **8**. **Ziphosuchia gen et sp. indet.**, right maxilla, FGGUB R.1945 in **a** – labial, **b** – lingual, **c** – palatal view, with **d** – close-up (x3) of 4th tooth; arrows point to the location of abrupt change in tooth size and morphology. **9. Eusuchia indet.**, right maxilla, FGGUB R.1782 in **a** – labial, **b** – lingual view, with **c** – close-up (x2) of the dentition; arrow point to the location of abrupt change in tooth size and morphology. **Scale bar**: 1 mm – figs. 1 -7; 5 mm – figs. 8, 9.

Acynodon or basal globidontans may turn out in other European Late Cretaceous localities as well.

The non-eusuchian crocodilians are represented in the Haţeg Basin by two ziphosuchians: *Doratodon* and the strange heterodont form. It can be confirmed that the genus *Doratodon* was present across Europe, where different Late Cretaceous species are reported from Spain (*D. ibericus*: Company et al., 2005) and from Austria (*D. carcharidens*: Buffetaut, 1979). Closely related ziphosuchians, the Baurusuchidae, are reported from the Late Cretaceous of South America and Pakistan (Carvalho et al., 2005), suggesting the cosmopolitan nature of these terrestrial forms. The second ziphosuchian is represented by a small heterodont form reminiscent of Early Cretaceous forms such as *Candidodon itapecuruensis* from South America (Nobre and Carvalho, 2002) or *Malawisuchus mwakasyungutiensis* from eastern Africa (Gomani, 1997). This taxon has never been reported from any other Late Cretaceous European localities and appears to be unique to the Haţeg fauna. Non-eusuchians crocodilians occupy an important position inside Late Cretaceous European ecosystems, but seem to differ between Western and Eastern Europe. The large trematochampsid *Ischyrochampsa* has not been reported from eastern European localities and seems restricted to southern France and northern Spain (Vasse, 1997; Buscalioni et al., 1999), whereas the heterodont ziphosuchian is for the moment only reported from Eastern Europe.

Ecology

The crocodilian fauna was ecologically diversified and can be divided into two groups. Eusuchians with the classic crocodilian Bauplan such as *Allodaposuchus* and possible alligatoroids mostly occupied amphibious habitats. A probably short-snouted taxon with spatulate dentition and closely related to *Acynodon* filled a specialized niche. On the other hand, non-eusuchian crocodilians, represented exclusively by ziphosuchians, may correspond to terrestrially adapted forms (Gasparini et al., 1993; Gomani, 1997; Carvalho et al., 2005). Judging from its serrated dentition, *Doratodon* seems to have filled a predatory niche. Finally, the heterodont ziphosuchian shows molariform teeth with either a tall single lingual cusp rostrally or a platform-like rear dentition with a labiolingually compressed concave occlusal facet. This latter morphology may have been useful for blocking, securing and then crushing small-sized prey. As in mammals, teeth would serve different functions along the tooth row for food processing. An insectivorous diet was suggested for *Malawisuchus* (Clark et al., 1989), which bears a comparable dentition; the small size of the Haţeg specimen is consistent with this idea.

Conclusions

The preliminary study of the crocodilian remains from the Maastrichtian of the Haţeg Basin, Romania, shows these were more diverse than previously recognized. Besides *Allodaposuchus*, known since the time of the early studies of Nopcsa, several other taxa are present, including both derived eusuchians and more basal ziphosuchians. The ziphosuchians are represented by *Doratodon* and a second taxon with a peculiar, unique heterodont dentition, while eusuchians include cf. *Acynodon* and another, for the moment indeterminate, taxon. From these, *Allodaposuchus* and *Doratodon* are widespread, being reported from other European Senonian localities, but other members of the assemblage seem to be restricted to the Haţeg fauna, emphasizing its peculiar, endemic composition. The diversity of dental specializations recognized in the crocodilian assemblage suggests they filled several different ecological niches, playing an important role within the local ecosystem.

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