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A new Pansirenian from the late Eocene of Romania

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Abstract

Palaeogene sea-grass communities of Tethyan shallow marine ecosystems encompassed a diverse range of animals, including the ancestors of present-day sirenians. The fossil record of this group from the Eocene of Romania is relatively extensive; however, most occurrences consist only of isolated ribs and, less frequently, skull bones, vertebrae, or elements of the appendicular skeleton. Until now, such remains have typically been identified as Sirenia indet. or assigned to the catch-all taxon *'Halitherium'*. Here we describe a three-dimensional, incomplete skull along with additional cranial and postcranial specimens from the late Eocene (Priabonian, Cluj Limestone Formation) of the Transylvanian Basin, Romania, and assign them to a new species within the stem group Pansirenia. The new taxon, *Prototherium transylvanicum* n. sp., possesses a dolichocephalic skull with large premaxillary symphysis, elongated nasals, enlarged infraorbital foramen, whereas the ventral extremity of jugal is positioned under the posterior edge of the orbit, but forward of jugal's postorbital process. In our parsimony analysis *P. transylvanicum* n. sp. was erected as the sister species of *P. ausetanum* and positioned crownward of *P. veronense* on the cladogram, whereas another member of the genus (*P. intermedium* s.l.) occupies a more crownward position on the stem as the sister taxon of *'Halitherium' taulannense*. Consistent with previous studies, we confirm that several endocranial features on the inner surfaces of the parietal and supraoccipital, such as the bony falx cerebri, tentorium osseum, and inner occipital protuberance, reported here for the first time in *Prototherium*, together with the morphology of muscular attachment on the ventral surface of the basioccipital, may carry the phylogenetic signal of, and contribute to, a better understanding of relationships among the pan-sirenian taxa. The paraphyletic arrangement of *Prototherium* in the phylogenetic tree, similar to that observed for *Eotheroides*, indicates that a comprehensive taxonomic revision of the group is warranted.

Keywords: Afrotheria, Phylogeny, Priabonian, Tethys, Transylvania

1. INTRODUCTION

The sirenians, or as they are commonly known as 'sea-cows', represent a group of mammals that have fully adapted to an aquatic lifestyle, are obligate herbivores (DOMNING, 1978, 2001a; DOMNING et al., 2010) and possess certain morphological characteristics: streamlined bodies, tails that have evolved into a fluke, presence of flippers instead of front legs and the hind limbs are completely reduced (DOMNING & DE BUFFRÉNIL, 1991; ROMERO, 2009; DE BUFFRÉNIL et al, 2010). Their skeletal structure can be recognized by the presence of pachyosteosclerosis (VERESS et al., 2025). This assemblage is classified in the superorder Afrotheria, a group of placental mammals (i.e., Tenrecoidea, Macroscelidea, Tubulidentata, Proboscidea, Hyracoidea, and Sirenia), of African origin (STANHOPE et al., 1998). Part of afrotherians (i.e., proboscideans, desmostylians, and sirenians) were included by MCKENNA (1975) in the mirorder Tethytheria, whose members would have diversified along the Tethyan coasts (DÍAZ-BERENGUER et al., 2022). The node-based phylogenetic definition of Sirenia includes the clade of Pansirenia comprising all species more closely related to *Trichechus manatus* LINNAEUS, 1758 than to any other living species (O'LEARY et al., 2013, supplementary material, table 4), while the clade of Sirenia refers only to the crown clade composed of the last common ancestor of *Trichechus manatus* and *Dugong dugon* (VÉLEZ-JUARBE & WOOD, 2018; DÍAZ-BERENGUER et al., 2022).

Divergence date estimates for Afrotherian mammals, based on the combined data sources of different authors, led to equivocal results. BININDA-EMONDS et al. (2007), using gene alignments in conjunction with fossil calibration points to construct a supertree, presumed that the end-Cretaceous mass extinction event had a minor role in driving the diversification of modern mammalian lineages and established the divergence times for Placentalia and Afrotheria well before the end-Cretaceous, while that for Sirenia into the early Eocene. MEREDITH et al. (2011), based on molecular time-tree analyses, found the divergence times for both Placentalia and Afrotheria in the Late Cretaceous, while that of Sirenia around the Eocene–Oligocene transition. In contrast, O'LEARY et al. (2013), using phenomic characters, combined with molecular sequences and fossil calibration points,

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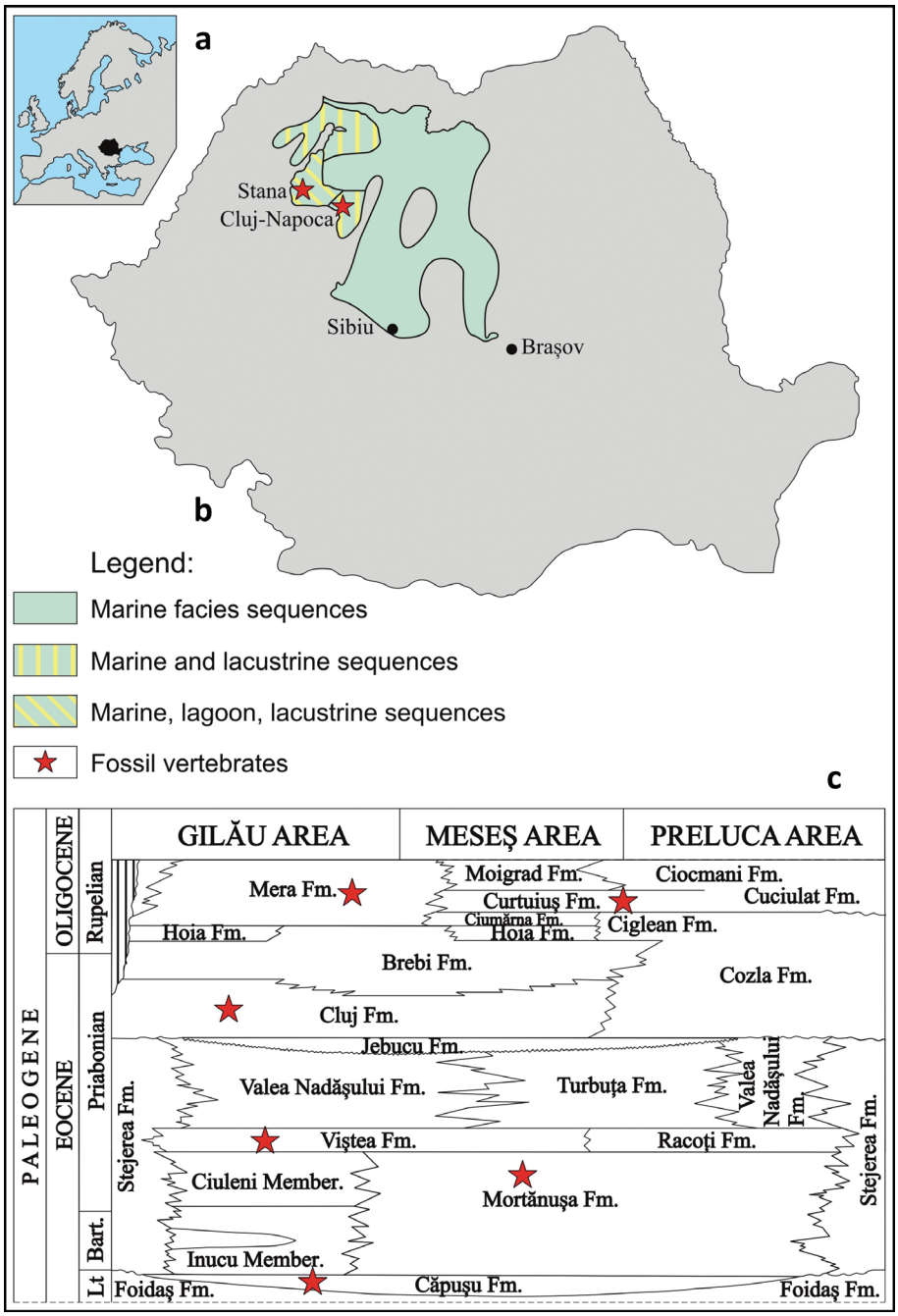


Figure 1. Map with geographic and geological details of the studied area: (**a**) position of Romania within Europe; (**b**) extension of marine, lagoonal and lacustrine sedimentation in the Transylvanian Basin during the Palaeogene (Romania with grey background) with the location of the holotype locality (Stana) and that of referred specimens (Cluj-Napoca); (**c**) lithostratigraphic units with sirenian fossils from the Palaeogene of the Transylvanian Basin, after POPESCU (1984), modified.

obtained a phylogenetic tree where all placental orders, including Sirenia, originated after the K-Pg boundary. The divergence date of the latter clade, based on the results of O'LEARY et al. (2013), is traced into the middle Eocene. Furthermore, the phylogenetic analysis of Sirenia using Bayesian tip-dating methods by HERITAGE & SEIFFERT (2022), links the rise of Pan-Sirenia to North Africa in the latest Palaeocene, and their subsequent diversification to the Eocene within the Tethyan realm.

The fossil record of sirenians from the Palaeogene of Romania is relatively extensive, spanning between the middle Eocene and early Oligocene (Fig. 1). The earliest record is known from the southern part of the Transylvanian Basin near Turnu Roșu (= Porcești), as a rib fragment identified in the collection of J.M. ACKNER from around 1850 (VERESS et al., 2025). However, except for Albești (Argeș County, Albești Limestone Formation, late Eocene) (GRIGORESCU, 1967), the remaining localities are known only from Transylvania, of which three occurrences are of middle Eocene (Lutetian–Bartonian) age, twelve localities of late Eocene (Priabonian) age and six localities of early Oligocene (Rupelian) age (VERESS et al., 2025). Nevertheless, the diagnostic value of these records is usually low, being represented by ribs, vertebrae, and more rarely by elements of the appendicular skeleton or skull (VERESS et al., 2022; VERESS & CODREA, 2023a, b) and are listed frequently as Sirenia indet. or

'Halitherium' sp. However, the latter was considered by VOSS et al. (2016) to be a catch-all taxon of paraphyletic nature (DOMNING, 1994; VOSS, 2013, 2014; VOSS et al., 2016, 2017), which is taxonomically invalid and therefore should be replaced (VOSS, 2014; VOSS & HAMPE, 2016; VOSS et al., 2016, 2017; VOSS, 2021).

We describe an incomplete pansirenian skull from the late Eocene (Priabonian) of Stana locality, Romania, previously included in a cladistic analysis, however not described in detail by SAGNE (2001a) in her PhD thesis, who referred to it as "*Prototherium* n. sp.". In addition, we report several dissociated cranial and postcranial specimens recovered from the late Eocene (Priabonian) Someș Dam locality in Cluj-Napoca, Romania. These specimens share a set of synapomorphies with the Stana skull and are assigned here collectively to a new four-legged pansirenian species. Both fossil localities are situated in the Gilău sedimentary area (Fig. 1), and all the pansirenian specimens originate from shallow marine deposits overlying a broad carbonate substrate (CHIRA & IGRIȚAN, 2004), as part of the Cluj Limestone Formation of late Eocene (Priabonian) age (MÉSZÁROS, 2000). Here, we: 1) describe the cranial and postcranial material and assign it, based on the combination of characters, to a new species of *Prototherium*; 2) test the phylogenetic relationships of the new taxon; and 3) discuss the palaeozoogeographical and palaeoenvironmental contexts of these pansirenian remains.

2. GEOLOGICAL SETTING

Located in Central Europe, in the centre of Romania, the current Transylvanian Basin is merely the physiographic expression of a sedimentary basin that originated at the end of the Cretaceous period. Sedimentation was completed at the end of the Late Miocene (CODREA & DICA, 2005; KRÉZSEK & BALLY, 2006). It is a subsiding block, outlined by the Carpathian orogenic structures (SĂNDULESCU, 1984).

Palaeogene marine sequences are observable only in limited outcrops located on the southern margin of the basin at Turnu Roșu (= Porcești; MÉSZÁROS, 1996), where diverse littoral deposits present challenges for correlation, due to their varied lithology. Additionally, the presence of faults complicates these correlations, as they have not been sufficiently mapped to date. Vertebrate fossils from these deposits include fish, particularly sharks (TRIF & CODREA, 2018 and references therein), crocodilians (KOCH, 1894; VENCZEL et al., 2023), but also fragments of sea-cow ribs (KOCH, 1894; VERESS et al., 2025). The most representative zone of Palaeogene sedimentation in the Transylvanian Basin is located in the northwestern side, where three sedimentation areas have been defined, each characterized by specific sedimentary features: Gilău, Meseș, and Preluca (POPESCU, 1976) (Fig. 1). The middle to late Eocene sedimentary sequence includes two transgressive–regressive cycles that constitute the Călata and Turea Groups, each composed of evaporites, shallow-marine carbonates, outer shelf marls, shallow-marine sands and completed by overlying fine-grained fluvial deposits (KOCH, 1894; POPESCU, 1984; RUSU, 1995; MÉSZÁROS, 2000; KRÉZSEK & BALLY, 2006). The Lutetian (Căpușu Fm.) and Priabonian (Cluj Limestone Fm.) carbonate platforms feature a rich invertebrate fauna, including foraminifera, bivalves, gastropods, and echinoderms, as well as vertebrates, particularly fish, crocodilians, and sea-cows (KOCH, 1894; RUSU, 1987; TRIF & CODREA, 2018; VENCZEL & CODREA, 2022; VERESS et al., 2022, 2025). In fact, the overwhelming majority of the fossil occurrences of the latter group are known from these two sedimentary cycles, since of the 22 sirenian localities listed by VERESS et al. (2025), 16 belong to the middle to late Eocene sequences and only six to the early Oligocene cycle (VERESS et al., 2025).

3. MATERIAL AND METHODS

The fossil material described here consists of a three-dimensionally preserved skull recovered from the Stana fossil locality, missing most of its rostrum, the right jugal and squamosal, both petrotympanic bones, whereas the exoccipital area is heavily damaged and in part covered by matrix. Additional cranial material originating from the Someș-Dam fossil locality consists of partly dissociated skull bones from a single individual preserving the rostrum and exposing on its inner posterior part, the ossified endocranial structures, and two pairs of partial jaws from two different individuals. The postcranial material consists of an atlas, an axis, a thoracal vertebra, several fragmentary ribs, a nearly complete humerus, a partially fused radius and ulna, and a fragmentary innominate bone. The fossil material described herein belongs to the collections of the Geological Department Paleontological Museum of the Babeș-Bolyai University (=UBB), Cluj-Napoca, Romania. The photographs used in this paper were taken at the Țării Crișurilor Museum, Oradea, Romania, using a Canon EOS R6 digital camera equipped with a Canon, RF 50 mm lens.

In order to test the phylogenetic relationships of the new taxon, we conducted parsimony analyses with the phylogenetic software package TNT version 1.6 (GOLOBOFF & MORALES, 2023) using the character-taxon matrix (CTM) with 89 phenotypic characters (ch.), provided by DÍAZ-BERENGUER et al. (2022). The CTM of the latter authors represents an updated version of that used by VÉLEZ-JUARBE & WOOD (2018), which is based on the work of many authors traceable back to DOMNING (1994).

The anatomical nomenclature used in this study follows ROBINEAU (1969), DOMNING (1978), and DÍAZ-BERENGUER et al. (2022). The skull, postcranial skeletal, and dental measurements are after ZALMOUT & GINGERICH (2012), and the standard anatomical orientation system is used throughout this paper.

4. SYSTEMATIC DESCRIPTION

Class Mammalia LINNAEUS, 1758

Superorder Afrotheria STANHOPE et al., 1998

Mirorder Tethytheria MCKENNA, 1975

Clade Pan-Sirenia O'LEARY et al., 2013 (sensu VÉLEZ-JUARBE & WOOD, 2018)

Genus: *Prototherium* DE ZIGNO, 1887

Type species: *Halitherium veronense* DE ZIGNO, 1875

Prototherium transylvanicum n. sp.

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Figs. 2–5

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Etymology: In reference to the Transylvanian region of Romania.

Holotype: Incomplete skull of an adult individual (UBB V. 115).

Referred specimens: Reasonably complete cranium of an adult individual (UBB V. 1149), a pair of maxillae (UBB V. 1150), one right squamosal + periotic (UBB V. 1151), a sphenopalatine (UBB V. 1152), two pairs of lower jaws (UBB V. 114, V. 116), an atlas (UBB V. 1153), an axis (UBB V. 1154), a thoracal vertebra (UBB V. 1155), a rib (UBB V. 1156), a humerus (UBB V. 1157), a partially fused radius+ulna (UBB V. 1158); a fragmentary innominate bone (UBB V. 1159).

Type locality and distribution: The holotype is known from the late Eocene (Priabonian) Stana fossil locality, which is part of the Cluj Limestone Formation; the referred material comes from the Someș-Dam fossil locality, which, like the holotype, is also late Eocene (Priabonian) in age and part of the Cluj Limestone Formation.

Diagnosis: Member of Pansirenia, based on a unique set of synapomorphies, as it follows: rostrum enlarged (ch. 1-2), external nares retracted and enlarged (ch. 4-1), premaxilla long contacting frontal (ch. 5-1), infraorbital foramen large (ch. 8-1), sagittal crest absent (ch. 21-1), supraoccipital wider ventrally than dorsally (ch. 22-1), cranial portion of squamosal extends to temporal crest (ch. 29-1), processus retroversus of squamosal moderately inflected (ch. 30-1), ventral extremity of jugal lies under posterior edge of orbit, but forward of jugal's postorbital process (ch. 34-1), posterior border of palatine incised (ch. 41-1), alisphenoid canal absent (ch. 43-1), pterygoid fossa present, extending above the level of the roof of internal nares (ch. 44-1), sphenopalatine region short with pterygoid process enlarged, thickened and downwardly projecting (ch. 46-1), permanent premolar 5 absent (ch. 65-1), tentorium osseum present (ch. 85-1), internal occipital protuberance present (ch. 86-1), basioccipital in ventral view hourglass-shaped (ch. 87-2), and insertions for the longus capitis muscle on the ventral side of the basioccipital form deep fossae (ch. 88-1).

4.1. Description of holotype

The UBB V. 115 holotype specimen represents an incomplete skull of an adult individual missing the symphyseal part of its rostrum, lacrimals, most part of the exoccipitals, right squamosal and jugal, and both petrotympanic bones (Fig. 2). In the maxillae the left partial M^2 and the M^3 only are preserved, and the specimen was lacking a permanent P^5. The occlusal surfaces of M^2 and M^3 are very worn, indicating the advanced age of the individual. Numerous cracks and shifts of bony margins produced alterations of the original three-dimensional skull morphology and part of the bony structures are covered by matrix.

Premaxillae: In the holotype, only the nasal processes are preserved, broken at the anterior limit of the mesorostral fossa (Fig. 2a, a'). The remaining nasal processes, about 105 mm long, are slightly sinuous, trend dorsoposteriorly and taper distally, but are slightly thickened dorsoventrally at the articulation point with the maxillae. The nasal processes of premaxillae, together with the dorsoposteriorly positioned nasals, enclose medially an enlarged mesorostral fossa about 100 mm long and of 38 mm maximal width (Table 1). They contact the maxillae ventrally and laterally, the nasals posteromedially and the frontals posterolaterally.

Nasals: The posterior parts of the paired nasals are positioned in sockets on the anteromedial sides of the frontals, where they are fused medially (Fig. 2a, a'). Their anterior parts are very damaged and displaced from their original positions.

Frontals: The dorsal surface of the fused frontals appears flat between the temporal crests and devoid of any knoblike boss (Fig. 2a, a'). The frontals contact the nasals anteromedially and widen considerably to form the prominent supraorbital processes. The latter structures are relatively robust with their posterolateral margins moderately flattened. Posteriorly, the frontals are fused to the parietal in the form of a V-shaped frontoparietal suture with some damage on the right dorsolateral margins. The mid-dorsal length of the frontals is smaller than that of the parietals and their lateral walls narrow posteriorly onto the frontoparietal suture (Table 1). The ratio of the maximum breadth across the supraorbital processes to the mid-dorsal length of the frontals is 1.1.

Parietals: The parietals are elongated (i.e., they contribute to the dolichocephaly) forming the skull roof from the frontoparietal suture to the dorsoposterior part of the skull, where they fuse to the supraoccipital (Fig. 2a, a'). The temporal crests are prominent, delimiting a narrow and concave dorsal surface, somewhat widening posteriorly (15 mm at the level of the frontoparietal suture and 45 mm at the level of the parietal-squamosal suture-line). The interparietal suture is lacking however, the parietal-supraoccipital suture is well-defined, and a triangle-shaped, shallow depression is present anterior of that structure.

Supraoccipital: The bone is almost complete, roughly of trapezoidal shape and exposed posteriorly forming an angle with the parietal of about 110° (Fig. 2e, e'). The bone is wider ventrally than dorsally and at the ventral tip of the supraoccipital the lower margins form a wide angle of about 140°. The nuchal crest is prominent with rounded margins, and its dorsolateral portion is fused with the dorsal process of the squamosal, preserved on the left side only. The external occipital crest is well-defined, bordered on both sides by deep concavities for the insertions of rectus capitis dorsalis muscles. The ventral margins are fused with the paired exoccipitals; their remnants are preserved on the right side of the holotype.

Exoccipitals: The dorsolateral parts are damaged, preserving only a small fragment on the left side exposing its rounded margin (Fig. 2e, e'). The occipital condyles are oval shaped; above the right occipital condyle, a shallow supracondylar fossa, partly filled by matrix, extends dorsolaterally (Fig. 2e, e'). The hypoglossal foramina are present and surrounded by bone (Fig. 2b, b'). Part of the downward projecting paroccipital process is preserved on the right side of the skull (Fig. 2e, e').

Basioccipital: The bone is hour-glass shaped with the anterior part strongly fused to the basisphenoid (Fig. 2b, b'). However, the midsection of the bone is displaced between two transversal fissures. On the left side, a well-defined oval depression for the attachment of the longus capitis muscle is preserved; on the right side, that depression is also discernible, but filled by matrix; the posterior part of the medial keel is

preserved extending beyond the limit of the longus capitis muscles attachment surfaces (Fig. 2b, b').

Alisphenoid: The bone is fused to the basisphenoid and pterygoid, extending downwards on the lateral side of the pterygoid process (Fig. 2c, c'); the alisphenoid canal is missing (ch. 43-1).

Pterygoid: The bone is deep and short anteroposteriorly (ch. 46-1); it is fused anteriorly with the palatine, dorsally with the basisphenoid and it is covered laterally by the alisphenoid (Fig. 2b, b'). The pterygoid process is large and projects ventrally, and the pterygoid fossa extends above the level of the roof of the internal nares (ch. 44-1); the posteromedial extension of the pterygoid process (i.e., hamular trochlea) is broken off.

Palatine: The bone is well preserved, fused posteriorly to the pterygoid and anteriorly and laterally to the maxilla (Fig. 2b, b'). Its anterior margin is missing, but the impression left on the maxillary surface indicates that it reached the level of P^4. The palatine posterior margin is incised up to the level of the M^3 anterior border (ch. 41-1), however, it remains thin at the level of M^2.

Maxilla: In ventral view (Fig. 2b, b'), the maxillae are well preserved and expose a lyre-shaped palate as in other pansirenians (ZALMOUT & GINGERICH, 2012; DÍAZ-BERENGUER et al., 2022). The ventral surface appears horizontal at the level of the upper molars (M^1-M^3) and a deflection point starts at the level of P^4 alveoli. The lateral side is shallowly concave and the zygomatic-orbital bridge of the

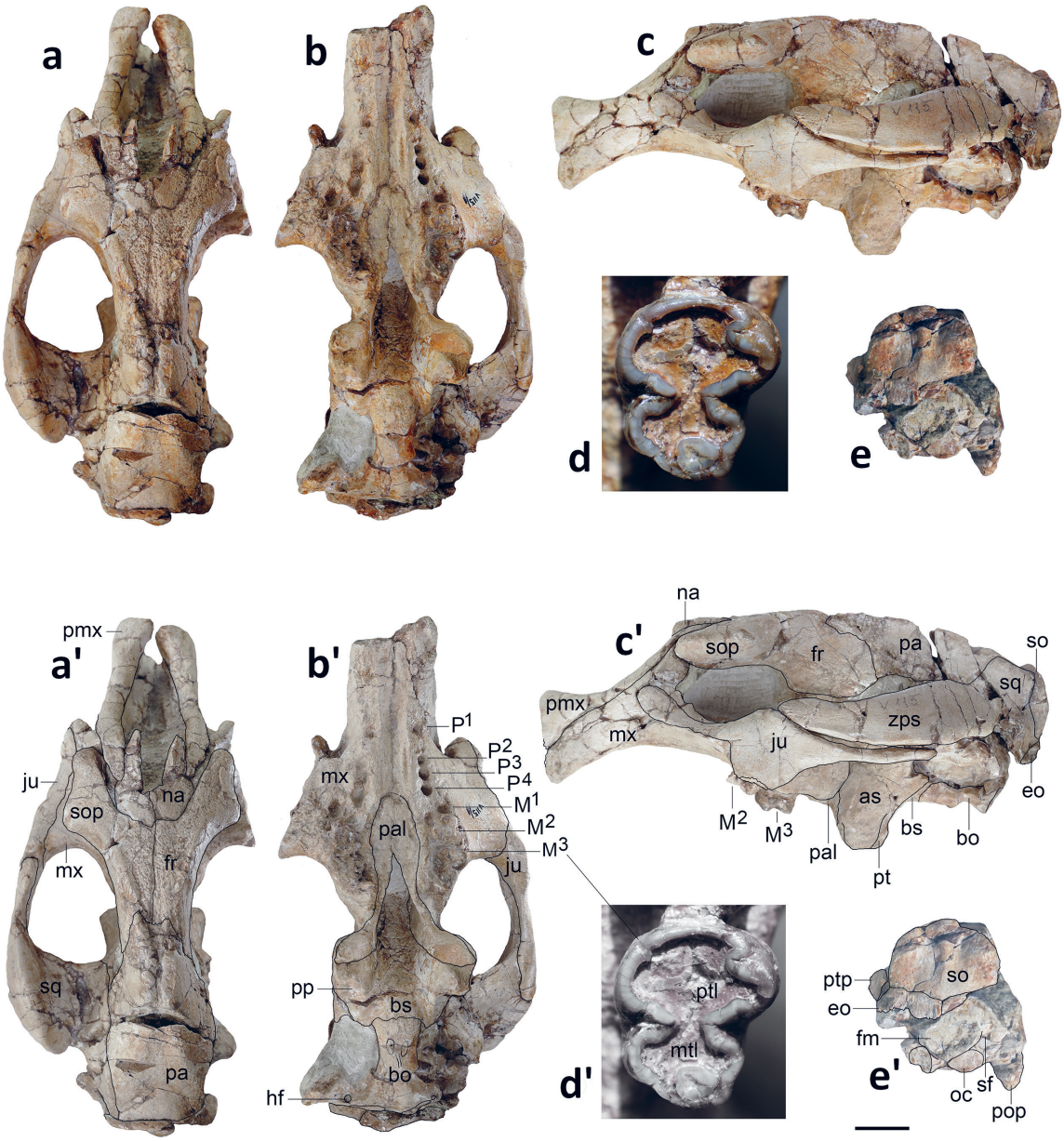


Figure 2. Holotype skull (UBB V. 115) of *Prototherium transylvanicum* n. sp. (**a–e**) with interpretative outlines of the relevant bony structures (**a'–e'**). (**a, a'**) – dorsal view; (**b, b'**) – ventral view; (**c, c'**) – left lateral view; (**d, d'**) – M^3 molar in occlusal view (not to scale); (**e, e'**) – posterior view. Abbreviations: as – alisphenoid, bo – basioccipital, bs – basisphenoid, eo – exoccipital, fm – foramen magnum, fr – frontal, hf – hypoglossal foramen, ju – jugal, M – upper molar, mtl – metaloph, mx – maxilla, na – nasal, oc – occipital condyle, P – premolar, pa – parietal, pal – palatine, pmx – premaxilla, pop - paroccipital process, pp – pterygoid process, pt – pterygoid, ptl – protoloph, ptp – posttympanic process, sf – supracondylar fossa, so – supraoccipital, sop – supraorbital process, sq – squamosal, zps – zygomatic process of squamosal. Scale bar = 3 cm.

maxilla is nearly on the same level with the alveolar margin (ch. 7-0). The maxillae enclose short (of about 13 mm) and relatively large infraorbital foramina (22 mm height x 15 mm width) (ch. 8-1), with their anterior medial margins situated at about 40 mm from each other. The anterior part of the zygomatic-orbital bridge is thin and sharp, whereas its posterior end is thickened and rounded. The dental arcade is concave medially, whereas the narrowest point of the palate is at the level of the P^1 (20 mm) and its maximal width is reached between the M^1 alveoli (40 mm).

Squamosal: On the left side of the holotype, the cranial portion of the squamosal extends dorsally up to the temporal crest (ch. 29-1) and fuses to parietal, whereas posteriorly it contacts the anterodorsal part of supraoccipital (Fig. 2c, c'). The zygomatic process has a roughly triangular cross section and slightly tapers anteriorly extending to the postorbital border, whereas its posterior section is bent medially, thickened ventrally and forms a moderately inflected processus retroversus (ch. 30-1).

Jugal: On the left side of the holotype, the jugal is almost completely preserved, except for the anteroventral margin of its most ventral extremity, which is broken off (Fig. 2c, c'). The preorbital process is thin and fused to the maxilla, joining the latter to the anterior margin of the orbit; however, the jugal is excluded from the contact with the premaxilla. The postorbital process is rounded abutting against the distal termination of the squamosal's zygomatic process. The ventral process is positioned under the posterior edge of the orbit, but forward to the jugal's postorbital process (ch. 34-1). The zygomatic process of the jugal is longer than the anteroposterior diameter of the orbit extending below the zygomatic process of the squamosal; the posterior part becomes extremely thin and flattened dorsoventrally.

Dentition: In the holotype, on both sides, only the M^2 and M^3 are preserved (Fig. 2b, b'), and only the left M^3 possesses a measurable surface (Fig. 2d, d'). However, the size of the preserved teeth and the impression left on the maxillae indicate that among the upper molars the crown of M^3 was the largest (ch. 66-0). The molars are three-rooted and where preserved, the occlusal surfaces are worn obliquely, higher labially than lingually. The occlusal surface of the M^3 is heart-shaped and nearly completely worn, indicating the advanced age of the holotype specimen. The tooth crown is of a bunolophodont type, partitioned by the protoloph and metaloph, which are clearly delimited by a mid-length constriction (i.e., the remnants of the transverse valley); the anterior and posterior cingula are preserved, whereas the posterior one possesses the remnants of a single cingular cuspule closed completely (Fig. 2d, d'). The presence of DP^5 is conceivable, as in other members of *Prototherium*, and replaced in the adult by the M^1, whereas the canines and P^1-P^4 series were single rooted (PILLERI et al., 1989; BALAGUER & ALBA, 2016). However, the positions of the canines cannot be determined with certainty due to the damaged ventral surface on that part.

4.2. Description of referred material

Fragmentary skull: The UBB V. 1149 specimen, recovered from the Someș-Dam locality, consists of an incomplete skull preserving the rostrum, articulated to the nasals and frontals, whereas the parietal is fused to the supraoccipital (Fig. 3a–c). Detached from the same individual are: the partial sphenopalatine region (UBB V. 1152, Fig. 3d); the pair of maxillae preserving on its right side an incomplete jugal (UBB V. 1150, Fig. 3e); the left squamosal with the left periotic (UBB V. 1151, Fig. 3f–h). The premaxillae are almost complete provided with a pair of lens-shaped I^1 alveoli; the premaxillary

Table 1. Cranial measurements in specimens of *Prototherium* after PILLERI et al. (1989, table 1, 6) and BALAGUER & ALBA (2016, table 1). Abbreviations: Pa – *Prototherium ausetanum*; Pv – *P. veronense*; Pi – *P. intermedium* s.l.; Pt1 – *P. transylvanicum* n. sp. (holotype); Pt2 – *P. transylvanicum* n. sp. (UBB V. 1149).

	Pa	Pv	Pi	Pt1	Pt2
Condylobasal length	>309	360	(320)	-	325
Length of frontals in midline	64	-	-	48	50
Length of frontals, level of tips of supraorbital processes to frontoparietal suture	77	127	90	92	105
Length of parietals, frontoparietal suture to rear of external occipital protuberance	91	70	70	105	105
Breadth of cranium at frontoparietal suture	27	40	27	35	38
Parietal, maximal dorsal breadth	52	38	48	55	60
Parietal, minimal dorsal breadth	25	34	20	33	36
Breadth across supraorbital processes	(130)	104	70	90	102
Length of mesorostral fossa	69	75	68	-	63
Width of mesorostral fossa	(58)	36	42	38	32
Maximum height of rostrum	53	68	37	-	55
Anteroposterior length of zygomatic-orbital bridge of maxilla	>57	-	-	64	-
Length of row of tooth alveoli, M1–M3	55	-	-	55	58
Anteroposterior length of root of zygomatic process of squamosal	-	(45)	37	35	-
Height of jugal below orbit	43	40	27	40	41
Maximum width between labial edges of left and right alveoli	65	72	64	72	73
Height of supraoccipital	43	-	-	47	46
Width of supraoccipital	53	-	-	62	61
Length of nasal	32	70	30	-	70
Breadth of nasal	24	56	20	18	18
Rostral deflection (RD)	47	50	-	-	45

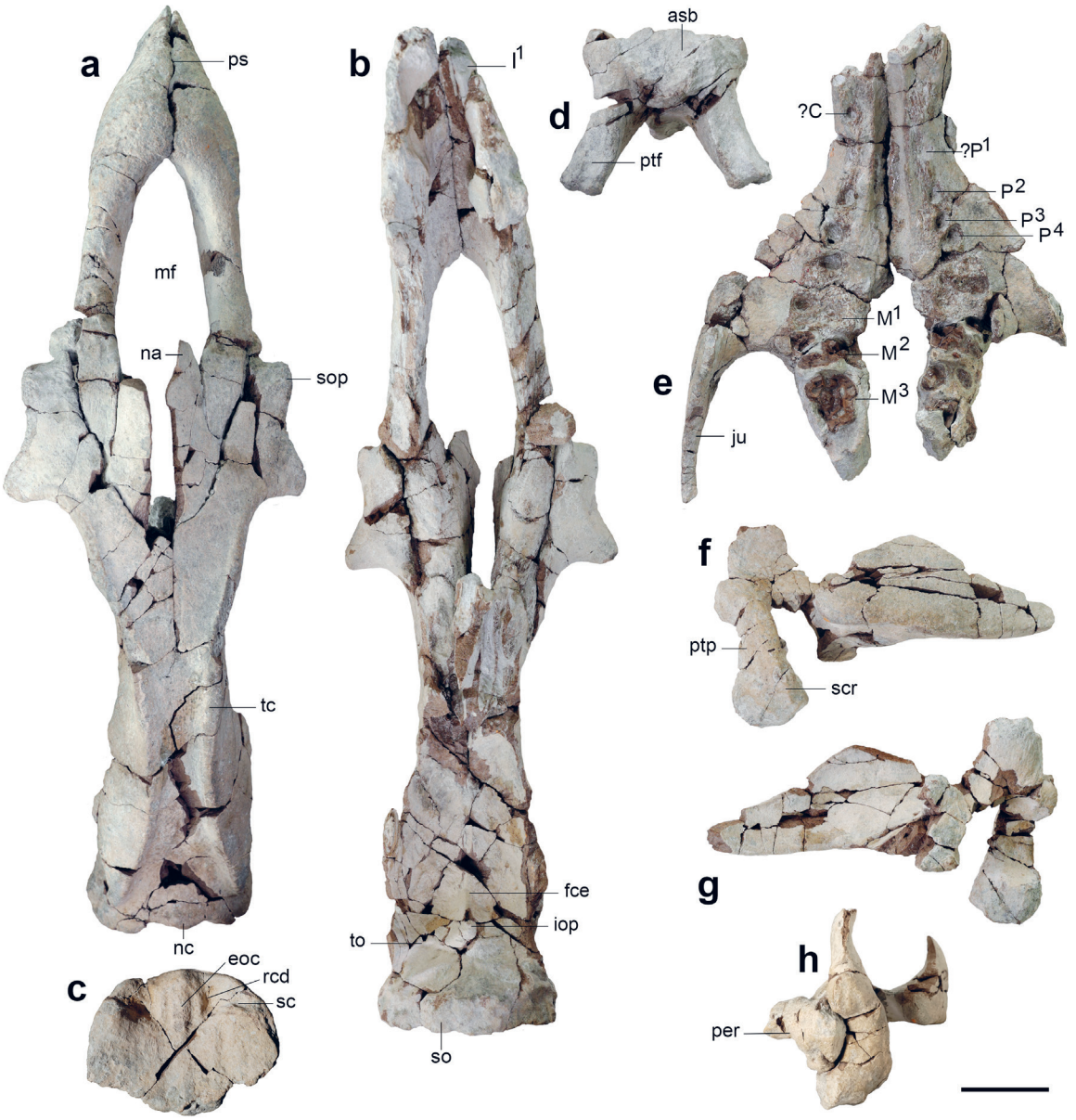


Figure 3. Referred partial skull (UBB V. 1149) and isolated cranial bones of *Prototherium transylvanicum* n. sp. (**a, b**) partial skull roof; (**c**) supraoccipital; (**d**) sphenopalatine (UBB V. 1152); (**e**) paired maxillae and right jugal (UBB V. 1150); (**f, g**) right squamosal; (**h**) right squamosal and right periotic (UBB V. 1151). a – dorsal view, b, e – ventral views, c, d, h – posterior views, f – lateral view, g – medial view. Abbreviations: asb – articular surface with basioccipital, C – canine, eoc – external occipital crest, fce – falx cerebri, I – incisive, iop – internal occipital protuberance, ju – jugal, M – upper molar, mf – mesorostral fossa, na – nasal, nc – nuchal crest, P – premolar, per – periotic, ptf – pterygoid fossa, ptp – post-tympanic process, rcd – insertion surface for rectus capitis dorsalis muscle, sc – insertion surface for semispinalis capitis muscle, scr – sigmoid crest, so – supraoccipital, sop – supraorbital process, tc – temporal crest, to – tentorium osseum. Scale bar = 3 cm.

symphysis (95 mm) is enlarged if compared to the condylobasal length (325 mm) (ch. 1-2). The anterior edge of the rostrum is wedge-shaped, but it becomes more rounded near the anterior margin of the mesorostral fossa; the rostral deflection is moderate, at about 45°. Distally, the contact point of the nasal processes with the paired nasals is nearly vertical, whereas the fusion points with the maxillae are on their ventral sides, marked by small remnants of broken bony surfaces in the vicinity of the frontal processes. The nasals are incomplete (their reconstructed length is 70 mm), fused laterally to the nasal process of the premaxillae and frontal, and form a wedge-shaped extension beyond the posterior part of the mesorostral fossa. The medial edges of the nasals are projected dorsomedially above the roof of the frontal (nevertheless, positioned on the same level as that of the parietal). In the living animal, the nasal margins were probably in contact medially and with a small incision anteriorly. The temporal crests on the frontal and the parietal are prominent and closely spaced; however, the supraorbital processes of the frontals appear less robust and are more flattened than those in the holotype. The inner parietal surface displays a prominent internal occipital protuberance connected anteriorly to a well-defined bony falx cerebri, and laterally to a relatively low tentorium osseum (Fig. 3b). The latter structure develops along the line of fusion between the fused parietals and supraoccipital (GINGERICH et al., 1994). The shape of the supraoccipital is

similar to that of the holotype (i.e., wider ventrally than dorsally), exposing a prominent nuchal crest with rounded margins and a relatively thick (about 1 cm), articulating surface for the exoccipitals; however, the external occipital crest is less prominent and relatively short, and on both sides a pair of oval concavities are present serving as the attachment surfaces for the rectus capitis dorsalis and the semispinalis capitis muscles insertions respectively (DÍAZ-BERENGUER et al., 2022). The sphenopalatine region is short, exposing posteriorly the roughened articulating surface for the basioccipital (Fig. 3d); the pterygoid process is enlarged, thickened and downwardly projecting (ch. 46-1); the pterygoid fossa is present and well developed as in the holotype (ch. 44-1). The pair of maxillae (the palatine is missing) are shallowly concave with the ventral margin of the zygomatic-orbital bridge positioned nearly on the same level with that of the alveolar margin (ch. 7-0); the remnants of the cheek teeth (M^1-M^3) and alveoli (P^1-P^4) are distributed similarly as in the holotype, but the position of the canine remains uncertain (Fig. 3e). The right squamosal is nearly complete with the cranial part positioned vertically and slightly bent laterally (Fig. 3f–h). The zygomatic process tapers anteriorly with a roughly triangular cross section; its medial surface is shallowly concave and the dorsal margin bent medially (ch. 33-0). The post-tympanic process of the squamosal projects anteroventrally beyond the ventral margin of the zygomatic process, possessing a prominent sigmoid ridge (ch. 28-1); the periotic sets in the close-fitting socket of the squamosal, however, it cannot be determined if it contacted the alisphenoid or not. The mastoid portion of the periotic was exposed only via fenestra in the dorsal occiput (ch. 48-1).

Mandibles: The mandibular symphysis is compressed laterally and displays a large mental foramen, accompanied by several accessory foramina (ch. 51-0) (Fig. 4a–b). The horizontal mandibular ramus is slender with the ventral margin moderately concave and sharply downturned anteriorly (ch. 50-1); the ventral margin of the horizontal ramus is not tangent to angle posteriorly (ch. 56-1). The masticating surface is narrow, scarcely wider than the two rows of mandibular teeth or alveoli. The anterior margin of the partially preserved coronoid process is roughly vertical (ch. 53-0), whereas the mandibular dental capsule of m_3 is completely enclosed by bone (ch. 54-0) (Fig. 4c).

The lower dentition is scarcely preserved, in the most complete mandible (UBB V. 114) only the m_2 and m_3 are present (Fig. 4). The transverse crests expose steep obliquely worn occlusal surfaces, where the lingual cusps are distinctly higher and sharper than the buccal cusps (Fig. 4d). In the UBB V. 114 specimen, the m_2 is smaller than the m_3 (Table 3), however both are double-rooted and bilophodont. In m_2 the protolophid appears narrower than the hypolophid, whereas in m_3 both structures appear to be of the same width; the proto- and hypolophids are separated by deep transverse valleys. The morphology of the hypoconulid is barely discernable on m_2 due to tooth wear, but on the m_3 it includes a larger anterior and a smaller posterior cuspule and both hypoconulids enclose distinct talonid basins.

Atlas: The UBB V. 1153 specimen is almost complete, except for the left anterior margin of the articular facet and the lower margin of the right transverse process that are broken off (Fig. 5a–b). The cotyles are kidney shaped with flaring

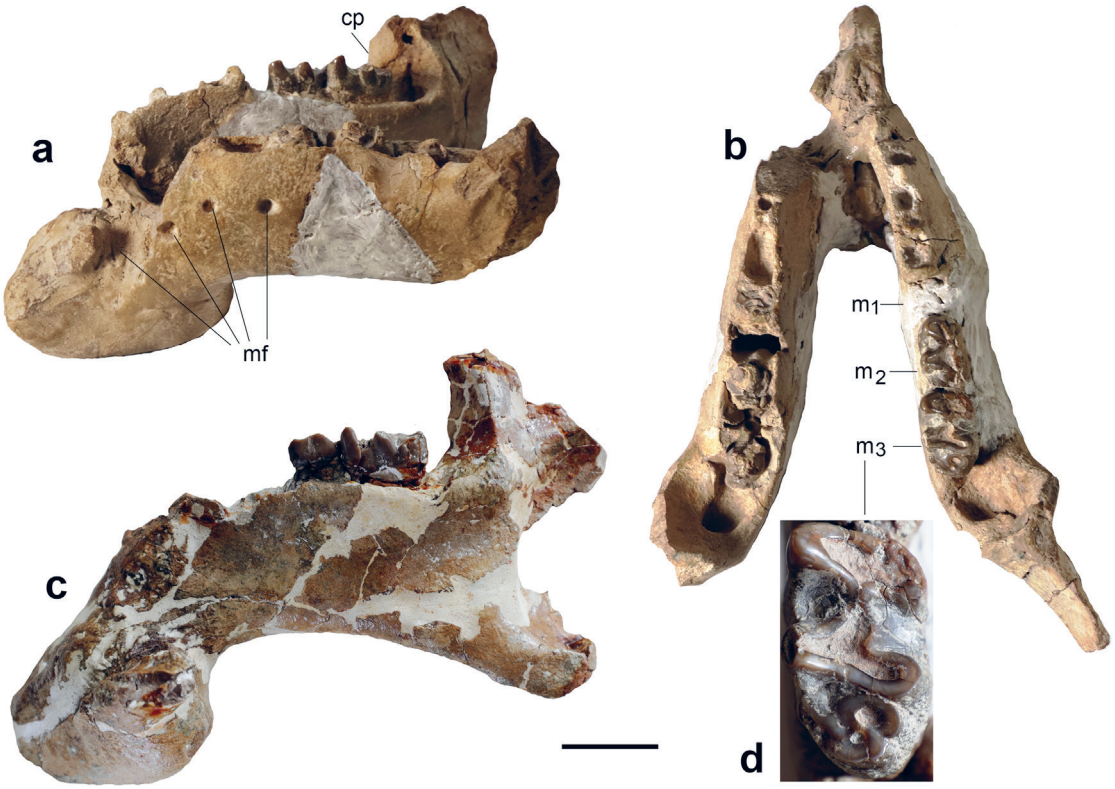


Figure 4. Referred lower jaws of *Prototherium transylvanicum* n. sp. (**a, b**) partial pair of dentaries (UBB V. 116); (**c**) right dentary (UBB V. 114); (**d**) right m_3 (not to scale). a – left lateral view, b – dorsal view, c – medial view; d – occlusal view. Abbreviations: cp – coronoid process, m – lower molar, mf – mental foramen. Scale bar = 3 cm.

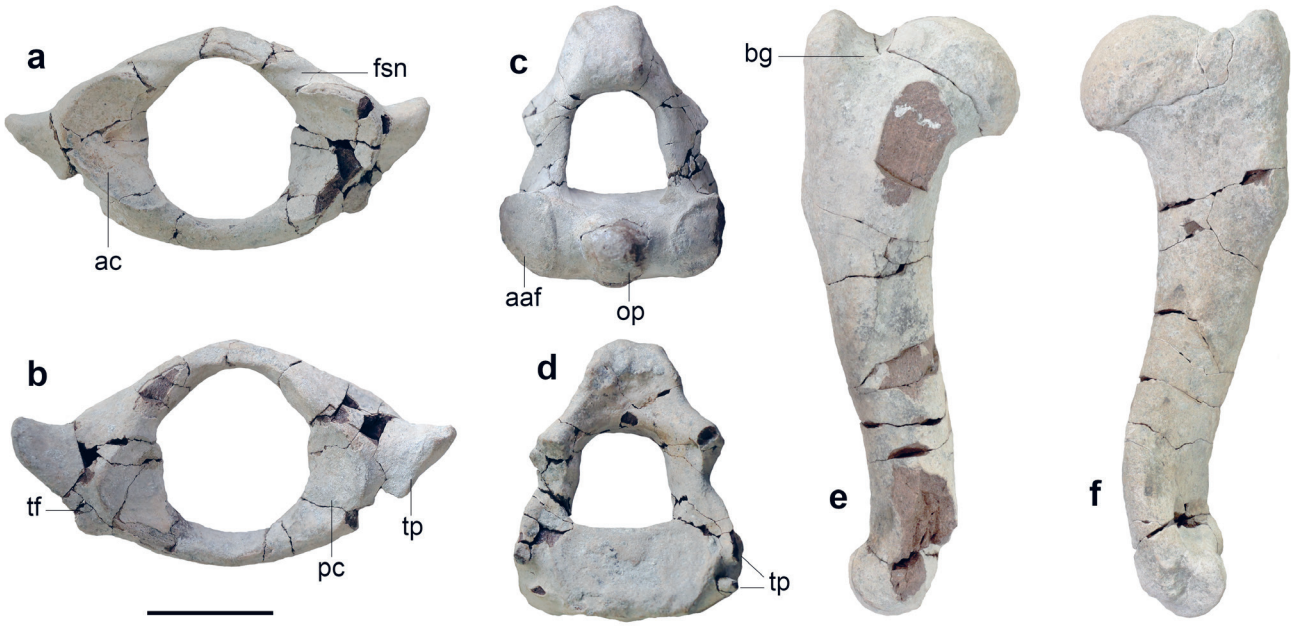


Figure 5. Referred vertebrae and humerus of *Prototherium transylvanicum* n. sp. (**a, b**) atlas (UBB V. 1153); (**c, d**) axis (UBB V. 1154); (**e, f**) right humerus (UBB V. 1157). a, c – anterior views, b, d – posterior views, e – medial view; f – lateral view. Abbreviations: aaf – anterior articular facet, ac – anterior cotyle, bg – bicipital groove, fsn – passage of first spinal nerve, op – odontoid process, pc – posterior cotyle, tf – transverse foramen, tp – transverse process. Scale bar = 3 cm.

dorsal sides, whereas the anterior cotyles possess more prominent margins than the posterior ones. The passages of the paired first spinal nerves are exposed behind the dorsal margins of the anterior cotyles, as seen in *Eotheroides sandersi* (ZALMOUT & GINGERICH, 2012) or *Metaxitherium albifontanum* (VÉLEZ-JUARBE & DOMNING, 2014, fig. 9a, h). The transverse processes are aliform with slightly longer dorsal margins and project posterodorsally, and pierced on each side by the transverse foramina. The anterior margin of the lower arch is shallowly concave, whereas its posterior margin exposes a small outgrowth medially.

Axis: The centrum is roughly rectangular with a flattened subcentral surface; however, it possesses a medial convexity at the base of the odontoid process (Fig. 5c–d). The latter is conical, bearing ventrally an anteroposteriorly extending oval facet. The anterior articular facets are oval in shape, higher than wide and with slightly convex surfaces. The transverse processes are not complete, connected dorsally to thin cristae up to the bases of postzygapophyses; the transverse foramina are large and positioned near to their lower margins. The neural canal is oval with a flat base, whereas the neural arch appears robust and upraised posteriorly; the neural spine is also thickened and rectangular, projecting anteriorly.

Thoracic vertebra: The vertebra (UBB V. 1155) is robustly built with an extremely high neural spine and narrowed vertebral canal (VERESS, 2025, fig. 84a–c). The centrum is provided with flattened articular surfaces and with a rounded subcentral margin. The neural spine is high with its anterior edge sharp, the lateral margins are slightly convex, whereas the posterior margin is thickened and displays a concave posterior surface; the transverse processes are short and robust and project anterodorsally.

In addition to the vertebrae, a number of fragmentary ribs, a humerus (UBB V. 1157), a partially fused radius+ulna (UBB V. 1158) and a fragmentary innominate bone (UBB V. 1159) have already been reported from the Someș-Dam locality (VERESS et al., 2022, 2025), and therefore we avoid their detailed description. However, it should be taken into consideration that the humerus recovered from that locality is robustly built (ch. 82-1) (Fig. 5e–f), possessing well separated humeral tubercles and a large bicipital groove (ch. 77-0). The innominate is fragmentary, retaining a flaring iliac shaft and small remnants of the ischium and pubis (VERESS et al., 2022).

4.3. Comparisons and comments

Prototherium transylvanicum n. sp. appears as a medium sized pansirenian, displaying signs of advanced dolichocephaly; it possesses a large premaxillary symphysis, elongated nasals and with retracted and enlarged external nares reaching to or beyond the level of the anterior margin of orbit. In the skull roof, the parietal is of the same length or slightly longer than the frontals, the rostral deflection is moderate (of about 45°), and the permanent P^5 is lacking. *P. transylvanicum* n. sp. differs from other congeners by the position of the ventral extremity of the jugal, that lies approximately under the posterior edge of the orbit, but forward of the jugal's postorbital process. Furthermore, it can be diagnosed within the members of this genus by a unique combination of characters, as follows: it differs from *P. ausetanum* and *P. veronense*, but resembles *P. intermedium* s.l. in its possession of an enlarged premaxillary symphysis; it resembles *P. ausetanum* and *P. intermedium* s.l., but differs from *P. veronense* in its possession of a zygomatic-orbital bridge of the maxilla, nearly level with the palate; it resembles *P. ausetanum*, but differs from *P. veronense* and *P. intermedium* s.l., in the possession of a supraoccipital that is wider ventrally than dorsally; it resembles *P. veronense*, but differs from the other members by its long nasals and by the

Table 2. Measurements of M1 – M3 teeth in members of *Prototherium*. Measurements of *P. ausetanum* and *P. veronense* are after BALAGUER & ALBA (2016, table 2) and PILLERI et al. (1989, table 7, 9).

	P. ausetanum			P. veronense			P. transylvanicum		
	M1	M2	M3	M1	M2	M3	M1	M2	M3
Mesiodistal length (L)	13.8	16.3	21.6	16	21	23	-	-	22.2
Anterior breadth (L)	-	18.3	19.9	18	21	20	-	-	20.1
Posterior breadth (L)	-	18.9	15.4	16	19	16.5	-	-	14.8
Mesiodistal length (R)	15.5	16.6	21.4	-	-	-	-	-	-
Anterior breadth (R)	-	-	19.7	-	-	-	-	-	-
Posterior breadth (R)	-	-	14.5	-	-	-	-	-	-

incised posterior border of the palatine. Based on the measurements of M^3 (the only available from the maxillary teeth), *P. veronense* possesses the largest M^3 (mesiodistal length = 23 mm, anterior breadth = 20 mm, posterior breadth = 16.5 mm), *P. intermedium* s.l. the smallest M^3 (mesiodistal length = 17 mm, anterior breadth = 16 mm, posterior breadth = 13 mm). In *P. ausetanum,* the mesiodistal length of M^3 (21.4 – 21.6 mm) and the anterior breadth of M^3 (19.7 – 19.9 mm) are slightly smaller than that of *P. transylvanicum* (22.2 mm and 20.1 mm respectively), while the posterior breadth values of M^3 (14.5 – 15.4 mm) are comparable to those of *P. transylvanicum* (14.8 mm) (Table 2).

Possible close relationships between the fossil sirenian specimens from the Transylvanian late Eocene (Priabonian) and *Sirenavus hungaricus* KRETZOI, 1941 were discussed by KORDOS (2002). KRETZOI (1941) proposed a close relationship between *Sirenavus* and the prorastomids, but subsequent studies by KORDOS (1981, 2002) and DOMNING (1994, 1996) highlighted its more advanced features, suggesting closer affinities with the dugongids rather than with the prorastomids or protosirenids (BALAGUER & ALBA, 2016). ZALMOUT & GINGERICH (2012) also noted similarities between *Sirenavus* and *Eotheroides clavigerum* and *E. sandersi*, particularly in the retention of strongly arched, upwardly concave nasals, large infraorbital foramina, and enlarged ribs associated with the partial skull. Additionally, these authors observed that certain components of the appendicular skeleton of *Sirenavus* – especially the femur – are reminiscent of *Eosiren* (ZALMOUT & GINGERICH, 2012). Based on the study of KORDOS (2002), *Sirenavus hungaricus* shares with the holotype skull and referred cranial material of *Prototherium transylvanicum* n. sp., a number of features, as follows: the zygomatic-orbital bridge of the maxilla is nearly level with the palate (ch. 7-0); the nasals are large and meet in the midline (ch. 15-0); the supraorbital process of the frontal is well developed and has a prominent, dorsoventrally flattened posterolateral corner (ch. 16-0). However, *Sirenavus* differs from *P. transylvanicum* in several diagnostic features, as follows: the zygomatic process of the jugal is shorter than the diameter of the orbit; the posterior border of the palatine is not incised; the coronoid process of the mandible extends anteriorly to the base of the process, and among the upper molars, the M^2 is the largest (KORDOS, 2002).

Paralitherium tarkanyense KORDOS, 1977, based on fossil specimens (e.g., mandible, vertebrae and ribs) from the late Eocene of Felsőtárkány–Várkút roadcut locality (KORDOS, 1977), was included in the synonymy of *Sirenavus* (KORDOS, 2002).

Anisosiren pannonica KORDOS, 1977 is based on fragmentary material (i.e., the holotype is a left maxilla with M^1–M^3, a fragment of P^4, and an independent ?P^3) from the middle Eocene (Lutetian) locality of Oroszlány, Hungary (KORDOS, 1977; DOMNING, 1996; KORDOS, 2002). The largest tooth in the holotype is the M^3 (mesiodistal length = 24 mm, anterior breadth = 22.2 mm), which might have belonged to a large sized pansirenian.

Sobrarbesiren cardieli DÍAZ-BERENGUER et al., 2018, appears as a more primitive pansirenian in possession of a small infraorbital foramen, an alisphenoid canal, a single rooted permanent P^5, a supraoccipital that is wider in its dorsal half than at the ventral extremities of the lateral borders and shallow depressions for the insertion of the longus capitis muscles (DÍAZ-BERENGUER et al., 2018, 2022). It resembles *Prototherium transylvanicum* n. sp. and *P. intermedium* s.l., but differs from the remaining members of *Prototherium*, in the possession of an enlarged rostrum and its zygomatic-orbital bridge of the maxilla is elevated above the palate, with its ventral surface more than 1 cm above the alveolar margin (also in *P. veronense*). It further differs from the members of *Prototherium* by its lesser degree of rostral deflection (of about 30°) and by the lack of dolichocephaly (DÍAZ-BERENGUER et al., 2018, 2022).

'Halitherium' taulannense shares with *Prototherium transylvanicum* n. sp. an enlarged rostrum. However, in the former, the rostral deflection is more accentuated at about 50° (SAGNE 2001a, b). Further synapomorphies shared by the above taxa, among others include: long premaxillae contacting the frontal (ch. 5-1); large infraorbital foramina (ch. 8-1); the

Table 3. Measurements of mandibular teeth in *Prototherium transylvanicum* n. sp. Abbreviations: R – right dentary – UBB V.114, L – left dentary – UBB V.116.

	P. transylvanicum		
	m_1	m_2	m_3
Mesiodistal length (R114)	-	19.9	25.3
Anterior breadth (R114)	-	12.4	15.6
Posterior breadth (R114)	-	14.3	15.5
Mesiodistal length (L116)	-	-	23.7
Anterior breadth (L116)	-	-	15.0
Posterior breadth (L116)	-	-	13.5
Mesiodistal length (R116)	-	-	24.4
Anterior breadth (R116)	-	-	15.2
Posterior breadth (R116)	-	-	13.5

cranial portion of the squamosal extends to the temporal crest (ch. 29-1); processus retroversus of the squamosal is present, and moderately inflected (ch. 30-1); the posterior border of the palatine is deeply incised (ch. 41-1); hourglass-shaped basioccipital (ch. 87-2); and, insertions for the longus capitis muscle on the ventral side of the basioccipital form deep fossae (ch. 88-1). Apomorphic character states present in *P. transylvanicum* n. sp. but lacking in *'Halitherium' taulannense* are: the supraoccipital is wider ventrally than dorsally (ch. 22-1); the ventral extremity of the jugal lies approximately under the posterior edge of the orbit, but forward of the jugal's postorbital process (ch. 34-1); and, the cross section of the I^1 crown appears lens-shaped, with sharp anterior and posterior edges (ch. 60-1). In contrast, *'Halitherium' taulannense* appears more derived in several apomorphies, as follows: supracondylar fossa of the exoccipital is deep and extends across the entire width of the occipital condyle (ch. 24-2); the anterior border of the mandibular coronoid process extends slightly anterior to the base of the process (ch. 53-1); the mandibular dental capsule is exposed posteroventrally (ch. 54-1); the first upper incisor is vestigial or absent (ch. 58-1); and, the basioccipital mid ventral keel is absent (ch. 89-1).

The endocranial structures (i.e., ossified falx cerebri, tentorium osseum, internal occipital protuberance), well-developed in *Prototherium transylvanicum* n. sp., are distributed variably among the different representatives of Pan-Sirenia. The ossified falx cerebri is lacking in *Pezosiren*, *Protosiren*, *Sobrarbesiren*, *Libysiren* and *Eotheroides lambondrano* (DÍAZ-BERENGUER et al., 2022), while it is present in the remaining members of *Eotheroides* (where it is known), *Eosiren* and *'Halitherium' taulannense*; unfortunately, in the remaining members of *Prototherium* it has not been reported. The tentorium osseum is present in *Sobrarbesiren*, *Eotheroides*, *Eosiren imenti* and *'Halitherium' taulannense*, but is lacking in *Pezosiren*, *Libysiren* and *Protosiren*; however, in the latter, some specimens may possess a low tentorium osseum (DOMNING & GINGERICH, 1994; GINGERICH et al., 1994). The internal occipital protuberance is lacking in *Pezosiren*, *Protosiren*, *Libysiren* and *Eotheroides lambondrano*, but is present in *Sobrarbesiren*, *Eotheroides*, *Eosiren imenti* and *'Halitherium' taulannense* (DÍAZ-BERENGUER et al., 2022). Nevertheless, the inner parietal surface of the single specimen (i.e., holotype) of *Eotheroides lambondrano* is not complete (SAMONDS et al., 2009), therefore, the character state of bony falx cerebri and internal occipital protuberance in that species may be considered equivocal.

5. RESULTS

In the parsimony analysis we added to the CTM of DÍAZ-BERENGUER et al. (2022) our scored character set of the new taxon (of the 89 phenotypic characters 71 are identified, representing 79% from the character list) (Table 4); the numbering of characters is the same in the character list and in the CTM (i.e., first numerals used by DÍAZ-BERENGUER et al., 2022). The resulting CTM, consisting of 63 operational taxonomic units (OTU) and 89 phenotypic characters, was analyzed using the 'New Technology search' option with sectorial search, ratchet, drift and tree fusing settings as the default parameters. A search for suboptimal trees, ten steps longer than that of the most parsimonious tree, was also completed in order to calculate the decay indices of BREMER (1994), and the common synapomorphies for all trees were also identified.

In the parsimony analysis, the TNT returned two most parsimonious trees of 314 steps from a total of 16.503.074 rearrangement examined (consistency index [CI] = 0.436; retention index [RI] = 0.777; homoplasy index [HI] = 0.564; rescaled consistency index [RCI] = 0.338). Both shortest trees recovered *Prototherium transylvanicum* n. sp. among the other pansirenians as the sister-species of *P. ausetanum* and located stemward to *Eotheroides aegyptiacus. P. veronense* and *Sobrarbesiren cardieli* are positioned successively stemward on the cladogram, whereas *E. lambondrano* and *Libysiren sickenbergi* are recovered in a successive nesting position crownward, as a distinct clade with members of *Protosiren* (*P. smithae* and *P. fraasi*) and *Ashokia antiqua*. In the more derived positions, the recovered members include *Eosiren* (*E. imenti* and *E. libyca*), the remaining members of *Eotheroides* (*E. sandersi* and *E. clavigerum*) and finally *'Halitherium' taulannense* and *Prototherium intermedium* as sister-species; the latter clade appears as the sister group of Sirenia. Nodal support is weak for most members of Pansirenia (decay index = 2), while for the clade of Sirenia the nodal support is moderate (decay index = 3).

The strict consensus tree differs from those of the two shortest trees in the rearrangement of particular dugongine genera in unresolved relationships (e.g., *Callistosiren, Kutchisiren, Rytiodus*), within the clade of Sirenia, while *P. transylvanicum* + *P. ausetanum* are positioned in an unresolved relationship with *Eotheroides aegyptiacus.* The sister-taxon relationship between *Prototherium transylvanicum* n. sp. and *P. ausetanum* is supported by a single synapomorphy: the supraoccipital is wider ventrally than dorsally (ch. 22-1). The node uniting *P. transylvanicum* + *P. ausetanum* with *Eotheroides aegyptiacus* is supported by two synapomorphies: (1) the zygomatic-orbital bridge of the maxilla is nearly level with the palate (ch. 7-0), and (2) the supracondylar fossa of the exoccipital is distinct but shallow, positioned directly dorsal to the condyle (ch. 24-1).

6. DISCUSSION

6.1. Cladistic analysis

The results from the parsimony analyses are quite surprising, if we take into consideration that *Prototherium transylvanicum* n. sp. is recovered on the shortest trees among pansirenian members (e.g., *P. ausetanum*, *P. veronense*, *Eotheroides aegyptiacus*), known from the earlier stages of the Eocene (i.e., Lutetian–Bartonian). In contrast, the coeval European pansirenian members, including *Prototherium intermedium* s.l. and *'Halitherium' taulannense*, are recovered in more crownward positions on the phylogenetic trees (see also, DÍAZ-BERENGUER et al., 2022) and are consistently positioned as the sister group of Sirenia. In fact, the body plan of *P. transylvanicum* n. sp., by preserving more plesiomorphic attributes, is reminiscent of geologically older taxa including *P. ausetanum*, *Sirenavus* or *Eotheroides*, while the pair of *P.*

intermedium s.l. and *'Halitherium' taulannense*, which are coeval with *P. transylvanicum* n. sp., but positioned more crownward on the cladogram, had already acquired more derived features, as seen on the exoccipitals (e.g., deep supracondylar fossa extending across the entire width of the occipital condyle – ch. 24-2) (VOSS, 2013; VOSS & HAMPE, 2017), basioccipital (e.g. absence of mid-ventral keel – ch. 89-1) (DÍAZ-BERENGUER et al., 2022), and mandibles (posterior border of the mandible bears no distinct processus angularis superior, but has a broadly convex outline beginning well below the condyle – ch. 52-2; anterior border of the coronoid process extends slightly anterior to the base of process – ch. 53-1; mandibular dental capsule exposed posteroventrally – ch. 54-1) (VOSS, 2013; VOSS & HAMPE, 2017); these characters in *P. transylvanicum* n. sp., exhibit the plesiomorphic condition, or are less derived or missing (see Table 4).

The new cranial characters observed on the endocranial surface of the fused parietals (i.e., development of the bony falx cerebri, tentorium osseum, and internal occipital protuberance), first introduced by DÍAZ-BERENGUER et al. (2022) for parsimony analysis, are largely unknown in most members of *Prototherium* (except *P. transylvanicum* n. sp.). Further additional new characters introduced by the same authors, located on the ventral surface of the basioccipital (i.e., the shape of the basioccipital in ventral view, the insertions for the longus capitis muscle on the ventral side of the basioccipital, and the presence vs. absence of a mid-ventral keel), are only partially known within *Prototherium*. The available information is as follows: in ventral view, the basioccipital is hourglass-shaped in *P. veronense*, *P. transylvanicum* n. sp., and *P. intermedium* s.l. (ch. 87-2); the insertions for the longus capitis muscles are marked by deep fossae in *P. transylvanicum* n. sp. and *P. intermedium* s.l. (ch. 88-1); and the mid-ventral keel of the basioccipital is present in *P. transylvanicum* n. sp. (ch. 89-0) but absent in *P. intermedium* (ch. 89-1). This gap in knowledge hinders a more complete understanding of the relationships in *Prototherium*.

Members of *Prototherium* and *Eotheroides*, as currently represented in phylogenetic analyses (e.g., BALAGUER & ALBA, 2016; VÉLEZ-JUARBE & WOOD, 2018; DÍAZ-BERENGUER et al., 2022; HERITAGE & SEIFERT, 2022), appear consistently as paraphyletic assemblages. Several species of *Prototherium* (*P. transylvanicum*, *P. veronense*, *P. ausetanum*) are placed in stemward positions, clustering with other genera such as *Sobrabesiren cardieli* and *Eotheroides aegyptiacum* (DÍAZ-BERENGUER et al., 2022, fig. 15; HERITAGE & SEIFERT, 2022, fig. 4). In contrast, *Prototherium intermedium* s.l. is positioned more crownward, grouping with derived forms such as *'Halitherium' taulannense* (DÍAZ-BERENGUER et al., 2022, fig. 15). A comparable pattern is observed within *Eotheroides*: some species (*E. aegyptiacum*, *E. lambondrano*) occupy stemward positions, whereas others (*E. clavigerum*, *E. sandersi*) are recovered in more derived placements (DÍAZ-BERENGUER et al., 2022, fig. 15; HERITAGE & SEIFERT, 2022, fig. 4). This phylogenetic distribution highlights the paraphyletic nature of both genera and may warrant a comprehensive taxonomic revision of these basal sirenian taxa (DÍAZ-BERENGUER et al., 2022).

6.2. Palaeozoogeographical links

There is a consensus between most authors that there might have been a clear partition between the northern and southern Peri-Tethyan fossil pansirenian populations, with *Sobrarbesiren*, *Prototherium*, *Sirenavus* occurring on the European side, while *Eotheroides*, *Libysiren*, *Protosiren*, *Eosiren* distributed on the African side of Tethys (HERITAGE & SEIFFERT, 2022). The dispersal of sirenians from western into more eastern European territories along the northern Tethyan coastal waters was facilitated by an extremely high eustatic level during most of the Eocene, when Europe looked like an archipelago (RAGE & ROČEK, 2003). The fossil record from the middle Eocene of the Pannonian Basin includes *Sirenavus hungaricus* KRETZOI, 1941 and *Anisosiren pannonica* KORDOS, 1977, and *Paralitherium tarkanyense* KORDOS, 1977 from the late Eocene of Felsőtárkány, Hungary; however, the latter form was synonymized with *Sirenavus hungaricus* by KORDOS (2002). Since the waterways between the Transylvanian Basin were largely open during the middle and late Eocene, the origin of *Prototherium transylvanicum* n. sp. from the late Eocene (Priabonian) might be linked to early waves of *Prototherium* pansirenian populations. A possible explanation for the conservative body plan of *P. transylvanicum* n. sp. (i.e., possession of many plesiomorphic traits) may be linked to the relatively isolated position of the Transylvanian Basin during the late Eocene, when marine connections with the Tethyan marine realm became rather limited (PALCU et al., 2023). Sea level drops that occurred around the Eocene–Oligocene transition further limited the connectivity with the global ocean and favoured the development of anoxic environments (PALCU et al., 2023). In such circumstances, the last reliable sirenian occurrences from the Transylvanian Basin are known from the early Oligocene (Rupelian) (VERESS et al., 2025).

6.3. Palaeoenvironmental circumstances

There is limited information regarding the complexity of late Eocene shallow-marine ecosystems from the fossil localities situated on the north-western side of the Transylvanian Basin, where pansirenians were evidently closely associated with seagrass palaeocommunities. In addition to various marine groups, such as calcareous algae, *Nummulites fabiani*, ostracods, gastropods, and bivalves, documented within the Cluj Limestone Formation (MÉSZÁROS, 2000), the most ecologically significant component may have been the presence of crocodilians (SABĂU et al., 2021; VENCZEL & CODREA, 2022), and potential bite marks of crocodilians have been reported in one of the recovered ribs (VERESS, 2025, fig. 96).

Table 4. Character states of *Prototherium transylvanicum* n. sp., based on the character list of DÍAZ-BERNEGUER et al. (2022). Unknown characters are marked with "?".

Ch.	10	20	30	40	50	60	70	80	89
	2001110100	0100000000	1101100111	0?010000??	101111?111	0?000??001	?010100011	??????0???	?10011210

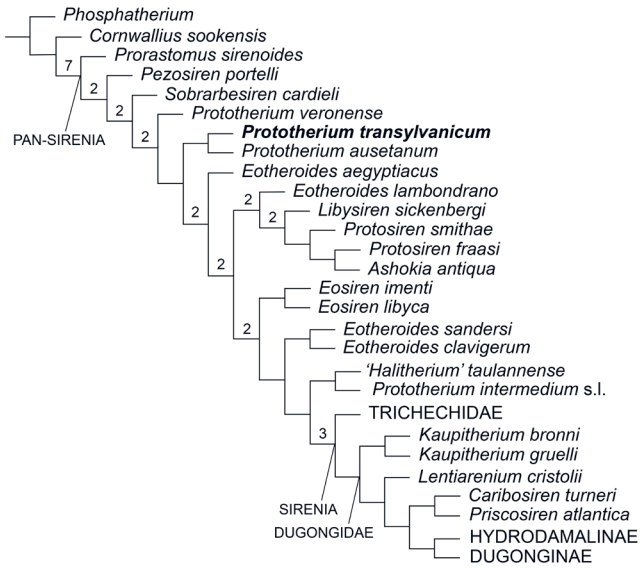


Figure 6. Relationships of *Prototherium transylvanicum* n. sp., based on parsimony analysis. Shortest most parsimonious tree generated by TNT, based on 63 operational taxonomic units with 89 phenotypic characters, derived from DÍAZ-BERENGUER et al. (2022). The numbers above the nodes indicate the decay indices of Bremer (= extra steps).

The development of seagrass communities in the Transylvanian Basin during the late Eocene was likely favoured by the mild climate and elevated eustatic sea levels. However, the so-called "Terminal Eocene Event," associated with global cooling and glacio-eustatic regression (SOTÁK, 2010), may have triggered substantial shifts within these communities.

When reconstructing the lifestyle of *Prototherium transylvanicum* n. sp., it is important to consider that these mammals were monogastric herbivores with post-gastric digestion and a low metabolic rate (BEST, 1981). Since all Eocene Transylvanian pansirenian occurrences come from marine sediments, this species was likely closely associated with shallow-marine environments. Rostral deflection in the sirenian skull represents an adaptation for feeding at different levels within the water column, as exemplified by representatives of extant Trichechidae (DOMNING & HAYEK, 1986). These authors observed that the modern Amazonian *Trichechus inunguis* possesses the smallest degree (25–41°) of rostral deflection among the sirenians, and its diet consists primarily of emergent and free-floating plant species (GUTERRES-PAZIN et al., 2014). In contrast, the modern *Trichechus manatus latirostris* exhibits a higher degree of rostral deflection (30–52°) (DOMNING & HAYEK, 1986), and two-thirds of its diet is composed of submerged plants (LEDDER, 1986). The narrow rostrum and narrow mandibular symphysis of *P. transylvanicum* n. sp., combined with its relatively high degree of rostral deflection (45°), indicate a selective browsing habit (DOMNING, 2001b), and its primary diet was likely composed of submerged aquatic macrophytes. However, in all the available maxillary and mandibular specimens of *P. transylvanicum* n. sp., the cheek teeth are either missing or heavily worn (Fig. 2d, 3e, 4a–d). This suggests that the horny pads surrounding the mouth may have taken over the primary role in food comminution after the cheek teeth became non-functional, as observed in modern dugongids (LANYON & SANSON, 2006).

7. CONCLUSION

Based on comparative studies and parsimony analyses of the pansirenian skull, as well as additional dissociated cranial material, vertebrae, and elements of the appendicular skeleton unearthed from the late Eocene (Priabonian) shallow-marine deposits of the Cluj Limestone Formation, we described a new species of pansirenian, *Prototherium transylvanicum* n. sp.

In our parsimony analyses, *Prototherium transylvanicum* n. sp. was erected as the sister species of *P. ausetanum*, positioned crownward of *P. veronense* on the cladogram. Unexpectedly, the remaining member of the genus, *P. intermedium*, often regarded as a catch-all taxon and coeval with *P. transylvanicum* n. sp. is placed even more crownward, as the sister taxon of *'Halitherium' taulannense*.

Endocranial structures exposed on the inner surfaces of the parietals and supraoccipital in one specimen (i.e., the bony falx cerebri, tentorium osseum, and inner occipital protuberance), reported here for the first time in *Prototherium*, underscore the phylogenetic relevance of such features, as previously emphasized by DÍAZ-BERENGUER et al. (2022). In contrast, other cranial traits, such as the rostral width and deflection, together with the morphology of the mandibular symphysis, likely reflect feeding adaptations shaped by selective pressures and may represent homoplasies (i.e., features lacking phylogenetic signal).

Consistent with other studies (e.g., BALAGUER & ALBA, 2016; VÉLEZ-JUARBE & WOOD, 2018; DÍAZ-BERENGUER et al., 2022; HERITAGE & SEIFERT, 2022), the paraphyletic nature of the genera *Prototherium* and *Eotheroides* suggests that a comprehensive taxonomic revision is warranted.

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