

The Rhabdodontidae (Dinosauria, Ornithischia), an enigmatic dinosaur group endemic to the Late Cretaceous European Archipelago

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Abstract

The Rhabdodontidae was one of the most important dinosaur groups inhabiting the Late Cretaceous European Archipelago. Currently, the clade comprises nine species within six genera, which have been found in southern France, northern Spain, eastern Austria, western Hungary and western Romania, ranging from the Santonian to the late Maastrichtian. Phylogenetic analyses consistently place the Rhabdodontidae at the very base of the iguanodontian radiation, whereas the in-group relationships of rhabdodontids are relatively poorly understood; nevertheless, the clade seems to have had a rather complicated biogeographical history. Generally, rhabdodontids were small- to medium-sized, probably habitually bipedal herbivores, characterised by a rather stocky build and a comparatively large, triangular skull. Several lines of evidence suggest that they were presumably gregarious animals, as well as selective browsers that fed on fibrous plants and occupied different ecological niches than sympatric herbivorous dinosaur clades. Moreover, the sympatry of at least two rhabdodontid taxa was rather common and can be explained, at least in some instances, by niche partitioning. While rhabdodontids disappeared prior to the K/Pg extinction event in Western Europe, they survived close to the end of the Cretaceous in Eastern Europe, where they were amongst the last non-avian dinosaurs still present before the end of the Cretaceous. In this paper, we provide an overview of the rhabdodontid taxonomic history, diversity, phylogenetic relationships and palaeobiogeographic history, as well as palaeoecology and extinction. In addition, we also highlight still open questions on each of these topics and suggest potential future research directions.

Key Words

Iguanodontia, Late Cretaceous European Archipelago, palaeobiogeography, palaeoecology, Rhabdodontidae, taxonomy

Introduction

Amongst the various dinosaur groups that inhabited the Late Cretaceous European Archipelago, the Rhabdodontidae is one of the most important, as these animals seem to have been exceptionally abundant and also relatively diverse, representing the most common medium-sized herbivores of Europe during the largest part of the later Late Cretaceous (Weishampel et al. 2004; Csiki-Sava et al. 2015). Currently, the Rhabdodontidae

comprises nine species within six genera, which have been found in southern France, northern Spain, eastern Austria, western Hungary and western Romania (Fig. 1) and which range in age from the Santonian to the late Maastrichtian (Matheron 1869; Bunzel 1871; Seeley 1881; Nopcsa 1902; Buffetaut and Le Loeuff 1991; Weishampel et al. 2003; Ósi et al. 2012; Godefroit et al. 2017; Párraga and Prieto-Márquez 2019; Augustin et al. 2022). The group looks back on a rather complicated taxonomic history that spans more than 150 years (see

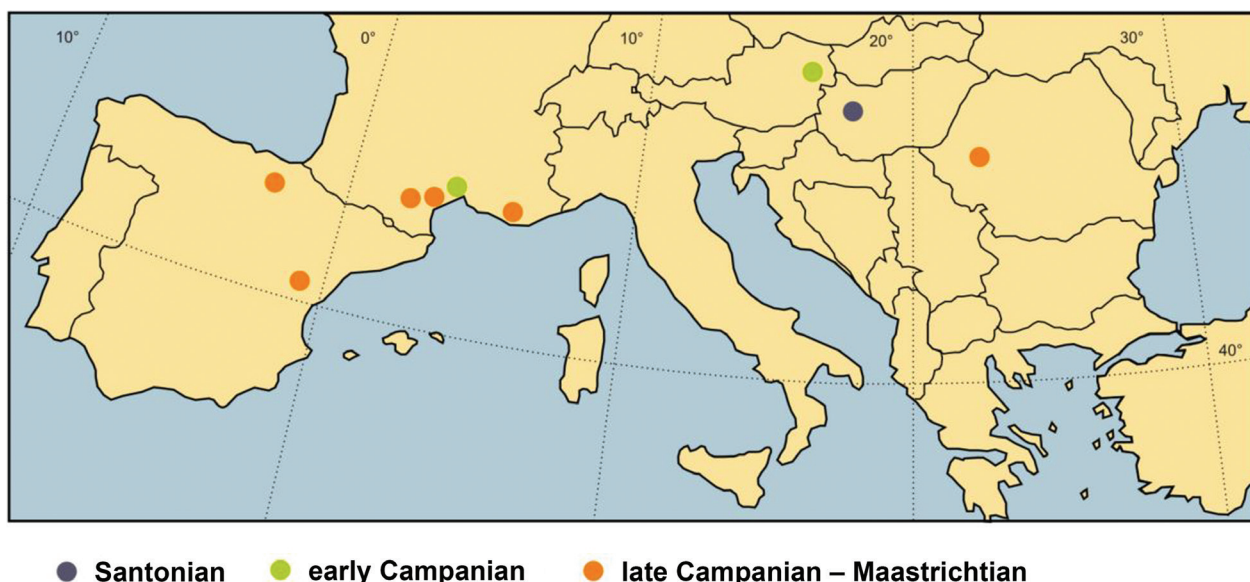


Figure 1. Distribution of the localities yielding remains of the Rhabdodontidae in Europe.

below), starting with the description of the eponymous *Rhabdodon* from southern France (Matheron 1869). In general, rhabdodontids were small- to medium-sized, probably habitually bipedal herbivores, characterised by a rather stocky build, with strong hind limbs, short forelimbs, a long tail and a comparatively large, triangular skull that tapers anteriorly and ends in a pointy snout (Weishampel et al. 1991, 2003; Garcia et al. 1999; Pincemaille-Quillevere 2002; Chanthasit 2010; Ösi et al. 2012).

Interestingly, unquestionable remains of rhabdodontids are currently only known from Upper Cretaceous (i.e. Santonian and younger) strata of Europe and, accordingly, the clade appears to have been endemic to the Late Cretaceous European Archipelago (Weishampel et al. 2003; Ösi et al. 2012; Godefroit et al. 2017; Párraga and Prieto-Márquez 2019; Augustin et al. 2022). A potential Early Cretaceous rhabdodontid from northern Spain, the unnamed ‘Vegagete ornithopod’, has been described recently and referred to the clade (Dieudonné et al. 2016, 2020; Yang et al. 2020), but according to a subsequent assessment, it might be a close relative of the Rhabdodontidae instead (Dieudonné et al. 2021). Within Ornithopoda, the Rhabdodontidae has consistently been found to be a basal clade of iguanodontians (see below), which, combined with their fossil record being limited to the Late Cretaceous, indicates a particularly long ghost lineage. Mapping their distribution and phylogenetic relationships offers intriguing insights into the complicated biogeographical history of these animals, but also that of the Late Cretaceous European Archipelago palaeofaunas overall (see below). Furthermore, several studies have focused on certain aspects of the palaeoecology of rhabdodontids, including their peculiar masticatory apparatus, potential niche partitioning, as well as their posture and locomotion (e.g. Weishampel et al. 2003; Bojar et al. 2010; Godefroit et al. 2017; Augustin et al. 2022; Ösi et al. 2022; Dieudonné et al. 2023).

In the past decades, a wealth of new rhabdodontid material has been discovered throughout Europe (e.g. Chanthasit 2010; Ösi et al. 2012; Godefroit et al. 2017) Párraga and Prieto-Márquez 2019; Augustin et al. 2022), which, combined with the renewed interest in this peculiar dinosaur group, has led to a dramatic increase of our knowledge on the Rhabdodontidae in recent years. This is well exemplified by the fact that three of the six genera currently recognised were named in the last decade (see below). Nevertheless, numerous new and, so far, undescribed specimens remain to be studied and several rhabdodontids still await taxonomic revision, likely leading to an even better understanding of rhabdodontids in the near future. The aims of this paper are to summarise the current state of the knowledge concerning their taxonomic history and diversity, phylogenetic relationships and palaeobiogeographic history, as well as their palaeoecology and extinction. Moreover, we highlight open questions on each of these topics and suggest potential future directions. Therefore, this overview is intended as a baseline for future research on rhabdodontids.

Institutional abbreviations

LPB (FGGUB), Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania; **MTM**, Hungarian Natural History Museum, Budapest, Hungary; **MCD**, Museu de la Conca Dellà, Isona, Spain; **MDE**, Musée des Dinosauriens, Espéraza, France; **MHN**, Muséum d’Histoire Naturelle d’Aix-en-Provence, Aix-en-Provence, France; **MMS/VBN**, Musée du Moulin seigneurial, Velaux-La Bastide Neuve, France; **MPLM**, Palais Longchamp Museum, Marseille, France; **NHMUK**, Natural History Museum, London, UK; **PIUW**: Paläontologisches Institut der Universität Wien, Vienna, Austria; **UBB**, Babeş-Bolyai University, Cluj-Napoca, Romania.

The taxonomic history and diversity of the Rhabdodontidae

For the taxonomic history of the Rhabdodontidae presented here, only unquestionable members of the family were considered; other putative rhabdodontids that were, however, subsequently mostly placed outside of the Rhabdodontidae (within the more inclusive clade Rhabdodontomorpha), are discussed in the following section (see also there the formal definitions of the two clades, Rhabdodontidae and Rhabdodontomorpha).

The first rhabdodontid that was scientifically described and which later served as the basis for the name of the family is *Rhabdodon priscum* (later amended to *R. priscus* by Brinkmann (1986), see below) from the uppermost Cretaceous (Campanian–middle Maastrichtian) of southern France (Matheron 1869). The material upon which Matheron (1869) erected *Rhabdodon priscum* included a fragmentary left dentary (Fig. 2A) and some postcranial elements. The fragmentary left dentary (MPLM 30) was later selected as the lectotype of *Rhabdodon priscus* (Brinkmann 1988), but has since deteriorated (Pincemaille-Quillevere 2002). The material was originally discovered in the 1840s at the construction site of a railway tunnel at la Nerthe in Bouches-du-Rhône, southern France (Taquet 2001). A few years after the discovery, Philippe Matheron, a geologist tasked with supervising the drilling work of the tunnelling project, preliminarily described the first vertebrate remains from La Nerthe, including a tooth that was reminiscent of *Iguanodon* (Matheron 1846; Taquet 2001). More than two decades later, he based a new genus and species of dinosaur, *Rhabdodon priscum*, on the material from la Nerthe (Matheron 1869).

Additional material of *Rhabdodon priscum* was described by Matheron (1892) and, much later, by Lapparent (1947). As a consequence of the intensified research on the Late Cretaceous vertebrates from southern France since the later part of the 20th century, numerous specimens have been uncovered and referred to *Rhabdodon* (e.g. Garcia et al. 1999; Pincemaille-Quillevere 2002; Allain and Suberbiola 2003; Pincemaille-Quillevere et al. 2006; Chanthasit 2010). The most important of the more recently collected specimens from southern France is a partial associated skeleton missing the cranium, forelimbs and several caudal vertebrae (MHN AIX PV 199) from the lower Maastrichtian of Vitrolles (Bouches-du-Rhône, southern France), which is one of the most complete rhabdodontid individuals known thus far (Garcia et al. 1999; Pincemaille-Quillevere 2002). In addition to the occurrences from southern France, *Rhabdodon* has also been reported from the Upper Cretaceous of north-eastern Spain (e.g. Pereda-Suberbiola and Sanz 1999; Ortega et al. 2006, 2015; Pereda-Suberbiola et al. 2015).

However, the referral of all of this material to just one species or even genus is currently debated and usually at least a second species, *R. septimanicus* from southern

France, is recognised (Buffetaut and Le Loeuff 1991; Chanthasit 2010). This second species was erected based on an isolated and incomplete right dentary of a juvenile individual (MDE D-30; Fig. 2B) from the upper Campanian–lower Maastrichtian “Grès à Reptiles Formation” of Montouliers (Hérault), southern France (Buffetaut and Le Loeuff 1991). Although they noted a high degree of variability in the *Rhabdodon* material from southern France, Allain and Pereda-Suberbiola (2003) regarded all this material as pertaining to just one species, characterised by a high degree of intraspecific variation and/or sexual dimorphism and, thus, considered *R. septimanicus* as a junior synonym of *R. priscus*. Later, Chanthasit (2010) described additional cranial and postcranial material from the upper Campanian–lower Maastrichtian of Hérault (southern France) referred to *R. septimanicus*, concluding that it, indeed, represents a valid species. In this context, it is worth noting that Ősi et al. (2012), in their analysis of histological thin sections of *Rhabdodon* long bones from southern France, have documented extreme differences in body size occurring within a single ontogenetic stage (i.e. adult individuals) indicating the presence of at least two, but possibly even more, different taxa.

The geologically oldest material ascribed to the genus *Rhabdodon* comes from the lower Campanian of the Villeveyrac Basin (Hérault, southern France) and comprises four teeth, dorsal and caudal vertebrae, a humerus and a partial femur (Buffetaut et al. 1996). The authors assigned the teeth to the genus *Rhabdodon*, while the vertebrae were referred to as cf. *Rhabdodon priscus* (Buffetaut et al. 1996). Conversely, the youngest occurrence of the genus comes from the upper Maastrichtian of Vitrolles-la-Plaine (Bouches-du-Rhône, southern France) and includes several isolated teeth (Valentin et al. 2012). Remarkably, the material from Vitrolles-la-Plaine also represents the youngest rhabdodontid occurrence from south-western Europe in general (see below); nevertheless, it should be noted that the vertebrate remains from this site might have been reworked (as indicated by weathering and abrasion of the fossils) and, thus, could ultimately turn out be older than currently thought (Valentin et al. 2012; Vila et al. 2016).

Soon after the description of *Rhabdodon* by Matheron (1869), a closely related taxon from the Upper Cretaceous (lower Campanian) of eastern Austria (Muthmannsdorf) was reported by Bunzel (1871), as *Iguanodon suessi*, for which Seeley (1881) later coined the new genus name *Mochlodon* (as *M. suessi*). The specimens referred to *Mochlodon suessi* were found in the ‘coal-bearing series’ of Muthmannsdorf, which was mined until the end of the 19th century and which is assignable to the lower Campanian Grünbach Formation of the Gosau Group (Bunzel 1871; Seeley 1881; Summesberger et al. 2007; Csiki-Sava et al. 2015). The first vertebrate fossil collected from Muthmannsdorf was an isolated tooth found by Ferdinand Stoliczka in 1859 during an excursion led by Professor Eduard Suess, which resembled



Figure 2. Type specimens of the nine rhabdodontid species described so far. **A.** The original drawing of the lectotype of *Rhabdodon priscus*, MPLM 30, a partial left dentary. The specimen has since deteriorated (Pincemaille-Quillevere 2002). Modified after Matheron (1869). **B.** Holotype of *Rhabdodon septimanicus*, MDE D-30, an incomplete right dentary. Photo kindly provided by Eric Buffetaut. **C.** Lectotype of *Mochlodon suessi*, PIUW 2349/2, a right dentary. **D.** Holotype of *Mochlodon vorosi*, MTM V 2010.105.1, a left dentary. **E.** Holotype of *Zalmoxes robustus*, NHMUK R.3392, a right dentary. Photo kindly provided by János Magyar. **F.** Holotype right dentary of *Zalmoxes shqiperorum*, NHMUK R.4900. Note that the holotype of *Z. shqiperorum* also comprises several postcranial elements that presumably belong to the same individual as the dentary. Photo kindly provided by János Magyar. **G.** Holotype of *Matheronodon provincialis*, MMS/VBN-02-102, a right maxilla. Modified after Godefroit et al. (2017). **H.** Holotype of *Pareisactus evrostos*, MCD 5371, a left scapula. Modified after Párraga and Prieto-Márquez (2019). **I.** Holotype of *Transylvanosaurus platycephalus*, LPB (FGGUB) R.2070, a partial skull comprising the articulated basicranium and both frontals. Scale bars: 1 cm.

the teeth of *Iguanodon* (Bunzel 1871). Following this discovery, more vertebrate material was collected by the mining manager Pawlowitsch and eventually described by the physician and amateur palaeontologist Emanuel Bunzel (1871), who erected the new species *Iguanodon suessi*. After further material had been collected, Harry Govier Seeley was invited to Vienna in 1879 to study the additional specimens, which resulted in a revision of the vertebrate material from Muthmannsdorf and the erecting of the new genus *Mochlodon* (Seeley 1881). Originally, Seeley (1881) also erected the taxa *Ornithomerus gracilis*, *Rhadinosaurus alcemus* and *Oligosaurus adelus* based on various fragmentary appendicular elements; subsequently, however, all three taxa have been considered to be synonymous with *M. suessi* (Norman 2004; Sachs and Hornung 2006). As the mining activity has stopped at Muthmannsdorf in the late 19th century, no further fossil vertebrate material has been collected at this site (Csiki-Sava et al. 2015).

The material assigned to *Mochlodon suessi* comprises a right dentary (Fig. 2C), a partial parietal, two teeth and fragmentary postcranial elements (Bunzel 1871; Seeley 1881), of which the dentary (PIUW 2349/2) was selected as the lectotype of the taxon by Sachs and Hornung (2006). Subsequently, *Mochlodon* was synonymised with *Rhabdodon* by Nopcsa (1915), a view that was upheld for decades (e.g. Abel 1919; Romer 1933, 1956; Huene 1956; Müller 1968; Steel 1969; Brinkmann 1988; Norman and Weishampel 1990). Much later, Sachs and Hornung (2006) considered *Mochlodon* to be a nomen dubium and referred the Austrian material to the genus *Zalmoxes* that was named shortly before (see below). However, more recent work showed that *Mochlodon*, indeed, likely represents a valid genus that is distinct from *Rhabdodon* and *Zalmoxes* (Ösi et al. 2012). Moreover, a second species of *Mochlodon*, *M. vorosi*, was also recently described by Ösi et al. (2012) from the Upper Cretaceous (Santonian) of Hungary based on a left dentary (holotype, MTM V 2010.105.1; Fig. 2D), as well as a referred left postorbital, two right quadrates, additional dentaries, isolated teeth and postcranial elements. The presence of rhabdodontids in the Upper Cretaceous of Hungary was originally reported a few years earlier based on three isolated teeth referred to an indeterminate rhabdodontid (Ösi 2004).

It is noteworthy that the name *Rhabdodon* was abandoned in favour of *Mochlodon* for several years during the 1980s (Bartholomai and Molnar 1981; Weishampel and Weishampel 1983; Milner and Norman 1984; Norman 1984, 1985; Weishampel 1984; Sereno 1986), when it was recognised that the genus name *Rhabdodon* was pre-occupied by a colubrid snake (Fleischmann 1831). As a consequence, a case was submitted to the ICZN in 1985 (No. 2536) by Brinkmann (1986) to conserve the name for the dinosaur. In the same submission, Brinkmann (1986) also suggested to change the species name from *R. priscum* to *R. priscus*. A decision by the ICZN on this case was reached in 1987 (opinion 1483), when it was decided unanimously to conserve the genus name for the dinosaur and change the species name to *R. priscus*,

as proposed by Brinkmann (1986) two years before (International Commission on Zoological Nomenclature 1988). Therefore, *Rhabdodon* is the valid genus name of the taxon described and named by Matheron (1869).

The first mentions of basal ornithopods from Transylvania (western Romania) were made by Nopcsa (1897, 1899a, b) in three short notes on the geology of the region around Sânpetru ('Szentpéterfalva') in the Hațeg Basin, referring the material to 'mochlodons', as well as to 'camptosaurus' (the latter being known mainly from the Upper Jurassic of the United States). Subsequently, Nopcsa (1900), in his monograph on the hadrosauroid dinosaur *Telmatosaurus* (originally named '*Limnosaurus*'), commented on three lower jaws that were found together with the type material of *Telmatosaurus* at his most prolific site, his 'Nest 1' (Quarry 1) from the Sibișel Valley near Sânpetru and which he referred to basal ornithopods. Two of these jaws were assigned to two new species, *Camptosaurus inkeyi* and *Mochlodon robustum* (Fig. 2E), whereas the third was referred to *Mochlodon suessi*. Despite erecting two new species and reporting the presence of a third one, Nopcsa (1900) did not figure the dentaries in this monograph and only very briefly described the element he assigned to *Camptosaurus inkeyi* in a footnote. The first thorough study of rhabdodontid material from the Hațeg Basin was published by Nopcsa (1902). In this monograph, he described a few cranial elements (three dentaries, an articular, two quadrates, three squamosals and several isolated teeth belonging to four individuals) referred to *Mochlodon* and synonymised *Mochlodon robustum* with *Mochlodon suessi*.

Two years later, Nopcsa published a second monograph on the cranial anatomy of *Mochlodon* reporting new elements (frontal, premaxilla, maxilla, nasal, prementary and tentatively referred braincases) from Sânpetru (Nopcsa 1904). In this publication, Nopcsa also re-identified the type dentary of *Camptosaurus inkeyi* as a maxilla and considered this taxon to be a junior synonym of *Mochlodon* (Nopcsa 1904: p. 245–246). The initial draft for this publication also included a new genus and species, *Onychosaurus hungaricus*, which was based on a right premaxillary (NHMUK R.3411) and a prementary (NHMUK R.3410), but the manuscript was subsequently retracted by Nopcsa himself (Nopcsa 1903) and *Onychosaurus* was referred to *Mochlodon* as Individual G (Nopcsa 1904: p. 231). Subsequently, Nopcsa (1905) regarded *Mochlodon robustum* again a valid species and listed both *M. robustum* and *M. suessi* as occurring at Sânpetru (Nopcsa 1905: p. 170). After first-hand examination of the *Rhabdodon* material from southern France described by Matheron (1869), Nopcsa (1915) synonymised *M. robustum* and *M. suessi* with *Rhabdodon priscum* and regarded the two former *Mochlodon* species from Transylvania as sexual variants of a single species (Nopcsa 1915: p. 4–7). Several years later, Nopcsa published his third monograph on the rhabdodontids from the Hațeg Basin, this time describing the vertebral column (Nopcsa 1925) and

mentioning, for the first time, the inventory numbers of his Transylvanian specimens housed in the London collection (NHMUK), to which Nopcsa previously sold his collection. In this third monograph, Nopcsa noted once again the presence of two morphotypes within his ‘*Rhabdodon*’ sample that he interpreted as most likely representing male and female individuals of the same species (Nopcsa 1925), a view later reiterated in an article on sexual dimorphism in ornithomimid dinosaurs (Nopcsa 1929), his last work dealing with the ornithomimid dinosaurs from the Hațeg Basin.

Following the work of Nopcsa, the rhabdodontids and, in fact, the entire latest Cretaceous vertebrate fauna from the Hațeg Basin slid into oblivion for several decades. Renewed interest began to form again in the 1970s and 1980s, with systematic excavations taking place at several of Nopcsa’s classical sites, as well as at new localities (for an overview of this restart, see Grigorescu 2010). As a consequence, an extensive review of the geology, taphonomy and palaeontology of the Hațeg Basin was given by Grigorescu (1983), incorporating both old and newly acquired data. Additionally, Weishampel et al. (1991) provided an updated overview of the dinosaur fauna from the Hațeg Basin with a discussion treatment of *Rhabdodon priscus* mainly based on the original Nopcsa specimens, but also reporting newly discovered material. A few years later, Jianu (1994) described a new dentary specimen from Sânpetru and assigned it to *Rhabdodon priscus*. Eventually, an extensive revision of the rhabdodontid material from the Hațeg Basin, both old and new, was published by Weishampel et al. (2003), in which the authors noted several important differences between *Rhabdodon* from southern France and the material from Romania. Consequently, the new genus *Zalmoxes* was erected for the rhabdodontid material from Romania, containing two species, the type species *Z. robustus* and *Z. shqiperorum*. The former represents a resurrection of Nopcsa’s *Mochlodon robustum* (amended to *robustus*), whereas the latter is a new species based primarily on a partial skeleton excavated by Nopcsa (NHMUK R.4900; Fig. 2F). These authors also designated the holotype of *Z. robustus*, represented by the right dentary (NHMUK R.3392; Fig. 2E), upon which Nopcsa (1900) originally based *M. robustum* and which he figured and described a few years later (Nopcsa 1902). In the same publication, Weishampel et al. (2003) also formally established the family Rhabdodontidae, at that time including the genera *Rhabdodon*, *Mochlodon* and *Zalmoxes*.

It is important to note, nonetheless, that the holotype of *Zalmoxes shqiperorum* does not come from the south-western Transylvanian Basin as stated by Weishampel et al. (2003), but from the Hațeg Basin. The locality of the type specimen of *Z. shqiperorum*, individual NHMUK R.4900, was originally given as “Unnamed formation (‘Bozeș strata’; upper Maastrichtian-Paleocene); Vurpăr, near Vințu de Jos, Alba County, Romania” (Weishampel et al. 2003: p. 95) and this information was later repeated by several other authors (e.g. Brusatte et al. 2013).

However, when first mentioning this individual, Nopcsa (1925: p. 286) clearly wrote that NHMUK R.4900 (his individual I) comes from Sânpetru (‘Szentpéterfalva’) in the south-central part of the Hațeg Basin. Accordingly, we amend here some of the basic information concerning *Zalmoxes shqiperorum* as stated by Weishampel et al. (2003: p. 95), respectively the position and identity of the type locality and horizon for this taxon; instead of Vurpăr, in the Transylvanian Basin, the corrected type locality is represented by the ‘Sibișel Valley, south of Sânpetru, Hațeg Basin, Hunedoara County, Romania’, whereas the type horizon can now be specified as the ‘Sânpetru Formation (Maastrichtian)’. Incidentally, since the only currently diagnostic rhabdodontid individual found at Vurpăr according to Nopcsa (1905) and identified later as Individual H (Nopcsa 1925; but indicated as originating from Vințu de Jos in this monograph), respectively specimen NHMUK R.3813, was referred to *Z. robustus* by Weishampel et al. (2003), the presence of a second species of *Zalmoxes* at this locality remains unsupported by currently available information. Although the occurrence of relatively abundant rhabdodontid remains had been reported subsequently from Vurpăr (e.g. Codrea et al. 2010; Vremir 2010; Vremir et al. 2015), these were not described in detail and were only generically referred to *Zalmoxes* (Codrea et al. 2010; Vremir et al. 2015). As such, the presence of *Zalmoxes shqiperorum* at Vurpăr, as well as the sympatry of *Z. robustus* and *Z. shqiperorum* in this locality (as proposed by, for example, Godefroit et al. 2009; Vremir et al. 2015) remains questionable for the time being.

In the years following the revision of the Transylvanian rhabdodontids by Weishampel et al. (2003), additional material referred to *Zalmoxes* was described from various parts of the Hațeg Basin, the Transylvanian Basin and the Ruscă Montană Basin, in Romania (Codrea and Godefroit 2008; Codrea et al. 2010, 2012; Brusatte et al. 2013, 2017; Dumbravă et al. 2013; Vremir et al. 2014, 2017; Botfalvai et al. 2017). Amongst these newly discovered specimens, a partial skull and skeleton referred to *Z. shqiperorum* from Nălaț-Vad (UBB NVZ1) is particularly noteworthy, as it represents one of the most complete *Zalmoxes* individuals known so far (Godefroit et al. 2009); recently, however, the referral of the entirety of this material to just one individual (or even taxon) was questioned (Brusatte et al. 2017; Augustin et al. 2023). Although the large majority of the material assigned to *Zalmoxes* comes from Maastrichtian strata (Csiki-Sava et al. 2016), one site from the south-western Transylvanian Basin (Petrești-Arini) yielded remains referred to *Zalmoxes* sp. from the uppermost Campanian (Vremir et al. 2014, 2015), representing the oldest rhabdodontid material from western Romania reported so far.

Besides *Rhabdodon*, *Mochlodon* and *Zalmoxes*, three more rhabdodontid genera were recently named and described, all of which are monospecific. The first of these is *Matheronodon provincialis*, which was based on a single, well preserved right maxilla (MMS/

VBN-02-102; Fig. 2G) from the Upper Cretaceous (Upper Campanian) of the Aix-en-Provence Basin in southern France (Godefroit et al. 2017). The second, *Pareisactus evrostos*, is represented by a nearly complete left scapula (MCD 5371; Fig. 2H) that was discovered in the Upper Cretaceous (lower Maastrichtian) Conques Member of the Tremp Formation in north-eastern Spain (Párraga and Prieto-Márquez 2019). To date, no further material has been assigned to either *Matheronodon* or to *Pareisactus* and, thus, both taxa are only known from their respective holotypes. Finally, Augustin et al. (2022) described the new genus and species *Transylvanosaurus platycephalus* based on a partial skull from the Hațeg Basin. The holotype and only known specimen of this taxon, LPB (FGGUB) R.2070, comes from the ‘middle’ Maastrichtian of the ‘Pui Beds’ (Csiki-Sava et al. 2016) and comprises the articulated basicranium together with the associated left and right frontals (Fig. 2I). The description of this new Romanian rhabdodontid has important consequences. As pointed out by Brusatte et al. (2017) and Augustin et al. (2022), in the past, rhabdodontid remains from the uppermost Cretaceous of Transylvania have been indiscriminately referred to the genus *Zalmoxes*, often without positive supportive evidence, on the account that it was the sole taxon represented in the local faunas. However, with the recent description of *Transylvanosaurus*, this practice has to be re-considered as the taxonomic diversity of rhabdodontids seems to have been actually higher than previously thought (at least in the Hațeg Basin, but potentially also in the Transylvanian and Rusca Montană basins). For an overview of the different rhabdodontids, as well as their temporal and stratigraphical distribution, see Table 1.

The phylogenetic relationships of the Rhabdodontidae and palaeobiogeographic implications

From the very beginning onwards, a close relationship between rhabdodontids and iguanodontian ornithopods was recognised. In fact, already Matheron (1869), in his initial description of *Rhabdodon*, noted the similarity of this form to *Iguanodon*, as did Bunzel (1871) by assigning the rhabdodontid from Muthmannsdorf, Austria, to *Iguanodon*, as the new species *I. suessi* (later placed in its own genus *Mochlodon*, see above, previous section). Nopcsa (1901) was the first to assign the rhabdodontids known at that time to a higher taxon, placing *Rhabdodon* and *Mochlodon* (the latter also including the rhabdodontid material from the Hațeg Basin, later to be named *Zalmoxes*) within the Hypsilophodontidae. This group was, in turn, considered to be part of the family Kalodontidae, a newly erected, paraphyletic grouping of non-hadrosaurid ornithopods (Nopcsa 1901). Later, Nopcsa (1902) confirmed this assignment in his first monograph on the rhabdodontid dinosaurs from the Hațeg Basin, noting the close resemblance of this material to *Hypsilophodon* from the Lower Cretaceous of England. After examination of further cranial material (see above) in his second monograph on the rhabdodontids from the Hațeg Basin, Nopcsa (1904) still regarded *Mochlodon* as a close relative of *Hypsilophodon*, although he noted that it also appears to be similar to *Camptosaurus* (see also Nopcsa 1903). His view, however, changed again several years later, when he regarded *Rhabdodon* (now including specimens referred previously to *Mochlodon* from both Austria and Romania)

Table 1. Overview of the different rhabdodontid taxa, as well as their geographical and stratigraphical distribution (for details and references, see text).

Taxon	Locality	Age
<i>Rhabdodon</i> Matheron, 1869		
<i>R. priscus</i> Matheron, 1869	various lithostratigraphic units, southern France	Campanian–‘middle’ Maastrichtian
<i>R. septimanicus</i> Buffetaut & Le Loeuff, 1991	“Grès à Reptiles Formation”, Hérault, southern France	Late Campanian–early Maastrichtian
<i>Mochlodon</i> Seeley, 1881		
<i>M. suessi</i> Bunzel, 1871 (= <i>Iguanodon suessi</i> Bunzel, 1871; <i>Ornithomerus gracilis</i> Seeley, 1881; <i>Rhadinosaurus alcemus</i> Seeley, 1881; <i>Oligosaurus adelus</i> Seeley, 1881)	Grünbach Formation, Muthmannsdorf, eastern Austria	Early Campanian
<i>M. vorosi</i> Ősi et al., 2012	Csehbánya Formation, Iharkút, western Hungary	Santonian
<i>Zalmoxes</i> Weishampel et al., 2003		
<i>Z. robustus</i> Nopcsa, 1900 (= <i>Mochlodon robustum</i> Nopcsa, 1900; <i>Camptosaurus inkeyi</i> Nopcsa, 1900; <i>Onychosaurus hungaricus</i> Nopcsa, 1902)	Sânpetru Formation, Densuș-Ciula Formation, Hațeg Basin, western Romania	early–late Maastrichtian
<i>Z. shqiperorum</i> Weishampel et al., 2003	Sânpetru Formation, Densuș-Ciula Formation, ‘Râul Mare River section’, Hațeg Basin, Jibou Formation, northwestern Transylvanian Basin, western Romania	early–late Maastrichtian
<i>Matheronodon</i> Godefroit et al., 2017		
<i>M. provincialis</i> Godefroit et al., 2017	Unnamed formation, Aix-en-Provence Basin, southern France	Late Campanian
<i>Pareisactus</i> Párraga and Prieto-Márquez, 2019		
<i>P. evrostos</i> Párraga and Prieto-Márquez, 2019	Tremp Formation, Basturs Poble, north-eastern Spain	early Maastrichtian
<i>Transylvanosaurus</i> Augustin et al., 2022		
<i>T. platycephalus</i> Augustin et al., 2022	‘Pui Beds’, Hațeg Basin, western Romania	‘middle’ Maastrichtian

as a member of the more derived Camptosauridae (Nopcsa 1915), an opinion also expressed in his later works (Nopcsa 1923, 1934). During the next decades, most authors followed this classification and *Rhabdodon* was assigned to the Camptosauridae or, alternatively, to the Iguanodontidae, which, during that time, was often used as a somewhat more inclusive clade also containing taxa traditionally placed within Camptosauridae, such as *Camptosaurus* (Abel 1919; Romer 1933, 1945, 1956; Huene 1956; Müller 1968; Steel 1969).

In the early 1980s, however, this view was challenged by some workers who classified *Mochlodon* (at this time including *Rhabdodon* and the Romanian rhabdodontid material, see above) as a non-iguanodontid ornithopod (Bartholomai and Molnar 1981) or as a potential hypsilophodontid (Norman 1985) or, at least, questioned its iguanodontid affinities (Weishampel and Weishampel 1983). All of these taxonomic opinions convergently regarded *Rhabdodon* as a more basal ornithopod than previously thought. The advent of cladistics in ornithischian systematics during the mid-1980s (Norman 1984; Sereno 1984, 1986; Cooper 1985; Maryanska and Osmólska 1985) also had a profound impact on the classification of *Mochlodon* and *Rhabdodon* within the dinosaur family tree. In the framework of these first cladistic analyses, *Mochlodon* (including *Rhabdodon*) was regarded either as a dryosaurid (Milner and Norman 1984) or else as a basal member of the clade Iguanodontia (Sereno 1986). Meanwhile, based on its supposedly more basal phylogenetic position and its hypsilophodontid-like tooth morphology, Brinkmann (1988) classified *Rhabdodon* as a member of the Hypsilophodontidae. Norman (1990) rejected dryosaurid affinities of *Rhabdodon* and, instead, considered it to be a hypsilophodontian. In contrast, Norman and Weishampel (1990) followed Sereno (1986) and classified *Rhabdodon* as Iguanodontia incertae sedis. Similarly, Weishampel et al. (1998) and Pincemaille-Quillever (2002) regarded *Rhabdodon* as a basal iguanodontian.

In their extensive revision of the rhabdodontid material from the Hațeg Basin, Weishampel et al. (2003) finally erected the family Rhabdodontidae (at this time containing *Rhabdodon*, *Zalmoxes* and, provisionally, *Mochlodon*) and defined it as “a node-based taxon consisting of the most recent common ancestor of *Zalmoxes robustus* and *Rhabdodon priscus* and all the descendants of this common ancestor (Weishampel et al. 2003: p. 69). In their phylogenetic analysis, Weishampel et al. (2003) recovered it as the sister-clade to Iguanodontia. Since then, the Rhabdodontidae has been consistently placed at the base of the iguanodontian radiation (Butler et al. 2008; McDonald 2012; Ósi et al. 2012; Boyd 2015; Dieudonné et al. 2016, 2021; Verdú et al. 2018, 2020; Madzia et al. 2018; Bell et al. 2018, 2019; Yang et al. 2020; Poole 2022; Augustin et al. 2022). Such a basal phylogenetic position within Iguanodontia, combined with their fossil record being limited to the later Late Cretaceous (Santonian–Maastrichtian), indicates an exceptionally long ghost lineage for rhabdodontids. Soon after the Rhabdodontidae

was erected and first defined by Weishampel et al. (2003), Sereno (2005) proposed a new definition for this taxon as the most inclusive clade containing *Rhabdodon priscus*, but not *Parasaurolophus walkeri*.

Based on the results of their phylogenetic analysis (indicating a particularly close relationship of the Rhabdodontidae with *Muttaborrasaurus*), Dieudonné et al. (2016) later erected the more inclusive clade Rhabdodontomorpha and defined it as “a node-based taxon consisting of the most inclusive clade containing *Rhabdodon priscus* Matheron, 1869 and *Muttaborrasaurus langdoni* Bartholomai & Molnar, 1981” (Dieudonné et al. 2016: p. 5). Subsequently, Madzia et al. (2018) suggested another definition for Rhabdodontomorpha, i.e. as a branch-based taxon with *Rhabdodon priscus* and *Muttaborrasaurus langdoni* as internal specifiers and *Iguanodon bernissartensis* as an external specifier. This definition was in turn slightly amended by Madzia et al. (2020), who defined the clade as a branch-based taxon with *Rhabdodon priscus* as an internal specifier and *Iguanodon bernissartensis* as an external specifier. Recently, formal definitions of the two clades Rhabdodontidae and Rhabdodontomorpha in compliance with the International Code of Phylogenetic Nomenclature (ICPN or PhyloCode) have been provided by Madzia et al. (2021). According to these definitions, Rhabdodontidae is defined as the smallest (most exclusive) clade containing *Rhabdodon priscus* and *Zalmoxes robustus*, while Rhabdodontomorpha is defined as the largest (most inclusive) clade containing *Rhabdodon priscus*, but not *Hypsilophodon foxii* and *Iguanodon bernissartensis* (Madzia et al. 2021). Potential close relatives of the Rhabdodontidae, belonging to the more inclusive clade Rhabdodontomorpha, include the ‘Vegagete ornithopod’ from the Lower Cretaceous (Barremian–Aptian) of northern Spain (Dieudonné et al. 2016), *Tenontosaurus* from the Lower Cretaceous (Aptian–Albian) of the western United States (Poole 2022), *Muttaborrasaurus* from the Lower Cretaceous (Albian) of north-eastern Australia (Bartholomai and Molnar 1981), *Fostoria* from the lowermost Upper Cretaceous (lower Cenomanian) of eastern Australia (Bell et al. 2019) and *Iani* from the lowermost Upper Cretaceous (Cenomanian) of the western United States (Zanno et al. 2023), albeit it should be noted that alternative positions within Iguanodontia have also been suggested for four of these five taxa (i.e. the ‘Vegagete ornithopod’, *Tenontosaurus*, *Muttaborrasaurus* and *Fostoria*).

The ‘Vegagete ornithopod’ has been originally proposed to be the basal-most and earliest member of the Rhabdodontidae itself (Dieudonné et al. 2016), although under the definition of Weishampel et al. (2003; see also Madzia et al. 2021), it would fall outside Rhabdodontidae (as the sister-group to it). Subsequently, this taxon was recovered in a sister-group relationship with *Mochlodon suessi*, together forming the sister-group to *M. vorosi* (Yang et al. 2020); on its turn, this small clade was found to be in a polytomy with the other two well-established rhabdodontid genera known at that time (*Rhabdodon*, *Zalmoxes*), each of which was shown to be monophyletic.

In an attempt to achieve better resolution within their tree, these authors decided to remove taxa identified as wildcards from a second run of their phylogenetic analysis, including here both *Zalmoxes* and *Rhabdodon*. Thus, whereas their resulting fully resolved agreement subtree did still return the same ‘Vegagete ornithopod’-*Mochlodon* clade, ironically, whether this grouping belongs to Rhabdodontidae (or even to Rhabdodontomorpha) or not, cannot be ascertained any longer as the specifiers for these clades (regardless of the details of their definition) were not included in the analysis. Indeed, there is no way to delineate Rhabdodontidae or its parent clade Rhabdodontomorpha at all in the fully resolved agreement subtree of Yang et al. (2020). Finally, the Early Cretaceous Spanish taxon was also recovered as a member of the Rhabdodontidae, closely related to *Rhabdodon* (Herne et al. 2019); however, more recently, it was recovered as the closest outgroup of Rhabdodontidae within Rhabdodontomorpha (Dieudonné et al. 2021).

Although *Tenontosaurus* is usually recovered outside of Rhabdodontomorpha (e.g. Dieudonné et al. 2016, 2021; Madzia et al. 2018; Bell et al. 2018, 2019; Andrzejewski et al. 2019; Yang et al. 2020; Barta and Norell 2021; Augustin et al. 2022), it has recently also been placed within this clade (Poole 2022; Zanno et al. 2023). *Muttaburrasaurus* is often regarded as a basal rhabdodontomorph (Dieudonné et al. 2016, 2021; Madzia et al. 2018; Bell et al. 2018; Barta and Norell 2021; Augustin et al. 2022), but it has also been recovered in a polytomy with the rhabdodontids *Rhabdodon* and *Zalmoxes* (McDonald et al. 2010); alternatively, it has been identified either as a more basal (Bell et al. 2019) or a more derived (Boyd 2015; Herne et al. 2019) iguanodontian compared to rhabdodontids and their close kin. *Fostoria*, on the other hand, has been found to be either a basal rhabdodontomorph (Dieudonné et al. 2021; Augustin et al. 2022) or a more basal iguanodontian (Bell et al. 2019). Meanwhile, the very recently described *Iani* has been recovered as a rhabdodontomorph by the only phylogenetic analysis including this taxon (Zanno et al. 2023). Given that derived rhabdodontomorphs (i.e. rhabdodontids) are, so far, exclusively known from Europe, a European origin of the Rhabdodontidae seems likely.

In addition to the phylogenetic position of the Rhabdodontidae within Ornithopoda, the interrelationships of the different rhabdodontids have been thoroughly scrutinised as well (Fig. 3). In most previous phylogenetic analyses, *Rhabdodon* spp. from southern France and north-eastern Spain has been recovered as the sister-taxon to a clade comprising *Mochlodon* spp. from Austria and Hungary and *Zalmoxes* spp. from Romania (Ösi et al. 2012; Madzia et al. 2018; Verdú et al. 2018, 2020; Barta and Norell 2021; Dieudonné et al. 2021). Notably, only a single phylogenetic analysis has found a closer relationship between *Rhabdodon* and *Zalmoxes* instead (Dieudonné et al. 2016), whereas the three genera have also been recovered in a polytomy by some phylogenetic analyses (e.g. Bell et al. 2019). Based on the results of these phylogenetic analyses and the geographic

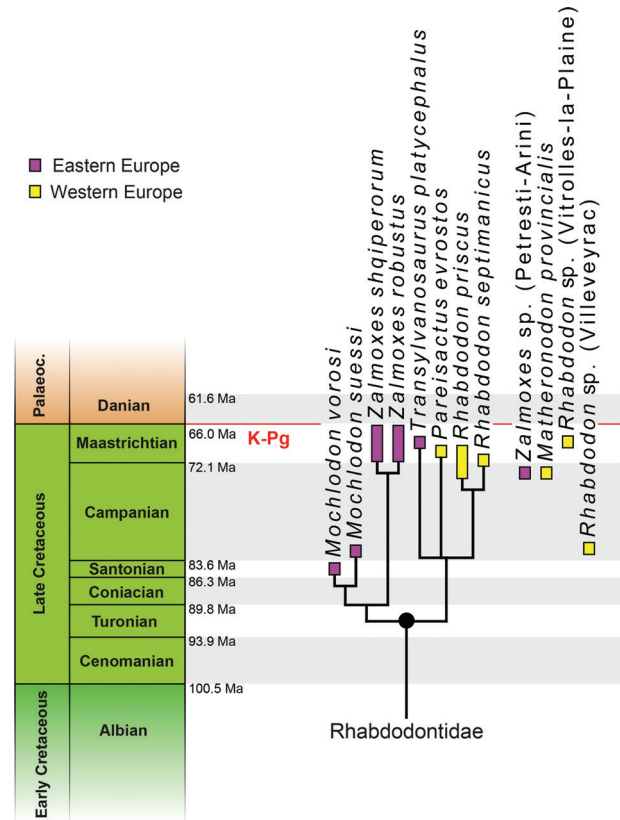


Figure 3. Phylogenetic relationships and temporal distribution of the Rhabdodontidae. The relationships within Rhabdodontidae primarily follow Dieudonné et al. (2021), as well as Párraga and Prieto-Márquez (2019) for the relationships of *Pareisactus*. The phylogenetic relationships of *Transylvanosaurus* follow Augustin et al. (2022), who suggested a particularly close relationship between this taxon and *Rhabdodon* spp. from southern France based on morphological comparisons. The relationships of *Matheronodon* have not yet been explored by a phylogenetic analysis nor by detailed comparisons and, thus, it is not included in the cladogram. Similarly, *Zalmoxes* sp. from Petrești-Arini, *Rhabdodon* sp. from Villevetryac and *Rhabdodon* sp. from Vitrolles-la-Plaine have not yet been incorporated into a phylogenetic analysis, but are included here, as these specimens represent the oldest respectively the youngest occurrences of rhabdodontids in Eastern and Western Europe (see text for explanations). The colour of the boxes denotes their distribution (purple for Eastern Europe, yellow for Western Europe).

distribution pattern of the then-known rhabdodontids, the presence of two rhabdodontid lineages has been suggested, one from Western Europe and the other from Eastern Europe (Ösi et al. 2012). The phylogenetic relationships of *Pareisactus evrostos* from north-eastern Spain were explored only by a single phylogenetic analysis that found it to be the sister-taxon to *Rhabdodon priscus*, thus making it a member of the same Western European rhabdodontid lineage (Párraga and Prieto-Márquez 2019). *Matheronodon* from southern France, on the other hand, has never been included in a phylogenetic analysis and, thus, its relationships with the other rhabdodontids remain currently unknown.

Intriguingly, a comparable ‘eastern vs. western’ dichotomous distribution pattern has been previously suggested for other latest Cretaceous European continental vertebrates as well, including turtles (Rabi et al. 2013; Csiki-Sava et al. 2015; Augustin et al. 2021), mammals (Csiki-Sava et al. 2015; Gheerbrant and Teodori 2021) and allodaposuchid crocodyliforms (Narváez et al. 2016; Blanco and Brochu 2017; Blanco 2021). Such a coherent pattern, as well as a high degree of regional faunal differences and endemism is usually linked to geographical isolation of the different islands of the Late Cretaceous European Archipelago (Fig. 4; for an overview, see Csiki-Sava et al. 2015). Meanwhile, the Santonian age of *Mochlodon vorosi* would indicate that the split between the western and the eastern rhabdodontid lineages must have occurred before the Santonian, after which the two clades evolved in isolation from each other through allopatric speciation (Ősi et al. 2012). Recently, however, this relatively simple and clear-cut biogeographical hypothesis has been challenged by Augustin et al. (2022), who postulated a particularly close relationship between the newly described *Transylvanosaurus* from western Romania and *Rhabdodon* spp. from southern France based on extensive morphological comparisons. Accordingly, these authors have, instead, suggested that at least one large-scale dispersal event must have happened within the ‘western’ European rhabdodontid lineage – either from western to eastern Europe or westward into the western European realm (Augustin et al. 2022).

At this point, it should be noted, however, that the in-group relationships of the Rhabdodontidae are still only

incompletely understood. One of the main reasons for this lies in the fact that several rhabdodontids are known from only relatively few and often non-overlapping elements (e.g. *Matheronodon*, *Pareisactus*, *Transylvanosaurus*), making it difficult to firmly establish phylogenetic hypotheses for these taxa. Moreover, the two best-known rhabdodontid taxa, *Rhabdodon* and *Zalmoxes*, both of which have regularly been included into phylogenetic analyses (e.g. McDonald 2012; Ősi et al. 2012; Dieudonné et al. 2016, 2021; Bell et al. 2018, 2019; Madzia et al. 2018; Verdú et al. 2018; Barta and Norell 2021; Augustin et al. 2022; Poole 2022), await taxonomic revision (see above). All of this currently hinders exploring the phylogenetic relationships of rhabdodontids in more detail, both within the group, but also with other ornithischian dinosaurs. Accordingly, the relationships of the different rhabdodontids, as well as the biogeographical scenarios based on these, should be viewed with caution pending the discovery of more complete specimens and the taxonomic revision of certain taxa.

The palaeoecology and extinction of the Rhabdodontidae

Assessments concerning rhabdodontid palaeoecology have been made early on and one of the first to hypothesise rather extensively on this topic was, again, Franz Nopcsa, considered one of the pioneers of dinosaur palaeobiology (Weishampel and Reif 1984). In his detailed description

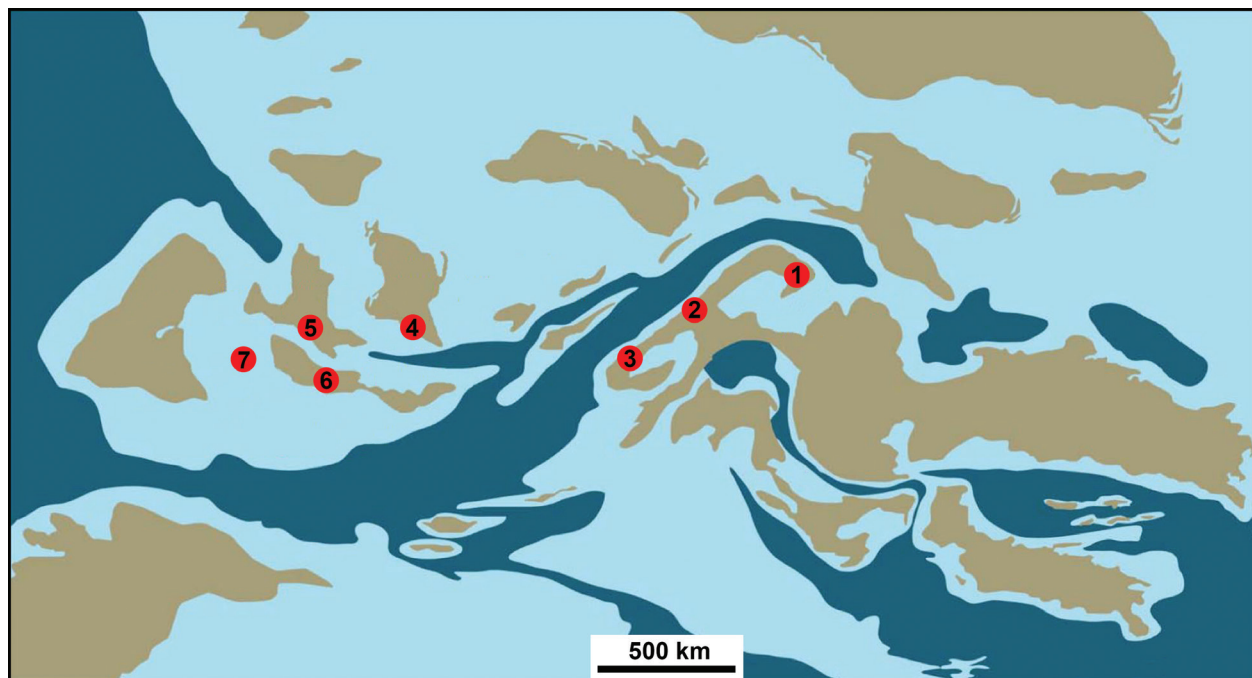


Figure 4. Palaeogeographic map of Europe during the latest Cretaceous (late Campanian), with the location of the most important rhabdodontid-bearing assemblages. **1** Transylvania (including the Hațeg, Transylvanian and Rusca Montană basins), western Romania. **2** Iharkút, western Hungary. **3** Muthmannsdorf, eastern Austria. **4** Eastern southern France. **5** Western southern France. **6** Northern Spain. **7** Central Spain. Note that the position and the extent of the different islands was slightly different before and after the late Campanian. In particular, during the Maastrichtian, the emergent landmasses were more extensive, meaning that the uppermost Cretaceous strata from central Spain (7) were deposited in a predominantly continental environment. Modified after Blanco (2021).

of the skull anatomy of the Transylvanian ‘*Mochlodon*’ (i.e. *Zalmoxes*), Nopcsa (1902) concluded that, based on tooth morphology, the movement of the jaws was exclusively vertical and that the abrasion pattern of the teeth indicates a scissor-like shearing action. He was, however, not the first to propose such a kind of masticatory mechanism since, two decades before, Seeley (1881) already suggested a scissor-like chewing action in *Mochlodon suessi* based on tooth wear. In addition, Nopcsa (1914) suggested that the presence of a sharp beak and the teeth adapted for chewing (Fig. 5A, G) indicate consumption of food items that were hard on the outside, but internally soft. He further reasoned that the rhabdodontids from ‘Szentpéterfalva’ (= Sânpetru) in the Hațeg Basin were living in the same area where their remains have been found, because they are so abundant at this locality and because juveniles have been found there (Nopcsa 1914). Since he interpreted the Sânpetru deposits as those of a shallow freshwater swamp, he regarded the rhabdodontids as swamp dwellers (Nopcsa 1914), a notion that he reiterated thereafter on several occasions (Nopcsa 1915, 1923). Contrary to Nopcsa’s interpretation, more recent sedimentological investigations demonstrated that the Sibișel Valley succession (i.e. the stratotype section of the Sânpetru Formation) were, in fact, deposited on a poorly channelised alluvial plain drained by braided river systems, which comprised active channels, wetlands, well-drained floodplains and higher-lying drier areas (e.g. Therrien 2006; Therrien et al. 2009).

Albeit this alternative sedimentological and palaeoenvironmental interpretation of the Sibișel Valley deposits was first proposed by Grigorescu (1983), he also noted that, based on taphonomical considerations, rhabdodontids (along with hadrosaurs and turtles) were likely residents of swampy areas within this diverse palaeoenvironmental mosaic – this conclusion appears to be largely a holdover of Nopcsa’s earlier habitat preference assessments. Subsequently, however, an extensive taphonomic survey of the latest Cretaceous vertebrates from the Hațeg Basin demonstrated that rhabdodontid remains are present in all of these different palaeoenvironmental settings and, despite earlier claims to the contrary, are commonly found in well-drained palaeoenvironments (Csiki et al. 2010). Therefore, these animals were almost certainly not limited to swamps or lacustrine environments as suggested before, but instead were inhabiting all palaeobiotopes represented by the deposits of the Hațeg Basin (Csiki et al. 2010). Interestingly, rhabdodontid remains with similar taphonomic features – and, thus, common taphonomic histories – pertaining to several different *Zalmoxes* individuals of different sizes have been found together in certain bonebeds in the Hațeg Basin, suggesting that these animals might have been gregarious (Csiki et al. 2010). A similar conclusion is suggested by the occurrence of at least six individuals of different sizes at the monotaxic Vegagete fossil locality that all belong to the ‘Vegagete ornithopod’, most probably a rhabdodontomorph (Dieudonné et al. 2020, 2021,

2023), indicating that the presence of a gregarious habit may have been the ancestral condition within this lineage.

During the past decades, especially the feeding behaviour and potential diet of rhabdodontids received a great deal of attention. In his monograph on ornithopod jaw mechanisms, Weishampel (1984) described the intracranial joints in more than 50 ornithopod taxa, including ‘*Mochlodon*’ (most specimens examined for this taxon pertain to *Zalmoxes*, albeit a few belong to *Rhabdodon* and *Mochlodon* as well). Based on the morphology and the distribution of these joints, it was concluded that the more derived ornithopods (including ‘*Mochlodon*’) utilised a transverse power stroke to chew their food that was accomplished by the mobilisation of the upper jaws (i.e. pleurokinesis; Weishampel 1984). The presence of this kind of cranial kinesis and the associated chewing mechanism was later suggested specifically for *Zalmoxes* as well (Weishampel et al. 2003), although the authors noted a deviation from the general pleurokinetic bauplan characterising the derived ornithopods, one that probably limited the degree of intracranial mobility and might represent an adaptation to process hard food items. Lately, the pleurokinetic skull model has been questioned in some hadrosaurs (Rybczynski et al. 2008; Cuthbertson et al. 2012). As no articulated cranial material, upon which the conditions for pleurokinesis can be demonstrated (Holliday and Witmer 2008), is yet available for *Zalmoxes* or, indeed, for any other rhabdodontid either, the occurrence of such a feeding mechanism cannot be currently confirmed for these basal ornithopods. Thus, the description of more complete and articulated cranial elements would greatly increase our knowledge of potential intracranial kinesis and the functioning of their masticatory apparatus.

Furthermore, large jaw adductor muscle chambers in *Zalmoxes* coupled with robust jaws and a well-developed coronoid process of the lower jaw are indicators of a high bite strength (Weishampel et al. 2003). Taken together with the mesiodistally enlarged teeth of certain rhabdodontids (i.e. *Matheronodon*) and the high-angled wear-surface of the teeth, these features indicate that the masticatory apparatus of at least some rhabdodontids was adapted for powerful slicing action (Godefroit et al. 2017), an interpretation very similar to those of Seeley (1881) and Nopcsa (1902) discussed above. Moreover, it was suggested that the relatively narrow jaw tips (Fig. 5E, F), which, in life, were most likely covered by a keratinous beak, could indicate that *Zalmoxes* was a selective feeder (Weishampel et al. 2003). Godefroit et al. (2017) further argued that the enlarged teeth of *Matheronodon* represent an adaptation for the crushing of tough and woody or fibrous food items. Taking the palaeobotanical data of various rhabdodontid-bearing localities into consideration, Godefroit et al. (2017) hypothesised that rhabdodontids fed primarily on tough plant parts with a high sclerenchyma fibre content, like the palms *Sabalites* and *Pandanites*, both of which are known from the Campanian Grünbach Formation of Austria (Kvaček and Herman 2004), the Maastrichtian of north-eastern

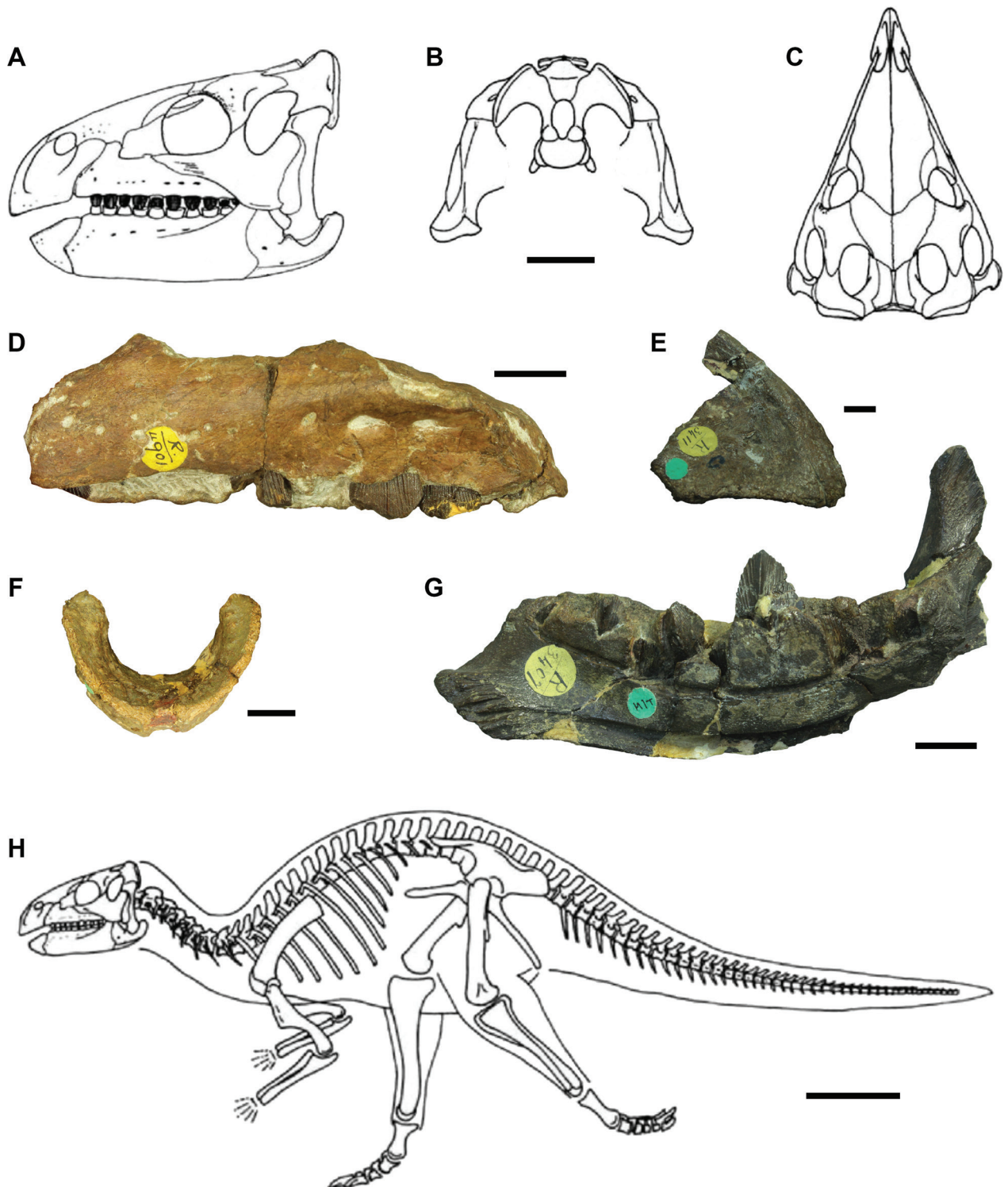


Figure 5. Anatomy of the Rhabdodontidae. A–C. Skull reconstruction of *Z. robustus* in left lateral view (A), posterior view (B), and dorsal view (C). Modified after Weishampel et al. (2003). D. Maxillary of *Z. robustus* (NHMUK R.4901) in medial view. E. Premaxillary of *Z. robustus* (NHMUK R.3411) in right lateral view. F. Prementary of *Z. robustus* (NHMUK R.3410) in dorsal view. G. Right dentary of *Z. robustus* (NHMUK R.3407) in medial view. H. Skeletal reconstruction of *Zalmoxes robustus*. Modified after Weishampel et al. (2003). All specimens figured (i.e. D–G) are historical Nopcsa specimens from his Quarry 1 (for details, see text). Photos (D–G) kindly provided by János Magyar. Scale bars: 5 cm (A–C); 1 cm (D–G); 20 cm (H).

Spain (Marmi et al. 2010, 2014) and the Maastrichtian of Transylvania (Popa et al. 2014).

Apart from cranial anatomy, two independent lines of evidence have also been used to infer the feeding ecology

of rhabdodontids – stable isotope analysis and multiproxy dentition analysis. Stable isotope analysis of rhabdodontid teeth from the Hațeg Basin suggested that these animals mainly ingested C3 plants (Bojar et al. 2010). Remarkably,

the similarity of $\delta^{13}\text{C}$ values between rhabdodontid and hadrosauroid teeth from the same locality of the Hațeg Basin was interpreted by Bojar et al. (2010) to reflect the absence of large-scale habitat partitioning between representatives of the two ornithopod clades. Furthermore, dental microwear analysis has been applied to teeth of *Mochlodon vorosi* from Iharkút (Hungary) revealing straight and parallel micro-striations that likely reflect orthal jaw movement, while the high tooth formation rates in this taxon imply an abrasive diet (Virág and Ósi 2017). The dental microwear pattern of *Mochlodon vorosi* further indicates that this animal was a low-browsing herbivore (browsing height up to 1 m above ground level) that fed on particularly tough vegetation (Ósi et al. 2022). Meanwhile, differences found in microwear pattern between this rhabdodontid and hadrosaurs likely reflect different feeding ecologies (Ósi et al. 2022), an observation that is consistent with (and explains) the large-scale habitat sharing of rhabdodontids and hadrosauroids noted in the Romanian faunas by Bojar et al. (2010). Despite a similar and partially overlapping browsing height in *Mochlodon* and hadrosaurs, the rhabdodontid probably fed on higher-growing plants, which were either tougher or were processed more vigorously (Ósi et al. 2022). Similarly, a different microwear pattern identified in the ankylosaurian *Hungarosaurus* (as compared to *M. vorosi*) demonstrates different feeding strategies and niche partitioning between these two sympatric herbivorous dinosaurs, with *Hungarosaurus* probably feeding on softer plants and/or processing its fodder less intensively (Ósi et al. 2022).

Recently, Augustin et al. (2022) suggested that niche partitioning was probably present between the two sympatric rhabdodontid genera from the Hațeg Basin, *Zalmoxes* and *Transylvanosaurus*. Although they attained a roughly similar body size, *Transylvanosaurus* differs considerably from the sympatric *Zalmoxes* in its cranial morphology having had a much wider and lower skull (Augustin et al. 2022). The markedly different skull proportions, such as a larger attachment site for *m. rectus capitis ventralis* and *m. protractor pterygoideus* in *Transylvanosaurus*, most likely were correlated with different development of the corresponding muscles involved in the feeding process (for details, see Augustin et al. 2022). Ultimately, such differences might reflect distinct feeding adaptations and corresponding niche partitioning between the sympatric rhabdodontids from the Hațeg Basin (Augustin et al. 2022). Generally, the co-occurrence of at least two rhabdodontid species was not uncommon: in the upper Campanian–lower Maastrichtian of north-eastern Spain, *Rhabdodon* sp. occurs alongside *Pareisactus evrostos* (Pereda-Suberbiola and Sanz 1999; Párraga and Prieto-Márquez 2019), while coeval deposits of southern France yielded the two species *Rhabdodon priscus* and *R. septimanicus*, as well as *Matheronodon provincialis* (Buffetaut and Le Loeuff 1991; Chanthasit 2010; Godefroit et al. 2017). Conversely, only one rhabdodontid has, so far, been described from the slightly older European deposits, including *Mochlodon vorosi* from the Santonian of western Hungary, *Mochlodon suessi* from the lower Campanian

of eastern Austria (Seeley 1881; Ósi et al. 2012) and cf. *Rhabdodon priscus* from the lower Campanian of southern France (Buffetaut et al. 1996). Apparently, the co-occurrence of at least two rhabdodontids is characteristic for the later part of their evolutionary history (i.e. Late Campanian–Maastrichtian), whereas single species occurrences are present earlier (i.e. during the Santonian–Early Campanian). The question of whether this pattern is a true evolutionary phenomenon or simply the result of a more extensive fossil record in the later part of the Late Cretaceous cannot be answered conclusively for the time being.

Interestingly, the different sympatric rhabdodontids largely overlapped in body size, as is the case for *Rhabdodon* and *Pareisactus* from northern Spain (Párraga and Prieto-Márquez 2019), *Rhabdodon* and *Matheronodon* from southern France (Chanthasit 2010; Godefroit et al. 2017), as well as *Zalmoxes* and *Transylvanosaurus* from western Romania (Weishampel et al. 2003; Ósi et al. 2012; Augustin et al. 2022). Whether niche partitioning was commonly present between the different sympatric rhabdodontids (as suggested for *Transylvanosaurus* and *Zalmoxes*) is currently unknown, but it is to be expected given their largely overlapping body sizes (and thus feeding heights/ranges). At least for some taxa, the different shapes and proportions of the dentaries (*Rhabdodon priscus* versus *R. septimanicus*), as well as that of the dentition itself (*Rhabdodon* versus *Matheronodon*), definitively suggest some kind of difference in skull shape and proportions and, accordingly, in feeding mechanisms and food preferences and, thus, some degree of niche partitioning. Such niche partitioning may be better understood in the future either based on new and more complete discoveries of these different taxa and/or by using other, complementary approaches. Several methods commonly used to reconstruct certain palaeoecological aspects in fossil vertebrates have yet to be applied rigorously to rhabdodontids. This includes, but is not limited to, stable isotope analysis of their bones and teeth, dental microwear analysis, finite element analysis, biomechanics and myological reconstructions. Some of these, but not others, have already been applied to select taxa; as outlined above, stable isotope analysis has only been used for *Zalmoxes* so far, while dental microwear analysis has only been used for *Mochlodon vorosi*.

In addition to the habitat preferences and feeding ecology of rhabdodontids, several remarks about their posture and locomotion have been made. In their monograph on *Zalmoxes*, Weishampel et al. (2003) noted that it was a medium-sized ornithopod with a comparatively stocky build (Fig. 5H), with several peculiarities of the postcranium suggesting that its locomotion differed from that of other ornithopods and that it had a particularly wide gait when walking and running. Subsequently, Dumbravă et al. (2013) reconstructed the musculature of the *Zalmoxes* hind limb, based mainly on the partial *Z. shqiperorum* skeleton from Nălaț-Vad (see also Godefroit et al. 2009) and other material from this locality, concluding that the rather ventral position of the fourth trochanter on the femur indicates that

Z. shqiperorum was not a particularly fast runner. Although rhabdodontids are mostly envisioned as bipedal animals (for *Zalmoxes*, see Weishampel et al. 1991: fig. 11 and Weishampel et al. 2003: fig. 36; for *Rhabdodon*, see Garcia et al. 1999: fig. 2; for *Mochlodon*, see Ösi et al. 2012: fig. 15), at least *Rhabdodon* was also portrayed as quadrupedal (Pincemaille-Quillevere 2002: fig. 1; Chanthasit 2010: p. 121). This uncertainty concerning the posture and locomotion of rhabdodontids is primarily due to a lack of relatively complete and articulated skeletons (albeit see Vremir et al. 2017). Even the most complete rhabdodontid skeletons described thus far (i.e. MHN AIX PV 199 assigned to *Rhabdodon priscus* and UBB NVZ1 assigned to *Zalmoxes shqiperorum*) lack substantial parts of the postcranium, such as the front limbs (in MHN AIX PV 199) or the majority of the vertebral column (in UBB NVZ1).

Recently, Dieudonné et al. (2023) used several proxies for the posture of ornithopods (based on hind limb morphology) to evaluate the possible posture of rhabdodontomorphs. They concluded that the ‘Vegagete ornithopod’ and *Mochlodon vorosi* switched from quadrupedality to bipedality during ontogeny, whereas *Muttaborrasaurus* and some derived rhabdodontids of the Late Cretaceous (i.e. *Zalmoxes* and *Rhabdodon*) retained a quadrupedal posture until late in ontogeny or even into adulthood. Moreover, based on the histology of long bones, these authors suggested that the rhabdodontomorph ‘Vegagete ornithopod’ grew very rapidly and likely had a high basal metabolic rate (Dieudonné et al. 2023). Conversely, the bone histology of *Zalmoxes* likely indicates relatively slow growth (Benton et al. 2010). Ösi et al. (2012) examined the growth stage of several different rhabdodontids based on histological thin sections of *Mochlodon vorosi*, *M. suessi*, *Zalmoxes robustus*, *Z. shqiperorum* and *Rhabdodon* spp. and concluded that they all had largely similar growth rates, despite their varying adult body sizes with reconstructed (sub-)adult body lengths of 1.4 m in *M. suessi*, 1.8 m in *M. vorosi*, 2.4 m in *Z. robustus*, 2.5 m in *Z. shqiperorum* and 5.9 m in *Rhabdodon* spp. Similarly, Prondvai (2014) found a consistent growth pattern in the three rhabdodontids examined (i.e. *Rhabdodon*, *Zalmoxes*, *Mochlodon*) that is characterised by the early onset of cyclical growth and secondary remodelling, although *Rhabdodon* seems to have undergone a prolonged phase of fast growth compared to *Zalmoxes* and *Mochlodon*. Interestingly, Ösi et al. (2012) were able to show that the ancestral body size of rhabdodontids was likely close to that of *Zalmoxes* by mapping the femoral length on to the results of their phylogenetic analysis. Therefore, *Zalmoxes* likely did not undergo dwarfism, as has been reconstructed for other dinosaurs from the latest Cretaceous Transylvanian Island, such as for the titanosaur *Magyarosaurus* (Stein et al. 2010) and, instead, *Rhabdodon* underwent autapomorphic gigantism, whereas *Mochlodon* might have been characterised by phylogenetic body size reduction (Ösi et al. 2012).

Interestingly, rhabdodontids seem to have died out well before the K/Pg extinction event in Western Europe (i.e. in the early late Maastrichtian), while they survived much

longer (i.e. well into the late Maastrichtian) in Eastern Europe (at the least, in Romania). In the Ibero-Armorican realm, the titanosaur-rhabdodontid-nodosaurid fauna of the Late Campanian–early Maastrichtian was replaced by a hadrosauroid-titanosaur dominated fauna in the later Maastrichtian, with rhabdodontids and nodosaurids apparently going extinct by the early late Maastrichtian, approximately 69 Ma ago (Le Loeuff et al. 1994; Buffetaut et al. 1997; Vila et al. 2016). Several vertebrate groups were affected by this faunal turnover in Ibero-Armorica, the main herbivores of the assemblage first of all; meanwhile and remarkably, such a faunal change did not occur in the Transylvanian realm despite the same clades being also represented there and all major herbivorous taxa appear to have survived for the quasi-entirety of the time span covered by the local fossil record, i.e. from the latest Campanian to late Maastrichtian (Csiki-Sava et al. 2016). Therefore, the Transylvanian landmass seems to be characterised by relatively higher-level faunal stability when compared to the Ibero-Armorican Island (Csiki-Sava et al. 2015, 2016). The reasons leading to the disappearance of rhabdodontids in Western Europe in the early late Maastrichtian are not entirely clear, but it has been hypothesised that palaeogeographic changes might have resulted in the immigration of new taxa on to the Ibero-Armorican landmass (Vila et al. 2016). In particular, the arrival of different clades of hadrosauroids and their subsequent dominance in the Maastrichtian faunas of the Ibero-Armorican Island might have caused the extinction of rhabdodontids, as they potentially occupied similar ecological niches (Vila et al. 2016; but see above). However, it cannot be ruled out that rhabdodontids (and nodosaurids) were already in decline because of another environmental or ecological factor(s) and hadrosauroids simply took advantage of unoccupied niches vacated through the demise of the former taxa (Vila et al. 2016).

One possible environmental factor that might have changed during this time interval, with impact on to the noted faunal replacement, is the nature of the primary producers, i.e. the structure and taxonomic composition of the vegetation supporting the megaherbivores. Although data from related forms in Western Europe are still scarce, tooth structure and tooth wear suggest that *Mochlodon* (and, by extension, possibly all rhabdodontids) and *Hungarosaurus* (and, by extension, possibly all struthiosaurine nodosaurids) show a tooth wear characterised by high number of pits, more typical of browsers (Ösi et al. 2022). The extremely wide teeth of *Matheronodon* were also adapted to cut tougher plant parts (Godefroit et al. 2017). In contrast, microwear patterns of hadrosauroid teeth are known to be scratch-dominated (Fiorillo 2011; Mallon and Anderson 2014; A. Ösi pers. obs.), which may indicate a fundamentally grazer-type lifestyle (Williams et al. 2009). What is clear concerning the faunal turnover in the western European fauna is that herbivorous groups with pit-dominated microwear patterns (rhabdodontids and nodosaurids) are followed by hadrosauroids with a scratch-dominated microwear pattern. This may indicate

a change in the available plant food, for example, the development of more open areas and the spread of a ‘grassland’-type ground vegetation. In contrast, the eastern part of the Archipelago may not have undergone such a dramatic change in flora, allowing rhabdodontids and nodosaurids to persist until the end of the Cretaceous. All this is only a hypothesis until at least more details of the floral record and evolution supports it. Regardless of the exact cause(s) of their demise in Western Europe, rhabdodontids survived until shortly before the K/Pg extinction event in Transylvania and were amongst the last non-avian dinosaurs still present before the end of the Cretaceous.

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