Spatial and Temporal Distribution of the Island-Dwelling Kogaionidae (Mammalia, Multituberculata) in the Uppermost Cretaceous of Transylvania (Western Romania)

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ABSTRACT

The latest Cretaceous kogaionid multituberculates from Transylvania (western Romania) were part of an endemic European clade of mammals that underwent an insular radiation at the end of the Cretaceous and then survived the end-Cretaceous mass extinction that extinguished many groups of contemporary therians. Transylvanian kogaionids lived on what was an island during the latest Cretaceous—"Haţeg Island"—and their fossils are found in the uppermost Campanian to upper Maastrichtian deposits of the Haţeg, Rusca Montană, and southwestern Transylvanian basins. This fossil record has improved dramatically over the past several decades, in part resulting from our decade-long joint Romanian-American-Scottish fieldwork, and comprises one of the most impressive and complete archives of Mesozoic mammals, including not only jaws and teeth but several incomplete skulls and partial skeletons.

We here review the fossil record of kogaionids from Transylvania. We report four new occurrences from the Haţeg Basin, update information on previously described ones, and use our database to reassess the chronostratigraphical and geographical distribution of kogaionids and their evolutionary patterns.

Although it was previously suggested that large and small kogaionids had largely mutually exclusive spatial distributions, we recognize the cooccurrence of small and large taxa in various units, suggesting a sympatric distribution across their entire chronostratigraphic range. We also identify a novel pattern: small kogaionids appear somewhat earlier than their larger relatives in all well-sampled sedimentary successions, suggesting that kogaionid colonizations of Haţeg Island and component regions took place at small body size and that body size increased only later through local evolution. We find correlations between body size, preservation style, and sedimentary context, which give insight into kogaionid paleobiology and diversity. Larger kogaionids are represented more often by partial skulls and occasionally skeletons compared with small kogaionids, which are usually represented only by isolated teeth, regardless of provenance. Larger kogaionids currently have a higher recognized local taxic diversity than their smaller relatives. We hypothesize that this may be in part a consequence of preservational bias related to body size, as more complete specimens may be more easily diagnosed as distinct taxa than those that are represented by more fragmentary and/or incomplete fossils. If true, the taxic diversity of smaller kogaionids may currently be underestimated. Finally, we identify correspondence between sedimentary facies and preservation style. Red-colored fine-grained rocks, suggestive of well-drained, oxidized floodplain paleoenvironments, yield more complete specimens than drab, greenish or grayish sediments deposited in more poorly drained parts of the floodplain. This pattern may suggest habitat preferences for better-drained floodplain environments and a semifossorial lifestyle for some taxa.

As the kogaionid fossil record improves, we can further test the hypotheses and patterns outlined above. The pace of new kogaionid discoveries by our team and others indicates that a more complete picture of kogaionid distribution, paleobiology, and evolution will emerge in the coming years, contributing to a more profound understanding of this peculiar group of island-dwelling Mesozoic mammals.

INTRODUCTION

The uppermost Cretaceous (uppermost Campanian-Maastrichtian) continental beds of the southwestern Transylvanian Basin and its neighboring areas (the Haţeg and Rusca Montană basins; Nopcsa, 1905; Grigorescu, 1992; Csiki-Sava et al., 2016; fig. 1) have been long celebrated for their fossil vertebrate assemblages, exemplified iconically by the famous dwarfed dinosaurs of Transylvania (Nopcsa, 1915, 1923; Weishampel et al., 1991; Benton et al., 2010; Csiki-Sava et al., 2015). These latest Cretaceous vertebrate assemblages of Transylvania inhabited an emergent land area placed along the northern margin of the Mesozoic Neo-Tethys oceanic domain, within the area of the so-called Mediterranean Seuil (Dercourt et al., 1993, 2000). This emergent land is customarily referred to as Haţeg

Island or the Transylvanian Landmass (e.g., Weishampel et al., 1991, 2010; Benton et al., 2010; Csiki-Sava et al., 2015).

The vertebrate faunas of this Hațeg Island included a fair number of dwarfed herbivorous dinosaurs (Nopcsa, 1923; Benton et al., 2010; Stein et al., 2010; Ősi et al., 2014), as well as morphologically aberrant nonavian and/or avian theropod dinosaurs (Csiki et al., 2010a; Brusatte et al., 2013; Cau et al., 2015; Buffetaut and Angst, 2020; Mayr et al., 2020a, 2020b). The dinosaurs lived alongside an array of other taxa that often also display island life-related paleobiological features. These taxa include a series of relictual groups such as turtles (Nopcsa, 1923; Gaffney and Meylan, 1992; Sterli and de la Fuente, 2013; Pérez-García and Codrea, 2018), crocodyliforms (Martin et al., 2010; Tennant et al., 2016; Venczel and Codrea, 2019), and hadrosauroid dinosaurs (Weishampel et al., 1993). These relicts were accompanied by isolated paleobiogeographical outliers such as madtsoiid snakes (Folie and Codrea, 2005; Vasile et al., 2013) as well as borioteiioid (Folie and Codrea, 2005) and possible teiioid (Venczel and Codrea, 2016; Codrea et al., 2017a) lizards; gigantic flying pterosaurs (Buffetaut et al., 2002; Vremir, 2010, Vremir et al., 2018); and a series of endemic taxa of frogs (Venczel and Csiki, 2003; Venczel et al., 2016), madtsoiid snakes (Vasile et al., 2013), dortokid pleurodiran turtles (Augustin et al., 2021), azhdarchid pterosaurs (Vremir et al., 2013; Solomon et al., 2020), and rhabdodontid dinosaurs (Weishampel et al., 2003). The island-related features of the latest Cretaceous Transylvanian vertebrate assemblage were first noted long ago by the pioneering paleontologist and paleobiologist Franz Nopcsa (Nopcsa, 1915, 1923; Weishampel et al., 1991; Benton et al., 2010; Weishampel et al., 2010), and were synthesized most recently by Csiki-Sava et al. (2015).

The Mammals of Hațeg Island

Among the groups of vertebrates that most eloquently exemplify the insular nature of the latest Cretaceous Hațeg Island fauna are the mammals. These latest Cretaceous Transylvanian mammals are, as currently documented, almost exclusively (but see Csiki and Grigorescu, 2002) members of the Multituberculata, a now completely extinct, derived nontherian clade within Allotheria (e.g., Kielan-Jaworowska et al., 2004). All of these Hațeg Island multituberculates, whose remains were identified for the first time in the Transylvanian area less than 40 years ago (Grigorescu, 1984a), are currently considered to belong to one family of cimolodontans, the Kogaionidae, erected in 1996 by Rădulescu and Samson (1996; see below). In the years since their first discovery in the Hațeg Basin, a large number of kogaionid specimens have been collected across the outcropping areas of the continental uppermost Cretaceous in southwestern Transylvania (fig. 2). The large number of kogainoid-bearing sites (figs. 2, 3) demonstrates that these animals were common, abundant, and widespread in this part of the Late Cretaceous European Archipelago at the end of the Cretaceous.

Furthermore, their fossil record is of high quality for Mesozoic mammals; it consists, as is often the case, of widely distributed isolated teeth, but also of tooth-bearing jaws or jaw fragments, and most remarkably, partial skulls, and in some cases even partial skeletons (Csiki-Sava et al., 2017; see review below). This situation stands in stark contrast with that documented for the uppermost Cretaceous of the western European areas where multituberculates are as yet completely unknown, and where the relatively rare mammals are represented mainly by the stem eutherian zhelestids (e.g., Gheerbrant and Astibia, 2012) as well as (much more rarely) by metatherians (Martin et al., 2005), with a fossil record that consists mainly of isolated teeth (with some recently identified notable exceptions; Tabuce et al., 2004, 2013; Gheerbrant and Teodori, 2021). The Kogaionidae thus represent a group that, apparently, was endemic to the Transylvanian area during the latest Cretaceous (Csiki and Grigorescu, 2002; Csiki-Sava et al., 2015). Furthermore, it boasts a plethora of
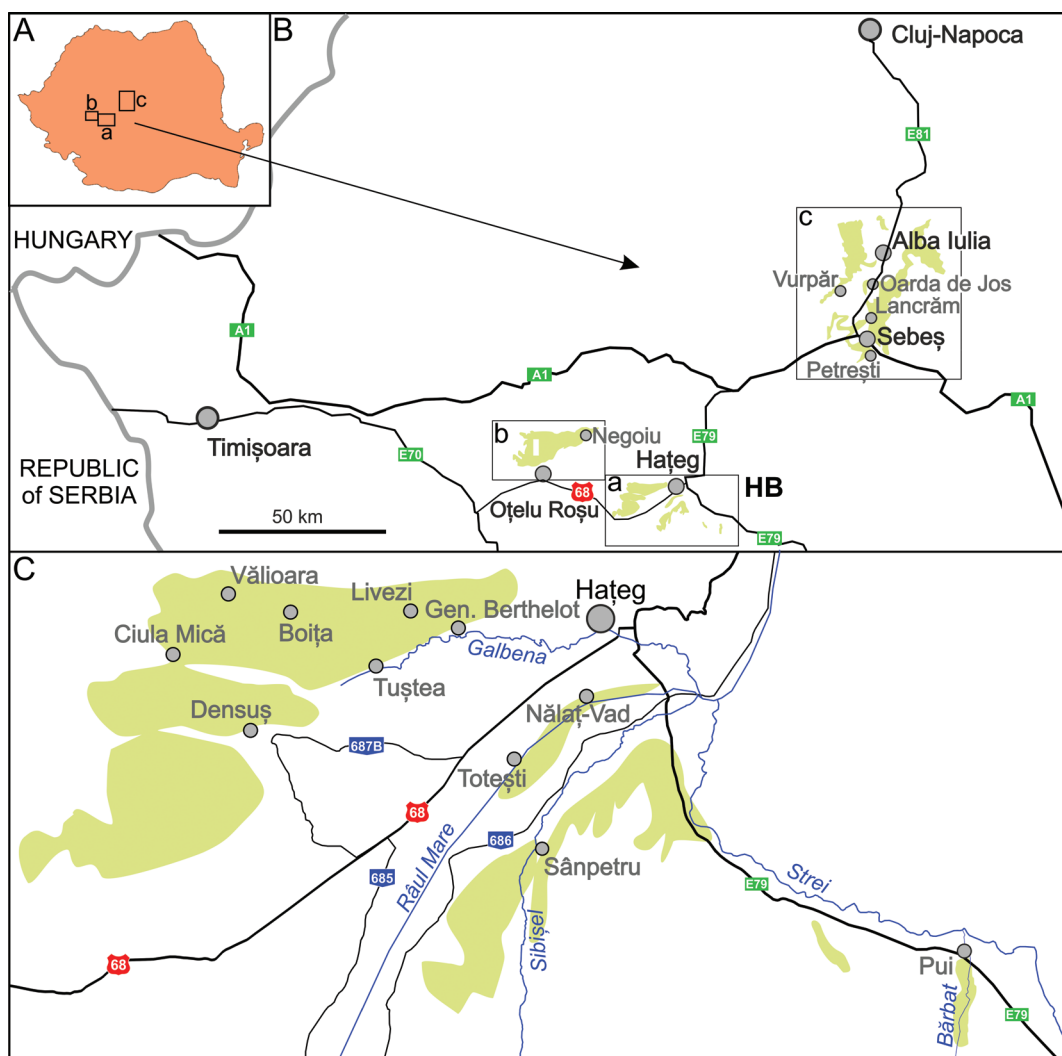
FIGURE 1. Areal distribution of the kogaionid multituberculate-bearing uppermost Cretaceous continental deposits in western Romania. **A.** Map of Romania showing the position of the main outcropping areas: **a.** Haţeg Basin; **b.** Rusca Montană Basin; **c.** southwestern Transylvanian Basin. **B.** Northwestern Romania, with the distribution of the uppermost Cretaceous continental deposits in green (simplified after Csiki-Sava et al., 2016); the area of the Haţeg Basin (HB) shown enlarged in C, for details. Names of major towns and cities in black, main uppermost Cretaceous fossiliferous localities in gray; important highways and roads indicated by number-letter codes. **C.** Distribution of the uppermost Cretaceous continental deposits in the Haţeg Basin.

largely sympatric taxa suggesting a moderate adaptive radiation of this clade within this area during the latest Cretaceous, and it also includes one of the most striking examples of island-related neuroanatomical adaptations known in Mesozoic mammals (Csiki-Sava et al., 2018).

In keeping with the ever-growing fossil record of the latest Cretaceous Transylvanian kogaionids, the literature dealing with them is also rather extensive, making them one of the best-studied vertebrate clades from the Haţeg Island fauna. The large number of kogaionid discoveries and studies
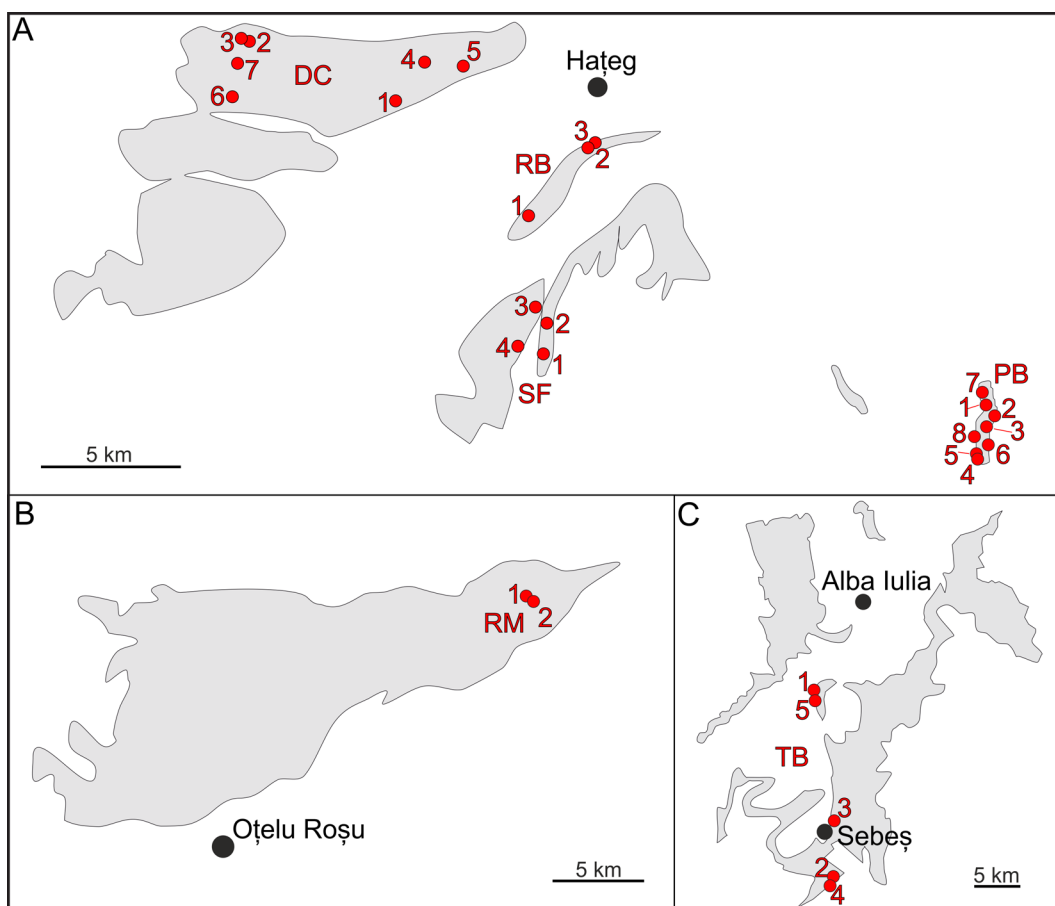
FIGURE 2. Kogaionid-bearing fossil sites (red dots) discussed in this review (see text for details and abbreviations) in the main areas with fossiliferous uppermost Cretaceous continental deposits of the Transylvanian area (in light gray; see fig. 1). **A.** Kogaionid occurrences from the Haţeg Basin; DC1–7**,** sites in the Densuş-Ciula Formation; PB1–8**,** sites in the Pui Beds; RB1–3**,** sites in the Râul Mare Beds; SP1–4**,** sites in the Sînpetru Formation. **B.** Kogaionid sites from the Rusca Montană Basin (RM1–2). **C.** Kogaionid sites from the southwestern Transylvanian Basin (TB1–5).

have also prompted a fair number of reviews of their Transylvanian fossil record over the years (e.g., Rădulescu and Samson, 1997; Csiki and Grigorescu, 2002; Smith and Codrea, 2003; Csiki, 2005; Csiki et al., 2005; Solomon et al., 2015, 2016; Codrea et al., 2017a). Each of these studies has reflected the then-current state-of-the-art information concerning their identity, diversity, and distribution. The most recently published overview—Codrea et al. (2017a)—aptly synthesized the existing body of knowledge available at the respective time about the distribution and diver-

sity of the latest Cretaceous Transylvanian kogaionids. Nevertheless, the rapid pace of new discoveries, together with ongoing efforts to describe older or newly collected specimens, has led to an accumulation of new data (e.g., Csiki-Sava et al., 2017, 2018; Smith et al., 2022) that already requires an update to the overview presented by Codrea et al. (2017a).

The purpose of this review is to introduce several new occurrences and discoveries of kogaionids in the uppermost Cretaceous of Transylvania, to insert the occurrences currently on record

FIGURE 3. Approximate chronostratigraphic distribution of the latest Cretaceous kogaionid occurrences from the Transylvanian area (red stars), alongside other important fossil sites (gray stars) using the biochronofaunal tier system developed by Csiki-Sava et al. (2016), in the main kogaionid-bearing successions: **A,** the Sînpetru Formation (SP sites); **B,** the Râul Mare Beds (RB sites); **C,** the Pui Beds (PB sites); **D,** the Densuș-Ciula Formation (DC sites), all in the Hațeg Basin; **E,** the Rusca Montană Basin (RM sites); **F,** the southwestern Transylvanian Basin, eastern (left column) and western (right column) outcropping areas (TB sites); dark gray, marine deposits; light gray, continental deposits. For kogaionid site abbreviations, see text and figure 2; for other abbreviations, see Csiki-Sava et al. (2016) and Botfalvai et al. (2021). Question mark added in the Râul Mare Beds succession reflects current lack of details as to the relative straigraphic positions of sites RB2 and RB3 (see text).

into the most recently available chronostratigraphic framework in order to better understand the spatial and temporal distribution of these animals within the Transylvanian Landmass, and to discuss the significance of some of the patterns unraveled by their known fossil record.

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ANATOMICAL TERMS: lower/UPPER case letters, lower/UPPER teeth; i/I, incisors; p/P, premolars, m/M molars (e.g., p4, fourth lower premolar; M1, first upper molar); L, left; R, right.

GEOLOGICAL SETTING AND MAMMALIAN FOSSILIFEROUS CONTENT OF THE CONTINENTAL UPPERMOST CRETACEOUS OF TRANSYLVANIA

Uppermost Cretaceous fossiliferous continental deposits are spread patchily over a rather extensive area of the western Transylvanian Basin and its surroundings (fig. 1), extending from the Jibou-Someş-Odorhei area in the north to Pui in the Haţeg Basin, to the south, and from Lunca Cernii de Jos, in the Rusca Montană Basin, in the west, to Sebeş in the east (e.g., Nopcsa, 1905; Grigorescu, 1992; Codrea and Dica, 2005; Codrea and Godefroit, 2008; Codrea et al., 2010c, 2012a; Vremir, 2010; Vasile et al., 2012; Vremir et al., 2015a; Csiki-Sava et al., 2016). Overall, these deposits are mostly purely continental, and mainly of alluvial origin, although transitional beds toward the underlying marine deposits have been also identified locally (Vremir et al., 2014). The lithology and lithostratigraphy of these uppermost Cretaceous (uppermost Campanian-Maastrichtian) deposits have been addressed in several previous contri-

butions, most recently reviewed by Csiki-Sava et al. (2016), and only the most salient points will be mentioned here; further details will be provided, whenever necessary, when discussing the nature of the local kogaionid fossil record.

In the main fossiliferous area, represented by the Haţeg Basin (fig. 1B: HB, 1C), the continental uppermost Cretaceous beds are divided traditionally between the northwestern, volcanoclast-bearing Densuş-Ciula Formation and the central-eastern Sînpetru Formation, mainly devoid of volcanoclasts (Grigorescu, 1992), although more recent fieldwork suggests a somewhat more complicated lithostratigraphic distribution (see Therrien, 2005; Csiki-Sava et al., 2016). In the southwestern Transylvanian Basin, coeval deposits are included into the Sebeş Formation (fig. 1B: c)—probably also subsuming the Vurpăr and, partly, the Şard formations of Codrea and Dica (2005) and Codrea et al. (2010c; see Vremir et al., 2015a)—whereas in the northwestern part of the same basin, synchronous beds have been included into the base of the Jibou Formation (Codrea and Godefroit, 2008). Finally, fossiliferous uppermost Cretaceous continental-volcanodetrital successions in the more westerly lying Rusca Montană Basin (fig. 1B: b) have been noted in several isolated locations (Vasile and Csiki, 2011; Codrea et al., 2012a, 2017a; Vasile et al., 2012), but no formal lithostratigraphic scheme had been proposed yet for their hosting beds.

In most of these areas, the fossil-bearing continental deposits sit above paleontologically well-dated uppermost Cretaceous marine deposits whose youngest components are currently considered upper Campanian (e.g., Grigorescu and Melinte, 2001; Neagu, 2006; Melinte-Dobrinescu, 2010; Vremir et al., 2014; Ţabără et al., 2022), thus bracketing the age of the continental beds as younger than latest Campanian. Further constraints on the age of these deposits (mainly from palynostratigraphy, magnetostratigraphy, and radiometric dating) suggest that the fossiliferous beds represent the uppermost Campanian-Maastrichtian interval, although the presence of the

uppermost Maastrichtian is as yet only assumed (see most recent review by Csiki-Sava et al., 2016). Integration of the different age-constraining data has allowed the development of a relatively robust chronostratigraphic framework of the uppermost continental fossiliferous deposits from the southwestern Transylvanian area, including also the relative positions of the major fossiliferous sites and localities that yielded multituberculate remains (Csiki-Sava et al., 2016).

Although vertebrate remains have been reported across the entire area with outcropping uppermost Cretaceous continental beds (which circumscribe roughly the core area of the emergent land known as the Hațeg Island), mammal remains are as yet restricted to the southern part of it, admittedly one with significantly better outcrop conditions. As such, their remains are currently recorded in the northeastern Rusca Montană Basin, across the entire Hațeg Basin, and into the southern and eastern parts of the southwestern corner of the Transylvanian Basin (see below; figs. 1, 2). Across this relatively extensive area, a large number of mammal-bearing sites have been reported over the past several years (fig. 2). The quality and quantity of the mammal remains recovered vary widely between the different fossil localities, ranging from few isolated (and often incomplete) teeth, to larger samples of isolated teeth (tens of specimens), eventually also associated with edentulous and tooth-bearing jaw fragments, and finally to partial skulls and even incomplete skeletons. As a result, the Transylvanian fossil record of multituberculates represents by far the best-preserved and richest mammalian fossil assemblage known from the entire Late Cretaceous in Europe (e.g., Kielan-Jaworowska et al., 2004; Csiki-Sava et al., 2015), documenting a unique and peculiar episode of mammalian evolutionary history.

KOGAIONIDAE IN PHYLOGENY, TIME, AND SPACE

In order to better understand the wider significance of the latest Cretaceous Transylvanian multituberculates, a brief outline of their place within Multituberculata is required. Multituberculates are members of Allotheria, a nontherian mammalian clade placed close to the origin of Theria (e.g., Kielan-Jaworowska et al., 2004). The clade Allotheria groups exclusively extinct mammals that are currently considered more derived than prototherians (hence, they are members of the crown-group Mammalia), but less derived than therians (Metatheria plus Eutheria) as well as several fossil groups leading up to the therian root (such as symmetrodonts, dryolestoids, and stem zatherians; e.g., Luo et al., 2002; Kielan-Jaworowska et al., 2004; Yuan et al., 2013; Han et al., 2017). The latest phylogenies find that, within Allotheria, multituberculates are the sister-group of Haramiyida, a probably paraphyletic assemblage of Late Triassic–Late Jurassic mammaliaforms with a superficially multituberculate-like, policusped postcanine dentition (e.g., Yuan et al., 2013; Han et al., 2017; fig. 4). Other analyses recovered multituberculates as allotherians closely allied to Haramiyida plus Gondwanatheria (Krause et al., 2014, 2020; but see, e.g., Huttenlocker et al., 2018, for an alternative placement of these clades), a group of mammaliforms with peculiar, hypsodont-crowned molars and which had an exclusively southern, Gondwanan distribution during the later Mesozoic and Paleogene-Miocene (e.g., Krause and Bonaparte, 1993; Gurovich and Beck, 2009; Chimento et al., 2015).

Among multituberculates, kogaionids are definitively members of the derived, probably monophyletic clade Cimolodonta (e.g., Kielan-Jaworowska and Hurum, 2001; fig. 4A), as supported conclusively by a large number of shared derived craniodental characters (e.g., Kielan-Jaworowska et al., 2004; Csiki et al., 2005; Csiki and Grigorescu, 2006; Smith and Codrea, 2015; Csiki-Sava et al., 2018; Smith et al., 2022). These characters include foremost the overall skull shape as well as the significantly reduced dental formula of the kogaionids (fig. 5). The dentition is reminiscent of the plesiomorphic cimolodontan condition (e.g., Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska et al., 2004),
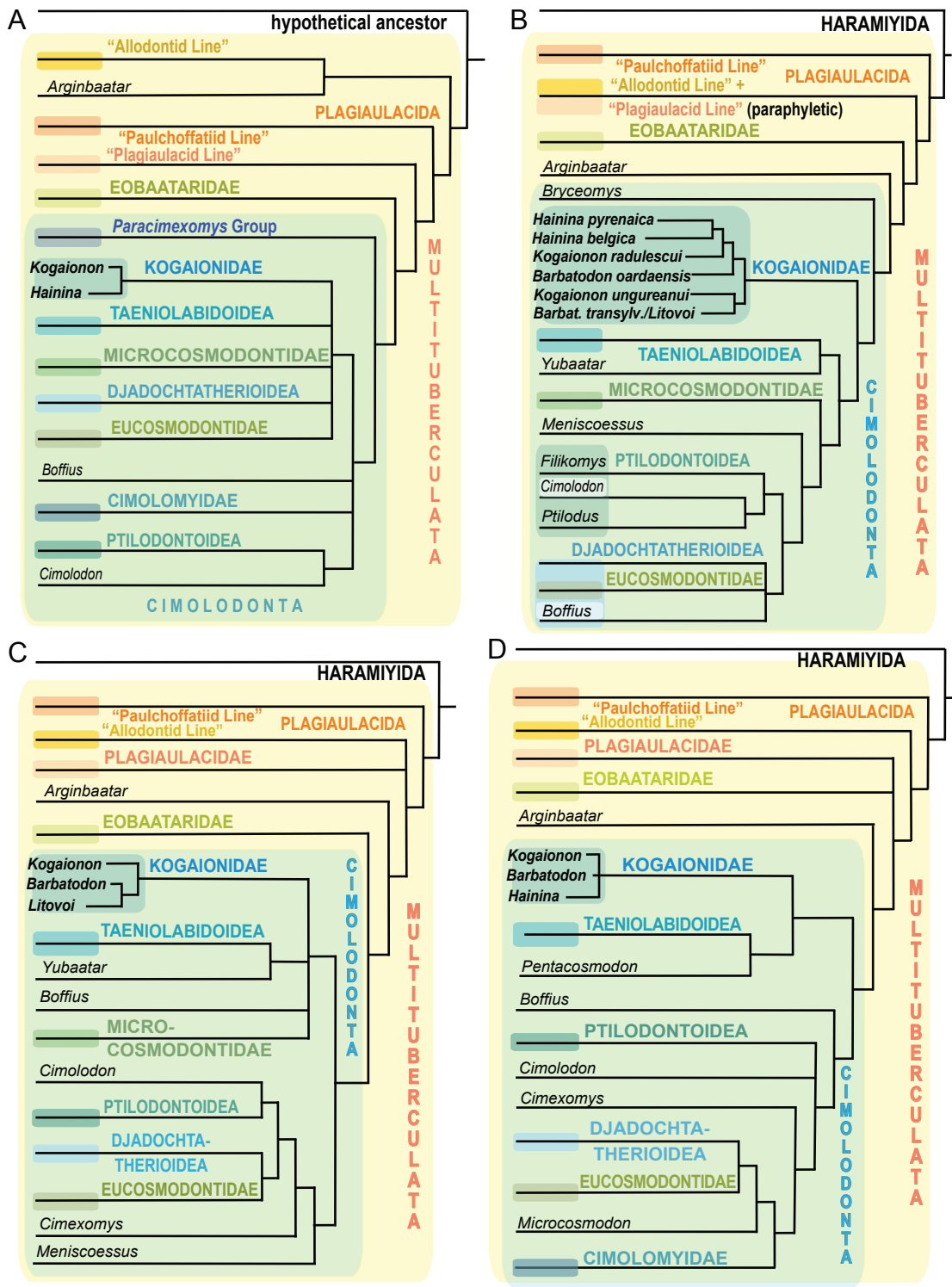
with an upper tooth row that consists of two incisors (I2 and I3), no canine, four premolars, and two molars (Rădulescu and Samson, 1996; Peláez-Campomanes et al., 2000; Smith and Codrea, 2015; Csiki-Sava et al., 2018; Smith et al., 2022; fig. 5C, F), as well as a lower tooth row with one incisor (i1), most probably only one premolar (p4; see below), and two molars (Csiki et al., 2005; Smith and Codrea, 2015). Further cimolodontan apomorphies recognized within Kogaionidae (see Csiki-Sava et al., 2018) include the rather simple, peglike I3 (although in kogaionids, this incisor is relatively large compared to I2, and may be slightly more complex in morphology than usually found in other cimolodontans); the arcuate, relatively high p4 that protrudes slightly above the level of the molar occlusal plan, and presents a single labiodistal structure (commonly a platformlike feature that is better developed and more complex in morphology than the comparable structure in other cimolodontans), as opposed to the row of labiobasal cusps seen in the more basal plagiaulacidan multituberculates; and the presence of a prismatic (gigantoprismatic: Fosse et al., 2001) enamel structure.

The exact position of Kogaionidae within Cimolodonta remains, however, controversial (fig. 4), in part due to the nature of the group's fossil record (which was mainly fragmentary until very recently), but also in part to the unstable nature of higher-level multituberculate relationships as currently understood. Accordingly, kogaionids have been placed alternatively in a large polytomy with a number of other important cimolodontan clades (Kielan-Jaworowska and Hurum, 2001; fig. 4A), as basal cimolodontans (e.g., Rougier et al., 1997, Smith et al., 2022; fig. 4B), even forming a nonmonophyletic assemblage of taxa that represent successively more derived lineages at the base of Cimolodonta (Csiki and Grigorescu, 2006), or as closely related to the clade of dominantly large Asian–North American taeniolabidoids (e.g., Smith and Codrea, 2015; Mao et al., 2016; Csiki-Sava et al., 2018; fig. 4C, D). These controversies stem to a great extent from the peculiar and highly autapomorphic craniodental anatomy of the kogaionids (fig. 5) that spurred the recognition of a distinct multituberculate family once the first relatively well-preserved remains of a kogaionid (the partial skull of the group namesake *Kogaionon*) was identified and described (Rădulescu and Samson, 1996).

The diagnosis of the Kogaionidae has evolved significantly over the years, as a more and more inclusive membership had been identified, as well as more completely preserved remains were uncovered and described; these changes in the diagnosis (reflecting our understanding concerning the nature of Kogaionidae) were most recently reviewed and commented upon by Csiki-Sava et al. (2018: Supplementary Appendix) as well as by Smith et al. (2022). According to our current ideas, the family is diagnosed by a series of cranial and dental features that are either autapomorphic to the clade, or else form a unique combination of characters. The skull of the kogaionids is as yet incompletely known, but at least in the case of four latest Cretaceous taxa (*Barbatodon transylvanicus*, *Kogaionon ungureanui* and *K. radulescui*, and *Litovoi tholocephalos*) enough of it is preserved so as to allow reasonably complete and detailed reconstructions (figs. 5A, B, D, E, 6A–H). In all of these four taxa, the skull appears to be autapomorphically constructed with a narrow and relatively long snout region followed by distal skull segment charac-

FIGURE 4. Hypotheses concerning the phylogenetic position of the Kogaionidae. **A.** In a polytomy with other derived cimolodontan clades (based on Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska et al., 2004). **B.** As a basal clade of the Cimolodonta (based on Smith et al., 2022; see also Rougier et al., 1997; Csiki and Grigorescu, 2006). **C, D.** Closely related to the Asian–North American Taeniolabidoidea (based on **C,** Csiki-Sava et al., 2018; **D,** Smith and Codrea, 2015).
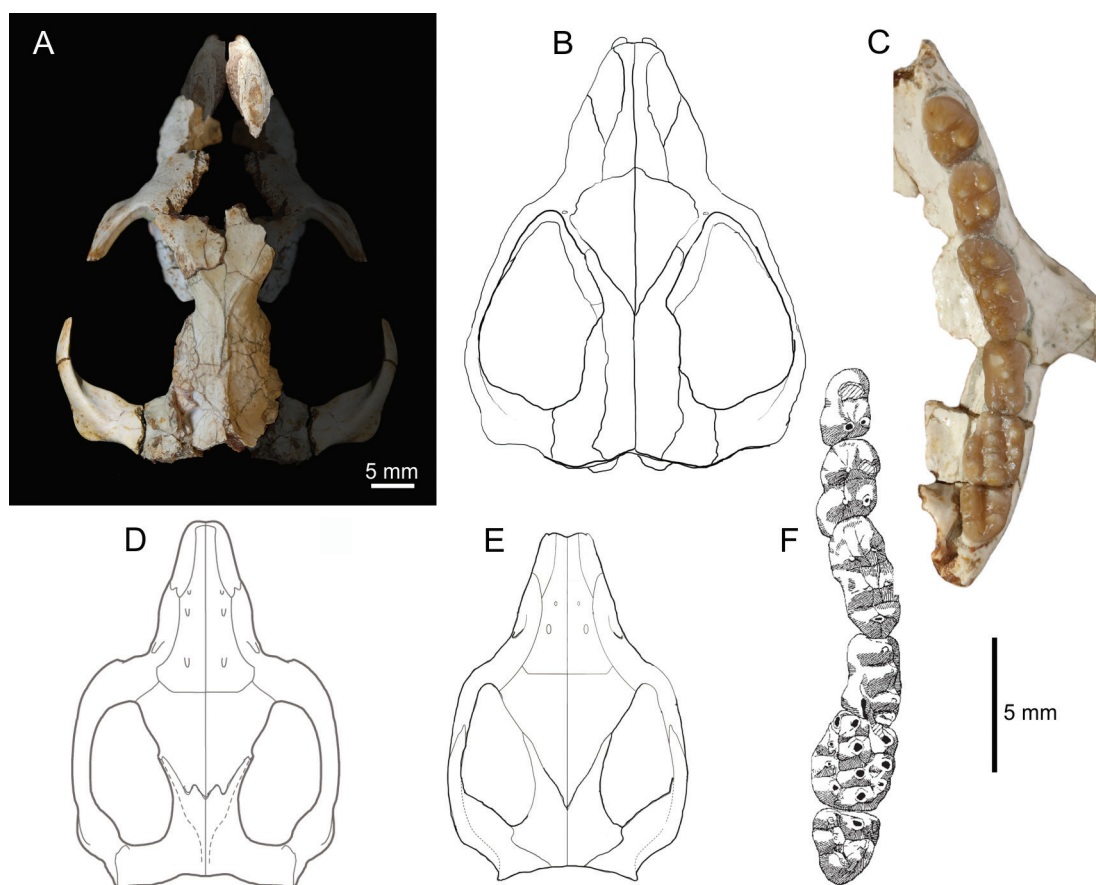
FIGURE 5. Craniodental morphology of the Kogaionidae. Skull structure in dorsal view (**A, B, D, E)** and occlusal view of upper dentition (**C, F**) in different kogaionid genera (skulls and tooth rows, respectively, drawn to the same scale). **A, B.** Skull of *Litovoi tholocephalos*, **A.** Reconstructed, with missing elements (shaded) mirrored from their counterparts, and **B.** Simplified outline drawing (from Csiki-Sava et al., 2018). **C.** Left-side upper dentition of *Litovoi tholocephalos* (from Csiki-Sava et al., 2018). **D.** Skull of *Kogaionon ungureanui*, simplified outline drawing (from Rădulescu and Samson, 1996: Kielan-Jaworowska et al., 2004). **E.** Skull of *Barbatodon transylvanicus,* simplified outline drawing (from Smith and Codrea, 2015). **F.** Left-side upper dentition of *Kogaionon ungureanui*, in occlusal view (from Rădulescu and Samson, 1996).

terized by widely diverging zygomatic arches that are oriented transversaly and arise at the level of the P3/P4 contact. Although neither of these characteristics is in itself unique to Kogaionidae (see discussions in Kielan-Jaworowska et al., 2004; Csiki-Sava et al., 2018: Supplementary Appendix), their combination is, and it is this combination that sets apart the skulls of kogaionids from those of other cimolodontans. Furthermore, kogaionids appear to have relatively large, massive, and tall premaxillae (fig. 6D, F). Detailed description of the known kogaionid cranial material is needed before further kogaionid apomorphies can be identified.

The most diagnostic feature of the kogaionids is, however, represented by their dentition, and especially their upper dentition (fig. 5C, F). Most remarkably, the premolar row is lenghtened relative to the molar row, often amounting to twice the length of the latter. Furthermore, the longest

element of the premolar row is represented by the elongated P3, although its relative development compared to P4 varies between the different taxa, from clearly longer than P4 to subequal with the latter. The P3 is often even longer than, or at least comparable in its length to, the largest upper molar (M1). In its turn, the P4 is remarkable in that it develops a unique occlusal morphology, unlike that seen in other cimolodontans, with an obliquely striking main labial cusp row seconded by a short and distally restricted lingual cusp row, a morphology first identified and recognized as diagnostic for the clade by Peláez-Campomanes et al. (2000). Finally, the M1 is characterized by a unique combination between a short and wide occlusal outline, a reduced cusp count (only four cusps are present in the median row in all known kogaionids), and a well-developed lingual cusp row that extends mesially for at least half the mesiodistal length of the crown.

In the lower dentition, the apomorphically arched p4 is associated with a relatively short m1 that shows a reduced cusp formula of 3–4 cusps in each row; the relative development of the p4 compared to m1 varies between the different taxa, from 50% longer than m1 to more than twice as long. Finally, another kogaionid synapomorphy may be represented by the unequally developed, lingually reduced enamel cover of the incisors (in i1 and I2, at the least), although this feature is currently documented only in the latest Cretaceous representatives of the clade. It should be also emphasized that although our knowledge concerning the anatomy of the kogaionids is limited mainly to their craniodental morphology, recent discoveries reveal details of their postcranial anatomy as well (Csiki-Sava et al., 2018; Vremir et al., 2018; Botfalvai et al., 2021; fig. 6I, J).

Due to their highly apomorphic craniodental morphology, the true affinities of the first discovered kogaionid remains, which at that moment were represented exclusively by isolated teeth, had been obscured by their fragmentary nature. Indeed, the first found kogaionid fossils, coming from the Paleocene of Western Europe (Belgium and France) and referred to the genus *Hainina*

(Vianey-Liaud, 1979, 1986), were left unassigned at a higher taxonomic level (Vianey-Liaud, 1979; McKenna and Bell, 1997), or else were tentatively included either in Cimolomyidae (Vianey-Liaud, 1986) or in Ptilodontoidea (Rougier et al., 1997). Meanwhile, the second identified kogaionid taxon (*Barbatodon* from the uppermost Cretaceous of Romania; Rădulescu and Samson, 1986) was considered related to the Asian djadochtatherioids (Rădulescu and Samson, 1986), or, alternatively, to the North American basal cimolodontans of the "*Paracimexomys* group" (Grigorescu and Hahn, 1987). Such widely diverging taxonomic opinions were the byproduct of the unique dental morphology of these multituberculates, with combinations of characters hard to fit into the diagnoses of previously separated taxonomic categories.

The discovery of *Kogaionon*, the third recognized kogaionid genus (also coming from the uppermost Cretaceous of Romania; Rădulescu and Samson, 1996; fig. 5D, F), finally offered the opportunity to understand the true taxonomic and systematic affinities of *Hainina* and *Barbatodon*. First *Hainina* (Peláez-Campomanes et al., 2000; Kielan-Jaworowska and Hurum, 2001), then *Barbatodon* as well (Csiki et al., 2005) were securely nested in the newly erected Kogaionidae, alongside *Kogaionon*. Recently, the family was enlarged with the description of a fourth genus (*Litovoi*) also originating from the uppermost Cretaceous of Romania (Csiki-Sava et al., 2018; figs. 5A–C, 6).

According to a series of discoveries spread over the past 40 years, the currently known fossil record of kogaionids is restricted exclusively to Europe, and the group is often regarded as a typical European endemic clade (e.g., Csiki-Sava et al., 2015). Its stratigraphically oldest representatives are reported from the uppermost Campanian–lowermost Maastrichtian of Romania (Vremir et al., 2014, 2015b), and they occur throughout the Maastrichtian of the southwestern Transylvanian area (fig. 3). Here, they are represented by the above-mentioned three genera (*Barbatodon*, *Kogaionon*, *Litovoi*), with *Bar-*
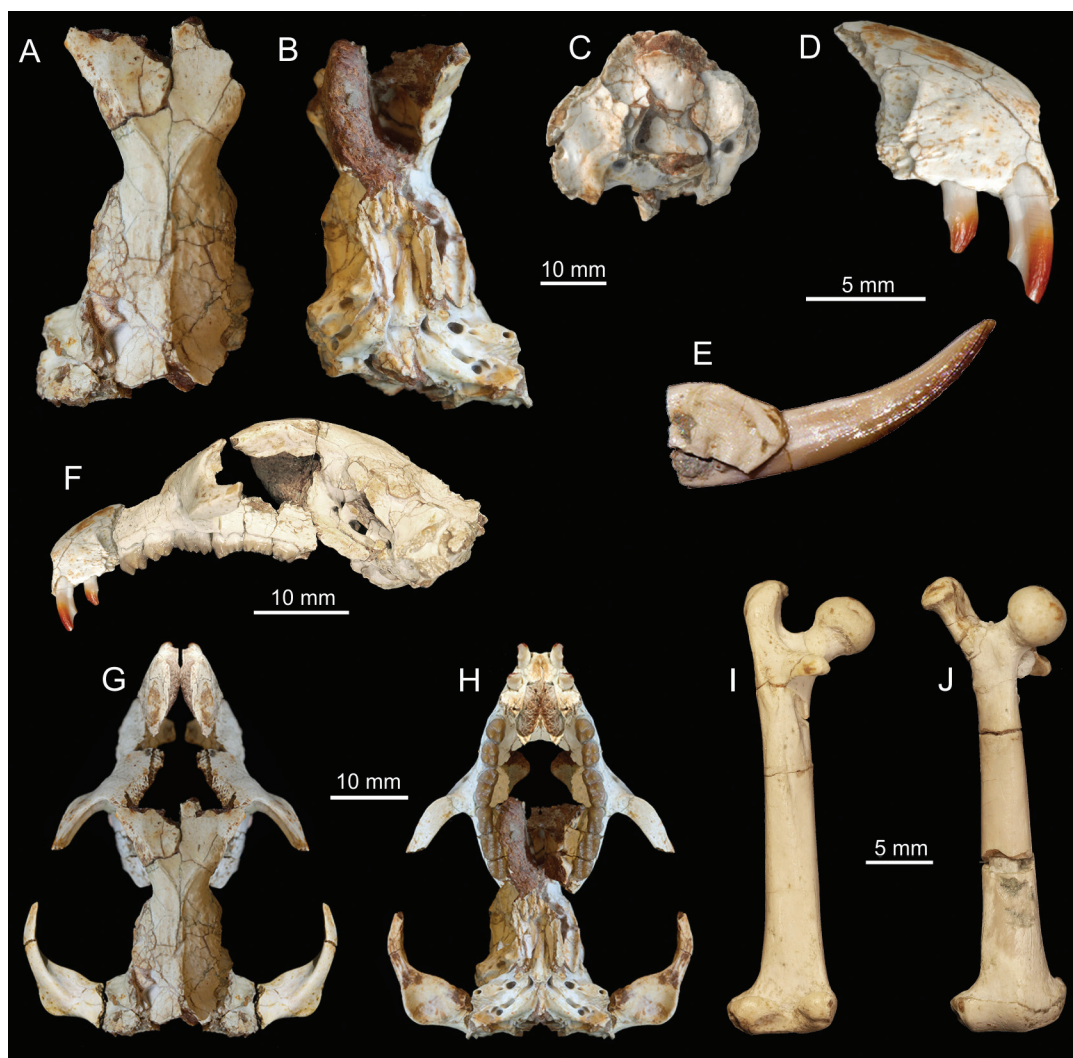
FIGURE 6. Selected skeletal elements of the holotype of *Litovoi tholocephalos* LPB (FGGUB) M.1700, one of the most completely known kogaionid individuals from Pui (site PB6), Haţeg Basin (modified and completed from Csiki-Sava et al., 2018). **A–C,** Skull roof, braincase and partial petrosals (specimen M.1700.1) in **A.** dorsal, **B.** ventral, and **C.** occipital views. **D.** Right premaxilla with red-pigmented, in situ I2 and I3 (specimen M.1700.5) in lateral view. **E.** Left symphyseal fragment with i1 (specimen M.1700.6) in medial view. **F.** Composite reconstruction of skull in lateral view, using specimens M.1700.5 (right premaxilla, mirrored), M.1700.2 (left maxilla with in situ P1-M2), and M.1700.1 (braincase and petrosal region). **G, H,** Composite skull reconstruction based on elements listed above (see **F**), as well as M.1700.4 (left posterior zygomatic arch), with preserved elements mirrored, in **G.** dorsal and **H.** ventral views. **I.** Left femur (specimen M.1700.19) in posterior view. **J.** Right femur (specimen M.1700.20) in anterior view.

batodon and *Kogaionon* each including two species—the medium-large type species *B. transylvanicus* (Rădulescu and Samson, 1986; Csiki et al., 2005; Smith and Codrea, 2015; Solomon et al., 2016) and the smaller *B. oardaensis* (Codrea et al., 2014, 2017a) in the case of the former, and the larger *K. ungureanui* (Rădulescu and Samson, 1996) and the smaller *K. radulescui* (Smith et al., 2022) for the latter. Although *Hainina* has been also reported from the same area and time interval (e.g., Csiki and Grigorescu, 2000, 2002; Kielan-Jaworowska et al., 2004), this original taxonomic referral should be now reconsidered, given the now significantly improved local fossil record of the group (see below).

Besides these four nominal taxa, kogaionid remains that are as yet unidentified at a genus and/or species level have also been reported from several locations across southwestern Transylvania. Some of these remains had been tentatively referred to already known genera, but left in open nomenclature at a species level, while others might represent even further new taxa or else remain indeterminate at a lower taxonomic level due to their fragmentary and/ or nondiagnostic nature. Besides the taxonomic diversity it already reveals, the known fossil record of these Transylvanian kogaionids is also characterized by a noticeable diversity in craniodental morphology and especially in body size (fig. 7; see also below). Most remarkably, according to our current knowledge all latest Cretaceous kogaionids were restricted exclusively to the Transylvanian Landmass, and the clade can be thus identified as being strictly endemic for this area at the end of the Cretaceous (Csiki and Grigorescu, 2002, 2006; Csiki-Sava et al., 2015; Smith and Codrea, 2015; Solomon et al., 2015, 2016). This could, of course, change with future discoveries of kogaionids in other Upper Cretaceous units in Europe, but for the time being their absence in otherwise well-sampled terminal Cretaceous faunas in France and Spain is striking (e.g., Csiki-Sava et al., 2015), and supportive of local endemicity in the Transylvanian area.

Starting at the very beginning of the Paleocene, kogaionids suddenly achieved a significantly wider spatial distribution, as their remains have been identified from the lowermost Paleocene of northern Spain (Peláez-Campomanes et al., 2000), the lower Paleocene of Belgium (Vianey-Liaud, 1979; De Bast and Smith, 2017), as well as the upper Paleocene of France, Romania, and possibly Spain (Vianey-Liaud, 1986; Gheerbrant et al., 1999, 2003; López-Martínez and Peláez-Campomanes, 1999). Despite this important paleobiogeographical range expansion, kogaionids remained constrained to Europe; they have not been found, for instance, in any of the well-sampled Paleocene rock units of North America (e.g., Rose, 2006). Furthermore, their higher-level taxonomic diversity apparently dropped in the Paleocene compared to the latest Cretaceous; only one genus, *Hainina*, is recorded throughout the epoch, with several temporally and—in part—spatially nonoverlapping species: the early Danian Spanish *H. pyrenaica*, the sympatric but differently sized, late Danian *H. belgica* and *H. godfriauxi* from Belgium, and the Thanetian *H. vianeyae* from France, while a currently indeterminate *Hainina* sp. has also been reported from the Thanetian of Romania.

The evolutionary fate of the kogaionids dwindled during the Paleocene. While they formed almost exclusively the European multituberculate assemblages during the Danian (Vianey-Liaud, 1979; Peláez-Campomanes et al., 2000; De Bast and Smith, 2017), kogaionids became subordinate by the early Thanetian to the neoplagiaulacid cimolodontans, introduced from North America in an as yet poorly understood mid-Paleocene dispersal event (Vianey-Liaud, 1986; De Bast and Smith, 2017). Kogaionids appear to have survived into the latest Paleocene in some marginal regions of Europe (Romania, Spain), where they still occured alongside more common placentals that were already represented by relatively modern groups (Gheerbrant et al., 1999; López-Martínez and Peláez-Campomanes, 1999). In other parts of Europe, however, kogaionids were either replaced entirely by the immigrant neoplagiaulacids (e.g.,
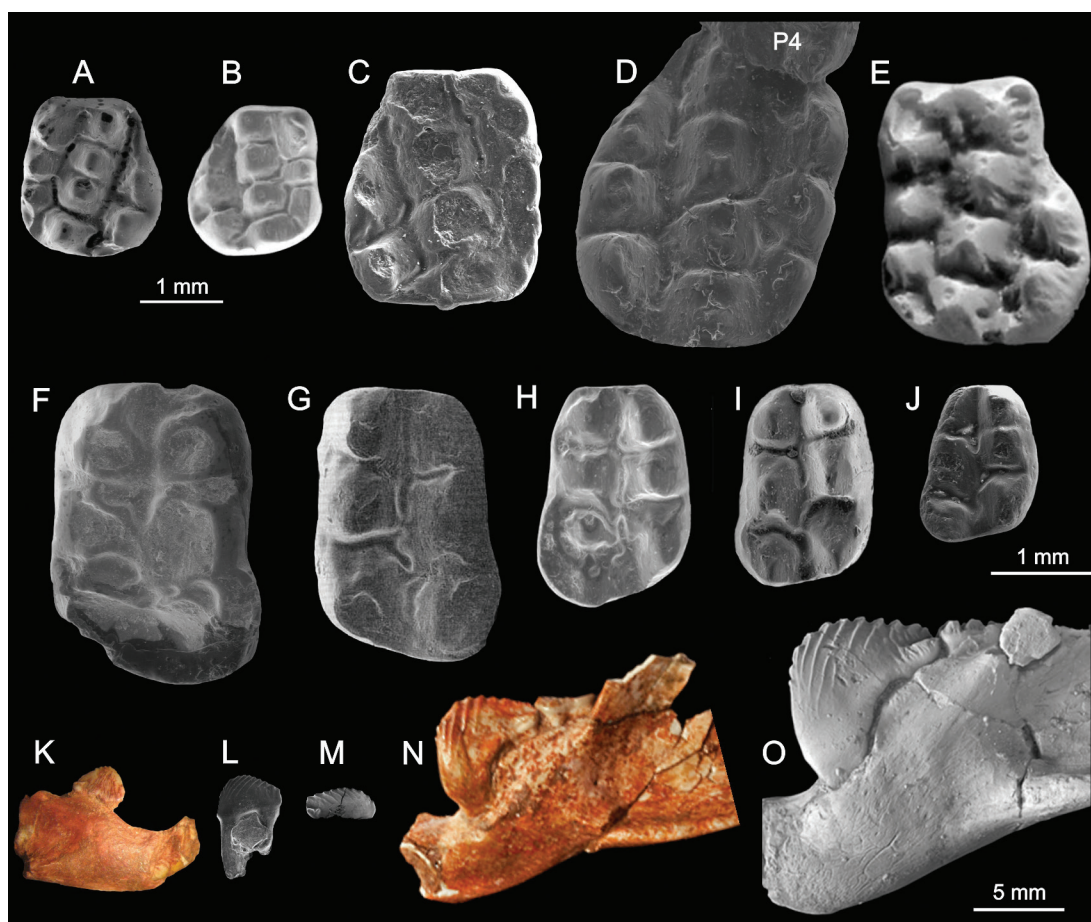
FIGURE 7. Morphological and size disparity within the latest Cretaceous Transylvanian kogaionids. **A–E.** First upper molars (M1), in occlusal view, drawn to the same scale. **A.** *Barbatodon oardaensis*, right M1 UBB ODAN-Mt-13, Oarda de Jos (site TB1), southwestern Transylvanian Basin (from Codrea et al., 2014). **B.** Small kogaionid (*Kogaionon* n. sp. or *Barbatodon oardaensis*; see text for details), left M1 UBB (specimen number not available), Totești-baraj (site RB1), Hațeg Basin (from Codrea et al., 2002). **C.** Indeterminate kogaionid (?*Kogaionon* n. sp. in Csiki and Grigorescu, 2002), left M1 LPB (FGGUB) M.1624, Fântânele, Vălioara (site DC2), Hațeg Basin (see Csiki and Grigorescu, 2002). **D.** *Kogaionon ungureanui*, left M1 ISER SPT/001 (P4 marks preceding last premolar), Sânpetru (site SP1), Hațeg Basin. **E.** *Barbatodon transylvanicus*, right M1 UBB P-Mt3-4, Pui (site PB5), Hațeg Basin (from Solomon et al., 2016). **F–J.** First lower molars (m1), in occlusal view, drawn to the same scale. **F.** *Barbatodon transylvanicus*, right m1 LPB (FGGUB) M.1635, Pui (site PB3), Hațeg Basin. **G.** Indeterminate kogaionid (*Hainina* sp. B in Csiki and Grigorescu, 2000), right m1 LPB (FGGUB) M.1613, Fântânele, Vălioara (site DC2), Hațeg Basin. **H.** Indeterminate kogaionid (*Barbatodon* n. sp. or *Barbatodon oardaensis*; see text for details), left m1 UBB TBM V.442, Nălaț-Vad (site RB2), Hațeg Basin (from Smith et al., 2002). **I.** *Barbatodon oardaensis*, left m1 UBB ODAN-Mt-15, Oarda de Jos (site TB1), southwestern Transylvanian Basin (from Codrea et al., 2014). **J.** Indeterminate kogaionid, left m1 LPB (FGGUB) M.1618, Fântânele, Vălioara (site DC2), Hațeg Basin. **K–O.** Ultimate lower premolars (p4), labial view, drawn to the same scale. **K.** Indeterminate kogaionid, right p4 in dentary fragment MMIRS 655, Petrești-Arini (site TB2), southwestern Transylvanian Basin (see Csiki-Sava et al., 2012). **L.** *Barbatodon oardaensis*, left p4 UBB ODAN-Mt-1, Oarda de Jos (site TB1), southwestern Transylvanian Basin (from Codrea et al., 2014). **M.** *Barbatodon oardaensis*, right p4 UBB Ng2-01, Negoiu (site RM2), Rusca Montană Basin (from Codrea et al., 2017a). **N.** *Barbatodon transylvanicus*, left p4 in dentary LPB (FGGUB) M.1635, Pui (site PB3), Hațeg Basin. **O.** *Barbatodon transylvanicus*, left p4 in dentary UBB P-Mt3-1, Pui (site PB5), Hațeg Basin (from Solomon et al., 2016).

Jehle et al., 2012), or else multituberculates disappeared altogether with the advent of the more derived, modern placental orders (e.g., Smith et al., 2014), following an important dispersal-related faunal turnover near the Paleocene-Eocene boundary (e.g., Hooker and Collinson, 2012; De Bast and Smith, 2017).

THE CURRENT FOSSIL RECORD OF THE LATEST CRETACEOUS TRANSYLVANIAN KOGAIONIDS

In this section, we review in detail the currently known kogaionid fossil record from the Transylvanian uppermost Cretaceous. Our review is organized, as much as possible, both chronologically (from earliest to latest, ordered by discovery date) and geographically (focusing on particular areas and lithostratigraphic units). For each kogaionid occurrence (fossiliferous site), we report details such as age and stratigraphic position, sedimentary context and paleoenvironmental assessment, fossil content, and history of discovery and research, completed with comments and discussions related to the kogaionid material known from the respective site, whenever possible based either on our personal inspection of the specimens or on available published data and illustrations. In addition, we also provide a comprehensive lithostratigraphic and geochronologic framework for the Transylvanian kogaionid distribution, and discuss some of the emerging distribution patterns, as a baseline for future research.

As already noted, kogaionid fossils are reported in three main areas with uppermost Cretaceous continental deposits across the Transylvanian area, the Hațeg Basin, the southwestern corner of the Transylvanian Basin, and the Rusca Montană Basin, respectively (figs. 2, 3). Chronologically, the first multituberculate fossils were identified in the Hațeg Basin, the best studied and paleontologically most well sampled of these three areas, starting in the late 1970s (e.g., Grigorescu, 1984a; Grigorescu et al., 1985). These first discoveries were fol-

lowed much later, in the late 2000s, by reports of kogaionid occurrences in the Rusca Montană Basin (Codrea et al., 2009, 2012; Feigi et al., 2010), and finally, roughly synchronously, in the southwestern Transylvanian Basin (Sebeș–Alba Iulia area) as well (Codrea et al., 2010a, 2010b, 2010c; Vremir, 2010).

KOGAIONID OCCURRENCES IN THE HAȚEG BASIN

Although identified significantly later in the Hațeg Basin than other latest Cretaceous vertebrates, the remains of kogaionids are rather common and occur in most of the at least moderately well-sampled microvertebrate localities, along with the more exceptional cases where their remains (usually much better preserved and more complete partial skulls and/or skeletons) have been identified through surface prospecting. Their fossils also show a remarkably wide areal and lithostratigraphic coverage, having been recovered from practically all major areas with vertebrate-bearing continental beds (e.g., Csiki-Sava et al., 2016); this demonstrates that kogaionids were both common and relatively abundant components of the local faunal assemblages throughout the temporal range of the latest Cretaceous Hațeg Basin paleofaunas. As the uppermost Cretaceous continental vertebrate-bearing deposits of the basin are currently divided into several lithostratigraphic entities (some formally defined as formations, while others referred to only informally, as beds; Csiki-Sava et al., 2016), the Hațeg fossil record of kogaionids will be presented separately for each of these subdivisions.

SÎNPETRU FORMATION

Although once considered to cover significantly larger areas across the central and eastern parts of the Hațeg Basin (e.g., Grigorescu, 1992; Van Itterbeeck et al., 2004), the outcropping areas of the Sînpetru Formation are currently restricted to the classical occurrences along the

FIGURE 8. Kogaionid-bearing fossiliferous localities from the Hațeg Basin–Sînpetru Formation and potentially correlative units. **A.** Deposits of the lower section of the Sînpetru Formation exposed on the right side of Sibișel Valley, near site SP2. **B.** Deposits of the lower section of the Sînpetru Formation exposed on the left side of the Sibișel Valley, in the La Scoabă section hosting site SP3. **C.** Overview of the Râul Mare Beds cropping out in the bed of the Râul Mare River at Nălaț-Vad locality; site RB2 located roughly in the middle of the riverbed, aligned with the powergrid tower. **D.** General view of the middle-upper part of the Pui Beds deposits, position of site PB3 located near the small ledge in the middle of the image. **E.** Excavations at site PB4 (Pui-Micro), in the uppermost section of the Pui Beds. **F.** Looking for fossils at the newly discovered site PB6 (year 2012), in the upper part of the Pui Beds; the stratigraphically higher site PB4 is located near the small ledge in the right background.

Sibișel Valley at Sânpetru and Săcel and closely neighboring areas, extending from Valea Dâljii to Sântămăria-Orlea (Therrien, 2005; Csiki-Sava et al., 2016; figs. 2:SP, 8A,B). These deposits have long been known to yield diverse latest Cretaceous vertebrate remains (e.g., Halaváts, 1897; Nopcsa, 1897, 1905), and they were also the first ones to yield multituberculate remains about a century after the first vertebrate fossil discoveries. Chronologically, the oldest kogaionid discovery in this unit is probably that of the partial cranium of *Kogaionon*, although it was described significantly later (see below). This was soon followed by the identification of rare isolated teeth from a small number of different vertebrate sites, recovered (sometimes together with other, most often isolated and fragmentary vertebrate remains) from experimental screenwashing at different levels within the local succession. It is noteworthy that, compared with other parts of the Hațeg Basin, proper microvertebrate accumulations—the most common source of kogaionid fossils—remain as yet unidentified in the deposits of the Sînpetru Formation. Below, we list and discuss the known kogaionid-bearing vertebrate sites from the Sînpetru Formation, identified as SP sites for convenience.

Site SP1
Kogaionon Type Locality

LOCATION, AGE: Tămășel Hill, along the right bank of Sibișel Valley (Rădulescu and Samson, 1996), upstream of Sânpetru village; no more precise locality data are available. Using the chronostratigraphic tier system developed by Csiki-Sava et al. (2016) and based on the coarsely estimated position of site SP1, it is most probably situated in the middle part of the Sînpetru Formation; its age should be thus close to the early-late Maastrichtian boundary (possibly upper part of Tier 2).

LITHOLOGY, PALEOENVIRONMENT: The lithology is not reported, but, based on the matrix still adhering to the specimen it was represented probably by gray-greenish sandy siltstone. This suggests a relatively low-energy, somewhat reducing depositional environment.

FOSSIL CONTENT: ISER SPT/001, the holotype of *Kogaionon ungureanui* (Rădulescu and Samson, 1996: fig. 1; figs. 5D, F, 7D, 9A), is an incomplete skull preserving the anterior and middle sections of the cranium from the tip of the rostrum to the anteriormost part of the braincase, with associated petrosals, and the nearly complete upper dentition (only the left I2, I3 and P2 are missing); no other fossils were reported from this site besides the holotype cranium.

HISTORY OF RESEARCH: The holotype skull was discovered and collected in 1979 by Costin Ungureanu, then an undergraduate student of the Faculty of Geology and Geography of the University of Bucharest. It was then painstakingly and carefully prepared for several years, and was finally described in a brief report by Rădulescu and Samson (1996). No further, more detailed description of this important specimen/taxon is yet available, although its authors were preparing a monographic description of the material at the moment of their untimely death (Z. Kielan-Jaworowska, personal commun. to Z. Cs.-S. in 2004–2005); this manuscript could not be located and is now probably lost.

COMMENTS: The almost complete cranium ISER SPT/001, one of the best-preserved Cretaceous mammalian fossils from Europe, became not only the holotype (and only known specimen) of the new multituberculate taxon *Kogaionon ungureanui*, but also the specimen that came to typify an entirely novel Bauplan of multituberculate cranial and dental morphology. As such, it laid the foundations for the recognition of the Kogaionidae, an endemic and peculiar European multituberculate radiation (e.g., Peláez-Campomanes et al., 2000; Csiki and Grigorescu, 2002). Although the authors of *Kogaionon* recognized the unique anatomy of their newly erected taxon, they failed to recognize its wider evolutionary and paleogeographic significance, despite the fact that following the original description they
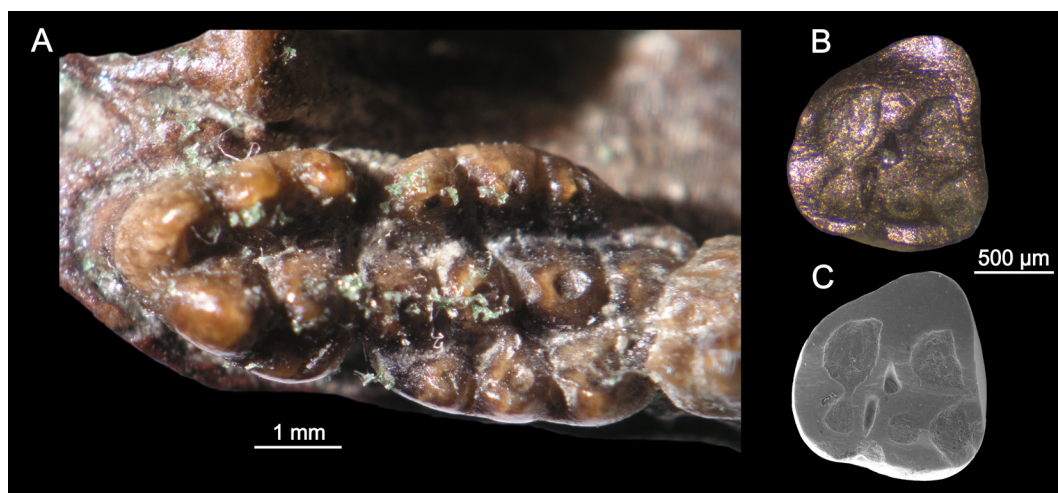
FIGURE 9. Kogaionid remains from the Sînpetru Formation. **A.** Close-up of the left upper molars (M1 and M2) of *Kogaionon ungureanui* (ISER SPT/001), site SP1. **B, C.** Isolated right M2, LPB (FGGUB) M.1631, of an indeterminate kogaionid, site SP3, occlusal view as **B.** reflected light stereomicroscopic image; **C.** SEM image.

subsequently addressed additional anatomical details of the cranium in several abstracts and short papers (e.g., Rădulescu and Samson, 1997, 1998; Petculescu et al., 1998). One further important contribution to the knowledge concerning this very important specimen is the study of its tooth enamel microstructure by Fosse et al. (2001) who demonstrated that *Kogaionon* had gigantoprismatic enamel. This is an autapomorphic type of enamel that is known to uniquely characterize a diverse grouping of derived cimolodontan multituberculates (e.g., Carlson and Krause, 1985; Fosse et al., 1985; Kielan-Jaworowska and Hurum, 2001; Wood and Rougier, 2005), and it is also known to occur in the kogaionid *Hainina* (Carlson and Krause, 1985).

Despite the fact that a fair number of other multituberculate skulls (some even more complete than ISER SPT/001) have been recovered in the Transylvanian area during the 40+ years that have passed since the discovery of the *Kogaionon* cranium (see below), this specimen still remains extremely important for the understanding of the unique morphology of kogaionids, and its detailed description is forthcoming.

Site SP2
Frezezen Locality

LOCATION, AGE: Coasta Mereuţă, neighborhood of La Cărare quarry (see Csiki et al., 2010b; fig. 8A), along the right bank of Sibişel Valley, upstream of Sânpetru village. No more precise locality data are available. Age estimated roughly to early Maastrichtian, probably lying within Tier 2 as defined by Csiki-Sava et al. (2016).

LITHOLOGY, PALEOENVIRONMENT: Fine-grained, "silty-argillaceous" sediments (Grigorescu, 1983); no further information is available. This information constrains site SP2 only to a hyrodynamically relatively quiet depositional environment, developed within the fluvially dominated succession of the Sînpetru Formation (Therrien et al., 2009).

FOSSIL CONTENT: LPB (FGGUB) M.1636, worn left I2; no other fossils were reported from site SP2 besides this isolated tooth.

HISTORY OF RESEARCH: The matrix yielding the isolated I2 was screenwashed in 1979, following the restart of the paleontological research activities in the Haţeg Basin, by Carmen Panaitescu, and the specimen itself was discovered by Georges Frezezen in 1980 (both undergraduate

students of the Faculty of Geology and Geography, University of Bucharest). This specimen became the first Mesozoic mammal fossil ever reported from Romania (and the entirety of Central and Eastern Europe); its discovery was mentioned preliminarily in several publications (Știucă et al., 1982; Grigorescu, 1983a, b, 1987a), and it was then briefly described and figured by Grigorescu (1984a, 1984b).

COMMENTS: The morphology of the worn I2 corresponds to that reported in situ in other kogaionid remains from Transylvania, and thus it suggests that LPB (FGGUB) M.1636 possibly belongs to a kogaionid (the only multituberculate group known in the Transylvanian area and, generally, in the Upper Cretaceous of Europe; Csiki-Sava et al., 2015; Solomon et al., 2015). The importance of this isolated and rather nondiagnostic specimen relies on the fact that it documented for the first time the presence of multituberculate mammals in the uppermost Cretaceous of the Transylvanian area. Furthermore, it also revealed the potential of these continental beds to yield microvertebrate assemblages if surveyed carefully and excavated using the screenwashing method of microfossil recovery; it thus opened up an avenue toward the subsequent important development of microvertebrate research in this area (e.g., Grigorescu et al., 1985, 1999; Folie and Codrea, 2005; Vasile and Csiki, 2010).

SITE SP3
LA SCOABĂ LOCALITY

LOCATION, AGE: La Scoabă locality (see Csiki et al., 2010b; Csiki-Sava et al., 2016), along the left bank of Sibișel Valley, upstream of Sânpetru village. Two different levels from the La Scoabă succession (Therrien, 2006; Csiki-Sava et al., 2016; fig. 8B) have yielded isolated multituberculate remains, one in the lower-middle part of the local succession, the second one placed in its upper part. The age of the La Scoabă succession is constrained to the early part of the early Maastrichtian (Panaiotu

and Panaiotu, 2010; Csiki-Sava et al., 2016), thus belonging to the very early transitional stage between tiers 1 and 2 as defined by Csiki-Sava et al. (2016).

LITHOLOGY, PALEOENVIRONMENT: Both of the beds yielding multituberculate remains are fine-grained, reddish-brown silty mudstones. The La Scoabă succession is interpreted as a stacked succession of relatively well-drained floodplain and channel deposits in a shifting mosaic of seasonal wetlands and floodplains (Therrien, 2006; Therrien et al., 2009).

FOSSIL CONTENT: LPB (FGGUB) M.1631, isolated and worn right M2 (fig. 9B, C), from the lower La Scoabă level; LPB (FGGUB) M.1699, incomplete left p4, anterior crown fragment, from the upper La Scoabă level. The M2 was found associated only with gastropod shell fragments and indeterminate bone chips, whereas the p4 is part of a richer microfossil assemblage, including characeans (Vicente et al., 2019), as well as gastropods, ostracods, and isolated amphibian remains (anurans, albanerpetontids), an assemblage that is still largely under study (see Csiki-Sava et al., 2016). The overall fossiliferous content of the La Scoabă succession was reviewed by Csiki-Sava et al. (2016).

HISTORY OF RESEARCH: The lower level yielding multituberculate remains was sampled in 2001, in a preliminary attempt to find important microvertebrate assemblages in the Sibișel Valley outcrops of the Sînpetru Formation (which are otherwise richly fossiliferous; Nopcsa, 1905; Grigorescu, 1983a, 1992; Csiki et al., 2010b; Csiki-Sava et al., 2016). Unfortunately, no such microvertebrate localities have been identified as yet in the Sânpetru area, hence the relatively low number of multituberculate remains, their isolated nature (with the notable exception of the *Kogaionon* holotype), and the very low taxic diversity of their associated fossil content. The upper level was also sampled in 2001 during a systematic micropaleontological survey of the La Scoabă local section by Anca Oprișoreanu and Marius Stoica (University of Bucharest) that aimed at discovering ostracod assemblages.

COMMENTS: Neither of the two specimens from La Scoabă is diagnostic at a lower taxonomic level. The preserved morphology of the fragmentary p4 implies that it was bladelike and relatively high, suggesting that it belongs to a derived cimolodontan. The morphology of the right M2 (fig. 9B, C) is also rather generalized, with two short cusp rows and a short anterolabial cingulum. Despite its heavily worn nature, its cusp formula can be identified as crest(1?):2:3. The bases of the median and lingual cusps are still discernible, whereas the mesiolabial corner is transformed by wear into a concave platform. The lingual cusps are somewhat smaller than the median ones; the first two lingual cusps appear twinned, more closely spaced and of similar size, whereas the distalmost lingual cusp is slightly larger and set apart. The contour of the crown is trapezoidal, with a distally convex labiodistal margin, differing in this respect from the more triangular M2 of *Kogaionon ungureanui* (figs. 5F, 9A) and being more reminiscent of the M2s referred to *Barbatodon transylvanicus* (e.g., Csiki et al., 2005) and *Kogaionon radulescui* (Smith et al., 2022) or of the isolated kogaionid M2 from Toteşti-baraj (Codrea et al., 2002: fig. 4i; see below). It is, furthermore, significantly smaller (1.16×1.26 mm) than the M2s referred to *Kogaionon* (fig. 9A), *Barbatodon transylvanicus* (e.g., Smith and Codrea, 2015), or *Litovoi* (Csiki-Sava et al., 2018), being roughly similar in size to and even marginally smaller than the smallest M2s referred to *B. oardaensis* by Codrea et al. (2014; see also Smith et al., 2022: table S1).

Both of these isolated teeth from the La Scoabă section have morphologies that are consistent with their possible kogaionid affinities, but no more detailed identification is possible. These specimens document the presence of small kogaionids in the lower part of the Sînpetru Formation, clearly different from *Kogaionon ungureanui* (in the case of the M2 LPB [FGGUB] M.1631, the only specimen that overlaps with ISER SPT/001) which has also been described from the same Sibişel Valley succession, but most probably comes from a higher stratigraphic level (fig. 3).

SITE SP4
VÂLCEA P3 LOCALITY

LOCATION, AGE: Vâlcea local section, along the left bank of Sibişel Valley, upstream of Sânpetru village. This locality is situated in the upper part of the lower half of the Sibişel Valley succession. A small number of vertebrate (including microvertebrate) remains have been found over the years in several points of the Vâlcea outcrop, but only one level (P3) has yielded an isolated multituberculate tooth. Based on its stratigraphic position, the probable age of the site falls into the early part of late Maastrichtian (Panaiotu and Panaiotu, 2010; Csiki-Sava et al., 2016).

LITHOLOGY, PALEOENVIRONMENT: The bed yielding the sole multituberculate fossil from Vâlcea is represented by a greenish silty mudstone level, suggesting a floodplain setting with slightly impeded drainage within the dynamic wetland-alluvial mosaic of the type Sînpetru Formation (Therrien et al., 2009).

FOSSIL CONTENT: LPB (FGGUB) M.1632, incomplete left i1, found associated only with gastropod shell fragments and indeterminate bone chips.

HISTORY OF RESEARCH: The Vâlcea P3 level was identified in 2001, in the same sampling effort that also identified the lower Scoabă multituberculate level (site SP3).

COMMENTS: The fragmentary nature and isolated state of M.1632 precludes any detailed taxonomic identification, although its general shape (elongated, evenly tapering to a point, with unevenly distributed enamel cover) is reminiscent of other, in situ Transylvanian kogaionid i1s (e.g., Csiki et al., 2005; Solomon et al., 2016; Smith et al., 2022) and is thus consistent with its probable kogaionid affinities.

RÂUL MARE BEDS

A series of outcrops, made up of almost vertically dipping beds, arrayed along the Râul Mare Valley from Unciuc in the south to near Sântămăria-Orlea in the north, represent the

"Râul Mare Beds" defined by Csiki-Sava et al. (2016) (figs. 1C, 2A: RB). The precise lithostratigraphic position of these deposits is still contentious, mainly due to their unique tectonic setting, their isolated geographic distribution, separated from other outcrops of the continental uppermost Cretaceous through much younger sedimentary cover, and their distinctive lithofacial and taphonomic characteristics (see, e.g., Van Itterbeeck et al., 2004). Historically, these deposits were considered to belong to the Sînpetru Formation and correlated with the terminal part of its stratotype succession along the Sibişel Valley (e.g., Van Itterbeeck et al., 2004; Therrien, 2006; Therrien et al., 2009), but more recently they have been provisionally separated as a distinct lithostratigraphic unit (Csiki-Sava et al., 2016). Despite the fact that Nopcsa (1905) already noted the presence of uppermost Cretaceous continental deposits along the Râul Mare River, these deposits were surveyed closely and were found to be fossiliferous only much more recently (e.g., Codrea et al., 2002; Smith et al., 2002). At that same moment, the presence of multituberculate remains was also reported from these deposits, where they most often occur in relatively rich and diverse microvertebrate assemblages. The known kogaionid-bearing vertebrate localities from the Râul Mare Beds—for sake of convenience identified as RB localities—will be listed and discussed briefly here.

SITE RB1
TOTEŞTI-BARAJ MICROVERTEBRATE LOCALITY

LOCATION, AGE: This locality is situated within the middle part of the local section exposed at the Toteşti-baraj fossiliferous site, very close to the right bank of the Râul Mare River (Van Itterbeeck et al., 2004). The age of these beds was first considered to be close to the early-late Maastrichtian boundary based on palynological grounds by Van Itterbeeck et al. (2005), but was later refined to the late Maastrichtian by Panaiotu et al. (2011) based on magnetostratigraphy, and its vertebrate remains were regarded as belonging to the youngest, Tier 4 local chronofaunal complex by Csiki-Sava et al. (2016).

LITHOLOGY, PALEOENVIRONMENT: The multituberculate-yielding microvertebrate accumulation at site RB1 was discovered in a dark gray silty mudstone capping a pedogenetic calcrete level associated with a megaloolithid dinosaur nest (Van Itterbeeck et al., 2004), a type of deposit probably accumulated in a small pond or a poorly drained floodplain depression. Overall, the local succession is interpreted to have been deposited in a mainly waterlogged wetland environment within a meandering fluvial setting (Van Itterbeeck et al., 2004).

FOSSIL CONTENT: The Toteşti-baraj fossil locality has yielded a large number of megaloolithid dinosaur eggs (Codrea et al., 2002), with at least some of these most probably referable to indeterminate titanosaurs (Grellet-Tinner et al., 2012), several partial turtle skeletons (e.g., Rabi et al., 2013; Pérez-García and Codrea, 2018), as well as one microvertebrate bonebed with a diverse microvertebrate assemblage including discoglossid frogs, albanerpetontids, scincomorph lizards, as well as hadrosauroid, theropod, and nodosaurid dinosaurs, along with the multituberculate remains represented by isolated teeth (Codrea et al., 2002; Smith and Codrea, 2003; fig. 7B).

HISTORY OF RESEARCH: The Toteşti-baraj local succession was first identified as potentially fossiliferous in 2000 and the first fossils—including the microvertebrate bonebed—were excavated here in 2001 (Codrea et al., 2002; Smith and Codrea, 2003). The multituberculates from site RB1 have been reported preliminarily by Codrea et al. (2002) and Smith and Codrea (2003), and the most recent taxonomic reassessment of the material belongs to Codrea et al. (2017a). The largest part of the available sample (over 14 specimens; 16, according to Smith and Codrea, 2003), however, was never described in detail and/or figured and the collection numbers of most multituberculate specimens (deposited at the UBB) were not published.

COMMENTS: According to previously published information (Codrea et al., 2002, 2017a; Smith and Codrea, 2003), two taxa are represented in the Toteşti-baraj multituberculate sample, one small and one medium in size (but see below), differentiated (at the genus level, according to these authors) mainly by their size. In the absence of a detailed account concerning this sample, the published information about its taxonomic composition is somewhat contradictory. In the original report of the local faunal assemblage, Codrea et al. (2002) mentioned the presence of a new, small species of *Kogaionon*, represented by over nine teeth, of which only one isolated M1 was figured (Codrea et al., 2002: fig. 4h; fig. 7B). The recovered material covers most upper dentition positions for this taxon, according to Smith and Codrea (2003), but also includes two lower (probably cheek) tooth positions, besides four upper ones, based on the original report (Codrea et al., 2002).

This small species of *Kogaionon* was reportedly accompanied at site RB1 by a somewhat larger taxon represented by a *Hainina*-like M2 (UBB TBM v.441) and identified only as Kogaionidae indet. by Codrea et al. (2002: fig. 4i). Shortly after, this second taxon from the RB1 sample was referred to as *Barbatodon transylvanicus* by Smith and Codrea (2003) based on the presence of an (undescribed and not figured) m1 in the local assemblage, one that was considered to be similar to the (overlapping) type specimen of this taxon, described from the Pui area by Rădulescu and Samson (1986; for correct identification of the nature of this specimen, see Csiki et al., 2005). Indeed, the previously reported (and figured) M2 from Toteşti, referred to a middle-sized *Hainina*-like Kogaionidae indet., shows certain suggestive similarities—trapezoidal outline, crestlike anterolabial crest, and twinned, incompletely separated two anterolingual cusps—with the isolated M2 of specimen LPB (FGGUB) M.1635 as well as the in situ M2 of specimen UBB P-Mt 1, both referred to *Barbatodon transylvanicus* (Csiki et al., 2005; Smith and Codrea, 2015). These shared similarities sug-

gest that *Barbatodon transylvanicus* (or a closely comparable taxon) might indeed be present at Toteşti-baraj, a possibility already hinted at by Csiki et al. (2005). If such a taxonomic identification is upheld by more detailed studies, this occurrence would mark an important range extension for *Barbatodon transylvanicus* both geographically and chronostratigraphically, as the type locality, as well as other sites yielding material referred to this taxon represent Tier 2 and 3 faunal complexes of Csiki-Sava et al. (2016; roughly "mid"-Maastrichtian; see also below), whereas site RB1 from Toteşti-baraj lies within Tier 4 (late Maastrichtian).

On the other hand, the only other multituberculate specimen figured from Toteşti-baraj, the diminutive left M1 referred to a new small species of *Kogaionon* (fig. 7B), shows indeed a distinctive feature of this genus, i.e., the presence of three lingual cusps in the inner cusp row (e.g., Smith et al., 2022), as opposed to only two in *Barbatodon* (Codrea et al., 2014; Smith and Codrea, 2015; Solomon et al., 2016) or in *Litovoi* (Csiki-Sava et al., 2018), and might support the recognition of this genus at Toteşti.

Intriguingly, an entirely new interpretation of the Toteşti-baraj multituberculate assemblage was put forth in the most recent general overview of the latest Cretaceous Romanian kogaionids by Codrea et al. (2017a), according to which the RB1 assemblage contains a small kogaionid provisionally referred to *Barbatodon oardaensis*, together with a middle-sized Kogaionidae indet. This change of view from those expressed previously by Codrea et al. (2002) and Smith and Codrea (2003) is unexpected, and remains as yet unsupported by comparative data except for the roughly similar small body size noted in both *B. oardaensis* and the small kogaionid sample from Toteşti. However, as already mentioned, the Toteşti M1 clearly has a cusp formula of 3:4:3 (see Codrea et al., 2002: fig. 4h; fig. 7B), unlike the 3:4:2 cusp formula reported in their overview to diagnose *B. oardaensis* (Codrea et al., 2017a: 31). Thus, based on the currently available published information, the referral of the small

kogaionid material from Toteşti-baraj to *Barbatodon* (and specifically to *B. oardaensis*) appears unsupported, unless the diagnosis of this taxon is expanded with regard to the M1 cusp formula so that this will overlap with that known to characterize *Kogaionon* (Rădulescu and Samson, 1996; Smith et al., 2022).

Meanwhile, Codrea et al. (2017a: table 1) returned to listing the "medium-sized" kogaionid from Toteşti as Kogaionidae indet., instead of referring it to *Barbatodon transylvanicus* as was suggested previously.

Detailed publication of this interesting multituberculate assemblage, ranking among the youngest in the uppermost Cretaceous of the Transylvanian area, is sorely needed before its true taxonomic composition and relevance can be fully assessed. Furthermore, Codrea et al. (2002) reported potential association between elements of lower and upper dentition in the case of the new small *Kogaionon* species from site RB1. If this assertion proves to be correct, the RB1 kogaionid assemblage might represent—following the recent description of *Kogaionon radulescui* (Smith et al., 2022)—the second instance when different elements from the lower dentition of this very important genus would be documented, furthering our knowledge regarding the type genus of the Kogaionidae, and allowing more detailed anatomical and paleoecological comparisons with other kogaionid taxa.

Site RB2
Nălaţ-Vad Microvertebrate Lens

LOCATION, AGE: The microvertebrate lens that yielded the first multituberculate assemblage from Nălaţ-Vad was discovered within the riverbed of the Râul Mare River, close to the right side bank, at about midlength of the Nălaţ-Vad outcrop as mapped by Smith et al. (2002); it is considered to occur in the lowermost part of the local succession (Van Itterbeeck et al., 2004). The age of the Nălaţ-Vad succession was identified as possibly "mid"-Maastrichtian both by palynostratigraphy (Van Itterbeeck et al., 2005) and

by magnetostratigraphy (Panaiotu et al., 2011), and it is included into the Tier 3 faunal complex of the latest Cretaceous Transylvanian faunal succession by Csiki-Sava et al. (2016).

LITHOLOGY, PALEOENVIRONMENT: According to Van Itterbeeck et al. (2004), the lenslike accumulation that forms the microvertebrate bonebed is hosted by a dark gray mudstone capping a thick reddish paleosol level; the fine-grained bed yielding the fossils can be traced laterally until it grades into a lenticular, coarser-grained channel deposit. The basal part of the fossil-bearing bed is heavily calcareous and was identified as a freshwater limestone coquina made up of eggshell fragments, whereas the upper part is represented by blackish marls that were interpreted as a pond deposit formed in a poorly drained portion of the floodplain. Overall, the Nălaţ-Vad succession, which is lithologically similar to that from Toteşti, represents a stacked succession of fluvial channel and floodplain deposits (fig. 8C) developed within a meandering river paleosetting (Van Itterbeeck et al., 2004; Săsăran et al., 2011).

FOSSIL CONTENT: The Nălaţ-Vad locality, in its entirety, has yielded a large number of vertebrate occurrences, represented by dinosaur eggs and nests, by isolated skeletal remains spread throughout the outcrop, by a few partial skeletons, and by microvertebrate accumulations. Megaloolithid eggs form the small nests commonly encountered at the site (Smith et al., 2002; Grigorescu et al., 2010). Two fossiliferous pockets yielded disarticulated remains of two partial skeletons, representing the rhabdodontid ornithopod *Zalmoxes* (Godefroit et al., 2009), and the titanosaur *Paludititan* (Csiki et al., 2010c). Partial turtle shells referable to the basal testudinate *Kallokibotion* are common (Csiki-Sava et al., 2016; Pérez-García and Codrea, 2018), as are diverse skeletal elements belonging to *Zalmoxes* (Brusatte et al., 2017). Isolated skeletal remains document the presence of further taxa at Nălaţ-Vad. These include indeterminate azhdarchid pterosaurs, the mysterious small theropod *Elopteryx*, a possible *Gargantuavis*-like

nonavian theropod (alternatively regarded as a flightless bird), an indeterminate midsized theropod, as well as indeterminate hadrosauroids (Smith et al., 2002; Csiki-Sava et al., 2016; Buffetaut and Angst, 2020; Mayr et al., 2020a, 2020b). The kogaionid-bearing fossiliferous black lens from site RB2 yielded the largest part of the currently known local vertebrate diversity. The fossil content of the lens is mainly made up of ornithoid eggshell fragments (Van Itterbeeck et al., 2004), but it also contains a diverse microvertebrate assemblage with albanerpetontids, scincomorph lizards, diverse small theropods, enantiornithine birds, and multituberculate mammals (Smith et al., 2002; Smith and Codrea, 2003; Wang et al., 2011a).

History of research: The fossiliferous nature of the Nălaţ-Vad outcrops along the Râul Mare River was first recognized in 2001. Following this moment, the site was surveyed closely and the first fossil localities were excavated here in 2002; this is also when the multituberculate remains from site RB2 were collected (Smith et al., 2002). Since then, the relatively active riverbed site of Nălaţ-Vad has been surveyed regularly, yielding (mainly isolated) macrovertebrate remains and small clutches of megaloolithid eggs, but only a very limited amount of further multituberculate remains have been found there (see below, site RB3). The 2002 multituberculate sample from site RB2 was only briefly mentioned and discussed by Smith et al. (2002) and Smith and Codrea (2003), and was addressed briefly again, without further details being added, in the kogaionid distribution overview of Codrea et al. (2017a). Unfortunately, no detailed description was published for the largest part of this material; one specimen (an isolated m1) had been figured previously (Smith et al., 2002: pl. 1, figs. 1, 2; fig. 7H), and a second specimen apparently coming from this site, a fragmentary left dentary with in situ i1 and p4, was referred very recently to a new kogaionid taxon by Smith et al. (2022; see below, site RB3).

Comments: According to the available information concerning the RB2 multituberculate sample from Nălaţ-Vad (Smith et al., 2002; Smith and Codrea, 2003; Codrea et al., 2017a), a total of 12 multituberculate teeth and three jaw fragments (one maxilla, 2 dentaries) were recovered from the microvertebrate lens. Almost since its discovery, the presence of two different taxa was suggested within this assemblage, mainly based on the distinctive morphologies shown by the different p4s, the most diagnostic overlapping elements from the sample (Smith et al., 2002; Smith and Codrea, 2003).

One taxon was identified provisionally as a new, small species of the genus *Barbatodon*. This identification was initially based on an isolated m1 (UBB TBM v.442; Smith et al., 2002: pl. 1, figs, 1, 2; see also Csiki et al., 2005: pl. II, figs. H, I; fig. 7H) that is roughly similar to but only about 60% the size of the holotype m1 of *Barbatodon transylvanicus* from Pui (Rădulescu and Samson, 1986). Minor morphological differences between the m1 specimen UBB TBM v.442 from Nălaţ-Vad and the *Barbatodon transylvanicus* holotype, respectively, also support such a taxonomic distinction (Smith et al., 2002; Csiki et al., 2005). Furthermore, Smith and Codrea (2003) tentatively associated with specimen UBB TBM v.442 one of the (not specifically described) dentigerous jaw fragments from site RB2, which reportedly retained in situ p4 and m1. Accordingly, this particular p4 that typifies one of the two distinct p4 morphologies recognized at site RB2, was identifed tentatively by Smith and Condrea (2003) as a *Barbatodon* p4, a dental position not previously documented for this taxon. However, from the brief preliminary characterization offered for this element as very long and rounded, it appears to be clearly distinct in shape from the highly vaulted, somewhat triangular in situ *Barbatodon transylvanicus* p4s documented in several other individuals that were referred to this taxon (Csiki et al., 2005; Smith and Codrea, 2015; Solomon et al., 2016; fig. 7N, O). Instead, it may be more reminiscent of the isolated p4 described by Codrea et al. (2017a) from the Rusca Montană Basin and referred to the smaller congeneric taxon *B. oardaensis* (fig. 7M),

although any assessment of either of these two alteratives remains very tentative given the limited amount of information available for this specimen. Smith and Codrea (2003) also noted that this dentary fragment lacks a p3, which they considered as an important feature that characterizes the unnamed *Barbatodon* species from site RB2. Indeed, the absence of even a rudimentary p3 is a feature that was subsequently clearly demonstrated in *Barbatodon transylvanicus* (Csiki et al., 2005; Smith and Codrea, 2015). Nevertheless, a similar condition was recently reported to occur in *Kogaionon radulescui* as well (Smith et al., 2022), suggesting that it represents a more widely distributed derived kogaionid character not restricted to *Barbatodon*. Meanwhile, this condition is currently impossible to verify in other known latest Cretaceous kogaionid taxa (*K. ungureanui*, *Litovoi*, *B. oardaensis*) due to the absence of relevant specimens.

The second kogaionid taxon from the Nălaț-Vad microvertebrate lens RB2 was identified initially as representing the genus *Kogaionon* (Smith and Codrea, 2003), and this identification appears to be more puzzling. The only tooth position referred explicitly to this second taxon is a p4, distinguished by its overall triangular shape from the p4 morphotype attributed by the same authors to the indeterminate small *Barbatodon* species from site RB2 (see above). However, at that moment *Kogaionon* was known only from its upper dentition (Rădulescu and Samson, 1996), and thus referral of isolated lower teeth to this taxon was tenous at best in the absence of their clear association with diagnostic upper teeth. Nevertheless, the occurrence of two distinctive p4 morphotypes reported from the microvertebrate bonebed certainly supports the presence of two sympatric taxa.

In the light of such definitive (although not explicitly presented in detail) evidence for the presence of two different taxa at site RB2, even more surprising was a more recent interpretation concerning this Nălaț-Vad multituberculate assemblage, offered in the overview of Codrea et al. (2017a), which lists only one taxon from

Nălaț-Vad. This taxon was considered to be potentially synonymous with *Barbatodon oardaensis*, apparently based on simple dimensional arguments ("small sized"), despite the fact that *Barbatodon oardaensis* is diagnosed by a m1 with a cusp formula of 3:3 (Codrea et al., 2014, 2017a; fig. 7I), whereas the only described and figured Nălaț-Vad m1 (UBB TBM v.442; fig. 7H) is reported to have a cusp formula of 4:3 (Smith et al., 2002).

In their recent report of a new kogaionid taxon (*Kogaionon radulescui*; see below, site RB3) from Nălaț-Vad, Smith et al. (2022) referred to this medium-sized species a fragmentary dentary with in situ i1 and p4 (UBB NV-Mt1), also from Nălaț-Vad. Although this is not stated explicitly by Smith et al. (2022), from the details of its discovery as supplied by these authors it appears highly probable that the referred specimen originates from site RB2. Whether such an inference for the origin of this specimen is correct, and whether it is the same dentary fragment as the one mentioned (without specimen number and not figured) by Smith and Codrea (2003) and referred to *Barbatodon* remain unclear for the present. The presence of an in situ i1, not mentioned in the 2003 report, as well as the absence of an m1 in specimen UBB NV-Mt1 suggests that these two dentary fragments are two different specimens, although such a tentative assessment should be clarified by future studies of the RB2 kogaionid assemblage.

Just as in the case of the Toteşti-baraj multituberculate sample from site RB1, detailed description and illustration of the entire Nălaț-Vad material from site RB2 is necessary in order to correctly assess the taxonomic composition of this assemblage and to understand the identity, relationships, and significance of the taxa represented here.

SITE RB3
Kogaionon radulescui TYPE LOCALITY

LOCATION, AGE: The locality yielding the holotype of the most recently described kogaio-

nid taxon from Transylvania (Smith et al., 2022) is located in the same Nălaț-Vad outcrop along the Râul Mare River that also contains site RB2 (fig. 2), but more precise locality data (for example, its spatial and stratigraphic position relative to site RB2, from where the referred specimen may originate; see above) are unavailable. As already noted for site RB2, the age of the Nălaț-Vad succession was identified as possibly "mid"-Maastrichtian (Van Itterbeeck et al., 2005; Panaiotu et al., 2011), corresponding to the Tier 3 faunal complex of the latest Cretaceous Transylvanian faunal succession as defined by Csiki-Sava et al. (2016).

LITHOLOGY, PALEOENVIRONMENT: Only very limited information is available on the local lithology at site RB3. According to Smith et al. (2022), the holotype (PSMUBB V-893) was discovered in a gray marl bed, most probably corresponding to a poorly drained, low-energy depositional environment developed within a meandering river paleosetting (Van Itterbeeck et al., 2004; Săsăran et al., 2011).

FOSSIL CONTENT: The overall fossil assemblage known from Nălaț-Vad locality was reviewed previously (see above, site RB2); as far as site RB3 in particular is concerned, no other fossil remains have been reported to occur together with specimen PSMUBB V-893.

HISTORY OF RESEARCH: As mentioned above, the first fossil occurrences at Nălaț-Vad were identified in 2001, with the kogaionid assemblage from site RB2 being recovered in 2002 through screenwashing. Meanwhile, site RB3 was discovered in 2004 by V. Codrea, most probably by surface prospecting of the beds exposed in the riverbed of Râul Mare River. The unique kogaionid specimen coming from this site, a well-preserved anterior section of a cranium with in situ upper dentition (except for the I2) and associated p4 (PSMUBB V-893), was thoroughly described and figured by Smith et al. (2022) as the holotype of a new kogaionid taxon, *Kogaionon radulescui*.

COMMENTS: The kogaionid material originating from site RB3 is remarkable in several respects. It represents the holotype of the fifth nominal multituberculate taxon erected from the uppermost Cretaceous of the Transylvanian area (Smith et al., 2022), thus supporting the view that a high taxonomic diversity of this endemic clade had existed within the ancient Hațeg paleoisland (as suggested previously by Csiki-Sava et al., 2017; Vremir et al., 2018). It definitively supports the presence of intrageneric taxonomic diversity within the genus *Kogaionon*, already hinted at previously by isolated but potentially diagnostic remains recovered from sites RB1 (see above; Codrea et al., 2002) and PB4 (see below), while for the first time also allows secure referral of lower dental elements (i1, p4) to a genus otherwise known until now exclusively from its upper dentition (Rădulescu and Samson, 1996). The new taxon also documents the presence of species-level body-size variability within *Kogaionon* as well, mirroring a similar pattern reported previously in its largely sympatric relative *Barbatodon* (Codrea et al., 2014). Moreover, it firmly establishes the occurrence of the genus *Kogaionon* outside its distribution previously restricted to the type Sînpetru Formation at Sânpetru, again in accordance with previous suggestions concerning a more widespread distribution of *Kogaionon*-type dental remains made by Codrea et al. (2002), Csiki and Grigorescu (2002), and Smith and Codrea (2003) (see also below).

At a wider scale, the identification of *Kogaionon radulescui* at Nălaț-Vad, in the Râul Mare Beds, confirms a higher taxonomic and body-size diversity of the kogaionids within this unit than that recognized in the most recent review of the latest Cretaceous Transylvanian multituberculates by Codrea et al. (2017a)—a higher diversity already hinted at by Codrea et al. (2002), Smith and Codrea (2003), and Csiki-Sava et al. (2017), and now also supported by our review (see below). Finally, description of this new taxon offers novel insights into the phylogenetic position and intragroup relationships of the kogaionids, establishing this clade as a very basal, monophyletic offshoot of the cimolodontan radiation, while also suggesting a major within-clade split between the larger

latest Cretaceous and the smaller latest Cretaceous-Paleocene members of the family, respectively (Smith et al., 2022; fig. 4B).

PUI BEDS

The Pui Beds represent the easternmost currently reported occurrence of the continental uppermost Cretaceous deposits from the Hațeg Basin (fig. 2: PB). They consist of a more or less continuous succession of stacked fluvial and floodplain deposits cropping out along the lower course of the Bărbat River south of Pui village (figs. 1C, 2A: PB), slightly upstream from its confluence with the Strei River. Just as in the case of the Râul Mare Beds, although these deposits were incorporated historically into the Sînpetru Formation (e.g., Stilla, 1985; Grigorescu, 1992), their lithostratigraphic identity and position remain poorly constrained, mainly because they are areally isolated, being widely separated from the other outcropping areas of the continental uppermost Cretaceous by large expanses hidden by younger deposits and vegetation cover. To further emphasize the individuality of these deposits, they are markedly different from the Sibișel Valley succession of the Sînpetru Formation as well as from the Râul Mare Beds in their lithology and sedimentological features, characterized by the widespread presence of heavily pedogenetically modified, calcrete-bearing red silty mudstones interbedded with greenish, coarse-grained channel sandstones (fig. 8D–F). These characteristics of the Pui Beds make their correlation with the other uppermost Cretaceous continental deposits from the basin rather difficult, leading Therrien (2005) to suggest that they might represent a distinct lithostratigraphic unit, an opinion carried forward by Csiki-Sava et al. (2016), although it is yet to be formalized.

Outcrops of "Danian" (uppermost Cretaceous) continental red beds along the Bărbat River were noted as early as the end of the 19th century (e.g., Halaváts, 1897; Nopcsa, 1905), but the presence of fossils in the Pui Beds was first reported only decades later by Mamulea (1953).

Furthermore, their relatively richly fossiliferous nature was only recognized later (Știucă, 1983; Grigorescu et al., 1985). As currently recorded, the Pui succession yielded one of the richest continental vertebrate samples from the Transylvanian uppermost Cretaceous; the local faunal list includes fish, anurans, albanerpetontids, diverse lizards (borioteiioiids, teiids), madtsoiid snakes, diverse crocodyliforms, azhdarchid pterosaurs, dinosaurs—rhabdodontids, hadrosauroids, theropods, and titanosaurs—and multituberculates (see review in Csiki-Sava et al., 2016; also Venczel and Codrea, 2016, 2019; Venczel et al., 2016, Vasile et al., 2019). Remarkably, multituberculate remains were recovered at Pui almost as soon as the first significant vertebrate accumulations were identified (Grigorescu et al., 1985). This discovery was followed before long by the description, also from Pui, of the first newly erected Mesozoic mammal taxon from Romania, named *Barbatodon transylvanicus* by Rădulescu and Samson (1986; see Solomon et al., 2016, for nomenclatural issues surrounding the name of this taxon).

During the 35 years plus that have elapsed since the naming of *Barbatodon*, a large number of multituberculate remains have been discovered within the Pui succession; a number of eight different multituberculate-bearing levels are currently on record (figs. 2, 3) with most of these containing more than one multituberculate specimen and often even the remains of more than one individual (see below). The Bărbat River section is also remarkable in that it yielded not only isolated teeth (as is usual in other areas with multituberculate-bearing fossiliferous sites across Transylvania), but also incomplete skulls (sometimes surpassing even the cranium of *Kogaionon ungureanui*, the first kogaionid skull ever discovered, in degree of preservation) and even partial skeletons. Altogether, the currently known multituberculate fossil record from Pui makes the local succession by far the richest and most important mammalian fossil-bearing locality not only across the entire Transylvanian area, but for the entire continental Upper Cretaceous from Europe (Csiki-Sava et al., 2015). The
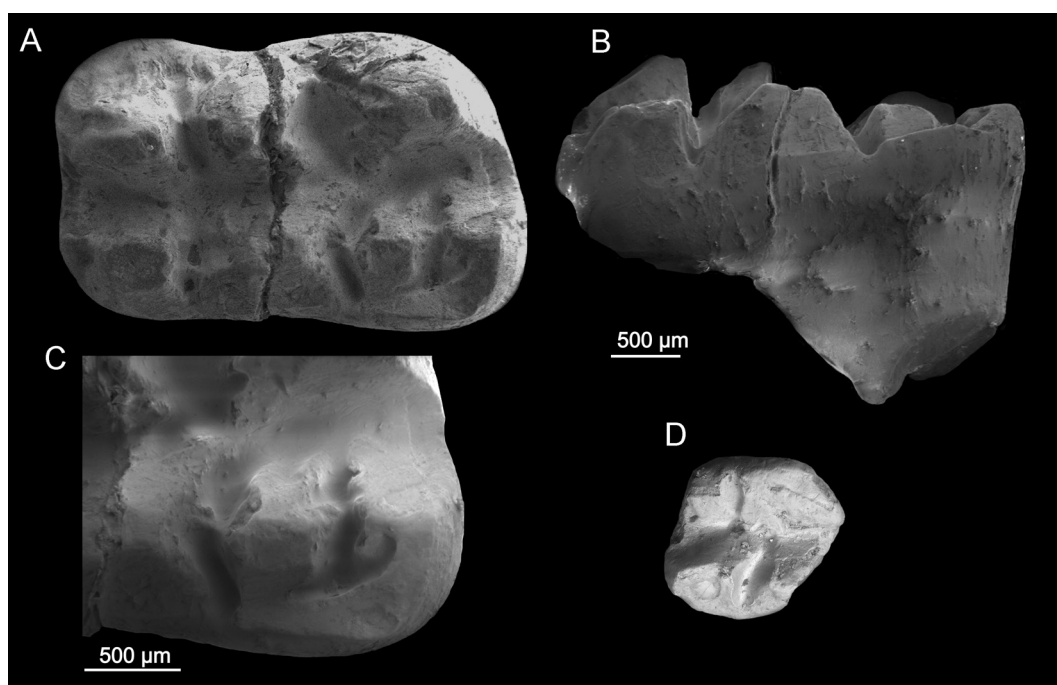
FIGURE 10. Kogaionid lower molars from the Pui Beds, site PB1. **A–C,** Isolated left m1, ISER PUI.001, the holotype of *Barbatodon transylvanicus*, in **A.** occlusal and **B.** labial views, with **C.** close-up of the labiodistal cingulumlike crest. **D.** Isolated right m2, ISER PUI.002, of an ideterminate kogaionid, in occlusal view.

known kogaionid-bearing vertebrate fossil sites from the Pui Beds, for the sake of convenience identified as PB localities, will be listed here.

Site PB1
Barbatodon Type Locality
(= Știucă locality)

Location, age: The *Barbatodon* type locality was discovered in the riverbed of Bărbat River, about 300 m south from the Pui road bridge crossing the river (Știucă, 1983); no further locality data are available. According to its reconstructed position, it falls within the lower part of the Bărbat River section. As the middle-upper part of this local section was palynologically placed near the lower/upper Maastrichtian boundary (Van Itterbeeck et al., 2005), the lower part of the Pui section—which includes the *Barbatodon* type locality discussed here—was considered to fall into the lower Maastrichtian

(Csiki-Sava et al., 2016). Accordingly, the age of the locality should be early Maastrichtian, corresponding to Tier 2 of the Transylvanian faunal succession as defined by Csiki-Sava et al. (2106).

Lithology, paleoenvironment: The *Barbatodon* type locality was identified in a dark, gray-greenish clayey-silty sandstone bed, intercalated into a succession of stacked sequences with pedogenetically modified red silty mudstones (well-drained floodplain paleosols) and green coarse pebbly sandstone channel deposits. The overall sedimentary setting can be reconstructed as a well-drained distal floodplain developed within a fluvial environment (Van Itterbeeck et al., 2004; Bojar et al., 2005; Therrien, 2005). The lithosome enclosing site PB1 accumulated within this wider paleoenvironment as an abandoned channel or as a fine-grained crevasse-splay deposit.

Fossil content: The *Barbatodon* type locality was initially reported as a lenticular microvertebrate bonebed, dominated by isolated teeth and
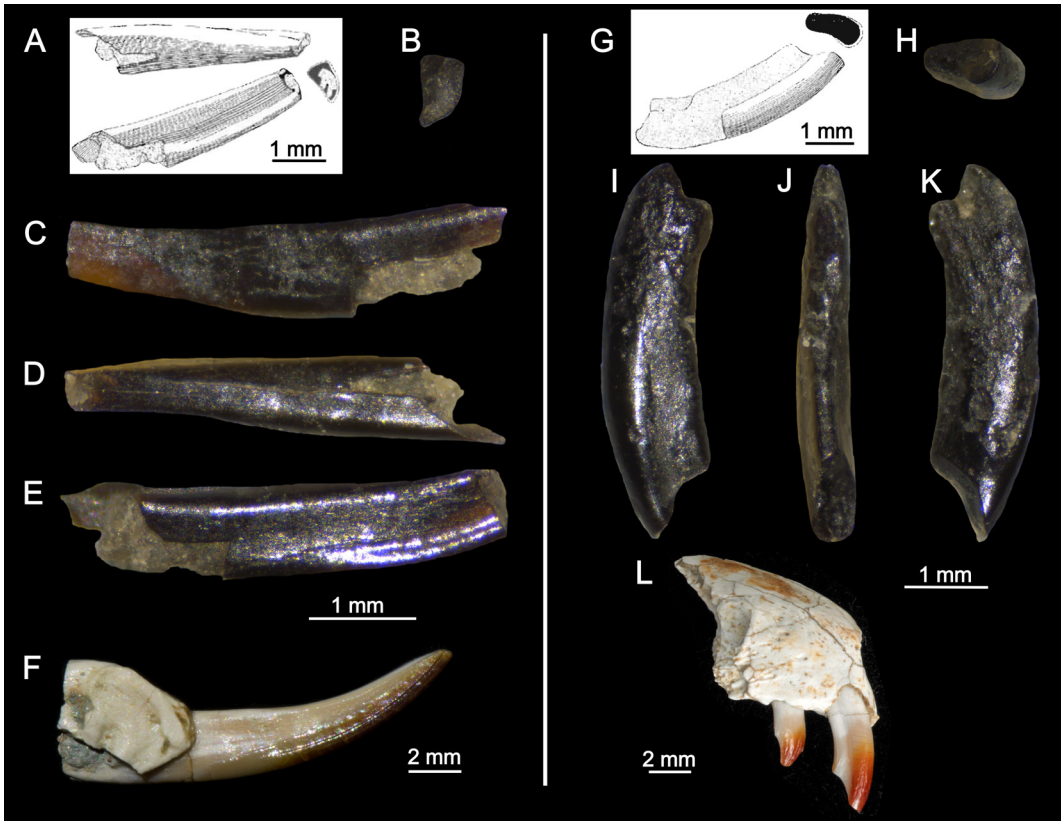
FIGURE 11. Isolated kogaionid incisors from the Pui Beds, site PB1. **A–E,** Isolated left i1, ISER PUI.004, of an indeterminate kogaionid, **A.** Specimen identified as "ptilodontoid," puncturing-grasping type of i1; drawing from Rădulescu and Samson (1997). **B.** apical, **C.** labial, **D**. dorsal, and **E.** lingual views. **F.** Holotype of *Litovoi tholocephalos*, LPB (FGGUB) M.1700, left i1 in lingual view, for comparison. **G–K,** Isolated left I2, ISER PUI.003, of an indeterminate kogaionid, **G.** Specimen identified as "taeniolabidoid," gnawing type of i1; drawing from Rădulescu and Samson (1997), **H.** apical, **I.** labial, **J.** dorsal, and **K.** lingual views. **L.** Holotype of *Litovoi tholocephalos*, LPB (FGGUB) M.1700, right premaxilla with in situ I2–I3 in labial view, for comparison.

other small skeletal remains, alongside gastropod shells (Grigorescu et al., 1985). Further accounts suggest that this assemblage of small remains was part of a more extensive fossil accumulation recovered from roughly the same stratigraphic level. It included the diverse microvertebrates from the lens, represented by remains of fish, anurans, albanerpetontids, squamates, crocodyliforms, dinosaurs—rhabdodontids, theropods, and titanosaurs—and multituberculates (Grigorescu et al., 1985; Rădulescu and Samson, 1986; Duffaud, 2000; Venczel et al., 2016). The same accumulation also yielded, however, a number of macrovertebrate remains referred to ornithopods (*Zalmoxes*, hadrosauroids), titanosaur sauropods, small theropods, basal eusuchian crocodyliforms, and chelonians (Ştiucă, 1983).

A total of four isolated multituberculate teeth have been reported from this site (see Rădulescu and Samson, 1997): ISER PUI.001, left m1; ISER PUI.002, right m2; ISER PUI.003, left I2; and ISER PUI.004, left i1 (figs. 10, 11)

Curatorial note: When mentioned at all, the registry numbers of these important multituberculate specimens have been quoted differently in different publications (table 1). Rădulescu and

TABLE 1

Taxonomic and Curatorial History of the Holotype Specimen of *Barbatodon transylvanicus* (boldface) and Associated Kogaionid Material from Site PB1, Bărbat River Section, Pui Locality, Haţeg Basin

Publication	Element identification	Taxon name	Registry number	Notes
Grigorescu et al., 1985	**left M1**	**cf. *Paracimexomys* sp.**	–	**figured, characterized briefly**
	right m2	Multituberculata indet.	–	figured
Rădulescu and Samson, 1986	**left M1**	***Barbatodon transylvanicum*, n. gen., n. sp.**	**IS.001**	**figured, described**
	i1 ("taeniolabidoid" type)	*Barbatodon transylvanicum* tentatively referred	IS.003	characterized briefly
Grigorescu and Hahn, 1987	**left m1**	***Paracimexomys*? *dacicus*, n. sp.**	–	**cast figured, described**
	right m2	*Paracimexomys*? *dacicus*, n. sp.	–	cast figured, described
Rădulescu and Samson, 1996	**M1**	***Barbatodon transylvanicus***	–	–
	m2	Multituberculata indet.	–	–
	i1 type 1	Ptilodontoidea	–	–
	i1 type 2	Taeniolabidoidea	–	–
Rădulescu and Samson, 1997	**left M1**	***Barbatodon transylvanicus***	–	**figured, described**
	right M2	Multituberculata indet.	–	described
	right i1	Multituberculata indet. ("taeniolabidoid")	–	figured, described
	left i1	Multituberculata indet. ("ptilodontoid")	–	figured, described
Csiki and Grigorescu, 2000	**right M1**	***Barbatodon transylvanicus***	–	**mentioned**
Csiki and Grigorescu, 2002	**m1**	***Barbatodon transylvanicus***	–	**commented briefly**
Smith et al., 2002	**right m1**	***Barbatodon transylvanicus***	–	**mentioned**
Kielan-Jaworowska et al., 2004	**left M1**	***Barbatodon transylvanicum***	–	**mentioned**
Csiki et al., 2005	**left m1**	***Barbatodon transylvanicus***	**ISB IS.001**	**figured, commented**
	i1 ("ptilodontoid" type)	probably not *Barbatodon transylvanicus*	ISB IS.003	commented
Smith and Codrea, 2015	**left m1**	***Barbatodon transylvanicus***	**ISB IS.001**	**mentioned**
Solomon et al., 2016	**left m1**	***Barbatodon transylvanicus***	**ISB IS.001**	**mentioned**
This paper	**left m1**	***Barbatodon transylvanicus***	**ISER PUI.001**	**figured, commented**
	right m2	Kogaionidae indet. (not *Barbatodon transylvanicus*)	ISER PUI.002	described, figured
	left I2	Kogaionidae indet. (not *Barbatodon transylvanicus*)	ISER PUI.003	described, figured
	left i1 ("ptilodontoid" type)	Kogaionidae indet. (not *Barbatodon transylvanicus*)	ISER PUI.004	described, figured

Samson (1986) listed these specimens as IS specimens—e.g., IS.001—whereas Csiki et al. (2005) and Smith and Codrea (2015) used the reference numbers ISB IS. (e.g., ISB IS.001). However, these specimen numbers should be updated to include the catalog abbreviation used by the Emil Racoviță Institute of Speleology, Bucharest, that is, ISER. Furthermore, the original boxes containing the specimens are accompanied by handwritten labels using the collection number format PUI—e.g., PUI.001. The labels show that this was the format intended by the authors of *Barbatodon* to be used for these specimens. This format is, coincidently, similar in composition to that used by the same authors for the holotype of *Kogaionon* (the format "locality/number"; see Rădulescu and Samson, 1996). Accordingly, from now on, this is the specimen number format by which the PB1 multituberculate teeth will be referred to (table 1), and we suggest that this same formatting of specimen numbers be followed in subsequent publications as well.

HISTORY OF RESEARCH: The PB1 microvertebrate lens was identified and excavated during the 1983 fieldtrip of a French-Romanian collaborative team including members from the University of Bucharest, Romania and Montpellier University, southern France (Grigorescu et al., 1985; Grigorescu, 1987a; Grigorescu and Hahn, 1987); the fossiliferous bed itself was discovered somewhat earlier (1982) by former University of Bucharest student Emanoil Știucă (Știucă, 1983). The first multituberculate remains from the locality—two isolated molars—were reported by Grigorescu et al. (1985; fig. 10). One of these specimens, considered to be more diagnostic and interpreted as an M1, was selected as the holotype of the first Mesozoic mammal taxon described from Romania, *Barbatodon transylvanicus* (as *Barbatodon transylvanicum*; Rădulescu and Samson, 1986), a taxon to which the same authors also referred tentatively an isolated i1 (otherwise neither identified by specimen number nor figured). The same molar specimen (but identified, correctly, as an m1) was used by Grigorescu and Hahn (1987) to erect the taxon

Paracimexomys? *dacicus*, an objective junior synonym of *Barbatodon transylvanicus* (see Kielan-Jaworowska et al., 2004). The occurrence of a second isolated i1 was briefly reported later from site PB1 by Rădulescu and Samson (1990), and the entire PB1 multituberculate sample was discussed in some detail by Rădulescu and Samson (1997). The identity of the holotype molar of *Barbatodon transylvanicus* (recognized as an m1 instead of an M1 as was originally assumed by the authors of the taxon; fig. 10A–C) was reassessed and established definitively by Csiki et al. (2005), and nomenclatural issues surronding the taxon name were discussed and cleared up by Solomon et al. (2016).

COMMENTS: Despite the great historical importance of the PB1 multituberculate sample, its true significance was muddled for a long time by misinterpretations surrounding the anatomical identity of some of the included specimens (all of them, isolated teeth). The holotype of *Barbatodon transylvanicus* (ISER PUI.001; fig. 10A–C) was long considered to represent an M1 (Grigorescu et al., 1985; Rădulescu and Samson, 1986, 1996, 1997; Grigorescu, 1987a; Kielan-Jaworowska et al., 2004), although Grigorescu and Hahn (1987) correctly recognized it to be an m1. These uncertainties have had a great impact on the identification of the true systematic and phylogenetic affinities of this isolated tooth, as well as those of the taxon based on it. Accordingly, *Barbatodon* was considered closely related to either the informal *Paracimexomys* group (Grigorescu et al., 1985; Grigorescu, 1987a; Grigorescu and Hahn, 1987; Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska et al., 2004) or it was linked alternatively to certain Mongolian djadochtatherioid multituberculates (Rădulescu and Samson, 1986). In their most recent review of the PB1 multituberculate assemblage, Rădulescu and Samson (1997) discussed this taxon as of uncertain affinities, probably more basal than either djadochtatherioids or the *Paracimexomys* group. It was only with the discovery of more complete associated remains referable to this taxon (see below) that the holotype molar

was definitively recognized as an m1 showing a peculiar, autapomorphic distolabial cingulum or crest (fig. 10C). This identification also allowed the recognition of the kogaionid affinities of *Barbatodon* (Csiki et al., 2005).

Despite these recent systematic clarifications, one further inconsistency concerning specimen ISER PUI.001 remained largely unnoticed: its dimensions, as reported by the different authors. In the first mention of this specimen, its dimensions—determined from scaled direct measurements from the figure (Grigorescu et al., 1985: fig. a)—should had been 3.52 mm long × 2.20 mm wide. Subsequently, Rădulescu and Samson (1986; see also Rădulescu and Samson, 1997) reported measurements of 3.38 mm × 2.20 mm for ISER PUI.001, while Grigorescu and Hahn (1987) described it as 3.40 mm × 1.96 mm in size and Kielan-Jaworowska et al. (2004) gave a measurement of 3.38 mm × 2.06 mm. Most intriguingly, Grigorescu (1987a) reported this specimen as 3 mm long and 1.5 mm wide. In order to resolve the uncertainty surrounding the correct dimensions of the holotype of *Barbatodon transylvanicus*, which is of great importance in assessing the relative size of the different Transylvanian multituberculate specimens reported subsequently (of which several were referred to *Barbatodon* and even to *Barbatodon transylvanicus* itself), we have remeasured (see below, Body size distribution, for details of the standard measurements used) this historically important specimen directly with digital calipers (0.01 mm precision) and digitally from the SEM picture with ImageJ software, and we can report a reliable measurement of 3.40 mm × 2.15 mm.

Further misinterpretations of the PB1 sample concern the anatomic and taxonomic identity of the second multituberculate molar specimen reported from here by Grigorescu et al. (1985). Different authors such as Grigorescu et al. (1985), Rădulescu and Samson (1986, 1996, 1997), and Grigorescu (1987a) have all noted that this specimen, a right m2 (ISER PUI.002; 1.30 mm × 1.30 mm; fig. 10D), is significantly smaller than the *Barbatodon transylvanicus* holotype m1 (by com-

paring, e.g., the width of 1.30 mm in this m2 with the "2.20 mm" reported at that time in ISER PUI.001), and thus they argued that it should represent a second, small taxon (Rădulescu and Samson, 1997). Nevertheless, Grigorescu and Hahn (1987) regarded this specimen as the paratype of their *Paracimexomys*? *dacicus*, and thus as referable to the same taxon as ISER PUI.001 (see also Grigorescu, 1987a). We agree with Rădulescu and Samson (1997) that the size discrepancy between the two molar specimens precludes their conspecificity, and through this, we emphasize the presence of two multituberculate taxa, of different body size, in the PB1 assemblage.

The generalized morphology and slightly damaged state of this m2 (fig. 10D) does not allow a more detailed taxonomic identification, but its morphology is nevertheless consistent with probable kogaionid affinities of the specimen. Previously, Grigorescu and Hahn (1987) and Rădulescu and Samson (1997) have both reported this tooth as having a cusp formula of 3:2, despite the fact that it clearly appears to show a 2:2 cusp formula when first figured by Grigorescu et al. (1985; fig. 1b). Nevertheless, Grigorescu and Hahn did note that "the cusps of the labial row are strongly worn; the first cusp is limited posteriorly by a slight transverse valley, but the second and third cusps are confluent, no longer separated one from the other" (Grigorescu and Hahn, 1987: 239) and, in our assessment, the absence of separation in the distal part of the labial row noticed by these authors is genuine, instead of a byproduct of advanced wear. Hence, we suggest that ISER PUI.002 appears to have a cusp formula of 2:2, with two unequal cusps in the labial row (the distal cusp twice as large as the mesial one) and two roughly subequal cusps in the lingual row; the distolingual corner of the tooth is damaged, and the distal half of the distal lingual cusp is missing. Due to this differential size distribution pattern of the cusps in the two rows, the transverse valley separating the lingual cusps is distally shifted compared to its labial counterpart.

It is worth noting here that, rather unexpectedly and inexplicably, Rădulescu and Samson (1997) mentioned ISER PUI.002 as a right M2, instead of a right m2, contrary to the identity of this specimen as well as to all its previous identifications (Grigorescu et al., 1985; Grigorescu and Hahn, 1987; Rădulescu and Samson, 1996); this must certainly be a *lapsus calami*.

Finally, there are serious previous misinterpretations surrounding the last two multituberculate specimens from site PB1, the two isolated incisors (fig. 11); these same misinterpretations gave rise to somewhat contentious interpretations about the higher-level composition of the Transylvanian multituberculate faunas. Our restudy of these specimens (ISER PUI.003 and ISER PUI.004) finally clarifies their anatomical identity, thus contributing to a more accurate understanding of the affinities of the latest Cretaceous Transylvanian multituberculates and of the composition of the local multituberculate assemblages.

As noted above, two markedly different morphotypes of incisors, both identified as lower incisors, were reported to have been found at site PB1, an observation first mentioned by Rădulescu and Samson (1990). These presumed i2 morphotypes were subsequently briefly described and figured by Rădulescu and Samson (1997: fig. 2; fig. 11A, G). Whether any of these incisors belong to *Barbatodon* (or even to *Barbatodon transylvanicus*, as was suggested tentatively by Rădulescu and Samson, 1986), is difficult to ascertain, given the dissociated and mixed nature of the microvertebrate remains from this locality (see also below). Regardless of this taxonomic uncertainty, a few comments concerning the nature of the PB1 incisors are nevertheless necessary.

Since the first mention of their cooccurrence at site PB1, these specimens (ISER PUI.003 and PUI.004) were interpreted to represent two different, morphologically widely divergent morphotypes of lower incisors (Rădulescu and Samson, 1990, 1997) in the terms of Kielan-Jaworowska (1980): one of taeniolabidoid affinities (Rădulescu and Samson, 1997: fig. 2.1; fig. 11G–K) and the other of ptilodontoid affinities (Rădulescu and Samson, 1997: fig. 2.2; fig. 11A–E). That is to say, the first morphotype was described as a robust, "gliroid," gnawing i1 with a reduced enamel cover, presenting a clearly delimited labiomesial enamel band, while the second incisor was identified as a more gracile, tapering, grasping-puncturing morphotype with an almost full enamel cover (see also Kielan-Jaworowska et al., 2004). No specimen numbers were assigned to these lower incisors when they were first figured, making it uncertain which of the two registry numbers (PUI.003 and PUI.004) refers to which specimen noted on the box where they are stored together. As the "gliroid" specimen is the one first mentioned and figured by Rădulescu and Samson (1997), it is to be assumed that it bears specimen number PUI.003. This assignment may be further supported by the fact that in a previous publication, Rădulescu and Samson (1986) tentatively referred to *Barbatodon transylvanicus* (under specimen number IS.003, but without illustrating and/or describing it in detail) an isolated and incomplete lower incisor with a ventrolabially restricted enamel band. Based on this brief account, the presence of the ventrolabially restricted enamel band identifies this particular incisor specimen as the "gliroid" morphotype figured by Rădulescu and Samson (1997: fig. 2.1; fig. 11G). Accordingly, the second, "ptilodontoid" lower incisor from PB1 (Rădulescu and Samson, 1997: fig. 2.2; fig., 11A) ought then to be referred to as ISER PUI.004.

It should be noted here that the absence of a clear identification of these PB1 incisor specimens (through figures and specimen numbers) in previous publications led Csiki et al. (2005: 78) to mistakenly refer to *Barbatodon transylvanicus*, under specimen number ISB IS.003, the lower incisor from site PB1 that best matched the morphology seen in the in situ i1 in the jaw of individual LPB [FGGUB] M.1635 that these authors were reporting and referring to the same taxon, that is, ISER PUI.004—this error is pointed out, and is corrected now and here.

We further point out here, that *Barbatodon transylvanicus* was considered previously, albeit tentatively, to have a "taeniolabidoid" type of lower incisor (Rădulescu and Samson, 1986). This inference was then used by Rădulescu and Samson (1986: 1829) to suggest affinities of this taxon with certain Asian djadochtatherioideans such as *Kryptobaatar* that also shows a limited enamel band on its relatively robust i1 (e.g., Kielan-Jaworowska, 1970; Wible and Rougier, 2000). However, the discovery in 2002 of an associated specimen referred to *Barbatodon transylvanicus* (LPB [FGGUB] M.1635; see below) allowed Csiki et al. (2005) to establish that this taxon had a "ptilodontoid" type of i1, although of a somewhat modified nature. The i1 of *Barbatodon transylvanicus* (see also Smith and Codrea, 2015; Solomon et al., 2016), although long and evenly tapering (thus corresponding to the "grasping-puncturing" morphotype), shows an unevenly developed enamel, with a clearly defined boundary that marks the edge of the thicker labioventral enamel cover. This pattern of enamel development roughly corresponds to the "djadochtatherioid pattern" identified by Kielan-Jaworowska et al. (2004: 278), although the overall shape of the tooth is more gracile and apically narrowing, thus somewhat reminiscent of the "ptilodontoid pattern" (Kielan-Jaworowska et al., 2004: 277).

This morphology—which we identify here as a novel kogaionid pattern of multituberculate i1 development (see also figs. 6E, 11F) and which may represent a kogaionid synapomorphy, as noted above (see section Kogaionids in phylogeny, space, and time)—fits that of specimen ISER PUI.004 (fig. 11B–E) instead of that shown by ISER PUI.003 (fig. 11H–K). Accordingly, we correct here the tentative referral of this latter, supposedly taeniolabidoid type of i1 as the i1 of *Barbatodon transylvanicus*, as was proposed previously by Rădulescu and Samson (1986). Such a reassessment, incidentally, also removes presumed *Kryptobaatar*-like features from *Barbatodon*, thus dismissing previously cited similarities in support of the proposed

djadochtatherioid affinities of the Transylvanian multituberculate. Finally, as already noted by Csiki et al. (2005: 78), the small size of ISER PUI.004 (fig. 11B–E) compared with that of the holotype m1 of *Barbatodon transylvanicus* (ISER PUI.001; fig. 10A–C) precludes its referral to this medium-to-large kogaionid taxon (see below) and suggests that it might belong instead to another, smaller kogaionid taxon, maybe that represented in the same site by the diminutive right m2 (ISER PUI.002; fig. 10D).

Under these circumstances, the unexpected presence in the Haţeg Basin of a multituberculate taxon with gnawing lower incisors, thus showing alleged taeniolabidoid affinities, as was suggested by Rădulescu and Samson (1990, 1997) based on the presumably diagnostic i1 morphotype identified in ISER PUI.003 (see fig. 11H–K), appears remarkable (see also note in Kielan-Jaworowska et al., 2004: 64), requiring further investigation. All other multituberculate i1s reported to date from the Transylvanian area (e.g., Csiki and Grigorescu, 2000; Csiki et al., 2005: Smith and Codrea, 2015; Solomon et al., 2016; Codrea et al., 2017a; Csiki-Sava et al., 2018; Smith et al., 2022) are but minor variants of the kogaionid pattern described above. Thus, the outstanding occurrence of a taeniolabidoid lower incisor, as exemplified by ISER PUI.003, would suggest the presence of a second group of multituberculates in the Transylvanian area, with a widely divergent dental morphology, probably different morphofunctional and dietary adaptations, and yielding a distinctive paleobiogeographic-evolutionary signal (e.g., Rădulescu and Samson, 1997; Williamson et al., 2016).

In order to verify the identity and potential affinities of this intriguing specimen, we have reexamined it firsthand (fig. 11H–K). It shows indeed a sharp demarcation line between the thick enamel-covered labiorostral and the more thinly enameled distolingual sides of the crown. Nevertheless, the enamel is not completely missing in any area of the crown (although it is locally removed, obviously through postmortem taphonomic damage), contrary to previous claims by

Rădulescu and Samson (1986, 1990, 1997). Instead, the apparently neat distinction between the thicker and thinner enameled surfaces of the crown is further emphasized by the presence of a longitudinal groove running along its labial face (fig. 11I), giving the crown its asymmetrically laterally compressed cross-sectional outline noted by Rădulescu and Samson (1997: fig. 2.1b; fig. 11G). The tip of the crown is obviously heavily worn, with a concave, slightly oblique, lingually oriented apical wear facet. The crown continues into a root of roughly similar diameter with the former, giving the specimen a slightly arched and labiolingually compressed tubular, cylindrical shape.

Overall, the morphology of ISER PUI.003 is strongly reminiscent of the worn first upper premolars (I2) of kogaionids, especially those of *Kogaionon* (ISER SPT/001), of the Pui specimen UBB P-Mt 1 referred to *Barbatodon transylvanicus* by Smith and Codrea (2015: fig. 4D), and of *Litovoi* (figs. 6D, 11L). Thus, we recognize this specimen as a worn first upper incisor of a kogaionid, and not as a taeniolabidoid first lower incisor as was proposed previously by Rădulescu and Samson (1997). Given this reassessment of ISER PUI.003, the presence of two completely different multituberculate clades in the uppermost Cretaceous of the Transylvanian area—as advocated by Rădulescu and Samson (1990, 1997)—is no longer a tenable hypothesis and all known multituberculate specimens can be accommodated within one group, that of the endemic Kogaionidae. Nevertheless, the referral of ISER PUI.003 to *Barbatodon transylvanicus*, as suggested by Rădulescu and Samson (1986), cannot be supported by positive evidence either. Such identification is also contradicted by the small size of this I2 specimen (fig. 11H–K) compared with the holotype m1 (fig. 10A–C) of *B. transylvanicus*, and thus it can be identified only as a Kogaionidae indet.

To conclude, the small but historically significant multituberculate sample from site PB1 documents the presence of two distinct kogaionid taxa, the medium-large *Barbatodon transylvani-* *cus* and an indeterminate small kogaionid. Our revision of this small kogaionid dental assemblage also helps clear up a long-standing paleobiogeographic enigma of the latest Cretaceous Transylvanian mammalian faunas put forth by Rădulescu and Samson (1990, 1997), the argument that these included members of two widely divergent multituberculate lineages. Our reassessment of the PB1 multituberculate material upon which this hypothesis was based shows that all these specimens can be accommodated within the typical kogaionid dentition and that the local mammalian assemblage is made up exclusively of kogaionids, thus alleviating the need to consider the presence of other, nonkogaionid multituberculate clades within the multituberculate fauna of the Transylvanian area.

Site PB2
Pui Islaz Locality

Location, age: The Pui Islaz locality is situated on the right bank of the Bărbat River, about 500 m south (upstream) of the Pui road bridge, at the level of the last houses of the locality (Folie and Codrea, 2005; GPS data provided in this publication appear to be somewhat imprecise, plotting into the active floodplain, an area covered by soil and Quaternary lags, instead of the riverbed), and a few tens of meters below the wooden (now replaced by metal) footbridge crossing the river (Codrea and Solomon, 2012). A relatively poor palynological assemblage sampled from a channel deposit immediately overlying the multituberculate-bearing fossiliferous bed suggests an age straddling the early/late Maastrichtian boundary (Van Itterbeeck et al., 2005), making this locality a geochronologically relatively well constrained one, an uncommon occurrence in the entire Transylvanian uppermost Cretaceous (Csiki-Sava et al., 2016).

Lithology, paleoenvironment: The Pui Islaz locality was discovered in a relatively (almost 2 m) thick stacked sedimentary body made up of mica-rich, calcrete-bearing red silty mudstone beds (Van Itterbeeck et al., 2004), the

dominant lithotype of the Bărbat River succession (Van Itterbeeck et al., 2004; Bojar et al., 2005; Therrien, 2005; fig. 8D). The silty mudstone locally passes laterally into greenish coarse, sometimes conglomeratic sandstones. In the lower third of the silty mudstone unit, two relatively mature, continuous calcrete horizons are individualized, the upper one of these being erosionally cross-cut by a lenticular sandstone body. A third, less well-developed, locally discontinuous calcrete layer is also present at about midthickness, cross-cut by a second lenticular sandstone body; finally, at the top of the outcropping succession, the stacked mudstone body is capped by a fourth calcrete layer. The multituberculate-bearing level, a microvertebrate bonebed, was discovered just above the third, discontinuous calcrete layer; meanwhile, right below the same calcrete level, a small macrovertebrate accumulation was also recorded (Van Itterbeeck et al., 2004). These deposits are interpreted to have been laid down in the confines of a distal floodplain undergoing prolonged pedogenesis under a semiarid climate, and crossed by a northeastward-flowing braided river.

Fossil content: The microvertebrate bonebed at Pui Islaz is reported to have yielded a diverse fossil assemblage (Van Itterbeeck et al., 2004), including gastropods, different types of eggshells (Garcia et al., 2002), discoglossid anurans, albanerpetontids, paramacellodid and borioteioiid lizards (it is the type locality of the endemic lizard taxa *Becklesius nopcsai* and *Bicuspidon hatzegiensis*), and indeterminate madtsoiid snakes (Folie et al., 2002; Folie and Codrea, 2005), as well as multituberculates. Right below the calcrete level underlying the microvertebrate bonebed, a titanosaur humerus and 10 articulated vertebrae were also recovered (Pui-Dino locality; Van Itterbeeck et al., 2004), whereas the laterally correlative channel sandstone yielded a rather poor palynological assemblage dominated by fern spores (Van Itterbeeck et al., 2005). The multituberculate material from this site, containing an unreported number of isolated teeth, is stated to represent four dental positions (Smith

and Codrea, 2003). No detailed description of this material is yet published, and neither figures nor specimen numbers are available for it.

History of research: The Pui Islaz locality was identified in 2000 by a Belgian-Romanian field party, and was excavated through screenwashing in 2000–2001. The multituberculate material originating from this site was only very briefly mentioned by Smith and Codrea (2003), which is the only published account concerning this important material.

Comments: Without offering any details in support of their identification, Smith and Codrea (2003) referred the multituberculate sample from site PB2 to a new, small species of the genus *Kogaionon*. As no detailed description of this material was published subsequently, we cannot comment further on the identity and affinities of these (presumably isolated) teeth, except to point out that: (1) they apparently support a higher taxonomic diversity within the genus *Kogaionon* than that recognized for a long time, an idea that is also emphasized now by the very recent description of a new, smaller species of the genus by Smith et al. (2022); (2) if correctly identified, this material documents a geographic range extension of the genus into the eastern part of the basin and into the Pui Beds; (3) this material also significantly augments the known local diversity of multituberculates; and (4) this occurrence fills an important gap in the stratigraphic succession of multituberculate localities from the Bărbat River succession (fig. 3; and see below).

Site PB3
2002 *Barbatodon* Locality
(Karlsruhe or Rücklin locality)

Location, age: The PB3 locality was discovered on the right bank of the Bărbat River, about 100 m upstream from the footbridge crossing the river (fig. 8D). The locality is situated about 700 m upstream from the Pui main road bridge, thus about 200 m upstream (roughly 45 m in stratigraphic section) from the *Barbatodon* holotype locality PB1, but 70 m downstream (about 15 m
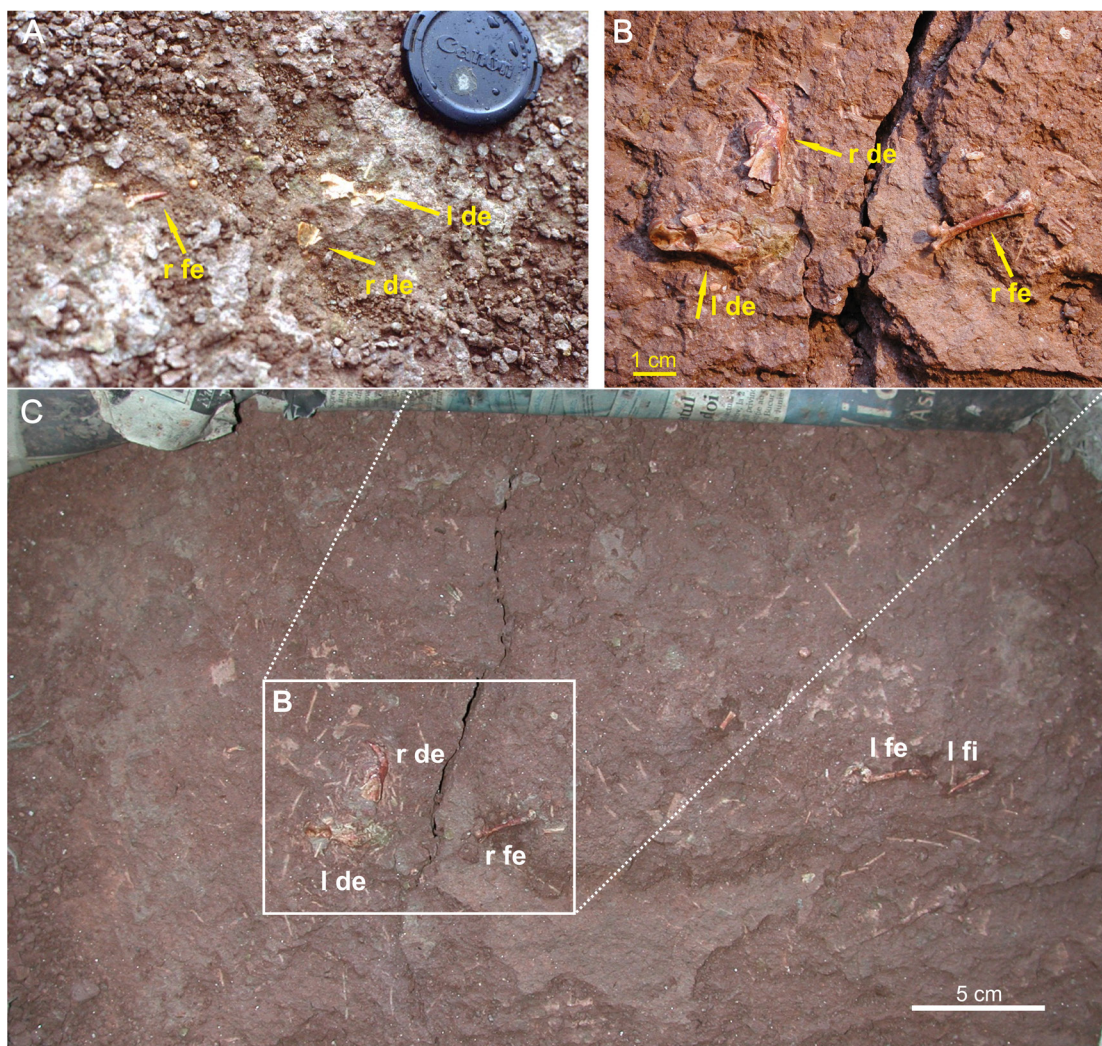
FIGURE 12. In situ remains of the referred specimen of *Barbatodon transylvanicus*, LPB (FGGUB) M.1635, Pui Beds, site PB3, documenting their associated nature. **A.** Remains of M.1635 as first spotted in the field, July 2002, showing the dentaries and one of the femora exposed on the bed surface by river erosion. **B.** Close-up from the initial preparation stage of the plaster jacket containing the partial skeleton M.1635, with the fully exposed dentaries and right femur. **C.** Presence of further postcranial remains revealed within the plaster jacket; boxed area in left center (B) highlights the position of the first discovered remains. Abbreviations: **de,** dentary; **fe,** femur; **fi,** fibula; **l,** left; **r,** right.

lower in stratigraphic thickness) from the Multi-Bed locality (see below, site PB6) yielding the holotype of the new kogaionid taxon *Litovoi tholocephalos* (Csiki-Sava et al., 2018), and some 100 m downstream (around 24 m thickness) from the site yielding the specimens described by Smith and Codrea (2015) and Solomon et al. (2016) (see below, site PB5; fig. 3). As its position is stratigraphically higher than that of the palynostratigraphically positioned site PB2, its age should be regarded tentatively as very early late Maastrichtian, based on the palynology-
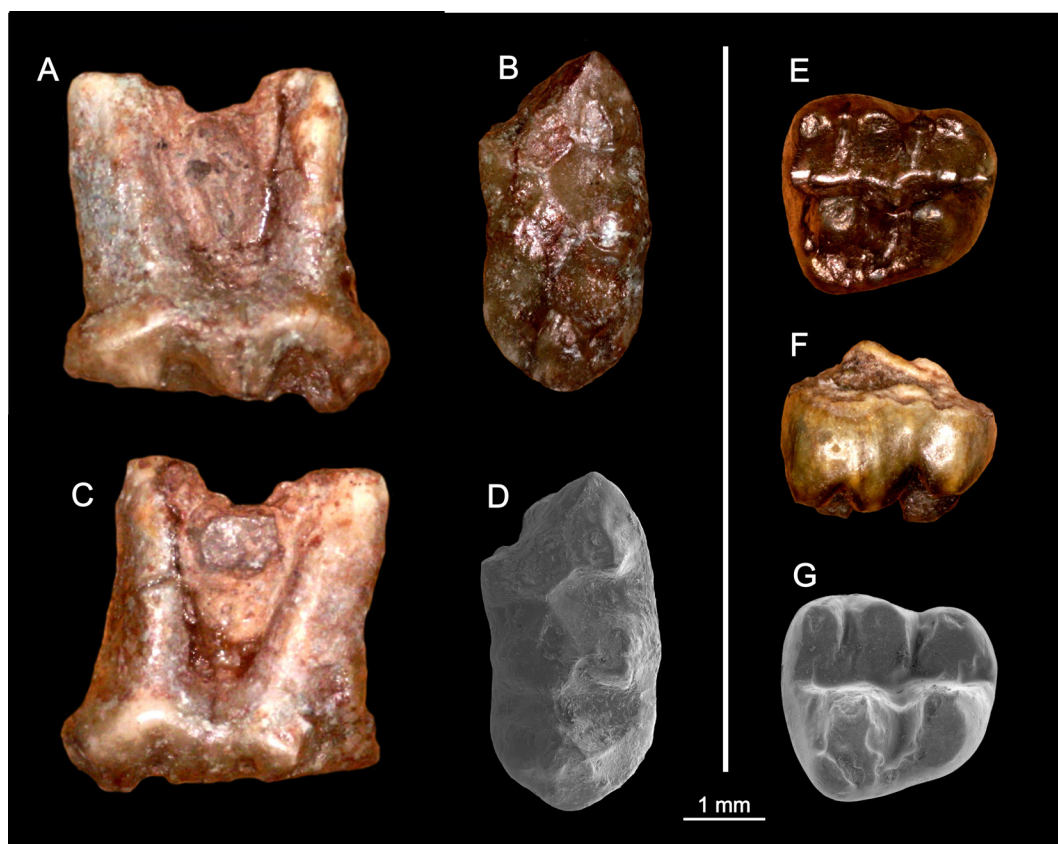
FIGURE 13. Isolated elements of the upper dentition, referred specimen of *Barbatodon transylvanicus*, LPB (FGGUB) M.1635, Pui Beds, site PB3. **A–D.** Left P3 in **A.** lingual, **B.** occlusal, and **C.** labial views; **D.** SEM microphotograph of the occlusal surface. **E–G**. Right M2 in **E.** occlusal, and **F.** lingual views; **G**. SEM microphotograph of the occlusal surface in slightly laterally oblique view to show relative development of cusps.

based age assessment suggested by Van Itterbeeck et al. (2005) for the Pui section.

LITHOLOGY, PALEOENVIRONMENT: The fossils from site PB3 were discovered in a dark red, very weakly calcareous, micaceous silty sandstone bed (figs. 8D, 12A), with diffuse horizontal lamination; the fossiliferous bed overlies a relatively thick, greenish-gray coarse conglomeratic sandstone. According to the sedimentological interpretation of the local succession (Van Itterbeeck et al., 2004; Bojar et al., 2005; Therrien, 2005), the fossil-bearing bed accumulated in a well-drained floodplain setting, within the confines of a braided river depositional environment, and most probably represents the distal reaches of a sheetlike crevasse splay deposit.

FOSSIL CONTENT: The fossiliferous bed yielded the disarticulated partial skeleton of one multituberculate individual, including cranial (incomplete dentaries with in situ teeth) and postcranial (femora, humerus, vertebrae) remains (specimen LPB [FGGUB] M.1635; Csiki et al., 2005; Vremir et al., 2018; fig. 12). Removal and screenwashing of the sediment from around the partial skeleton revealed the presence of several isolated teeth (left i1, left P3: fig. 13A–D; and right M2: fig. 13E–G). These isolated teeth most probably belong to the same individual, as no other vertebrate remains have been recovered from around the skeleton, and they are roughly commensurate in size with the in situ lower teeth (i1, p4, m1)

preserved in the dentaries (fig. 7N). The only other organic remains from this site are represented by cyclophorid gastropod operculae, a common occurrence in the red-colored, fine-grained floodplain deposits from Pui (Pană et al., 2002; Van Itterbeeck et al., 2004).

HISTORY OF RESEARCH: Specimen LPB (FGGUB) M.1635 was discovered by M. Rücklin, member of a joint Romanian-German field team led by D. Grigorescu (Bucharest) and E. "Dino" Frey (Karlsruhe), during a brief prospection of the Bărbat River outcrops in July 2002. Only the two dentaries and parts of the right femur were exposed when the specimen was discovered and removed in plaster jacket from the field (fig. 12A). Preparation of the jacket at the LPB (FGGUB) revealed the presence of further skeletal elements in the proximity of the exposed ones (fig. 12B, C), including the complete left femur, parts of the humerus and ulna, as well as the isolated left i1. Preliminary screenwashing of the matrix that resulted during preparation also yielded an isolated right M2.

The discovery of this specimen was reported and its dentition (i1, p4, m1, and M2) and dentary morphology were described in some detail by Csiki et al. (2005; see also figs. 7F, N, 13E–G), who referred it to *Barbatodon transylvanicus*. Subsequent to this preliminary report, an isolated left P3 (fig. 13A–D) was also recovered from nearby the skeletal remains and it will be described here in detail; as its size is commensurate with the other dental remains known in individual LPB (FGGUB) M.1635, this isolated P3 is thus most parsimoniously also referred to the same individual. The postcranial remains associated with the dentaries were briefly discussed by Vremir et al. (2018).

COMMENTS: The partial skeleton LPB (FGGUB) M.1635 represented a crucial specimen for understanding the anatomy, taxonomic affinities, and systematic relationships of the Transylvanian latest Cretaceous multituberculates as it documented the first cooccurrence of cranial and postcranial material and, more importantly, that of upper and in situ lower dentition. It allowed researchers to

definitively establish the kogaionid affinities of *Barbatodon transylvanicus* (Csiki et al., 2005), thus removing any arguments for the presence of the mainly North American basal cimolodontan "*Paracimexomys*" group in Transylvania based on the occurrence of this taxon (e.g., Grigorescu et al., 1985; Grigorescu and Hahn, 1987; Kielan-Jaworowska et al., 2004). It also offered the first opportunity for direct comparisons—through overlapping dental elements—between the roughly sympatric and similarly sized kogaionids *Barbatodon transylvanicus* (previously known solely from the holotype m1, i.e., its lower dentition; fig. 10A–C) and *Kogaionon ungureanui* (represented exclusively by its upper dentition; figs. 5F, 9A), the only two nominal Transylvanian kogaionid taxa known at that time. The preliminary description of this individual (Csiki et al., 2005) is supplemented here by that of the isolated P3, allowing further comparisons with other kogaionids, especially with those known from their upper dentition, such as *Kogaionon ungureanui* or *Litovoi tholocephalos*. In order to more completely document this important specimen, we also report confident dental measurement values for LPB (FGGUB) M.1635 as these have not been explicitly presented before (table 2).

The isolated left P3 referred to individual LPB (FGGUB) M.1635 (fig. 13A–D) shows the typical kogaionid pattern, offering further support for the kogaionid affinities of this specimen recognized previously by Csiki et al. (2005). It is a relatively well-preserved double-rooted tooth (the mesial root being more massive that the distal one; fig. 13A, C), damaged only on the mesiolingual corner of the crown; it is thus unclear whether it also developed a proximal platform similar to that described in the P3 of *Kogaionon*, where this platform overlaps the distal heel of P2 (Rădulescu and Samson, 1996). The crown has a mesiodistally elongated oval outline (fig. 13B, D), with a mildly tripartite convex labial margin and a medially waisted, largely concave lingual margin; the distal margin is pointed, roughly triangular.

The crown bears five cusps, four of which are placed within its mesial two-thirds and pair up

TABLE 2

Dental Measurements of *Barbatodon transylvanicus*, Individual LPB (FGGUB) M.1635, Bărbat River Section, Pui Locality (site PB3), Haţeg Basin

Position	Side	Length (mm)	Width (mm)	Height (mm)
p4	right	6.70	2.19	3.53
	left	6.78	2.14	3.70
m1	right	3.35	2.20	–
	left	3.35	2.15	–
P3	left	4.03	1.94	–
M2	right	2.45	2.31	–

to form two rows both mesiodistally and transversely. The cusps in the labial row are smaller, somewhat transversely compressed and more widely spaced than those in the lingual row, which are separated only by a very narrow valley; this condition differs from that seen in *Kogaionon*, where the first four cusps of the P3 are roughly equally well developed and separated. Transversely, the corresponding cusps of the labial and lingual rows are closely appressed, to the extent that the two cusps of the mesial transverse row are virtually touching each other. The fifth cusp is located in the distal quarter of the crown, slightly lingually offset from the midline and almost collinear with the two cusps of the lingual row. The enamel covering the crown is generally smooth, with only very few ridges radiating from the tips of the cusps, especially that of the fifth, unpaired cusp (fig. 13D).

This fifth, distalmost cusp is connected to the midpoint of the second lingual cusp through a straight, low crest. Meanwhile, the second labial cusp also connects loosely to the labial side of the same fifth cusp through a long, curved ridge that closely parallels the labiodistal margin of the crown, and is very well visible on the labial slope of the fifth cusp. This labiodistal ridge, together with the second (median) transverse cusp row and the distalmost cusp, encloses a roughly hexagonal basin on the distal third of the crown. In this respect, the P3 morphology of individual LPB (FGGUB) M.1635 is reminiscent of that

described in another specimen from Pui (UBB P-Mt 1) also referred to *Barbatodon transylvanicus* by Smith and Codrea (2015), but departs from that seen in *Kogaionon ungureanui* (Rădulescu and Samson, 1996), where—although the P3 cusp formula is similarly 2:3—the distalmost cusp is relatively larger, more bulbous, more centrally placed, and not connected to a well-individualized labiodistal ridge. As a consequence, in *K. ungureanui* the corresponding posterior basin is less well defined and smaller, shaped more like a transversely oblique oval. In the smaller *K. radulescui* (Smith et al., 2022), the cusp formula of P3 is again identical to that of LPB (FGGUB) R.1635 (i.e., 2:3), but the tooth itself differs in several morphological details such as the more rounded (instead of angular) distal edge of the crown in occlusal view, the more precise alignment of the three lingual cusps within the lingual row, a relatively larger distal lingual cusp, and, most importantly, the presence of a small flat surface in the labiodistal corner of the crown that contrasts the basined morphology seen in the P3 from site PB3.

In the significantly smaller *Barbatodon oardaensis* (Codrea et al., 2014), the cusp formula of P3 is slightly higher (3:3), through the addition of a small, but distinct conical third (distal) labial cusp. Finally, in *Litovoi* (Csiki-Sava et al., 2018), the occlusal crown morphology of P3 is significantly more complex than in either *Barbatodon* or *Kogaionon*, with a cusp formula of 2:5, and

with a mesiodistally flattened cusplet individualized in the labiodistal corner, instead of a continuous crest connecting labial cusp 2 to the distalmost lingual cusp (which would correspond topologically to the fifth, unpaired cusp in LPB [FGGUB] M.1635).

In most derived multituberculates, the P3 is considered part of a piercing mechanism (e.g., Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska et al., 2004) and does not usually wear significantly. However, in the P3 of LPB (FGGUB) M.1635 the tips of most cusps are affected by clearly defined subhorizontal wear facets, whereas no obvious wear can be detected along the slopes of the cusps or within the valleys separating the cusps. Wear on the cusp tips is more important mesially and lingually; consequently, the distalmost, fifth cusp is the highest-protruding and least worn cusp of the crown (fig. 13C). The advanced wear affecting the cusps of P3 is reminiscent of the relativey heavily worn condition shown by both m1s (fig. 7F) as well as by the labiodistal platform and labiodistal face of the bladelike p4s of individual LPB (FGGUB) M.1635. Such an advanced wear in the dentition of this specimen suggests that it was a rather old, possibly senescent individual, unlike the *Barbatodon transylvanicus* specimen reported by Smith and Codrea (2015) or the holotype of *Litovoi tholocephalos* (Csiki-Sava et al., 2018), both of which are roughly similar in size to the individual from site PB3, but have relatively unworn molars and, especially, premolars. Remarkably, the isolated right M2 of the same individual (fig. 13E–G), previously described by Csiki et al. (2005), shows a less advanced degree of wear, with the cusps well individualized and worn mostly on their tips.

Both the strongly elongated oval outline of the P3 and, partly, its cusp formula are highly reminiscent of the autapomorphic kogaionid condition (Kielan-Jaworowska et al., 2004; Csiki-Sava et al., 2018), first reported in *Kogaionon* by Rădulescu and Samson (1996). Although no other upper premolars were recovered from specimen LPB (FGGUB) M.1635 to compare

them with P3, this latter tooth is obviously elongated both relative to the only other known element of the upper dentition, the right M2 (M2/P3 length ratio = 0.608), as well as compared to the largest element of the lower dentition (P3/p4 length ratio = 0.612). This degree of P3 elongation, despite being somewhat lower, is reminiscent of that found in *Kogaionon ungureanui* (ISER ST/001: M2/P3 ratio = 0.580), in the specimen UBB P-Mt 1 referred to *Barbatodon transylvanicus* (M2/P3 = 0.548, P3/p4 = 0.553; Smith and Codrea, 2015) and in the holotype of *Litovoi* (M2/P3 = 0.564; Csiki-Sava et al., 2018), but is distinctly more pronounced than that reported in the smaller *K. radulescui* (PSMUBB V-893, M2/P3 = 0.828–0.862; Smith et al., 2022), suggesting that in this latter taxon, the P3 remains relatively shorter compared with the condition present in the other, larger kogaionid taxa from Transylvania.

These ratios, where available, also differ significantly in the species of *Hainina* (M2/P3 = 0.782 in *Hainina vienayae*; P3/p4 = 0.451–0.513 in *Hainina belgica*; Vianey-Liaud, 1979, 1986; De Bast and Smith, 2017), showing that the P3 is relatively less elongated in the Paleocene kogaionids for which corresponding dental elements are known, compared with the condition seen in the different previously described latest Cretaceous kogaionids except for *K. radulescui*. The same significant difference between LPB (FGGUB) M.1635 and the different species of *Hainina* is also present in the size of P3 relative to m1 (P3/m1 = 1.203, compared to P3/m1 = 0.770 in *Hainina pyrenaica*, 0.941 in *H. vianeyae*, 1.020–1.087 in *H. belgica*; Vianey-Liaud, 1979, 1986; Peláez-Campomanes et al., 2000; De Bast and Smith, 2017). These comparisons also support the presence of a shorter P3 relative to other cheekteeth in the dentition of the different *Hainina* species compared to the PB3 individual.

Furthermore, in its overall proportions (width-to-length ratio, W/L = 0.481), the P3 of LPB (FGGUB) M.1635 is reminiscent of the P3 of individul UBB P-Mt 1 (W/L = 0.500; Smith and Codrea, 2015) referred to *Barbatodon tran-*

sylvanicus, an observation consistent with previous referral of the PB3 individual to the same taxon. This W/L ratio appears to be higher in several specimens referred to *B. oardaensis*, with a value of 0.540 in UBB ODAN-Mt-69 and as high as 0.638 in UBB ODAN-Mt-29 (Codrea et al., 2014; Smith et al., 2022). It is also significantly higher in some species of *Hainina* (W/L = 0.607 in *H. vianeyae*; Vianey-Liaud, 1979, 1986; with this ratio, as originally reported, as high as 0.649 in *H. belgica*, according to Vianey-Liaud, 1979), in agreement with the less elongated shape of the P3 in the Paleocene genus, although not as much (P3 W/L ratio 0.579 in UCM FNT 3-9, respectively 0.554 in UCM FNT 3-10) in the chronostratigraphically oldest species of the genus, *H. pyrenaica* (Peláez-Campomanes et al., 2000). It should be noted, however, that De Bast and Smith (2017) reported significantly lower W/L ratios in P3s referred to *H. belgica*, ranging from 0.488 to 0.559. These values are roughly comparable to those found in *K. radulescui* (0.496–0.533; Smith et al., 2022); in both of these taxa, the P3s are thus still marginally to moderately less elongated than in LPB (FGGUB) M.1635. Meanwhile, the W/L ratio is somewhat lower in the P3 of *Litovoi* (0.469; Csiki-Sava et al., 2018), and especially in that of *Kogaionon ungureanui* (0.450; Rădulescu and Samson, 1996), suggesting that these taxa had even relatively more elongated P3s compared with LPB (FGGUB) M.1635. Finally, one specimen referred to *B. oardaensis* (UBB ODAN-Mt-35; Smith et al., 2022: table S1) seems to be very elongated (W/L ratio = 0.426), significantly more than any other P3 specimen referred to this taxon, as well as compared with any currently known kogaionid including the *B. transylvanicus* individual from site PB3.

Site PB4
Pui-Classic (or Pui micro) Locality

Location, age: The Pui-Classic locality is located on the left bank of the Bărbat River, close to the uppermost, currently outcropping part of the local section, about 160 m upstream from the footbridge, and less than 10 m upstream from the important multituberculate locality reported by Smith and Codrea (2015; site PB5, see below). This locality is currently the stratigraphically highest-lying multituberculate occurrence recorded in the Bărbat River succession, well above the palynologically dated PB2 locality, thus most probably it is of (early?) late Maastrichtian age, belonging to the Tier 3 chronofaunal unit as defined by Csiki-Sava et al. (2016).

Lithology, paleoenvironment: The PB4 locality occurs in a relatively thick, richly calcareous, pale red to brick-red, silty mudstone bed (fig. 8E); these mudstones overlie a greenish, laterally extensive microconglomerate-coarse sandstone channel deposit. There is no continuous calcrete horizon developed in the fossil-bearing bed, as reported for similar lithologies from other parts of the section (e.g., Van Itterbeeck et al., 2004; Therrien, 2005); instead there is a large number of relatively small calcareous concretions dispersed throughout the upper half of the silty mudstone, although they tend to concentrate into a more compact layer toward the top of the bed. According to the paleoenvironmental interpretations of the Râul Bărbat succession (Van Itterbeeck et al., 2004; Bojar et al., 2005; Therrien, 2005), the fossiliferous silty mudstone can be interpreted as a pedogenetically immature, well-drained floodplain deposit.

Fossil content: A significant number of vertebrate fossils, represented exclusively by microvertebrate remains, were collected at this site both by surface collecting and by screenwashing. The assemblage is dominated by shed dinosaur (especially rhabdodontid) and crocodyliform teeth (e.g., Vasile and Csiki, 2010), while cyclophorid operculae (Pană et al., 2002) as well as thin pseudogeckoolithid (= maniraptoran theropod) eggshell fragments (Choi et al., 2020a) are also very abundant here. Three isolated multituberculate teeth were identified in this locality through screenwashing the fossiliferous matrix; the first two specimens discovered here (LPB [FGGUB] M.1670, a left I3, and M.1671, a left

M1) were reported, but not described, by Vasile and Csiki (2010), whereas the third specimen, represented by a left I2 (LPB [FGGUB] M. 1706), was identified in the concentrated residue resulted from screenwashing only in 2020.

HISTORY OF RESEARCH: The Pui-Classic locality was identified by FGGUB student field parties in 2004 by spotting a lag of different disperse microvertebrate remains lying atop the subaerially exposed, weathered, and calcrete nodule-enriched top of the fossiliferous bed (fig. 8E). The site was continuously surveyed and surface collected over a period of about eight years, and around 500 kg of sediment were also screenwashed from here. More recently, the top of the bed started to be covered by soil and vegetation, making access to it, as well as natural erosion that exposes and concentrates further fossils on the bed surface, more difficult. Its fossil content was reviewed briefly, without mentioning the name of the locality specifically, by Vasile and Csiki (2010), and the site itself was described briefly by Choi et al. (2020b).

COMMENTS: One isolated left I2 (LPB [FGGUB] M.1706; fig. 14A–C) was discovered at this locality. It is similar to other kogaionid I2s reported from the Transylvanian area (e.g., Grigorescu, 1984a; Csiki and Grigorescu, 2000; Smith and Codrea, 2015; Codrea et al., 2017a; Csiki-Sava et al., 2018) in that it is bicuspid, with a rather worn, large, and mesially positioned main cusp paired at its base with a small accessory cusp placed in the midline of the distal face of the crown (fig. 14B); on the labial face of the crown (fig. 14A), an apicobasal furrow separates the two cusps. The labiodistal edge of the crown, just basal to the accessory cusp, is strongly bulging near the crown-root juction. The enamel cover of the incisor is unevenly developed; the enamel is thicker, even mildly brownish-to-yellow colored, in the mesial and lateral-distolateral sides of the crown, but becomes less shiny, thinner, and slightly translucent distolingually. A line of demarcation between the two enamel regions is visible both on the lingual and on the labiodis-
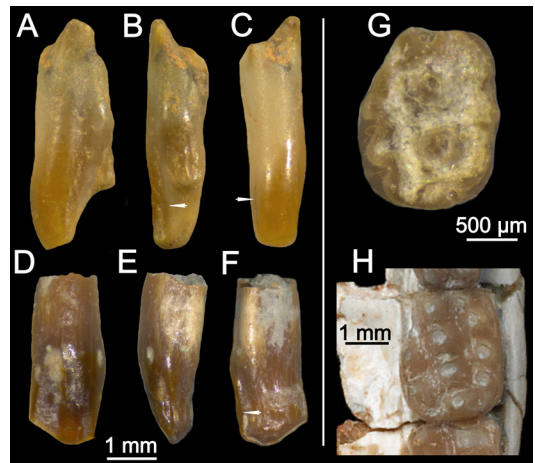

FIGURE 14. Isolated kogaionid teeth from the Pui Beds, site PB4. **A–C.** Isolated left I2, LPB (FGGUB) M.1706, in **A.** labial, **B.** distal, and **C.** mesial views. **D–F.** Isolated left I3, LPB (FGGUB) M.1670, in **D.** mesial, **E.** labial, and **F.** distal views. Arrows in B, C, and F point to the demarcation line between thicker and thinner enamel cover. **G.** Isolated left M1, LPB (FGGUB) M.1671, in occlusal view. **H.** Holotype of *Litovoi tholocephalos*, LPB (FGGUB) M.1700, left M1 in occlusal view, for comparison.

tal faces of the crown (fig. 14B, C). The root is slightly elliptical, longer mesiodistally than labiolingually, in cross section. Due to the lack of potential diagnostic features recognized on kogaionid upper incisors, LPB (FGGUB) M.1706 can be identified only as Kogaionidae indet., although it is definitively smaller than the corresponding teeth in *Barbatodon transylvanicus* (e.g., Smith and Codrea, 2015) and in *Litovoi tholocephalos* (Csiki-Sava et al., 2018; figs. 6D, 11L).

The isolated I3 from site PB4 (LPB [FGGUB] M.1670; fig. 14D–F) stands out in that it is large (in both absolute and, especially, relative terms) compared with the I2 from the same site, described previously. Normally, in kogaionids just as in most other cimolodontans, the I3 is significantly smaller than I2 (see, e.g., fig. 11L). The I3 is about half the size of its corresponding I2 in kogaionids where these teeth are known in association, as reported in *Kogaionon ungureanui*

(Rădulescu and Samson, 1996), in *Barbatodon transylvanicus* (Smith and Codrea, 2015), and in *Litovoi tholocephalos* (Csiki-Sava et al., 2018; figs. 6D, 11L), whereas the I3 can become even more reduced relative to I2 in other cimolodontans (e.g., Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska et al., 2004). To the contrary, the isolated I3 LPB (FGGUB) M.1670 from site PB4 is roughly comparable in its absolute dimensions to the isolated I2 LPB (FGGUB) M.1706 from the same locality, suggesting that they most probably belong to different taxa, one small (M.1706) and one medium to large (M.1670).

This left I3 (LPB [FGGUB] M.1670) preserves the crown and the basal part of the root. The crown is spatulated, chisellike, with a sharp cutting edge on the occlusal surface. This cutting edge is due to the differential development of the enamel, thicker and darker colored on the mesial face, but very thin on the distal face of the crown, with a well-marked, stepped boundary between these two regions visible both on the lateral and the occlusal margins of the crown (fig. 14E, F). The mesial face of the chisel-shaped crown is largely convex both apicobasally and labiolingually, with a rounded bulge crossing it slightly obliquely apicobasally; corresponding to the apical termination of this bulge, the occlusal edge of the crown shows a protuberance that gives this edge an asymmetrical, labially skewed triangular contour in mesial view (fig. 14D, F). The distal face of the crown is still convex labiolingually, although less markedly so than the mesial face, but concave apicobasally. The labial side of the crown is rounded, slightly angular due to the demarcation line between the differently enameled regions, and shows a lateral deflection near the crown-root junction; corresponding to this deflection, the distal side of the crown presents a basally situated bulge in its labial half. The lingual side of the crown is more acute, edgelike. The root is circular in cross section. Just as in the case of the I2 from site PB4, the morphology of the I3 is rather generalized, reminiscent of the in situ I3s found in *Barbatodon transylvanicus* (Smith and Codrea, 2015) and *Litovoi* (Csiki-

Sava et al., 2018; figs. 6D, 11L). Thus, its precise taxonomic identity remains unclear, although it seems to differ in morphology from the less spatulate, peglike I3 of *Kogaionon ungureanui* (Rădulescu and Samson, 1996).

The most important multituberculate specimen from site Pu4 is the isolated left M1 LPB (FGUB) M.1671, of very small size (1.82 × 1.42 mm; fig. 14G). The specimen preserves only the crown, without any signs of the roots; the cusps show rather pronounced wear surfaces and are locally damaged, but otherwise the state of preservation of this specimen is good. It shows the typical kogaionid morphology of short and wide crown with a small number of cusps in each of the three cusp rows (Csiki-Sava et al., 2018); its cusp formula is most probably 3:4:3 (but see below). The contour of the crown in occlusal view resembles a mesiolingually incomplete rectangle, with a shorter and straight mesial edge and a longer, largely rounded distal edge; the labial edge is straight, but with minute undulations marking the positions of the three labial cusps, whereas the lingual margin is made up of two kinked segments, one somewhat longer, parasagittal, and slightly convex segment distally, joined by a shorter, labiomesially slanting straight segment mesially.

The four cusps of the median row are the most robust ones; they are large and pyramidal, with the exception of the distalmost cusp, which is labiolingually elongated and connected by low ridges to the distalmost labial and lingual cusps along the distal margin of the crown. The mesialmost cusp of the median row also seems to have been connected to the mesial cusp of the labial row by a crest, although extensive wear in this area makes this difficult to ascertain. Abrasion due to wear, possibly augmented by postmortem damage as the tips of the cusps are barely affected, is so heavy in the median part of the crown that the enamel cover is almost completely removed from the median cusps, which curently consist mainly of dentine. The heavy wear and removal of the enamel obviously also enlarged the transverse valleys

separating the cusps, but it is nevertheless clear that these valleys were deep to begin with, especially those lying between median cusps two, three, and four.

The three cusps of the labial row are definitively smaller and less pyramidal than the median ones, and display an alternative placement with the latter, aligned with the transverse valleys separating the median cusps. Heavy wear, affecting mainly the lingual side of the labial cusps, reduced their height significantly, so that it is difficult to determine whether these projected as far apically as the median cusps. The degree of wear increases progressively from cusp to cusp backward, with the third, distal labial cups almost completely obliterated. The second labial cusp appears to be the smallest, whereas damage to the mesiolabial corner of the crown (due to wear and/or abrasion) makes it impossible to ascertain whether there was just one large mesial cusp or two closely twinned ones in this area. Due to the convex distal margin of the crown, the labial cusp row is somewhat shorter than the median cusp row.

The lingual cusp row, although incomplete, extends for about 80% of the crown length. Of the three lingual cusps, the second and third are subequal in size, somewhat smaller than the cusps of the median row, and of a labiolingually flattened pyramidal shape. The first, mesialmost cusp is significantly smaller, although not less elongated mesiodistally, and ridgelike, corresponding to the slanted mesial segment of the lingual margin; it extends mesially to the level of the transverse valley that separates median cusps 1 and 2, gradually merging with the base of the first median cusp. The lingual cusps have their labial sides flattened and their tips removed by wear that affects mainly the lingual valley separating the median and lingual cusp rows. Despite this wear, the transverse valleys dividing the cusps of the lingual cusp row are still deeply incised and clearly visible, which makes the identification of the presence of the third, mesialmost and ridgelike lingual cusp straightforward.

The cusp formula of LPB (FGGUB) M.1671 differentiates it from the M1s of *Barbatodon* and *Litovoi*, both of which have only two cusps in the lingual row (Codrea et al., 2014, 2017a; Smith and Codrea, 2015; Csiki-Sava et al., 2018), and in this respect it resembles the M1s of *Kogaionon ungureanui* (Rădulescu and Samson, 1996; figs. 5F, 7D, 9A) and *K. radulescui* (Smith et al., 2022), both of which have three cusps in their still incomplete, but relatively more elongated lingual rows. Although Smith et al. (2022) noted this uniquely shared similarity between the latter two taxa, they stopped short of identifying the presence of three lingual cusps on M1 as a synapomorphy of the genus *Kogaionon*. Instead, they surprisingly stated that *Kogaionon* can be differentially diagnosed relative to the genus *Hainina* in displaying a "shorter lingual row of M1 with only 2–3 cusps" (Smith et al., 2022: 4), despite the facts that no known specimen of *Kogaionon* has two lingual cusps on its M1 and that the presence of three lingual cusps had been recognized previously as a diagnostic feature of *Kogaionon* (e.g., Codrea et al., 2002). However, the M1 from site PB4 is markedly smaller, at less than half the size of the M1 of *K. ungureanui*, and is only about 72% of that of middle-sized *K. radulescui*. It further differs from *K. ungureanui* in presenting a crestlike, elongated mesialmost lingual cusp instead of a bulbous, short, and pyramidal one, as seen in the latter taxon (fig. 9A). Also, in the labial cusp row, the size of the cusps diminishes gradually backward in *K. ungureanui* (fig. 9A), unlike the alternating cusp size seen in the labial row of the Pui specimen. Meanwhile, the M1 of *K. radulescui* (Smith et al., 2022) also differs from LPB (FGGUB) M.1671 in several morphological details, such as the minute dimensions of the distal lingual cusp, significantly smaller than the preceding ones, and the subpyramidal, bulbous shape of the mesial lingual cusp instead of an elongated one as seen in the PB4 specimen. Finally, the Pui specimen also differs in its relatively longer and less wide contour (W/L ratio = 0.780) from the M1s of *K. ungureanui* (W/L = 0.821) and especially of *K. radulescui* (W/L ratio over 0.855). Based on its apomorphic cusp formula, with three lingual

cusps, and its small overall size, LPB (FGGUB) M.1671 appears to represent a new, diminutive species of *Kogaionon*, although we refrain here from formally erecting such a species, given the limited amount and relatively poor preservation state of the material available.

Remarkably, M.1671 is strikingly reminiscent in several of its morphological traits of the isolated kogaionid M1 from Toteşti-baraj (site RB1) figured by Codrea et al. (2002) and referred by them to a new, small species of *Kogaionon* (fig. 7B). The two specimens have roughly similar overall size and they share both the same general cusp formula and, perhaps most importantly, details of the cusp development, such as the small size of the second labial cusp wedged between two clearly larger ones, the elongation of the lingual row that approaches in development the total mesiodistal length of the crown, the triangular rather than pyramidal shape of the mesial lingual cusp, and the labiolingually elongated and mesiodistally flattened pyramidal shape of the distalmost median cusp; this last-mentioned feature also appears to be shared by *K. radulescui* (Smith et al., 2022: fig. 5b, e). The different preservation state of the two specimens (the Toteşti one being much better preserved) makes further comparisons, such as the precise shape of the first lingual and labial cusps, difficult. Nevertheless, it is worth noting that the Toteşti M1 specimen seems to be significantly more square shaped, wider and less elongated (W/L ratio 0.890) compared with that from site PB4, and also with those of the two nominal *Kogaionon* species.

Overall, despite this important shape difference it appears clear that, when compared with all other previously described kogaionid M1s from Transylvania, LPB (FGGUB) M.1671 from site PB4 shares the closest morphological and dimensional similarities with the isolated M1 from Toteşti-baraj (site RB1), perhaps suggesting possible close taxonomic affinities between the two. But, regardless of the possible relationships, if any, between the Toteşti (site RB1) and Pui (site PB4) M1s, it is also worth remarking that

both of these specimens, which suggest the presence of a small *Kogaionon*-like taxon, occur in the uppermost part of their local fossiliferous sections. Nevertheless, based on the current assessment of their relative stratigraphic positions/ages (see fig. 3), the M1 specimen from site PB4 appears to be somewhat older (early to mid late Maastrichtian, belonging to Tier 3 of Csiki-Sava et al., 2016) compared with the Toteşti-baraj specimen (later late Maastrichtian, Tier 4 of Csiki-Sava et al., 2016).

The importance of site PB4, despite yielding a very small multituberculate sample, lies in the fact that it represents the youngest (highest-lying) multituberculate occurrence known at Pui, and it documents the presence of a small multituberculate taxon (possibly a species of *Kogaionon*) high in the local succession, whereas all other known occurrences from the upper half of the same section represent medium-to-large-sized taxa (Smith and Codrea, 2015; Solomon et al., 2016; Csiki-Sava et al., 2018; see below). This small taxon is associated within the same stratigraphic level with a second, medium-to-large kogaionid, just as was noted in the case of the *Barbatodon* type locality (site PB1) positioned much lower in the local section, and at Toteşti-baraj (site RB1; Codrea et al., 2002). Finally, the presence of the more diagnostic M1 at site PB4 shows that a third kogaionid taxon different from both *Barbatodon* and *Litovoi* in size and M1 morphology and possibly related to *Kogaionon* based on its cusp formula is also represented at Pui.

Site PB5
Pui-UBB Locality

Location, age: According to Smith and Codrea (2015: fig. S1), this locality was discovered on the left bank of the Bărbat River, close to the uppermost outcropping part of the local section. It lies a few meters downstream (about 1.5 m lower in stratigraphic section) from site PB4 and about 30 m upstream from the *Litovoi* type locality (site PB6). Located significantly higher in the section than site PB2, which was palynologi-

cally placed around the early/late Maastrichtian boundary (Van Itterbeeck et al., 2005), it is probably late Maastrichtian in age.

LITHOLOGY, PALEOENVIRONMENT: The fossil-bearing unit is reported to be a relatively thick red siltstone, covered by a several decimeter-thick bed of greenish channel sandstones with a mildly erosional base. According to the sedimentological interpretation of the local Maastrichtian succession (Van Itterbeeck et al., 2004; Bojar et al., 2005; Therrien, 2005), this unit represents a well-drained floodplain deposit; the absence of well-marked calcrete horizons suggests that pedogenetic processes might not have been advanced at this site.

FOSSIL CONTENT: The presence of only multi-tuberculate remains has been reported until now from the fossiliferous bed at site PB5. These remains belong to at least three different individuals, based on associated cranial and dental remains: individual UBB P-Mt1, represented by a rostrum with anterior zygomatic arches and complete in situ cheektooth row, left premaxillary with I2–I3, left squamosal, both petrosals, and both associated dentaries with in situ p4–m2 (Smith and Codrea, 2015); individual UBB P-Mt2, including a left dentary with i1–m2, a right dentary with i1 (broken)–m1, a left I2, the left and right P2, and the left P4–M2 row; and individual UBB P-Mt3, with a left dentary preserving i1 (broken)–m2, the left P1–P2, P4, and M2, as well as the right M1 (Solomon et al., 2016; fig. 7E, O). Further isolated multituberculate incisors (UBB P-Mt 4-1, an I2; UBB P-Mt 4-2, an I3; and UBB P-Mt 4-3, an i1), reported by Smith and Codrea (2015), may possibly originate from the same bed as the other, associated specimens, but their exact locality data were not published.

HISTORY OF RESEARCH: The fragmentary but associated skulls of the three individuals from site PB5 were reported to have been discovered while surveying the fossil-yielding bed during different fieldwork campaigns, between 2001 and 2010. From these, the best-preserved and most complete UBB P-Mt1 specimen was described briefly and figured by Smith and Codrea (2015;

fig. 5D), whereas specimens UBB P-Mt2 and P-Mt3 were described and discussed by Solomon et al. (2016); all these indiviuals were referred to *Barbatodon transylvanicus*. Teeth of individual UBB P-Mt1, together with the isolated incisors registered as UBB P-Mt 4 specimens, were used to document for the first time the occurrence of red iron pigments in the dentition of a Mesozoic mammal (Smith and Codrea, 2012, 2015).

COMMENTS: The scientific significance of the UBB mammal lens and of the multituberculate fossils it yielded is severalfold. First, as already noted, Smith and Codrea (2012, 2015) reported the occurrence of reddish to deep red pigmentation in several of the tooth positions in these *Barbatodon transylvanicus* specimens, and further discoveries, primarily from Pui, do indeed support the presence of such pigmentation in other multituberculate individuals as well. These include the previously referred *Barbatodon transylvanicus* individual LPB (FGGUB) M.1635 from site PB3 and individual LPB (FGGUB) M.1700, the holotype of *Litovoi tholocephalos* (Csiki-Sava et al., 2018; fig. 7D, 11L) from site PB6, as well as other specimens yet to be described.

Second, by producing the first more or less complete kogaionid cranial specimens with both lower and upper dentition in association (especially in the case of specimen UBB P-Mt1), the discoveries from site PB5 allowed the first in-depth analysis of the phylogenetic position of the Kogaionidae (Smith and Codrea, 2015; fig. 4D), after several previous attempts which included kogaionids (*Kogaionon*, *Hainina*) that were coded only very incompletely due to the limited availability of relevant fossil material (e.g., Rougier et al., 1997; Kielan-Jaworowska and Hurum, 2001; Csiki and Grigorescu, 2006; fig. 4A). The analysis of Smith and Codrea (2015) grouped Kogaionidae with Taeniolabidoidea, a phylogenetic hypothesis further supported by the discovery and description of *Litovoi tholocephalos* (Csiki-Sava et al., 2018; see also Mao et al., 2016; fig. 4C), although this special relationship was not recovered in the most recent and comprehensive phylogenetic

analysis of the kogaionid clade (Smith et al., 2022; fig. 4B). And third, the large sample derived from the UBB locality allowed the identification of morphological and dimensional intraspecific variability in *Barbatodon transylvanicus*, together with a thorough documentation of the patterns of this variability (Codrea and Solomon, 2014; Solomon et al., 2016).

Site PB6
Multi-Bed Locality
(= *Litovoi* Type Locality)

Location, age: The Multi-Bed locality is located on the right bank of the Bărbat River, within the upper third of the outcropping section (fig. 8F). It lies about 80 m upstream of the 2002 *Barbatodon* locality (site PB3; some 24 m higher in stratigraphic section), and somewhat below the uppermost multituberculate localities, sites PB4 and PB5 (about 5–8 m lower in stratigraphic section). Like these localities, site PB6 also lies significantly higher than the palynologically dated site PB2 (Pui Islaz) and is thus younger than PB2, that is, its age should be regarded as (early?) late Maastrichtian.

Lithology, paleoenvironment: The fossiliferous deposit at site PB6 is represented by a 0.5 m thick red, sparsely calcrete-bearing mudstone, a common lithotype in the Bărbat River section (e.g., Therrien, 2005; figs. 8F, 15A); a detailed petrological study of the fossiliferous bed identified the local lithology as a pebble-bearing sandy mudstone. This multituberculate-bearing red mudstone paleosol level corresponds to bed no. 25 in the local stratigraphic succession as recorded by one of us (M.V.). Based on the general sedimentological interpretation of the Bărbat River succession, the Multi-Bed can be identified as a multistoried, well-drained floodplain deposit that underwent incipient pedogenesis.

Fossil content: The Multi-Bed has yielded—from slightly superimposed levels—several multituberculate specimens ranging from isolated teeth (e.g., LPB [FGGUB] M.1703) to associated teeth and tooth-bearing jaw fragments (LPB

[FGGUB] M.1701, M.1702), and finally to associated partial skeletons with both cranial and postcranial remains preserved (e.g., LPB [FGGUB] M.1698) and the holotype of the newly erected kogaionid *Litovoi tholocephalos* (LPB [FGGUB] M.1700, Csiki-Sava et al., 2018; fig. 6). Besides the multituberculates, this bed has also yielded several other macro- and microvertebrate remains (see Csiki-Sava et al., 2018: SI Appendix) that represent different dinosaurs (such as isolated teeth and caudal vertebrae of the rhabdodontid ornithopod *Zalmoxes*; isolated teeth and a partial dentary of a hadrosauroid ornithopod, possibly *Telmatosaurus*; one isolated shed tooth of the incertae sedis coelurosaurian theropod *Richardoestesia*), crocodyliforms (isolated teeth of the basal eusuchian *Allodaposuchus*), and turtles. Some of the skeletal remains discovered at site PB6 show traces of bioerosion. Based on its currently known fossil content, this accumulation can be characterized as a relatively specimen-poor mixed macrovertebrate-microvertebrate bonebed.

History of research: The fossiliferous nature of the Multi-Bed locality was initially recognized in June 2012 (fig. 15A), when the first multituberculate remains were discovered and excavated here during a joint Romanian-American field trip. Since then, this bed had been surveyed and surface collected regularly; sediment samples had been screenwashed occasionally on a small scale and, in 2014, a limited excavation of the bed was also conducted. As yet, the only remains described in any detail from this assemblage are represented by the associated partial skeleton of the holotype of the kogaionid *Litovoi tholocephalos* (Csiki-Sava et al., 2018; Vremir et al., 2018; figs. 6, 15B, C), that is, individual LPB (FGGUB) M.1700.

Comments: The description of *Litovoi* (Csiki-Sava et al., 2018) represented a major addition to our knowledge concerning the latest Cretaceous Transylvanian kogaionids, as the first new genus identified after more than 20 years in this multituberculate clade. Its presence shows that taxonomic variability is higher within the
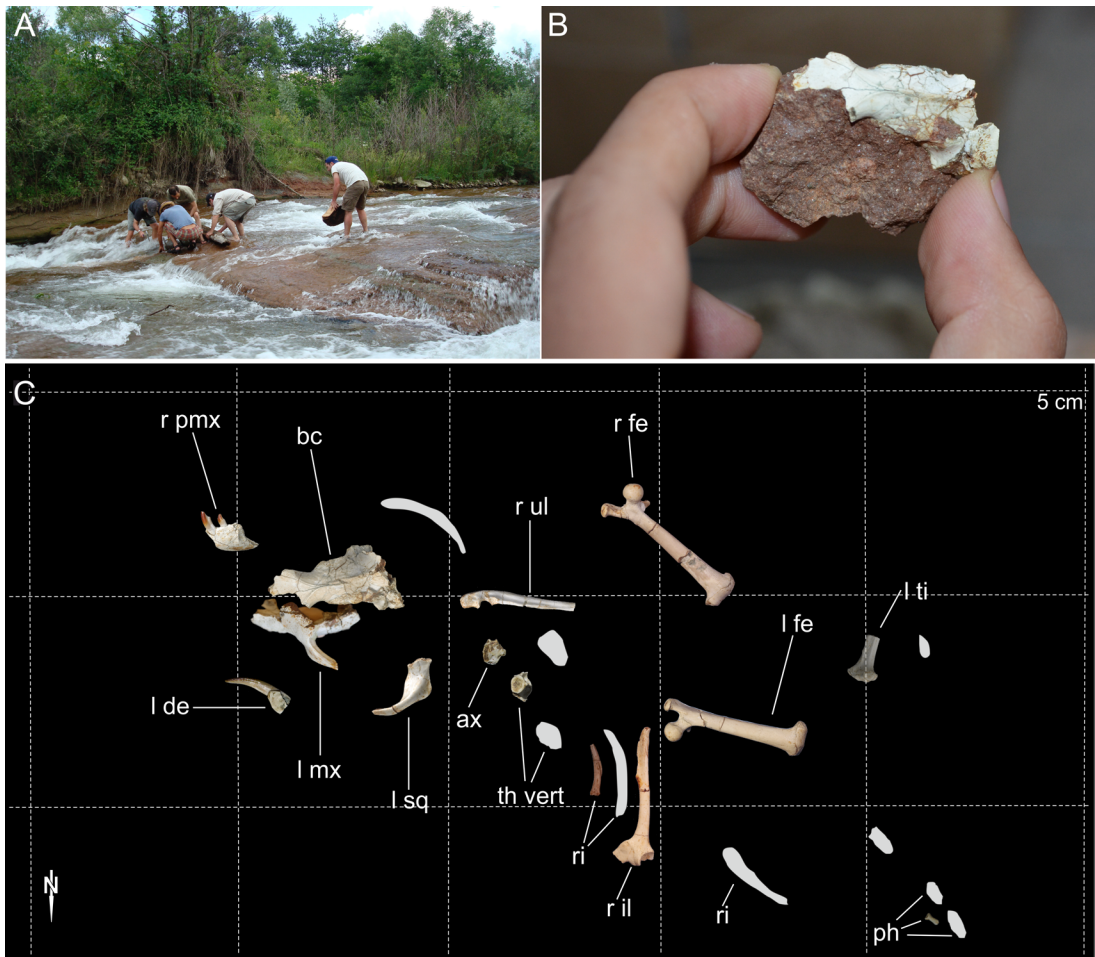
FIGURE 15. Discovery and taphonomy of the holotype of *Litovoi tholocephalos*, specimen LPB (FGGUB) M.1700, Pui Beds, site PB6. **A.** Excavation conditions at site PB6 (Multi-Bed locality), in the upper part of the Bărbat River succession of the Pui Beds; members of the Romanian-American-UK team building an improvized dam to protect newly exposed tiny fossils (June 2012). **B.** The braincase of *Litovoi tholocephalos* (see also fig. 6A–C) shortly after it was salvaged from under flowing water. **C.** Reconstructed partial quarry map of site PB6 documenting the associated nature of the cranial, dental, and postcranial remains belonging to the holotype individual (see also Csiki-Sava et al., 2018: Supplementary Appendix). The quarry map is a redrawn version of an ad hoc sketch made in June 2014 by one of us (M.V.) during the salvage excavation of the holotype specimen in underwater conditions, with the already prepared individual elements subsequently overlaid.

Pui multituberculate sample than previously suggested, with a minimum of three taxa (*Barbatodon transylvanicus*, *Litovoi tholocephalos*, and at least one small taxon represented by the isolated m2 specimen from site PB1 and/or the isolated M1 from site PB4) present here. The occurrence of a fourth, small taxon (formerly mentioned as *Kogaionon* sp. from site PB2) is a distinct possibility, but this cannot be definitively verified until the detailed description of the PB2 material becomes available.

The identification of *Litovoi* also represented an important advance in that its holotype preserves, for the first time in the case of a kogaio-

nid, significant amounts of cranial, dental, and postcranial material in association (fig. 15C), including the first reasonably complete braincase of a kogaionid (figs. 6A–C, 15B). As such, the cranial and postcranial anatomy of *Litovoi* could be reconstructed in unprecedented details for a kogaionid (fig. 6). This detailed reconstruction also allowed recognition of what were interpreted as island habitat-related neurological changes (reduction of relative brain mass, correlated with relative increase in the size of the olfactory bulbs and paraflocculi) that occured in this taxon. The case of *Litovoi* represents the first such instance reported in a multituberculate, and one of the very few pre-Cenozoic examples of habitat-driven anatomical and physiological modifications reported in insular mammals (see also Krause et al., 2014, 2020; Hoffmann et al., 2014), whereas such changes are more commonly identified in Cenozoic insular eutherians (e.g., Köhler and Moyà-Solà, 2004; Weston and Lister, 2009; Van der Geer et al., 2010).

Furthermore, the multituberculate material collected from site PB6, most of which is not yet studied or described in detail, suggests the presence of at least one other small taxon at Pui, taxon that can be differentiated from either *Kogaionon*, *Barbatodon*, or *Litovoi* by its size and P1 morphology (for details, see Csiki-Sava et al., 2018: SI Appendix). It is to be expected that once this material is published, it will contibute to a more complete understanding of the Transylvanian multituberculate diversity.

SITE PB7
PUI SWAMP LOCALITY

LOCATION, AGE: The Pui Swamp locality (see Csiki-Sava et al., 2016) is located in the left bank of the Bărbat River, about 130 m upstream from the Pui road bridge, near a small metallic bridge and a hydrometric station, and just downstream from the main building of a sawmill. As the locality is placed in the local stratigraphic section well below the Pui Islaz locality (site PB2) that was dated palynostratigraphically to around the

early/late Maastrichtian boundary, its age is most probably early Maastrichtian (thus belonging to chronofaunal Tier 2 as defined by Csiki-Sava et al., 2016).

LITHOLOGY, PALEOENVIRONMENT: The lithology at PB7 is represented by dark gray to blackish, mica-rich silts with pyrite concretions and coalified wood remains (Codrea and Solomon, 2012; Vasile and Panaitescu, 2012; Vasile et al., 2019), unlike the common Pui lithology of reddish to dark red, calcrete-bearing sandy siltstones and silty mudstones. This bed (together with a few others with similar lithofacies from the Pui succession) was interpreted as being deposited in standing, poorly oxygenated waters within spatially restricted, waterlogged areas (ponds or oxbow lakes) developed within an otherwise well-drained floodplain (Codrea and Solomon, 2012; Vasile and Panaitescu, 2012; Vasile et al., 2019).

FOSSIL CONTENT: The Pui Swamp locality yielded one of the richest and most diverse vertebrate accumulations reported to date from the Bărbat River outcrops. Although Codrea and Solomon (2012) mentioned only indeterminate sauropod remains associated with plant fragments from this bed, a significantly more diverse microvertebrate assemblage has been described by Vasile and Panaitescu (2012; see also Csiki-Sava et al., 2016), including frogs (*Paralatonia transylvanica*), albanerpetontids (?*Albanerpeton*), lizards, turtles (*Kallokibotion*), various crocodyliforms (*Acynodon*, *Theriosuchus*, *Doratodon*, *Allodaposuchus*), as well as theropod (*Richardoestesia*) and ornithopod (*Zalmoxes*) dinosaurs, associated with eggshells, indeterminate gastropod shell fragments, and charred fructifications. The most recently reported additions to the local vertebrate assemblage (Voicu et al., 2018; Vasile et al., 2019) are the presence of at least three morphotypes of eggshells (including *Pseudogeckoolithus*) at the site, as well as that of the first multituberculate fossil, represented by an isolated, unworn I2 (LPB [FGGUB] M.1705) that documents the presence of this group at Pui Swamp.

HISTORY OF RESEARCH: The Pui Swamp locality (site PB7) was discovered in 2011, during an

important drop in water level after several years of heavy erosion by the swift-flowing Bărbat River that exposed the lowest part of the local outcropping succession, from downstream to slightly upstream of the main road bridge in Pui. Once uncovered through erosion, it was preliminarily prospected by teams from the Babeș-Bolyai University, Cluj-Napoca (Codrea and Solomon, 2012), and screenwashed by teams from the University of Bucharest (Vasile and Panaitescu, 2012). The screenwashing activities of material from this locality by the University of Bucharest teams continued up to 2017 when the bed was covered by large concrete blocks dumped in the riverbed, practically prohibiting access to the fossiliferous layer.

COMMENTS: The multituberculate evidence at site PB7 is til now very scarce and rather nondiagnostic. The overall morphology of the unworn, bicuspid right I2—with a large and mesially positioned, slightly curved main cusp paired at its base with a small accessory cusp (Vasile et al., 2019)—is reminiscent of in situ upper incisors known in *Barbatodon* (Smith and Codrea, 2015) or in *Litovoi* (Csiki-Sava et al., 2018; figs. 6D, 11L), as well as of the isolated I2s from Pui (site PB4, fig. 14A–C) and from Tuștea (Csiki and Grigorescu, 2000), and only suggests the presence of an indeterminate kogaionid at the site. However, its main importance lies in its stratigraphic position, very close to the outcropping base of the local succession (see Csiki-Sava et al., 2016; fig. 3), making this specimen the oldest known occurrence of kogaionids in the Pui Beds.

Site PB8
MJ18 Locality

LOCATION, AGE: The MJ18 locality, the most recently identified multituberculate occurrence in the Pui succession, is located on the left bank of the Bărbat River, downstream from the richly fossiliferous Multi-Bed locality (site PB6) and upstream of the 2002 *Barbatodon* locality (site PB3), at about middistance (and stratigraphically lying) between these two (fig. 3). Due to its posi-

tion well above site PB2, which was dated palynologically close to the early/late Maastrichtian boundary (Van Itterbeeck et al., 2005), its age is most probably (early?) late Maastrichtian.

LITHOLOGY, PALEOENVIRONMENT: The lithology at site PB8 is represented by brownish red, micaceous sandy-silty mudstones, with locally developed diffuse calcrete nodules. The multituberculate remains are also surrounded by weakly developed concretionary nodules. According to the sedimentological interpretation of the Pui succession (Van Itterbeeck et al., 2004; Bojar et al., 2005; Therrien, 2005) the fossiliferous layer was formed in a well-drained floodplain environment, and most probably represents either sediments laid down during the waning stages of a flood, or those of a distal sheet crevasse splay which underwent very early stages of pedogenesis under a semiarid, seasonally variable climate.

FOSSIL CONTENT: Other than the multituberculate remains representing one single individual (based on their commensurate size and field association), only a few isolated crocodyliform teeth (not yet studied in detail), alongside small indeterminate bone fragments, represent the vertebrates recovered from site PB8. These are associated, however, with a large number of thin eggshell fragments (including some of the *Pseudogeckoolithus* type) and with a similarly abundant assemblage of gastropods, dominated by cyclophorid operculae. In this respect, the MJ18 site is reminiscent of several other Pui occurrences preserved in the dominant fine-grained red-colored lithofacies types of the local succession in that it is relatively specimen and species poor as far as vertebrates are concerned, with a large number of small indeterminate bone chips that are associated with abundant and diverse eggshell fragments as well as with (mainly terrestrial) gastropods (e.g., Grigorescu et al., 1999; Garcia et al., 2002; Pană et al., 2002; Vasile and Csiki, 2010; Choi et al., 2020a, b).

HISTORY OF RESEARCH: The MJ18 locality (site PB8) was discovered in June 2018, during field prospection at the Pui locality by a joint Romanian-American team. The multituberculate

specimen was spotted when partly under water and was excavated rapidly from the water-soaked and partly submerged bed together with a small amount of surrounding sedimentary matrix. Immediate survey of the fossiliferous bed near the specimen failed to reveal any other fossils visible macroscopically, whereas several fossils (although no further multituberculate remains) were recovered subsequently by screenwashing the matrix collected from around the specimen. To our knowledge, this is the first report of a fossil occurrence at this site.

COMMENTS: The specimens recovered from site PB8, consisting of dissociated skull remains that preserve in situ dentition, are currently under preparation and study, and thus no further comments will be made here. For now, the importance of the locality, apart from the already impressive multituberculate fossil record registered from the Pui Beds, is that it fills the stratigraphic gap between the 2002 *Barbatodon* locality (site PB3) and the Multi-Bed locality (site PB6; see fig. 3), thus complementing the local kogaionid fossil record.

DENSUŞ-CIULA FORMATION

The Densuş-Ciula Formation (Grigorescu, 1992) groups uppermost Cretaceous continental deposits cropping out along the northwestern and northern borders of the Haţeg Basin, extending from Densuş and Ciula Mica in the west, to Crăguiş in the east (fig. 2: DC). Their most outstanding characteristic is the important contribution of the volcanic and volcanoclastic material to the composition of the mainly siliciclastic deposits (Grigorescu, 1992; Csiki-Sava et al., 2016), although the volcanogenic component varies quantitatively from locality to locality. Based on the nature and proportional contribution of this volcanoclastic material, three different subunits (members) were separated historically within the formation, which are considered to be arranged from older (Lower Member, richest in volcanoclastic material, with even volcanic material represented) in the west to pro-

gressively somewhat younger (vertebrate-bearing Middle Member, with local minor participation of reworked volcanoclastics), and then to youngest (Upper Member, purportedly lacking volcanoclastics, and devoid of vertebrate remains) toward the east, with the possibility that the uppermost deposits of the unit may even extend into the Paleogene (e.g., Weishampel et al., 1991; Grigorescu, 1992). New discoveries show, however, that the proposed lithological distinctions between the middle and upper subunits might have been overestimated and that both of these contain latest Cretaceous vertebrate remains as well as beds with reworked volcanoclasts (Vasile et al., 2011a, 2011b).

The Densuş-Ciula Formation is considered to be roughly time-correlative with the Sînpetru Formation deposits and other uppermost Cretaceous occurrences (Râul Mare Beds, Pui Beds) in the central-eastern parts of the Haţeg Basin. However, it should be noted that precise and direct correlation between the Densuş-Ciula Formation deposits and those from the central-eastern areas of the basin is practically impossible due to their patchy and discontinuous outcropping conditions (with large areas that present a Quaternary sedimentary cover separating the northwestern and central outcropping areas of the continental uppermost Cretaceous), the absence of regionally traceable marker beds, and the presence of often substantial lithological differences between the deposits from these different areas (Csiki-Sava et al., 2016).

Occurrence of uppermost Cretaceous fossiliferous continental deposits in the northwestern marginal areas of the Haţeg Basin was noted as early as the first quarter of the 20th century (Nopcsa, 1905, 1915; Kadić, 1916; Laufer, 1925), but multituberculate mammalian remains were discovered and reported from these only much later (Grigorescu et al., 1999; Csiki and Grigorescu, 2000). Such multituberculate fossils usually occur in microvertebrate accumulations, within which they are geographically widespread although not particularly abundant (e.g., Vasile and Csiki, 2010; Csiki-Sava et al., 2016; fig. 2);

occasionally they also show up in the micro-vertebrate component of multitaxic bonebeds (e.g., Csiki and Grigorescu, 2000; Botfalvai et al., 2017, 2021). Regardless of their origin, the multituberculate remains currently known in the Densuş-Ciula Formation are represented almost exclusively by isolated teeth. The kogaionid-bearing vertebrate occurrences from this unit will be listed and identified in the following as DC sites.

Site DC1
Tuştea Nesting Locality
(= Oltoane Hill Locality)

Location, age: The Tuştea nesting locality is located in the topmost part of the eastern slope of Oltoane Hill, north of Tuştea village. It is represented by an isolated outcrop first opened up in 1988 by an accidental landslide, and subsequently quarried systematically (in part with heavy machinery, to remove the overburden) until the early 2010s (Grigorescu et al., 1990; Botfalvai et al., 2017). It was first considered to lie within the uppermost part of the Middle Member of the Densuş-Ciula Formation (e.g., Weishampel et al., 1991; Grigorescu et al., 1994), but subsequently its position was reconsidered to be within the middle-to-upper part of the same subunit (Grigorescu and Csiki, 2008; Csiki-Sava et al., 2016), and is thus probably early to mid late Maastrichtian in age, belonging to the Tier 3 faunal complex defined by Csiki-Sava et al. (2016).

Lithology, paleoenvironment: The local succession at site DC1 is dominated by red, calcrete-bearing silty and sandy mudstones, with locally developed minor grayish-green sandy intercalations or greenish mudstones. In the upper part of the succession, a thick multistorey, gray-greenish sandy-conglomeratic bed (made up of several fining-upward sequences showing oblique and through cross-lamination, with common red mudstone rip-up clasts and altered andesitic pebbles) covers the main fossil-bearing unit, a thick red mudstone with several calcrete levels (Grigorescu et al., 1994; Botfalvai et al., 2017; fig. 16A). The local succession is inter-preted to have been deposited in distal, well-drained floodplain reaches of an alluvial fan fluvial environment draining the highlands lying toward the north (e.g., Therrien, 2005; Botfalvai et al., 2017), with the red silty mudstones representing alternating floodsheet mud and paleosol deposits, interspersed with crevasse splay (greenish sandstone sheets) and major channel deposits (coarse, cross-bedded sandy conglomerates and sandstones) formed during river avulsion.

Fossil content: The Tuştea nesting site is one of the major fossiliferous localities in the Transylvanian uppermost Cretaceous, represented by a multilevel accumulation of multitaxic bonebeds formed in a well-drained floodplain environment. The locality was initially reported as a nesting horizon with megaloolithid eggs, referred to as *Megaloolithus* cf. *siruguei* (Grigorescu, 2010, 2017; Grigorescu et al., 2010). These eggs were ascribed first to titanosaur sauropods (Grigorescu et al., 1990) but were subsequently considered to belong instead to hadrosauroids, based on their cooccurrence with diagnostic hatchling skeletal remains (Grigorescu et al., 1994; Grigorescu, 2017). Continuing excavations at the locality have revealed that the dinosaur nests (found in two superposed levels, according to Botfalvai et al., 2017) are associated with a large number of vertebrate skeletal remains dispersed throughout the two nesting horizons, but also at other levels of the fossiliferous, calcrete-bearing red mudstone body (e.g., Vasile and Csiki, 2010). The fossil content of the locality was most recently summarized by Botfalvai et al. (2017), and it includes indeterminate anurans, albanerpetontids, and lizards, madtsoiid snakes (*Nidophis*), abundant turtles (*Kallokibotion*, dortokids), various crcodyliforms (*Sabresuchus* = "*Theriosuchus,*" *Allodaposuchus*), pterosaurs (cf. *Hatzegopteryx*), ornithopods (*Zalmoxes*, *Telmatosaurus*), theropods (*Richardoestesia*, velociraptorines), and as yet indeterminate titanosaurs. The locality is particularly noteworthy due to the cooccurrence of megaloolithid eggs and hadrosauroid (?*Telmatosaurus*) hatchling remains; it is also the type locality of the madtsoiid snake

FIGURE 16. Kogaionid-bearing fossiliferous localities from the Densuş-Ciula Formation, Haţeg Basin. **A.** The Tuştea-Oltoane nesting locality, corresponding to site DC1; large-scale excavation on the newly created platform, August 1998. **B.** Close-up of the fossiliferous bed at Vălioara-Fântânele, hosting site DC2; **C.** Close-up of the fossiliferous bed at Vălioara-Fântânele 2, location of site DC3. **D.** Ravines north of Livezi with outcrops of uppermost Cretaceous continental beds; in the middle foreground, below the grass cover, is site DC4; **E.** Limited exposures of the uppermost Cretaceous continental beds north of General Berthelot, locality GB1, with the lower red silty mudstones hosting site DC5.

Nidophis insularis (Vasile et al., 2013) and of the neosuchian crocodyliform *Sabresuchus* ("*Theriosuchus*") *sympiestodon* (Martin et al., 2010). Multituberculate remains are rather rare elements within the microvertebrate component of the local assemblage (e.g., Csiki and Grigorescu, 2000; Vasile and Csiki, 2010) and are represented both by isolated teeth and by small tooth-bearing jaw fragments.

HISTORY OF RESEARCH: The Tuştea locality was discovered in 1988 due to a fortuitous landslide that opened up access to uppermost Cretaceous deposits in the Oltoane Hill, within an area covered normally by grasslands or even heavier vegetation. After a few years of small-scale exploratory excavations at the locality, the overburden was removed using heavy machinery; the large-scale quarrying excavation that started in the almost

horizontal platform created lasted between 1997 and 2011, yielding a large number of dinosaur egg nests and of vertebrate skeletal remains (see review in Botfalvai et al., 2017). Small-scale screenwashing activity, usually focusing on the surroundings of the larger dinosaur egg nests, also revealed the sparse presence of microvertebrate remains at the locality, including of multituberculate fossils. Only one of these multituberculate remains, an isolated I2, has been described briefly by Csiki and Grigorescu (2000).

COMMENTS: The Tuştea locality was the first to yield multituberculate remains in the Densuş-Ciula Formation, represented by specimen LPB (FGGUB) M.1609, a right I2 referred to an indeterminate kogaionid (Csiki and Grigorescu, 2000). Subsequently, several other multituberculate specimens have been recovered from this locality through screenwashing, including LPB (FGGUB) M.1658, a left i1, LPB (FGGUB) M.1657, a tricuspid left P1, and LPB (FGGUB) M.1709, a right p4, as well as a very fragmentary specimen (LPB [FGGUB] M.1659, possibly a P4?). All these specimens show features that are consistent with their kogaionid identity. The gracile i1 presents the partly reduced enamel cover seen in more complete in situ specimens such as LPB (FGGUB) M.1635 referred to *Barbatodon transylvanicus* and LPB (FGGUB) M.1700, the holotype of *Litovoi tholocephalos* (figs. 6E, 11K), a morphology that was identified here as the kogaionid pattern. Similarly, the cusp pattern of the P1 is similar to that reported in *Barbatodon transylvanicus* (Smith and Codrea, 2015) and *Litovoi* (Csiki-Sava et al., 2018; fig. 5C). Nevertheless, their morphology and characteristics are not diagnostic enough to identify them beyond Kogaionidae indet.

The most significant multituberculate specimens from site DC1 are represented by a left p4–left m1 pair, registered as LPB (FGGUB) M.1655 and M.1656, respectively. These specimens were discovered while screenwashing a relatively small sample of matrix that resulted from the preparation of one of the megaloolithid nests. Both of these teeth are still implanted into small fragments of the dentary; they show comparable preservation style, and are commensurate in size. Moreover, the two fragments match rather well, although obviously the fragmentary nature of the specimens and the damage inflicted during the screenwashing process makes their perfect retrofitting impossible. Based on these observations, it appears highly probable that the two specimens belong to the same individual; these specimens are currently under study. The small DC1 kogaionid faunule, including this more diagnostic associated material, will be described later, once the ongoing efforts to review and study the Densuş-Ciula Formation kogaionids is completed.

SITE DC2
Fântânele Locality
(Fântânele-Vălioara, Fântânele 1)

LOCATION, AGE: The Fântânele locality is located on the left bank of the Fântânele creek, upstream of the uphill exit from Vălioara village (fig. 2), at the confluence of this temporarily active small creek with a minor left-side gulch. Based on its position, it is situated in the lower part of the middle subunit of the Densuş-Ciula Formation (fig. 3). The age of this subunit around Vălioara was first proposed to be late Maastrichtian based on palynostratigraphy (Antonescu et al., 1983), but was later reconsidered as Maastrichtian (e.g., López-Martínez et al., 2001; Csiki et al., 2008). Radiometric ages reported from the basal part of the middle subunit (Bojar et al., 2011) suggest that its deposition started during the early-mid part of the early Maastrichtian, and thus the age of the Fântânele locality can be most probably constrained to the later part of the early Maastrichtian, which makes it a Tier 2 fossil locality (Csiki-Sava et al., 2016).

LITHOLOGY, PALEOENVIRONMENT: The local lithology at the Fântânele site is represented by a gray-greenish, locally slightly variegated silty mudstone (Grigorescu et al., 1999; Vasile and Csiki, 2010), with dispersed pebbles up to 1 cm in size; white, globular calcrete concretions are

locally present. The fossiliferous bed covers a red silty mudstone bed with a diffuse and thin calcrete layer toward its top, and grades upward into a variegated, reddish-greenish silty mudstone (fig. 16B). The bed is interpreted to have been formed within a poorly drained, spatially restricted ponding floodplain environment (Vasile and Csiki, 2010).

Fossil content: The site DC2 is a typical microvertebrate bonebed (MvBB; see Eberth et al., 2007, for a definition), where most of the fossil remains are small (<5 cm in maximum dimension, recovered through screenwashing), representing mainly small (<5 kg body size) vertebrate taxa both in sheer number, in abundance, and in diversity. The Fântânele MvBB has yielded one of the most diverse (micro)vertebrate assemblages recorded in the Transylvanian uppermost Cretaceous, with remains of fish (the gar cf. *Atractosteus*); anurans (the alytid *Paralatonia transylvanica*, the bombinatorid *Hatzegobatrachus grigorescui*, and an indeterminate pelobatid); albanerpetontids (*Albanerpeton* sp.); lizards (mostly indeterminate scincomorphs); snakes (*Nidophis insularis*); turtles (*Kallokibotion*); various crocodyliforms (*Allodaposuchus* sp., *Sabresuchus* (= "*Theriosuchus*") *sympiestodon*, *Doratodon* sp., *Acynodon* sp.); ornithopod (*Zalmoxes* sp., hadrosauroid), titanosaur, and nonavian theropod (*Richardoestesia*, *Euronychodon*, velociraptorines) dinosaurs; ornithurine birds; and multituberculates (e.g., Grigorescu et al., 1999; Csiki and Grigorescu, 2000, 2002; Vasile and Csiki, 2010; Wang et al., 2011b; Vasile et al., 2013; Martin et al., 2014; Venczel et al., 2016). Based on its fossil content, the Fântânele MvBB can be classified as a high-diversity multidominant multitaxic MvBB, the most commonly occurring type of MvBBs in the fossil record (Eberth et al., 2007). The vertebrate remains are associated within the site with gastropod shell fragments, rare ostracods, and insect eggs. In total, over 50 isolated multituberculate teeth were recovered from site DC2, the largest single sample known to date from the entire Densuș-Ciula Formation (table 3) and one of the most

specimen rich from the entire uppermost Cretaceous of Transylvania.

History of research: The Fântânele MvBB was identified in 1996 by one of us (Z.C.-S.) together with R. Limberea, former undergraduate geology student of the University of Bucharest (Grigorescu et al., 1999). Material collected from the locality has been screenwashed regularly since then, amounting to a total of several tons of fossiliferous matrix until 2013, after which the access to the fossiliferous bed became difficult; the locality is currently largely overgrown by vegetation. A thorough study of the locality, its taphonomy and fossil content is not available, although material discovered at Fântânele and belonging to different vertebrate taxa had been described and discussed in different publications (see above); a brief overview of the vertebrate assemblage, based on data available as of late 2009, was presented by Vasile and Csiki (2010). Some of the multituberculate specimens originating from site DC2 were preliminarily discussed by Csiki and Grigorescu (2000, 2002), Csiki (2005), and Vasile (2008a).

Comments: As noted above, site DC2 yielded the richest multituberculate sample currently available from the Densuș-Ciula Formation, as well as one of the largest known assemblages of isolated kogaionid teeth from the entire Transylvanian uppermost Cretaceous (table 3, fig. 7C, G, J). A total of 54 isolated and often fragmentary teeth are currently on record from this site in the collections of the University of Bucharest, representing most tooth positions except m2 and I3, in addition to several other nonregistered minute tooth fragments. Registered specimens include 10 i1s, 3 p4s, 7 m1s, 4 I2s, 4 P1s, 4 P2s, 6 P3s, 5 P4s, 5 M1s, and 4 M2s (see table 3), whereas two other specimens are too fragmentary for precise anatomical identification.

In a preliminary report of the first, newly discovered DC2 multituberculate remains, Csiki and Grigorescu (2000) noted the presence of specimens considered to be diagnostic and referable to the genus *Hainina*, a taxon previously known only from the Paleocene of West-

TABLE 3

List of Multituberculate Teeth from Site DC2 (Vălioara-Fântînele MvBB), Middle Subunit of the Densuş-Ciula Formation, Haţeg Basin

All specimen numbers in full share the prefix LPB (FGGUB); the side of the specimen (L, left, R, right) is provided in parentheses (if determined) or, if not known due to incompleteness/poor preservation, a ? indicates uncertainty; *N*, sample size.

Tooth position	*N*	Specimen numbers
i1	10	M.1612 (L), M.1616 (R), M.1627 (L), M.1664 (R), M.1665 (L), M.1674 (?), M.1682 (L), M.1683 (R), M.1686 (R), M.1687 (R)
p4	3	M.1622 (?), M.1678 (R), M.1688 (L)
m1	7	M.1613 (R), M.1618 (L), M.1619 (L), M.1625 (R), M.1666 (R), M.1696 (R), M.1695 (R)
I2	4	M.1621 (L), M.1669 (R), M.1684 (?), M.1685 (?)
P1	4	M.1610 (L), M.1611 (R), M.1620 (R), M.1667 (R)
P2	4	M.1617 (L), M.1676 (L), M.1679 (?), M.1680 (L)
P3	6	M.1614 (?), M.1626 (?), M.1633 (?), M.1660 (L), M.1677 (L), M.1691 (R)
P4	5	M.1615 (R), M.1661 (L), M.1662 (R), M.1690 (L), M.1697 (R)
M1	5	M.1624 (L), M.1663 (L). M.1689 (L), M.1692 (L), M.1693 (L)
M2	4	M.1623 (L), M.1675 (?),M.1676 (L), M.1694 (R)
Indet.	>2	M.1668 (?molar?), M.1681, other uncataloged fragments

ern Europe. Furthermore, given the marked size differences existing between the different specimens known at that moment, two indeterminate species of *Hainina* were tentatively identified at Fântânele: a small *Hainina* sp. A, based on two isolated P1s (LPB [FGGUB] M.1610, M.1611), and a medium-sized *Hainina* sp. B, based on an isolated m1 (LPB [FGGUB] M.1613; fig. 7G), whereas a few other specimens (i1, P3) were left as indeterminate cimolodontans.

The rather surprising recognition of the presence of the Paleocene *Hainina* in the uppermost Cretaceous of Transylvania relied on two distinctive features of the referred Fântânele specimens, features that—at the moment of their initial reporting—were recorded within Cimolodonta exclusively in this Western European Paleocene multituberculate. These features are represented by the very low cusp count on both the P1 (2 cusps, reported previously only in the Thanetian *Hainina vianeyae*—as *H. godfriauxi*—by Vianey-Liaud, 1986), and on the m1 (3:3, mentioned previously solely in the two Montian species of *Hainina*, *H. belgica* and *H. godfriauxi*; Vianey-

Liaud, 1979). Roughly in the same time period, the exact same characters were also reported to occur in the earliest Paleocene representative of the genus, *H. pyrenaica* from northern Spain (Peláez-Campomanes et al., 2000), further suggesting that the original taxonomic identification of the latest Cretaceous Fântânele specimens was correct.

It should be emphasized, nevertheless, that at the moment of these preliminary taxonomic identifications of specimens from site DC2, the only other multituberculate lower molar known from the Haţeg Basin (the holotype of *Barbatodon transylvanicus*; fig. 10A–C) was still considered to represent an M1 with a low cusp formula (e.g., Kielan-Jaworowska and Hurum, 2001; see table 1). However, with the reidentification of the *B. transylvanicus* holotype as an m1, with a low-count cusp formula comparable to that of LPB (FGGUB) M.1613 (Csiki et al., 2005), and with the discovery of isolated two-cusped P1s in other fossiliferous localities in the Transylvanian area (e.g., Codrea et al., 2012a; Vremir et al., 2015b; Csiki-Sava et al., 2018), the previ-

ously quoted support for the referral of these first reported Fântânele specimens to *Hainina* has been weakened, because their low cusp formulas were shown to not be autapomorphic for *Hainina*, but also occurring in several other latest Cretaceous kogaionids. Accordingly, the presence of the Paleocene genus *Hainina* in the uppermost Cretaceous of Transylvania should be regarded as doubtful (see also Codrea et al., 2017a, and below), until (and unless) it can be supported by more complete and diagnostic material (see also below).

The only other previously reported and tentatively identified Fântânele multituberculate specimen is represented by a medium-to-large M1 (LPB [FGGUB] M.1624; fig. 7C) described briefly by Csiki and Grigorescu (2002: fig. 1) and considered by these authors to represent a new species of *Kogaionon*. This identification was, again, influenced fundamentally by the comparison of the DC2 specimen with the only other correctly identified kogaionid M1 known at that moment in the uppermost Cretaceous of Transylvania, that of *Kogaionon ungureanui* (Rădulescu and Samson, 1996; figs. 7D, 9A), with which LPB (FGGUB) M.1624 shares an overall short and wide shape as well as a reduced cusp formula (with only four cusps in the middle row) coupled with a short, incomplete lingual cusp row. These features shared by the two latest Cretaceous Transylvanian M1 specimens were considered to differentiate them from the Paleocene M1s referred to *Hainina* (Vianey-Liaud, 1979, 1986; De Bast and Smith, 2017). For the sake of correctedness, it should also be noted that this DC2 specimen (fig. 7C) does not represent a right M1, as stated by Csiki and Grigorescu (2002), but is instead a left M1, in accordance with the details of the brief description of the specimen presented by these authors (see also Csiki, 2005).

Since the preliminary description of this isolated multituberculate M1 from site DC2, however, several other multituberculate M1s have been recovered from different Transylvanian localities (e.g., Codrea et al., 2002, 2014; Solo-

mon et al., 2016; fig. 7A, B, E), including some preserved in situ together with other elements of the upper dentition (Smith and Codrea, 2015; Csiki-Sava et al., 2018; figs. 6C, 14H). These subsequent discoveries revealed that the characters that were listed by Csiki and Grigorescu (2002) to unite LPB (FGGUB) M.1624 with *Kogaionon* are actually more widely distributed within the clade, and probably represent synapomorphies of a subgroup of latest Cretaceous kogaionids. Accordingly, LPB (FGGUB) M.1624 can no longer be referred to *Kogaionon* based on these previously noted similarities. Furthermore, the presence of three lingual cusps on M1 appear to characterize the genus *Kogaionon* (fig. 7D; Smith et al., 2022), possibly also including here the isolated M1s reported from site RB1 at Toteşti-baraj (Codrea et al., 2002: fig. 1h; fig. 7B) or from site PB4 at Pui (see above; fig. 14G), whereas the presence of only two lingual cusps—as seen in LPB (FGGUB) M.1624 (fig. 7C)—is known to occur both in *Barbatodon* (Codrea et al., 2014; Smith and Codrea, 2015; Solomon et al., 2016; fig. 7A, E) and in *Litovoi* (Csiki-Sava et al., 2018; fig. 14H). Unfortunately, the labial cusp row of the DC2 specimen is heavily worn and damaged, which makes a reliable cusp count difficult. It is thus unclear whether there were five labial cusps, as described by Csiki and Grigorescu (2002), or only four, similar to the condition reported in *Litovoi* (Csiki-Sava et al., 2018; fig. 14H) as well as in several referred specimens of *Barbatodon transylvanicus* (Solomon et al., 2016; fig. 7E), with the distalmost, oval wear depression seen in LPB (FGGUB) M.1624 representing only the imprint of a labio-distal crest uniting the distal cusps of the labial and median rows. Accordingly, the true taxonomic identity of this specimen remains difficult to ascertain for the moment, and might become clearer once the entire DC2 multituberculate sample has been studied.

In the most recent overview of the latest Cretaceous Transylvanian multituberculate record (Codrea et al., 2017a), some of the previously reported DC2 multituberculate specimens were

referred to *Barbatodon oardaensis*, a small kogaionid taxon first described from the early-late Maastrichtian aged locality of Oarda de Jos, in the Transylvanian Basin (Codrea et al., 2014; see below), and then also identified in the Negoiu-Fărcădeana 1 and 2 localities from the Rusca Montană Basin (Codrea et al., 2017a). This referral was based mainly on the overall similarities between the isolated bicuspid P1 (UBB Ng1-02) described by Codrea et al. (2017a; see also Codrea et al., 2012) from the Rusca Montană Basin and referred to *B. oardaensis*, and the minute bicuspid P1s from site DC2 referred to as *Hainina* sp. A by Csiki and Grigorescu (2000), as well as on the generally small size of the specimens. Nevertheless, it should be noted that there are minor dimensional and morphological differences between the Negoiu and the DC2 P1s, such as the relative development of the cusps (only shallowly separated by a cleft in UBB Ng1-02, but more deeply divided in LPB [FGGUB] M.1610 and M.1611), which call into question their taxonomic identity.

Most importantly, however, it must be emphasized that whereas Codrea et al. (2017a) suggested that, based on their overall small size, all previously described multituberculate specimens from DC2 belong to *Barbatodon oardaensis*, in fact there is a wide range of dimensions represented in the Fântânele sample as already noted by Csiki and Grigorescu (2002; see also Csiki, 2005; fig. 7G, J). Presence of such size differences within the Fântânele sample was previously cited by Csiki and Grigorescu (2000) in order to support the taxonomic distinctiveness between specimens referred by these authors to *Hainina* sp. A. and *Hainina* sp. B. Now, with the discovery of positively associated in situ kogaionid upper and lower dentition in *Barbatodon transylvanicus* (Smith and Codrea, 2015), it is even more apparent that the minute P1s LPB (FGGUB) M.1610 and M.1611 from Fântânele (= *Hainina* sp. A of Csiki and Grigorescu, 2000) cannot belong to the same taxon with the significantly larger m1 (LPB [FGGUB] M.1613 = *Hainina* sp. B of Csiki and Grigorescu, 2000; fig. 7G) and M1 (LPB

[FGGUB] M.1624; fig. 7C) from the same locality; meanwhile, the specimen M.1624 had been considered potentially conspecific with M.1613 by Csiki and Grigorescu (2002).

Indeed, based on the range of dimensions represented within the significant ($n = 7$) sample of kogaionid m1s from site DC2, Csiki and Grigorescu (2002) had suggested that at least three differently sized kogaionid taxa could be represented at this locality, one minute (even smaller than *B. oardaensis*; fig. 7J), one small (roughly the same size with *B. oardaensis*), and one medium sized, somewhat smaller than *B. transylvanicus* (compare fig. 7G with 7F). The precise taxonomic identity of the kogaionids represented in the Fântânele sample can be disentangled only once more complete and associated specimens known from other localities (Pui, Petreşti-Arini) have been described, and the intra- and interspecific morphological and taxonomic diversity and disparity of the Transylvanian kogaionids can then be better understood in the context of all currently known specimens.

SITE DC3
FÂNTÂNELE 2 LOCALITY
(SENSU VASILE, 2008A, 2008B)

LOCATION, AGE: The Fântânele 2 locality represents a minor MvBB located in the close proximity of site DC2, in the right side of Fântânele valley upstream of Vălioara village (Vasile, 2008a, 2008b; fig. 2), and most probably lying at a marginally lower stratigraphic level than the latter (fig. 3). Based on its stratigraphic position, it has the same age as site DC2, that is, probably early Maastrichtian (Tier 2; Csiki-Sava et al., 2016).

LITHOLOGY, PALEOENVIRONMENT: The lithology at site DC3 is reminiscent of that found at site DC2 (gray-greenish massive mudstone containing subrounded ruditic clasts of metamorphic origin; fig. 16C), but the size of the clasts is somewhat larger than in the latter (up to 3 cm long), the overall lithology is slightly coarser, and the reddish variegated component appears to be missing. Nonetheless, lithology that is roughly

the same suggests a comparable depositional setting, i.e., a waterlogged floodplain depression (Vasile, 2008a, 2008b).

FOSSIL CONTENT: The fossil content yielded by site DC3 is also reminiscent of that found at DC2, although comparatively less diverse and with a different relative abundance of the elements (most probably related to a somewhat higher basin energy during the sediment accumulation; Vasile, 2008a, 2008b). Although anurans (possibly *Paralatonia*) and albanerpetontids (possibly *Albanerpeton*) are both recognized at this site, as is the turtle *Kallokibotion*, their remains are very rare. Crocodyliform remains are more abundant as well as more diverse, with *Doratodon*, *Acynodon*, and *Sabresuchus* (= *Theriosuchus*) being represented by isolated teeth at the site. Small theropods are similarly diverse, with the presence of indeterminate velociraptorines, *Euronychodon*, and *Richardoestesia* documented based on distinct tooth morphotypes. The vertebrate assemblage is completed by very rare megaloolithid eggshells, as well as by one multituberculate specimen represented by an isolated tricuspid right P1 (LPB [FGGUB] M.1654), and the vertebrate remains are also associated with gastropod shell fragments. The locality can be tentatively classified as a typical MvBB, of the high-diversity multidominant multitaxic type (Eberth et al., 2007), despite the significantly lower number of recovered specimens compared with site DC2.

HISTORY OF RESEARCH: Site DC3 was discovered by one of us (Ş.V.) in 2007, and a small amount of material derived from here was screenwashed following the discovery. Due to the relatively low fossiliferous content, screenwashing was discontinued after a few years.

COMMENTS: Despite the relatively poor fossil content of site DC3, it is remarkable that it also yielded multituberculate remains. The single tricuspid P1, referred to only as an indeterminate kogaionid by Vasile (2008b), is morphologically more reminiscent of the P1 of *Kogaionon ungureanui* (Rădulescu and Samson, 1996; fig. 5F) and, to a lesser extent, that of *K. radulescui*

(Smith et al., 2022) than those of *Barbatodon* (Smith and Codrea, 2015; Solomon et al., 2016) and *Litovoi* (Csiki-Sava et al., 2018; fig. 5C) in that the mesial cusp is relatively large and widely separated from the pair of subequal distal cusps that are obviously smaller than the mesial cusp. Until the dental morphological diversity and intraspecific variability of the Transylvanian kogaionids is better understood, the P1 from DC3 is here very tentatively referred to the genus *Kogaionon*. If this taxonomic assignment is upheld in the future, LPB (FGGUB) M.1654 would represent an as yet indeterminate small species of the genus and, as such, would document an increased taxic diversity within the genus and may extend the fossil record of *Kogaionon* into the Densuş-Ciula Formation.

SITE DC4
LIVEZI MICRO2 LOCALITY

LOCATION, AGE: The Livezi Micro2 locality is situated uphill of Livezi village (fig. 2), at the southern foothills of Prislop Hill, in the basal (southernmost) section of the largest ravine within which uppermost Cretaceous deposits crop out (fig. 16D). Based on the overall lithological make-up of these outcropping deposits, the Livezi site was considered to belong to the upper part of the middle subunit of the Densuş-Ciula Formation (Grigorescu and Csiki, 2008) and is thus of probably early to mid late Maastrichtian age (Csiki-Sava et al., 2016), slightly younger than the Tuştea (= site DC1) locality (fig. 3).

LITHOLOGY, PALEOENVIRONMENT: The lithology at this site is represented by a 60–70 cm thick layer of dark gray mudstone, markedly differing from the dominant lithologies reported from Livezi (red silty-sandy mudstones and matrix-supported conglomerates; Grigorescu and Csiki, 2008). The transition between the gray mudstone layer and the over- and underlying brick-red mudstones is gradual. Based on their general sedimentological features, the fossiliferous sediments were probably accumulated in a localized, poorly drained, and poorly oxygenated

ponding environment within the confines of an otherwise well-drained floodplain.

FOSSIL CONTENT: The Livezi locality, represented by a series of ravines exposing the uppermost Cretaceous deposits (fig. 16D), has yielded mainly megaloolithid eggs and eggshells, including two large megaloolithid nests (Grigorescu and Csiki, 2008; Flintaşu et al., 2017). Besides these eggs, only rare remains of turtles (*Kallokibotion*) and titanosaurs were discovered in different locations within the locality, alongside rare microvertebrates—including indeterminate lizard jaw fragments and fragmentary anuran postcranial remains—identified at three distinct levels (this microvertebrate material is as yet unpublished due to its fragmentary and largely nondiagnostic nature). One of these microvertebrate-bearing levels, the low-diversity microvertebrate locality DC4 has yielded the only multituberculate fossil known from Livezi (see Csiki-Sava et al., 2016).

HISTORY OF RESEARCH: The fossiliferous nature of the Livezi deposits was first recognized in 2005 and the locality has been surveyed since then regularly for vertebrate remains. Several levels were sampled for microvertebrates starting with 2006 with very moderate success and one of these levels (Micro2) yielded in 2007 an isolated multituberculate upper molar.

COMMENTS: The small (2.18 × 1.68 mm), isolated right M1 (LPB [FGGUB] M.1672; Csiki-Sava et al., 2016: fig. 12R, S) from site DC4 is unfortunately extremely worn. Despite its very advanced wear, it is otherwise reasonably well preserved, with both roots quasicomplete. The two roots are wide labiolingually; the distal root is mesiodistally subequal with or even very slightly smaller than the mesial one in labial view, but is enlarged, about twice as thick as the latter in lingual view. In occlusal view, the crown shows the typical short and wide kogaionid morphology, with three short rows of cusps. The contour of the crown is incompletely rectangular, missing its mesiolingual corner, as usually occurs in Late Cretaceous kogaionids where the lingual cusp row is well developed, but incomplete and

does not reach the mesial edge; in this specimen, the lingual cusp row extends for about 60%–65% of the mesiodistal length of the crown.

The extreme wear obliterated almost all the cusps of this M1, so that establishing its exact cusp formula is difficult. The least worn median row contains four cusps, as in all known kogaionid M1s (see Csiki-Sava et al., 2018; Smith et al., 2022), and it appears that the lingual row was made up of two large cusps; the labial row, however, is nearly leveled by wear, especially in its distal half, so that counting the number of cusps present there is virtually impossible. By comparison with better preserved and in situ M1s known in *Kogaionon*, *Barbatodon transylvanicus*, and *Litovoi* (Rădulescu and Samson, 1996; Smith and Codrea, 2015; Csiki-Sava et al., 2018; Smith et al., 2022; figs. 7D, E, 14H), it looks possible that there were as many as four cusps in the labial row, and that the distalmost one was connected to the distalmost median cusp through a ridge.

In their overview of the Transylvanian latest Cretaceous multituberculates, Codrea et al. (2017a) regarded LPB (FGGUB) M.1672 from site DC4 as possibly referable to *Barbatodon oardaensis*. However, even in its deeply worn condition, the morphology of the Livezi M1 suggests that its labial row included possibly four cusps, whereas according to the diagnosis of *B. oardaensis*, its M1 cusp formula is 3:4:2 (invariably recorded in the nine known M1 specimens, including the holotype UBB ODAN Mt-13, from the type locality; Codrea et al., 2014). Due to the absence of any clear synapomorphies uniting the Oarda de Jos and the Livezi M1 specimens and the potential presence of a morphological difference (four labial cusps instead of three) that is very difficult to ascertain given the advanced wear of the tooth, the referral of LPB (FGGUB) M.1672 to *B. oardaensis* based simply on its size may not be appropriate. Such a referral is especially questionable considering the probable presence of more than one small kogaionid taxon in the Transylvanian area (as already noted above in discussing sites RB1, RB3, PB1, PB2, and PB4; see also Smith et al., 2022, and below). Accord-

ingly, this M1 specimen from site DC4 may instead represent another small kogaionid and not *Barbatodon oardaensis*; thus, given its poor preservation and isolated nature for the moment it is advisable to list this record simply as Kogaionidae indet.

Site DC5
General Berthelot 1 (GB1) Locality

Location, age: Site DC5 is situated just uphill of the Orthodox church in General Berthelot village (fig. 2), along the footpath leading up toward the hills lying to the north (Vasile et al., 2011a), and is represented by a small outcrop exposed from below the vegetation cover (fig. 16E). Although the deposits around General Berthelot have been considered to belong to the upper subunit of the Densuş-Ciula Formation, thus possibly Paleocene in age (e.g., Weishampel et al., 1991; Grigorescu, 1992), discovery of Cretaceous fossils (such as dinosaur eggshells) has prompted the reconsideration of their age and stratigraphic position, and as a result these deposits have been recently reallocated to the middle subunit of the formation (Vasile et al., 2011a; fig. 3). Accordingly, the age of site DC5 is now considered to be probably middle-late late Maastrichtian, probably belonging to the youngest, Tier 4 local faunal complex (Csiki-Sava et al., 2016).

Lithology, paleoenvironment: The lithology at site DC5 is represented by dark red, massive silty micaceous mudstones, interbedded with grayish, poorly consolidated coarse conglomeratic sandstones (fig. 16E). Although the outcrops are very limited in extent, and thus detailed sedimentological interpretation is difficult, the general lithological similarities with the Tuştea fossil locality (site DC1, above) suggest a similar depositional environment, that is, a well-drained floodplain.

Fossil content: The fossil content at site DC5 is represented mainly by megaloolithid eggshell fragments and cyclophorid gastropod operculae, associated with extremely rare anuran and multituberculate remains, as well as pseudogeckoolithid eggshells (Vasile et al., 2011a).

History of research: The first fossils (megaloolithid eggshells) at site DC5 were discovered in 2009, and continuing survey at the small patchy outcrops in the area was also supplemented by screenwashing of exploratory samples from several levels. Although most of these levels were barren or have contained only megaloolithid eggshells, the GB1 locality has also yielded—besides megaloolithid and pseudogeckoolithid eggshell fragments—a few microvertebrate remains, including those of multituberculates, first reported by Vasile et al. (2011a; see also Csiki-Sava et al., 2016).

Comments: The only multituberculate specimen known from site DC5 is represented by a distal fragment of a molariform tooth (LPB [FGGUB] M.1673) preserving the partial distal root and the distalmost part (about one-fourth) of the crown. Despite its fragmentary preservation state, the specimen was identified as a left M1 of an indeterminate kogaionid by Vasile et al. (2011a: fig. 3e, f), based on the presence of three cusp rows and through comparisons with other, better preserved kogaionid M1s from the Transylvanian area (see, e.g., Rădulescu and Samson, 1996; Smith and Codrea, 2015; Csiki-Sava et al., 2018; figs. 7A–E, 14H). Of the three cusp rows, the labial and median ones each preserve the distalmost pyramidal cusp as well as the distal halves of their penultimate cusps. Meanwhile, only the distalmost part of the lingual cusp row is present, represented by the crestlike distal end of the distal lingual cusp connecting laterally with the distolingual corner of the distal median cusp, a pattern that is reminiscent of that seen in several other kogaionid M1s (fig. 7A–E). Wear is minor to moderate on this M1 and mainly affects the labial and lingual sides of the median cusp row, while the tips of the preserved cusps are barely touched.

A more precise taxonomic identification of this M1 from site DC5, beyond that given by Vasile et al. (2011a; see also Csiki-Sava et al., 2016: fig. 12T), is impossible in its current state

of preservation, as neither its size and proportions, nor its cusp formula can be established with any certainty. Nevertheless, Codrea et al. (2017a) tentatively referred this specimen to *Barbatodon oardaensis* in account of its small size. It is worth pointing out, however, that the only measureable dimension (width, 1.24 mm) of this M1 is slightly less than 80% of the (mean) width of the Oarda M1 specimens, making this specimen from site DC5 the smallest kogaionid M1 known from the entire Transylvanian area (see Smith et al., 2022; table S1), comparable in size only to the smallest known kogaionid M1s referred to the minute Paleocene species *Hainina belgica* (De Bast and Smith, 2017). Due to these circumstances (smaller size and absence of any shared apomorphy), the referral of LPB (FGGUB) M.1673 to *B. oardaensis* is questionable, and this specimen is here retained as Kogaionidae indet. It is nonetheless important because it represents the youngest kogaionid record currently known from the Densuş-Ciula Formation and one of the youngest records overall in the Transylvanian area (see Csiki-Sava et al., 2016; fig. 3); furthermore, it records the presence of a minute kogaionid taxon in the uppermost part of the fossiliferous succession of this unit.

Site DC6
K1 Locality, Ciula Mică

LOCATION, AGE: Site DC6 was identified in the uppermost, red paleosol-bearing part of the outcropping section along the Pârâul Vârtopilor ravine, southwest of Vălioara and near Ciula Mică (Botfalvai et al., 2021; fig. 2), in deposits belonging to the basal part of the middle subunit of the Densuş-Ciula Formation (fig. 3). Based on the stratigraphic position of this locality, its age should be early early Maastrichtian (Botfalvai et al., 2021), representing either a Tier 1/2 or an earliest Tier 2 occurrence according to the chronofaunal succession stages of Csiki-Sava et al. (2016).

LITHOLOGY, PALEOENVIRONMENT: The lithology at site DC6 is represented by red, calcrete-bearing silty mudstones with vertical root traces, interpreted as well-drained floodplain deposits that underwent pedogenesis under conditions of fluctuating groundwater levels (Botfalvai et al., 2021).

FOSSIL CONTENT: The relatively meagre fossil content at site DC6 was reported to include isolated teeth of crocodyliforms (*Doratodon*) and indeterminate titanosaurians, as well as turtle (*Kallokibotion*) plates, alongside various indeterminate bone fragments, whereas two probably associated rhabdodontid (*Zalmoxes*) vertebral centra were recovered as loose elements near the locality itself. The only mammal remains identified at this locality is represented by a fragmentary i1 (Botfalvai et al., 2021).

HISTORY OF RESEARCH: The locality was first identified and preliminarily searched in autumn 2019, during the attempt to relocate the historical Vălioara fossiliferous sites excavated by Kadić more than a century ago (Kadić, 1916). Only very preliminary surface collecting took place at the locality. Although situated in the very close proximity of Kadić's exacavation site no. I, it most probably represents a different fossiliferous level (Botfalvai et al., 2021).

COMMENTS: The sole multituberculate specimen known from site DC6 is an apical fragment of a left i1 (LPB [FGGUB] M.1707; Botfalvai et al., 2021: fig. 11J). As noted by Botfalvai et al. (2021), its overall morphology is reminiscent of previously described kogaionid i1s from the Haţeg Basin, showing the typical kogaionid pattern, thus most probably it also represents an indeterminate kogaionid. Its relevance consists in that it is probably the oldest currently known kogaionid occurrence from the Haţeg area (Botfalvai et al., 2021; fig. 3). Furthermore, it documents (besides other multituberculate specimens from sites DC7 and DC3) the presence of relatively small kogaionids in the basal beds of the Densuş-Ciula Formation Middle Member; it is also of roughly similar size with the isolated i1 LPB (FGGUB) M.1612 described from Vălioara-Fântânele (site DC2) by Csiki and Grigorescu (2000).

Site DC7
K3 Locality, Vălioara

Location, age: Site DC7 is situated west of Vălioara (fig. 2), near the upstream branching point of Pârâul Neagului ravine, a right-side tributary of Vălioara Valley that exposes deposits of the basal Middle Member of the Densuş-Ciula Formation (Botfalvai et al., 2021). Based on the preliminary work by these authors, site DC7 is roughly contemporaneous with or marginally younger than site DC6, which dates it, too, as early early Maastrichtian in age. According to their relative geographic and stratigraphic positions, both of these sites are slightly older than the classical multituberculate-yielding locality Vălioara-Fântânele (site DC2) (Botfalvai et al., 2021; fig. 3).

Lithology, paleoenvironment: The lithology of the sedimentary succession around site DC7 is dominated by reddish calcrete-bearing paleosols and the single mammal specimen from this area originates from such a paleosol horizon, representing a well-drained, more elevated floodplain setting that underwent moderate pedogenesis (Botfalvai et al., 2021).

Fossil content: The currently known fossil content originating from around site DC7 was recovered mainly from a grayish-bluish mudstone that represents a poorly drained wetland environment; this bed yielded isolated turtle shell elements as well as rare remains of *Zalmoxes* (tooth), titanosaurs (vertebra), and possibly pterosaurs, besides plant fragments and gastropod shells. The mammal-bearing reddish paleosol bed is far less fossiliferous, with only one isolated turtle shell fragment found alongside a right distal humerus of a multituberculate.

History of research: Site DC7 was identified in 2019 during the attempt to rediscover the historical Kadić sites (Botfalvai et al., 2021) and was only very preliminarily prospected. The sole mammal remains known from this locality was recovered as an isolated surface find. Although it came from a relatively thin stratigraphic sequence that hosts several other, more fossil-rich horizons, including Kadić's localities II to V, it definitively represents a different fossiliferous level from these.

Comments: Site DC7 yielded one mammal specimen, a right distal humerus (LPB [FGGUB] M.1708; Botfalvai et al., 2021: fig. 11K) that is the first such specimen ever reported and preliminarily described from the entire Transylvanian area. It is currently under study, but it further supports the presence of small multituberculates (probably kogaionids) in the basal part of the Densuş-Ciula Formation Middle Member and it is also one of the oldest multituberculate remains known from the Haţeg area.

KOGAIONID OCCURRENCES IN THE
RUSCA MONTANĂ BASIN

The Rusca Monană Basin is the area from the Transylvanian region with outcropping uppermost Cretaceous deposits (figs. 1, 2) that was the latest to yield vertebrate remains. Although the presence of uppermost Cretaceous continental beds in this region was noted more than a century ago (e.g., Nopcsa, 1905), including reports of their fossil content consisting of plant remains (Tuzson, 1913), vertebrates have been discovered here only recently (e.g., Codrea et al., 2009, 2012a; Feigi et al., 2010; Vasile and Csiki, 2011; Vasile et al., 2012).

The uppermost Cretaceous continental deposits of the Rusca Montană Basin are widespread in the eastern part of the area (fig. 2: RM), and they show a somewhat distinctive lithofacial development contrasting with those described from the Haţeg and Transylvanian basins. These deposits are characterized by the widespread presence of volcanoclastic interbeds, even volcanic tuffs, the dominance of coarse detrital sedimentary rocks, and the occurrence of coal-bearing sequences (e.g., Dincă, 1977; Csiki-Sava et al., 2016), but were not yet formalized in the form of lithostratigraphic units. Plant remains are relatively common and widespread in these beds (e.g., Popa et al., 2014, 2016), but only very few vertebrate localities are on record to date (see Csiki-Sava et

al., 2016). Nevertheless, two of these vertebrate localities have also yielded multituberculate remains since their early-stage excavation (e.g., Codrea et al., 2009, 2012a); this suggests that kogaionid multituberculates were a common component of the Rusca local ecosystems as well. Exclusively isolated multituberculate teeth, recovered from microvertebrate accumulations, have been reported until now from this area, unlike the situation known from the Hațeg and Transylvanian basins.

The kogaionid-bearing vertebrate occurrences from the Rusca Montană Basin will be listed here, for sake of convenience identified in the following as RM sites.

<center>SITE RM1
NEGOIU-FĂRCĂDEANA 1 (NG1)
OR FĂRCĂDEANA LOCALITY</center>

LOCATION, AGE: The site RM1 was identified in a bed cropping out on the left side of Fărcădeana Creek, at Negoiu near Lunca Cernii de Jos (fig. 2), in the northeastern part of the Rusca Montană Basin (Csiki-Sava et al., 2016; Codrea et al., 2017a). Although the local litho- and chronostratigraphy is rather poorly constrained, the age of the deposits at Fărcădeana were estimated to be mid to early late Maastrichtian by Csiki-Sava et al. (2016; fig. 3).

LITHOLOGY, PALEOENVIRONMENT: According to Codrea et al. (2017a), the fossil-bearing layer is represented by a thin bed of black clay and sand, in a mainly reddish succession of fluvial deposits (fig. 17A). It probably represents a poorly drained, depressionary area developed within the floodplain.

FOSSIL CONTENT: The black deposits from locality Ng1 (fig. 17A) have yielded, besides the multitubeculate remains, a small amount of other micro- and macrovertebrate fossils, including anurans (*Paralatonia*), albanerpetontids (cf. *Albanerpeton*), turtle shell fragments (*Kallokibotion*), common crocodyliform skeletal remains and teeth (including some referred to *Doratodon*), theropod teeth (velociraptorines,

Richardoestesia, and *Paronychodon*), and scarce fossils of sauropods and ornithopods (*Zalmoxes*) (Codrea et al., 2009, 2012a; Vasile and Csiki, 2011; Vasile et al., 2012; Csiki-Sava et al., 2016; Venczel et al., 2016). These are associated with *Pseudogeckoolithus* type of (probably maniraptoran theropod) eggshells, diverse gastropods, and angiosperm fructifications (Vasile and Csiki, 2011; Vasile and Csiki-Sava, 2012). Only two multituberculate specimens were found at this locality: a right I2 (UBB Ng1-01) and a left P1 (UBB Ng1-02) (Codrea et al., 2012a, 2017a).

HISTORY OF RESEARCH: Site RM1 was identified and excavated independently in 2009–2010 by teams from the Babeș-Bolyai University, Cluj-Napoca (Codrea et al., 2009; Feigi et al., 2010), and the University of Bucharest (Vasile and Csiki, 2011; Vasile et al., 2012). Over the years, several hundred kilograms of fossiliferous matrix was screenwashed from the locality (Codrea et al., 2012a; Csiki-Sava et al., 2016) and the multituberculate fossils discovered here have been discussed in several publications (e.g., Codrea et al., 2012a), most recently by Codrea et al. (2016, 2017a).

COMMENTS: In the most recent review of the Rusca Montană multituberculate material (Codrea et al., 2017a) the RM1 multituberculate teeth were referred, based on their size, to the small kogaionid *Barbatodon oardaensis* erected by Codrea et al. (2014), representing the first definitive report of this taxon outside its type locality. The isolated P1 UBB Ng1-02 also shows some resemblances in its bicuspid morphology to the isolated P1s described by Csiki and Grigorescu (2000) from Fântânele (site DC2); these latter specimens are, nevertheless, still somewhat smaller than the RM1 premolar, and details of their morphology also differ (see above, DC2). This gross morphological and (to an extent) size similarity may suggest certain taxonomic affinities between the multituberculates represented by the bicuspid P1s from RM1 and DC2, but more and better preserved material from both localitis is needed for a reliable assessment.
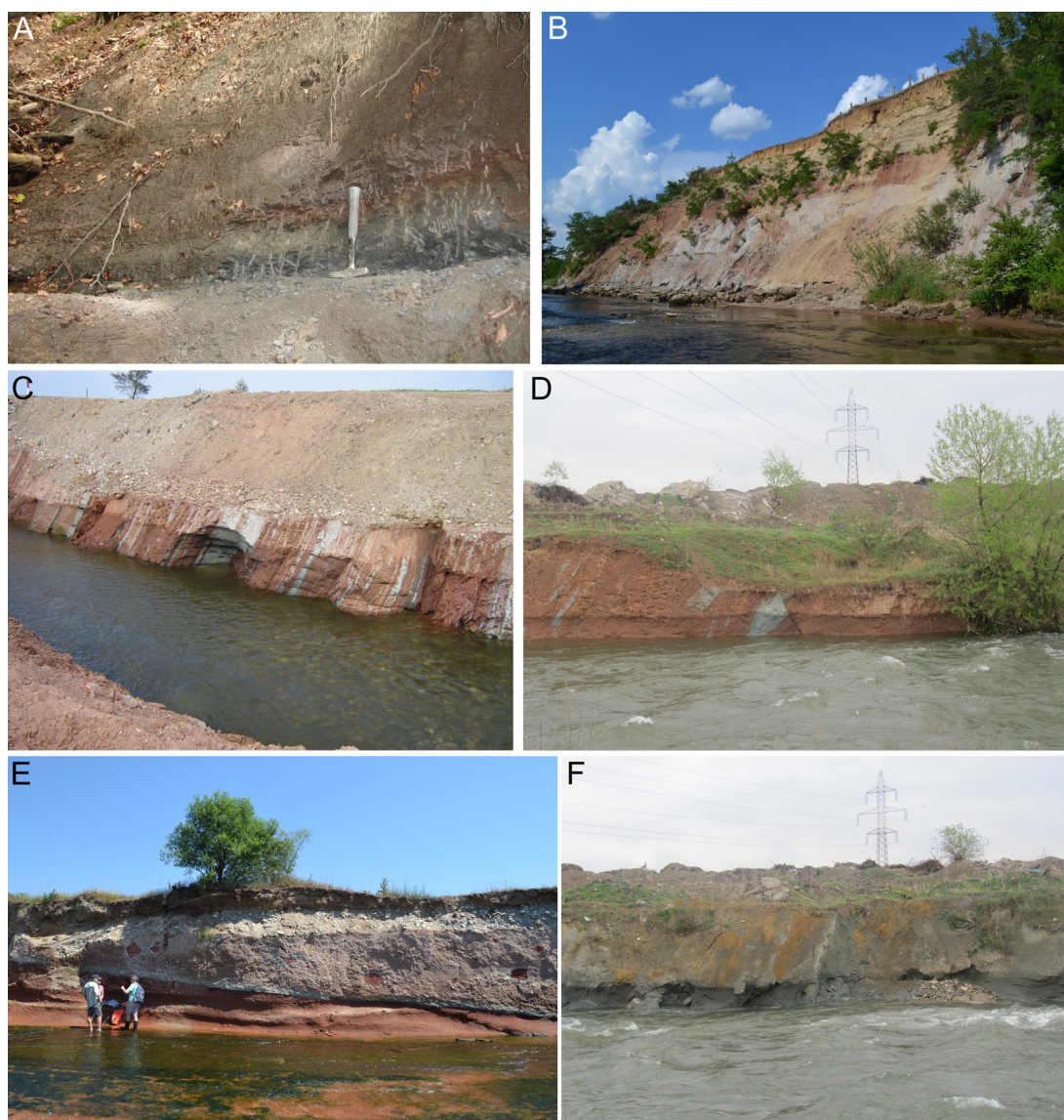
FIGURE 17. Kogaionid-bearing fossiliferous localities from the Rusca Montană (A) and southwestern Transylvanian (B–F) basins. **A.** Exposures of uppermost Cretaceous continental beds along Fărcădeana Creek at Negoiu, Lunca Cernii de Sus, eastern Rusca Montană Basin. Hammer marks the position of the fossilfierous bed hosting site RM1. **B.** Overview of the Oarda de Jos A locality, south of Alba Iulia, on the right side of Sebeş River (in the foreground). The fossiliferous bed hosting site TB1 is located in the upper part of the outcropping succession. **C.** Strongly tilted beds of the continental Sebeş Formation outcropping at Petreşti-Arini, covered by flat-lying Quaternary sandy-pebbly deposits and recently created anthropic sediment heaps. **D.** Red mudstone-dominated part of the basal section of the Sebeş Formation at Petreşti-Arini, hosting site TB2. **E.** Outcrops of the Sebeş Formation at Sebeş-Glod, along the Sebeş River, locality Sebeş-Glod A, with kogaionid site TB3 near the group of people to the left. **F.** The transitional sequence from the estuarine-brackish uppermost Bozeş Formation (right) to the continental, gray-colored basalmost Sebeş Formation (left, more ochre-colored rocks) at Petreşti-Arini, hosting the Black Lens fossiliferous level (site TB4).

Site RM2

Negoiu-Fărcădeana 2 (Ng2) Locality

Location, age: The Negoiu-Fărcădeana 2 locality is situated in close proximity to the Ng1 locality (fig. 2), on the right bank of the Fărcădeana brook at Negoiu, in the northeastern part of the Rusca Montană Basin (Codrea et al., 2017a). Its age is, accordingly, similar to that of the Ng1 locality, that is, mid (roughly early late) Maastrichtian (fig. 3).

Lithology, paleoenvironment: The lithology at site RM2 is reportedly made up of red and yellowish-grayish siltstones, within a succession of fluvial red beds (Codrea et al., 2017a). Although no paleoenvironmental interpretation was proposed for the locality, based on the regional setting of the uppermost Cretaceous continental deposits from Transylvania, it can be suggested that the fossiliferous deposits formed within a well-drained floodplain setting.

Fossil content: According to the published data, only a small number of multituberculate teeth have been discovered at site RM2, including left and right i1 (UBB Ng2-02, UBB Ng2-03), a right p4 (UBB Ng2-01; fig. 7M), and a right P4 (UBB Ng2-04) (Codrea et al., 2012a, 2017a).

History of research: Site RM2 was discovered and excavated at the same time as site RM1 (Codrea et al., 2009; Feigi et al., 2010) and the multituberculate remains found here have been described by Codrea et al. (2012a, 2017a).

Comments: The i1s from site RM2 show the characteristic kogaionid pattern of morphology reported in several kogaionid specimens from the Transylvanian area, with a gracile, elongated, and pointed shape, and a partially reduced lingual enamel cover, demarcated from the thicker labioventral enamel cover by an easily visible longitudinal line on the lingual side (e.g., Csiki and Grigorescu, 2000; Smith and Codrea, 2015; Csiki-Sava et al., 2018; see fig. 11F). Accordingly, these specimens can be reliably identified as kogaionid i1s. Similarly, the p4 and the P4 from locality Ng2 display features also found in other kogaionid premolars.

In particular, the P4 (UBB Ng2-04) shows the typical, autapomorphic kogaionid morphology of a rectangular crown with an obliquely slanting, mesiolingual-to-distolabial main cusp row and a lingual row restricted to the distal half of the crown, converging mesially with the oblique labial row (e.g., Peláez-Campomanes et al., 2000; Csiki-Sava et al., 2018). In this respect, as well as in the presence of four cusps in the oblique labial cusp row, UBB Ng2-04 is reminiscent of other P4s known in various other Transylvanian kogaionids (e.g., Codrea et al., 2014; Smith and Codrea, 2015; Solomon et al., 2016; Csiki-Sava et al., 2018; Smith et al., 2022; fig. 5C, F), as well as in the Western European Paleocene kogaionids (e.g., Peláez-Campomanes et al., 2000; De Bast and Smith, 2017). In the most recent review of the Rusca Montană multituberculates, teeth from site RM2, based on their size, were also referred to the small kogaionid *Barbatodon oardaensis* described from Oarda de Jos, in the Transylvanian Basin (Codrea et al., 2017a).

KOGAIONID OCCURRENCES IN THE TRANSYLVANIAN BASIN

The Transylvanian Basin is historically less well known for its latest Cretaceous continental vertebrates than the much smaller Hațeg Basin. Nevertheless, it was the first region to yield such vertebrate remains during the 19th century, although the nature of these fossils (whether they represent mammals or dinosaurs) remained contentious for over a century, and most of the recovered remains were cataloged as large mammals (see, e.g., Codrea and Mărginean, 2007). A notable exception to this trend was the work of Nopcsa (1905) who noted the presence of dinosaur remains in several locations in the southwestern as well as northwestern marginal areas of the basin. Nevertheless, for over a century, the presence of latest Cretaceous reptile remains within the thick successions of dominantly red-colored continental deposits that crop out especially in the southwestern parts of the Transylvanian Basin was considered to be largely

allochthonous, the result of their reworking into younger, Paleogene or Miocene beds (e.g., Grigorescu, 1987b; Codrea and Vremir, 1997; Jianu et al., 1997; Codrea et al., 2008).

The latest Cretaceous age, and the autochthonous fossil-bearing nature of these deposits were recognized gradually at the beginning of the 21st century (e.g., Vremir and Codrea, 2002; Codrea and Dica, 2005; Codrea and Godefroit, 2008; Vremir et al., 2009; Codrea et al., 2010c; Solomon et al., 2010; Vremir, 2010). As a result of these studies, it is now firmly established that a thick succession of mainly red-colored uppermost Cretaceous continental deposits, forming the basal part of the posttectonic cover of the latest Cretaceous Second Getide structures of the Southern Carpathians and Apuseni Mountains, blanket the southwestern, western, and northwestern marginal areas of the Transylvanian Basin (e.g., Codrea and Dica, 2005; Codrea et al., 2010c; Vremir, 2010; Vremir et al., 2015a; Csiki-Sava et al., 2016).

These continental deposits form the basal part of the time-comprehensive (uppermost Cretaceous-Eocene) Jibou Formation in northwestern Transylvania (Codrea and Godefroit, 2008). In the southwestern corner of the Transylvanian Basin, around Alba Iulia and Sebeş, facially similar deposits were included in the Sebeş Formation by Vremir (2010—corresponding to the Vurpăr, Şard, and Sebeş formations of Codrea and Dica, 2005; see also Csiki-Sava et al., 2016; fig. 2: TB)—and range in age from the latest Campanian to the (late?) late Maastrichtian (see reviews in Vremir et al., 2015a; Csiki-Sava et al., 2016; fig. 3). They are dominated by red-colored detrital beds that range from coarse conglomerates through sandstones to calcrete-bearing mudstones, although darker, greenish or gray fine-grained deposits also occur locally (e.g., Therrien et al., 2002; Codrea and Dica, 2005; Therrien, 2005; Codrea et al., 2010c; Vremir, 2010; Jipa, 2012; Vremir et al., 2014, 2015a; Csiki-Sava et al., 2016). Plant (e.g., Givulescu et al., 1995, Iamandei et al., 2005) as well as algal and invertebrate (Jipa, 2012) fossils have been also reported from these beds, but their fossil content is mainly represented by vertebrate remains (see Codrea et al., 2010c; Vremir, 2010; Jipa, 2012; Vremir et al., 2015a), including the only Cretaceous dinosaur footprints known from Romania (Vremir and Codrea, 2002).

Among these vertebrate remains, those of kogaionid multituberculates are also present, although these appear to be less common and less widely distributed than in the coeval deposits of the Haţeg Basin. Unlike their meager fossil record in the Rusca Montană Basin but similar to the situation known in the Haţeg Basin, kogaionids are represented in southwestern Transylvania mainly by isolated teeth, but also by dentigerous jaw fragments, and in rare cases even by partial skeletons, although their state of preservation and degree of completeness are poorer than that recorded in the Haţeg area. The currently known kogaionid-bearing vertebrate localities from the Transylvanian Basin will be listed here and, for the sake of convenience, identified as TB localities.

Site TB1
Oarda de Jos A Lens (or ODAN) Locality, Oarda de Jos

Location, age: The ODAN locality (site TB1) was identified in 2007 within a bed cropping out in the upper part of the Oarda de Jos A (ODA) outcrop, on the right bank of the Sebeş River (fig. 2), slightly upstream of its confluence with the Mureş River and the bridge leading to Oarda de Jos (see Codrea et al., 2010c; Vremir, 2010; Jipa, 2012). The Oarda de Jos A section is estimated to be situated in the middle part of the Sebeş Formation (e.g., Vremir, 2010; Vremir et al., 2015a), and is thus most probably mid (i.e., latest early to early-late Maastrichtian) in age, representing the Tier 3 faunachron of Csiki-Sava et al, (2016; fig. 3).

Lithology, paleoenvironment: Although the ODA section itself is dominated by reddish sandy channel deposits, silty crevasse splays, brownish-red floodplain mudstones, with rare

calcareous mudstone and thin coal interbeds (e.g., Vremir et al., 2015a; fig. 17B), the multituberculate fossil-bearing layer (ODAN) is represented by an intercalated lenticular bed of gray-greenish sandy-silty mudstone in the upper part of the local succession (Codrea et al., 2010c; Jipa, 2012). This MvBB is interpreted to have been formed through the infilling of a ponding, abandoned channel, within a meandering fluvial environment (Vremir, 2010; Codrea et al., 2014).

Fossil content: The lenslike ODAN MvBB has yielded a rich assemblage of vertebrates, including lepisosteiform and characiform fish, anurans (*Paralatonia*, *Hatzegobatrachus*), albanerpetontids (*Albanerpeton*), turtles (*Kallokibotion*, dortokids), lizards (*Oardasaurus*), crocodyliforms (*Allodaposuchus*, *Acynodon*, *Doratodon*), pterosaurs (*Albadraco*), diverse dinosaurs (*Zalmoxes*, *Telmatosaurus*, *Struthiosaurus*, titanosaurs, *Richardoestesia*, *Paronychodon*, dromaeosaurids), and possible bird teeth, besides characeans, ostracods, gastropods, and crab chelipedes (Codrea et al., 2010a, 2010b, 2010c, 2017b; Vremir, 2010; Jipa, 2012; Vremir et al., 2015a; Venczel et al., 2016; Solomon et al., 2020). Meanwhile, other parts of the ODA outcrop also yielded diverse eggshell fragments (Fernández et al., 2019) and even the remnants of an enantiornithine bird-nesting colony (Dyke et al., 2012). The vertebrate fossil remains from the ODAN MvBB were associated with what was reported to be the richest sample of kogaionid remains (over 70 isolated teeth) derived from one single site from the entire Transylvanian area and one within which all cheektooth positions representing a new, small kogaionid taxon are recorded (Jipa, 2012; Codrea et al., 2014).

History of research: The site TB1 was identified and excavated starting in 2007 by teams from the Babeş-Bolyai University, Cluj-Napoca (Codrea et al., 2010a, 2010b, 2010c; Jipa et al., 2010; Jipa, 2012), with about 2.5 tons of sediments screenwashed from the fossiliferous lens. The large multituberculate sample derived from the lens allowed Codrea et al. (2013, 2014) to erect from here a new, small species of the

genus *Barbatodon* (*B. oardaensis*; fig. 7A, I, L), after these remains had been referred to as indeterminate kogaionids in several previous publications (e.g., Codrea et al., 2010a, 2010b, 2010c, 2012b; Jipa et al., 2010).

Comments: The large kogaionid sample known from site TB1 also allowed Codrea et al. (2014) to identify some degree of intraspecific morphological and dimensional variability within *B. oardaensis* as far as P4, M2, m1, and m2 are concerned, whereas the M1s referred to this taxon (including the holotype specimen) are considered to be rather uniform in size, shape, and morphology. However, it is worth noting that Codrea et al. (2012b) rather surprisingly have noted the presence of two distinctive M1 morphologies in the TB1 sample, one reminiscent of *Kogaionon* and one considered closely comparable to that seen in *Barbatodon*, although detailed description and illustrations of the available material published subsequently elsewhere do not appear to support their original claim.

Site TB2
Level L1a, Petreşti-Arini

Location, age: The site TB2 was identified on the right bank of an artificial canal dug for the regularization of the Sebeş River downstream of Petreşti village (fig. 2), a newly created anthropogenic ouctrop that was first reported in 2010 (Codrea et al., 2010c; Vremir, 2010). The local succession exposes a continuous transition from the marine deposits of the uppermost Cretaceous (Campanian) Bozeş Formation to the continental deposits of the uppermost Campanian–Maastrichtian Sebeş Formation (Vremir et al., 2014; Ţabără et al., 2022; fig. 17C). As the TB2 fossiliferous bed yielding the multituberculate remains (level L1a of Vremir et al., 2014) is located in the basal part of the red continental beds of the Sebeş Formation (fig. 17D), slightly above their contact with the basalmost, gray-greenish transitional beds of the unit, it is most probably of an earliest Maastrichtian age (Vremir et al., 2014; Csiki-Sava et al., 2016; fig. 3).

Lithology, paleoenvironment: As reported by Vremir et al. (2014), the fossil-bearing layer is represented by a bioturbated, pale brownish-red silty mudstone with calcareous nodules, formed in a well-drained floodplain environment.

Fossil content: The multituberculate remains-bearing level of site TB2 is not particularly rich in identifiable fossils, most of which are represented by indeterminate bone fragments. Only one isolated rhabdodontid tooth (referred to as *Zalmoxes* sp.) was recovered in addition to an associated partial multituberculate skeleton that includes parts of the skull with elements of the dentition, as well as postcranial remains (Csiki-Sava et al., 2012, 2021a; Vremir et al., 2014, 2018).

History of research: Site TB2 was identified and excavated in 2011 by one of us (M.V.) who recovered and preliminarily prepared the multituberculate specimen (MMIRS 655). It was first reported, while still undergoing preparation, as a small indeterminate kogaionid in Csiki-Sava et al. (2012; fig. 7K), and subsequently mentioned, without description, by Vremir et al. (2015a), while a block containing some of the postcrania was figured in Vremir et al. (2014). The specimen was fully prepared only recently, and is currently under study.

Comments: Although the TB2 multituberculate specimen has only been reported and discussed previously as an indeterminate kogaionid, recently Codrea et al. (2017a) suggested that, based mainly on the size of the specimen, it may represent the small kogaionid *Barbatodon oardaensis* whose type material is known from the younger TB1 locality. Detailed study and description of this important specimen, currently underway, is required to test this assertion. The main importance of specimen MMIRS 655 rests in that it probably represents the oldest and one of the best-dated partial skeletons of a kogaionid known to date (Csiki-Sava et al., 2021a).

Site TB3
SbG/B Locality, Sebeş-Glod

Location, age: The site TB3 is situated in the riverbed and banks of the Sebeş River downstream

of Sebeş locality, upstream of and close to Lancrăm village, in proximity to the Sibiu-Orăştie-Sebeş motorway junction (Vremir, 2010; Vremir et al., 2015a; fig. 2). Based on the regional dip of the continental beds belonging to the Sebeş Formation exposed along the Sebeş River, this locality is intermediate in age between the older site TB2 and the younger site TB1, and thus probably of early Maastrichtian age, a Tier 2 fossil locality (fig. 3; see also Csiki-Sava et al., 2016).

Lithology, paleoenvironment: The local section at TB3 is dominated by red, often calcrete-bearing siltstones and silty mudstones, interbedded with grayish-whitish cross-laminated sandy-pebbly and poorly sorted conglomeratic channel deposits with abundant mudstone rip-up clasts (Vremir, 2010; Vremir et al., 2015a; fig. 17E). These are interpreted as a succession formed within a high-sinuosity meandering fluvial environment. The multituberculate-yielding bed corresponds to the locally dominant, reddish silty-muddy floodplain facies, representing a well-drained distal floodplain environment.

Fossil content: The local succession at site TB3 is the most fossil-rich one in the suite of different Sebeş-Glod localities (Vremir et al., 2015a). It has yielded a large number of vertebrate fossils, including several associated (even articulated) skeletons, such as the holotypes of the dromaeosaurid theropod *Balaur* (Csiki et al., 2010a) and the medium-sized azhdarchid pterosaur *Eurazhdarcho* (Vremir et al., 2013). These are accompanied within the locality by remains of anurans, turtles (*Kallokibotion*, dortokids), crocodyliforms, and several herbivorous dinosaurs (*Zalmoxes*, *Telmatosaurus*, titanosaurs). The single multituberculate specimen known from site TB3 was recovered from a small fossil pocket where it was found together with associated remains of hadrosaurs and titanosaurs and the holotype of *Eurazhdarcho*.

History of research: Site TB3 was identified in 1998 and has been explored subsequently in a regular manner since then, because, as a very dynamic riverbed site, it is characterized by a high degree of river erosion and fossil destruc-

tion. The unique multituberculate specimen known from this locality (MMIRS 666) was discovered in 2012 and was subsequently mentioned in passing in the reviews by Vremir et al. (2015a) and Csiki-Sava et al. (2017), but has never received a proper description. This specimen is currently under study.

COMMENTS: Despite its fragmentary nature (a dentigerous jaw fragment), specimen MMIRS 666 from site TB3 represents an important kogaionid record as it fills the stratigraphic (and thus, temporal) gap between the two previously described multituberculate occurrences (TB2, respectively TB1; fig. 3); moreover, it hints at a higher morphological and body-size variability present in the Transylvanian Basin kogaionid fossil record than previously acknowledged by Codrea et al. (2017a; see below).

SITE TB4
LEVEL L0/C (= BLACK LENS), PETREŞTI-ARINI

LOCATION, AGE: The site TB4 was discovered in the same Petreşti-Arini succession that hosts site TB2 (fig. 2). It lies a few meters stratigraphically below (i.e., upstream of) site TB2 and only slightly above the Bozeş-Sebeş formational contact (fig. 3). Given that this contact had been dated as latest Campanian or near the Campanian/Maastrichtian boundary in age (Vremir et al., 2014; Ţabără et al., 2022), the age of locality TB4 should be also near the Campanian/Maastrichtian boundary or it may be even slightly older, very latest Campanian (Vremir et al., 2015b), thus representing the chronostratigraphically earliest Tier 1 faunachron of Csiki-Sava et al. (2016).

LITHOLOGY, PALEOENVIRONMENT: The fossil-bearing layer at site TB4 is represented by a dark gray, massive mudstone grading into a concretionary, brecciated calcareous mudstone horizon. This lithon is topping the brackish, basal dark gray siltstone-sandstone section of the Sebeş Formation (fig. 17F) and lies immediately below the thick, grayish sandy-pebbly channel fill sandstone that marks the transition toward the purely

continental basal part of the Sebeş Formation in the Petreşti-Arini succession (Vremir et al., 2014). Although the petrology and sedimentology of the fossiliferous bed are currently under close scrutiny, on preliminary assessment it most probably represents a ponding water body developed within a coastal wetland environment (see also Choi et al., 2020b).

FOSSIL CONTENT: The Black Lens locality can be defined as a microvertebrate bonebed, although macrovertebrate remains up to 30 cm in length were also discovered here (Vremir et al., 2015b; Choi et al., 2020b). It has yielded a diverse vertebrate fauna that includes—besides the kogaionid multituberculates—lepisosteid fish, anurans, rare albanerpetontids, lizards, rare turtles, diverse and common crocodyliforms (*Allodaposuchus*, *Doratodon, Sabresuchus*, *Acynodon*), dinosaurs (*Zalmoxes*, nodosaurids, small theropods) (Vremir et al., 2015a, 2015b; Vasile et al., 2021), along with theropod eggshells (*Pseudogeckoolithus*; Choi et al., 2020a), gastropods, and charred wood remains.

HISTORY OF RESEARCH: Site TB4 was first identified in 2014 and was excavated and screen-washed since then in successive field seasons. The locality has yet to be addressed by a thorough investigation, which is currently underway, although its fossiliferous content, including the presence of kogaionid multituberculates (represented exclusively by isolated teeth) was preliminarily reported by Vremir et al. (2015b) and Vasile et al. (2021), supplemented by Choi et al. (2020b). The vertebrate assemblage recovered from the Black Lens, including the TB4 kogaionid material, is currently under study (Csiki-Sava et al., 2021a; Vasile et al., 2021).

COMMENTS: Given the position of site TB4 in the very basal part of the Sebeş Formation, the kogaionid remains it has yielded are definitively the oldest such fossils known in the Transylvanian area, and also the oldest known kogaionids to date (Csiki-Sava et al., 2017, 2021b). With a decent sample size (about 20 isolated teeth), these fossils document the presence of small kogaionids on the Haţeg Island in the very latest

Campanian or near the Campanian/Maastrichtian boundary. Of the material published to the present (Vremir et al., 2015b; Csiki-Sava et al., 2021a, 2021b), the incisors conform to the general kogaionid morphology reported from other taxa and other areas (e.g., Csiki and Grigorescu, 2000; Smith and Codrea, 2015; Solomon et al., 2016; Csiki-Sava et al., 2018). The somewhat more diagnostic bicuspid P1 is reminiscent of P1 specimens described from the Rusca Montană Basin (site RM1; Codrea et al., 2017a) or the Hațeg Basin (site DC2; Csiki and Grigorescu, 2000). The kogaionid material discovered at site TB4 is currently under study.

Site TB5

ODB Fossiliferous Lens, Oarda de Jos

Location, age: The site TB5 was discovered only very recently (Codrea et al., 2021) within the same general sedimentary succession that also contains site TB1 (fig. 2). It is located within the basal part of the second large outcrop at Oarda de Jos, in a new section that was recently exposed through fluvial erosion; thus only very limited information is available as yet concerning it. The site is situated somewhat upstream of and thus probably stratigraphically slightly below site TB1 (fig. 3). Judging by their spatial closeness within the middle-upper section of the Sebeş Formation (Vremir et al., 2015a), the age of sites TB1 and TB5 should be roughly the same, that is, most probably mid (i.e., latest early to early-late) Maastrichtian (Csiki-Sava et al., 2016; fig. 3).

Lithology, paleoenvironment: The fossil-bearing bed at site TB5 is a lens-shaped lithon several square meters in size, which has been briefly reported by Codrea et al. (2021) as consisting of two superposed, slightly differently colored, fine-grained layers: a coarser, basal dark gray mudstone overlain by a bluish mudstone. Preliminary paleoenvironmental assessment of the fossiliferous bed (within which the dark-colored fossils were concentrated preferentially in the coarser basal section) suggests rapid accu-

mulation of the remains in a quiet and poorly oxygenated setting within the otherwise fluvially dominated, reddish-colored, coarser, sandy local succession (Codrea et al., 2021).

Fossil content: The ODB lens appears to represent a multitaxic microvertebrate bonebed, although the occurrence of macrovertebrate remains was also noted (Codrea et al., 2021). It was reported to have yielded remains of fish, albanerpetontids, frogs, lizards, turtles, crocodilians, different dinosaurs (theropods, ornithopods, and sauropods), and pterosaurs (none of which was described yet in more detail), in addition to isolated teeth of kogaionid multituberculates (Codrea et al., 2021; Smith et al., 2022).

History of research: Site TB5 was reported only very recently and details of its discovery are not yet available. In addition to a brief conference abstract reporting the identification of the ODB lens locality and summarizing its overall faunal content, including the kogaionids (Codrea et al., 2021), some very basic information regarding the kogaionid teeth from this site (see below) was presented by Smith et al. (2022: table S1).

Comments: Given its recent identification, only very few details are available concerning the kogaionid fossils (represented apparently only by isolated teeth) from this site. Their presence was first mentioned by Codrea et al. (2021) and subsequently Smith et al. (2022) listed the measurements of three of these, representing several upper premolar positions including P2 (UBB ODBL-Mt-2), P3 (UBB ODBL-Mt-4), and P4 (UBB ODBL-Mt-5). All the TB5 specimens from this list were referred to the small kogaionid *Barbatodon oardaensis*, a taxon whose type locality (site TB1) is both spatially and stratigraphically close to site TB5, a proximity that might support such a taxonomic referral, despite minor size differences to be noted between the ODB specimens and the *B. oardaensis* type material. Description of this interesting new kogaionid assemblage appears to be forthcoming, according to Smith et al. (2022).

SPATIOTEMPORAL DISTRIBUTION PATTERNS OF THE LATEST CRETACEOUS TRANSYLVANIAN KOGAIONIDS

In the most recent general review of kogaionid distribution in the uppermost Cretaceous of the Transylvanian area (Haţeg, Transylvanian, and Rusca Montană basins), Codrea et al. (2017a) recognized only four taxa present in this region, including the formally described *Kogaionon ungureanui* (from Sânpetru, site SP1, in the Haţeg Basin), *Barbatodon transylvanicus* (from Pui, similarly in the Haţeg Basin), and *B. oardaensis* (with its type locality at Oarda de Jos, in the Transylvanian Basin, site TB1, but considered to be present in all three sedimentary basins), plus a taxonomically indeterminate medium-sized kogaionid from Toteşti-baraj (site RB1, also in the Haţeg Basin). In their review, these authors referred to several occurrences of small kogaionids previously reported from the Transylvanian (Petreşti locality), Haţeg (Vălioara, Tuştea, Livezi, General Berthelot, Nălaţ-Vad, Toteşti localities), and Rusca Montană (Negoiu locality) basins as *Barbatodon oardaensis* (see Codrea et al., 2017a: table 1), mainly based on the roughly similar small size of all these multituberculate fossils.

Using this taxonomic interpretation of the latest Cretaceous Transylvanian kogaionid fossil record, Codrea et al. (2017a) also established a rather straightforward and simple body-size related spatial distribution pattern of the kogaionids across the former Transylvanian landmass during the latest Cretaceous. According to this pattern, taxonomically uniform small kogaionids—represented exclusively by *Barbatodon oardaensis*—were spread across the entire Transylvanian landmass, occurring in several largely coeval lithostratigraphic units. Meanwhile, they considered large kogaionids such as *Kogaionon ungureanui* or *B. transylvanicus* restricted strictly to the Sînpetru Formation (in its widest acceptance; see Therrien, 2005, and Csiki-Sava et al., 2016, for a more nuanced view on the lithostratigraphic affinities of the different outcropping units in the Haţeg Basin), showing a spatially

exclusive distribution with *Kogaionon* occurring only at Sânpetru and *B. transylvanicus* represented only at Pui. Finally, in the assumed Sînpetru Formation–correlative beds along the Râul Mare River, the small *B. oardaensis* was considered to occur alongside a medium-sized indeterminate kogaionid.

The identification of the fourth nominal latest Cretaceous kogaionid taxon (belonging to a new, third genus), *Litovoi tholocephalos*, described by Csiki-Sava et al. (2018) from Pui (site PB6), appeared to conform to the same general spatial distribution pattern outlined in Codrea et al. (2017a), as this large taxon was also reported from Pui. Nevertheless, its presence at Pui, at a stratigraphic level different from those yielding the known specimens of *Barbatodon transylvanicus* (see our review, above; fig. 3), suggested that the distribution of large kogaionids was not entirely governed by strict allopatry (see below, and fig. 18). The discovery of *Litovoi* also hinted at the fact that the precise chronostratigraphic distribution of the different kogaionid occurrences (fig. 3)—a factor not considered by Codrea et al. (2017a)—should also be taken into account to arrive at a more detailed and correct image of the spatiotemporal distribution of kogaionids during the latest Cretaceous.

Similarly, Smith et al. (2022) recently reported a fifth kogaionid taxon from Nălaţ-Vad (site RB3), in the Haţeg Basin, which they identified as a small species of the genus *Kogaionon* (*K. radulescui*); this fifth species still largely fits the same general distributional pattern outlined by Codrea et al. (2017a), i.e., the presence of only small and medium-sized kogaionids in the Râul Mare Beds. On the other hand, however, the identification of this second smaller kogaionid in the Transylvanian uppermost Cretaceous demonstrated presence of a higher local taxic diversity within the group than acknowledged until recently. Consequently, the soundness of the referral of several previously reported kogaionid fossil occurrences to *B. oardanesis* (the sole small latest Cretaceous kogaionid taxon formally defined before K. *radulescui*), as was suggested by Codrea et al. (2017a)
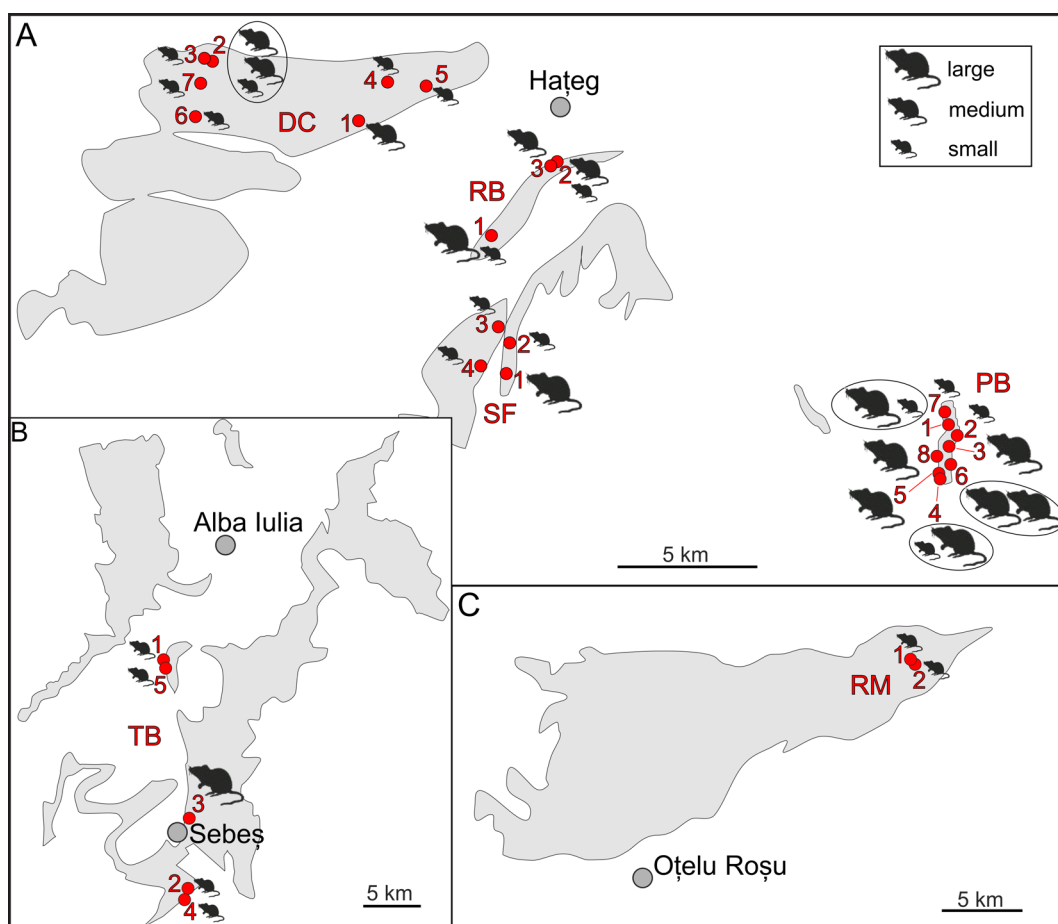
FIGURE 18. Latest Cretaceous Transylvanian kogaionid occurrences, highlighting the spatial distribution of their estimated body size (see text and figure 2 for identity of the fossiliferous sites marked in red in figures 18–23; see text and tables 4–7 for details of body size estimates). **A.** Haţeg Basin; **B.** southwestern Transylvanian Basin; **C.** Rusca Montană Basin.

based simply on their size, became questionable; in light of an increased taxic diversity of smaller-size kogaionids, such tentative referrals should be backed up with the identification of uniquely shared apomorphies between these specimens and *B. oardaensis*. Indeed, as we have pointed out in several instances in our review of the Transylvanian kogaionid-bearing localities (e.g., at sites RB1, RB2, DC2, and DC4), morphological differences identified between kogaionid specimens reported from these sites and the type material of *B. oardaensis* appear to seriously undermine such simply size-based taxonomic assertions, whereas

for other localities (e.g., SP2, DC1, DC5) the previously described material is not diagnostic enough to support lower-level taxic identifications. As a result of these uncertainties, the proposed widespread geographic distribution of the small *B. oardaensis* (in contrast with the very localized distribution of all three large kogaionid taxa, *K ungureanui*, *B. transylvanicus*, and *Litovoi tholocephalos*) may also represent an oversimplification and should undergo closer scrutiny as our knowledge on the distribution and content of the different kogaionid-bearing localities grows (as summarized in our present review).

Before considering the more subtle and complex latest Cretaceous kogaionid distribution patterns that are emerging from our review of their available fossil record, it should be also emphasized here that the overview of Codrea et al. (2017) appears to have omitted previously published information that would have already suggested a somewhat more complicated distribution pattern than that outlined in the cited research. For example, Smith and Codrea (2003) reported the presence of a small kogaionid, tentatively referred to the genus *Kogaionon*, from Pui (site PB2)—this occurrence is not discussed or even mentioned in Codrea et al. (2017a). Similarly, Rădulescu and Samson (1986, 1997) had already pointed out the presence of two taxa of differing body sizes in the *Barbatodon transylvanicus* type locality at Pui (site PB1), a suggestion likewise not considered in Codrea et al. (2017a). Finally, at Vălioara-Fântânele (site DC2), Csiki and Grigorescu (2000) emphasized the presence of two differently sized kogaionid taxa, one of which was identified as a medium-sized representative of the genus *Hainina*. Although this taxonomic assignment should be reevaluated in light of our current understanding of local kogaionid morphology, taxonomy, and diversity (see comments for site DC2, above), it is nevertheless clear that at least two, potentially three, different sized kogaionids are represented at this locality (fig. 7G, J; see also Csiki and Grigorescu, 2002). By adding only these occurrences to the list compiled by Codrea et al. (2017a: table 1), the resulting distribution pattern would had been more complex, whereby small kogaionids (regardless of their precise taxonomic identification) would be represented in the Sînpetru Formation and, more specifically, in the Pui Beds cropping out along the Bărbat River south of Pui and a cooccurrence of small and medium-sized kogaionids would also characterize the Densuș-Ciula Formation in addition to the Râul Mare Beds (fig. 18).

Integrating the entire fossil record of latest Cretaceous Transylvanian kogaionids, amounting to 29 fossiliferous sites reviewed in the first part of this contribution, draws an even more complex picture of their spatiotemporal distribution across the former Transylvanian landmass.

One important aspect commonly neglected when reconstructing the geographic distribution of the latest Cretaceous Transylvanian kogaionids is the number of fossiliferous sites that have yielded their remains. A "fossiliferous site" is defined here as a distinct fossil occurrence restricted to a particular bed or short succession of beds, at most a smaller-scale outcrop, that yields one localized fossil accumulation—taphocoenosis—with a particular preservation style and a unique set of taphonomic features (see, e.g., Csiki et al., 2010b for details concerning the taphonomic modes and preservation styles represented in the uppermost Cretaceous of Transylvania), and whose genesis is usually linked to one particular depositional event, regardless of its temporal duration and areal extent. Under this definition, a fossiliferous site (often referred to as fossil site or simply site) can be represented either by an isolated bone fragment or by an extensive bonebed; two fossil occurrences located within the same bed, but recovered at some distance and obviously genetically unrelated represent two distinct fossil sites. We would like to note here that this definition of the term corresponds to what Csiki-Sava et al. (2016) defined as a "fossiliferous locality," and we take this opportunity to emphasize this terminological change we are introducing here, as it appears to correspond more strictly to the ways it is commonly used in the literature, as well as in technical and/or common parlance in the field.

Instead of precision pinpointing to a particular, unique fossiliferous site, very often one or another of the previously reported kogaionid occurrences is cited only as to its fossiliferous locality, i.e., a wider geographic area, represented usually by the name of a village, valley, or hillside that can be used to mark the location of (a) smaller or larger outcropping succession(s) belonging to (a) particular fossiliferous lithostratigraphic unit(s). According to the definitions introduced here, one locality can host a
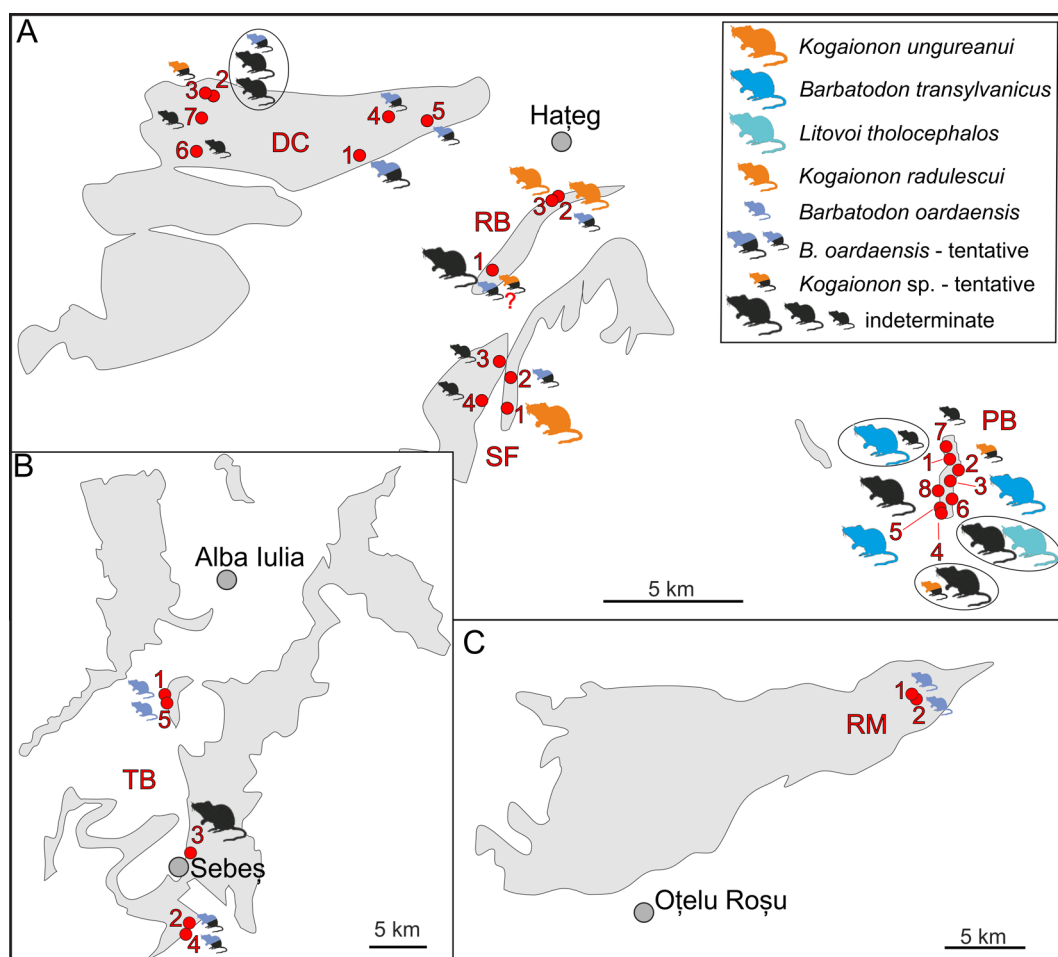
FIGURE 19. Latest Cretaceous Transylvanian kogaionid occurrences, highlighting the spatial distribution of the different taxa; estimated body sizes taken from figure 18. **A.** Haţeg Basin; **B.** southwestern Transylvanian Basin; **C.** Rusca Montană Basin. Question-mark refers to taxonomical uncertainty concerning the small kogaionid taxon from site RB1, in the Haţeg Basin.

large number of fossil occurrences (i.e., sites) with very different taphonomic and depositional histories, sedimentological context, and/or fossiliferous content. Lumping together different sites based on their shared wider locality can lead to an oversimplified (and potentially erroneous) distributional pattern of the fossil remains under study.

In the case of the Transylvanian latest Cretaceous kogaionids, marking only "Pui" as the origin of kogaionid fossils discovered in various spots over a period of several years near Pui village along the Bărbat River (i.e., within the Pui locality) can be very misleading, as these occurrences are spread along the entire local outcropping succession, differ in age, sometimes originate from very different depositional environments, and represent distinct taphonomic histories (fig. 3; see also our review, above). These different occurrences (i.e., sites) are thus actually distinct snapshots recording the faunal succession preserved in the respective sedimentary sequence and may contain not strictly synchronous and/or sympatric taxa. As an example, simply listing Pui as the
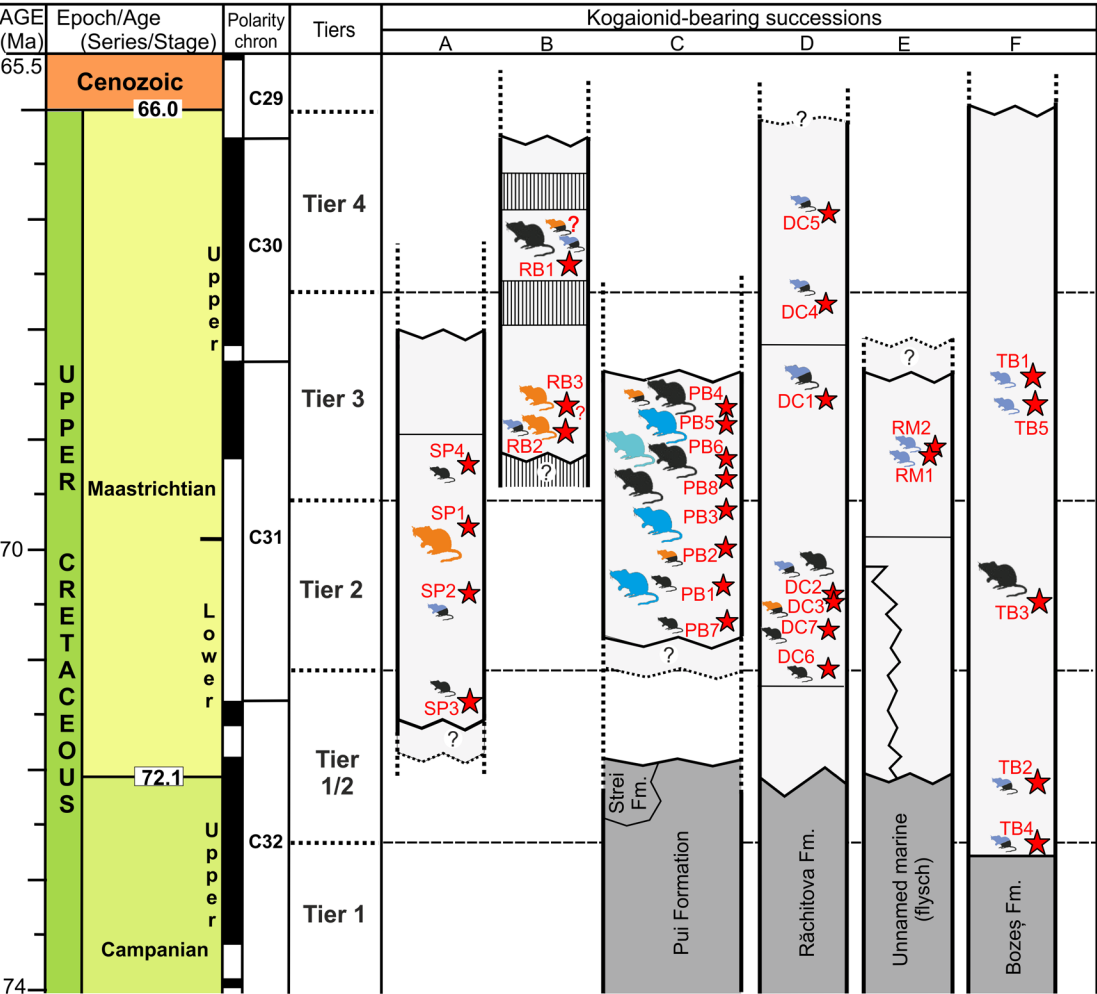
FIGURE 20. Chronostratigraphic distribution of the different kogaionid taxa identified in the uppermost Cretaceous beds of Transylvania. Dark gray, marine deposits; light gray, continental deposits. For color-coding of the taxa, see legend in figure 19.

locality of origin for *Barbatodon transylvanicus* hides the fact that this taxon appears to have a rather extended stratigraphic range in the local succession, having been recovered from at least three distinct layers (see figs. 3, 19, 20).

In order to mitigate such shortcomings, our review contains a breakdown of the Transylvanian kogaionid fossil record to the finest possible level of detail (i.e., fossiliferous site), allowing a much finer-grained representation of their known spatiotemporal distribution than any

attempted previously. Using this database of 29 currently registered kogaionid fossil sites, outlined above (see also tables 4–7), we will explore the topic of kogaionid distribution from five distinct viewpoints: temporal (chronostratigraphical), taxonomical, body size, sedimentological, and preservational (figs. 3, 18–23) to get as detailed an image as possible, in terms of both their patterns of distribution in time and space and some of the biotic and abiotic factors that may have controlled this distribution.

TABLE 4

Selected Dental Measurements Used to Estimate Relative Body Size in Latest Cretaceous Transylvanian Kogaionids from the Sînpetru Formation and the Râul Mare Beds (Haţeg Basin)

See text for details. Fossiliferous sites abbreviated as and arranged according to the order in which they are discussed in the text (see fig. 2). Abbreviations: **L,** left; **R,** right; preserved elements: **C,** cranial fragments; **IT,** isolated teeth; **JT,** dentigerous jaw fragments; **PC,** postcrania.

Site/preservation	Taxon/specimen number [reference]	Element	Dimensions length × width (mm)	Estimated body size
SP1 C	*Kogaionon ungureanui* ISER SPT/001[a]	P1	3.20 × 1.85	large
		P3	5.00 × 1.25	large
		P4	3.70 × 2.15	large
		M1	3.90 × 3.20	large
		M2	2.90 × 2.70	large
SP3 IT	Kogaionidae indet. LPB (FGGUB) M.1631[b, c]	M2	1.16 × 1.26	small
RB1 IT	*Kogaionon* n. sp.[d] or *B. oardaensis* [e]	M1	1.81 × 1.61	small
	Kogaionidae indet.[d, e] or *B. transylvanicus*[f] UBB TBM v.441	M2	2.47 × 2.43	large
RB2 IT, JT	*Barbatodon* n. sp.[g] or *B. oardaensis*[e] UBB TBM v.442	m1	2.14 × 1.47	small-medium
	Kogaionon radulescui[h] UBB NV-Mt1 (specimen possibly from this site, see text for details)	p4	4.48 × 1.52	medium
RB3 C, IT	*Kogaionon radulescui*[h] PSMUBB V-893	p4	4.30 × 1.46	medium
		P1	1.98 × 1.13 (R) 2.10 × 1.16 (L)	medium
		P3	2.68 × 1.33 (R) 2.53 × 1.35 (L)	small
		P4	2.18 × 1.35 (R) 2.24 × 1.31 (L)	small-medium
		M1	2.53 × 2.21 (R) 2.62 × 2.24 (L)	small-medium
		M2	2.22 × 2.13 (R) 2.18 × 2.14 (L)	medium-large

[a] Rădulescu and Samson, 1996.
[b] Csiki, 2005.
[c] This paper.
[d] Codrea et al., 2002.
[e] Codrea et al., 2017a.
[f] Smith and Codrea, 2003.
[g] Smith et al., 2002.
[h] Smith et al., 2022.

TABLE 5

Selected Dental Measurements Used to Estimate Relative Body Size in Latest Cretaceous Transylvanian Kogaionids from the Pui Beds (Haţeg Basin)

See text for details. Fossiliferous sites abbreviated as, and arranged according to the order in which they are discussed, in the text (see fig. 2). Abbreviations: **L,** left; **R,** right; preserved elements, **C,** cranial fragments; **IT,** isolated teeth; **JT,** dentigerous jaw fragments; **PC,** postcrania.

Site/preservation	Taxon/specimen number [reference]	Element	Dimensions length × width (mm)	Estimated body size
PB1 IT	*Barbatodon transylvanicus* ISER PUI.001 [a,b]	m1	3.40 × 2.15	large
	Kogaionidae indet. ISER PUI.002 [a,b]	m2	1.3 × 1.3	small
PB3 IT, JW, PC	*Barbatodon transylvanicus* LPB (FGGUB) M.1635 [b]	p4	6.70 × 2.19 (R) 6.78 × 2.14 (L)	large
		m1	6.70 × 2.19 (R) 6.78 × 2.14 (L)	large
		P3	4.03 × 1.94	large
		M2	2.45 × 2.31	large
PB4 IT	Kogaionidae indet. (*Kogaionon* sp. ?) LPB (FGGUB) M.1671 [b]	M1	1.82 × 1.42	small
PB5 IT, JT, C	*Barbatodon transylvanicus* UBB P-Mt 1 [c]	p4	7.60 × 2.20 (R) 7.60 × 2.20 (L)	large
		m1	3.10 × 2.20 (R) 3.00 × 2.10 (L)	medium-large
		m2	2.00 × 2.10 (R) 2.00 × 2.10 (L)	medium-large
		P1	2.70 × 2.10 (R) 2.60 × 2.10 (L)	large
		P3	4.20 × 2.10	large
		P4	3.30 × 1.90	large
		M1	3.20 × 2.50	medium-large
		M2	2.40 × 2.30 (R) 2.30 × 2.30 (L)	medium-large
	Barbatodon transylvanicus UBB P-Mt 2 [d]	p4	8.60 × 2.40 (R) 7.99 × 2.40 (L)	large
		m1	4.01 × 2.48 (R) 3.37 × 2.39 (L)	large
		m2	2.49 × 2.48	large
		P4	3.82 × 2.10	large
		M1	4.12 × 2.30	large
		M2	2.63 × 2.52	large
	Barbatodon transylvanicus UBB P-Mt 3 [d]	p4	8.60 × 2.40	large
		m1	3.80 × 2.57	large
		m2	2.85 × 2.56	large
		P1	3.05 × 2.49	large
		P4	3.79 × 2.10	large
		M1	3.94 × 3.08	large
		M2	2.85 × 2.59	large

TABLE 5 *continued*

Site/preservation	Taxon/specimen number [reference]	Element	Dimensions length × width (mm)	Estimated body size
PB6 IT, JT, C, PC	*Litovoi tholocephalos* LPB (FGGUB) M.1700[e]	P1	3.15 × 2.32	large
		P3	4.95 × 2.32	large
		P4	3.69 × 1.93	large
		M1	3.52 × 2.33	large
		M2	2.78 × 2.33	large
	Kogaionidae indet. LPB (FGGUB) 1698[b]	p4	7.15 × 2.58	large
		P1	3.33 × 2.12 (R) 3.31 × 2.18 (L)	large
		M1	3.75 × 3.05 (R) 3.75 × 2.98 (L)	large
PB8 JT, C	Kogaionidae indet. LPB (FGGUB) unnumbered[b]	m1	3.93 × 2.40	large
		m2	2.19 × 2.42	medium-large
		P1	2.70 × 1.92	large

[a] Rădulescu and Samson, 1986.

[b] This paper.

[c] Smith and Codrea, 2015.

[d] Solomon et al., 2016.

[e] Csiki-Sava et al., 2018.

Chronostratigraphic Distribution

As summarized in the first part of our review (see also figs. 3, 21), instead of representing one largely synchronous and sympatric assemblage, the latest Cretaceous Transylvanian kogaionids are known to have been spread across a range of several millions of years, ranging possibly from the very latest Campanian or very earliest Maastrichtian to the late Maastrichtian. The precise temporal duration of their presence in the region remains currently uncertain due to the dating limitations of the fossiliferous continental successions (see Csiki-Sava et al., 2016). It is nevertheless clear that the different occurrences and taxa cover a span of at least three and possibly as much as seven million years. Recognizing such a wide chronostratigraphic distribution of the latest Cretaceous Transylvanian kogaionids is of paramount importance, as the rate of evolutionary change is often known to speed up significantly in island environments (e.g., Millien, 2006; Evans et al., 2012; Cucchi et al., 2014), the type of environment these Transylvanian kogaionids inhabited (e.g., Benton et al., 2010).

Given such a wide chronostratigraphic distribution, it follows that temporal separation between the different kogaionid occurrences may suggest the diachronous and allopatric nature of the taxa represented within the respective occurrences. Based on the currently available fossil record, it is clear, for example, that although *Litovoi* and *Barbatodon transylvanicus* were probably partly synchronous and sympatric, this cooccurrence happened for only a short time, sometime during the early late Maastrichtian, and possibly not for the entire stratigraphic range documented for the latter taxon, which is better represented by a number of individuals (figs. 19, 20). On the other hand, whether *Kogaionon ungureanui*, *Barbatodon transylvanicus*, and *Litovoi*—the currently known large kogaionids—were all synchronous and sympatric, cannot be established with any certainty, due to the limitations in dating and correlating the different stratigraphic successions. Their occurrence at different localities and sites may at the least suggest a certain degree of allopatry in their distribution (fig. 19).

TABLE 6

Selected Dental Measurements Used to Estimate Relative Body Size in Latest Cretaceous Transylvanian Kogaionids from the Densuş-Ciula Formation (Haţeg Basin) and the Rusca Montană Basin
See text for details. Fossiliferous sites abbreviated as and arranged according to the order in which they are discussed in the text (see fig. 2). Abbreviations: **L,** left, **R,** right; preserved elements, **C,** cranial fragments; **IT,** isolated teeth; **JT,** dentigerous jaw fragments; **PC,** postcrania.

Site/preservation	Taxon/specimen number [reference]	Element	Dimensions length × width (mm)	Estimated body size
DC1 IT, JT	Kogaionidae indet. LPB (FGGUB) M.1655-M.1656[a]	p4	5.3 × 1.76	medium
		m1	2.14 × 1.66	small-medium
DC2 IT	*Hainina* sp. A[b] or *B. oardaensis*[c] LPB (FGGUB) M.1610, M.1611 (P1), M.1618, M.1619 (m1)	m1	1.45 × 1.00 1.52 × 1.05	small
		P1	1.01 × 0.92 1.03 × 0.93	small
	Hainina sp. B[b] or *B. oardaensis*[c] LPB (FGGUB) M.1613	m1	2.67 × 1.96	medium
	Kogaionon n. sp. or *Hainina* sp. B LPB (FGGUB) M.1624[d]	M1	2.85 × 2.35	medium
	Kogaionidae indet. LPB (FGGUB) M.1625[a, e]	m1	2.12 × 1.35	small-medium
DC3 IT	Kogaionidae indet. (?*Kogaionon* sp.) LPB (FGGUB) M.1654[f]	P1	1.44 × 0.86	small
DC4 IT	Kogaionidae indet.[g] or *B. oardaensis*[c] LPB (FGGUB) M.1672	M1	2.18 × 1.68	small
DC5 IT	Kogaionidae indet.[g, h] or *B. oardaensis*[c] LPB (FGGUB) M.1673	M1	– × 1.24	small
RM1 IT	*Barbatodon oardaensis*[c] UBB Ng1-02	P1	1.20 × 1.09	small
RM2 IT	*Barbatodon oardaensis*[c] UBB Ng2-01 (p4), Ng2-04 (P4)	p4	3.36 × 1.00	small
		P4	1.78 × 1.00	small

[a] This paper.
[b] Csiki and Grigorescu, 2000.
[c] Codrea et al., 2017a.
[d] Csiki and Grigorescu, 2002.
[e] Csiki, 2005.
[f] Vasile, 2008b.
[g] Csiki-Sava et al., 2016.
[h] Vasile et al., 2011a.

Conversely, the taxonomic reinterpretation proposed by Codrea et al. (2017a) according to which all assumedly small latest Cretaceous Transylvanian kogaionids are referred to *Barbatodon oardaensis* makes this taxon both geographically very widely spread (fig. 19) as well as extremely long lived (figs. 20, 21). If such a reinterpretation is upheld by future studies, *B. oardaensis* would then be present in all three main sedimentary areas known to have yielded kogaionid fossils. Moreover, the presence of small kogaionids is currently documented in all major kogaionid-bearing sedimentary successions (figs. 18, 19), that is, not only in Rusca Montană, southwestern Transylvania, the Densuş-Ciula Formation, and the Râul Mare Beds, as listed previously by Codrea et al.

TABLE 7

Selected Dental Measurements Used to Estimate Relative Body Size in Latest Cretaceous Transylvanian Kogaionids from the Southwestern Transylvanian Basin

See text for details. Fossiliferous sites abbreviated as, and arranged according to the order in which they are discussed, in the text (see fig. 2). Abbreviations: **L,** left; **R,** right; preserved elements, **C,** cranial fragments; **IT,** isolated teeth; **JT,** dentigerous jaw fragments; **PC,** postcrania. For site TB1 we use both dimension ranges (l_r, w_r) and mean values (l_m, w_m), for the tooth positions represented by several specimens (for sample size of these tooth positions, see Codrea et al., 2014), as well as the smallest and largest known elements for each tooth position (see Smith et al., 2022: table S1).

Site/preservation	Taxon/specimen number [reference]	Element	Dimensions length × width (mm)	Estimated body size
TB1 IT	*Barbatodon oardaensis*[a] type material, all listed specimens are UBB ODAN specimens (see[a,b] for more details)	p4 Mt-1	3.85 × 1.20	small
		m1 Mt-15 (smallest)	1.91 × 1.26	small
		m1 Mt-14 (largest)	2.24 × 1.48	small
		m1	l_r: 1.91–2.24 l_m: 2.09 w_r: 1.41–1.75 w_m: 1.58	small
		m2 Mt-68	1.20 × 1.48	small
		m2 Mt-77	1.27 × 1.28	small
		m2	l_r: 1.20–1.24 l_m: 1.22 w_r: 1.26–1.48 w_m: 1.34	small
		P1 Mt-38	1.20 × 0.72	small
		P3 Mt-24 (smallest)	1.80 × 0.88	small
		P3 Mt-69 (largest)	2.00 × 1.08	small
		P3	l_r: 1.80–2.10 l_m: 1.89 w_r: 0.8–1.20 w_m: 1.04	small
		P4 Mt-22 (smallest)	1.56 × 0.88	small
		P4 Mt-26 (largest)	2.04 × 1.20	small

TABLE 7 *continued*

Site/preservation	Taxon/specimen number [reference]	Element	Dimensions length × width (mm)	Estimated body size
TB1 IT	*Barbatodon oardaensis* [a] type material, all listed specimens are UBB ODAN specimens (see [a,b] for more details)	P4	l_r: 1.56–2.04 l_m: 1.80 w_r: 0.88–1.20 w_m: 1.04	small
		M1 holotype Mt-13 (close to mean)	2.03 × 1.56	small
		M1 Mt-12 (smallest)	1.93 × 1.55	small
		M1 Mt-65 (largest)	2.32 × 1.72	small
		M1	l_r: 1.93–2.32 l_m: 2.09 w_r: 1.41–1.75 w_m: 1.58	small
		M2 Mt-37 (smallest)	1.18 × 1.41	small
		M2 Mt-16	1.91 × 1.76	medium
		M2	l_r: 1.18–1.91 l_m: 1.51 w_r: 1.16–1.76 w_m: 1.43	small
TB2 IT, JT, C, PC	Kogaionidae indet. [c,d,e] or *B. oardaensis* [f] MMIRS 655	p4	3.54 × 1.35	small
		m1	2.31 × 1.66	medium
		m2	1.53 × 1.64	small
		P1	1.45 × 0.93	small
		M1	2.45 × 1.89	small-medium
TB3 JT	Kogaionidae indet. [e,g] MMIRS 666	p4	7.90 × 2.00	large
TB4 IT	Kogaionidae indet. [e,g,h] EME material, unnumbered	m1	2.50 × 1.20 2.28 × 1.21	medium
		m2	1.80 × 1.50	medium
		P1	1.00 × 0.90	small
		P4	2.10 × 1.30	small
		M1	2.24 × 1.66 2.30 × 1.76	small
TB5 IT	*Barbatodon oardaensis* [b] UBB ODBL-Mt-4 (P3), UBB ODBL-Mt-5 (P4)	P3	2.06 × 1.15	small
		P4	1.75 × 1.03	small

[a] Codrea et al., 2014.
[b] Smith et al., 2022.
[c] Csiki-Sava et al., 2012.
[d] Vremir et al., 2014.
[e] This paper.
[f] Codrea et al., 2017a
[g] Vremir et al., 2015a.
[h] Vremir et al., 2015b.
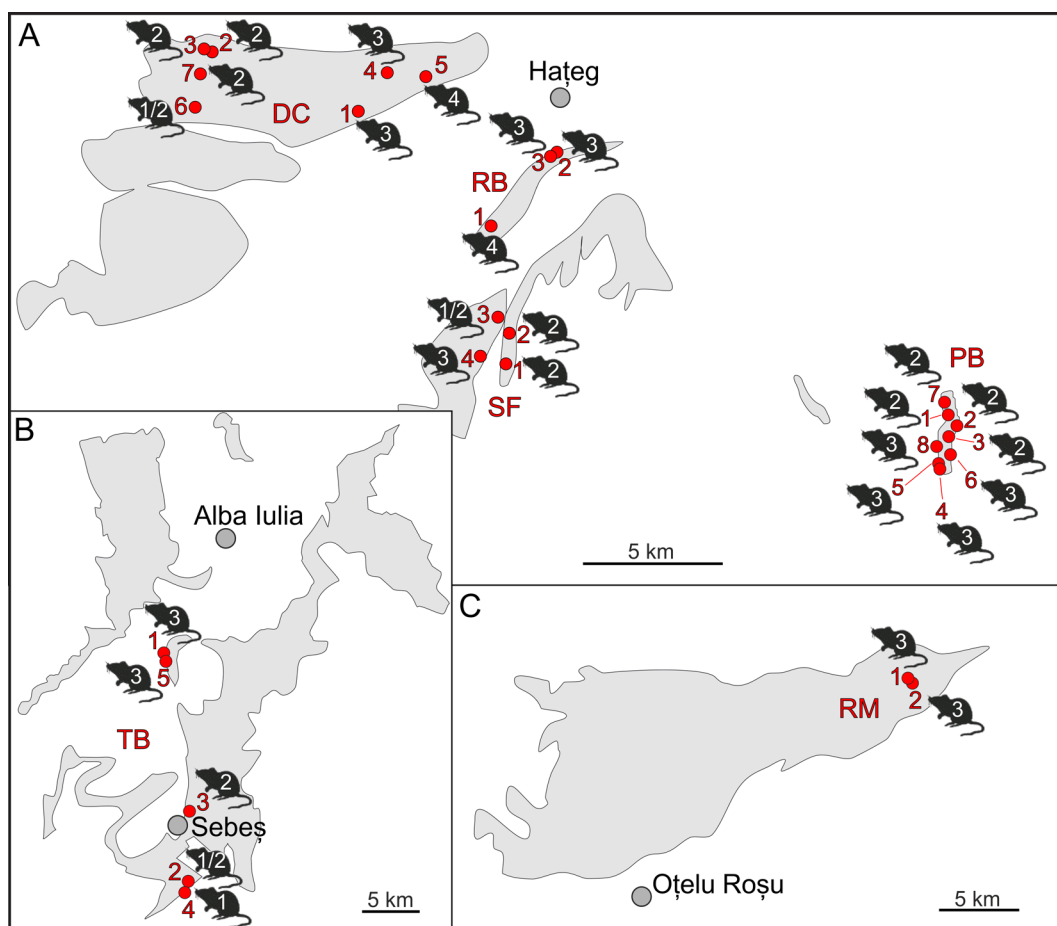
FIGURE 21. Latest Cretaceous Transylvanian kogaionid occurrences, highlighting the spatial distribution of the different chronofaunal tiers represented. Numbers within kogaionid silhouettes refer to their respective tiers (see fig. 3). **A.** Haţeg Basin; **B.** southwestern Transylvanian Basin; **C.** Rusca Montană Basin.

(2017a), but also in the Sînpetru Formation and the Pui Beds. Given this, on the same grounds it should be assumed that *B. oardaensis* was distributed across the entire known geographic range of the latest Cretaceous Transylvanian kogaionids. On the other hand, the temporal extension of *B. oardanesis*, defined according to the reinterpretation given by Codrea et al (2017a)—i.e., *the* small Transylvanian kogaionid—would cover the entire known chronostratigraphic range of the latest Cretaceous Transylvanian kogaionid fossil record (figs. 3, 20, 21), from the latest Campanian into the late Maastrichtian (possibly as much as 4 to 6 Ma). Such an extensive temporal range of *B. oardaensis* stands in marked contrast with that documented for all its larger relatives from the Transylvanian landmass, all of which have a much more restricted temporal distribution (and extremely localized ones in the cases of *Kogaionon ungureanui* and *Litovoi*, both currently represented by only one individual; fig. 20). Incidentally, a similarly restrictive chronostratigraphic distribution is also known to characterize the species of the Paleocene kogaionid *Hainina*, despite the fact that some species of that genus (*H. belgica*, *H. pyrenaica*) overlap with *B. oardaensis* in body size (Peláez-Campomanes et al., 2000; De Bast and Smith, 2017). We also note
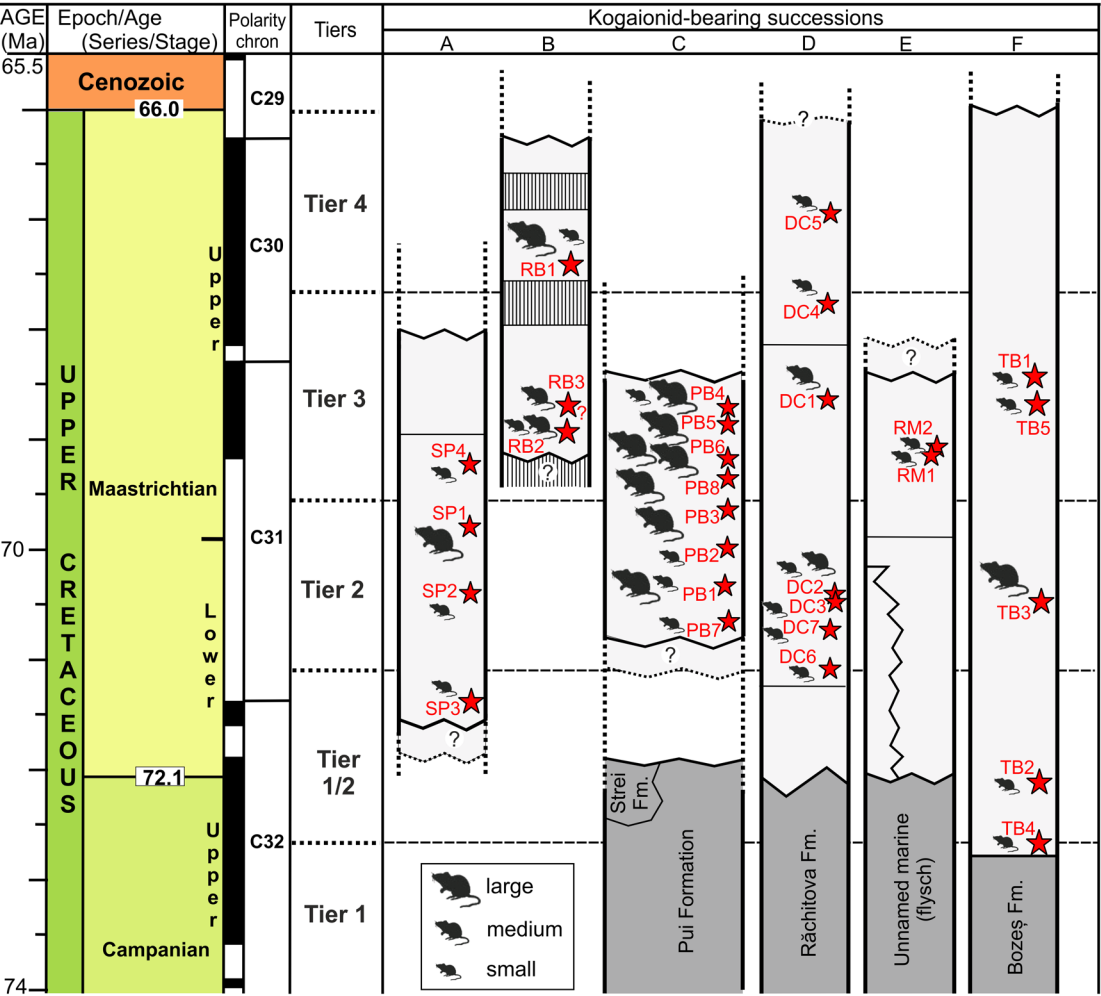
FIGURE 22. Chronostratigraphic distribution of the estimated body sizes of known latest Cretaceous Transylvanian kogaionid occurrences. Dark gray, marine deposits; light gray, continental deposits.

that, in theory, it might be surprising for a single small mammal species to persist for 4–6 million years in any environment, much less in an island environment where evolutionary rates are likely to have been higher with selective pressures different from the mainland (e.g., Cucchi et al., 2014).

Whether the taxon-related distributional pattern proposed by Codrea et al. (2017a) is real or is biased by differential preservation and recovery of the remains of the different taxa and/or by current, partly unsubstantiated taxonomic inter-

pretations can be established only with the discovery of further kogaionid fossil occurrences, as well as with detailed description and sound taxonomic identification of the material available for study. In particular, we need to untangle whether there is a single small kogaionid species spanning the temporal and geographical spread of the Transylvanian deposits (figs. 19, 20) that can be confidently diagnosed by a set of apomorphies or whether these small kogaionid specimens represent a constellation of species, each with its own clear diagnosis.
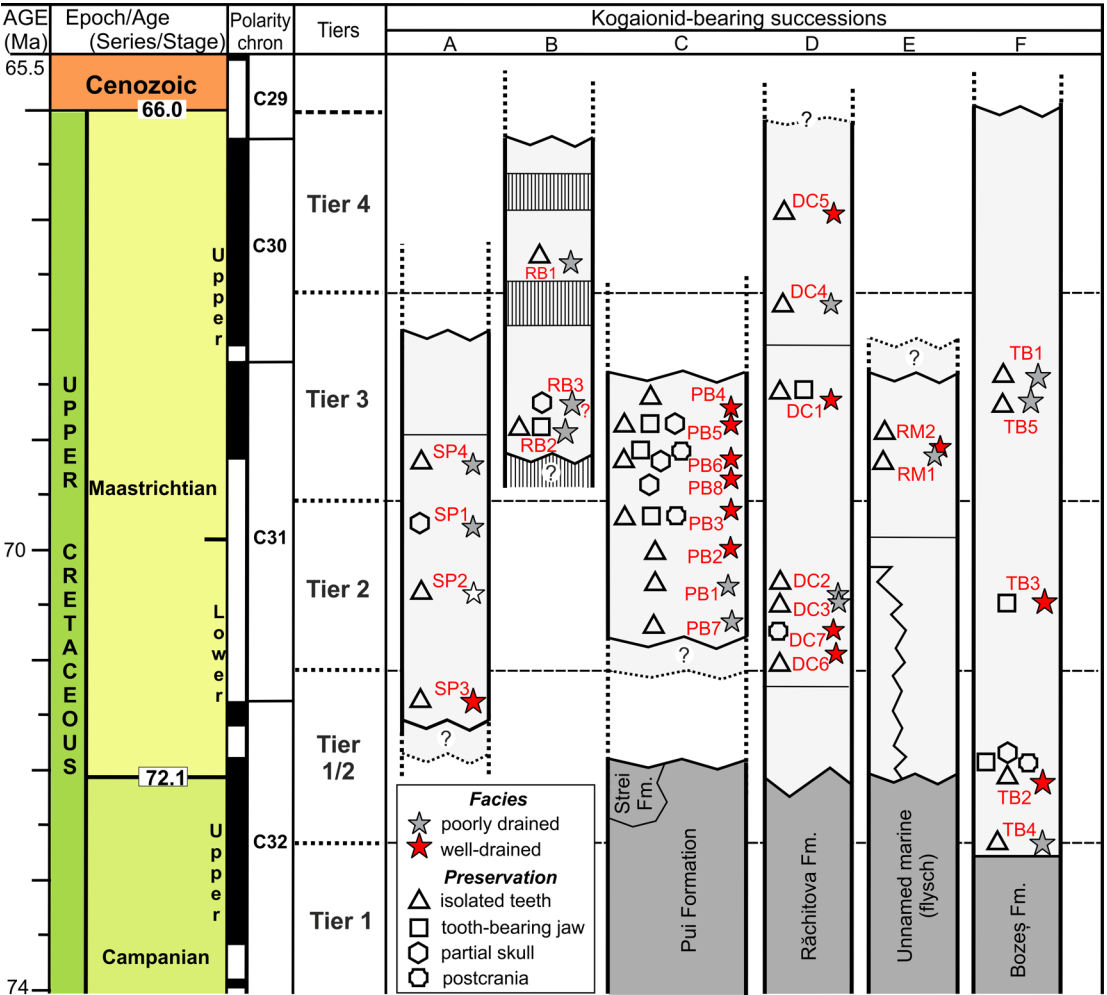
FIGURE 23. Chronostratigraphic distribution of the sedimentary facies represented, combined with the nature of the kogaionid remains recovered, at the different uppermost Cretaceous Transylvanian kogaionid sites. Dark gray, marine deposits; light gray, continental deposits.

Body-Size Distribution

Codrea et al. (2017a) noted an apparently partially exclusive spatial distribution of the latest Cretaceous Transylvanian kogaionids depending on their estimated body size. According to their model, whereas only small kogaionids (assumed to be represented by *Barbatodon oardaensis*) were present in the Transylvanian and Rusca Montană basins, as well as in the Densuş-Ciula Formation (while occurring together with medium-sized taxa locally in the Râul Mare

Beds), the Sînpetru Formation and the Pui Beds were dominated by large multituberculate taxa (represented by *Kogaionon ungureanui*, and by *Barbatodon transylvanicus* and *Litovoi*, respectively).

Our review of the currently known latest Cretaceous Transylvanian fossil record of the kogaionids suggests, however, a much more complex and mosaiclike body-size distribution pattern, both in space and in time (figs. 18, 22). In order to arrive at a semiquantitative, albeit preliminary and rather coarse, estimate of the body size of the dif-

ferent kogaionids, we have tabulated absolute dimensions (length, whenever available) of the cheekteeth (especially the upper and lower fourth premolars and first molars; see below) of the different Transylvanian kogaionids (tables 4–7), and these raw dimensions were used as very rough proxies for body size (see Csiki-Sava et al., 2018, for more detailed approaches to body-size estimates in kogaionids; converting tooth measurements to mass estimates is difficult because the lack of any extant multituberculates makes identifying accurate scaling formulas problematic).

For all specimens available to us, including as yet undescribed ones, the length of the teeth were measured directly (see below). Other dental measurements were taken either from publications in cases where such data are reported (e.g., Rădulescu and Samson, 1996; Codrea et al., 2014, 2017a; Smith and Codrea, 2015; Solomon et al., 2016; and especially Smith et al., 2022: table S1) or the length of the teeth was measured using published figures in the few cases when the specimens themselves (or their measurements) were unavailable to us (e.g., Codrea et al., 2002: fig. 4h, i; Smith et al., 2002: pl. I, fig. 1, 2; fig. 7B, H). The measurements were made using ImageJ software on available digital microphotographs and/or SEM images, checked whenever possible through direct measurements of the specimens themselves using a 0.1 mm precision digital caliper. Whenever a taxon and/or a dental position was represented by several individuals/specimens, we have included as many individual measurements as possible to account for potential intraspecific size differences (e.g., Csiki et al., 2005; Codrea et al., 2014; Smith and Codrea, 2015; Solomon et al., 2016). In cases where individual tooth measurements were not expressly listed in the original publication (Codrea et al., 2014), we have relied on the published mean dimensions to estimate rough body size based on tooth size values that were considered representative for that specific taxon (i.e., *B. oardaensis*), but also tried to take into account the reported ranges of dimensions, by assessing estimated body size based on the smallest and largest specimens referred to that

particular taxon and using the raw dental measurements provided in Smith et al. (2022: table S1). Finally, in one particular case (site PB2) where published information about the existing kogaionid material is extremely scarce, restricted to a very brief comment in a conference abstract (Smith and Codrea 2003), we will employ the authors' own general size assessment.

In order to arrive at a coarse relative body size estimate for the different latest Cretaceous Transylvanian kogaionids, we have divided the documented size (length) range for the different measured tooth positions into three equal intervals that would roughly correspond to small, medium-sized, and large taxa. To achieve an even finer resolution in kogaionid body size variability, we have also defined transitional categories between the main ones, demarcated as the upper quartile of the corresponding lower body size division (i.e., small-to-medium body size corresponds to teeth falling into the 75% to 100% length range of their respective "small" category). We have employed these transitional categories alongside the major ones (small, medium, large) in the size estimates tabulated in tables 4–7 in order to offer a detailed overview of the currently known body-size variability within the latest Cretaceous kogaionids, although for the sake of simplicity we presented only the major categories in the corresponding figures (figs. 18–20, 22). Whenever possible, we have used as many postcanine tooth positions as were available for the same individual to check whether these additional teeth give a coherent signal as to the estimated body size of the individual. In cases where mean length values and range of lengths were tabulated in previous publications instead of individual tooth dimensions (e.g., Codrea et al., 2014), we checked whether the reported intraspecific ranges still fall within the same size category as that suggested by the mean as well as by the smallest and largest referred tooth specimens. Admittedly, our preliminary approach to estimating kogaionid body size is very coarse, but it still gives a more reliable picture of the relative body size distribution within the studied

material than the widespread previous practice that qualitatively noted the "small" or "large" size of the described specimens. Also, it should be emphasized that these size categories are devised simply to illustrate relative kogaionid body size and do not allow for comparing kogaionids directly with other multituberculates (or more distantly related mammals) sizewise.

Using this straightforward approach to estimate size, a more complex overall picture of body size–related kogaionid distribution pattern emerges (figs. 18, 22). First of all, by integrating the entire known kogaionid fossil record, the previously suggested and largely exclusive scenario of two-sided body-size distribution (small kogaionids in some of the fossiliferous sedimentary units, large kogaionids in others; Codrea et al., 2017a) collapses almost entirely. One exception to this is the Rusca Montană Basin, where small kogaionids continue to be the only ones represented. However, it is worth emphasizing that the kogaionid fossil record is also the poorest in this sedimentary succession, with a very small number of isolated teeth reported from two very closely located sites. It is thus possible that the exclusive presence of small kogaionids here is biased by the available sample size. Other than in the case of the Rusca Montană Basin, however, smaller and larger kogaionids cooccur everywhere in the different fossiliferous successions and even within the same fossiliferous site, although small-scale spatial distinctions still appear to hold. Thus, in the Densuș-Ciula Formation small kogaionids are the most commonly found and are associated in this unit with only medium (at most, medium-to-large) taxa, whereas large kogaionids are yet to be reported from here. Meanwhile, in the Pui succession large kogaionids appear to dominate. Nevertheless, they are associated here along the entire thickness of the outcropping succession with small taxa, occasionally even within the same site (e.g., in sites PB1, PB4).

One pattern that appears to emerge, however, is a delayed first occurrence date of the larger kogaionids compared to their smaller relatives,

regardless of the fossiliferous succession considered (fig. 22; see also Csiki-Sava et al., 2021b). Indeed, the oldest kogaionid occurrences in the entire Transylvanian landmass, as well as within each individual succession, are represented by taxa of small (more rarely small-to-medium) body size, and large kogaionids make their appearance only somewhat later, well within the early Maastrichtian at the earliest. Although this pattern may also represent the byproduct of a biased sample (i.e., the presence of comparatively few and more fossil-poor early localities compared with younger ones), such an alternative explanation seems to be less parsimonious because: (1) the same pattern of early small taxa appears to be generalized across the entire landmass (figs. 18, 22); (2) remains of larger taxa, if present, would have probably been easier to spot and recover than the minute remains of smaller ones; and (3) at least in some of the chronostratigraphically early occurrences (such as site TB4 from Petrești) the kogaionid fossils are decently abundant and probably would have revealed the presence of differently sized taxa.

Furthermore, these oldest known kogaionid occurrences originate from deposits accumulated in both poorly drained and well-drained floodplain environments (fig. 23), and thus a possible paleoenvironmental/paleoecologial body size bias can also be ruled out. This is not to say that larger taxa might not have been present around the Campanian-Maastrichtian boundary on the Transylvanian landmass (although this remains a distinct possibility), but even if present, these were definitively less common than their smaller relatives in the paleoenvironments and areas sampled by their earliest fossil record. This may indicate that not only the Transylvanian island as a whole, but individual geographic regions of the island as well, were first settled by small colonizers, and while some of their possible descendants remained small, others got larger over time. The fact that the latest Cretaceous large kogaionids from the Transylvanian area do seem to form a tight clade within Kogaionidae (see Csiki-Sava et al., 2018;

Smith et al., 2022; fig. 4B, C) is consistent with such a hypothetical scenario of in situ evolution toward larger body size.

One other pattern that appears to emerge is a correlation between body size and preservation style (see also below). Virtually all small kogaionid specimens for which there is available information, whether taxonomically diagnosable or not, are represented by isolated teeth (e.g., Codrea et al., 2014, 2017a); one remarkable exception to this pattern is the small, associated kogaionid specimen from site TB2 reported by Vremir et al. (2014; see also Csiki-Sava et al., 2012; fig. 7K, table 7), currently under study. On the other hand, virtually all large kogaionids are represented at least by tooth-bearing jaw elements associated with isolated teeth (e.g., Solomon et al., 2016), but more commonly also by skull remains or even by associated cranial, dental, and postcranial elements (e.g., the holotypes of *Kogaionon ungureanui* and *Litovoi*); in this regard, the only medium-sized nominal taxon erected so far, *K. radulescui*, also conforms to the pattern found in the large taxa. The fact that larger individuals seem to be preserved more commonly as more complete, associated specimens makes the finding of exclusively small individuals—represented almost entirely by isolated teeth—near the base of each succession all the more striking, and probably all the more likely to represent a genuine evolutionary signal.

The emerging pattern thus suggests that increasing body size appears to be an important driver for quality and type of preservation and through this it may also further impact the diagnostic nature of the recovered remains—it is probably not accidental that the number of nominal taxa, as well as that of the positively diagnosable specimens, within the currently known latest Cretaceous Transylvanian kogaionid assemblage is higher at larger body size (three taxa) than at medium (one taxon) or small (one taxon) size. This pattern of taxic diversity may be thus in part a byproduct of body size–related differential preservation and may not reflect the true taxic diversity within the assemblage. If so,

this may indicate that many individual small species are currently being lumped together as a single, small taxon (*Barbatodon oardanesis* in the taxonomic scheme of Codrea et al., 2017a) because the limited dental material is not sufficient for establishing confident diagnoses of multiple taxa. Such diagnoses would be easier if there were more complete and associated remains of these small kogaionids, as is the case with the larger taxa higher in the successions.

SEDIMENTARY FACIES DEPENDENCE AND
PRESERVATION STYLE

One final combination of distribution patterns to be considered here preliminarily is the facies-dependant distribution of the kogaionid fossils and its potential correlation with preservation style and quality. As already mentioned, the latest Cretaceous Transylvanian fossil record of kogaiond multituberculates is remarkable in that it includes a decent number of very nicely preserved and rather complete specimens, including partial skulls and associated postcrania, along with a large number (well over 100) of isolated teeth. This stands in stark contrast both with the contemporaneous Western European mammalian fossil record (represented mainly by lainodontine zhelestid eutherians, with very rare remains of metatherians and peculiar eutherians; Martin et al., 2005; Gheerbrant and Astibia, 2012; Gheerbrant and Teodori, 2021), as well as with the later, Paleocene fossil record of the kogaionids themselves, represented there exclusively by isolated teeth (e.g., Vianey-Liaud, 1979, 1986; Gheerbrant et al., 1999; Peláez-Campomanes et al., 2000; De Bast and Smith, 2017). In this regard, the Transylvanian kogaionid fossil record is remarkable even at a global level for the latest Cretaceous, for which mammalian (and especially multituberculate) remains are often rather incomplete (see Kielan-Jaworowska et al, 2004), despite examples of remarkable mammalian fossil preservation reported from Mongolia (e.g., Kielan-Jaworowska et al., 2000), China (e.g., Xu et al., 2015), and North America (Weaver et al., 2021).

Based on our review of the latest Cretaceous Transylvanian kogaionids, their remains appear to be widespread and not linked to one particular type of facies (fig. 23). Admittedly, fine-grained floodplain facies deposits are relatively more likely to preserve the remains of these animals that in the grand scheme of vertebrate size classes are small and fit into the microvertebrate category (body size less than 5 kg; see Csiki-Sava et al., 2018 for more precise body size estimates of some Transylvanian kogaionids). Indeed, virtually all known kogaionid remains have been discovered in fine-grained (at most fine sandy-silty) deposits of floodplain or pond origin. But within the fine-grained sediment category, kogaionid remains are equally well represented (considering the number of kogaionid-yielding sites) both in reddish-brownish sediments that suggest well-drained floodplain environments (14 sites) and in greenish-gray to dark gray-blackish sediments formed in more poorly drained, even ponding floodplain settings (also 14 sites; fig. 23).

Beyond this nonselective overall facies-related distribution of the kogaionid remains, however, certain patterns seem to emerge if sedimentary facies is correlated with preservation style (fig. 23). Our review suggests that poorly drained floodplain deposits are more prone to yield assemblages of isolated teeth and the more complete kogaionid remains recovered from these deposits are usually represented only by rare examples of tooth-bearing jaw fragments (e.g., Smith et al., 2002). Meanwhile, better-preserved and more complete kogaionid specimens occur more commonly in red-colored, often calcrete-bearing floodplain paleosols. With the notable exception of the holotype crania of the two *Kogaionon* species (*K. ungureanui* from site SP1 and *K. radulescui* from site RB3) derived from gray-colored sediments, all other examples of associated partial kogaionid skeletons (i.e., those that also include skull remains and/or postcrania) have been found in red calcareous paleosols, whether at Petreşti (site TB2) or at Pui (sites PB3, PB5, PB6, and PB8). There is an even more

marked imbalance in this respect when the number of individuals represented is considered: a total of two individuals, one from each site, come from the gray facies deposits, compared with a minimum of eight individuals recovered from red facies deposits. This pattern of preservational style-related differential facies distribution is independent of relative body size—red-colored paleosols yielded both small (at Petreşti; site TB2) and large (at Pui, site PB6) kogaionid partial skeletons, whereas dark-colored ponding deposits similarly yielded isolated teeth representing different sized taxa, often coming from the same site such as at Toteşti-baraj (site RB1) or Vălioara-Fântânele (site DC2). Remarkably, partial skeletons (represented by incomplete crania) recovered from gray, reductive facies deposits belong exclusively to medium-sized (site RB3) or large (site SP1) taxa.

One final consideration regarding the sedimentary facies-related preservation pattern of the kogaionids emerges when separately considering the localities that yielded attritional assemblages of isolated teeth and dentigerous jaw elements, usually from either specimen-rich or specimen-poor MvBBs. In their case, the kogaionid-bearing MvBBs tend to occur more commonly in poorly drained, gray deposits (8 sites conserving more than one or two isolated teeth: RB1, RB2, PB1, DC2, RM1, TB1, TB4, TB5) compared with those identified in red-colored, well-drained beds (4 sites: PB2, PB4, DC1, RM2). The facies-related differences between these two types of MvBBs become even more trenchant once the quality and quantity of their respective kogaionid fossil assemblages are compared: whereas the MvBBs discovered in gray-colored deposits often yielded tens (even several tens, in the cases of sites DC2 and TB1) of kogaionid teeth, sometimes also associated with dentigerous jaw elements, those identified in red-colored deposits are less specimen-rich (at least three of the four sites listed above yielded fewer than 10 specimens, with no reliable quantitative data available for site PB2), and dentigerous jaw elements are also exceedingly rare in these MvBBs.

If we further consider that in most cases better preservation and presence of skeletal association also equates with autochthony (or, at most, para-autochthony) of the respective remains, whereas the assemblages of isolated kogaionid teeth are commonly recovered from microvertebrate bonebeds of attritional origin (and thus are most likely para-autochthonous to allochthonous), it appears that at least some kogaionids had a certain habitat preference for better-drained, pedogenetically modified dry floodplain areas. Such a preference for semiarid, dry, and open floodplain environments identified for the kogaionids would be consistent with the widespread, assumed habitual presence and often in situ preservation of various other cimolodontan multituberculates in similar environments in both North America (e.g., Weaver et al., 2021) and Asia (e.g., Kielan-Jaworowska and Gambaryan, 1994). Such a presumed habitat preference of the latest Cretaceous Transylvanian kogaionids may find further support in the detailed study of their postcranial anatomy and their detailed taphonomy.

In particular, we suspect that some of the best preserved and associated multituberculate skeletons from Transylvania belong to taxa and/or individuals that may have been living in burrows, and were killed, buried, and fossilized in situ. Multituberculates had been considered historically as mainly saltatorial terrestrial animals (Gidley, 1909) or as having a semiarboreal (Simpson, 1926) or arboreal (Jenkins and Krause, 1983; Krause and Jenkins, 1983) lifestyle. Nevertheless, there is a growing amount of evidence to suggest that at least some multituberculates were semifossorial instead; inferences for such a lifestyle have been based on details of their cranial (e.g., Miao, 1988; Ladevèze et al., 2010; Rougier et al., 2016) and postcranial (Kielan-Jaworowska, 1989; Kielan-Jaworowska and Qi, 1990) anatomy. The recent discovery of the spectacular multituberculate burrowing assemblage in the uppermost Cretaceous of North America by Weaver et al. (2021) provides definitive evidence that some multituberculates were fossorial, making our conjecture even more plausible, but it will need to be tested in the future by: (1) assessing whether the Transylvanian multituberculates had burrowing adaptations in their cranial and/or postcranial skeletons; and (2) careful field work establishing whether there is sedimentological evidence for burrows in these floodplain environments and, in particular, whether individual kogaionid skeletons are found within identifiable burrows.

CONCLUDING SUMMARY

We present a thorough review of the latest Cretaceous (?latest Campanian–Maastrichtian) fossil record of the European endemic clade of kogaionid multituberculates, restricted solely at that time to the Transylvanian area of present-day Romania, a region that can be reliably reconstructed as an isolated landmass (the Hațeg Island or Transylvanian Landmass) for this time interval. Overall, 29 different latest Cretaceous kogaionid fossil occurrences are reported from the Transylvanian area (see table 8), mainly from the Hațeg Basin (22 occurrences), followed by the Transylvanian Basin (five occurrences), and the Rusca Montană Basin (two occurrences). The large number of kogaionid-bearing fossiliferous sites, together with the nature of their fossil record, which also includes partial skulls and incomplete skeletons, makes the Transylvanian area unique within Europe, as does the exclusive presence of the kogaionids.

We explore in detail the sedimentological and paleontological context of each individual fossil occurrence (site), review its history of research, and comment on the nature and implications of the kogaionid remains discovered there. Besides simply reviewing the previously already reported kogaionid fossil sites, we also report here four new kogaionid occurrences (two at Sânpetru—sites SP3 and SP4, and two at Pui—sites PB4 and PB8) and describe the material discovered in most of these newly reported sites, as well as offer further details concerning some of the already known localities.

TABLE 8

Overview of the Latest Cretaceous Transylvanian Kogaionid Fossil Record
For details and relevant references for each fossiliferous site, see text. Collecting method abbreviations used:
SC, surface collecting; **SW,** screenwashing.

Area/unit Locality/site	Estimated age/ chronofauna tier	Lithofacies/ collecting method	Kogaionid taxa present	Skeletal parts represented	Body size estimate
Haţeg Basin, Sînpetru Formation					
Sânpetru, Sibişel Valley, SP1	early-late Maastrichtian boundary, Tier 2 or Tier 3	gray-green siltstone; reducing floodplain/SC	*Kogaionon ungureanui* type locality	cranium with upper dentition	large
Sânpetru, Sibişel Valley, SP2	early Maastrichtian, Tier 1/2	"silty"; ?/SW	Kogaionidae indet.	isolated tooth	small
Sânpetru, Sibişel Valley, SP3	early early Maastrichtian, Tier 2	reddish-brown silty mudstone; oxidized floodplain/SW	Kogaionidae indet.	isolated teeth	small
Sânpetru, Sibişel Valley, SP4	late early Maastrichtian; probably Tier 3	greenish silty mudstone; reducing floodplain/SW	Kogaionidae indet.	isolated tooth	small
Haţeg Basin, Râul Mare Beds					
Toteşti-baraj, RB1	late Maastrichtian; Tier 4	dark gray silty mudstone; reducing floodplain/SW	*Kogaionon* n. sp. or *Barbatodon oardaensis* (see text for details)	isolated teeth	small
			Kogaionidae indet. (or *Barbatodon transylvanicus*)	isolated teeth	large
Nălaţ-Vad, RB2	early-late Maastrichtian boundary, Tier 3	dark gray mudstone; reducing floodplain/SW	*Barbatodon* n. sp. or *Barbatodon oardaensis*	isolated teeth, tooth-bearing jaw fragments	small-medium
			? *Kogaionon* sp.	isolated teeth, tooth-bearing jaw fragments	small?
			Kogaionon radulescui	tooth-bearing jaw element	medium
Nălaţ-Vad, RB3	early-late Maastrichtian boundary, Tier 3	gray marl; reducing floodplain/SC	*Kogaionon radulescui*	cranium with upper dentition and p4	medium
Haţeg Basin, Pui Beds					
Pui, Bărbat River, PB1	early Maastrichtian; Tier 2	gray-green silty sandstone; reducing floodplain/SC, SW	*Barbatodon transylvanicus* type locality	isolated tooth	large
			Kogaionidae indet.	isolated teeth	small
Pui, Bărbat River, PB2	early-late Maastrichtian boundary, Tier 3	red silty mudstone; oxidized floodplain/SW	*Kogaionon* n. sp.	isolated teeth	small

TABLE 8 *continued*

Area/unit Locality/site	Estimated age/ chronofauna tier	Lithofacies/ collecting method	Kogaionid taxa present	Skeletal parts represented	Body size estimate
Pui, Bărbat River, PB3	early-late Maastrichtian boundary, Tier 3	red sandy siltstone; oxidized floodplain SC, SW	*Barbatodon transylvanicus*	associated teeth, tooth-bearing jaws, postcrania	large
Pui, Bărbat River, PB4	early late Maastrichtian; Tier 3	red silty mudstone; oxidized floodplain/SW	Kogaionidae indet. (?*Kogaionon* sp.)	isolated teeth	small
			Kogaionidae indet.	isolated teeth	large
Pui, Bărbat River, PB5	early late Maastrichtian; Tier 3	red siltstone; oxidized floodplain/SC, ?SW	*Barbatodon transylvanicus*	associated teeth, tooth-bearing jaws, crania	large
Pui, Bărbat River, PB6	early late Maastrichtian; Tier 3	red mudstone; oxidized floodplain/SC, SW	*Litovoi tholocephalos* type locality	associated teeth, tooth-bearing jaws, cranium, postcrania	large
			Kogaionidae indet.	associated teeth, tooth-bearing jaws, cranium	large
Pui, Bărbat River, PB7	early Maastrichtian; Tier 2	dark gray silts; reducing floodplain/SW	Kogaionidae indet.	isolated teeth	small
Pui, Bărbat River, PB8	early late Maastrichtian; Tier 3	red silty mudstones; oxidized floodplain/SC, SW	Kogaionidae indet.	associated tooth-bearing jaws, cranium	large

Hațeg Basin, Densuș-Ciula Formation

Tuștea, DC1	early to "mid" -Maastrichtian; Tier 2	red silty mudstones; oxidized floodplain/SW	Kogaionidae indet. or *Barbatodon oardaensis*	isolated teeth, associated tooth-bearing jaw fragments	medium
Fântânele, Vălioara, DC2	early Maastrichtian; Tier 2	gray-green silty mudstone; reducing floodplain/ SW	*Hainina* sp. A or *Barbatodon oardaensis*	isolated teeth	small
			Hainina sp. B or Kogaionidae indet.	isolated teeth	medium
			Kogaionidae indet.	isolated teeth	medium
Fântânele 2, Vălioara, DC3	early Maastrichtian; Tier 2	gray-green silty mudstone; reducing floodplain/ SW	Kogaionidae indet. (? *Kogaionon* sp.)	isolated teeth	small
Livezi, DC4	early late Maastrichtian; Tier 3	gray mudstone; reducing floodplain/SW	Kogaionidae indet. or *Barbatodon oardaensis*	isolated teeth	small
GB1, General Berthelot, DC5	early late Maastrichtian; Tier 3	red silty mudstones; oxidized floodplain/SW	Kogaionidae indet. or *Barbatodon oardaensis*	isolated tooth	small

TABLE 8 *continued*

Area/unit Locality/site	Estimated age/ chronofauna tier	Lithofacies/ collecting method	Kogaionid taxa present	Skeletal parts represented	Body size estimate
K1, Ciula Mică, DC6	early Maastrichtian; Tier 2	red silty mud-stones; oxidized floodplain/SC	Kogaionidae indet.	isolated tooth	small
K3, Vălioara, DC7	early Maastrichtian; Tier 2	red silty mud-stones; oxidized floodplain/SC	Kogaionidae indet.	postcrania	small
Rusca Montană Basin, unnamed unit					
Fărcădeana, Negoiu 1, RM1	early late Maastrich-tian; Tier 2 or 3	black sandy clay-stone; reducing floodplain/SW	*Barbatodon oardaensis*	isolated teeth	small
Fărcădeana, Negoiu 2, RM2	early late Maastrich-tian; Tier 2 or 3	red siltstones; oxidized flood-plain/SW	*Barbatodon oardaensis*	isolated teeth	small
Transylvanian Basin, Sebeș Formation					
ODAN, Oarda de Jos, TB1	early late Maastrich-tian; Tier 3	gray-greenish silty mudstone; reducing flood-plain /SW	*Barbatodon oardaensis* type locality	isolated teeth	small
Level L1a, Petreşti-Arini, TB2	Early Maastrichtian, Tier 1/2	red silty mud-stones; oxidized floodplain/SC	Kogaionidae indet. or *Barbatodon oardaensis*	associated teeth, jaws, cranium, postcrania	small-medium
Sebeș-Glod A, TB3	Early Maastrichtian, Tier 2	red silty mud-stones; oxidized floodplain/SC	Kogaionidae indet.	tooth-bearing jaw fragment	large
Level L0/c, Petreşti-Arini, TB4	latest Campanian or near Campanian-Maastrichtian boundary, Tier 1	gray mudstone; reducing flood-plain/SW, SC	Kogaionidae indet.	isolated teeth	small-medium
ODB lens, Oarda de Jos, TB5	early late Maastrich-tian; Tier 3	dark gray to blu-ish mudstone; reducing flood-plain/SW	*Barbatodon oardaensis*	isolated teeth	small

Most importantly, we (1) discuss the nature and identity of the (scarce) kogaionid material reported from the type locality of *Barbatodon transylvanicus*, the first Transylvanian kogaionid taxon to be described; by doing so, we note the presence of a higher kogaionid taxic diversity at this site than it was often acknowledged in the past and reassess the identity of the multituberculate incisors reported previously from here, and which were used to suggest the presence of two different higher-level multituberculate clades on the Haţeg Island;

(2) report and describe new, previously unknown dental locations for an associated skeleton of *Barbatodon transylvanicus* from Pui (site PB3) and provide reliable dental measurements for this specimen; and (3) report newly discovered kogaionid material from previously known sites, most of which is currently under evaluation.

Based on our comprehensive review of their fossil record, we also reassess our current views concerning the spatiotemporal distribution of the latest Cretaceous Transylvanian kogaionids.

By doing so, we identify a much more complex picture of this distribution, one in which:

(1) The temporal duration of the kogaionid presence in the Haţeg Island is evaluated for the first time to range across several millions of years, suggesting that all these kogaionids were probably not strictly synchronous, but instead represent members of successive chronofaunas;

(2) The relatively simple, twofold small-versus-large body-size-based geographic distribution pattern of the kogaionids, as described by Codrea et al. (2017a), is reevaluated and a more complex pattern is identified in which smaller and larger taxa cooccur for long time intervals in most kogaionid-bearing sedimentary successions;

(3) Although the previously suggested simple body size-related geographic distribution is modified by our review, we were able to identify instead a similar pattern through time, with smaller taxa occurring earlier than larger ones, regardless of the sedimentary succession or geographic area considered;

(4) Another possibly emerging body size-related pattern links body size to preservation quality, according to which larger taxa are represented regularly by better preserved and more complete specimens than smaller ones;

(5) We identified preservational and sedimentary facies-based patterns in the distribution of the kogaionids. According to these patterns, despite the fact that kogaionid remains are distributed in both red, well-drained as well as gray, poorly drained fine-grained deposits, the quality of preservation is often better and more complete in the red-colored paleosols, regardless of body size. As preservation (including degree of completeness and skeletal articulation) is also correlated with autochthony of the specimens, it appears that many of the latest Cretaceous Transylvanian kogaionids preferred the semiarid, dry, and pedogenetically modified floodplain environments over the wetter, wetland habitats. We suggest that some of the Transylvanian kogaionids may have burrowed in these well-drained floodplain habitats, increasing their likelihood of preservation.

The emerging new and more complex picture of kogaionid spatiotemporal distribution is still incomplete, as the material discovered in several fossil sites remains undescribed in detail or is currently under study. Once further kogaionid occurrences will be discovered, and the already existing material has been studied in detail, the emerging picture may be refined, modified, or changed entirely. Regardless of its final details, the in-depth understanding of the spatiotemporal distribution pattern(s) of the endemic Transylvanian kogaionids will provide novel insights into the intriguing evolutionary history and unique island radiation of a very peculiar multituberculate group around the Cretaceous-Paleogene boundary.

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On the cover: Maastrichtian continental beds at Pui (Haţeg Basin) yielded key kogaionid fossils including the holotype of *Litovoi tholocephalos*. Inset: skull of *Litovoi* in lateral view.