

New data on *Barbatodon oardaensis* Codrea, Solomon, Venczel & Smith, 2014, the smallest Late Cretaceous multituberculate mammal from Europe

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art. 21 (13) — Published on 5 April 2022
www.cr-palevol.fr



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Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

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ISSN (imprimé / print): 1631-0683/ ISSN (électronique / electronic): 1777-571X

New data on *Barbatodon oardaensis* Codrea, Solomon, Venczel & Smith, 2014, the smallest Late Cretaceous multituberculate mammal from Europe

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Submitted on 17 August 2020 | Accepted on 29 December 2020 | Published on 5 April 2022

[urn:lsid:zoobank.org:pub:BA405524-E57A-4DAE-A012-E6650C0D9491](https://zoobank.org/pub:BA405524-E57A-4DAE-A012-E6650C0D9491)

Solomon A. A., Codrea V. A., Venczel M. & Smith T. 2022. — New data on *Barbatodon oardaensis* Codrea, Solomon, Venczel & Smith, 2014, the smallest Late Cretaceous multituberculate mammal from Europe. *Comptes Rendus Palevol* 21 (13): 253-271. <https://doi.org/10.5852/cr-palevol2022v21a13>

ABSTRACT

Surprisingly, after the Early Cretaceous taxonomic diversity recorded in Europe, which probably is largely an artifact of inadequate taxonomy and inflation of taxa, multituberculate mammals became extremely scarce in the Late Cretaceous in this continent, being reported exclusively from the uppermost Cretaceous continental deposits of the so-called “Haţeg Island” in Transylvania, Romania. Such mammals have been documented from the Haţeg and Rusca Montană sedimentary basins, as well as from the southwestern area of the Transylvanian Basin. All these records belong to the endemic family

KEY WORDS

Kogaionidae,
multituberculates,
Late Cretaceous,
“Hațeg Island”,
diversity.

Kogaionidae. The present paper reports additional data related to the smallest Cretaceous kogaionid, *Barbatodon oardaensis* Codrea, Solomon, Venczel & Smith, 2014 based on a series of new isolated teeth recovered mainly from the type locality, Oarda de Jos (Oarda A). Furthermore, the fossil localities Oarda B and Vălioara are other new occurrences for the species. Based on this new material, the intraspecific variability of *B. oardaensis* is confirmed and its presence is attested in the three basins. Details related to the diversity of the “Hațeg Island” kogaionids are also provided.

RÉSUMÉ

Nouvelles données sur Barbatodon oardaensis Codrea, Solomon, Venczel & Smith, 2014, le plus petit mammifère multituberculé du Crétacé supérieur d'Europe.

Après la diversité taxonomique enregistrée au Crétacé inférieur en Europe, qui serait en grande partie un artefact résultant d'une taxonomie inadéquate et d'une inflation des taxons, les mammifères multituberculés de ce continent sont devenus extrêmement rares au Crétacé supérieur, étant signalés exclusivement dans les dépôts continentaux du Crétacé terminal de ladite «île de Hațeg» en Transylvanie (Roumanie). Ces mammifères ont été documentés dans les bassins sédimentaires de Hațeg et Rusca Montană, ainsi que dans le sud-ouest du Bassin de Transylvanie. Tous ces enregistrements appartiennent à la famille endémique des Kogaionidae. Le présent article apporte des données supplémentaires concernant le plus petit kogaionidé du Crétacé, *Barbatodon oardaensis* Codrea, Solomon, Venczel & Smith, 2014, sur base d'une série de nouvelles dents isolées, découvertes principalement dans la localité type, Oarda de Jos (Oarda A). En outre, les localités fossiles Oarda B et Vălioara représentent d'autres nouvelles occurrences de l'espèce. La variabilité intraspécifique de *B. oardaensis* est confirmée sur base de ce nouveau matériel et sa présence est attestée dans les trois bassins. Des détails relatifs à la diversité des kogaionidés de l'île de Hațeg sont également mis en évidence.

MOTS CLÉS

Kogaionidae,
multituberculés,
Crétacé supérieur,
«île de Hațeg»,
diversité.

INTRODUCTION

Often called “the rodents of the Mesozoic”, for multituberculate mammals several important questions related to their origin and phylogeny persist (e.g. Luo *et al.* 2002; Kielan-Jaworowska *et al.* 2004; Butler & Hooker 2005; Martin 2018; Averianov *et al.* 2020). Recently, Averianov *et al.* (2020) suggested that Siberia could be a “center of origin for Multituberculata”. In Europe, multituberculates were clearly present since the Middle Jurassic (Butler & Hooker 2005; see Solomon *et al.* 2015a for an overview of European Mesozoic multituberculates). In the Early Cretaceous, they reached their highest taxonomic diversity on this continent (Solomon *et al.* 2015a, and references therein), while in the Late Cretaceous, European multituberculates were recorded exclusively from the landmasses of the “Hațeg Island” (Grigorescu 1984; Grigorescu *et al.* 1985; Rădulescu & Samson 1986, 1996, 1997; Csiki & Grigorescu 2000, 2001, 2006; Codrea *et al.* 2002, 2009, 2012a, 2012b, 2014, 2017a; Smith *et al.* 2002; Smith & Codrea 2003, 2015; Csiki *et al.* 2005; Vremir *et al.* 2014; Solomon 2016; Solomon *et al.* 2016, 2019; Csiki-Sava *et al.* 2018). On that isolated landmass (although see Krause *et al.* 2020 for a different interpretation of this emerged area), the endemic family Kogaionidae (Rădulescu & Samson 1996) documents a completely different evolutionary trend compared to the lineages in the Late Cretaceous of Asia and North America. Recent phylogenetic analyses place the kogaionids within Cimolodonta (Smith & Codrea 2015; Csiki-Sava *et al.* 2018), more precisely as a basal group of Cimolodonta (Smith & Codrea 2015). To date, three genera and four species have been described from the Late Cretaceous of Transylvania: *Barbatodon transylvanicus* Rădulescu & Samson, 1986, *Kogaionon*

ungureanui Rădulescu & Samson, 1996, *B. oardaensis* Codrea, Solomon, Venczel & Smith, 2014, and *Litovoi tholocephalos* Csiki-Sava, Vremir, Meng, Brusatte & Norell, 2018. The present paper focuses on old but unpublished, as well as new material assigned to *B. oardaensis*, the smallest Cretaceous kogaionid. It is a rich sample, including isolated teeth originating from the type locality (Oarda de Jos A) and from three other fossil sites (Oarda de Jos B, Negoiu and Vălioara).

GEOLOGICAL SETTING

Upper Cretaceous terrestrial deposits crop out in Romania only in the so-called “Hațeg Island” (i.e., Nopcsa 1914, 1915, 1923; Codrea & Godefroit 2008; Benton *et al.* 2010; Codrea *et al.* 2010, 2012a, 2012b; Weishampel *et al.* 2010; Weishampel & Jianu 2011; Smith & Codrea 2015; Csiki-Sava *et al.* 2015, 2016; Solomon *et al.* 2020). This paleo-island is famous worldwide for its peculiar endemic vertebrate assemblages (Nopcsa 1914; Codrea *et al.* 2014; Csiki-Sava *et al.* 2015, 2016), including dwarf dinosaurs, first reported at the end of the 19th century (Halaváts 1897; Nopcsa 1897; for more details, see Grigorescu 2010). In fact, the first dinosaur bone ever recorded from the “Hațeg Island”, and even from Romania, was found in the Transylvanian Basin, not the Hațeg Basin (see Codrea & Mărginean 2007), although it was first assigned to a large mammal (Téglás 1886; Koch 1894, 1900). This paleo-island, with an estimated area of about 80.000 km² (Benton *et al.* 2010), was part of the western Tethys Archipelago, located at that time in present-day southern Europe (Dercourt *et al.* 2000; Csontos & Vörös 2004; Csiki-Sava *et al.* 2015). Evidence

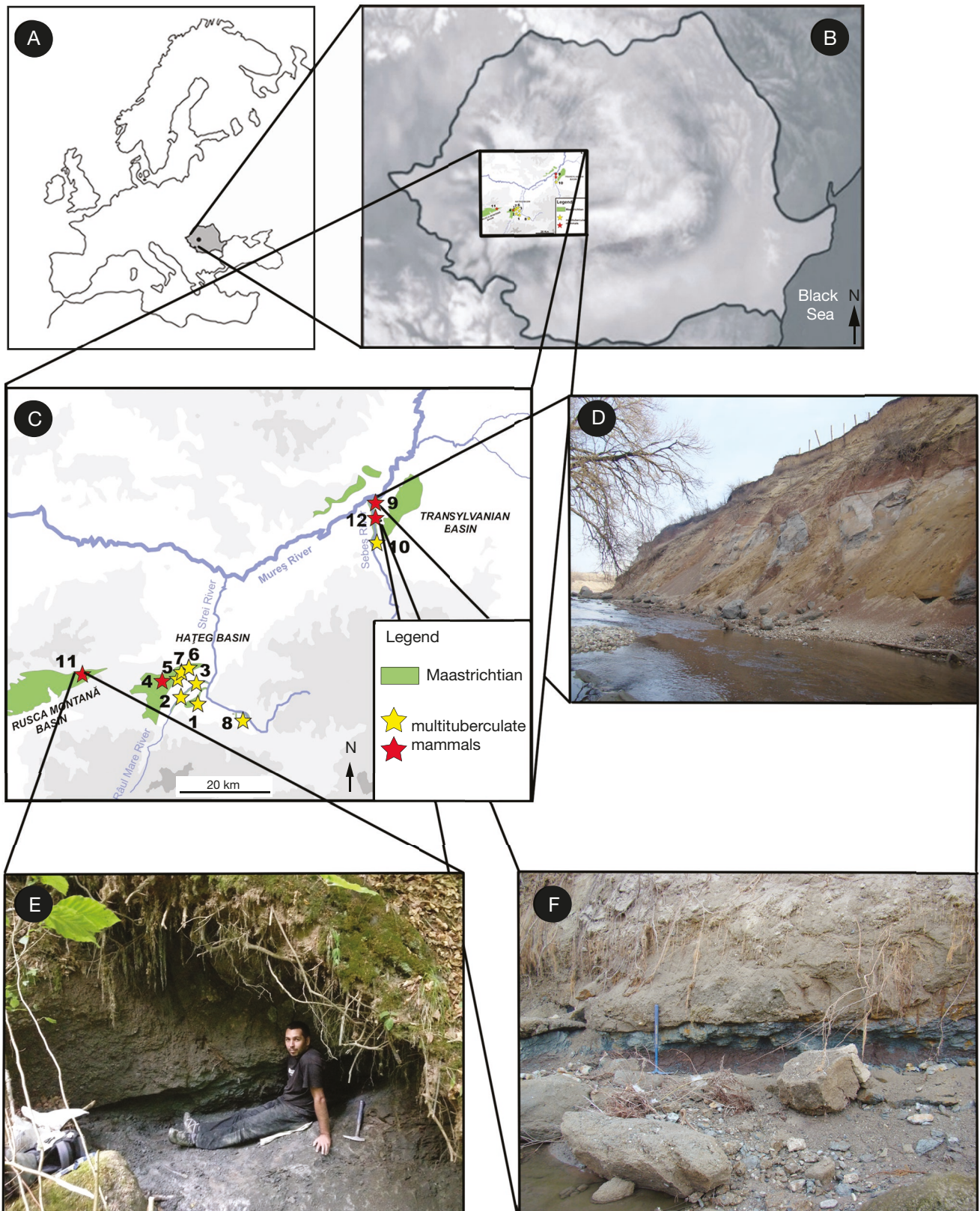


Fig. 1. — Distribution of latest Cretaceous kogaionid multituberculate mammals in Romania: **A**, location of Romania on the map of Europe; **B**, map of Romania with the indication of the areas the multituberculates originated from; **C**, map of Romanian latest Cretaceous (Maastrichtian) localities (marked by **stars**) that yielded kogaionid multituberculates (modified from Codrea *et al.* 2017a): **1**, Sânpetru; **2**, Totești-baraj; **3**, Nălaț-Vad; **4**, Vălioara-Fântânele; **5**, Tuștea; **6**, Livezi; **7**, General Berthelot; **8**, Pui; **9**, Oarda de Jos (ODA section); **10**, Petrești de Jos; **11**, Negoiu-Fărcădeana; **12**, Oarda de Jos (ODB section); **red stars** indicate the origin of the materials from this study; **D**, photograph of ODA outcrop; **E**, photograph of Negoiu-Fărcădeana outcrop; **F**, detail of caliche-layer from ODB section.

of this Late Cretaceous island is present in Transylvania, Romania (Fig. 1A, B), where several vertebrate-bearing localities are located in five regions, namely in the Hațeg and Rusca Montană sedimentary basins, and in the Transylvanian Basin on its southwestern border, at the contact between the folded structures of the Apuseni Mountains in Alba County, as well as in the western side, at Ierii Valley, Cluj County, and in the northwestern side, in Sălaj County (e.g. Halaváts 1897; Nopcsa 1897, 1905, 1914, 1915, 1923; Groza 1983; Weishampel *et al.* 1993, 2003, 2010; Codrea *et al.* 2002, 2009, 2010, 2012a, 2012b, 2014, 2017a, 2017b; Smith *et al.* 2002; Codrea & Godefroit 2008; Delfino *et al.* 2008; Benton *et al.* 2010; Csiki *et al.* 2010a, b; Grigorescu 2010 and references therein; Vasile & Csiki 2011; Codrea & Solomon 2012, 2019; Vasile 2012; Vremir *et al.* 2013; Ősi *et al.* 2014; Csiki-Sava *et al.* 2015, 2016, 2018; Grellet-Tinner & Codrea 2015; Solomon & Codrea 2015; Solomon *et al.* 2015b, 2016, 2020; Solomon 2016; Venczel & Codrea 2016, 2019; Venczel *et al.* 2016; Mayr *et al.* 2020a, 2020b). Within this area of Romania, multituberculates have been found only in the Hațeg and Rusca Montană basins as well as in the Metaliferi Sedimentary Area (Codrea & Dica 2005), located in the southwestern part of the Transylvanian Basin (Fig. 1C; for details see Solomon *et al.* 2015a, and references therein; Codrea *et al.* 2017a; Csiki-Sava *et al.* 2018). The newly available sample was also collected from the same areas. The largest part of the sample originates from the southwestern part of the Transylvanian Basin, from two outcrops at the Oarda de Jos (OD) locality, respectively A and B. ODA contains the lens (ODAN) which is the type locality and level of *Barbatodon oardaensis*, while ODB contains a newly discovered lens (ODBL). Inasmuch as the geology of most of the localities that yielded the available specimens has been detailed in several studies, we briefly present the lithology from ODB (Codrea *et al.* 2010) only, because this is a new kogaionid occurrence from Romania. For details about the Oarda section ODA (Fig. 1D) see Codrea *et al.* (2010, 2013, 2014, 2017a) and Solomon *et al.* (2020, and references therein), for Ng1 (Fig. 1E) see Codrea *et al.* (2009, 2012b, 2017a) and Solomon (2016, and references therein), and for Vă see Csiki & Grigorescu (2000) and Csiki-Sava *et al.* (2015, 2016 and references therein).

ODB is located along the right riverbank of the Sebeș River, approximately 300 m south of ODA (Codrea *et al.* 2010, 2013). The larger outcrop (Figs 1F; 2) has nearly the same lithology as ODA (Codrea *et al.* 2010). In fact, both outcrops from Oarda de Jos are part of the Șard Formation (= Sebeș Formation in Csiki-Sava *et al.* 2016), which is strictly continental and has evolved in a braided fluvial system, with a prevalence of red beds (see Codrea *et al.* 2010 and Solomon *et al.* 2020 for details). Until now, microvertebrate-bearing pond-like or even small lake sediments have been recognized only at ODA (see Solomon *et al.* 2020 for details). Here we report the first microvertebrates represented by kogaionid mammals from ODB. The ODB outcrop (Figs 1F; 2) is more than 70 m in length, and approximately 17 m in height (Fig. 2). From base to top (Fig. 2), the following succession can be observed: a mudstone with fossilized wood and vertebrate remains, a caliche layer (Fig. 1F), a relatively thick (c. 3 m) layer of cross-

bedded sand, a mudstone that yielded macrovertebrates, a thin laminitic sandy clay layer, sand and pebbles, capped by recurrent rhythms of alternating conglomeratic sandstones and sandstones. Between the members of the penultimate rhythm from the mentioned alternate, a thin mudstone can be observed. The top of the succession is covered by vegetation and river terrace deposits (Fig. 2). Despite the fact that in the last decade the outcrop is beginning to be covered by invasive vegetation or by fallen debris (Fig. 1F), erosion by the water stream recently exposed in the riverbed a mudstone that yielded both macro- and microvertebrates (Fig. 2, base of lithological column). Although the faunal content of the lens is still under study, we may report preliminarily an extremely rich assemblage including fish remains, albanerpetontids, frogs, lizards, turtles, crocodilians, dinosaurs (theropods, ornithopods, sauropods), pterosaurs (probably cf. *Albadraco* Solomon, Codrea, Venczel & Grellet-Tinner, 2020) and mammals. Here we focus on the multituberculate sample originating from the lens. The remaining faunal assemblage will be published elsewhere.

MATERIAL AND METHODS

The material available for this study was collected from various Late Cretaceous continental localities of the “Hațeg Island”, in Transylvania (Romania). The sample from the *Barbatodon oardaensis* type locality ODA (Codrea *et al.* 2014) consists of twelve as yet unpublished teeth and of six new finds. From ODB five multituberculate teeth are available for study. One isolated lower incisor originates from Negoiu (Rusca Montană Basin), and one tooth fragment is from Vălioara (Hațeg Basin). All the teeth are isolated and have been recovered by screen-washing as follows: 500 kg for the new finds from ODAN; 250 kg from ODBL; 100 kg from Ng and 100 kg from Vă. Photographs of some of the studied specimens were taken with a low environmental scanning electronic microscope (ESEM Quanta 200) at the Royal Belgian Institute of Natural Sciences, Brussels, while for photographs of other specimens we used a D7000 Nikon camera mounted on a 20–80x Nikon binocular. Several photographs taken on each tooth were combined using the photo stacking technique. The cusp formula of the cheek teeth is counted from the labial to the lingual side. The position of the upper premolars follows Kielan-Jaworowska & Hurum (2001, see addendum p. 426 for more details). All measurements are given in millimeters (mm).

ABBREVIATIONS

FGGUB	Faculty of Geology and Geophysics, University of Bucharest;
ISB	Institute of Speleology Emil Racoviță, Bucharest;
Mt	multituberculata;
Ng1	Negoiu-Fărcădeana layer 1;
ODAN	the name given for all the fossil material originating from the lens-like accumulation from Oarda de Jos section ODA;
ODBL	the name given for all the fossil material originating from the newly discovered lens-like accumulation from Oarda de Jos section ODB;
UBB	UBB – Babeș-Bolyai University of Cluj-Napoca;

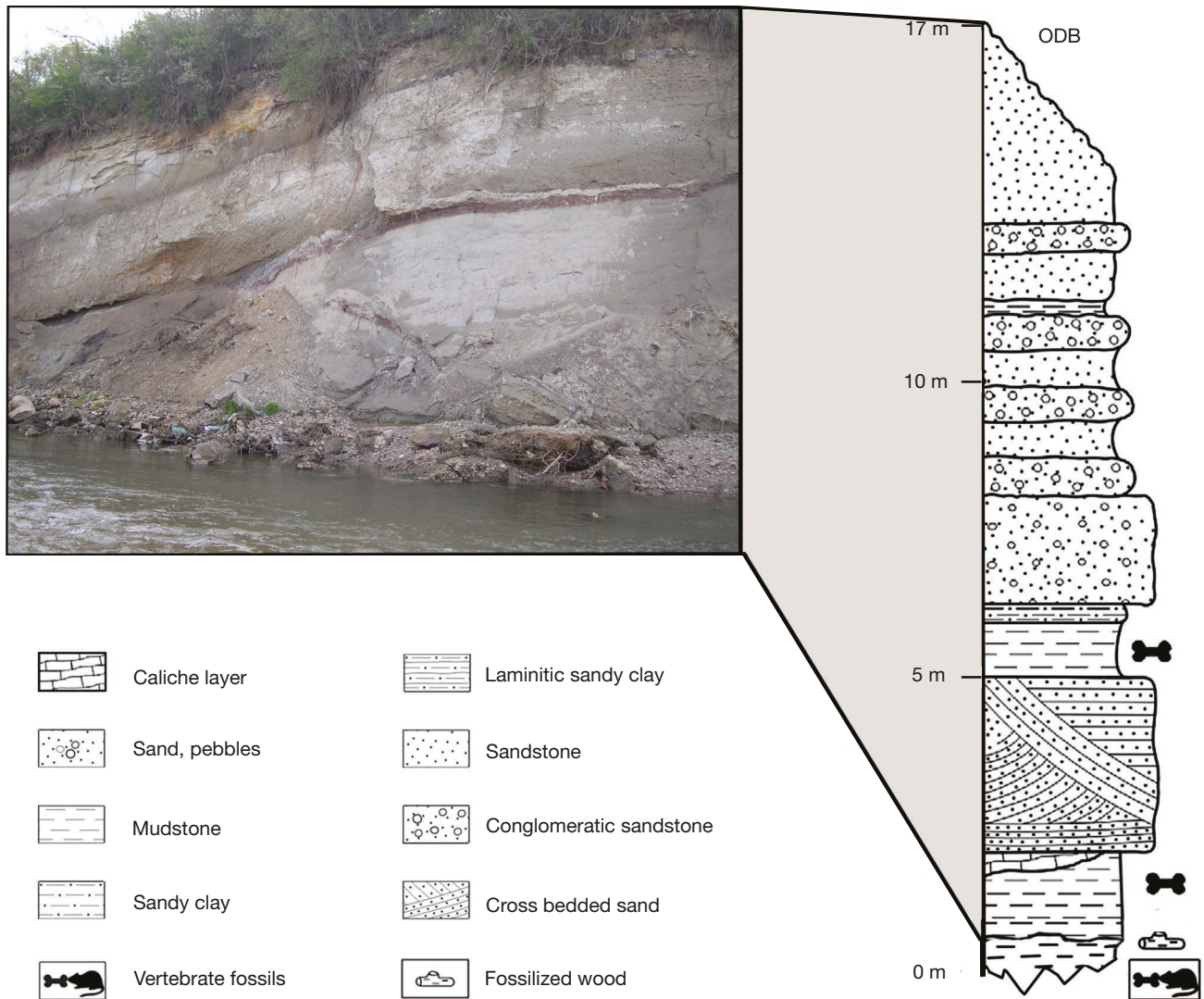


FIG. 2. — Photograph of ODB section when it was clearly exposed (left) and its lithologic column (right); modified after Codrea *et al.* 2010).

Vă
X

Vălioara;
number for each specimen.

UBB ODAN-Mt-X; UBB ODBL-Mt-X; UBB Ng1-Mt-X;
UBB Vă-Mt-X are specific abbreviations for tooth/teeth from
the mentioned sites.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Subclass ALLOOTHERIA Marsh, 1880
Order MULTITUBERCULATA Cope, 1884
Suborder CIMOLODONTA McKenna, 1975
Family KOGAIONIDAE Rădulescu & Samson, 1996

Genus *Barbatodon* Rădulescu & Samson, 1986

Barbatodon Rădulescu & Samson, 1986: 1825-1829, pl. I.

TYPE SPECIES. — *Barbatodon transylvanicus* Rădulescu & Samson, 1986.

OTHER SPECIES. — *Barbatodon oardaensis* Codrea, Solomon, Venczel & Smith, 2014.

Barbatodon oardaensis (Codrea, Solomon,
Venczel & Smith, 2014)
(Fig. 3)

Barbatodon oardaensis Codrea, Solomon, Venczel & Smith, 2014:
492-497, fig. 2, table 2.

HOLOTYPE. — UBB ODAN-Mt-13, isolated M1 (Codrea *et al.* 2014,
fig. 2J1-J2).

REFERRED SPECIMENS. — The material described by Codrea *et al.* 2014,
2017a.

NEW AVAILABLE REFERRED SPECIMENS. — UBB ODAN-Mt-44,
46, 47, 48 and UBB ODBL-Mt-3: left I2; UBB ODAN-Mt-45:
left I3; UBB ODAN-Mt-74: right I3; UBB ODBL-Mt-2: P2 frag-
ment; UBB ODBL-Mt-4: right P3; UBB ODBL-Mt-5: left P4;
UBB Vă-Mt-1: M1 fragment; UBB ODAN-Mt-49, 51, 61, 78 and

UBB ODBL-Mt-1: left i1; UBB ODAN-Mt-50, 53 and UBB Ng1-Mt-03: right i1; UBB ODAN-Mt-2: left p4; UBB ODAN-Mt-4: right p4; UBB ODAN-Mt-76: left m1; UBB ODAN-Mt-75, 80: right m1; UBB ODAN-Mt-77: right m2.

TYPE HORIZON. — ODAN lens, Oarda de Jos, Șard Formation, uppermost Cretaceous (Maastrichtian).

TYPE LOCALITY. — Oarda de Jos (ODA section), Alba county, Transylvanian Basin, Romania.

OCCURRENCES. — Oarda de Jos (ODA, and ODB sections), Alba County, Transylvanian Basin, Romania; uppermost Cretaceous (Maastrichtian), Șard Formation; Lunca Cernii de Jos, Negoiu, Fărcădeana Creek (Negoiu-Fărcădeana layers 1 and 2), Hunedoara County, Rusca Montană Basin, Romania; uppermost Cretaceous (Maastrichtian), unnamed formation; Vălioara (Fântânele site), Hunedoara County, Hațeg Basin; uppermost Cretaceous (Maastrichtian), Densuș-Ciula Formation.

EMENDED DIAGNOSIS. — Modified from Codrea *et al.* (2014, 2017a). Small species of *Barbatodon* with the following cusp formula: I2 bicuspid; I3 single cusped; P1 1:1-2; P2 2:2; P3 3:3; P4 (1):4:2-3; M1 3:4:2; M2 2:3; i1 single cusped and elongated; p4 with ten to eleven serrations, six to seven ridges and two labio-distal cuspules; m1 3-4:3; m2 2-3:2. It differs from *B. transylvanicus* in being approximately 40-45% smaller and by the cusp formula of P3 (3:3 in *B. oardaensis*; 2:3 in *B. transylvanicus*).

DESCRIPTION OF THE NEW MATERIAL AND COMPARISONS WITH OTHER KNOWN KOGAIONIDS

Upper dentition

I2. Five specimens are available for study; four of them were recovered from the type locality of *B. oardaensis* (Fig. 3A-D) and one from ODBL (Fig. 3E). All available I2s are from the left part of the dentition. The first upper incisors bear a recurved main mesial cusp forming the major part of the crown, and an additional cusp, which is placed in the lower third of the crown. In labial view, a depression-like structure (= groove in Csiki & Grigorescu 2000) separates the two cusps. All the I2s have similar sizes (see Table 1), UBB ODBL-Mt-3 (Fig. 3E) being the largest and the most robust one. The cusps of the incisors are strongly worn with the exception of UBB ODAN-Mt-47 (Fig. 3C). In most cases the accessory cusp is almost lost due to wear, but in UBB ODAN-Mt-47 (Fig. 3C), it is well preserved and ventrally directed.

The I2s are bicuspid as seen in the I2 of *B. oardaensis* from Rusca Montană Basin (Codrea *et al.* 2017a), *B. transylvanicus* (see Smith & Codrea 2015, fig. 5; Solomon *et al.* 2016: fig. 2a) and *L. tholocephalos* (Csiki-Sava *et al.* 2018). The bicuspid morphology of the new material, with a main mesial cusp and one accessory much smaller distal cusp, also resembles the small incisor from Sibișel valley (Grigorescu 1984) and FGGUB M.1609 described from Tuștea (Csiki & Grigorescu 2000). The I2 of *B. oardaensis* is considerably smaller than that of *Kogaionon* (Rădulescu & Samson 1996), *B. transylvanicus* (Smith & Codrea 2015; Solomon *et al.* 2016) and *Litovoi* (Csiki-Sava *et al.* 2018). Similar wear, with the almost lost accessory cusp, is present in *B. transylvanicus* (the I2 of UBB P-Mt1, Smith & Codrea 2015) and *L. tholocephalos* (Csiki-Sava *et al.* 2018). However, there are some incisors of *B. transylvanicus* that as in UBB ODAN-Mt-47 (Fig. 3C) show

a reduced state of the wear of the cusps and a mesially directed accessory cusp (UBB P-Mt4-1 from Smith & Codrea 2015, and UBB P-Mt2-3 from Solomon *et al.* 2016). The crown of the new incisors is completely covered by enamel of uniform thickness as in FGGUB M.1609 (Csiki & Grigorescu 2000), *B. transylvanicus* and *L. tholocephalos* (Smith & Codrea 2015; Solomon *et al.* 2016; Csiki-Sava *et al.* 2018), but differing in this aspect from the reduced enamel band reported in the poorly described I2 of *K. ungureanui* (Rădulescu & Samson 1996, 1997). The I2 is unknown in all the four known *Hainina* Vianey-Liaud, 1979 species (Vianey-Liaud 1979, 1986; Peláez-Campomanes *et al.* 2000; De Bast & Smith 2017).

I3. Two second upper incisors (UBB ODAN-Mt-45, left, Fig. 3F, F' and UBB ODAN-Mt-74, right, Fig. 3G) are available. The I3s are single-cusped and both preserve the crown and the root. The sizes of the teeth are comparable (see Table 1). The tip is severely worn in UBB ODAN-Mt-45 (Fig. 3F), while in UBB ODAN-Mt-74 (Fig. 3G) the wear is more pronounced in the labial part of the tip. The crown is spatulate and fully covered by enamel. In anterior view (Fig. 3F'-G) the enamel is wrinkled, whereas in posterior view of UBB ODAN-Mt-45 (Fig. 3F), on the smooth enamel surface some cracks can be noticed. We assign these I3s to *B. oardaensis* due to the fact they were recovered from the type-locality of this species, from where no other kogaionid was reported, and based on their size which fits with the sizes of other teeth of this kogaionid. These two specimens are the first I3s ever reported for *B. oardaensis*.

A similar spatula-like I3 is also known in other Late Cretaceous kogaionids such as *B. transylvanicus* (Smith & Codrea 2015) and *Litovoi* (Csiki-Sava *et al.* 2018), but they are seemingly different from the peg-like I3 of *Kogaionon* (cf. Rădulescu & Samson 1997). The enamel is wrinkled on the anterior face in *B. oardaensis* as it is in *B. transylvanicus* and *Litovoi*, differing from the smooth enamel reported for the I3 of *Kogaionon* (cf. Csiki-Sava *et al.* 2018). The size of the new I3s is smaller than those of the other known Late Cretaceous kogaionids. Unfortunately, the I3 is unknown in any *Hainina* species, thus preventing a comparison with the I3 of *B. oardaensis*.

P2. A distal crown fragment of a right P2 and its distal root (UBB ODBL-Mt-2, Fig. 3H) is available. Despite the fragmentary state of the tooth, we can recognize two distinct cusps which are separated by a longitudinal valley. Unfortunately, the labial one is broken, but the lingual one is conical. In labial and lingual views, the preserved part of the crown shows a slope extending from the distal cusps of each row toward the distal margin of the tooth. The apex of the distal lingual cusp is slightly damaged. No wear facets can be noticed on the preserved part of the crown. The enamel is extremely damaged, but fine enamel radial wrinkles diverge from the apex towards the crown base.

The general pattern of the tooth morphology is similar to that of the P2 described in *B. oardaensis* (Codrea *et al.* 2014) and also to the one known in other Late Cretaceous kogaionids (Rădulescu & Samson 1996, 1997; Smith & Codrea 2015;



FIG. 3. — New isolated teeth assigned to *Barbatodon oardaensis* Codrea, Solomon, Venczel & Smith, 2014: **A**, UBB ODAN-Mt-44, left I2 in labial view; **B**, UBB ODAN-Mt-46, left I2 in lingual view; **C**, UBB ODAN-Mt-47, left I2 in lingual view; **D**, UBB ODAN-Mt-48, left I2 in lingual view; **E**, UBB ODBL-Mt-3, left I2 in lingual view; **F**, UBB ODAN-Mt-45, left I3 in posterior (F), and anterior (F') views; **G**, UBB ODAN-Mt-74, right I3 in posterior view; **H**, UBB ODBL-Mt-2, fragment of right P2 in occlusal view; **I**, UBB ODBL-Mt-4, right P3 in occlusal view; **J**, UBB ODBL-Mt-5, left P4 in occlusal (J) and labial (J') views; **K**, UBB Vă-Mt-1, fragment of ?left M1 in occlusal view; **L**, UBB ODAN-Mt-49, left i1 in lingual view; **M**, UBB ODAN-Mt-51, left i1 in lingual view; **N**, UBB ODAN-Mt-53, right i1 in lingual view; **O**, UBB ODAN-Mt-50, right i1 in lingual view; **P**, UBB ODAN-Mt-61, left i1 in lingual view; **Q**, UBB ODBL-Mt-1, left i1 in lingual view; **R**, UBB ODAN-Mt-78, left i1 in lingual view; **S**, UBB Ng1-Mt03, right i1 in lingual view; **T**, UBB ODAN-Mt-2, fragmentary left p4 in lingual view; **U**, UBB ODAN-Mt-4, fragmentary right p4 in lingual view; **V**, UBB ODAN-Mt-75, right m1 in occlusal view; **X**, UBB ODAN-Mt-76, left m1 in occlusal view (X) and detail of the presence of two labio-distal cusps (X'); **Y**, UBB ODAN-Mt-80, right m1 in occlusal view; **Z**, UBB ODAN-Mt-77, fragmentary right m2 in occlusal view. Scale bar: 1 mm.

TABLE 1. — Measurements (in mm) of the new teeth referred to *Barbatodon oardaensis* Codrea, Solomon, Venczel & Smith, 2014. *, for incisors we measured the preserved length; #, fragmentary tooth.

Specimen	Locality	Position	Cups formula/ no. of cusps/ serrations	L*	W
UBB ODAN-Mt-44	Oarda de Jos (ODAN lens)	L I2	bicuspid	2.20	—
UBB ODAN-Mt-46	Oarda de Jos (ODAN lens)	L I2	bicuspid	1.87	—
UBB ODAN-Mt-47	Oarda de Jos (ODAN lens)	L I2	bicuspid	2.20	—
UBB ODAN-Mt-48	Oarda de Jos (ODAN lens)	L I2	bicuspid	1.85	—
UBB ODBL-Mt-3	Oarda de Jos (ODBL lens)	L I2	bicuspid	2.42	—
UBB ODAN-Mt-45	Oarda de Jos (ODAN lens)	L I3	single cusp	2.39	—
UBB ODAN-Mt-74	Oarda de Jos (ODAN lens)	R I3	single cusp	2.80	—
UBB ODBL-Mt-2#	Oarda de Jos (ODBL lens)	R P2	—	—	0.97
UBB ODBL-Mt-4	Oarda de Jos (ODBL lens)	R P3	3:3	2.06	1.15
UBB ODBL-Mt-5	Oarda de Jos (ODBL lens)	L P4	4:2	1.74	1.03
UBB Vă-Mt-1#	Vălioara	?L M1	—	—	1.40
UBB ODAN-Mt-49	Oarda de Jos (ODAN lens)	L i1	single cusp	4.20	—
UBB ODAN-Mt-50	Oarda de Jos (ODAN lens)	R i1	single cusp	2.41	—
UBB ODAN-Mt-51	Oarda de Jos (ODAN lens)	L i1	single cusp	2.51	—
UBB ODAN-Mt-53	Oarda de Jos (ODAN lens)	R i1	single cusp	5.99	—
UBB ODAN-Mt-61	Oarda de Jos (ODAN lens)	L i1	single cusp	3.96	—
UBB ODAN-Mt-78	Oarda de Jos (ODAN lens)	L i1	single cusp	6.73	—
UBB ODBL-Mt-1	Oarda de Jos (ODBL lens)	L i1	single cusp	5.57	—
UBB Ng1-Mt-03	Negoiu-Fărcădeana layer 1	R i1	single cusp	5.10	—
UBB ODAN-Mt-2#	Oarda de Jos (ODAN lens)	L p4	10	3.45#	1.15
UBB ODAN-Mt-4#	Oarda de Jos (ODAN lens)	R p4	7+	—	0.89
UBB ODAN-Mt-75	Oarda de Jos (ODAN lens)	R m1	3:3	1.91	1.28
UBB ODAN-Mt-76	Oarda de Jos (ODAN lens)	L m1	4:3	2.03	1.25
UBB ODAN-Mt-80	Oarda de Jos (ODAN lens)	R m1	73:3	2.04	1.18
UBB ODAN-Mt-77#	Oarda de Jos (ODAN lens)	R m2	3:2	1.27#	1.28

Solomon *et al.* 2016; Csiki-Sava *et al.* 2018) and even in the P2 (P3 in Vianey-Liaud 1979, revised as P2 by De Bast & Smith 2017) of the Paleocene species *H. belgica* Vianey-Liaud, 1979 and *H. godfriauxi* Vianey-Liaud, 1979. When complete, the crown should bear four distinct cusps. The width of the new P2 fragment (Table 1) closely matches that found in *B. oardaensis* (Codrea *et al.* 2014: table 2, fig. 4). Also, the fine wrinkled enamel seen on the preserved fragment resembles that seen in *B. oardaensis*. The P2 of *B. oardaensis* is about half of the size of the P2 of *Kogaionon* (= P3 cf. Peláez-Campomanes *et al.* 2000) and *B. transylvanicus* (Rădulescu & Samson 1996; Codrea *et al.* 2014; Solomon *et al.* 2016). The width of the new fragment (Table 1) also resembles this condition, being almost half of the width known for the P2 of *Litovoi* (Csiki-Sava *et al.* 2018, suppl. table 1). Thus, based mainly on its small size, we assign this fragment to this small Maastrichtian kogaionid. The preserved width is comparable to that of *H. belgica*, being narrower than in *H. godfriauxi* (Vianey-Liaud 1979; De Bast & Smith 2017). In occlusal view, the crown shows a slope starting from the distal cusps of each row towards the distal margin of the crown as in the larger species *B. transylvanicus* (Solomon *et al.* 2016) and as it can be observed in the other two Late Cretaceous kogaionid genera, *Kogaionon* and *Litovoi*. This slope is likely shorter in *H. belgica* (Vianey-Liaud 1979: fig. 3c-d) and visibly shorter in *H. godfriauxi* (Vianey-Liaud 1979: fig. 5; De Bast & Smith 2017: fig. 6B1-B2). The enamel is wrinkled as in the P2 of *B. transylvanicus* (Solomon *et al.* 2016), *Litovoi* and *Kogaionon* (AAS personal observations), resembling in this aspect the Paleocene species *H. belgica* and *H. godfriauxi*, as well.

P3. One right P3 (UBB ODBL-Mt-4; Fig. 3I) is available for study. Only the crown is preserved and bears six cusps placed in two parallel longitudinal rows. Both the labial and lingual rows bear three conical cusps (3:3). All the cusps are distinct, being separated by clear longitudinal and transverse valleys. The labio-distal cusp is the smallest, whereas the lingual-distal one is broken lingually. In labial and lingual views, clear “V” shaped valleys are separating the cusps. In lingual view, the lingual row is higher than the labial one, the second lingual cusp being the highest. There is no noticeable wear facet present on the surface of the cusps. The enamel is ornamented with radial wrinkles which diverge from the apex of each cusp towards their base.

The new P3 from ODBL shares the general pattern of the cusps and valleys and a similar ornamented enamel with the P3s of *B. oardaensis* recovered from the type-locality (Codrea *et al.* 2014). Moreover, the dimensions (Table 1) fit the mean size seen in *B. oardaensis* (Codrea *et al.* 2014: table 2, fig. 4). Based on these similarities, we assign the new P3 to *B. oardaensis*. The P3 (including the new one) of *B. oardaensis* is more than twice as small as in *Kogaionon* (P3=P4 cf. Peláez-Campomanes *et al.* 2000), *B. transylvanicus* and *Litovoi* (Rădulescu & Samson 1996; Smith & Codrea 2015; Csiki-Sava *et al.* 2018), differing from these larger kogaionids also by the cusp formula. It bears one extra cusp on the labial row compared to *Kogaionon* and *B. transylvanicus* and when compared to *Litovoi*, an extra labial one, but two fewer on the lingual row. Six cusps are present in some P3 specimens of *H. belgica* (P4 in Vianey-Liaud 1979, but P3 in De Bast & Smith 2017), but their distribution pattern is totally different compared to *B. oardaensis*. However, De Bast & Smith (2017) pointed out

an intraspecific variability for the P3 of *H. belgica*. As such the P3 of *B. oardaensis* differs from *H. belgica* by its cusp formula (3:3 vs 1-3:5). *Barbatodon oardaensis* has two fewer lingual cusps on the P3 compared to *H. pyrenaica* Peláez-Campomanes López-Martínez, Álvarez-Sierra & Daams, 2000. The size of the P3 in *B. oardaensis* is slightly larger than those of *H. belgica* and *H. pyrenaica*. The elongated shape and the conical cusps of the P3 are shared with the other Late Cretaceous kogaionids that inhabited the “Hațeg Island”. Conical cusps are also known in the Paleocene *H. belgica* and *H. pyrenaica*, but the distal margin of their P3 is narrower (Peláez-Campomanes *et al.* 2000: fig. 2.1; De Bast & Smith 2017: fig. 5D-E). The enamel is wrinkled as in *H. belgica*, *H. pyrenaica*, *Kogaionon* (AAS personal observation), *B. transylvanicus* and *Litovoi*.

P4. One double-rooted left fourth upper premolar is available in the new sample (UBB ODBL-Mt-5; Fig. 3J, J'). The crown is subrectangular and bears six cusps aligned on two mesially convergent crests (Fig. 3J). The labial crest consists of four (?) conical cusps, the mesial one being the largest, whereas the lingual crest consists of two extremely worn cusps. The labial crest is higher than the lingual one (Fig. 3J'), its height decreasing towards the distal part of the tooth. A longitudinal valley starts from the confluence between the mesio-lingual and the second labial cusps and deepens through the distal part of the tooth. The mesial root is higher than the distal one. The enamel surface appears relatively smooth, but this could be due to the advanced stage of wear which affects the tooth crown. Wear facets affect different parts of the crown. These can also be seen on the lingual side of the labial cusps, and on the apices of the third and fourth labial cusps.

The lingual side of the crown is highly abraded; the cusps being almost lost. UBB ODBL-Mt-5 shares the general pattern of the P4s of *B. oardaensis* from the type locality and from Rusca Montană Basin (Codrea *et al.* 2014, 2017a), whereas its dimensions (Table 1) fit the mean size seen in *B. oardaensis* (Codrea *et al.* 2014: table 2, fig. 4; Codrea *et al.* 2017a: fig. 5). The P4 of *K. ungureanui* (= P5 cf. Peláez-Campomanes *et al.* 2000), *B. transylvanicus* and *L. tholocephalos* is almost twice as large as the new P4 (and as the P4 of *B. oardaensis* in general). The P4 from ODBL is quite similar in size to those of *H. belgica*, *H. pyrenaica* and cf. *Hainina* sp. from Jibou (however, the tooth from Jibou is wider; Vianey-Liaud 1979; Gheerbrant *et al.* 1999; Peláez-Campomanes *et al.* 2000; De Bast & Smith 2017), but smaller than that of *H. godfriauxi* (Vianey-Liaud 1979). The general outline and the conical (less worn) cusps are similar to the other Late Cretaceous and Paleocene kogaionids. The first labial cusp is inflated as in *Kogaionon*, *B. transylvanicus* and *Litovoi*. The cusp formula is variable in the P4 of *B. oardaensis* [(1):4:2-3; Codrea *et al.* 2014, 2017a], but resembles that of *Kogaionon* (4:2; Rădulescu & Samson 1996), *B. transylvanicus* (4:2-3; Solomon *et al.* 2016) or *Litovoi* (4:2). However, the P4 cusp formula seems difficult to be used as a character to discriminate species if it is likely variable, and as long as *Kogaionon* and *Litovoi* are known from single specimens. The higher labial crest combined with the lower lingual one is a condition also

seen in other known kogaionids as well as in many other multituberculates (for details, see Kielan-Jaworowska & Hurum 2001; Luo *et al.* 2002; Kielan-Jaworowska *et al.* 2004). The centrally situated ridge seen in *B. oardaensis* (Codrea *et al.* 2014, 2017a) and *H. pyrenaica* (Peláez-Campomanes *et al.* 2000) is lost in the new P4 due to advanced wear. In Codrea *et al.* (2017a), we stated wrongly that the labial part of the P4 of *B. oardaensis* and *H. pyrenaica* is affected by wear. We correct this here, and emphasize that the lingual side is worn (as written in Peláez-Campomanes *et al.* 2000 and Codrea *et al.* 2014). Similar wear facets that mostly affect the lingual side of the tooth and cusps are present in *B. oardaensis* from ODAN and Negoiu (Codrea *et al.* 2014, 2017a) and in *H. pyrenaica* (Peláez-Campomanes *et al.* 2000). Moreover, the larger species *B. transylvanicus* has a similar wear pattern (Solomon *et al.* 2016) as in the new P4. Codrea *et al.* (2014, 2017a) already discussed the development of enamel ornamentation (smooth vs wrinkled) which is due to the state of wear. However, this advanced state of wear with “smooth” enamel is similar to that seen in *H. pyrenaica* (also a highly worn P4; Peláez-Campomanes *et al.* 2000) differing from the wrinkled enamel seen in *B. transylvanicus* (Smith & Codrea 2015; Solomon *et al.* 2016), *Kogaionon* and *Litovoi* (AAS personal observation). A P4 of *H. belgica* from Hainin (De Bast & Smith 2017: fig. 4D1-D2) shares a comparable stage of wear with the new P4 of *B. oardaensis*. However, De Bast & Smith (2017) noted that the mentioned P4 of *H. belgica* could be a deciduous tooth (DP4), which is not the case for UBB ODBL-Mt-5.

M1. The only specimen is represented by a distal fragment of a ?left M1 (UBB Vă-Mt-1; Fig. 3K), preserving also the distal root. The tooth fragment is identified as an M1 due to the presence of three cusp rows, as well as by the shape of the distal margin which resembles the distal margin of M1 of known kogaionids. Although very worn, three cusp rows are recognized on the preserved part of the crown. This advanced state of wear indicates that the M1 fragment originates from a very old individual. Even though its state of preservation precludes a detailed comparison to other kogaionid M1s, we decided to figure this tooth because it is the first kogaionid fragment from the UBB collections originating from Vălioara.

Csiki & Grigorescu (2000) described some small kogaionid teeth from Vălioara and assigned them to various “species” of *Hainina*. However, Codrea *et al.* (2017a: table 1) stated that these *Hainina* species are of the same size with *B. oardaensis*. Based on the intraspecific variability (in size and morphology) shown by this small-sized Late Cretaceous kogaionid, Codrea *et al.* (2017a) considered that the teeth from Vălioara likely belong to *B. oardaensis*. The width of the M1 fragment (Table 1) approaches closely that of the M1 of *B. oardaensis* (Codrea *et al.* 2014: table 2, fig. 4). Also, the shape is similar to that of *B. oardaensis*. Based on the above remarks, we assign UBB Vă-Mt-1 to *B. oardaensis*. Thus, this M1 fragment strengthens our previous remark (Codrea *et al.* 2017a) that some of the specimens from Vălioara reported by Csiki & Grigorescu (2000) can be referred to *B. oardaensis*.

Lower dentition

i1. Four mesial extremities of lower first incisors (UBB ODAN-Mt-51, 61: left i1, Fig. 3M, P; UBB ODAN-Mt-53, 50: right i1, Fig. 3N, O), and four more complete lower incisors (UBB ODAN-Mt-49, 78; UBB ODBL-Mt-1: left i1, Fig. 3L, Q, R; UBB Ng1-Mt-03: right i1, Fig. 3S) are available for study. The incisors have a slightly curved elongated crown and their preserved sizes are variable (Table 1). On the lingual side of these teeth, a prominent curved line can be noticed in the basal third of the crowns. The tip of the incisors is worn. The wear degree varies, some of the incisors being extremely worn (e.g. UBB ODAN-Mt-49, Fig. 3L; UBB ODBL-Mt-1, Fig. 3Q; UBB Ng1-Mt-03, Fig. 3S). The enamel is present both on the labial and lingual sides of the crowns, disappearing towards the basal part (e.g. Fig. 3L, Q-S). The enamel band seems to be more developed on the labial side than on the lingual one, a feature more distinct on the highly worn specimens. The enamel is almost lost on the dorsal side of the teeth, exposing the dentine, due to advanced wear. Also, the dorsal curvature of these teeth varies, being directly dependent on the state of wear (gently curved vs almost no curvature).

Although these incisors originate from three distinct sites (ODAN, ODBL and Ng1) they share the same general morphology. Most of them (six out of eight) come from the type locality of *B. oardaensis*. They share the general morphology and aspect of wear with the i1s from Negoii assigned to *B. oardaensis* (Codrea *et al.* 2017a). Based on the above situation, we assign all the new available incisors (mesial parts or more complete ones) to *B. oardaensis*. Overall, the i1 of *B. oardaensis* is elongated, gently curved, covered with enamel on both lingual and labial sides, but more developed on the labial side, and with a clear distinct curved line in the basal third of the lingual side. Similar elongated and relatively gracile i1s are also known in the larger species *B. transylvanicus* (Csiki *et al.* 2005; Smith & Codrea 2015; Solomon *et al.* 2016). Also, the i1 of this small kogaionid shares the similar enamel distribution, with the enamel cover disappearing towards the distal part of the tooth, with the i1s described in *B. transylvanicus* and the indeterminate i1s described by Rădulescu & Samson (1997) and Csiki & Grigorescu (2000). The i1 of *B. oardaensis* is clearly smaller than that of *B. transylvanicus* (Csiki *et al.* 2005; Smith & Codrea 2015; Solomon *et al.* 2016), that of *Litovoi* (Csiki-Sava *et al.* 2018), and that of *H. godfriauxi* (cf. De Bast & Smith 2017). The new i1 specimens are comparable in size to FGGUB M.1612 from Vălioara (Csiki & Grigorescu 2000). The i1 is unknown in *H. belgica*, *H. vianeyae* Peláez-Campomanes, López-Martínez, Álvarez-Sierra & Daams, 2000., *H. pyrenaica* and *K. ungureanui* (Vianey-Liaud 1979, 1986; Rădulescu & Samson 1996, 1997; Peláez-Campomanes *et al.* 2000; De Bast & Smith 2017).

p4. Two partially preserved p4s are available for study (UBB ODAN-Mt-2: left, Fig. 3T and UBB ODAN-Mt-4: right, Fig. 3U). Both specimens have their roots broken, but UBB ODAN-Mt-4 preserves a part of its distal root (Fig. 3U). They have a blade-like, arcuate, asymmetrically rounded crown and



FIG. 4. — Comparison between the lateral outlines of different p4s referred to *B. oardaensis* Codrea, Solomon, Venczel & Smith, 2014 originating from Oarda de Jos; the dotted lines indicate the areas where UBB ODAN-Mt-2 and UBB ODAN-Mt-4 are broken. Note – despite the broken area – their similarity with the profile of UBB ODAN-Mt-1 (full line profile). Scale bar: 1 mm.

oblique ridges as in other cimolodontans (Kielan-Jaworowska & Hurum 2001). The left p4, UBB ODAN-Mt-2, preserves ten serrations (Fig. 3T) on the edge, whereas the right p4 fragment, UBB ODAN-Mt-4, preserves seven serrations (Fig. 3U). The first two serrations of UBB ODAN-Mt-2 are directed mesially, whereas the others are directed dorsally and distally with the highest point situated at the level of the fourth to fifth serrations. In UBB ODAN-Mt-4, all the preserved serrations are directed distally. All serrations are conical and separated by “U”-shaped gentle slopes. In labial and lingual views, the left p4 bears seven ridges below the third to ninth serrations. In labial view, there is a distinct labio-distal platform that apparently might have had two cusps, removed by wear. In front of this platform several fine enamel ridges are present. The other specimen, UBB ODAN-Mt-4, preserves the labial and lingual ridges between the level of the ?third to eighth serrations. On its labial side, the enamel is almost completely broken, but the position of the labio-distal platform can be recognized. Both specimens have their maximum width in their distal part, at the level of the labio-distal platform (Table 1).

The general pattern (Fig. 4) and the measurable dimensions of the new p4s are similar to those of the p4 of *B. oardaensis* (Codrea *et al.* 2014, 2017a). The left p4 has ten serrations on its edge and two heavily worn cusps on its platform, resembling in this aspect the p4 of *B. oardaensis* from Negoii, but differing by one less serration compared to UBB ODAN-Mt-1 (Codrea *et al.* 2014). This is very probably the result of intraspecific variability. A variable number of serrations on the edge was already reported in the larger *B. transylvanicus* (Solomon *et al.* 2016) and related also to intraspecific variability. Thus, we assign these newly described specimens to the small *B. oardaensis*. A similar arcuate p4 is present in the larger *B. transylvanicus* (see Solomon *et al.* 2016: fig. 6, for details) and in the Paleocene *H. belgica* (Vianey-Liaud 1979). The p4 of *B. oardaensis* (including the newly described specimens) has the highest point placed at the level of the fourth to fifth cusps as in *B. transylvanicus*, UBB ODAN-Mt-2 sharing

with the p4 of the larger species the number of serrations and lateral ridges. Also, fine enamel ridges are observed on UBB ODAN-Mt-2 in front of the labio-distal platform, a feature shared with the p4s of UBB P-Mt2 and UBB P-Mt3 (Solomon *et al.* 2016) and with the p4 of *B. oardaensis* from Negoiu (Codrea *et al.* 2017a). The maximum width of the p4 of *B. oardaensis* is at the level of the labio-distal platform, differing in this aspect from *H. belgica* which appears to have this maximum width in its mesial part (De Bast & Smith 2017: fig. 4F2). Wear affects the labio-distal platform in UBB ODAN-Mt-2 as in *B. transylvanicus* (Solomon *et al.* 2016). The p4 of *Kogaionon*, *Litovoi*, *H. godfriauxi*, *H. vianeyae* and *H. pyrenaica* is unfortunately unknown, thus preventing any comparisons with the p4 of *B. oardaensis*.

m1. Three lower first molars are available (UBB ODAN-Mt-76: left m1, Fig. 3X; UBB ODAN-Mt-75, 80: right m1, Fig. 3V, Y) all originating from the type locality of *B. oardaensis*. They display a nearly rectangular outline in occlusal view, with two mesio-distally aligned rows of pyramidal cusps. The cusp formula is 3:3 for UBB ODAN-Mt-75, 80 (Fig. 3V, Y); the labio-distal cusps of UBB ODAN-Mt-75 are surrounded by a long cingulid (Fig. 3V), whereas UBB ODAN-Mt-76 bears an extra labial cusp (Fig. 3X'). The cusps are separated by "V"-shaped transverse valleys, whereas the cusp rows are separated by a deep longitudinal valley. The sizes of these m1s are comparable (Table 1). The enamel appears smooth, but the wear facets affect various parts of the crown and the cusps. One diverging ridge is present in two specimens, UBB ODAN-Mt-75 and -80 extending from the disto-lingual part of the median labial cusps to the third lingual cusps. Moreover, in UBB ODAN-Mt-76, the two distal labial cusps are connected by a ridge. On the lateral sides of this ridge, two round-shaped depressions are present, the labial one being deeper (Fig. 3X). UBB ODAN-Mt-80 is highly affected by wear, so the morphological details of this tooth are almost totally lost, exposing the dentine (Fig. 3Y). In the other two specimens the wear affects the labial side of the tooth, and both the lingual and labial sides of the longitudinal valley and the apices of the cusps. The lingual side of the left m1 (UBB ODAN-Mt-76) is abraded, but the one of the right m1 (UBB ODAN-Mt-75) is less affected by wear. Also, in the left m1, on the labial side of the crown the enamel was removed by advanced wear, exposing the dentine.

The new m1s share the general patterns with *B. oardaensis*, and their dimensions (Table 1) fit the mean size of the m1s of this species (Codrea *et al.* 2014: table 2, fig. 4). A similar outline of the crown is also present in the m1 of the larger species *B. transylvanicus* (Rădulescu & Samson 1986; Csiki *et al.* 2005; Smith & Codrea 2015; Solomon *et al.* 2016), in the Paleocene *H. belgica* and *H. godfriauxi* (Vianey-Liaud 1979; De Bast & Smith 2017), and in the isolated m1s from Nălaț-Vad (Smith *et al.* 2002: pl. 1, figs 1-2) and Vălioara (Csiki & Grigorescu 2000). The new m1s of *B. oardaensis* are smaller than those of *B. transylvanicus* (Rădulescu & Samson 1986; Csiki *et al.* 2005; Smith & Codrea 2015; Solomon *et al.* 2016), *H. godfriauxi* (Vianey-Liaud 1979; De Bast & Smith 2017)

and FGGUB M.1613 (Csiki & Grigorescu 2000), slightly larger than that of *H. belgica* and similar in size to the m1 from Nălaț-Vad. The pyramidal cusps and the "V"-shaped valleys that separate them resemble those seen in *B. transylvanicus*, *H. belgica*, *H. godfriauxi*, as well as in the m1s from Nălaț-Vad and Vălioara. The number of cusps in the new m1s is variable, 3-4:3, but they are aligned in two short rows as in other kogaionids, as well as in other cimolodontan groups such as djadochtatherioideans and the *Paracimexomys*-group (for details, see Kielan-Jaworowska & Hurum 2001; Luo *et al.* 2002; Kielan-Jaworowska *et al.* 2004). A variable cusp formula is known in the m1 of *B. transylvanicus* and it is related to intraspecific variability (Solomon *et al.* 2016). Therefore, we also interpret the presence of a fourth labial cusp on the crown of UBB ODAN-Mt-76 as an intraspecific variation (Fig. 3X'). Based on the discussions above as well as on the size of the new m1's, argumentatively, we assign these new teeth to the small latest Cretaceous kogaionid, *B. oardaensis*. The enamel of UBB ODAN-Mt-75, 76 is similar to that seen in *H. belgica*, FGGUB M.1613 and the specimen from Nălaț-Vad, with small divergent ridges interconnecting some of the cusps of the two rows, but differing from the more wrinkled enamel of *H. godfriauxi* and *B. transylvanicus*. Wear facets similar to those described in UBB ODAN-Mt-75, 76 are also seen in FGGUB M.1613 (Csiki & Grigorescu 2000), the isolated specimen from Nălaț-Vad (Smith *et al.* 2002), *H. belgica* and *H. godfriauxi* (Vianey-Liaud 1979; De Bast & Smith 2017), and in the larger *B. transylvanicus* (Solomon *et al.* 2016). The m1 is unknown in the other two Maastrichtian kogaionids, *Kogaionon* and *Litovoi*, preventing a comparison to *B. oardaensis*.

m2. One right m2 is available (UBB ODAN-Mt-77, Fig. 3Z). The tooth is broken in its mesio-lingual part, but the cusp formula can be recognized as 3:2. The crown outline when complete should have been sub-rounded with pyramidal cusps, which are separated by longitudinal and transverse valleys, except the last two labial cusps which appear almost interconnected. The preserved part of the mesio-lingual cusp is connected by a divergent ridge with the second labial cusp. The lingual cusps are larger than the labial ones. Fine enamel wrinkles can be observed on the labial surface of the disto-lingual cusp and on the lingual surface of the last two labial cusps. Fine wear facets can be distinguished on the labial side of the disto-lingual cusps, on the apices of the last two labial cusps and on the distal part of the tooth.

The tooth has a similar general morphology to the m2s of *B. oardaensis* (Codrea *et al.* 2014). A similar sub-rounded m2 is known also in *B. transylvanicus* and the Paleocene *H. belgica*, *H. godfriauxi* and *H. pyrenaica*. The new m2 is about half the size of that of *B. transylvanicus* (see Solomon *et al.* 2016: table 1 for mean dimensions of the m2 of this species), being somewhat smaller than that of *H. godfriauxi* (Vianey-Liaud 1979; De Bast & Smith 2017) and *H. pyrenaica* (Peláez-Campomanes *et al.* 2000), but somewhat larger than that of *H. belgica* (Vianey-Liaud 1979; De Bast & Smith 2017). The new m2 fits within the mean dimensions of the small

multituberculate mammal *B. oardaensis* (Codrea *et al.* 2014: table 2, fig. 4). Based on the above, we assign the new m2 to this species. The new m2 is similar in size and morphology to the m2 described by Grigorescu & Hahn (1987) as “*Paracimexomys? dacicus*” (this name is considered a junior synonym of *B. transylvanicus*). However, if the dimensions of the tooth (measured from a cast) figured by Grigorescu & Hahn (1987) are correct, then that tooth is half the size of the m2 of *B. transylvanicus* (Solomon *et al.* 2016: table 1), and should belong to a smaller species (as Grigorescu *et al.* 1985 remarked), very possibly to *B. oardaensis*. Similar pyramidal cusps separated by longitudinal and transverse valleys are seen in *B. transylvanicus* and in *Hainina* species for which the m2 is known. The divergent enamel wrinkles are similar to those observed in the m2 of *B. transylvanicus* (Solomon *et al.* 2016), differing from the more pronounced wrinkles of *H. godfriauxi* (Vianey-Liaud 1979, 1986; De Bast & Smith 2017). The wear aspect is similar to that seen in the larger species; the m2 of the two known species of *Barbatodon* is the least worn tooth from the lower dentition (Codrea *et al.* 2014; Solomon *et al.* 2016). The m2 is still unknown in *Kogaionon* and *Litovoi*. We notice here the error made by Csiki-Sava *et al.* (2018) in the caption of their fig. 1F. The figured tooth is a right M2, not a right m2. However, they correctly identified this tooth as an upper M2 in their supplementary material (Csiki-Sava *et al.* 2018: suppl. mat., p. 5).

REMARKS

The genus *Barbatodon*, with the type species *B. transylvanicus*, was first described based on a single m1 (ISB IS.001) that was erroneously identified as an “M1” (Rădulescu & Samson 1986). On the other hand, Grigorescu & Hahn (1987) correctly identified the tooth in discussion as m1 but proposed a new species, *Paracimexomys? dacicus*. Finally, Csiki *et al.* (2005) reinterpreted the holotype of *B. transylvanicus* and by comparison with their newly discovered material, they confirmed its position as a m1. Comparing their new material (FGGUB M.1635; Csiki *et al.* 2005), the holotype (ISB IS.001) of *B. transylvanicus* and the known material belonging to *Hainina* (Vianey-Liaud 1979, 1986; Peláez-Campomanes *et al.* 2000), they placed *B. transylvanicus* into the family Kogaionidae (Rădulescu & Samson 1996). For a long time, *B. transylvanicus* was the single species of the genus, but Codrea *et al.* (2014), based on a rich sample from Oarda de Jos locality (ODAN lens), described another, small species, as *B. oardaensis*. This small kogaionid was initially restricted to the Transylvanian Basin (Codrea *et al.* 2014), but afterward the species was also recognized from the Rusca Montană Basin (Codrea *et al.* 2017a). It was predictable that the species should have been present in the Hațeg Basin as well (Codrea *et al.* 2017a: table 1). The M1 fragment described here, originating from Vălioara, attests to the presence of this species in the Hațeg Basin. Additional data are now available, and they allow us to provide a more complete picture of the dentition of this small Maastrichtian kogaionid. Although the described material of *B. oardaensis* consists exclusively of isolated teeth, through comparisons to other kogaionids where

the dentition is preserved *in situ* (Rădulescu & Samson 1996; Csiki *et al.* 2005; Smith & Codrea 2015; Solomon *et al.* 2016; Csiki-Sava *et al.* 2018), some remarks related to its dentition can be summarized. Based on the available sample of teeth belonging to this small kogaionid and on the known data from *Kogaionon*, *B. transylvanicus* and *Litovoi*, an upper dental formula of 2:0:4:2 and a lower one of 1:0:1:2 is proposed for *B. oardaensis*. The upper incisors are the I2 and I3. The I2 is bicuspid with a main mesial cusp and an accessory small one as in *Kogaionon*, *B. transylvanicus* and *Litovoi* (Rădulescu & Samson 1996; Smith & Codrea 2015; Solomon *et al.* 2016; Csiki-Sava *et al.* 2018). The I3 is single-cusped as in the above-mentioned taxa. The P1 of the species bears two or three cusps, whereas P2 has two short rows with two cusps each. Also there is a slope starting from the distal cusps of each row of P2 similar to the one seen in the other latest Cretaceous kogaionids (Rădulescu & Samson 1996; Smith & Codrea 2015; Solomon *et al.* 2016; Csiki-Sava *et al.* 2018), but longer than in the Paleocene *H. belgica* and *H. godfriauxi* (Vianey-Liaud 1979; De Bast & Smith 2017). The P3 bears a constant number of six cusps (3:3) differing in this aspect from the other known kogaionids (see Section Upper dentition, for details), but sharing with them an elongated outline. The P4 has a variable cusp formula; the cusps are disposed on two mesially convergent crests, but the dimensions of the available sample (see Codrea *et al.* 2014, 2017a, and this study) are comparable. In sum, the P4 of *B. oardaensis* is very similar to that known in other kogaionids (Vianey-Liaud 1979, 1986; Rădulescu & Samson 1996; Gheerbrant *et al.* 1999; Peláez-Campomanes *et al.* 2000; Smith & Codrea 2015; Solomon *et al.* 2016; De Bast & Smith 2017; Csiki-Sava *et al.* 2018). The M1 has a constant formula of 3:4:2, and the lingual row bears the smallest number of cusps, as in *B. transylvanicus* (Smith & Codrea 2015; Solomon *et al.* 2016) and *Litovoi* (Csiki-Sava *et al.* 2018), contrary to the condition seen in all *Hainina* species (Peláez-Campomanes *et al.* 2000). Peláez-Campomanes *et al.* (2000) noted that *Kogaionon* shares with *Hainina* the long lingual cusp row of M1, but we have to add that although *Kogaionon* bears three lingual cusps, the lingual row of the M1 is the shortest in *Kogaionon* (AAS personal observation) as it is in the other known Late Cretaceous kogaionids, including *B. oardaensis*. The M2 is short with a square to triangular outline (Codrea *et al.* 2014). The i1 of the species is clearly reported from three distinct localities (ODAN, ODBL and Ng), sharing the same pattern at all these sites (see Section Lower dentition, for details). The stage of wear clearly influences the general aspect of this tooth, which may appear gently curved when the wear is incipient or almost devoid of curvature when highly worn. The p4 bears ten to eleven serrations (*sensu* Weaver & Wilson 2020), six to seven ridges, two labio-distal cuspules, and has an arcuate profile typical for cimolodontans (Kielan-Jaworowska & Hurum 2001). The variability in the number of serrations, ridges, and the presence or absence (a condition interpreted by us as the result of advanced wear) of the labial cusps was also reported in *B. transylvanicus* (Solomon *et al.* 2016). As such, this aspect of variability seems to be characteristic for the p4

of the genus *Barbatodon*. Until now, the m1 of *B. oardaensis* was known to be a short tooth with a constant cusp formula of 3:3, but one m1 from the new sample has an extra labial cusp and demonstrates that intraspecific variability is present in this tooth position as well, just as reported in the m1 of *B. transylvanicus* (Solomon *et al.* 2016). The m2 of this species has a variable cusp formula of 2-3:2, and represents the less worn tooth from the lower tooth row as in the larger species of the genus (Solomon *et al.* 2016). As documented above, morphological and size variations are present in various tooth positions of *B. oardaensis* (Codrea *et al.* 2014, 2017a, and this study). However, all of these are related to intraspecific variability, as already demonstrated when the species was erected (Codrea *et al.* 2014). Moreover, the intraspecific variability seems to be quite common in kogaionids, being also reported in *B. transylvanicus* (Solomon *et al.* 2016) or *H. belgica* (De Bast & Smith 2017). In the Late Cretaceous kogaionids in which the upper dentition is known *in situ*, as in *Kogaionon*, *B. transylvanicus* and *Litovoi* (Rădulescu & Samson 1996; Smith & Codrea 2015; Csiki-Sava *et al.* 2018), P3 is the largest tooth of the cheek teeth row. Analyzing the available sample of upper teeth assigned to *B. oardaensis*, we note that the M1 of this species seems to be the largest upper tooth (see Codrea *et al.* 2014: table 2 for details). The enamel on the various teeth of *B. oardaensis* is variable (for details see Codrea *et al.* 2014, 2017a, and Section Systematic paleontology). A gigantoprismatic enamel type was identified for the P2 of *Kogaionon* (Fosse *et al.* 2001) and also for *Hainina* (Carlson & Krause 1985). Although as yet, no enamel analyses have been done on teeth from *B. oardaensis*, because they belong to the same family we may assume a gigantoprismatic enamel for this small kogaionid. Although in the anterior premolars (P1-P3) wear is absent or insignificant, on the P4-M2 the wear facets are clearly distinct. These wear facets from the P4-M2 complex have their corresponding ones on the surfaces of the p4-m2. As such, the pattern of wear is likely similar to that in *B. transylvanicus* (see Solomon *et al.* 2016, for a detailed discussion related to the wear stages of this kogaionid). Moreover, as Codrea *et al.* (2014) mentioned, the character of the wear on the P4-M1 of *H. pyrenaica* (see Peláez-Campomanes *et al.* 2000, for detailed discussion) is similar to that in *B. oardaensis*. Seemingly, the kogaionids shared the same orthal cycle.

DISCUSSION

STRATIGRAPHIC DISTRIBUTION OF ROMANIAN KOGAIONIDS

The origin of kogaionids is still unclear and poorly understood (Csiki & Grigorescu 2001, 2006; Codrea *et al.* 2014, 2017a; Smith & Codrea 2015; Solomon *et al.* 2016). Like other inhabitants of the “Hațeg Island”, some dinosaurs for example (Weishampel *et al.* 1993, 2003; Godefroit *et al.* 2014, 2009; Weishampel & Jianu 2011), Late Cretaceous kogaionids retained some archaic characters, but they also show derived characters (see Csiki & Grigorescu 2001). Such an archaic morphological character is the simple morphology of the

cheek teeth, with the number of cusps reduced in comparison with other Late Cretaceous multituberculates or with the more derived Paleocene ones (Codrea *et al.* 2014). However, in some respects, kogaionid cheek teeth (premolars, molars) are derived by having more cusps than at least some other Late Cretaceous cimolodontans (certain djadochtatherioids, *Paracimexomys*-group, see Eaton 1995; Kielan-Jaworowska & Hurum 1997; Eaton & Cifelli 2001; Luo *et al.* 2002). The Paleocene representatives are considered a stock of more derived kogaionids (Csiki & Grigorescu 2001). Some studies recovered the kogaionids as a derived subgroup of Cimolodonta (Kielan-Jaworowska & Hurum 2001; Kielan-Jaworowska *et al.* 2004), but those authors did not include *Barbatodon* in the Kogaionidae because they still considered the holotype m1 an “M1”. Although they likely appeared in the latest Cretaceous, the kogaionids represent a basal cimolodontan family (Csiki & Grigorescu 2006; Smith & Codrea 2015). It is likely that the genetic isolation offered by their (?) island habitat was the main reason for the differences between kogaionids and other latest Cretaceous multituberculates. Moreover, Csiki-Sava *et al.* (2018) also considered the reduced brain size of *Litovoi* indicative of an adaptation of kogaionids to an island life. For a long period of time, the stratigraphic distribution of this endemic multituberculate family was restricted to the Sânpetru Formation of the Hațeg Basin (Rădulescu & Samson 1996). Starting with 2000, several discoveries pointed out that their distribution was not restricted to this formation. Recently, Codrea *et al.* (2017a: 35) summarized the distribution of these mammals on the landmasses of the “Hațeg Island”. The discovery of *Litovoi* (a large sized kogaionid; Csiki-Sava *et al.* 2018) strengthens our observations (Codrea *et al.* 2017a) related to the distribution of larger forms. Csiki-Sava *et al.* (2016) separated several chronostratigraphic tiers (T1-T4) when they summarized the distribution of vertebrates in the Hațeg and Rusca Montană basins and southwestern part of the Transylvanian Basin. Based on their data, kogaionids were present on a stratigraphic interval that comprises the uppermost Campanian-upper Maastrichtian of the “Hațeg Island”. Until now, only the small forms are attested from all three above-mentioned basins (Codrea *et al.* 2017a, and references therein). The overall distribution of kogaionids on the island shows that they were an important component of the local vertebrate fauna (see Csiki-Sava *et al.* 2016; Codrea *et al.* 2017a). Moreover, the presence of kogaionids was confirmed in the Paleocene of Jibou (Gheerbrant *et al.* 1999), and taking into account that in that area the presence of the uppermost Cretaceous terrestrial deposits is also confirmed (Nopcsa 1905; Codrea & Godefroit 2008) it is predictable that future discoveries will extend the distribution of the latest Cretaceous kogaionids toward the northeastern part of present-day Transylvania. However, a different opinion proposed by Csiki & Grigorescu (2001) suggests that a derived stock of kogaionids were able to spread before their extinction eastward and, together with eutherians, repopulated the landmasses of present-day Transylvania. Future discoveries could establish which of these hypotheses, if any, is correct (but see discussion below).

DIVERSITY OF LATE CRETACEOUS KOGAIONIDS

Although kogaionids were present in various areas of the “Hațeg Island”, we have to be very cautious when referring to their taxonomic diversity. For a long time, because their remains were scarce and fragmentary, the systematic relationships of the Romanian multituberculates were rather poorly understood (Rădulescu & Samson 1986, 1997; Grigorescu & Hahn 1987). For example, all isolated incisors were regarded as *Multituberculata* indet. (e.g. Grigorescu 1984; Rădulescu & Samson 1997; Csiki & Grigorescu 2000). Some researchers proposed the idea that more than one multituberculate group was present on the island (Rădulescu & Samson 1990, 1996, 1997). The discovery of *Kogaionon*, which led to the establishment of the new family Kogaionidae (Rădulescu & Samson 1996), together with the reassignment of the Paleocene *Hainina* to this family (Peláez-Campomanes *et al.* 2000), represented great progress for the systematics of Romanian multituberculates. Later, Csiki *et al.* (2005) placed *B. transylvanicus* in this family. To date, three genera belonging to the endemic family Kogaionidae (Rădulescu & Samson 1996) have been described from the Late Cretaceous of Romania: *Kogaionon* (Rădulescu & Samson 1996), *Barbatodon* (with two species: *B. transylvanicus* [Rădulescu & Samson 1986; Csiki *et al.* 2005; Smith & Codrea 2015; Solomon *et al.* 2016] and *B. oardaensis* [Codrea *et al.* 2014, 2017a]), and *Litovoi* (Csiki-Sava *et al.* 2018). Csiki & Grigorescu (2000) also reported the possible presence of the genus *Hainina*, but based on a large sample Codrea *et al.* (2014, 2017a) considered that those *Hainina* “species” are uncertain, and some of the teeth are similar in size to those of *B. oardaensis* (Codrea *et al.* 2017a: table 1). Moreover, a possible synonymy between the larger forms has to be taken into account. *Barbatodon transylvanicus* was established on a single lower molar (Rădulescu & Samson 1986), whereas *K. ungureanui* was based on the upper dentition (Rădulescu & Samson 1996). *Litovoi tholocephalos* was defined based on a fragmentary skull with dentition (Csiki-Sava *et al.* 2018) without considering the already demonstrated dental intraspecific variation of *B. transylvanicus* (Solomon *et al.* 2016). It is intriguing that the two latter genera with very close morphology and size were erected from the same stratigraphic level and locality. There is no evidence of a specific diet for either of these two taxa. However, in the character-taxon matrix of the phylogenetic analysis of *Litovoi*, Csiki-Sava *et al.* (2018) did not use characters already known in *B. transylvanicus* (see Solomon *et al.* 2016) even though they stated that “The coding of *B. transylvanicus* is based on direct study of the specimens referred to this taxon and available to us, as well as literature (Csiki *et al.* 2005; Smith & Codrea 2015)” (Csiki-Sava *et al.* 2018: suppl. mat., p. 40). If they consider the materials from Solomon *et al.* (2016) wrongly assigned to *B. transylvanicus*, a discussion regarding this aspect would have been appropriate. Thus, it is astonishing how, for the diagnosis of the new genus *Litovoi*, comparisons to the already published data were not used, ignoring the well-known intraspecific variability of kogaionid multituberculates. However, a detailed discussion regarding the size and morphological differences of the same

kogaionid species was made by Solomon *et al.* (2016; see also references therein) and it would be redundant to repeat it here. When referring to the systematic diversity of insular mammals, a good example is shown by the more recent faunas from the Mediterranean islands. The mammalian faunas of these islands are characterized by a low taxonomic diversity (see Boekschoten & Sondaar 1966; Azzarolli 1982; Lister 1996; Marra 2005; Raia & Meiri 2006; De Vos *et al.* 2007; Palombo 2008, 2018; Benton *et al.* 2010; Van der Geer *et al.* 2010 and references therein; Krause *et al.* 2020). The presence of a ?therian in the Hațeg Basin was mentioned (without ever being figured) by Csiki & Grigorescu (2001), but this assumption has to be tested. In such a context, it seems more likely that kogaionids were the sole mammals that populated the “Hațeg Island”. Taking this aspect into account, a high local diversity of kogaionids may be accepted. Unpublished data (work in progress) suggest that Csiki & Grigorescu (2001) correctly recognized three size classes of kogaionids. However, the scarce material originating from the same species apparently led to the suggestion of a very high taxonomic diversity (Rădulescu & Samson 1986, 1996, 1997; Csiki & Grigorescu 2000; Codrea *et al.* 2002, 2012b; Smith *et al.* 2002). The well-documented sample of *B. oardaensis*, originating from the same site (Codrea *et al.* 2014), supports the idea that intraspecific variation should be an important aspect to be taken into account when studying kogaionids. Later, the intraspecific variability was also confirmed for the larger species of *Barbatodon* (Solomon *et al.* 2016). Moreover, Codrea *et al.* (2017a, and this study), demonstrated that *B. oardaensis* was not restricted to the Transylvanian Basin only, or to one particular site. In fact, intraspecific variability was also confirmed for the Paleocene *Hainina* (De Bast & Smith 2017) and, moreover, for *Boffius splendidus* Vianey-Liaud, 1979, another cimolodontan multituberculate that originates from the same site as *H. belgica* and presents intraspecific variability (De Bast & Smith 2017). The discovery of the partial skeleton of a small kogaionid, including skull elements, was reported from the Transylvanian Basin (Csiki-Sava *et al.* 2012; Vremir *et al.* 2014). Unfortunately, that material is still undescribed, which is regrettable for direct comparisons. However, the dimensions of the figured *in situ* p4 (Csiki-Sava *et al.* 2012: fig. 2B) are comparable to those of *B. oardaensis* (Codrea *et al.* 2014, 2017a). This aspect, together with the fact that they originate from the same area (Metaliferi Sedimentary Area; Codrea & Dica 2005) are arguments in favor of considering these to belong to the same genus and species.

To date, the origin of kogaionids is still unclear, but this endemic family dispersed westward in the early Cenozoic (Fig. 5). This hypothesis was put forward by Csiki & Grigorescu (2001), supported by the fact that to date, the only known Late Cretaceous kogaionids have been recorded from uppermost Cretaceous deposits of the “Hațeg Island”. But, after the mass extinction at the K/Pg boundary, the kogaionids are reported (although so far only by isolated teeth) from the earliest Paleocene of Spain, the early Paleocene of Belgium, and the late Paleocene of France and Romania (Vianey-

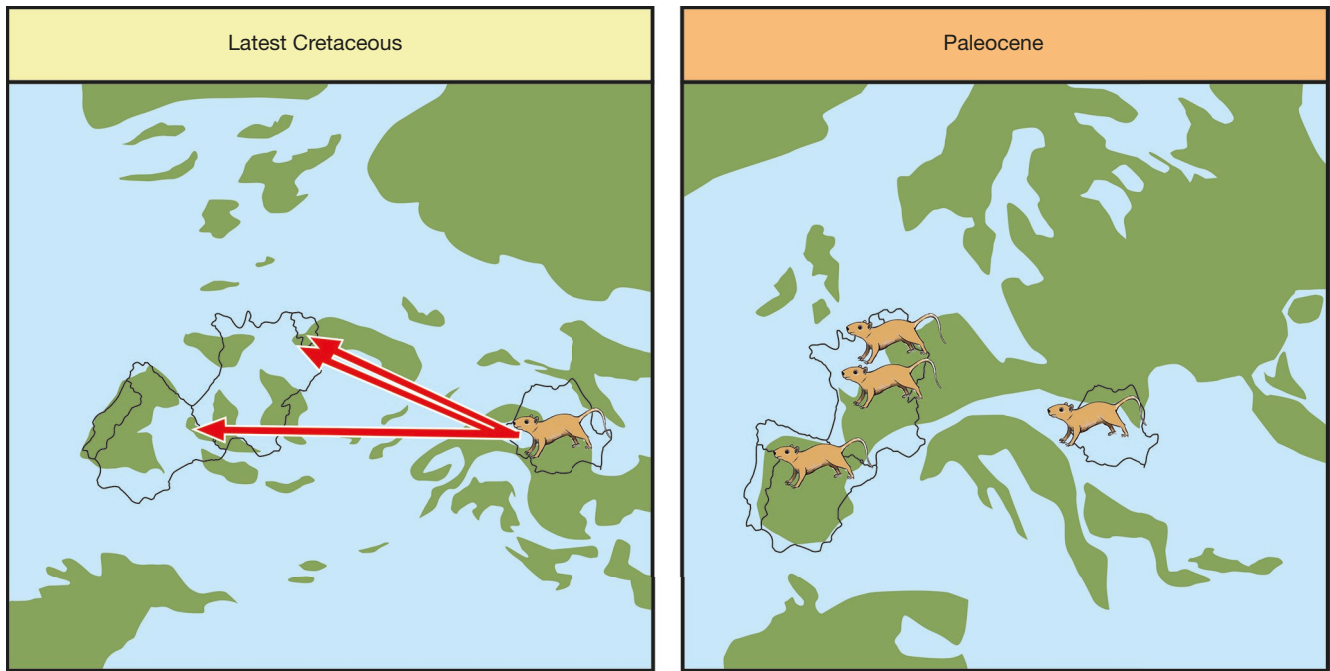


FIG. 5. — Schematic distribution of the kogaionids during the latest Cretaceous (left) and the Paleocene (right); arrows indicate their presumed dispersal direction. Late Cretaceous map, courtesy of Ron Blakey ([deeptimemaps.com/](https://www.deeptimemaps.com/) (accessed on 26 June 2020)) – modified and simplified. Paleocene map modified and simplified after Scotese (2014).

Liaud 1979; Vianey-Liaud 1986; Gheerbrant *et al.* 1999; Peláez-Campomanes *et al.* 2000; De Bast & Smith 2017). Csiki & Grigorescu (2001) proposed a scenario (see Section “Stratigraphic distribution of Romanian kogaionids”) for the re-appearance of kogaionids in the Paleocene of Romania. De Bast & Smith (2017) demonstrated that the kogaionids were the dominant multituberculates of the mammalian fauna from the early Paleocene of Hainin, whereas the late Paleocene mammalian fauna of Cernay was dominated by the family Neoplagiaulacidae Ameghino, 1890, with *Hainina* being by far less abundant than the other multituberculates (Vianey-Liaud 1986). We consider that probably the kogaionids did not cease to exist in Transylvania until the Thanetian, and a repopulation hypothesis is poorly supported, as long as in the late Paleocene of Cernay, the North American genus *Neoplagiaulax* Lemoine, 1982 was the most abundant taxon (Vianey-Liaud 1986; De Bast & Smith 2017). In the late Paleocene of Jibou (Romania), the presence of kogaionids is confirmed (Gheerbrant *et al.* 1999). Although the material from Jibou is still under study, it is clear that kogaionids were the dominant multituberculates of the local fauna (VAC personal observation). In such a circumstance, if the kogaionids were able to return to Transylvania, there is no reason why other multituberculates such as neoplagiaulacids for example, did not reach this part of Europe on their turn. Or if they did it, why did they not become the dominant family, as long as in the late Paleocene of France they were very common, as a successful group? As such, the “absence” of kogaionids in Transylvania from the end of the Maastrichtian until the Thanetian is likely nothing more than a consequence of the lack of outcrops with deposits during this interval.

CONCLUSIONS

The new multituberculate sample presented in this study confirms the presence of a single taxon at the type locality of *B. oardaensis* (Codrea *et al.* 2014). New occurrences of this small kogaionid are also reported in the Metaliferi Sedimentary Area and in the Hațeg Basin. Based on isolated specimens originating from various sites, the intraspecific variability of this multituberculate is supported, even documenting new morphological variations (e.g. in the cusp formula of the m1). The first I3s of the species, originating from the type locality (ODAN), are herein described, and based on a rich sample attention is drawn to the essential importance of intraspecific variability, in particular for kogaionids, when erecting new multituberculate genera and/or species. As such, the taxonomic diversity of the latest Cretaceous kogaionids was of particular interest for the present study (see Section “Diversity of Late Cretaceous kogaionids”). A latest Cretaceous-early Paleocene westward dispersal for kogaionids, as proposed by Csiki & Grigorescu (2001), is accepted, but a repopulation hypothesis from west to east during the Paleocene is not supported. Probably, kogaionids may have continuously populated the landmasses of Transylvania until they became extinct.

Acknowledgements

The authors are grateful to all the colleagues (too numerous to be mentioned here) involved over a decade in the field missions in the outcrops documenting the “Hațeg Island”. We thank Julien Cillis (RBINS) for assistance with SEM photographs. Also, we thank Cristina Fărcaș (Cluj-Napoca) and Nicolae

Trif (Sibiu and Cluj-Napoca) for producing some of the computer drawings, and Marian Bordeianu (Cluj-Napoca) for photographing some of the specimens. Also, we thank Dr Alexander Averianov and an anonymous reviewer, as well as the Associate Editor Dr Lorenzo Rook, for their useful comments that greatly helped to improve the manuscript. We thank Dr Kevin Padian for some English improvements. This work was supported by a grant of the Romanian Ministry of Education and Research, CNCS – UEFISCDI, project number PN-III-P1-1.1-PD-2019-0723, within PNCDI III (to AAS). VAC thanks Babeş-Bolyai University of Cluj-Napoca grants AGC: 30850, 30851, 30852, 31509, 32164 that partially supported part of the field-work.

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Submitted on 17 August 2020;
accepted on 29 December 2020;
published on 5 April 2022.