

A NEW MULTITUBERCULATE SPECIMEN FROM THE MAASTRICHTIAN OF PUI, ROMANIA AND REASSESSMENT OF AFFINITIES OF *BARBATODON*

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Abstract - *Barbatodon transylvanicus* is the first mammal described from the Mesozoic of Romania, based on an isolated molar found in the Maastrichtian continental deposits near Pui village. This tooth was subject of controversies since its discovery, being considered either a first upper or lower molar by different authors, even receiving different names. The systematic affinities and paleobiogeographic significance of this taxon were accordingly poorly understood. The peculiar morphology of the holotype was the main reason for the uncertainties concerning the specimen, hindering for long time the understanding of its true affinities and relationships. *Barbatodon* was listed until recently as probable member of the *Paracimexomys* group, a "Middle" - Late Cretaceous North American clade.

The discovery of a partial multituberculate skeleton at Pui allows the critical reassessment of the validity and relationships of *Barbatodon transylvanicus*. The new specimen includes the almost complete lower dentition, associated with M2; comparisons with other Hațeg multituberculate remains suggest it is referable to *Barbatodon transylvanicus*. *Barbatodon transylvanicus* is shown to be a valid taxon, that belongs together with other multituberculates from the Hațeg Basin and the Cretaceous-Paleogene genus *Hainina* to the European endemic family Kogaionidae. This taxonomic reinterpretation has also important systematic and paleobiogeographic consequences.

Keywords - Hațeg Basin, Maastrichtian, multituberculates, *Barbatodon transylvanicus*, Kogaionidae

INTRODUCTION

European Late Cretaceous mammals are exceedingly rare; this picture is only beginning to change with recent discoveries from Portugal, Spain, France and Romania.

Their first published account dates back only as far as 1966, when an isolated molar was reported from the French locality of Champ-Garimond (Ledoux *et al.*, 1966). For more than 15 years, it was the only European Late Cretaceous mammal record, being mentioned as such in the first edition of a comprehensive treatise of Mesozoic mammals (Clemens *et al.*, 1979). More recently, several isolated mammal teeth were recovered from Campanian-Maastrichtian deposits of Portugal (Taveiro; Antunes *et al.*, 1986), France (Champ-Garimond, Sigé *et al.*, 1997; Vitrolles, Tabuce *et al.*, 2004; Cruzy, Buffetaut, 2005) and Spain (Laño, Gheerbrant & Astibia, 1999; Quintanilla de Coco, Pol *et al.*, 1992). These teeth have eutherian affinities, most of them belonging to a probably endemic European group related to the zhelestids (Gheerbrant & Astibia, 1999; Tabuce *et al.*, 2004).

The Late Cretaceous continental deposits of the Hațeg Basin (western Romania) had also yielded a mammal fauna, but, unlike the western European ones, one almost exclusively made up of multituberculates. Their presence was first reported by Grigorescu (1984) based on an isolated upper incisor. From 1984 onward, a considerable amount of fossil mammal material was discovered in different localities within the basin (Rădulescu & Samson, 1996; Csiki & Grigorescu, 2000; Codrea *et al.*, 2002; Smith *et al.*,

2002), revealing the presence of a rich local mammal fauna. Mammals were not only relatively diverse, but apparently abundant and widespread as well, making up one of the most important Late Cretaceous mammal assemblages worldwide (although less diverse than the rich assemblages of North America and central-eastern Asia) and the only from Europe with multituberculates.

One of the earliest multituberculate discoveries from Hațeg is represented by an isolated first molar, the holotype of *Barbatodon transylvanicus*, the first mammal taxon to be named from the Cretaceous of Romania. Due to its peculiar morphology and to the absence of associated material, taxonomic affiliation, phylogenetic and paleobiogeographic affinities, even nature of this material and validity of the taxon erected on it, were unclear and subject of controversies (see below).

A newly discovered multituberculate partial skeleton from Pui is referred here to *Barbatodon transylvanicus*. It allows the review of the systematic position of *Barbatodon*, with implications on the phylogeny of the derived multituberculates (Cimolodonta) and the paleobiogeographic affinities of the Hațeg fauna.

Institutional abbreviations: FGGUB – Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania; ISB – Institute of Speleology "Emil Racoviță", Bucharest, Romania; TBM – Transylvanian Basin Museum, "Babeș-Bolyai" University, Cluj-Napoca, Romania.

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Other abbreviations: i, p, m and M are used to designate lower incisors, premolars and molars and upper molars, respectively.

GEOLOGICAL SETTING

The Hațeg Basin (Fig. 1) is an intra-montane, post-tectonic depression formed after the climax of the Laramian orogenic phase (Late Senonian) responsible for the final structuring of the nappe pile of the Southern Carpathians (Willingshofer, 2000). The subsidence following the main thrusting phase and subsequent regional emersion led to the accumulation of a thick succession of continental deposits within the Hațeg Basin, now divided into two distinct, but partly time-correlative lithostratigraphic units, the Densuș-Ciula and the Sînpetru formations (e.g. Grigorescu, 1992).

Sedimentological studies of these continental, siliciclastic deposits suggest that their deposition took place in slightly different sedimentary environments. While the Densuș-Ciula Formation was deposited in alluvial fan, fluvial and palustrine settings locally recording traces of volcanic activity taking place in their close vicinity, the mostly fluvial and floodplain deposits of the Sînpetru Formation are almost completely devoid of volcanic components (Grigorescu, 1992).

The age of the continental deposits, first interpreted as Danian (e.g. Nopcsa, 1905), was then considered as being Late Maastrichtian, based on palynology, invertebrates and proposed similarities of the Hațeg vertebrate assemblage

with those from better dated western European deposits (Antonescu *et al.*, 1983). More recently, biostratigraphical studies focusing on the marine deposits unconformably underlying the Densuș-Ciula Formation (Grigorescu & Melinte, 2002) and paleomagnetical studies of the Sînpetru Formation (Panaïotu & Panaïotu, 2002; Therrien, 2004) independently proposed a somewhat older, Maastrichtian age for these deposits.

Regional geological and paleomagnetical studies suggest the Hațeg area was part of a larger emerged land having a southern position relative to its present location (at about 27°N latitude in the Late Cretaceous), well inside the subtropical climatic belt (Panaïotu & Panaïotu, 2002), a conclusion supported also by independent geochemical, sedimentological and paleobotanical data (e.g. Petrescu & Dușa, 1982, van Itterbeek *et al.*, 2004, Therrien, 2004, 2005, Therrien *et al.*, 2002, Bojar *et al.*, 2005). Most paleogeographical reconstructions show this emerged land as being largely isolated from the northern, European margin of the Tethys by deep-water marine basins with flysch deposition during the Late Cretaceous-Paleogene (e.g. Dercourt *et al.*, 2000). The paleogeographical reconstructions seem to be in good agreement with the endemic character of the vertebrate fauna from the Hațeg Basin.

The Maastrichtian deposits outcropping along the Bărbat River valley, south of Pui village, represent the easternmost occurrence of the Maastrichtian vertebrate-bearing deposits from the

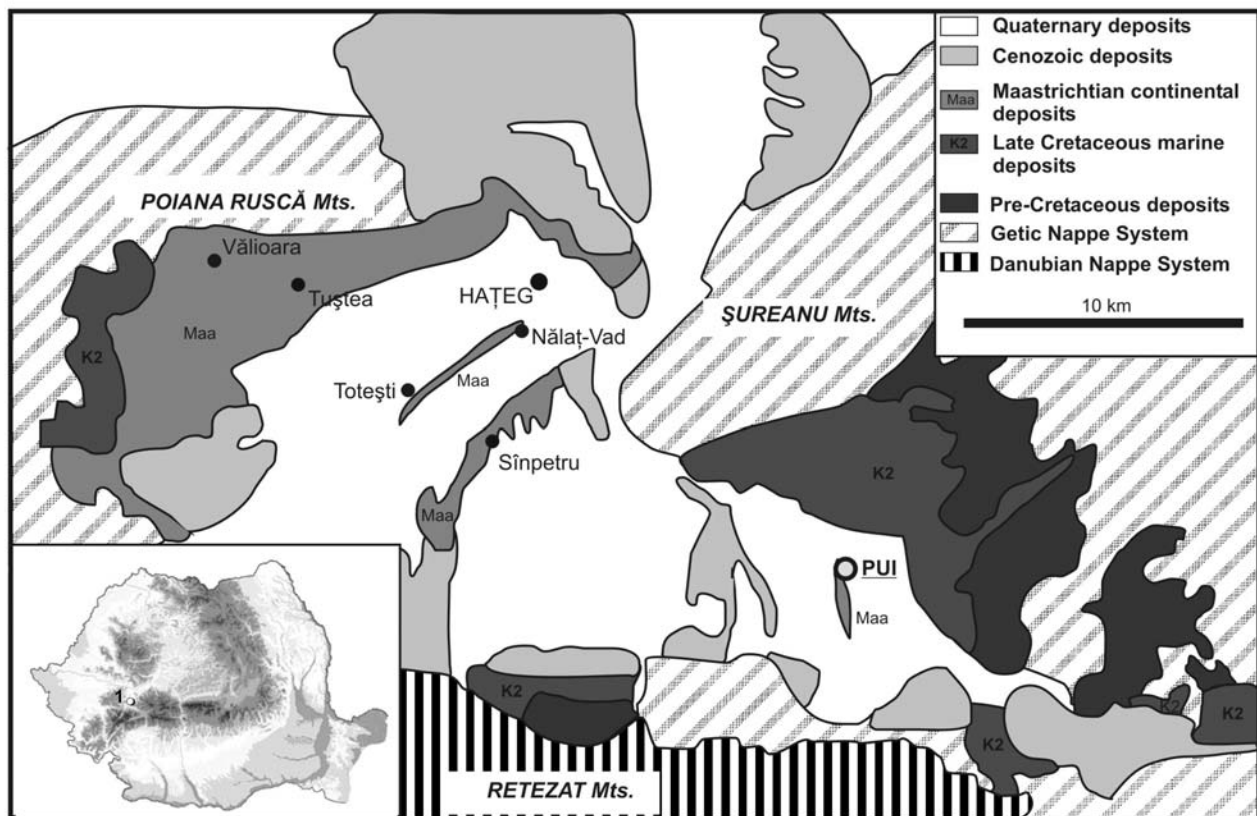


Fig. 1. Geological sketch of the Hațeg Basin (redrawn and completed after Bojar *et al.*, 2005), showing the most important multituberculate localities. Inset shows position of the Hațeg Basin (1).

Hațeg Basin. Reported as early as the beginning of the 20th century by Nopcsa (1905), their presence was subsequently overlooked until the regional geological synthesis of Stilla (1985) and the first Romanian-French paleontological researches (Grigorescu *et al.*, 1985).

The deposits at Bărbat River are somewhat different from the type section of the formation at Sînpetru, along the Sibișel valley, being represented mostly by brick-red and variegated micaceous siltstones and silty mudstones, with frequent, cm-thick calcret horizons. Cylindrical burrows are frequent, being especially abundant in and around the calcret horizons. Grey-green silty and sandstone beds, as well as rare conglomeratic bodies, appear intercalated in the red beds. The Maastrichtian age of the deposits is supported by the palynological content (van Itterbeek *et al.*, 2005), similar to those reported from the Sînpetru and Densuș-Ciula formations. Dinosaur remains occur usually as isolated bones or in microvertebrate fossil sites along with small vertebrates (Grigorescu *et al.*, 1985, 1999, Folie *et al.*, 2002, Folie & Codrea, 2003, 2005, Van Itterbeek *et al.*, 2004) or eggshells (Garcia *et al.*, 2002). Multituberculates were apparently quite abundant at Pui (Grigorescu *et al.*, 1985; Rădulescu & Samson, 1990; Smith & Codrea, 2003; Van Itterbeek *et al.*, 2004).

Recently, the deposits were the focus of several detailed studies on geochemistry, sedimentology, clay mineralogy and paleopedology (Van Itterbeek *et al.*, 2004; Therrien, 2005; Bojar *et al.*, 2005). According to these, the sediments were deposited distal to the major fluvial channels, experiencing long episodes of intense pedogenesis in periodically waterlogged, but mostly well-drained floodplain paleoenvironments.

The new multituberculate specimen was discovered in July 2002 by one of the co-authors (MR) during a Romanian-German fieldtrip in the Hațeg Basin following the 7th European Workshop on Vertebrate Paleontology, in the upper part of the Bărbat River section, in dark red coarse sandy siltstones with a diffuse horizontal lamination and small calcareous concretions. It was collected using a plaster jacket, and the matrix around the jacket was also bagged for screen-washing. The preparation of the jacketed specimen revealed the presence of both mandibles, the isolated left i1 and postcranial elements. The matrix yielded an isolated right M2, comparable in size to the lower dentition; it is consequently referred to the same specimen (FGGUB M.1635).

THE BARBATODON CONTROVERSIES

The holotype material of *Barbatodon transylvanicum*, an isolated molar, was recovered from the first microvertebrate fossil site from the Maastrichtian of the Hațeg Basin, a sandy lens in the Bărbat River valley succession, excavated by a Romanian-French team in 1983 (Grigorescu *et al.*, 1985). The microvertebrate material yielded four

isolated multituberculate teeth: two molars and two lower incisors, representing more than one taxon (Rădulescu & Samson, 1990, 1997).

The most diagnostic specimen from this sample, mentioned and figured as a left M1 was referred to as cf. *Paracimexomys* (“peut être rapprochée du genre *Paracimexomys*”; Grigorescu *et al.*, 1985: p. 1367), and compared to “quelques genres de Multituberculés primitifs, fréquents dans le Crétacé supérieur de l’Amérique du Nord, mais beaucoup plus rares dans celui de Mongolie.. les genres *Cimexomys* et *Paracimexomys*... (et) *Kryptobaatar*” (op. cit., p. 1367).

This molar (ISB IS.001) was designated soon thereafter as the holotype of two new taxa. Rădulescu & Samson (1986), based on this tooth, considered to represent a left first upper molar, erected the new taxon *Barbatodon transylvanicum* (sic), to which they also referred a fragmentary lower incisor coming from the same locality (ISB IS.003). *Barbatodon* was considered to be probably related to the Mongolian *Kryptobaatar* (= *Gobibaatar*), and as such, showing Asian (Mongolian) paleobiogeographic affinities (“ce genre pourrait être considéré comme représentant l’extension maximale vers l’Europe de la faune de Multituberculés de Mongolie.”; op. cit., p. 1829).

The same tooth, considered a left m1, was chosen as the holotype of *Paracimexomys? dacicus*, erected by Grigorescu & Hahn (1987) and diagnosed by “m1 with 4:3 cusps, m2 with 3:2 cusps, last labial cusp of m1 with a cingulum-like structure unknown in other species of *Paracimexomys*” (op. cit., 238). Implicitly, the taxon was seen as a close relative of relatively generalized Late Cretaceous North American multituberculates. The authors also referred to the new taxon the isolated m2 discovered in the same site, despite the significant size differences between the molars.

Although both papers (and names) were published within a short time span, since that of Rădulescu & Samson appeared earlier, their proposed name (*Barbatodon transylvanicus*) has precedence over *Paracimexomys? dacicus*, which thus became the junior synonym of the former one. According to this, the publications following 1987 referred to the Pui taxon as *Barbatodon*, considering *P.? dacicus* is synonymous with it.

The interpretation given to *Barbatodon* raised several problems. Admitting that its affinities are poorly understood, its authors continued to consider the holotype specimen an M1 in all discussions they made, which profoundly influenced their understanding of the specimen. After considering it related to the Mongolian Late Cretaceous multituberculates grouped in the Djadochtherioidea (Kielan-Jaworowska & Hurum, 1997), the possibly endemic nature of the taxon was also suggested (Rădulescu & Samson, 1997), the retention of primitive characters in *Barbatodon*, *Kryptobaatar* and members of the *Paracimexomys* group being interpreted as “developed

independently... rather than reflecting a close phyletic relationship.” (op. cit., p. 248).

However, recent comprehensive reviews and phylogenetic analyses of the multituberculates grouped, although tentatively, *Barbatodon* with members of the *Paracimexomys* group, a possibly paraphyletic basal assemblage of the Cimolodonta (Kielan-Jaworowska & Hurum, 2001; Kielan-Jaworowska *et al.*, 2004) or placed it, together with “paracimexomyians”, *Uzbekbaatar*, *Clemensodon* and *Hainina*, as *incertae sedis* within the basal members of the Cimolodonta (McKenna & Bell, 1997). Even in these recent reviews, the holotype molar of *Barbatodon* is discussed as a M1 (e.g. Kielan-Jaworowska *et al.*, 2004); only Smith *et al.* (2002) has considered this specimen as m1.

Both of these alternative hypotheses preclude thus a close relationship of *Barbatodon* with the endemic Asiatic djadochtatherioideans, as advocated by Rădulescu & Samson. Moreover, its inclusion into the informal *Paracimexomys* group, of late Early-Late Cretaceous North American distribution (Archibald, 1982; Eaton, 1995; Eaton & Cifelli, 2001; it is noteworthy, however, that recently *Uzbekbaatar* from the Late Cretaceous of Middle Asia was also suggested to belong to this group, Averianov & Archibald, 2003) points to North American paleobiogeographical ties, instead of Asiatic ones.

Either of these taxonomic allocations of *Barbatodon* stands in contrast with the systematic affinities of the other multituberculates from the Hațeg Basin that seem to belong to the peculiar Kogaionidae family. The family was first erected to include *Kogaionon unguereanui* (Rădulescu & Samson, 1996), a taxon based on an almost complete skull with upper dentition (ISB SPT/001). Although the skull is virtually complete, the authors published only the drawings of the anterior part of the skull and that of the dentition; reconstruction of the complete skull is published by Kielan-Jaworowska *et al.* (2004: fig. 8.42A).

The relationships of the Kogaionidae, as defined initially by Rădulescu & Samson (1996, 1997), to the other derived multituberculate groups of the suborder Cimolodonta were rather poorly understood and controversial. McKenna & Bell (1997) listed the family, together with the Bolodontidae (including *Eobaatar*) and Arginbaataridae, as less derived than the Cimolodonta. Kielan-Jaworowska & Hurum (2001) established the cimolodontan affinities of the family, suggesting that the Late Cretaceous – Paleocene genus *Hainina* (Vianey-Liaud, 1979, 1986) probably also belongs to this family (see also e.g. Peláez-Campomanes *et al.*, 2000; Csiki & Grigorescu, 2001). The relationship between *Hainina* and *Kogaionon* is further supported by the study of Fosse *et al.* (2001), showing that both genera share a gigantoprismatic enamel type.

Subsequently, a large sample of multituberculate remains was recovered from different sites in the Hațeg Basin, including

potentially new species of the genera *Kogaionon*, *Hainina* and *Barbatodon* (Csiki & Grigorescu, 2000, 2002; Codrea *et al.*, 2002; Smith *et al.*, 2002; Smith & Codrea, 2003), all of these being referred (explicitly or implicitly) to the Kogaionidae.

Isolated m1's from the Fântânele fossil site at Vălioara, referred to *Hainina*-like kogaionids, are remarkably similar in general morphology to the holotype of *Barbatodon transylvanicus* (Csiki & Grigorescu, 2001), suggesting that this specimen is indeed m1, as first hinted at by Grigorescu & Hahn (1987) and that it might have kogaionid rather than *Paracimexomys*-group affinities.

Multituberculate specimens referred to *Barbatodon* were described recently from Totești and Nălaț-Vad localities (Smith *et al.*, 2002; Smith & Codrea, 2003). The Nălaț-Vad locality yielded several teeth that seem to represent a second, small-sized species of the genus (see Plate II, H, I), while teeth referred to *B. transylvanicus* were reported from Totești; this taxon is probably the same to the one mentioned as Kogaionidae indet. by Codrea *et al.* (2002) from this locality (Plate II, M). In both instances, referral to *Barbatodon* was made based on the inferred similar morphology of the m1's, thus considering (without discussing the underlying reason) the holotype of *B. transylvanicus* a lower molar.

In conclusion, the *Barbatodon* controversy involves four different issues: nomenclatural (*Barbatodon transylvanicus* Rădulescu & Samson, 1986 vs. *Paracimexomys? dacicus* Grigorescu & Hahn, 1987), morphological (M1 vs. m1), systematic-phylogenetic (endemic, *Kryptobaatar*-like or related to the *Paracimexomys*-group) and correlative paleobiogeographical (suggesting Asian or North American relationships) ones.

Moreover, if ISB IS.001 represents a *Hainina*-like (thus kogaionid) m1, its diagnostic value should be re-evaluated. When compared to the different species of *Hainina* (the only kogaionids with known lower dentition), it reveals the same basic morphological pattern, with a short and relatively wide, rectangular shape and a reduced cusp formula with 3-4 cusps in each row. Looking into more detail, it shares with *Hainina vianeyae* a cusp formula of 4:3, while all other species of *Hainina*, as well as all other Hațeg kogaionids have a cusp formula of 3:3. However, reduced sample size does not allow full understanding of the range of potential individual variation of cusp formulae in kogaionids, while this kind of variation occur frequently in other cimolodontans. Consequently, due to its generalized kogaionid morphology and isolated nature, ISB IS.001 is possibly not diagnostic at species, let aside genus level.

To further complicate the problem, reinterpreting the holotype of *Barbatodon* as a m1 raises other, more fundamental, issues as well. Rădulescu & Samson (1996), comparing the newly erected *Kogaionon unguereanui* to *Barbatodon*, found clear-cut differences between the M1 of *Kogaionon* and the (supposed) M1 of *Barbatodon*,

differences that justified in their view the taxonomic distinction between the two taxa. They even allocated the two taxa into entirely different groups, an idea followed by McKenna & Bell (1997), Kielan-Jaworowska & Hurum (2001) and Kielan-Jaworowska *et al.* (2004). If, however, ISB IS. 001 represents a kogaionid m1, the problem of the synonymy of the two taxa is open to discussion.

Since only the upper dentition of *Kogaionon* and lower dentition of *Barbatodon* are known, both of typical kogaionid patterns, one might consider that they in fact represent the same taxon (an issue already raised by Csiki & Grigorescu, 2002). And, indeed, the m1-to-M1 length ratio observed within this composite dentition is inside the range of variation seen in the different Paleocene kogaionids (unpubl. data); morphological details (e.g. absence of ornamentation, known in some *Hainina* species) may also support the idea of synonymy.

In case the two formally named taxa from the Hațeg Basin would have proven to be synonyms, *Barbatodon transylvanicum* will obviously have precedence over *Kogaionon ungureanui*, which will become its junior synonymy.

Be that as it may, *Kogaionon*, a taxon represented by much more complete and diagnostic material and that had already been involved in discussions concerning the systematics and phylogeny of multituberculates, will be subduced to *Barbatodon*, a taxon established on an isolated and potentially not diagnostic molar.

Consequently, the problem of the systematic affinities of the genus *Barbatodon* (and that of *Barbatodon transylvanicus*), as well as that of the synonymy of *Barbatodon* and *Kogaionon*, must represent a matter of new, detailed enquiry, one that should use better material referable to the former taxon, eventually presenting unambiguously associated upper and lower dentition, since several different kogaionid taxa, based on no more than isolated teeth, are known from the deposits yielding *Barbatodon*.

THE NEW PUI SPECIMEN

The new multituberculate specimen to be discussed was found in the Maastrichtian deposits outcropping in the right bank of the Bărbat River valley bed, about 1.3 km upstream of the Pui bridge. It consists of associated cranial and postcranial remains of an individual, including both (incomplete) mandibles, with *in situ* p4-m1 and (in the right ramus) i1, isolated left i1, and right M2, as well left femur, fragmentary vertebrae and pelvic girdle. Associated to the specimen only bone debris, pieces of gastropod shells and diverse eggshell fragments were recovered.

Only the mandibles and dentition will be shortly described here, in order to compare it to *Barbatodon transylvanicus* and other multituberculates and to discuss the affinities and relationships of *Barbatodon*. A revised diagnosis of the family Kogaionidae and of the genus

Barbatodon is also provided; emendations are based chiefly on the new *Barbatodon* specimen from Pui.

SYSTEMATICS

Order **Multituberculata** Cope, 1884

Suborder **Cimolodonta** McKenna, 1975

Family **Kogaionidae** Rădulescu & Samson, 1996

Revised diagnosis (based in part on Rădulescu & Samson, 1996; Kielan-Jaworowska *et al.*, 2004). – Shares with other members of Cimolodonta the dental formulae of upper dentition (known in *Kogaionon* - 2:0:4:2) and lower dentition (known in *Barbatodon* - 1:0:1-2:2). Differ from other cimolodontans by strongly elongated upper premolars, of which P3 is the longest, by the upper premolar tooth row twice as long as molar row and M1 short and wide, with 4 cusps in middle row and almost complete or complete lingual row. Incisors (i1, i2) with limited enamel band, differing in this respect from the members of the Ptilodontoidea. The p4 arched, slightly raised above the level of molar occlusal plane, but to a lesser extent than in Ptilodontoidea, with small number of cusps (9-10). The m1 short, rectangular, with a low cusp formula (3-4:3), lower than in most other cimolodontans and remembering certain plagiaulacids. Molar enamel smooth in *Kogaionon* and *Barbatodon*, but ornamented with grooves in some species of the genus *Hainina*. Enamel microstructure (known in *Hainina* and *Kogaionon*) gigantoprismatic, differing in this respect from Ptilodontoidea.

The skull (only known in *Kogaionon*) has short basicranial region, strongly elongated snout and transversely oriented anterior part of the zygomatic arches. Share with Ptilodontoidea a short premaxilla, a nearly transverse suture between the nasals and frontals, far posteriorly placed foramina on the nasals and posteriorly pointed frontals (also present in taeniolabidoids). The suture between the frontals and parietals is autapomorphically digitated.

Genera assigned. – *Kogaionon* Rădulescu & Samson, 1996, *Barbatodon* Rădulescu & Samson, 1986 and *Hainina* Vianey-Liaud, 1979.

Distribution. – Late Cretaceous (Maastrichtian), Romania, Paleogene (Early Paleocene, Spain; Middle Paleocene, Belgium; Late Paleocene, France, Spain, Romania).

Genus ***Barbatodon*** Rădulescu & Samson, 1986

Type species: *Barbatodon transylvanicus* Rădulescu & Samson, 1986; Pui, Hațeg Basin (Romania); Sînpetru Formation, Maastrichtian

Revised diagnosis. – *Barbatodon* is middle-large sized kogaionid multituberculate, characterized by a lower dental formula 1:0:1:2. The i1 is elongated, with unevenly developed enamel, thicker ventrolabially. Triangular-rounded p4, slightly raised over the occlusal level of the molars, with a small number of cusps (9). It differs from *Hainina* (*H.*

belgica) by the presence of a well-developed labio-distal shelf on p4; distal width of p4 larger than mesial width. The m1 rectangular, with low cusp formula ((3?)4:3 – only present in *Hainina vianeyae*, while all other species of *Hainina*, in which m1 is known, have a cusp formula of 3:3) and an autapomorphic labio-distal crescentiform crest. In occlusal view, the crown shows a slight midline waist. M2 with a cusp formula crest (1):2:3, with a small, crest-like labial cusp, relatively less developed than in *Kogaionon*. Relatively smooth enamel, similar to *Kogaionon* and certain species of *Hainina* (*H. pyrenaica*, *H. belgica*), but different from *H. vianeyae* and *H. godfriauxi*.

Distribution. – Sînpetru Formation, Maastrichtian, localities Pui, Totești and Nălaț-Vad.

Barbatodon transylvanicus Rădulescu & Samson, 1986

(syn. *Paracimexomys* ? *dacicus* Grigorescu & Hahn, 1987)

Pl. I, Figs. A-D, Pl. II, Figs. A-G, J, K, M

Holotype: ISB IS.001, a left first lower molar, figured by Rădulescu & Samson (1986: Pl. I, 1a-c; see Pl. II, Fig. G). A cast of the specimen is deposited in the collections of the Laboratory of Paleontology, University of Bucharest (FGGUB M.1634)

Diagnosis: Large species of the genus *Barbatodon*, characterized by a rectangular m1 compared to rostrally narrowing m1 in the undescribed species from Nălaț-Vad. The labio-distal crest is less well developed, shorter than in the undescribed species from Nălaț-Vad.

Some of the apomorphic features of the genus *Barbatodon*, noted above, might in fact prove to be autapomorphies of this species, when the abundant material from Nălaț-Vad will be described in detail by T. Smith and V. Codrea.

Distribution. – Sînpetru Formation, Maastrichtian, localities Pui and possibly Totești.

Referred material:

- ISB IS.003, isolated fragmentary i1, Pui (Rădulescu & Samson, 1986, figured by Rădulescu & Samson, 1997: fig. 2.2); the relatively small size of the specimen, compared to the i1 of FGGUB R.1635, suggests the specimen might not have been correctly referred to *B. transylvanicus*

- FGGUB M.1635, associated incomplete mandibles, isolated left i2 and right M2, postcranial remains, Pui.

Description of FGGUB R.1635

Mandible: Both mandibles (Plate I A, B) are incomplete, but preserve different segments of the bone, so that the shape of the complete mandible can be reconstructed (Plate I, D), except the distal part of the coronoid process. The total length of the reconstructed mandible (measured in occlusal view, with the molar occlusal surface held horizontal) should be around 32.4 mm. The mandibular diastema is relatively short,

representing 60% of the rostro-distal length of p4, comparable with the condition seen in ptilodontids (*Ptilodus montanus*), cimolodontids (*Cimolodon nitidus*) or djadochtatherioideans with large p4 (*Nemegtbaatar*, *Kamptobaatar*, *Sloanbaatar*). The relatively large mental foramen is slightly distal to the base of i1, in the upper third of the labial face of the diastema. The angle between the ventral margin and the occlusal surface of the molars is low, about 10° (this represents the plesiomorphic state of the character, cf. the analysis of Kielan-Jaworowska & Hurum, 1997), similar with the taeniolabidoid *Taeniolabis* or the basal djadochtatherioideans *Nemegtbaatar* and *Kamptobaatar*, but differing from ptilodontoids (*Ptilodus*), *Lambdopsalis* and derived djadochtatherioideans (*Djadochtatherium*, *Catopsbaatar* and especially *Sloanbaatar*).

Distally, there is a deep, triangular masseteric fossa on the labial face. The mesial base of the coronoid process is placed labio-ventrally to the distal margin of the mesial root of m1, the coronoid process hiding m2 in labial view. The mesial margin of the coronoid process makes an angle of 57° with the occlusal plane of the molars, showing the plesiomorphic state similar to *Ptilodus*, *Sloanbaatar* or *Catopsbaatar*, slightly lower than in *Lambdopsalis*, *Nessovbaatar* or *Taeniolabis*, but higher than in *Kryptobaatar*, *Chulsanbaatar* or *Nemegtbaatar*. The pterygoid fossa is very deep, extending mesially to the distal end of m2.

Dentition: The lower dental formula is 1:0:1:2.

The i1 is elongated, relatively gracile (but less so than in ptilodontoids) and slightly curved. The enamel cover is unequally developed, restricted to the ventro-labial face. It is similar to those described previously by Rădulescu & Samson (1997: fig. 2) and Csiki & Grigorescu (2000: fig. 3), but significantly larger.

There is no p3, neither is accommodation space for it in the front of p4. From this point of view, the Pui specimen resembles certain derived cimolodontans such as eucosmodontids (*Stygimys*, *Eucosmodon*), taeniolabidoideans (*Catopsalis*, *Lambdopsalis*, *Taeniolabis*), *Buginbaatar* and microcosmodontids (*Acheronodon*, *Pentacosmodon*, but not *Microcosmodon*). Loss of p3 represents the apomorphic state within Cimolodonta, although its significance is highly dependent on the phylogenetic scheme adopted.

Few examples of p4's were described in kogaionids. A single isolated p4 was referred to *Hainina belgica* by Vianey-Liaud (1979); a small mesial fragment from Vălioara (FGGUB M.1615) was referred to the small-sized *Hainina* sp. A by Csiki & Grigorescu (2000). A small depression seen on the basalmost mesial crown in FGGUB M.1615 was interpreted as accommodating a small peg-like p3; a similar depression is present on the mesial face of the anterior root of p4 in *Hainina belgica* (pers. observ.), but completely absent in M.1635. It is thus possible that either the previous

interpretation of these depressions is erroneous, and p3 is missing altogether in kogaionids, or that this character is polymorphic within the family as it is in microcosmodontids.

The single premolar, a blade-like p4 (Plate I, A-C, Plate II, A-D) shows the typical cimolodontan pattern. It is asymmetrical, rounded, with the highest point placed slightly mesially, at the level of cusps 4-5. The crown is slightly raised over the occlusal surface of m1 and shows 9 cusps. The first cusp is conical and mesially projected; a similar pattern is present in FGGUB M.1615 from Vălioara, described by Csiki & Grigorescu (2000: fig. 2G), but this tooth is much smaller.

All other cusps are directed dorsally and distally, and cusp 9 is only visible in lingual view. Labial ridges are present only under cusps 2-7, while all cusps have lingual ridges; these run parallel with each other. The anterior triangular lobe is shallow, rostro-distally wide and rectangular, unlike the typical triangular shape seen in e.g. *Nessovbatar*, *Mimetodon*, *Cimexomys* or *Cimolodon*. Distally, a well-developed labio-distal shelf is present beginning level with cusp 8 and continuing to the distal edge of the crown; due to this platform, in occlusal view the crown is widest distally, and not mesially, at the level of the anterior triangular lobe, as usually seen in multituberculates (Plate 1, C; Plate 2, C, D). Advanced wear make unclear whether cusps were present on this platform. The shelf is continuous with the labial cusp row of m1, while the blade itself is placed in the front of the lingual row.

The p4 differs from that described for *Hainina belgica* by Vianey-Liaud (1979) by its much larger size, higher blade, morphology of the first cusp, better developed labio-distal platform and smaller cusp count (9 vs. 10, better developed cusps in *Hainina*).

Both m1's are present, but are worn and incomplete distally (Plate II, E, F). In occlusal view the contour of the crown is rectangular, slightly trapezoidal (length: 3.35 mm; maximum width: 2.15 mm – right, 2.2 mm – left) with a midline waist. The mesial margin is largely rounded, while the distal margin is oblique, so that the labial length is greater than the lingual one.

Cusp formula was apparently 3-4?:3. Both rows preserve the first two cusps; because the distal part is damaged in both specimens, the number of cusps in this area is unclear. However, taken into account the size of the damaged area, only one cusp per row (eventually 2 small ones labially) might have had existed.

The cusps are pyramidal, massive and slightly distally leaning; they are opposite in the mesial part, contrasting *Paracimexomys*, *Bryceomys* or *Cedaromys* (Eaton & Cifelli, 2001), where these are alternate, and become slightly alternating farther distally. The enamel is smooth, unlike different species of *Hainina*, where it is ornamented. Distally, there is a crescent-shaped labio-distal crest on the labial margin, starting level

with the distal edge of the second cusp and being distally confluent with the distal margin of the crown. The length of the crest represents 42% of the crown length.

Although the m2 is not preserved, the empty tooth locus (Plate I, C) allows estimation of its size; it might have had a length slightly over 2 mm, and a width of slightly less than 2 mm.

The isolated right M2 (Plate II, J, K; 2.45 mm x 2.2 mm) has a subcircular-trapezoidal outline and two roots. The cusp formula is crest (1):2:3. The labio-mesial cusp is small, low and crest-like; the other cusps are massive, sub-pyramidal, slightly mesially leaning. The first two cusps of the lingual row are closely spaced, separated only by a shallow incisure. The enamel is smooth.

COMPARISONS AND DISCUSSIONS

The importance of FGGUB M. 1635 resides in preserving dentition *in situ*, as well as in the association of upper and lower dental elements, allowing thus comparison with both previously named multituberculate taxa from Hațeg: *Barbatodon transylvanicus* and *Kogaionon ungureanui*.

Comparison of the *Barbatodon* holotype to the m1's of FGGUB M.1635 reveals striking similarities. The dimensions of ISB IS.001, as reported by Rădulescu & Samson (1986: length 3,38 mm, width 2,20 mm) are practically identical with those of the m1's of the Pui specimen (see Plate II, F, G). The largely rectangular contour, with a midline waist, and proportions are also similar. Although the distal part of the m1's of FGGUB M.1635 are damaged, making difficult to establish the cusp formula, the shape and dimensions of the preserved cusps suggest a formula of 3(?4):3, which, together with the presence of the crescentiform labio-distal crest, also evokes ISB IS.001. The relative development and proportions of the individual cusps are again comparable. Moreover, both ISB IS.001 and FGGUB M.1635 are recovered from the relatively small outcrop sequence of the Bărbat River valley, suggesting the age difference between the two specimens is minimal, if any. These observations suggest that FGGUB M.1635 is referable to *Barbatodon transylvanicus*.

The *in situ* preservation of the m1's and their morphological similarity to the *Barbatodon* holotype also settles the morphological controversy noted above, showing that ISB IS.001 is indeed a m1 as suggested by Grigorescu & Hahn (1987) instead of a M1 as supported by Rădulescu & Samson (1986). Consequently, the initial diagnosis of *Barbatodon transylvanicus* should read as: "middle-large sized multituberculate, characterized by a m1 with low cusp formula (3-4:3) and by the presence of a labio-distal crescentiform crest. In occlusal view, the crown shows a midline waist. Smooth enamel." Moreover, the diagnosis of the taxon can be supplemented and emended based on

informations derived from the associated dentition of FGGUB M.1635 (see *Revised diagnosis* and below).

Comparing *Barbatodon transylvanicus* (based on the reinterpreted holotype and the referred specimen from Pui) with other multituberculates from the Hațeg Basin and elsewhere suggests this taxon is valid and can be differentially diagnosed. It is different from most Late Cretaceous multituberculates by its low cusp formula on m1 (3-4:3; also present in other Hațeg multituberculates, *Hainina* and most *Paracimexomys*-group multituberculates, but not cf. *Paracimexomys perplexus*, *P. priscus*, cf. Eaton & Cifelli, 2001, *Cimexomys*, Archibald, 1982, Montellano *et al.*, 2000, as well as *Uzbekbaatar wardi*, if considered member of the group, Averianov & Archibald, 2003). It also differs from most members of the *Paracimexomys* group (*Bryceomys*, *Cedaromys*, *Paracimexomys*, *Cimexomys*) in that the central valley of m1 is straight, and especially in the first cusps being of the same size and opposite instead of alternate (in this respect it also differs from *Dakotamys* and *Uzbekbaatar*).

The presence of a labio-distal cingulum on m1 occurs very rarely among cimolodontans. A labio-distal cingulum was reported in the early Campanian *Cimolodon electus* by Fox (1971), who mentions the occurrence of this feature also in *C. nitidus*. In these cases, however, the cingulum presents a marked individual variation from missing to well-developed, and is associated with elongated, multicusped (5-8:4-7) typical cimolodontan m1. A short supplementary labial cusp row is reported in one specimen of *Neoplagiaulax serrator* by Scott (2005), but whether this is comparable to the cingulum of *Barbatodon* is not clear.

When compared to other kogaionids with known lower dentition, *Barbatodon transylvanicus* is remarkable by its large size (its m1 is at least 25% larger than all known kogaionid m1's), relatively wider shape of m1 and the presence of a well-individualized labio-distal cingulum (also known in the *Barbatodon* n. sp. from Nălaț-Vad; Smith *et al.*, 2002). Moreover, *Barbatodon* (including also *Barbatodon* n. sp. from Nălaț-Vad) differs from most known kogaionids (but not *Hainina vianeyae*) by its slightly higher cusp formula (3?-4:3 compared to 3:3), from *H. godfriauxi* and *H. vianeyae* by the smooth (vs. ornamented) enamel of the molars, and from *H. pyrenaica* by its opposite (vs. alternating) cusps.

Moreover, as FGGUB M.1635 also includes associated elements of the upper dentition (M2), for the first time *Barbatodon transylvanicus* can be directly compared to *Kogaionon unguoreanui*. The comparison is enlightening, since (besides the generally similar shape and morphological details) it reveals several differences (see Plate II, K, L). The most important of these concerns the shape and development of the labial cusp (crest), which is longer, more bulbous and labially expanded in

Kogaionon than in *Barbatodon*. In occlusal view, the outline of M2 is roughly triangular in *Kogaionon*, with an obliquely sloping labio-distal margin, but trapez-shaped in *Barbatodon*, with a rounded labio-distal margin. *Kogaionon* is also marginally (about 18%) larger than *Barbatodon*. Thus, although admittedly the possibilities of direct comparisons are limited, *Kogaionon unguoreanui* seems to be different from *Barbatodon transylvanicus*.

These comparisons suggest that, despite the limited nature of the holotype material of *Barbatodon transylvanicus* (an isolated left m1), the taxon can be diagnosed and shown to be different from all other cimolodontans.

Moreover, the Pui specimen referred here to *Barbatodon transylvanicus* (FGGUB M.1635) allows a more detailed diagnosis of this taxon, to also include other characters of the dentition (a more complete diagnosis of the taxon will emerge after the completion of the preparation and detailed description of FGGUB M.1635).

The presence of *Barbatodon*-like material at Nălaț-Vad was reported by Smith *et al.* (2002: pl. I, fig. 1, 2; TBM V.442). Size (*B. transylvanicus* is estimated to be 70% larger) and morphological differences (e.g. m1 narrower mesially than distally) suggest the Nălaț-Vad material probably belongs to a new species of the genus *Barbatodon*. It shows that the presence of a crescent-like labio-distal crest on m1, the smooth enamel and the opposite arrangement of the cusps on m1 (yielding a straight longitudinal valley) represent probably apomorphies of the genus *Barbatodon*, instead of being diagnostic to *Barbatodon transylvanicus*, as proposed before by Rădulescu & Samson (1986).

PHYLOGENETIC AND PALEOBIOGEOGRAPHIC IMPLICATIONS

The holotype m1 of *Barbatodon transylvanicus* is strongly reminiscent of those of other kogaionids; the main similarities include a relatively short and wide crown (also found in *Eobaatar*, *Arginbaatar* and members of the *Paracimexomys*-group) with a low cusp formula (3-4:3) occurring extremely rarely within the Cimolodonta. *Barbatodon* is surely not referable to the Arginbaataridae (due to the differences in the structure and morphology of p4) or the Eobaataridae (presence of only one lower premolar, non-coalescing cusps). Neither is it referable to the *Paracimexomys*-group, due to the different morphology and opposite (vs. alternating) arrangement of the cusps in m1. It is thus referred here to the family Kogaionidae, an endemic Late Cretaceous – Paleocene group from Europe.

The referral of *Barbatodon* to the Kogaionidae allows a more complete diagnosis of the family, to include characters of the lower dentition, too. This, in turn, may allow a better understanding of the systematic position and phylogenetic relationships

of this peculiar group of cimolodontan multituberculates (work in progress).

Another important consequence of the reinterpretation of *Barbatodon* as a kogaionid concerns the paleobiogeographic significance of the taxon. Previous referral of the taxon was to the basal cimolodontan *Paracimexomys*-group, whose members are known only from the Middle-Late Cretaceous of North America (Eaton, 1995; Eaton & Cifelli, 2001; Kielan-Jaworowska & Hurum, 2001; Kielan-Jaworowska *et al.*, 2004), with the possible exception of the provisionally referred *Uzbekbaatar* from the Late Cretaceous of Middle Asia (Averianov & Archibald, 2003). Based on this, *Barbatodon* was interpretable as a European immigrant member of the *Paracimexomys*-group, thus suggesting paleobiogeographical connections and faunal exchange with North America during the Late Cretaceous. This was at odds with the biogeographical affinities of other Late Cretaceous mammals of Europe, members of either the endemic Kogaionidae or that of the probably endemic zhelestid-like group including the eutherians *Labes*, *Lainodon* and *Valentinella*.

If, however, *Barbatodon* is a member of the Kogaionidae, no connections to the North American multituberculate faunas should be hypothesized before the Middle-Late Paleocene, when representatives of typical North American multituberculates (neoplagiaulacids, cimolodontids) entered western Europe (e.g. Vianey-Liaud, 1986). Their subsequent diversification stands in contrast with the constantly low diversity of kogaionids during the Paleocene. Decline and disappearance of the kogaionids after the Paleocene suggests that competition with the North American multituberculate immigrants (and with rodents) probably was responsible for the demise of this endemic clade of European multituberculates.

CONCLUSIONS

A new, incomplete but associated, multituberculate skeleton (FGGUB M.1635) allows the taxonomic and systematic reassessment of *Barbatodon transylvanicus* Rădulescu & Samson, 1986, the first Mesozoic mammal taxon named from Romania.

The *in situ* preserved lower dentition of the new specimen demonstrates that the holotype of *Barbatodon transylvanicus* is a m1, as suggested previously by Grigorescu & Hahn (1987). Similarities in size and morphology between the *B. transylvanicus* holotype and the m1's of FGGUB M.1635 from Pui strongly argues for a taxonomic identity of the two. Thus, the new specimen is here referred to *Barbatodon transylvanicus*.

The morphological reinterpretation of ISB IS.001 has profound influences on the systematic affinities of *Barbatodon*, previously referred to the *Paracimexomys*-group. It can belong instead to the European endemic family Kogaionidae, to which all other multituberculates from Hațeg were also referred.

Through the referral of FGGUB M.1635 to *Barbatodon transylvanicus*, this taxon is shown to be valid. A more complete diagnosis is also possible, to include characters of the i1, p4 and M2 as well. Based on this specimen and other discoveries from the Hațeg Basin, referred to the genus *Barbatodon*, it is possible to identify apomorphies of *Barbatodon*, as well as autapomorphies of the species *B. transylvanicus*.

All Hațeg multituberculates appear to belong to the Kogaionidae, a group of endemic European multituberculates from the Maastrichtian-Paleocene, whose relationships to other cimolodontan clades are yet poorly understood (Kielan-Jaworowska & Hurum, 2001). The reinterpretation of *Barbatodon* as a kogaionid weakens support for the presence of potential paleobiogeographical ties of the Hațeg fauna with North America, as was previously suggested by its proposed membership within the *Paracimexomys*-group.

ACKNOWLEDGMENTS

The authors thank the participants of the July 2002 fieldtrip for their efforts in excavating the specimen. The late Costin Rădulescu kindly made access to the holotype of *Kogaionon unguoreanui* and shared information and ideas on Hațeg multituberculates. Thierry Smith (Royal Belgian Institute of Natural Sciences, Bruxelles) and Vlad Codrea (Babeș-Bolyai University, Cluj-Napoca) are thanked for the informations and discussions about the Hațeg multituberculates; Vlad Codrea is also thanked for access to the unpublished kogaionid material from the Late Paleocene of Jibou (Romania). ZCs wishes to thank Zofia Kielan-Jaworowska (Institute of Paleobiology, Warsaw) for introduction in the field of multituberculate studies, and access to her extensive collection of multituberculates. Zofia Kielan-Jaworowska, Richard Cifelli (Oklahoma Museum of Natural History, Norman) and Thierry Smith helped with important references. Julien Cillis (RBINS) made the microphotographs. Comments and suggestions by Zofia Kielan-Jaworowska and Thierry Smith helped to improve the manuscript. Financial support, through grant G95 CNCSIS/2003 and EC FP5 Project ABC 95/2003, for ZCs is acknowledged.

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PLATE CAPTIONS

PLATE I

Barbatodon transylvanicus (FGGUB M.1635). **A** – right mandible, labial view; **B** – left mandible, labial view; **C** – outline drawing of the left mandible, occlusal view; **D** – reconstruction of the left mandible, in labial view (composite drawing, based on incomplete right and left rami). Abbreviation: m. f. – mental foramen.

PLATE II

Barbatodon transylvanicus (FGGUB M. 1635). **A** – right p4-m1, lingual view; **B** – left p4-m1, lingual view; **C** – left p4-M1 and **D** – right p4-m1, occlusal view; **E** – right m1 and **F** – left m1, occlusal view. *Barbatodon transylvanicum*, holotype m1 (ISB IS.001), **G** – occlusal view (from Rădulescu & Samson, 1986). *Barbatodon* sp. (Nălaț-Vad, TBM V.442), left m1, **H** – occlusal view; **I** – labial view (from Smith *et al.*, 2002). *Barbatodon transylvanicus* (M.1635), **J** – right M2, oblique labio-ventral view, (the rostral margin is to the left); **K** – right M2, occlusal view. *Kogaionon unguoreanui* (ISB SPT/001), **L** – left M2, occlusal view (from Rădulescu & Samson, 1996). *Kogaionidae* indet. (*Barbatodon transylvanicus?*, Totești, TBM V.441), **M** – right M2, occlusal view (from Codrea *et al.*, 2002). A-F, H-K and M SEM microphotographs.

PLATE I

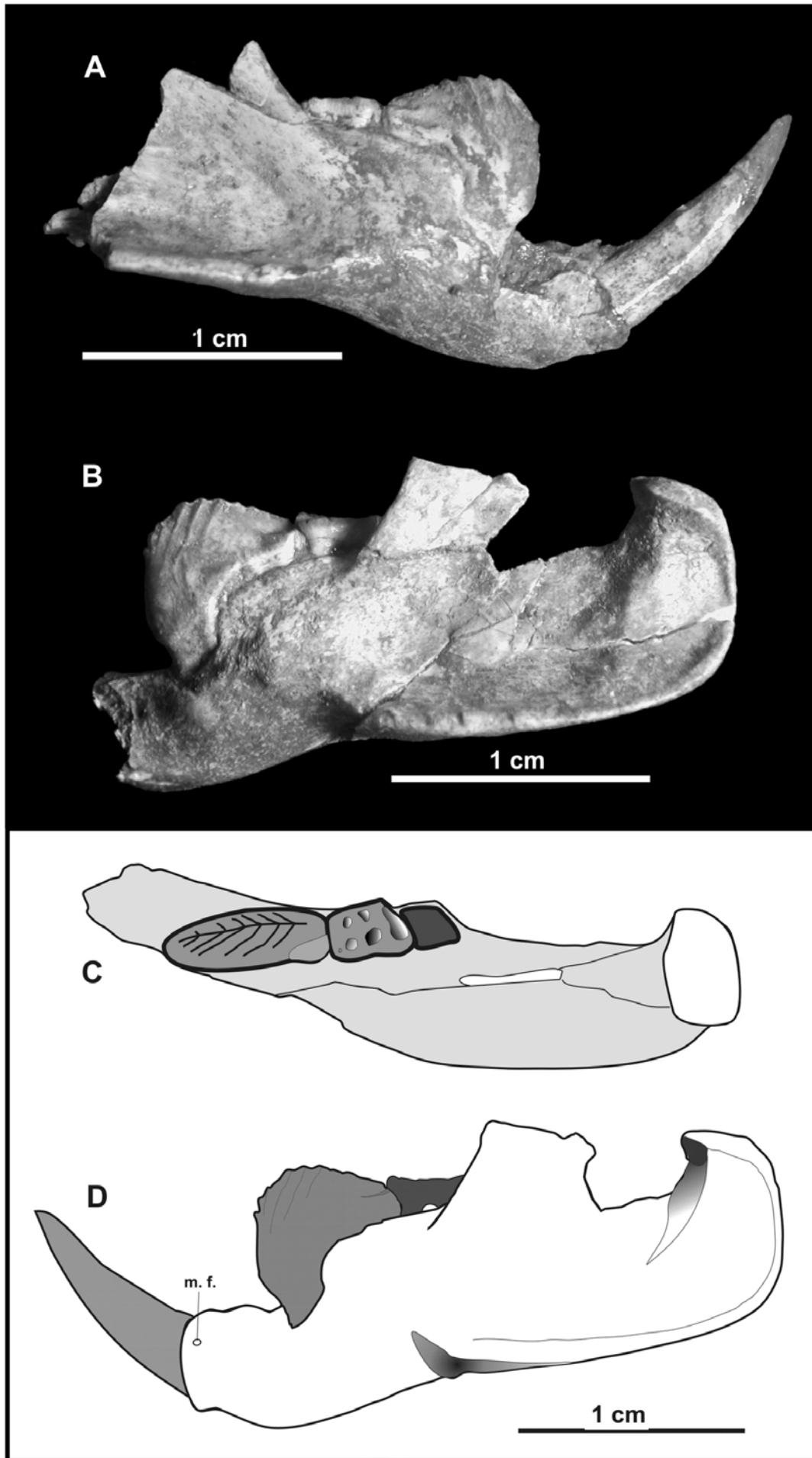


PLATE II

