SUPPORTING INFORMATION FOR:

An aberrant island-dwelling theropod dinosaur from the Late Cretaceous of Romania

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1. Etymology

Balaur is an archaic Romanian term that designates a mythical ophidian, dragon-like creature, and this word is often used as synonym for dragon in contemporary Romanian. However, the origin of the term "balaur" is complex. Although ophidian characters are usually of evil nature in Romanian mythology, the "balaur," representing a peculiar metamorphosed snake, has a more ambivalent character. According to Romanian folklore, the genesis of the "balaur" is an exceptional event: "within a certain time period, specifically during reproduction, large numbers of snakes might gather in a remote location. Here, they fight each other, while spitting balls of foam; this foam coalesces and is sprung into a 'priceless stone' (sometimes equated with a diamond). This snake gathering is usually called 'the boiling of the priceless stone.' One of the snakes (the sharpest, the largest, and/or the more valiant) engulfs the stone and becomes "balaur", as it grows wings and flies up to the sky" (Coman, 1996, p. 209). An alternative myth holds that the origin of the "balaur" is traced back to a snake that enters ascetic seclusion for seven years. If it manages to complete the magical seven years unseen by human eyes the snake becomes a "balaur", a winged reptiliomorph creature, master of the storms and repository of great secrets (Coman, 1996). Accordingly, our choice of the name *Balaur* is motivated both by the classical association between dinosaurs (especially theropods) and dragon-like creatures, as well as by the fact that balaur is a mythological creature with links to both reptiles (snakes) and birds (wings), a "winged reptile" – in other words, a paravian theropod, a group that includes the dromaeosaurid *Balaur*.

Bondoc is a Romanian folk word used to designate a clumsy, chubby creature (human or animal). The term itself is of Turkish origin (bunduk), and means "small ball". The specific name alludes both to the small and autapomorphically robust shape of the animal (due to the wide pelvis and increased femoral extensor muscle mass), as well as its Asiatic biogeographical connections (as it is originally a Turkic word).

2. Geological and taphonomic background

Uppermost Creteceous fossiliferous continental deposits have been known in Romania for more than a century, dating to the description of the classic eastern European dinosaur fauna of the Haţeg Basin by Franz Nopcsa (e.g., Nopcsa, 1905, 1923). Recently, increased exploration has determined that these fossil-bearing deposits are widely distributed spatially, across the western margin of the Transylvanian Basin and also within several small, intermontane basins (including the Haţeg Basin; see Codrea et al. [2009] for a recent review). All of these units were deposited subsequent to the latest Cretaceous (Laramidian or Late Getian) orogenetic phase that produced the earliest remnants of the Carpathian Mountains, and correspond to the oldest molasse deposits created by erosion of these mountains (Săndulescu, 1984; Willingshofer, 2000; Willinghofer et al., 1999, 2001; Krézsek & Bally, 2006) The most productive vertebrate-bearing localities from these deposits are distributed along the southwestern edge of the Transylvanian Basin and in the smaller Haţeg Basin, where several distinct lithostratigraphic units have been identified (see Codrea et al., 2009; Grigorescu, 2010).

The type specimen of *Balaur bondoc* (EME VP.313) was discovered at the Sebeş Glod (SbG/A) locality, which is located approximately 2.5 kilometers north of Sebeş town, downstream and along the Sebeş River, in Alba County, Romania. The specimen was collected by MV and his family (V. Gábor, V. Bence) in September 2009 and given a preliminary field number (SbG/A-Sk1) during collection and preparation. The holotype comes from the lower third of the Sebeş Formation, approximately 100 meters above the conformable contact with the underlying marine-transitional Bozeş Formation and approximately 450 meters below a major mid-Miocene unconformity that caps the Sebeş Formation at its stratotype locality (Râpa Roşie).

The Sebeş Formation was named by Codrea and Dica (2005) but was never formalized; it has been extensively mapped by MV. It represents a thick succession of continental "red beds," dominated by coarse, poorly sorted conglomerates and pebbly sandstones with sandstone and mudstone interbeds. Some of the best exposed outcrops are along the Mures River, downstream from the Alba Iulia locality, in the southwestern Transylvanian Basin. Originally, the Sebeş Formation was regarded as Lower-Middle Miocene (see review in Codrea et al., 2008), and thus its rare vertebrate fossils (dinosaurs, turtles, crocodilians) were considered as being reworked from the underlying Maastrichtian deposits (Grigorescu, 1992; Jianu et al., 1997; Codrea & Vremir, 1997; Codrea & Dica, 2005; Codrea et al., 2008). Only recently, however, has evidence emerged that the Sebeş Formation is (at least partially) latest Cretaceous (Maastrichtian) in age. This evidence includes clearly autochthonous vertebrate fossils from the stratotype section (Vremir et al., 2009) and from the Sebeş Glod locality (see below), as well as dinosaur footprints identified in beds roughly correlative with those from the holotype locality (Vremir and Codrea, 2002).

Near the type locality of *Balaur*, several restricted outrcrops of red continental deposits of the Sebeş Formation can be followed along the Sebeş River (codified as sites SbG/A-D in local maps). The stratigraphic position of the type locality within the local geological framework suggests that it is probably late Early Maastrichtian in age, based on its position well above the Campanian-Maastrichtian boundary (dated by palynology, calcareous nannoplankton, and forams: Antonescu, 1973; Antonescu et al., 83; Balc et al., 2007) and below Upper Maastrichtian deposits of the upper Sebeş Formation cropping out nearby. The type locality and proximal outcrops are dominated by coarse, mainly cross-bedded channel deposits (gravels, sandy gravels), with occasional interbeds of finer grained overbank and floodplain deposits (sandstones, silty red clays, mudstones). Contact between the floodplain deposits and the channel deposits is often erosional, and marked by several calcrete-bearing red silty clay horizons (up to 2 m thick) that are identified as well drained, moderately mature calcic paleosols. These represent floodplain mud deposits that have undergone subsequent pedogenesis. A large number of vertebrate fossils have been found in these deposits during the last decade, particularly at sites SbG/A and B. Most are fragmentary and isolated bone fragments, some referable to dinosaurs, turtles, crocodilians, pterosaurs, and possibly birds (see also Codrea et al., 2009). However, the pedogenetically modified red mudstones occasionally yield more complete specimens, such as the holotype of *Balaur*. Sedimentological and taphonomic evidence suggests that the specimen was transported in a low energy current as a partially rotted carcass during waning flood conditions, then subaerially exposed for a short time, partially disarticulated, and buried relatively rapidly due to additional sediment input.

The referred specimens of *Balaur* were discovered about 100 kilometers from the type locality, at the Tuştea dinosaur nesting site (near Tuştea village, Hunedoara County, Haţeg Basin, Romania) by a collecting party led by Prof. Dan Grigorescu (University of Bucharest) in 1997. This site is located in the fossiliferous middle member of the

Maastrichtian-?Palaeogene Densuş-Ciula Formation (Grigorescu, 1992), a continental succession with a significant volcanogenic component (tuffs, tuffites, agglomerates). Vertebrate fossils are found only in the middle member of the unit, as the lower member has yielded only isolated plant fossils and is dominated by volcanogenic sediments, and the upper member is entirely devoid of fossils. A Late Maastrichtian age was previously reported for the Densus-Ciula Formation (Antonescu et al., 1983), but recent data suggest that it also includes the Lower Maastrichtian (as it rests on Upper Campanian marine deposits: Melinte-Dobrinescu, 2009). Furthermore, the uppermost part of the unit may extend into the Palaeocene, but this suggestion is based mainly on the absence of definitive Mesozoic vertebrate fossils in this part of the formation, and is thus poorly supported. Despite the lack of any definitive chronostratigraphic markers in the proximity of the Tuştea nesting site, it can be confidently referred to the Maastrichtian, and possibly even to the "middle" to Upper Maastrichtian, based on its stratigraphic position in the middle-upper part of the vertebrate-bearing middle member.

The Tuştea nesting site is represented by an originally vertical outcrop exposing near-horizontal continental deposits. Subsequently, the outcrop was converted into a horizontal surface to allow excavation along the nesting horizon (see Grigorescu et al., 2010). The local succession is dominated by a thick unit of massive, red silty mudstone with several calcrete horizons, topped by a composite body of poorly sorted, matrix-supported conglomerates and coarse sandstones with through cross-bedding. The contact between the two distinct beds is represented by a well-developed erosional surface. The mudstone body, representing the main fossil-bearing unit and including the nesting horizon and the fossils of *Balaur*, is underlain by a thin layer of medium-grained sandstone and a second thick bed of red mudstone reminiscent of the egg-bearing mudstones (Grigorescu et al., 1994, 2010). The succession is interpreted to have been deposited within the distal part of a well-drained floodplain, where the fine-grained deposits brought by flood waters subsequently underwent extensive pedogenesis (e.g., Bojar et al. 2005, Therrien, 2005).

A large number of vertebrate fossils have been discovered at several levels at the Tuştea nesting site, including abundant turtles, a diverse array of dinosaurs, crocodilians and pterosaurs, as well as microvertebrates (frogs, multituberculates). Besides dinosaur nests and eggs, numerous neonate remains have also been discovered and referred to the hadrosaurid *Telmatosaurus transsylvanicus* (Grigorescu et al., 1994, 2010; Grigorescu and Csiki, 2000). Preliminary taphonomic analysis of the site suggests attritional, but dominantly autochthonous, accumulation of the vertebrate remains on the surface of incipiently developed paleosols, followed by a variable amount of subaerial weathering and postmortem disturbance (scattering, trampling, scavenging) before final burial by subsequent flooding events (Grigorescu and Csiki, 2000). Although the occurrence of isolated bones and bone fragments is most common, associated skeletal elements and rare articulated partial skeletons have also been found, suggesting that at least some degree of skeletal completeness was present in several individuals just before burial. Indeed, it is common for skeletal elements from the same body part of a taxon to be scattered about a small distance, with shared taphonomic modifications, commensurate size, and (in case of skull bones) sutural relationships suggesting that these elements belonged to one individual.

The material here referred to *Balaur* was discovered under such conditions. The six forelimb elements were discovered during the same excavation session, dispersed over a relatively small area. Moreover, all of these belong to the left forelimb, exhibit theropod affinities, are similar in size, and exhibit a common feature: the presence of a peculiar, rugose, woven surface texture (see below, **4.**, **5.**). Additionally, there are no duplicate elements and most elements exhibit autapomorphies of *Balaur*, as identified on the more complete holotype. Accordingly, these elements can be reliably considered as belonging to the same individual, despite the different specimen numbers (which only reflect that they were found isolated during the excavation).

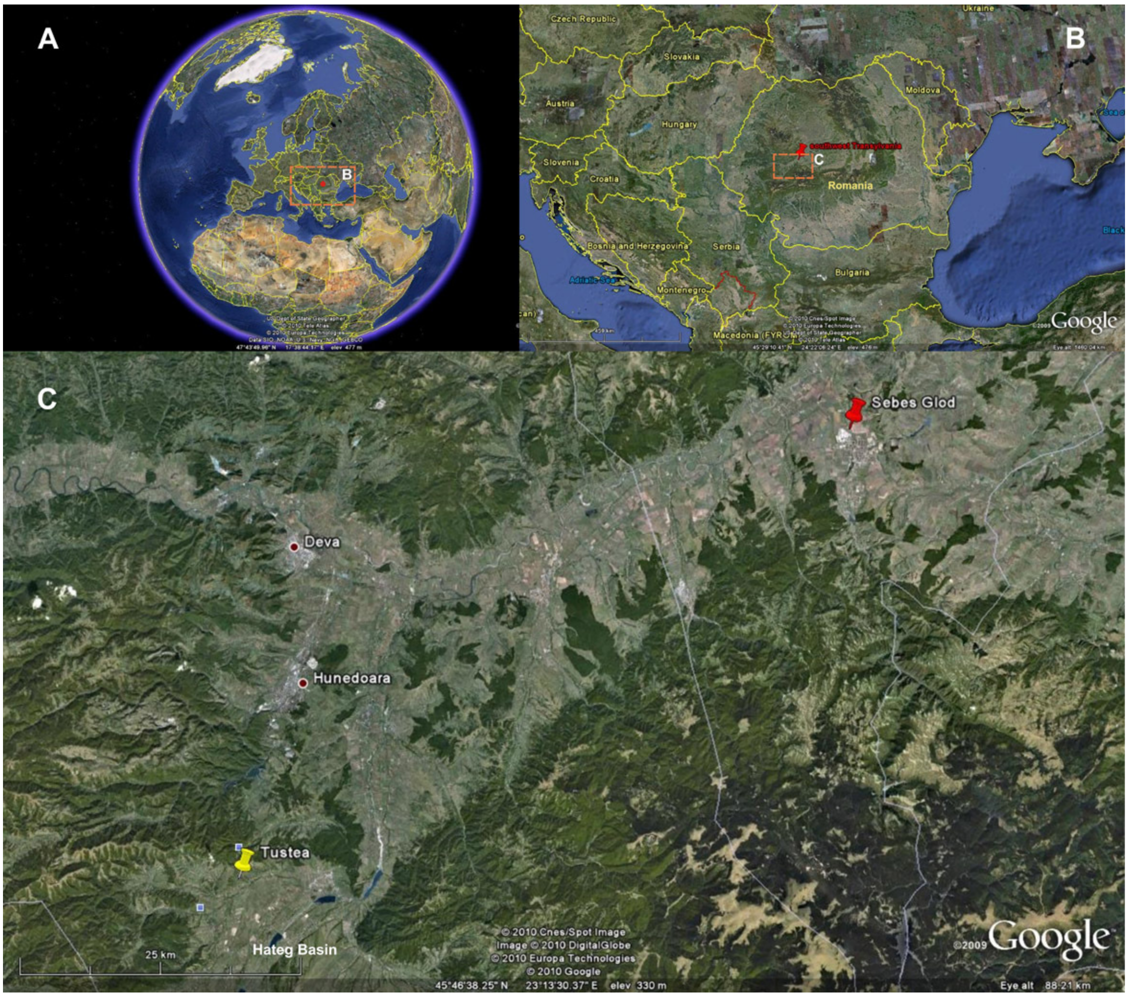

Figure S1. The type locality (Sebeş, upper right corner of C) for *Balaur bondoc* and the discovery site of the referred specimen (Tuştea, lower left corner of C) indicated on a map of Romania. The two localities are separated by slightly less than 100 kilometers.

Figure S2. The type locality for *Balaur bondoc*: the Sebeş Glod (SbG/A) locality during high river level, located approximately 2.5 kilometers north of Sebeş, downstream and along the Sebeş River, in Alba County, Romania. In the background, the outcrops of the type section of the Sebeş Formation are visible.

3. Details of type specimen

The type specimen belongs to a single, associated and partially articulated individual. No cranial bones or cervical vertebrae are present. The preserved fossils include: one anterior and seven more posterior dorsal vertebrae, the sacrum (made up of at least 4 sacrals) in articulation with the pelvis (including incomplete ilia preserving only the circum-acetabular region, pubes and ischia, all preserved in life position), one caudosacral, five anterior caudals, fragmentary right and left scapulacoracoids, complete right and almost complete left (missing metacarpal and digit III) forelimbs, left distal limb in articulation (tibiotarsus, metatarsals and complete digits) and right tarsometatarsus. The ossified, paired sternal plates were observed in the field, mainly as moulds of the original thin bone plates, but their excavation was largely unsuccessful. Additionally, several incomplete dorsal ribs (pertaining to the posterior dorsal vertebrae) and indeterminate bone fragments were also recovered.

It is likely that the holotype represents a mature or near-mature individual, although this is somewhat tenuous. Histological age assessment was not possible due to fungal damage in the interior of preserved long bones. Maturity is suggested by the high degree of skeletal fusion: the neural arches and centra are completely fused in all dorsal, sacral, and caudal vertebrae; the scapulocoracoid is fused; the carpals and metacarpals are fused; the pelvis is fused; the tibia, fibula, and proximal tarsals are fused; and the distal tarsals and metatarsals II-V are fused. However, the referred specimen is approximately 45% larger than the holotype (see below, **4**.), so it is clear that *Balaur* was able to attain larger size than the holotype individual, and that growth continued after fusion of numerous regions of the skeleton. Without independent histological age assessment for both specimens, however, it cannot be ruled out that such size difference is due to individual variation or dimorphism. What is important, however, is that both the holotype and referred specimen are within the size range of close dromaeosaurid relatives (e.g., *Velociraptor*, *Deinonychus*), so there is no evidence for dwarfism or gigantism.

4. Details of referred specimens

Previously, the referred specimen (FGGUB R. 1580-1585) was preliminarily identified and described as a possible caenagnathid oviraptorosaur by Csiki and Grigorescu (2005). However, these specimens can be referred to *Balaur* based on the possession of unique characters (autapomorphies) exhibited by the corresponding skeletal elements of the holotype (EME VP.313). The referred humerus (Figure S3) possesses the autapomorphic sinuous ridge on the lateral surface of the distal end and the autapomorphic prominent ridge on the medial surface of the distal half of the bone, the referred ulna (Figure S4) possesses the autapomorphic flat anterior surface bisected by a longitudinal ridge, and the referred metacarpal II possesses the autapomorphic ridge that laterally overhangs metacarpal III and a distal articular surface that autapomorphically does not extend onto the plantar surface of the bone. In addition, all referred bones possess the unusual mottled ridged surface texture characteristic of the *Balaur* holotype (Figure S5; either an autapomorphy of *Balaur* or a synapomorphy of a restricted European clade, see below), and are nearly identical in overall morphology to corresponding bones in the holotype, despite their larger size (Figures S3-4). Although the holotype and referred specimens come from different lithostratigraphic units in different basins, both units are roughly the same age (Maastrichtian) and were deposited in the same palaeogeographic area (a relatively large Transylvanian landmass often referred to as the “Haţeg Island”: e.g., Codrea and Godefroit, 2009; Benton et al., 2010).

Figure S3. A comparison of the holotype (A) and referred (B) left humeri of *Balaur bondoc*, illustrating the size differences between them and the autapomorphies that they share. Both bones are shown in anterior (A1, B1) and lateral (A2, B2) views. The sinuous lateral ridge and medial crest are autapomorphies of *Balaur bondoc* that are present in both specimens. The radial condyle is also autapomorphically located on the anterior surface of the bone; this is clear in the referred specimen (B1), and is present but difficult to discern in the holotype (A1) due to poor preservation in this region, as only a small portion of the condyle remains.

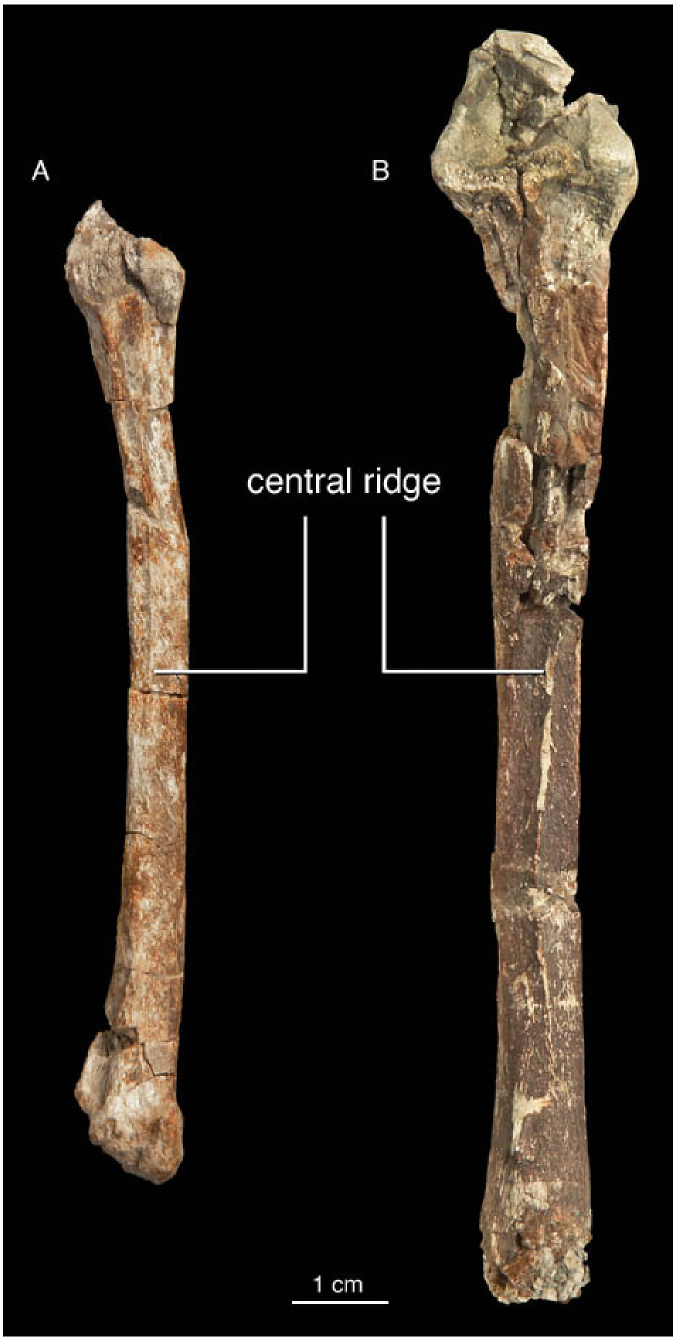

Figure S4. A comparison of the holotype (A) and referred (B) left ulnae of *Balaur bondoc* in anterior view, illustrating the size differences between them and the autapomorphies that they share. The flat anterior surface, which is bisected by a long, thin ridge, is an autapomorphic complex of characters present in both specimens.

5. Bone texture

One of the most unusual, and striking, features of the *Balaur* holotype and referred specimens is a heavily sculptured bone texture, which covers the external surfaces of all of the appendicular bones of both specimens (Fig. S5). This texture is not likely to be size related, an ontogenetically ephemeral character, or a taphonomic artifact, since it is present on both specimens, which greatly differ in body size (and presumed ontogenetic state) and were found at different localities characterized by different depositional and taphonomic settings. Additionally, similar bone texture has been noted on other isolated theropod bones from throughout the Late Cretaceous deposits of Romania (e.g., Andrews, 1913; Le Loeuff et al., 1992; and Kessler et al., 2005). It is possible that this bone texture is diagnostic of *Balaur bondoc* itself, but it has also been described on isolated bones that possess alvarezsaurid characteristics (Naish and Dyke, 2004; Kessler et al., 2005). Therefore, pending a careful revision of this other material, it is possible that this bizarre sculpturing is present on multiple small theropods from Romania, and perhaps may be tied to localized environmental conditions.

Unfortunately, histological examination of this texture in *Balaur* is hampered by fungal damage to the interior of the bone, so it is unknown whether the texture is also expressed internally. Similar bone texture is unknown in other Mesozoic dinosaurs, to our knowledge, but juvenile dinosaurs often possess a characteristic external texturing comprised of elongate, subparallel bone grains. The external texture of the type specimen of *Balaur* is comprised of subparallel grains in places (Fig. S5A), but these grains exhibit greater relief than the characteristic juvenile texture of dinosaurs. It is worthwhile to note that the external texture of the holotype, which is a smaller and presumably younger individual than the referred specimen, is comprised of more elongate, subparallel ridges, similar to juvenile bone texture. The larger holotype, however, has a more randomly mottled surface texture comprised of branched, curving, and anastomosing ridges (Fig. S5B). Whether this difference is ontogenetic in nature, or simply random, awaits further testing with additional discoveries.

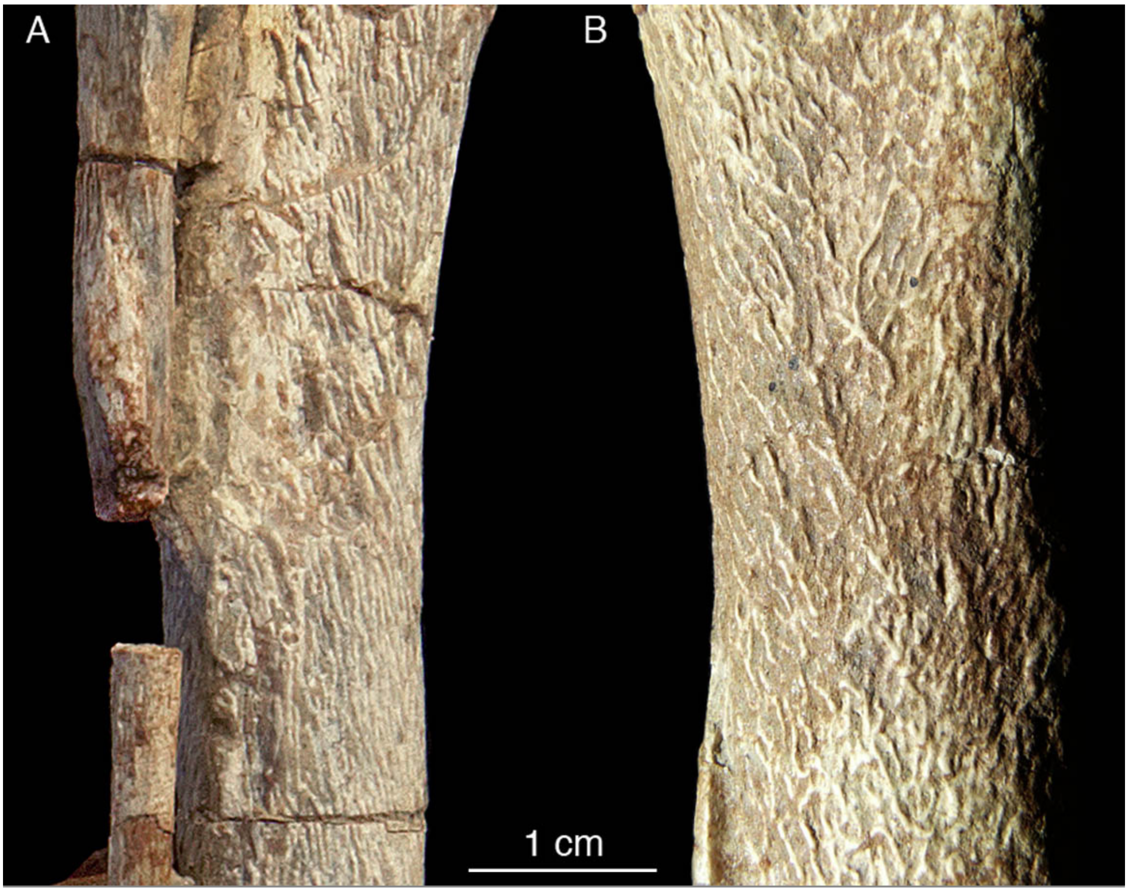

Figure S5. The unusual surface bone texture as preserved on the holotype left tibia and fibula (A, midshaft in oblique posterolateral view) and the referred left humerus (B, midshaft in anterior view).

6. Body size comparison with other dromaeosaurids

Balaur bondoc is within the size range of its closest relatives and is not substantially smaller or larger than its sister taxon. Unfortunately, both the holotype and referred specimen of *Balaur* are lacking a femur, the most common and confident estimator of body mass (Christiansen and Farina, 2004). Furthermore, it is misleading to compare the tibiotarsus or metatarsus of *Balaur* with other taxa, since both elements are autapomorphically shortened in *Balaur*. Therefore, the most reasonable bone to compare among taxa is the humerus. As is shown in Table S1, the humerus of the type specimen of *Balaur* is somewhat smaller than the humerus of one of the best exemplar specimens of its sister taxon, *Velociraptor mongoliensis*. The humerus of the referred specimen of *Balaur*, however, is somewhat larger than the *Velociraptor* specimen. Additionally, the humerus of the *Linheraptor* type is also intermediate in size between the humeri of the type and referred specimens of *Balaur*. Unfortunately, because there is no histological evidence to assess the absolute age of the *Balaur* specimens, it is difficult to make explicit comparisons between individuals of similar ontogenetic stage. What is clear, however, is that *Balaur* is generally similar in body size relative to other dromaeosaurids, and that there is currently no evidence that it was a dwarfed taxon that was approximately 50% smaller than its sister taxon and other close relatives, as is the case with Haţeg ornithopods and sauropods (e.g., Benton et al., 2010).

Table S1. Comparative measurements for the holotype and referred specimen of *Balaur bondoc* and several other dromaeosaurid taxa. All measurements are in millimeters. Symbols: ^{e} – estimated; ^{1} – estimated based on holotype; ^{2} – estimated based on close relative *Linheraptor*.

Taxon	Specimen number	Reference	Skull length	Humerus length	Femur length	Tibia length	Metatarsus length
Balaur bondoc	EME PV.313	this study	-	117	-	153	62
Balaur bondoc	Tustea specimen	this study	-	170^{e}	-	- (222^{e1})	-
Velociraptor mongoliensis	IGM 100/982	Norell and Makovicky, 1999	-	140	175	200	110
Velociraptor mongoliensis	IGM 100/986	Norell and Makovicky, 1999	-	-	238	255	99.1
Deinonychus antirrhopus	AMNH 3015	Ostrom, 1969	-	237^{e}	-	312	151
Deinonychus antirrhopus	MCZ 4371	Ostrom, 1976	-	254	336	368	164.4
Saurornitholestes langstoni	MOR 660	Photos	?	?	225	257	113
Tsaagan mangas	IMG 100/1015	Norell et al., 2006	201	-	-	- (227.8^{e2})	-
Linheraptor exquisitus	IVPP V16923	Xu et al., 2010	225	155^{e}	230	255	125
Buitreraptor gonzalezorum	MPCA 245	Makovicky et al., 2005	190	135	145	> 152	-
Unenlagia comahuensis	MCF PVPH 78	Novas et al., 2009	-	265^{e}	368	> 418	-
Austroraptor cabazai	MML-195	Novas et al., 2009	-	262	560	565	330^{e}
Rahonavis ostromi	UA 8656	Forster et al., 1998	-	-	88	119.8	48
Sinornithosaurus millenii	IVPP V12811	Xu et al., 1999	130^{e}	134	148^{e}	> 125	93
Microraptor zhaoianus	IVVP V12330	Xu et al., 2000	45^{e}	-	53	68	-
Microraptor zhaoianus	CAGS 20-8-001	Hwang et al., 2004	-	62.9	74.8	95.5	49.4

Mahakala onmogovae	IGM 100/1033	Turner et al., 2007	-	35-40[e]	79	110	82

7. Comparisons with other specimens from the Haţeg Basin and the Late Cretaceous of Europe

7.1. Previous derived theropod reports from the Upper Cretaceous of Transylvania

Theropod dinosaur remains are relatively rare in the uppermost Cretaceous continental deposits of the Transylvanian area. Several specimens that Nopcsa (1915) and others once thought belonged to theropods actually belong to other clades (e.g., Csiki and Grigorescu, 1998). The best known theropod taxon from Transylvania is *Elopteryx nopcsai* (Andrews, 1913), an enigmatic taxon based on fragmentary fossils whose relationships are poorly understood (see below). Other theropod fossils, likely belonging to derived coelurosaurs (paravians or close relatives), include teeth that were referred to dromaeosaurids and other taxa such as troodontids and the enigmatic tooth genera *Richardoestesia*, *Paronychodon*, and *Euronychodon* (Grigorescu, 1984; Grigorescu et al., 1985; Csiki & Grigorescu, 1998; Codrea et al., 2002; Smith et al., 2002; Vassile, 2008). However, the fragmentary nature and often poor preservation of these teeth makes taxonomic identification and palaeobiological interpretation difficult.

More complete and diagnostic fossils of derived theropods are exceedingly rare. Jianu and Weishampel (1996) reported the presence of *Saurornitholestes*-like derived dromaeosaurids based on associated frontal and parietals, fossils that unfortunately cannot be compared to *Balaur* (which lacks known cranial remains). Smith et al. (2002) described an isolated dorsal centrum of an indeterminate theropod and Kessler et al. (2005) referred a distal femur to *Elopteryx*, whose holotype is considered to belong to an alvarezsaurid (Kessler et al., 2005; Choiniere et al., 2010). Naish and Dyke (2004) also argued that a specimen previously referred to *Elopteryx* (see below), a distal tibiotarsus, represents an alvarezsaurid. Most recently, Ősi and Főzy (2007) reinterpreted a fragmentary sacrum, referred previously to the Early Cretaceous pterosaur genus *Ornithodesmus* by Nopcsa (1915, 1923), as representing an indeterminate paravian, probably most closely related to dromaeosaurids or birds. Unfortunately, it is difficult to compare this specimen to the *Balaur* holotype sacrum, which is mostly encased in matrix.

In sum, the latest Cretaceous Romanian record of derived coelurosaurian theropods is poorly understood. Several specimens suggest the presence of dromaeosaurids, perhaps even derived velociraptorine members of the group (e.g., Grigorescu, 1984; Jianu & Weishampel, 1996). It is tempting to speculate that some or all of these specimens belong to *Balaur*, but this is difficult to test in most cases due to a lack of overlapping material or the absence of diagnostic features on fragmentary specimens. It is worth noting that several other derived coelurosaurian clades, such as oviraptorosaurs, alvazrzsaurids, and troodontids, have also been reported from Translyvania, but on extremely fragmentary material that is usually undiagnostic. Some of this material may also belong to *Balaur* or close relatives, but this is also difficult to test.

7.2. *Elopteryx nopcsai*: a taxon with a checkered taxonomic history and comparisons to *Balaur bondoc*

The best known, best preserved, and most diagnostic theropod taxon from the Late Cretaceous of Romania (and indeed Europe) is *Elopteryx nopcsai*, named by Andrews (1913) and based on two proximal femoral fragments, and possibly a distal tibiotarsus, from the Maastrichtian Sînpetru Formation of Sibişel Valley, in the central Haţeg Basin. Of the available material, Andrews informally designated specimen BMNH (NHM, Natural History Museum, London) A1234, the less complete but better preserved proximal femur, as the holotype of the new taxon, by basing his description mainly on this specimen. The other proximal femur, BMNH A1235, was referred to the same taxon due to its comparable morphology. However, the rationale for referring the distal tibiotarsus (BMNH A4359) to *Elopteryx* was based solely on a similar, roughened surface texture, which Andrews (1913:195-196) held as suggestive of a common taxonomic origin.

Some subsequent authors referred additional material to *Elopteryx*, whereas others argued that some material could not be reliably referred to this taxon. Lambrecht (1929) referred to *Elopteryx* additional specimens from Sînpetru: two tibiotarsi collected by Nopcsa (BMNH A1528) and Lady Woodward (BMNH A1588), respectively. He included both *Elopteryx* and the Eocene taxon *Eostega lebedynskyi* from Cluj (Transylvania, Romania) in the family Elopterygidae, presumed to belong to the Pelecaniformes (Lambrecht, 1933). However, reexamination of the referred material by Harrison and Walker (1975) led to the removal of the tibiotarsi from *Elopteryx* and their referral to two new taxa of presumed giant owls: *Bradycneme draculae* and *Heptasteornis andrewsi*, for which the authors erected a new family (Bradycnemidae) within the Strigiformes. They accepted, however, the pelecaniform affinities of the type femora of *Elopteryx*, echoing the initial interpretation of Andrews (1913). A few years later, Grigorescu and Kessler (1981) referred an isolated limb bone (FGGUB R.351), identified as a distal left femur, to *Elopteryx*. Later authors disagreed with this referral, and this bone likely is the distal end of a large hadrosaur metatarsal (Csiki & Grigorescu, 1998; Kessler et al., 2005).

Along with debates about taxonomy and referred specimens, the phylogenetic affinities of *Elopteryx* have long been a source of contention. Several bird specialists disputed the avian nature of the material (e.g., Brodkorb, 1978; Elzanowski, 1983; Martin, 1983; Olson, 1985), and Martin (1983) and Grigorescu (1984) suggested that the fossils instead belonged to small, indeterminate coleurosaurian theropods. Later authors considered some or all of this material to belong to troodontids, but no strong evidence has ever been used to support this referral (e.g., Norman, 1985; Osmólska, 1987; Paul, 1988; Osmólska and Barsbold, 1990; Howse and Milner, 1993). Meanwhile, Le Loeuff et al. (1993) considered the *Elopteryx* holotype and all referred material to belong to a single taxon, probably a dromaeosaurid, and Csiki and Grigorescu (1998) suggested that at least some of the material belonged to a derived maniraptoran. More recently, Naish and Dyke (2004) argued that some of the *Elopteryx* referred material (“*Heptasteornis*”: BMNH A4359) represents an alvarezsaurid, whereas other material belongs to other maniraptoran theropods. In the most recent revision of this collection of fragmentary fossils, Kessler et al. (2005) described a new specimen from Sînpetru, a distal femur (FGGUB R.1957), which they assigned to *Elopteryx* based on comparable size and matching surface texture to the holotype. They advocated possible alvarezsaurid affinities for not only BMNH A4359, but for the holotype and all material currently referred to *Elopteryx*, which was followed by Choiniere et al. (2010).

The tortured taxonomic history of *Elopteryx* is due mostly to the fragmentary and poorly-preserved nature of the specimens, not a single one of which is even a remotely complete bone. The uncertain nature of this material is highlighted by the fact that all of the Haţeg taxa were considered troodontids in the second edition of the Dinosauria (Makovicky and Norell, 2004), whereas Hope (2002) still listed *Elopteryx* as a pelecaniform bird in her overview in the Mesozoic Birds volume. Despite the numerous papers written about *Elopteryx*, there is currently no widely accepted and well supported opinion as to the phylogenetic affinities of the holotype and various referred specimens. This may be a debate that can only be solved with additional specimens, hopefully more complete than the fragments that have been volleyed over by specialists for the last century.

For the sake of the present paper, however, it is important to note that *Balaur* cannot be compared to the holotype of *Elopteryx* (the name-bearing specimen of the genus and species) because there is no overlapping material (i.e., *Balaur* does not preserve a proximal femur). Therefore, *Balaur* cannot be synonymized with *Elopteryx*, even in the two do turn out to be the same taxon. It is noteworthy, however, that the type and referred material of *Elopteryx* share one potential apomorphy with the holotype and referred material of *Balaur*: the preserve of the pervasive woven and rugose bone surface texture. As already noted, this peculiar feature caught the attention of Andrews (1913), Le Loeuff et al. (1992), and Kessler et al. (2005), who used it to unite all these specimens into one taxon. However, we do not consider the presence of this single character to represent strong evidence for the referral of *Balaur* to *Elopteryx*. It could very well represent a synapomorphy of a larger group, or perhaps an environmentally-controlled feature, as it is known to be present on several isolated fossils restricted to Transylvania that have been assigned to numerous different theropod clades (see above). Additionally, the referred distal tibiotarsi of *Elopteryx* can be compared to *Balaur*. Although these specimens do share some characters, such as fusion into a tibiotarsus, the supposed *Elopteryx* tibiotarsi are more mediolaterally expanded and anteroposteriorly flattened distally.

7.3. Derived theropods from the Late Cretaceous of Europe and comparisons with *Balaur bondoc*

Fossils of derived coelurosaurian theropods are known from other Late Cretaceous sites in Europe, although these are also rare. No definitive paravian remains (exclusive of Avialae) from this time are known from the United Kingdom, the Netherlands, Belgium, Germany, Austria, or Italy, and their record is restricted to isolated teeth in Portugal, Spain, and Slovenia (see Weishampel et al., 2004). However, somewhat complete and diagnostic coelurosaurian fossils are known from the Late Cretaceous of Hungary (Ősi and Rabi, 2006; Ősi et al., 2010) and France (see reviews in Vullo et al. [2007] for the Cenomanian; Chantasit & Buffetaut [2009] for the Campanian-Mastrichtian). Most of these can be directly compared to *Balaur*, and it is clear that none of them represent the same taxon.

France, Cenomanian: Vullo et al. (2007) reported the isolated teeth of troodontids and dromaeosaurids, the latter of which were described as reminiscent of derived velociraptorines due to the strong size dissimilarity on the mesial and distal denticles. However, direct comparison with *Balaur* is not possible due to the lack of overlapping elements.

France, Campanian-Maastrichtian: Derived theropods are represented by only teeth at most sites of this age in France, and many of these isolated specimens are referred to dromaeosaurids (e.g., Buffetaut et al., 1986). However, two more complete and potentially diagnostic specimens are also known, and have been named as two taxa: *Variraptor mechinorum* (Le Loeuff and Buffetaut, 1998) and *Pyroraptor olympius* (Allain and Taquet, 2000). *Pyroraptor* can be directly compared to *Balaur* and the two exhibit obvious differences: *Pyroraptor* lacks the flat anterior surface of the ulna that is autapomorphic of *Balaur*, and *Balaur* lacks the deep muscle attachment site on the lateral surface of the proximal ulna that is described as autapomorphic of *Pyroraptor* (Allain and Taquet, 2000). Similarly, *Variraptor* can be compared with *Balaur*, and the two exhibit obvious differences. Most prominently, the humerus is more robust and straight in *Variraptor*, and exhibits a pronounced posteromedial protuberance level with the distal margin of the deltopectoral crest, which is not present in *Balaur* and is potentially autapomorphic (Le Loeuff and Buffetaut, 1998). Additionally, the sacrum of *Variraptor* exhibits a ventral groove only on the fourth sacral, whereas these structures are present anteriorly in *Balaur* (Chantasit and Buffetaut, 2009). Furthermore, two more fragmentary and unnamed specimens can also be differentiated from *Balaur*. An isolated manual ungual described by Chantasit and Buffetaut (2009) lacks the autapomorphic Y-shaped lateral and medial grooves of *Balaur*, and a caudosacral reported by Le Loeuff et al. (1992) (described in concert with a femur and a cervicodorsal that cannot be compared directly to *Balaur*) possesses a dorsolaterally oriented transverse process, unlike the more laterally oriented condition in *Balaur*.

Hungary, Santonian: The Santonian dinosaur assemblage from Hungary (Ősi and Rabi, 2006; Ősi et al., 2010) is interesting because it fills the gap between the earliest Late Cretaceous faunas and the much better known Campanian–Maastrichtian faunas from elsewhere in Europe. Although the presence of dromaeosaurids and *Richardoestesia* was first reported based only on isolated teeth (Ősi, 2004), further derived coelurosaurian remains were reported recently, one of which (a scapulocoracoid) was referred to a new taxon, *Pneumatoraptor fodori* (Ősi et al., 2010). This bone can be compared directly to the scapulacoracoids of *Balaur*, and the two taxa exhibit clear differences. Most importantly, *Balaur* lacks the large pneumatic foramen on the coracoid that is autapomorphic of *Pneumatoraptor*, and *Pneumatoraptor* lacks the hypertrophied coracoid tubercle that is autapomorphic of *Balaur*. Additionally, it is worth noting that the *Pneumatoraptor* scapulocoracoid is much smaller than that of the *Balaur* holotype. However, although different, the scapulocoracoids of *Pneumatoraptor* and *Balaur* do share some derived features, such as the L-shaped morphology characteristic of paravians in general and the fusion between the elements that is seen elsewhere in *Velociraptor* and *Microraptor* (Norell and Makovicky, 1999; Turner et al., 2007). Therefore, *Pneumatoraptor* may be a dromaeosaurid closely related to *Balaur*, but this will likely remain uncertain until more complete and associated material of *Pneumatoraptor* comes to light.

Additionally, a fused tarsometatarsus was reported from the same Santonian deposits by Ősi and Rabi (2006) and Ősi (2008) and referred to an enantiornithine bird. Although this specimen is indeed comparable to enantiornithines in the proximal fusion of the metatarsals, it also exhibits similarities with the corresponding element of *Balaur*. In fact, all characters cited to unite this Hungarian specimen with enantiornithines (fusion reduced to the proximalmost part of the metatarsals; mt II shortest; mt IV most gracile) are also present in *Balaur*, suggesting that this specimen belongs to a *Balaur*-like dromaeosaurid and/or that convergence between some dromaeosaurid and enantiornithine metatarsal morphologies was rampant. Regardless of the affinities of the Hungarian specimen, it exhibits clear differences when compared to *Balaur*. Most prominently, the tarsometatarsus is much shorter proximodistally relative to its mediolateral width in *Balaur*, the metatarsals are more closely appressed across their lengths in *Balaur*, the Hungarian specimen lacks the autapomorphic ridges on the plantar surfaces of the central metatarsals of *Balaur*, and the Hungarian specimen appears to lack a metatarsal V that is fused to metatarsal IV as in *Balaur*.

8. Comparisons with enigmatic four-toed Late Cretaceous footprints

Theropods with four functional pedal digits are rare, and body fossils of such taxa are limited to one aberrant basal theropod (*Tawa*: Nesbitt et al. 2009), derived therizinosauroids (Clark et al. 2004), and derived avialans. However, an enigmatic four-toed theropod footprint, *Saurexallopus*, is known from the Late Cretaceous of western North America (Harris et al., 1996; Lockley et al., 2003). The affinities of these tracks have been the subject of debate (Lockley et al., 2003), but it is clear that *Balaur* or a similar four-toed dromaeosaurid is not the source. *Saurexallopus* has an unusual morphology in which the four functional digits (I-IV) radiate outwards from a small central metatarsal imprint, indicative of a tightly bunched metatarsus (Harris et al., 1996). Similarly, differences in topographic relief on well-preserved tracks suggest that the trackmaker's foot may have been webbed (Harris et al., 1996). These features would not be present in a footprint made by a *Balaur*-like animal: the digits of *Balaur* do not radiate outwards, the metatarsus of *Balaur* is not tightly bunched, digit I of *Balaur* is not as reduced relative to digits II-IV as in *Saurexallopus*, and well-preserved tracks of dromaeosaurids indicate that the hyperextensible digits (digits I and II in *Balaur*) would be held free of the ground and thus would not be registered in a footprint (Li et al. 2007; Kim et al. 2008). It is more likely that *Saurexallopus* represents a derived avialian (e.g., Farlow et al., 2000) or a still unknown group of aberrant non-avian theropods. The unexpected discovery of *Balaur*, a functionally four-toed dromaeosaurid, raises the possibility that supernumerary digits may have also been present in other groups, and future discoveries may solve the mystery of the *Saurexallopus* trackmaker.

9. Details of phylogenetic analysis

To determine the phylogenetic affinities of *Balaur* we added this taxon to a modified version of the most recent version of the Theropod Working Group (TWiG) dataset (Turner et al. 2007). The modified dataset includes 70 taxa scored for 251 characters, 18 of which are ordered (see Turner et al. 2007 for details). Because characters follow those of Turner et al. (2007) they are not repeated here, but the final taxon-character matrix is presented below.

The dataset was subjected to a parsimony analysis in TNT v 1.1 (Goloboff et al. 2008). As a first step, we analyzed the matrix under the "New Techonology search" option, using sectorial search, ratchet, tree drift, and tree fuse options with default parameters. The minimum length tree was found in 10 replicates, which tried to sample as many tree islands as possible. The generated trees were then analyzed under traditional TBR branch swapping, to more fully explore each tree island, which resulted in 5832 most parsimonious trees of length 880 (consistency index = 0.35; retention index = 0.71). To further check our results, we also subjected the dataset to a new technology search (with the same options as above) that first consisted of 1000 iterations of heuristic tree searches, instead of saving the shortest tree in 10 replicates, and this returned trees of the same minimum length that, when combined, produced the same strict consensus topology. Bootstrap and Bremer supports were also calculated using TNT, the latter by saving topologies up to 10 steps longer than minimum length.

The strict consensus of the 5832 most parsimonious trees is shown below. Individual bootstrap and Bremer support values are not shown for each clade, but we note that all dromaeosaurid ingroup clades (as well as Dromaeosauridae itself) have a Bremer support of 1 and a bootstrap support of less than 50%. Although this may appear alarming, similar levels of support have characterized dromaeosaurid clades in all previous versions of the TWiG analysis, and are likely more a function of extreme missing data in some taxa rather than genuine poor support. Indeed, numerous synapomorphies unite major dromaeosaurid clades, including the *Velociraptor* + *Balaur* sister grouping (see main text).

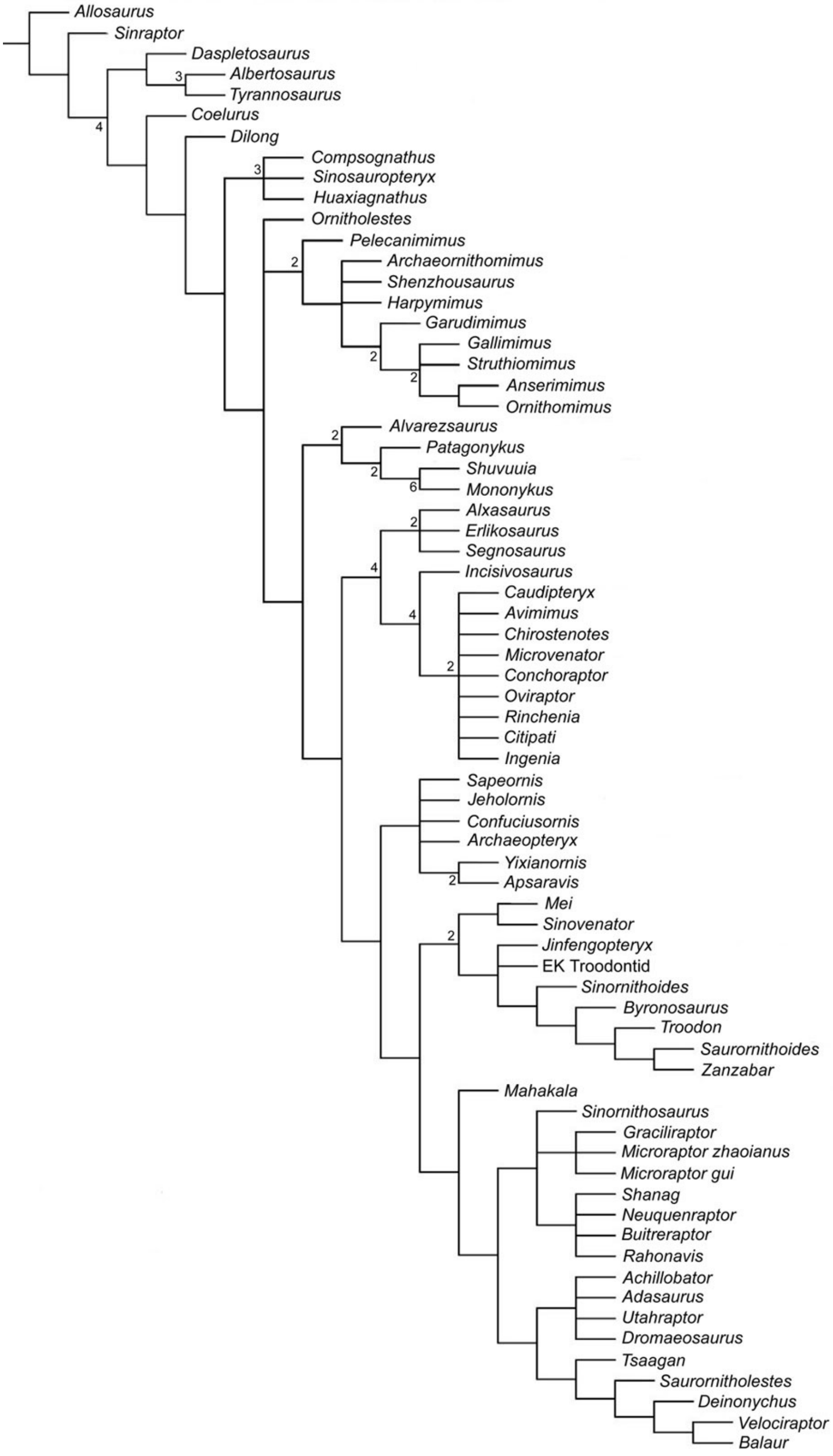

Figure S6. Strict consensus of 5832 most parsimonious trees (length = 880; CI = 0.35; RI = 0.71) recovered by the phylogenetic analysis. Numbers next to clades represent Bremer support values; clades without numbers have a Bremer of 1.

10. Character list and matrix

Our TNT dataset is presented here:

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