NYMPHAEA Folia naturae Bihariae	XLVIII	77 - 108	Oradea, 2021

Crocodylian remains from the late Paleocene of Jibou, Romania

Márton VENCZEL[1,2], Izabella SABĂU[1,], Vlad A. CODREA[1,3]*

[1] Laboratory of Paleotheriology and Quaternary Geology, Department of Geology, Faculty of Biology-Geology, Babeș-Bolyai University, 1 Kogălniceanu Street, Cluj-Napoca, 400084, Romania
[2] Department of Natural History, Țării Crișurilor Museum, 1/A Armatei Române, Oradea, 410087, Romania
[3]Department of Natural Sciences, Mureș County Museum, 24 Horea Street, Târgu Mureș, 540036, Romania
[*]Corresponding author. e-mail: sab.iza99@yahoo.com

Abstract. Here we report the presence of a planocraniid crocodyliform from the late Paleocene of Jibou (N-W Romania) representing one of the geologically earliest fossil records of this group from Europe. The recovered cranial and postcranial remains resulted probably from an attritional assemblage and may have belonged to a single planocraniid taxon. The morphological traits of this taxon (cf. *Boverisuchus*) include among others an interlocking occlusion in the premaxilla, a flat cranial table with upturned orbital margins, a large exposure of the supraoccipital on the dorsal skull table, procoelous presacral vertebrae, keeled paramedian osteoderms lacking an anterior process, and mediolaterally compressed teeth possessing fine and irregularly distributed serrations on the mesiodistal carinae of the tooth crowns. The planocraniid crocodyliforms identified from the Paleocene of Romania mark an important paleogeographic link between the Chinese, European and North American occurrences. The lacustrine taphonomic context in the Jibou fossil locality is suggested by the presence of strictly limnic ostracods and gastropods, as well as other freshwater preferring groups including teleostei fishes and dortokid turtles. The planocraniid crocodyliforms might have acted as top predators in these freshwater habitats.

Keywords: Crocodylia, Jibou, Paleocene, Planocraniidae, Romania.

Introduction

Crocodylomorpha, is a clade of pseudosuchian reptiles which also includes crocodiles, the only representatives of the clade that have survived to the present day. Their first occurrence (i.e., *Trialestes*) is known from the Late Triassic (Carnian) of Argentina (Irmis et al. 2013; Sues, 2019). The first representatives were of moderate size, reaching lengths of maximum 2.5 m (Nesbitt, 2011), being by far smaller than the subsequent Mesozoic dinosaur-eating crocodiles *Deinosuchus riograndensis* Colbert & Bird, 1954 (Brochu, 1999, 2003 and references therein; Cossette and Brochu, 2020) or *Sarcosuchus imperator* Broin & Taquet, 1966 (Sereno et al., 2001), both exceeding 10 m in length.

Throughout their evolution, crocodylomorphs reached various sizes, but from a morphological viewpoint they did not record major changes, actual representatives sharing similar physiognomies with their ancient forerunners. This is an illustrating example of conservatism tendencies in evolution. Crocodylomorph fossils were found in the Mesozoic and Cenozoic sedimentary deposits on nearly all continents, which constitutes proof of their worldwide distribution.

In Romania, knowledge regarding the paleontology of this group is still lacking. Evidence about the first stages of their evolution are missing both in this country, and in the neighboring ones. Triassic deposits are generally extremely scarce in vertebrate fossils, and the vertebrate localities (e.g., Lugașu de Sus, Peștiș in Bihor District; Agighiol, in Tulcea District) of this age yielded other groups of reptiles, but not crocodilians: placodonts, tanystropheids, notosaurs or ichthyosaurs (Simionescu, 1913; Jurcsák, 1982; Huza et al., 1987; Popa et al., 1992; Posmoșanu, 2008, 2013). Such a situation is predictable if we are considering the group's origin and evolution, since the Triassic rocks where the fossil vertebrates originated from are too old (Anisian) compared to the first occurrence of these reptiles, in the Late Triassic. A similar situation refers to areas situated nearby Western Romania, in Hungary, where systematically comparable Triassic reptiles were reported from younger deposits (Ladinian), in the Villány area (Segesdi and Ősi, 2021).

After the Triassic, the whole territory of present-day Romania has been covered by the Tethys Ocean, and the possibility to find fossil crocodiles is weak. Terrestrial sequences are extremely few, and are related to the early Cimmerian tectonic phase, but fossil vertebrate remains are missing in such deposits.

Therefore, the geologically oldest crocodile in Romania is the one reported from Săndulești, near Turda town, unearthed from the Săndulești Formation (late Oxfordian – early Beriassian). According to Dragastan et al. (1987), this limestone level is related to a carbonate platform, once located on the distal area of a shelf, nearby the continental slope. Probably, the platform recorded the emerging episodes of the late Cimmerian tectonic pulse (middle Jurassic – early Cretaceous), followed by karst genesis. However, the intensity of these processes was weaker in the Western Transylvanids (Săsăran, 2006) compared to the inner Dacids, considering this type of relief and the related accumulation of bauxites in the karst deposits (Ianovici et al. 1976; Cociuba, 2000). In the Early Cretaceous (Beriassian) of the area there was a Tethys Ocean archipelago where a lake system occurred under tectonic control, that is to say, a transition from marine (carbonate platform) to terrestrial environments took place. Săsăran (2006) interpreted the Cretaceous environments from Săndulești as related to a continental slope, nearby the shelf ridge, with Stramberk-type limestone with reefs erected by various organisms, microbialites included. The geological age specified by Săsăran is ”Upper Jurassic-Lower Cretaceous” (Săsăran, 2006: 41), without any other detail.

The crocodile from Săndulești was reported by Nițulescu (1936), former Prof. Ion Popescu-Voitești’s assistant at the geological University of Cluj, who noticed these fossils in an interwar collection once curated at the main office of the limestone quarry by someone named Gărduș. Nițulescu assigned these fossils (an isolate tooth and some rib fragments inside a limestone block, unprepared) to ”*Teleosaurus suprajurensis* Schlosser, 1881”, junior synonym of *Dakosaurus maximus* (Plieninger, 1846). Unfortunately, he did not illustrate these fossils, neither the crocodiles, nor the invertebrates stored in the same collection (corals, brachiopods, sea urchins, cephalopods, crustaceans) or the fish *Asterachantus ornatissimus* Agassiz, 1837 assigned based on a dentary plate of 36 mm in length vs. 16 mm width. If we exclude the rib fragments, the single piece on which the species assignation was based on, is a single isolated tooth. However, he did not describe useful characters for a correct assignation that would refer to the large size, the serrated margins of the tooth and its strong lateral compression, all diagnostic for this genus. In this situation, Nițulescu’s brief description remains problematic and should be kept in mind as such. A justified question concerns the level where the fossil originated from. The fossils from the old Săndulești collection resulted from fortuitous finds carried on by the quarry workers and the technical staff. Until Nițulescu’s paper, the single fossil vertebrates ever mentioned from this locality exclusively referred to fish teeth (*Sphaerodus maximus* Wagner, 1863) that Koch (1900) reported in his list of taxa.

If the assignation of this crocodile is however valid, it is important to say that there is extremely scarce data about the life and behavior of this crocodile, while it is rather unclear whether it was an exclusively marine, or a terrestrial animal that episodically intruded the marine realm, a presumed scenario that remains to be solved regarding other fossil crocodiles as well in Transylvania (e.g., Sabău et al., 2021). This crocodile was a large sized one, reaching 4.5 m in length (Fraas, 1902; Steel, 1973), being probably among the top predators of the ancient ecosystem. However, in the already mentioned context it is not possible to establish the origin level, and currently it is impossible to establish whether the invertebrates and the hybodont shark (which has concordant time span distribution with the crocodile) were found together with the crocodile remains in the same level, or originated from different ones, which would mean different ecosystems. Trying to estimate the geological age of the crocodile from Săndulești, it is very likely that it could originate from Upper Jurassic rocks. Săsăran's (2006) data for the new Săndulești limestone quarry could constitute the base for the credibility of this suposition.

The value of Nițulescu's contribution, even with its gaps, remains essential for the vertebrate paleontology of Romania, since he enriched the list of fossil taxa. Nonetheless, the Săndulești finds were of short fame among the contemporary paleontologists and geologists, even more so among the next generations. Nițulescu's paper was briefly mentioned by Rugonfalvi (1939), but it was completely ignored by the authors who made fossil vertebrate lists of taxa, such as Simionescu and Barbu (1943) or Macarovici and Turculeț (1982). On our turn, one of us (VAC) strived to retrieve these fossils, but seemingly the Săndulești collection was lost.

A very long time span completely devoid of data concerning crocodiles is between the Săndulești find and the following, geologically younger taxa. Newer materials originate only from the latest Cretaceous. The explanation for this lack of discoveries may be related to the specific paleogeography, with dominance of deep marine environments, where the terrestrial influences were either completely absent, or very faint. Evidence could however exist related to the mid-Cretaceous tectonic pulse (”Austrian”), but crocodiles of this age are lacking from the fossil record.

From the latest Cretaceous (Maastrichtian) terrestrial deposits of Romania a diversity of crocodylomorphs was reported, discoveries originating from only a few sedimentary basins, such as Hațeg (Venczel and Codrea, 2019 with references therein) from the Sânpetru and Densuș-Ciula Formations, Rusca Montană (Codrea et al., 2012) or from the Șard Formation, in the Metaliferi sedimentary area (Delfino et al., 2008; Codrea et al., 2010). All of these belong to the paleogeographic unit known as the ”Haţeg Island”. The common denominator of these associations of crocodylomorphs refers to the trophic chains, where the top predator was the eusuchian *Allodaposuchus precedens* Nopcsa, 1928 (Delfino et al., 2008, Codrea et al., 2010, Solomon and Codrea, 2015, Narváez et al., 2019), while the smallest was *Aprosuchus ghirai* Venczel & Codrea, 2019 (Venczel and Codrea, 2019).

Besides the mentioned taxa that mark extreme forms of the latest Cretaceous of Transylvania, there were also other representatives. One of the small sized *Theriosuchus* like taxa was assigned to *Sabresuchus* (=*Theriosuchus*) *sympiestodon* (Martin, Rabi & Csiki, 2010) by Tenant et al. (2016). Another crocodile from the Maastrichtian formations of Transylvania is the alligatoroid *Acynodon* (Martin et al., 2006; Solomon and Codrea, 2015), a small, extremely specialized taxon, with a significantly short snout. The diet of *Acynodon* is rather unclear (Delfino et al., 2008). In Romania, this form is known only based on isolated teeth, from the Haţeg basin (cf. *Acynodon* sp., in Martin et al., 2006; *Acynodon* sp., in Solomon and Codrea, 2015). Another genus known from the ”Haţeg Island” is *Doratodon* (Martin et al., 2006). Not far from Romania, *D. charcaridens* (Bunzel, 1871) is known from the ”Senonian” deposits of the Grünbach Formation (lowermost Campanian, Muthmannsdorf, Austria; Buffetaut, 1979 considers this species valid), but also from Hungary (Csehbánya Formation, Iharkút, late Santonian; Rabi, 2008).

Crocodylomorphs crossed the Cretaceous/Paleogene (”K/T”) boundary, but in the lowermost Cenozoic their taxa renewed. In Romania, data about the earliest representatives are known from the Jibou Formation (NW Transylvania; Maastrichtian-Lutetian; Codrea and Godefroit, 2008; Baciu, 2003). Apart from an isolated tooth found in a drill core sample at Someș-Odorhei (Sălaj County; Posewitz, 1906) that could have originated from a Cretaceous representative, all other evidences are originating from the Rona Limestone Member (Thanetian-?Sparnacian; Hofmann, 1879; Codrea and Săsăran, 2002; Baciu, 2003). Gheerbrant et al., (1999) mentioned in a list of taxa two types of crocodylomorphs, cf. *Doratodon* and Crocodylidae s.l. indet., without any description and illustration. If the assignations were correct, it would demonstrate that *Doratodon* survived until the end of the Paleocene.

Knowledge about the Cenozoic basalmost representatives of crocodylomorphs is extremely poor, with scarce data throughout Europe. In such context the Paleocene terrestrial vertebrates from Romania are of outstanding value, as they are unique for the entire Eastern Europe. This study is focused on crocodylian fossils collected from Paleocene lithostratigraphic units, at Jibou and Rona localities, in Sălaj County. The fossils consist of isolated specimens representing fragmentary cranial and postcranial remains that were probably part of an attritional assemblage. The skeletal parts reached the burial place probably after a high energy transport, like a flash flood, causing the disarticulation and fragmentation of most specimens. The available remains probably have belonged to a single group of eusuchian crocodylomorphs, which based on several unique characters (e.g., mediolaterally narrow but dorsoventrally deep snout and labiolingually compressed tooth crowns bearing finely serrated crests) may be attributed to Planocraniidae Li, 1976, a group never reported previously from the eastern part of Europe. However, the present report may correspond to one of the geologically oldest fossil records (late Paleocene) from the whole continent.

Geological setting and age of the lithostratigraphic units

Situated in central Romania, the Transylvanian Depression is the widest in the country, being surrounded by the Carpathian Mountains. Geologically it resulted from the evolution of succeeding overlaying sedimentary basins as defined by Balintoni et al. (1998), who specifies four Permian-Mesozoic and three Cenozoic basins. Krézsek and Bally (2006) discuss about four sedimentary megacycles for this area, which were closely related to and influenced by the Alpine Orogenesis of the Carpathians.

In the latest Cretaceous (Maastrichtian; Codrea and Godefroit, 2008 and references therein), after the ceasing of the extensional processes, the basin’s basement located nearby the northeastern margin of the Apuseni Mountains was uplifted, and terrestrial sedimentary deposits began to accumulate on the emergent surface. During the Paleogene megacycle, after the „Laramide” tectogenesis, freshly eroded sediments originating from the newborn relief of the Carpathians accumulated in subsidiary sag basins associated with a foreland area (Hosu, 1999). As a result, the Paleocene-lower Eocene sequence is characterized by terrigenous sedimentary rocks that begin with the alluvial fan deposits of the Jibou Formation (Maastrichtian-Lutetian; Fig. 1).

The Jibou Formation coined by Hofmann (1879; Fig. 2), also known as the “Lower Variegated Red Shales” in older stratigraphic nomenclature (a detailed historical evolution of its name, in Mészáros and Moisescu, 1991), exposed on large areas and with remarkable thickness of strata (+1500 meters at the type section), is constantly present in all three sedimentary areas (Gilău, Meseș and Preluca; Rusu, 1970, 1987; Popescu, 1976) on the NW side of the Paleogene Transylvanian basin and is characterized by facies uniformity. In the Gilău and Preluca areas at the same stratigraphic level, the counterpart clastic Stejerea Formation is present (Rusu, 1987; Codrea et al., 2010). The area of interest for this study is situated in the Meseș sedimentary area, between Jibou and Rona localities, in Sălaj

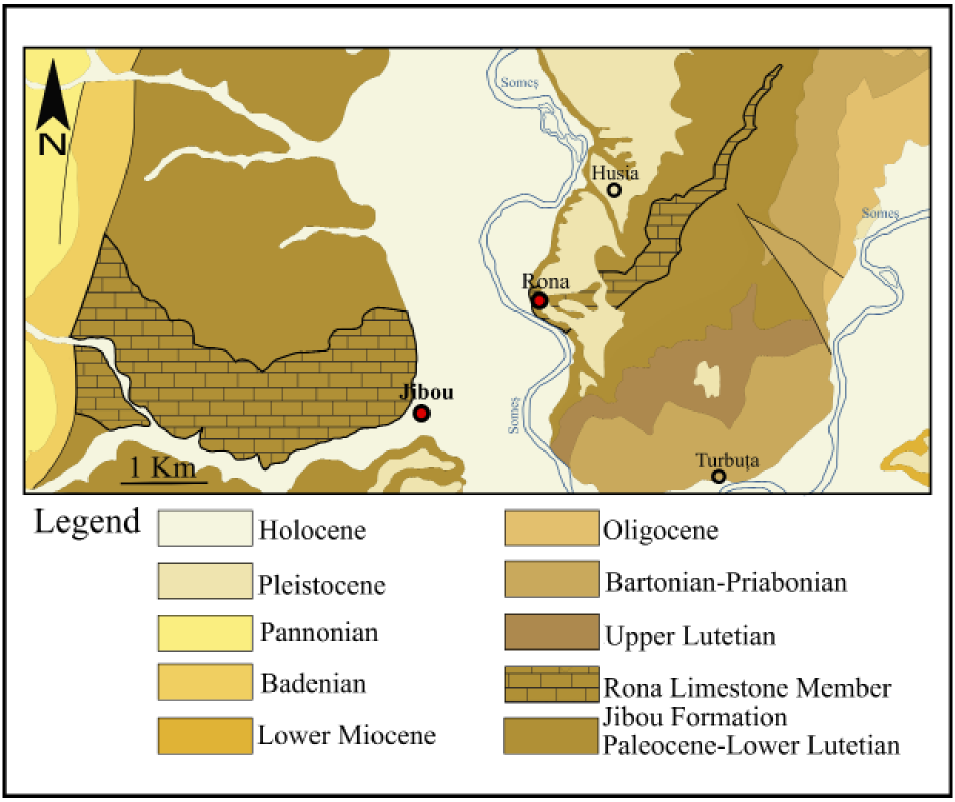

Figure 1. Geological map of the Jibou-Rona area, in Sălaj County (after the Geological map 1:50 000, folio 29b Jibou and folio 29a Zalău), modified.

County (Figs. 1 and 2). The studied formation presents the overlay of retrograde alluvial fan deposits that cover directly the post-“Laramide” unconformity surface of the metamorphic basement represented by the Someș Lithogroup (Fig. 3), and possibly the subsequent Mesozoic sedimentary deposits with a tectonically controlled thickness across the sedimentary basin (Hosu, 1999).

Proust and Hosu (1996) mentioned a specter of four alternating lithofacies composed of conglomerates, sandstones and red silty shales. In the lowermost section of the terrigenous deposits a layer of conglomerates is present, composed of metamorphic clasts and red silty-arenitic matrix. In the Gilău sedimentary area a level of interspersed pyroclastic deposits is present at the base of the mentioned formation (Mureșan, 1980), which has never been found in the proximity of the Jibou-Rona area. Further above, there are fluvial red-bed deposits with intertwined channel-fill deposits involving silty-conglomeratic sediments, and over-bank deposits with red silty clays related to fluvial plain environments, all composing the alluvial fans (Proust and Hosu, 1996; Hosu, 1999; Codrea and Hosu, 2001). Hosu (1999) also mentions a level of kaolinite at the basal part of the formation, and specifies the quartz rich composition of the red arenites. The striking red colour of these deposits was explained by Voitești (1935) on one hand, as a result of the Cretaceous lateritic soils that were transported in the Transylvanian basin from the nearby Gilău Mountains during rainy seasons. On the other hand, Hosu (1999) has a different explanation focusing on the mineralogical composition of sediments. He related the red color to diagenesis of the ferrous minerals and migrations of pigments.

Another peculiar feature of the studied formation is the presence of restricted lake deposits, as interbeddings in the red-beds succession. We refer to the Agârbiciu Dolomites (part of the ”Inferior marine series”, sensu Mureșan, 1980), the Horlacea Limestone Member (Rusu, 1995), and the Hășdate Limestones. But by far, the most important lacustrine deposits from the perspective of areal distribution, thickness and fossiliferous content are the ones of the Rona Limestone Member (Codrea and Săsăran, 2002), first mentioned by Hauer and Stache (1863), but described in detail by Hofmann (1879). The initial description of strata was based on an outcrop located on the geographic right shore of the Someș River, in Rona locality (Fig. 4). Hofmann considered these deposits as exclusively Eocene, based on some fossil mollusks. About three decades ago, new outcrops became available for study as a consequence of the botanical garden enlargement works in Jibou locality. Consequently, the team realized that 2/3 of the lake deposits have been unknown until that point (Codrea and Săsăran, 2002). The Rona Member lake deposits having a thickness of about 250 meters start with marls, mudstone layers, and sandstones, followed by organically rich shales and limestones, with final layers of red-greenish shales and channel-fill deposits (Codrea and Hosu, 2001).

Hofmann described the red shales of the Jibou Formation as being completely devoid of any fossil material and he also mentioned some *Chara* remains in the freshwater limestones of the Rona Member. Indeed, at first glance the red shales seem to be devoid of fossil remains, but in truth these are not completely lacking, the fossils are plain and simple uncommon. Historically, the oldest vertebrate remains were reported by Baron Nopcsa (1905), who collected the fossil remains of the dinosaur „*Rhabdodon priscus*” (formerly known as ”*Mochlodon suessi*”) together with indeterminate chelonian and crocodile remains from Someș-Odorhei locality, near Rona. Based on these, he established Danian age for the basal part of the Jibou Formation. Later, this contribution was either forgotten, or ignored by the followers. Codrea and Godefroit (2008) collected from the same level the remains of the ornithopod dinosaur *Zalmoxes shquiperorum*, a discovery that confirmed the uppermost Cretaceous (Maastrichtian) age for

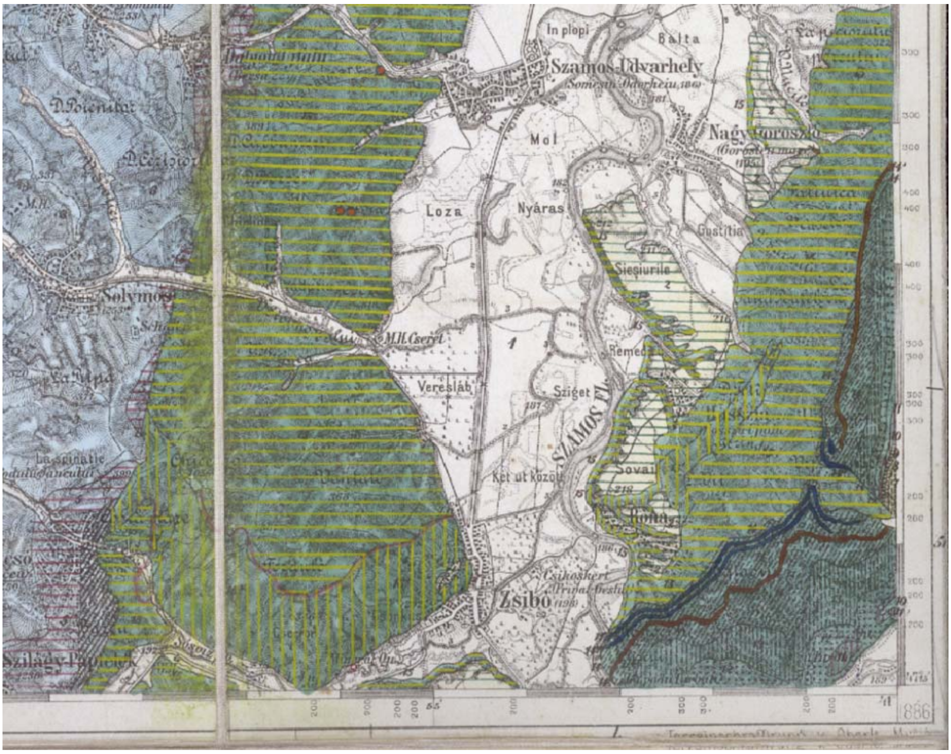

Figure 2. Historical geological map of the Jibou (= Zsibó) area 1: 75 000 by Hofmann et al. (1888).

the lowest portion of the Jibou Formation. Concerning the uppermost boundary of the Jibou Formation, Mészáros and Diószegi (1988) reported an assemblage of five nannoplankton taxa and some ostracods, which from their point of view emphasized a middle Eocene age for the rocks from Giurtelecul Șimleului outcrop. From the same locality, Codrea and Fărcaș (2002) reported the presence of turtles assigned to "*Paleochelis*" s. l., and *Neochelis*. Later, Vremir (2013) completed the list with cf. *Ronella* and other taxa with questionable systematic assignments. The presence of these fossils in the top of the Jibou Formation is indicative for an Ypresian-Lower Lutetian age.

Regarding the Rona Member, from the basal part of the freshwater sequence a palynological association was reported by Petrescu and Codrea (2003 a, b), Codrea et al. (2003) and Petrescu (2003), indicating a late Thanetian age. Baciu (2003) concluded the same age based on charophytes, to which Gheerbrant et al. (1999) added studies based on gastropods and ostracods, with similar results. Considering vertebrates, Gheerbrant et al. (1999) together with Codrea and Hosu

Figure 3. Lower boundary of the Jibou Formation at Dumbrava, Cluj County; the red waved line is marking the unconformity of the terrestrial sedimentary rocks with the underlying metamorphic Someș Lithogroup as basement of the Transylvanian basin.

Figure 4. The Rona Limestone Member outcrop located on the Someș's left shore, at Rona locality; based on these rocks Hofmann (1879) described the lithology of this member.

(2001) outlined an association with participants such as the dortokid turtle *Ronella botanica*, crocodylians (cf. *Doratodon* sp.) and multituberculate mammals, such as cf. *Hainina* sp., cf. *Paschatherium* sp., a.o. (Gheerbrant et al., 1999; Codrea and Hosu, 2001). Gaudant et al. (2005) added the Amiidae fish genus *Cyclurus* to the association from the late Paleocene. The above-mentioned taxa are indicative for a paleoecosystem established close to the Paleocene lake at Rona. Petrescu and Codrea (2003 a, b) interpreted a subtropical climate based on specific plant communities.

From a tectonic point of view, strata in the Jibou area have a monoclinal placement, with a dip angle of about 15°-20° SSE on the left shore of the Someș River, whereas on the right side the strata are dipping only about 5° SSE, with a decreasing value towards the center of the sedimentary basin (Hofmann, 1879). According to Koch (1894), at Someș-Odorhei an anticlinal aspect of the deposits can be noticed, which does not continue over the Someș valley, on the right bank of the river, and which is the result of the uplift of the underlying metamorphic substratum that is continuing underground, below the Meseș Mountains. The Paleocene-Eocene boundary is not easy to draw, since the deposits of both ages are parts of a continuous terrestrial sedimentation, in the same facies. During the Eocene, the continental sedimentation has been replaced by a marine one, after deepening of the basin and transgression of the marine waters.

Material and methods

The crocodile fossils were collected from two localities, both exposing the Rona Member of the Jibou Formation, in Sălaj County: in Jibou (Jb), from the rocks cropping out in the Botanical Garden, in the concentration levels B2 and B4 (in Gheerbrant et al. 1999), and from Rona (Ro), from outcrops located on the right bank of the Someș River.

The fossil bones and teeth were found scattered in the rock as isolated pieces. Therefore, they were collected inside blocks of various size, without using plaster jackets. When necessary, the vertebrate fossils were reinforced with professional polymers. The majority of teeth were retrieved by washing-sieving large amounts of sediments (24 tons in total, during successive field missions), the majority originating from the level B4. The sieves were disposed as washing tables with 0.3 and 0.5 mm meshes. For washing, usual garden pumps were used.

The bones were cleaned of the matrix rock in the Laboratory of Paleotheriology and Quaternary Geology of the Babeș-Bolyai University in Cluj-Napoca (abbreviated: LPQG BBU) using classical laboratory gear: needles, chisels, Air-Scribe, scalpels, under frontal magnifier or binocular magnifier. The small teeth were retrieved from the washed-sieved sediment concentrate with tweezers, under binocular magnifier Nikon SMZ 1000. When the teeth and bones were fissured, they were reinforced with professional polymers (mowillite) dissolved in acetone, at various concentrations.

The fossils are stored in the LPQG BBU collection. The registry numbers are following the formula: PJb(Ro)BxCr – x, where P means Paleocene, Jb (Ro) the name of the vertebrate locality, Bx the concentration level, Cr from crocodile, x the registration number.

The photographs were captured with a Nikon D-7000 camera and Nikon AF S Micro Nikkor 60 mm lens, and a lighting system. For the small teeth the photos were captured with the same camera mounted on a Nikon SMZ 1000 binocular magnifier. All photos were processed using the CombineZP software by Alan Hadley, using the overlaid images technique. Images were lastly processed in Adobe Photoshop CC 2019 and Adobe Illustrator CC 2019 computer programs. Common English terms and the standard anatomical orientation system are used throughout this paper; the anatomical nomenclature of crocodylians follows Brochu (2013).

Systematic paleontology

Class Reptilia Laurenti, 1768

Order Crocodylia Gmelin, 1789

Suborder Eusuchia Huxley, 1875

Family Planocraniidae Li, 1976

The family Planocraniidae, following Brochu (2013) and Sues (2019), represent a clade of eusuchian crocodylians that include *Planocrania datangensis* and all crocodylians more closely related to it than to *Alligator mississippiensis*, *Crocodylus niloticus*, *Gavialis gangeticus*, *Borealosuchus sternbergii*, *Thoracosaurus macrorhynchus*, *Allodaposuchus precedens*, or *Hylaeochampsa vectiana*. Li (1976) assigned the group Planocraniidae based on the basal taxon *Planocrania datangensis* Li, 1976, which has been recovered from the Paleogene red-bed deposits of the Nongshan Formation from China. Later, Li assigned a new species to the group, *Planocrania hengdongensis* Li, 1984, again originating from Paleogene red-bed deposits of the Lower Lingcha Formation from China, both of these fossils are considered unique specimens to this day (Li, 1984). The members of Planocraniidae possess a moderately long, mediolaterally narrow and dorsoventrally deep rostrum, whereas the tooth crowns are labiolingually compressed and bear finely serrated cutting edges, some can have hoof-like ungual phalanges (Brochu, 2013; Sues, 2019). Brochu (2013) and Narváez et al. (2015) found *Borealosuchus* and Planocraniidae as successive sister taxa to Brevirostres which includes Alligatoroidea and Crocodyloidea.

The fossil record of Planocraniidae is restricted to the Paleogene of China, the Paleocene-Eocene of the United States, Western Europe: Eocene of

France, Lutetian of Germany, Italy, and Spain (Kuhn, 1938; Li, 1976, 1984; Brochu, 2013; Sues, 2019), the Indian subcontinent (Eocene of Nepal and Northern India; Panadés I Blas et al., 2004; Sah and Schleich, 1990), Eocene of Kazakhstan (Rossmann, 1998) and lastly Romania (this report).

Genus *Boverisuchus* Kuhn, 1938

Previously, the genus *Boverisuchus* was widely known as "*Pristichampsus*", but the type material, on which the species name *Pristichampsus rollinati* (Gray, 1831) is based, is lacking diagnostic characters at species level (Langston, 1975), and therefore Brochu (2013) regarded it as a *nomen dubium*. Both the American and European members of the genus *Boverisuchus* (i.e., *B. vorax*, known from the Bridger Formation, Wyoming, USA and *B. magnifrons*, known from Geiseltal near Halle, Germany) are restricted to the middle Eocene; another taxon name *Weigeltisuchus geiseltalensis* Kuhn, 1938 (the holotype known from Geiseltal near Halle, Germany), is presently considered a junior synonym of *B. magnifrons* (Brochu, 2013).

Cf. *Boverisuchus* sp.

Material examined: one fragmentary left premaxilla [PJb(Ro)B4Cr-1]; one frontal [PJb(Ro)B4Cr-2]; one fragmentary frontal + parietal [PJb(Ro)B4Cr-3]; one posterior fragment of supraoccipital + parietal [PJb(Ro)B4Cr-4]; one squamosal [PJb(Ro)B4Cr-5]; one posteroleft fragment of neurocranium [PJb(Ro)B4Cr-6]; one fragmentary quadrate [PJb(Ro)B4Cr-7]; one fragmentary surangular + articular [PJb(Ro)B4Cr-8]; three fragmentary angulars [PJb(Ro)B4Cr-9/1-3]; one fragmentary dentary [PJb(Ro)B4Cr-10]; one scapulocoracoid [PJb(Ro)B4Cr-11]; two fragmentary humeri [PJb(Ro)B4Cr-12/1-2]; one fragmentary femur [PJb(Ro)B4Cr-13]; osteoderms [PJb(Ro)B4Cr-14]; vertebrae [PJb(Ro)B4Cr-15]; isolated teeth [PJb(Ro)B4Cr-16].

Description of the material

Premaxilla: The only premaxilla [PJb(Ro)B4Cr-1] is badly preserved missing its anterior and posterior margins; it displays some deformation on the anterolateral part of the labial surface (Fig. 5A, B). The specimen appears mediolaterally narrow, dorsoventrally deep and shallowly bent medially with its labial surface bearing a sculpture consisting of numerous small pits. The narial margin is slightly elevated on the posterior part, whereas the medial margin is gently curved medially indicating that the external naris was longer than wide. The bony margin delimiting the incisive foramen is broken off, therefore the size of that structure is unclear. Remnants of the premaxillary teeth are still present in the third and fourth alveoli, but their tooth crowns are broken off. The fourth premaxillary tooth is larger than the third and their shaft is slightly compressed labiolingually. Remnants of the second and fifth alveoli are partially preserved, whereas the first alveolus is broken off. The occlusal pits left by the dentary teeth are situated between the third and fourth alveoli and between the fourth and fifth alveoli, both pits being placed in line with the premaxillary tooth row; a partially preserved pit is situated lingually to the second alveolus.

Frontal, parietal, supraoccipital: The specimen PJb(Ro)B4Cr-2, represents a partially preserved frontal with its left posterolateral part missing (Fig. 5C, D). Due to its heavily built bony structure, it may have belonged to a mature individual. The bone's reconstructed shape approaches an elongated triangle with the medial part slightly depressed, whereas its lateral part is upturned near the orbital margins. The anterior process, about the same length as the remaining posterior bony part, is relatively narrow and subparallel, exposing laterally the sutural surfaces with the prefrontals. The dorsal anteriormost surface of that process displays the sutural imprints left by the paired nasals; the articulation appears as a simple acute point. The dorsal sculpture consists of enlarged and deep pits on the posterior half of the bone, whereas on the anterior process the pits tends to become elongated or replaced by shallow grooves. The posterior margin of the frontal exposes the sutural surface with the parietal that is more or less transversal, whereas on the right posterolateral side, there is a well-defined and deep contact surface with the postorbital.

The specimen PJb(Ro)B4Cr-3, representing a significantly smaller individual, preserves a fragmentary frontal and also the right anterolateral part of a parietal (Fig. 5E, F). The main difference between the PJb(Ro)B4Cr-2 and PJb(Ro)B4Cr-3 specimens is that the orbital margin is more deeply curved in the latter, that may be interpreted as an ontogenetic variation (i.e., in younger individuals the orbital spaces are relatively larger). The frontoparietal fusion line is transversal and does not enter into the supratemporal fenestra. The reconstructed width of the parietal between the supratemporal fossa appears narrower than that of the interorbital width. The dorsal sculpture consisting of rounded pits on the frontal and parietal is similar, and there is no overhang above the parietal's medial supratemporal margin.

The specimen PJb(Ro)B4Cr-4, represents a fused fragment of a supraoc-

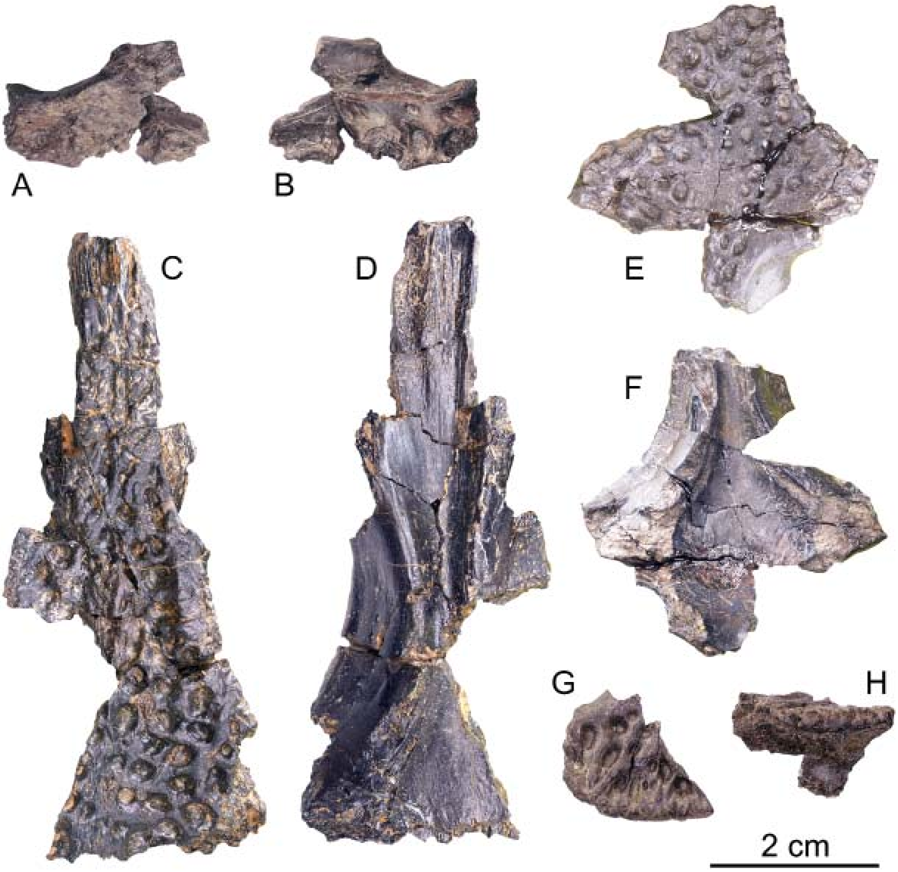

Figure 5. Cf. *Boverisuchus* sp. Left premaxilla (A, B), frontal (C, D), partial frontal + parietal (E, F) and partial supraoccipital + parietal (G, H) in lateral (A), medial (B), dorsal (C, E, G), ventral (D, E) and posterior (H) views.

cipital and posterior parietal fragment. The posterior margin of the supraoccipital projects downward into the occipital surface, whereas the dorsal part is exposed as a strongly sculptured, triangular flange, where it is fused anterolaterally with the parietal's posterior process.

Squamosal: The specimen PJb(Ro)B4Cr-5 is a nearly completely preserved squamosal of a large individual, excepting the postero-medial margin of the dorsal side, which is broken off. The dorsal surface is more or less flat and strongly sculptured with rounded or irregular deep pits. The surface of the postorbital-squamosal suture passes medially. The anteromedial margin of the squamosal circumscribes the lateral side of a relatively small supratemporal fossa; the posterolateral corner of the bone appears relatively long and shallowly bent ventrally. In lateral view, the dorsal and ventral rims of the squamosal groove for the insertion of the external ear musculature is more or less parallel, whereas the posterior margin of the otic aperture is flush with the lateral margin of the squamosal's ventral process. The ventral surface displays on the anteromedial part the articulation surface with the quadratojugal, whereas posteriorly the sutural surface with the exoccipital.

Neurocranial fragment: The posteroleft fragment of neurocranium [PJb(Ro)B4Cr-6], preserves a partial exoccipital, a small portion of the basioccipital, a small part of the basisphenoid and a partial quadrate. Despite of numerous cracks and shifts of bony margins that modified the morphology of the cranial surface, several important anatomical features could be identified, as it follows: close to the margin of the foramen magnum a single larger foramen may correspond to the exit of the paired hypoglossal nerves (cranial nerve XII); anteroventrally to the latter structure there is a paired foramina in a common recess, that may correspond to the exit of the glossopharyngeal and vagus nerves (cranial nerves IX-XI); the lateral carotid foramen is situated posteroventrally to the exit of the cranial nerves IX-XI and above to the basisphenoid exposure; the metotic crest in form of a sharp bony lamella extends laterally to the carotid foramen parallel with and closely above the exoccipital-quadrate contact line; the ventral surface of the quadrate ramus bears a prominent knob that serves as an attachment scar to the posterior mandibular adductor muscle.

Quadrate: The fragmentary quadrate [PJb(Ro)B4Cr-7] preserves the right distal quadrate ramus of a mature individual. It exposes an elongated articular surface with the quadratojugal, whereas the passage of the cranio-quadrate canal is preserved in form of a shallow groove starting from the posteromedial margin of the quadrate-exoccipital articulation contact. The foramen aereum is located near the posteromedial margin of the quadrate ramus. The medial hemicondyle is ventrally deflected and somewhat smaller than the lateral hemicondyle. Despite some distortion observed on the dorsal side of the quadrate condyle, the surface of the quadrate is projected dorsally between the hemicondyles.

Posterior mandible fragment: The specimen PJb(Ro)B4Cr-8, consists of a fragmentary articular and surangular preserving mainly the section with the glenoid fossa. The articulation between the articular and the surangular appears simple, flush against each other with an anteroposterior orientation. The surangular extends dorsally to the tip of the lateral wall of the glenoid fossa delimiting laterally the latter structure. Due to damage, the posterior extent of the surangular remains unknown. The tip of the retroarticular process is damaged, but its remnants sug-

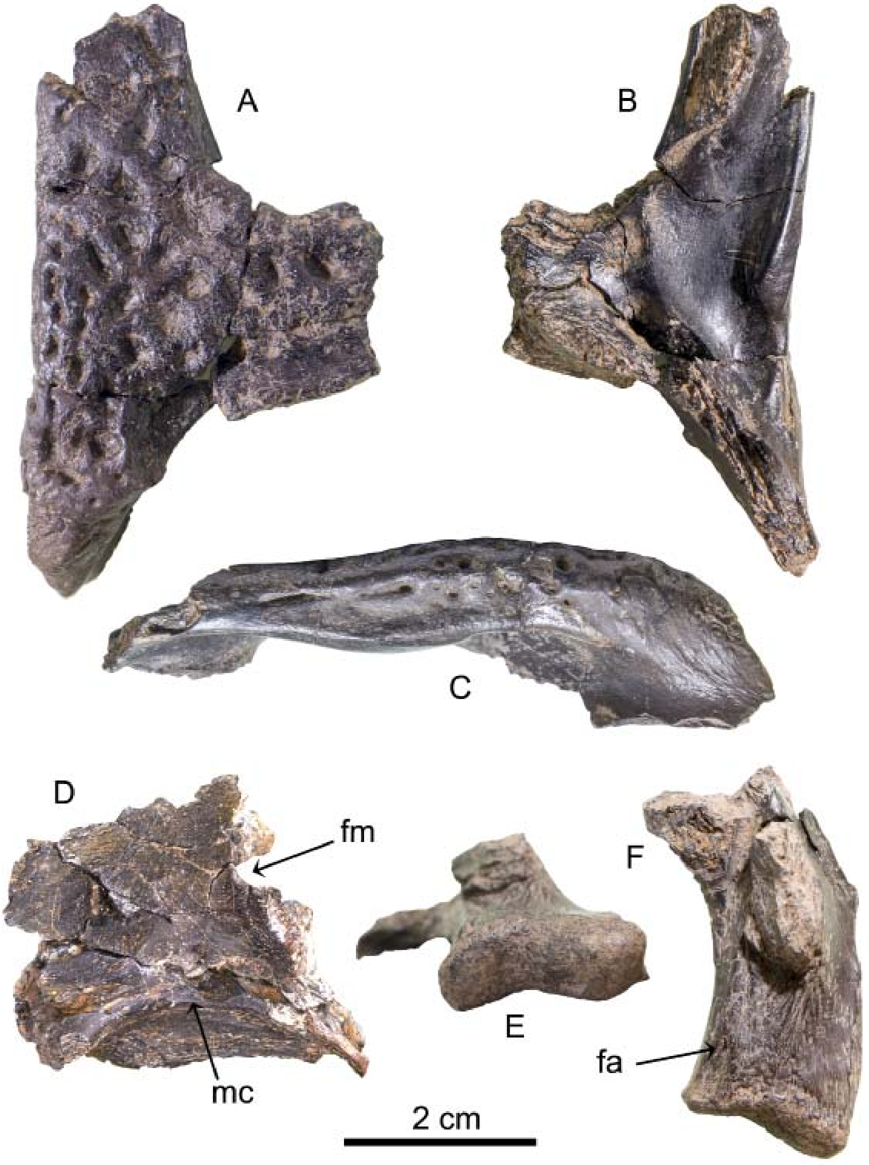

Figure 6. Cf. *Boverisuchus* sp. Left squamosal (A-C), Fragmentary neurocranium (D) and right quadrate in dorsal (A, F) ventral (B), lateral (C) and posterodorsal (D, E) views. Abbreviations: fm - foramen magnum, mc - metotic crest, fa - foramen aereum.

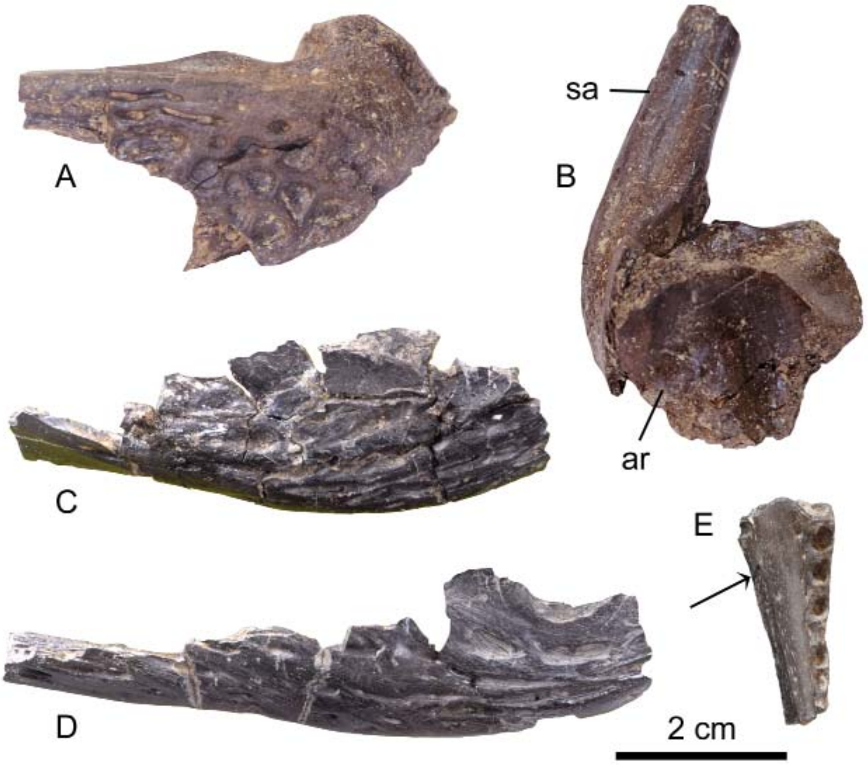

Figure 7. Cf. *Boverisuchus* sp. Partial mandible (A, B), left partial angulars (C, D) and right anterior dentary fragment (E) in lateral (A-C) and dorsal (B, E) views. Abbreviations: ar - articular, sa - surangular; arrow points to the anterior limit of the imprint of the splenial.

gest that it had a posterodorsal orientation.

Angular: Three fragmentary left angulars [PJb(Ro)B4Cr-9/1-3] were available for study. The specimens are strongly damaged with their labial surface strongly sculptured by a network of elongated grooves; their convex and smooth ventral margin displays several foramina. Each angular preserves a short section of the intact external mandibular fenestra suggesting that the external mandibular fenestra was of modest size. Imprints left by the surangular on the dorsal margin of the angulars indicate that the surangular-angular suture contacted the external mandibular fenestra at its posterior angle.

Dentary: The specimen PJb(Ro)B4Cr-10 represents a fragmentary right anterior part of a dentary that might have belonged to an immature individual; the anteriormost margin with the symphysys, the posterior shaft and the medial margin are

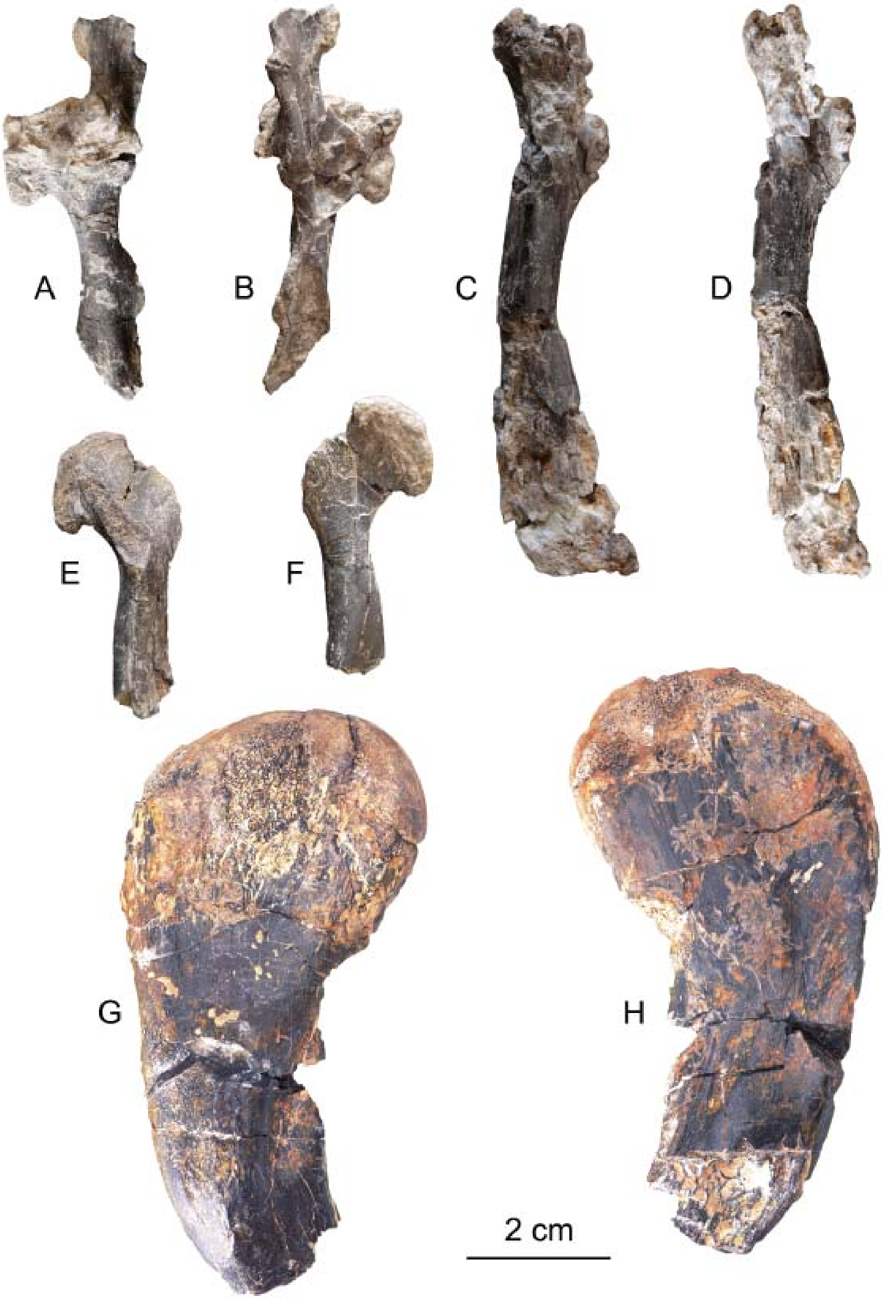

Figure 8. Cf. *Boverisuchus* sp. Right scapulocoracoid (A, B), humerus (C-F) and femur (G, H) in medial (A, D, F), lateral (B, C, E), ventral (G) and dorsal (H) views.

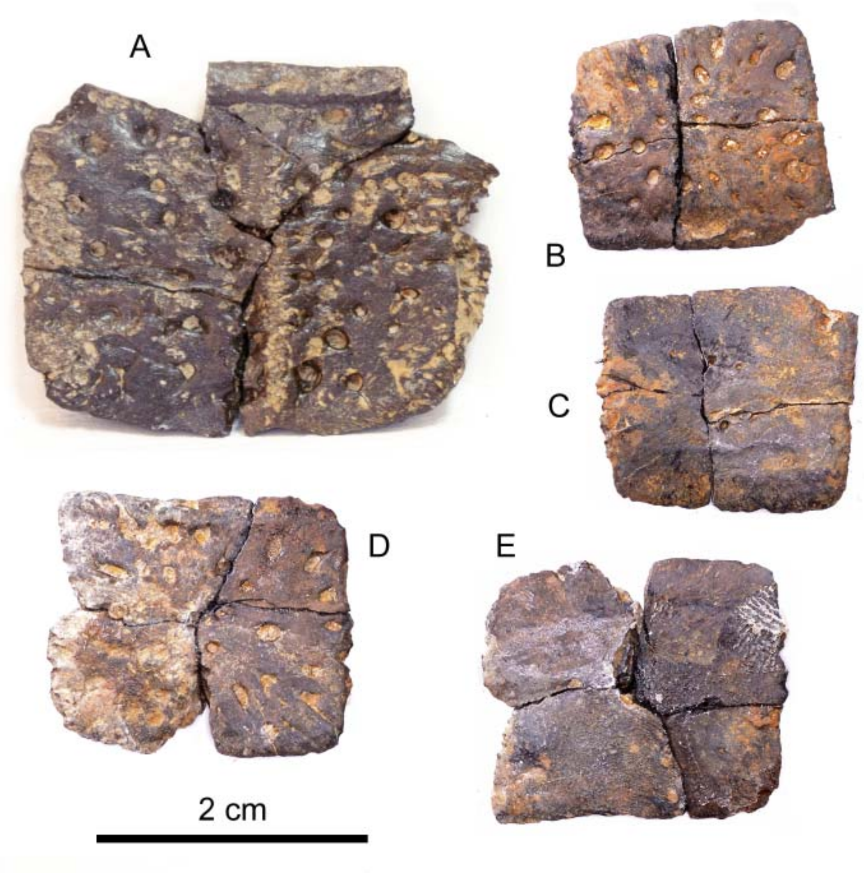

Figure 9. Cf. *Boverisuchus* sp. Dorsal (A) and ventral osteoderms (B-E).

broken off. Anteriorly, the dentary is widened bearing on its mediodorsal limit the imprint of the splenial and ventrally to the latter the lateral margin of the Meckel's groove. Six alveoli are preserved in the specimen, of which the posteriormost two are nearly confluent. The dorsal surface of the dentary lacks any sign of occlusion from the premaxillary or maxillary teeth. The tooth row appears linear and the alveoli have a moderate labiolingual compression. In the second alveolus a replacement tooth is preserved with its crown compressed laterally and provided with smooth mesiodistal carinae.

Vertebrae: The available vertebrae are strongly damaged preserving various parts of the procoelous centrum, neural arch and apophyses.

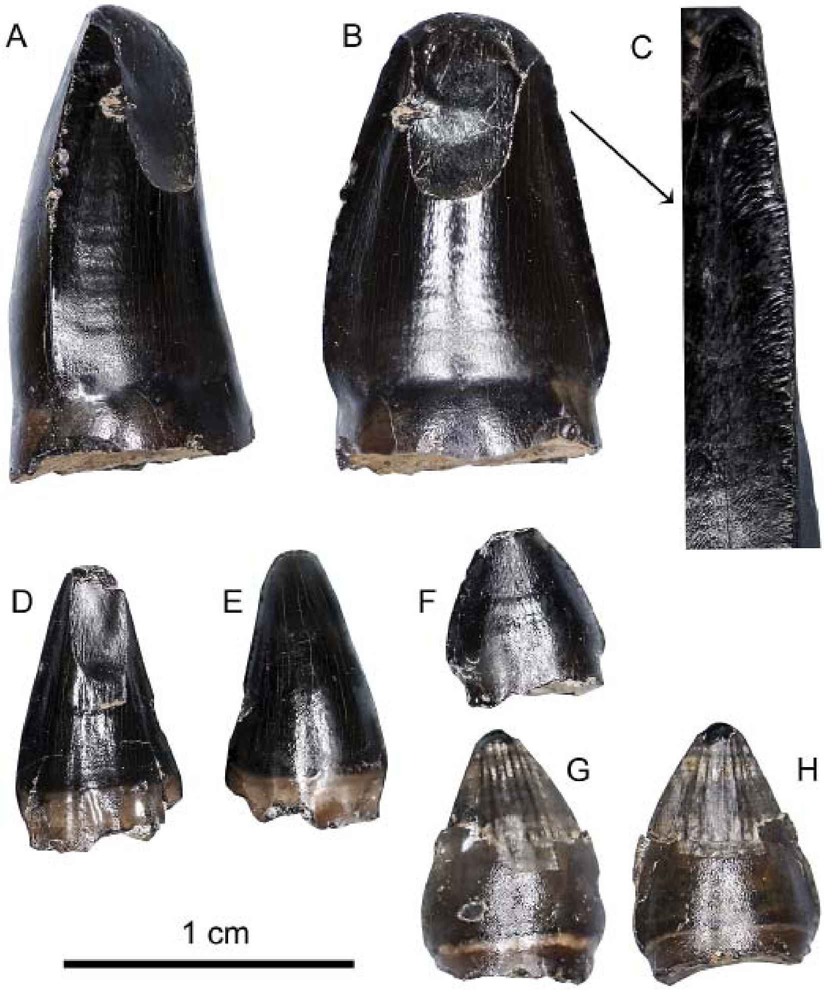

Figure 10. Cf. *Boverisuchus* sp. Isolated teeth. Arrow points to tooth carina with enlarged view preserving finely serrated margin.

Scapulocoracoid: In lateral view, the right scapulocoracoid specimen [PJb(Ro) B4Cr-11] is positioned vertically being readjusted from its originally angled position during the taphonomic process. The scapular blade is broken off distally but its remnants suggest that it flared dorsally, whereas the deltoid crest of the scapula appears relatively wide and twice longer than the diameter of the glenoid fossa. The scapulocoracoid facet anterior to the glenoid fossa appears uniformly narrow.

The coracoid also flares distally with a distinct ridge on its lateral surface.

Humerus: The two available specimens preserve rather limited morphological information. PJb(Ro)B4Cr-12/1 has both its extremities strongly crushed with the deltopectoral crest also slightly deformed. However, the latter structure suggests that the deltopectoral crest was well-developed emerging abruptly from the humeral proximal end. PJb(Ro)B4Cr-12/2 preserves its proximal end only, but the deltopectoral crest is completely broken off.

Femur: The proximal part of a sigmoid shaped left femur [PJb(Ro)B4Cr-13] may have belonged to an extremely large, mature individual. A deep pit on the dorsal side of the proximal epiphysis connected to several fracture lines may represent a bite mark produced by scavengers. The fourth trochanter on the ventral side is relatively short and prominent, flanked by a deep pit serving as the insertion surface for the M. pubo-ischio-femoralis internus.

Osteoderms: The dorsal osteoderms are more or less rectangular and provided with a prominent keel; the dorsal sculpture consists of deep rounded pits of various sizes. The anterior margin is smooth lacking any trace of convexity or embayment; the ventral surface is also smooth. The ventral osteoderms appear single and lacking a ventral keel. However, on some osteoderms a short thickening of the ventral surface is present. The sculpture consists of rounded or elongated pits, distributed irregularly on the ventral surface.

Isolated teeth: The main character of the available teeth is that their tooth crowns are mediolaterally compressed and provided with mesiodistal keels that frequently bear finely serrated margins. Three morphotypes have been identified: 1) the caniniform morphotype, that is large and shallowly curved, three to four times higher than wide at its base, and provided with mesiodistal keel bearing finely serrated edges; sometimes the cutting edges remain smooth; 2) the lanceolate morphotype, that is moderately high, the mesiodistal carinae are more or less symmetrically developed preserving variably fine serrations and 3) the low crowned morphotype, that is compressed mediolaterally and is wider than high; the mesiodistal carinae are present but usually do not preserve serrated margins. The tooth base, preserved in few specimens, is slightly constricted and below that point is of the same width as the tooth crown. However, from a morphological viewpoint some tooth specimens can be of intermediate form, as it is well presented in Fig. 10, where for instance specimen A-B is not typically “caniniform” and the “low crowned” specimen G-H is actually higher than wide.

Comparisons and comments

In the premaxilla of Planocraniidae the distribution of the occlusal pits is different in the European members (i.e., in *Boverisuchus magnifrons*, the dentary teeth occluded between the premaxillary alveoli) and in those of American members (i.e., in *B. vorax* the occlusal pits are situated lingually to the premaxillary alveoli; Brochu, 2013) with the exception of the Uintan planocraniid, where the occlusal pits are positioned between the alveoli (Busbey, 1986; Brochu, 2013). If our interpretation is correct, the morphology of the Jibou planocraniid should be intermediate between those of European and American members.

The frontal and parietal appear as azygous bones without signs of sagittal crests or division on their dorsal surfaces. As noted by Langston (1975), persistent median division is apparent between the paired frontals and parietals in *Boverisuchus vorax* (at least in FMNH PR 399). Upturned orbital margins, observed in both the available frontal specimens from Jibou are similar to members of *Boverisuchus* and *Planocrania datangensis*, but this condition is lacking in the earliest gavialoids, crocodyloids and alligatoroids (Brochu, 2013). The presence of palpebrals has been documented by Li (1976) in *Planocrania datangensis*, but there is no sign of articulation surface on the frontals from Jibou. Nevertheless, we cannot exclude the presence of palpepbrals in the Jibou specimens, because these bones should have been in contact mainly with the prefrontals, as demonstrated by the type material of *P. datangensis* (Li, 1976: fig. 1). On the anterior process of the larger frontal specimen, the exposed articular surfaces for the prefrontals and nasals indicate that the prefrontals were largely separated by the frontal. On the other hand, the frontal is excluded from the supratemporal margins by the parietal and postorbital. Larger dorsal exposure of the supraoccipital in the PJb(Ro)B4Cr-4 specimen may be reminiscent of *Boverisuchus magnifrons* (Kuhn, 1938), nevertheless, the parietal was not excluded by the supraoccipital from the posterior margin of the skull table.

In the dentary fragment the presence of the imprint of the splenial indicates that it did not contact the mandibular symphysis and the Meckel's groove passed below the anterior limit of the splenial. In the members of *Boverisuchus* and *Planocrania datangenis* the splenials are in contact medially, whereas in *P. hengdongensis* the splenial does not extend to the mandibular symphysis (Brochu, 2013).

The scapulocoracoid specimen preserved both the scapula and the coracoid and their proximal bony surfaces indicate that these were not completely ossified. Nevertheless, lithostatic pressure aligned the bones from their original angled position. The scapulocoracoid facet appears uniformly narrow anterior to the glenoid fossa.

The dorsal osteoderms possessed dorsal keels, but their anterior margins were smooth and without an anterior lamina, similar to alligatoroids, crocodyloids and planocraniids (Brochu, 2013). All the available ventral osteoderms represented single units without signs of suture at their margins. Composite ventral osteoderms are typical in the members of some alligatoroids, like *Diplocynodon* (Rio et al., 2020).

The isolated teeth are highly variable in shape and size, but all are laterally compressed and provided with finely serrated edges on their mesiodistal keels. On the other hand, many specimens possess strongly worn keels or apical margins and the serrated edges are not preserved. The serrations are highly variable and irregular and always significantly smaller than those seen in the members of *Boverisuchus* (Brochu, 2013). The presence of serrated edged teeth have been reported in *Planocrania datangensis* (Li, 1976: fig. 2) and also in *P. hengdongensis* (Li, 1984), but as stated by the latter author, these are less evident on the mesiodistal keels and are usually lacking from the apical part of the tooth crowns. This condition seems to be present in the Jibou specimens. Probably, the earlier identification of “*Doratodon*” from the Rona Limestone Member of Jibou by Gheerbrant et al. (1999) was based mainly on the ziphodont nature of the recovered isolated teeth.

Paleobiogeography

The presented fossil material is of peculiar interest, since Planocraniid remains have never been signaled from Eastern Europe, while taking into account the geological age of the Jibou Formation, where our fossils originated from, we can pronounce it being one of – if not the oldest European apparition of the group.

Li (1976, 1984) assigned the type species of *Planocrania*, from the Paleocene Nongshan Formation, Nanxioing sedimentary basin and the lower Lingcha Formation’s Paleocene deposits in the Hengdong sedimentary basin, from China. The Lingcha Formation is composed of fossiliferous red-bed deposits with a fluvial aspect, which shows similarities with the Transylvanian Jibou Formation’s red-beds. While the Chinese deposits yielded numerous well-preserved, complete cranial bones, our material from Jibou is rather fragmentary, which somewhat affects the observation of morphological characters.

Other ziphodont crocodile teeth have been reported from the Paleocene-Lower Eocene of Northern India (Panadés I Blas et al., 2004; Gupta and Kumar, 2013), the Eocene of South Nepal (Sah and Schleich, 1990) and Kazakhstan (Rossmann, 1998). The only intermediary area where planocraniid remains have been discovered and which seems to connect Asia to Western Europe through its similar aged fossiliferous sedimentary deposits and similar fossil remains is the Transylvanian region (Gheerbrant et al., 1999; Gaudant et al., 2005; De Lapparent et al., 2004). In Western Europe Planocraniid remains were found in the Middle Eocene (Lutetian, possibly also the Paleocene) of Germany, the Lutetian of Italy, the Eocene of France (Brochu, 2013; Kotsakis et al., 2004) and some remains that could possibly belong to the same group, from the Paleocene of Belgium (Groessens-Van Dyck, 1986). Regarding Northern America, relative fossils originate from the Bridgerian (Ypesian-Lutetian) of Wyoming, with appearances of extremely fragmented remains throughout the Paleocene-Uintan (Lutetian). The oldest presence of a Planocraniid in America has been recorded in the basal Paleocene of the Bighorn Basin, from the Puercan Mantua Lentil, based on a single ziphodont tooth assigned by Bartels (1980), while sadly the tooth has not been illustrated, today it is considered lost, as stated by Brochu (2013). Other planocraniid fossils have been signaled from the Eocene of Western Texas (Busbey, 1986), some problematic materials have been reported from Australia and Africa, while other ziphodont crocodylid remains originate from the Eocene of Jamaica (Brochu, 2013).

Regarding the origin and dispersal of Planocraniids, one of the possible scenarios refers to the much discussed and largely accepted Asiatic origin of the group, where they migrated from towards Europe, North America and later to India, in the Paleocene. Scotese (2014) has remarkably useful paleogeographic maps for the Danian and Thanetian (55.8 Ma) illustrating water to landmass ratio at +40m and +120m ocean level. From his illustrations we conclude two possible migration routes, especially at times when ocean levels were low and landmasses arose from the water, creating continental bridges and dispersal routes for various tetrapods, including crocodiles. Both of our speculated routes start in Asia and extend towards Europe. While the first one follows a northern path, across the – at the time closed – Turgai Strait (Western Siberia) which permitted passage of land fauna towards Northern Europe and later towards Southern Europe (France and Italy). The second scenario envisions a southern path, again starting from Asia, but this time, from the South-Western side with continuation on an elongated insular type archipelago, with a North-West direction, towards the region of today’s Turkey, continuing towards Bulgaria, the ex-Jugoslavian countries, then to the West, towards the Alps and Italy. The latter is the pathway that could have intersected the present Transylvanian Depression.

Paleoecology

Even though postcranial remains are quite scarce for the presented material, the cranial morphological characters allow us to believe that the planocraniid crocodile from Jibou-Rona was acquainted with terrestrial locomotion, rather than supporting aquatic adaptations. We assimilate this supposition of the Planocraniid etiology to their known hoof-like limb extremities instead of them being claw-like and a general rather slender build. Based on this strong physiological factor, we can suppose that individuals were capable of quick terrestrial locomotion, maybe even running after their prey while on the hunt.

The diet of these organisms remains yet obscure, but if we are referring back to the Paleocene fauna of Jibou, it should not be hard to imagine that these planocraniid crocodiles could have feasted on small sized terrestrial tetrapods like multituberculates (eg. *Hainina*), small reptiles like lizards and even chelonians (eg. *Ronella botanica* – proved by some unpublished bite marks). There are no proofs yet, but we should not ignore the possibility that the crocodiles could have made short incursions into the Rona Lake, and they could have completed their diets with amiid fish. In the absence of evidence regarding this matter, this detailed supposition is nothing but guessing, as of yet.

For the Paleocene of Transylvania, a warm, subtropical climate was characteristic (showed by a study of pollen and spores by Petrescu and Codrea, 2003 a,b), with specific fauna composed of Juglandaceae and Fagaceae in the proximity of the Rona Lake. The subtropical type climate could have permitted the development of serious floods, which could have been responsible for the transportation of fossil material in the lacustrine basin, since the crocodiles most likely lived in the lake's proximity. The fragmented aspect of the presented material undoubtedly indicates transportation of the bones before deposition of sediments and fossilization.

Concluding remarks

Abundant fragmentary cranial and postcranial remains of eusuchian crocodyliforms, recovered from the fossil locality of Jibou, suggest that all these isolated bones may have belonged to a single planocraniid taxon. This group of crocodylians is for the first time identified in Romania, while it represents one of the geologically earliest fossil records in Europe. The only other Paleocene occurrence from Europe is a possible planocraniid, which has been reported from the Paleocene of Walbech, Germany (Berg, 1969).

The planocraniid crocodyliforms from the Paleocene of Jibou complete the list of a peculiar terrestrial vertebrate assemblage that included dortokid turtles (*Ronella botanica*), multituberculates (cf. *Hainina*), palaeoryctid proteutherians

(*Aboletylestes*), hyopsodontid condylarthrs (cf. *Paschaterium*), undetermined eutherian mammals, anurans, lizards and possible snakes (Gheerbrant et al., 1999). The occurrence of ostracodes and gastropods closely associated with limnic environments, along with teleostei fish, dortokid turtles and crocodiles (Gheerbrant et al., 1999), suggest the presence of freshwater habitats in the area, where the crocodiles might have acted as top predators.

The presence of planocraniid crocodyliforms in the Paleocene of Romania represent an important paleogeographic link between the Chinese, European and American occurrences. Nevertheless, the planocraniid from Jibou shows closer affinities to Chinese planocraniids (e.g. finely serrated teeth in the Chinese and Romanian forms vs. more robust serrations in the European and American *Boverisuchus*), and it may represent a new taxon.

Acknowledgments

This research was kindly supported by a special scholarship offered for excellence in scientific research: “Bursa specială pentru cercetare științifică 2021-2022” offered by the Babeș-Bolyai University to one of of the authors (I. S.- MS student), and is part of the research project “Systematic, biostratigraphic and paleoecologic details on early Cenozoic crocodilians from Romania” which mainly regards the topic of Planocraniid crocodile fossils present in Romania.

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