



Dome-headed, small-brained island mammal from the Late Cretaceous of Romania

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The island effect is a well-known evolutionary phenomenon, in which island-dwelling species isolated in a resource-limited environment often modify their size, anatomy, and behaviors compared with mainland relatives. This has been well documented in modern and Cenozoic mammals, but it remains unclear whether older, more primitive Mesozoic mammals responded in similar ways to island habitats. We describe a reasonably complete and well-preserved skeleton of a kogaionid, an enigmatic radiation of Cretaceous island-dwelling multituberculate mammals previously represented by fragmentary fossils. This skeleton, from the latest Cretaceous of Romania, belongs to a previously unreported genus and species that possesses several aberrant features, including an autapomorphically domed skull and one of the smallest brains relative to body size of any advanced mammaliaform, which nonetheless retains enlarged olfactory bulbs and paraflocculi for sensory processing. Drawing on parallels with more recent island mammals, we interpret these unusual neurosensory features as related to the island effect. This indicates that the ability to adapt to insular environments developed early in mammalian history, before the advent of therian mammals, and mammals with insular-related modifications were key components of well-known dwarfed dinosaur faunas. Furthermore, the specimen suggests that brain size reduction, in association with heightened sensory acuity but without marked body size change, is a novel expression of the island effect in mammals.

Mammalia | Cretaceous | Multituberculata | insular environments | islands

Islands are regarded as laboratories of evolution, where species isolated in a resource-limited environment often drastically alter their anatomy and behaviors (1, 2). Many of the best examples are modern and Cenozoic mammals, with numerous documented species that drastically changed their body sizes and proportions, or developed bizarre morphological and behavioral characteristics, after being marooned in isolation (3–9). However, we know little about how more ancient, Mesozoic mammals responded to insular habitats.

Since the turn of the twentieth century, the Late Cretaceous vertebrates of Transylvania (Romania) have been lauded as a prime example of the island effect in the Mesozoic fossil record (10, 11), characterized by dwarfed herbivorous dinosaurs (12), morphologically bizarre carnivorous dinosaurs (13), and relict turtles and crocodylomorphs. Many of these unusual taxa were first recognized by the pioneering paleobiologist Franz Nopcsa over a century ago (10). More recently, fossils of distinctive multituberculate mammals, the kogaionids, have been found in Transylvania (14–16), but their largely isolated, fragmentary, and highly unusual remains have made them challenging to study. It has been particularly difficult to untangle their phylogenetic relationships and understand their paleobiology (17), and hence to determine how they may have been influenced by their island environment.

Here we describe a partial skeleton of a previously undiscovered genus and species of kogaionid from the latest Cretaceous (Maastrichtian) of Transylvania, which for the first time to our knowledge includes dentition, a skull, and substantial postcranium of a kogaionid reported in association. This specimen allows us to

describe the anatomy of kogaionids in detail, include them in a comprehensive phylogenetic analysis, estimate their body sizes, and present a reconstruction of their brain and sense organs. This species exhibits several features that we interpret as related to its insular habitat, most notably a brain that is substantially reduced in size compared with close relatives and mainland contemporaries, demonstrating that some Mesozoic mammals were susceptible to the island effect like in more recent species.

Systematic Paleontology

Mammalia Linnaeus, 1758; Multituberculata Cope, 1884; Cimolodonta McKenna, 1975; Kogaionidae Rădulescu and Samson, 1996; *Litovoi tholocephalos* gen. et sp. nov.

Holotype

Laboratory of Paleontology (LPB), Faculty of Geology and Geophysics, University of Bucharest (FGGUB) M.1700. An associated partial skeleton including much of the skull (partial skull roof, complete braincase and ear region, right premaxilla with incisors, left maxilla with complete cheek tooth row, and i1) and postcranial elements (vertebrae, ribs, pelvic and limb bones) (Fig. 1 and *SI Appendix*, Figs. S1–S9).

Significance

Island-living animals often differ from close relatives and mainland contemporaries in unusual ways, as best demonstrated by modern and Cenozoic mammals that are dwarfed or evolved aberrant anatomical features. However, it is unclear whether mammals from the Age of Dinosaurs followed this same pattern. We describe the fossil skeleton of a previously undiscovered peculiar Cretaceous island-dwelling mammal from Romania, which has a domed skull and one of the smallest brains (proportional to body size) of any mammal, living or extinct, but retains enlarged regions of the brain related to sensory processing. These unusual features were probably related to the species' island habitat and demonstrate that the ability to adapt to island environments developed early in mammalian history.

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Etymology

Litovoi, a voivode (local ruler) in thirteenth-century southwestern Romania; “tholo,” refers to the domed skull “cephalos.”

Horizon and Locality

“Multi-bed” level, Bărbat River succession, Pui, Hațeg Basin, Romania; Maastrichtian “Pui beds” (see *SI Appendix, Figs. S1 and S2* for detailed information on the holotype and its discovery).

Diagnosis

Litovoi tholocephalos is a large-sized kogaionid (14, 16, 17) diagnosed by an autapomorphically vaulted skull roof with the highest point of the arch at the level of the supraorbital notch, as well as a unique combination of characters: very elongated upper postcanine tooth row with apomorphically elongated P1 and P2, an elongated P3 having a cusp formula of 2:5, and an inflated first labial cusp on P4 (*SI Appendix*).

Description and Comparisons

The upper dentition is preserved in situ and exhibits the typical kogaionid pattern (14, 17): dental formula 2:0:4:2, premolars elongated relative to molars, P3 longest of the upper teeth, M1 short and wide with a small number of cusps (four) in the median row (Fig. 1). The postcanine tooth row is sinuous in labial view, defined by ventrally projecting cusp tips at the P3/P4 junction; this is also present in the sympatric kogaionids *Barbatodon* (16) and *Kogaionon* (14), and may be a synapomorphy of the group. In occlusal view, the tooth row bulges laterally, due to the distolabial deflection of P3, as in *Kogaionon* (14). P3 has the highest cusp count in a single row among any of the upper teeth (2:5), more reminiscent of the Paleocene kogaionid *Hainina* (18)

than the Cretaceous species. The length-to-width ratio of M1 is the lowest of any known kogaionid. Red pigmentation is present on the upper incisors, similar to other Transylvanian multituberculates (16, 19), but absent on the postcanines.

Much of the skull is preserved to enable reconstruction of a virtually complete kogaionid cranium (Fig. 1 and *SI Appendix, Fig. S3*). The μ CT imaging reveals details of the internal anatomy and brain architecture (Fig. 2 and *SI Appendix, Figs. S5–S7*). Most salient, the skull roof is distinctively domed in lateral view, a feature unique to *Litovoi* among all multituberculates (*Kogaionon* has a slight dome; *SI Appendix, Fig. S4*). The dorsal-most point of the dome corresponds to the highest point of the enlarged olfactory bulbs internally (Fig. 2 *A* and *F*), suggesting these two features are linked. The premaxilla is high dorsoventrally but narrow labiolingually, imparting a tall but narrow rostrum (Fig. 1 *A–C*). The zygomatic arch extends sharply laterally in dorsal view, producing a squared-off outline of the skull reminiscent of taeniolabidoids, aberrant multituberculates that thrived in North America and Asia after the end-Cretaceous extinction (20, 21). The braincase is exceptionally well preserved. The large anterior lamina of the petrosal overlaps the parietal and forms the sidewall of the braincase. The promontorium is long and fingerlike, with a convex ventral surface.

The μ CT scans reveal the brain endocast to be narrow in dorsal view, as reflected by the narrow skull roof. A narrow skull roof is also present in *Kogaionon* (14, 17) and *Barbatodon* (16) (*SI Appendix, Fig. S8*), suggesting that a narrow endocast may be a kogaionid feature, distinctive from the much wider endocasts of well-studied mainland Late Cretaceous and Paleogene multituberculates [ptilodontoids (20, 22) and djadoctatherioids (23–25)]. The olfactory bulbs are extremely large, especially compared with endocranial mass, and there is no distinct annular

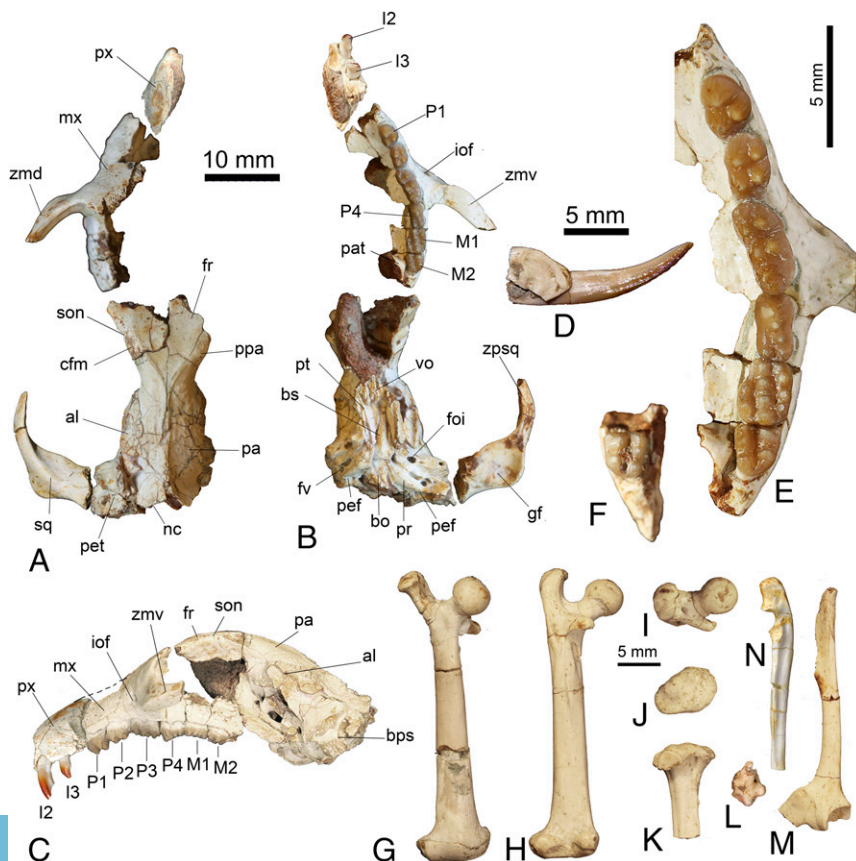


Fig. 1. Holotype of *Litovoi tholocephalos* [LPB (FGGUB) M.1700]. Skull elements: premaxilla with I2 and I3 (flipped from the right bone), left maxilla with postcanine teeth, skull roof and braincase, and squamosal in (A) dorsal view, (B) ventral view, and (C) lateral view, with the different elements restored in their anatomical position to show the distinctive arching of the skull roof (*SI Appendix, Fig. S4*). (D) Lingual view of left lower incisor with part of the symphysis; (E) left upper cheek teeth in occlusal view; (F) right m2 in occlusal view; (G) right femur in anterior view; (H) left femur in posterior view; (I) proximal view of the left femur; (J) proximal view of the left tibia; (K) proximal portion of the left tibia; (L) partial left calcaneum in dorsal view; (M) lateral view of the left ilium; (N) proximal portion of left ulna in lateral view. A full list of all holotype bones and their specimen numbers is provided in the *SI Appendix*. Abbreviations: al, anterior lamina of the petrosal; bo, basioccipital; bps, breakage between the petrosal and squamosal; bs, basisphenoid; cfm, contact facet (on the frontal) for the parietal; foi, foramen ovale inferium; fr, frontal; fv, fenestra vestibuli; gf, glenoid fossa; I2, second upper incisor; I3, third upper incisor; M1, first upper molar; M2, second upper molar; mx, maxilla; nc, nuchal crest; P1, first upper premolar; P2, second upper premolar; P3, third upper premolar; P4, fourth upper premolar; pa, parietal; pef, perilymphatic foramen; pet, petrosal; ppa, anterior prong of the parietal; pr, promontorium of the petrosal; pt, pterygoid; px, premaxilla (horizontally flipped); son, supraorbital notch; sq, squamosal; vo, vomer; zmd, zygomatic process of the maxilla (dorsal); zmv, zygomatic process of the squamosal.

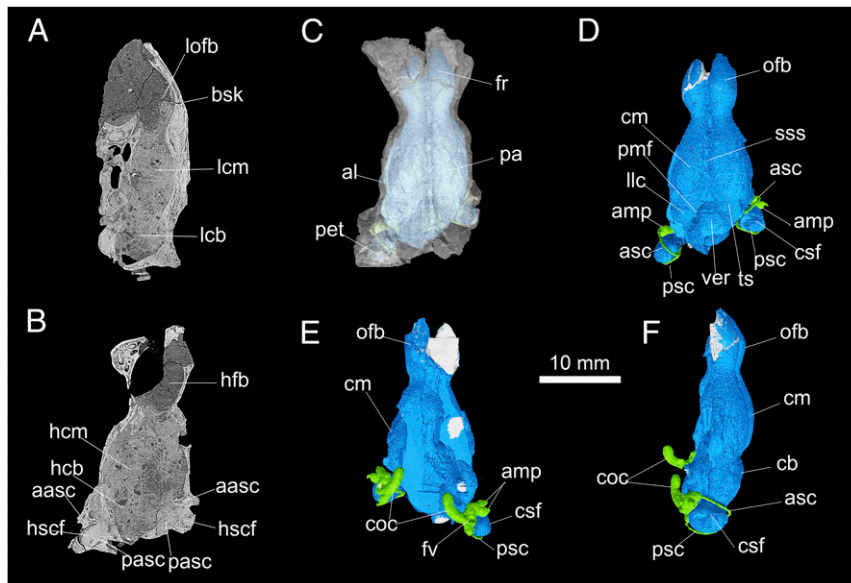


Fig. 2. Sections of X-ray microcomputerized tomography of cranium and reconstructed virtual cranial endocast of *Litovoi* (see also *SI Appendix, Figs. S5 and S6*). (A) The μ CT image along the longitudinal section of the braincase; (B) μ CT-image in horizontal section through the braincase. (C) Reconstructed cranium (with bone in semitransparency) and the enclosed endocast (light blue) in dorsal view. (D) Virtual endocast and inner ear (in green) in dorsal view. (E) Virtual endocast and inner ear in ventral view. (F) Virtual endocast and inner ear in lateral view. Abbreviations: aasc, anterior cross-section of anterior semicircular canal; al, anterior lamina of petrosal; amp, cast of ampulla; asc, cast of anterior semicircular canal; bsk, bending point of the skull roof (corresponding to the dorsal-most point of the olfactory bulb); cb, cast of cerebellum; cm, cast of cerebrum; coc, cast of cochlear canal; csf, cast of subarcuate fossa (for paraflocculus); fr, frontal; fv, fenestra vestibuli; hcb, horizontal section of the cerebellar space; hcm, horizontal section of the cerebral space; hfb, horizontal section of the olfactory bulb space; hscf, horizontal section of the fossa for paraflocculus; lcb, longitudinal section of the cerebellar space; lcm, longitudinal section of the cerebral space; llc, cast of the lateral lobe of cerebellum; lofb, longitudinal cross-section of the olfactory bulb space; ofb, cast of olfactory bulbs; pa, parietal; pasc, posterior cross-section of the anterior semicircular canal; pet, petrosal; pmf, paramedian fissure; psc, cast of posterior semicircular canal; sss, superior sagittal sinus; ts, transverse dural venous sinus; ver, cast of vermis. (Note: the left side of the skull is less distorted, although the left olfactory bulb is partly damaged).

fissure separating them from the remainder of the forebrain. The cast of the subarcuate fossa that contains the petrosal lobe of the paraflocculus is also large, corresponding to highly arched semicircular canals of the inner ear, and the cochlea is proportionally long and slightly curved (*SI Appendix, Figs. S6, S7, and S9*).

It was once argued that multituberculates had a therianlike brain, with a large vermis bulging from the center of the cerebellum (20, 23). However, this was later reinterpreted as the superior cistern, and the structures lateral to it as transversely elongated paraflocculi (24), differing considerably from the brain of Cretaceous therian mammals, which have a prominent vermis and cerebellar hemispheres laterally (17). The endocast of *Litovoi* clearly indicates a central vermis, as already documented convincingly in *Kryptobaatar* (25), but also lateral cerebellar hemispheres, identified here in multituberculates, with the subarcuate fossa for the paraflocculus located farther laterally (Fig. 3B and *SI Appendix, Fig. S7*). This architecture suggests that a remarkably therian-style brain may have evolved earlier in mammalian evolution than currently recognized (perhaps present in all multituberculates, where the vermis and cerebellar hemispheres are obscured by poor endocast preservation). Alternatively, some multituberculates may have independently evolved a therianlike brain, indicating that neural evolution in early mammals was extremely homoplastic.

The well-preserved femora (Fig. 1 G–I) exhibit typical multituberculate characters, including a spherical head, a long neck forming an angle of $\sim 55^\circ$ with the shaft, a greater trochanter extending beyond the head, a prominent lesser trochanter projecting ventromedially, a fissurelike posttrochanteric fossa, and absence of the third trochanter (17, 26). The proximal end of the tibia is mediolaterally wide and asymmetrical, and has a hooklike

process that contacts the fibula (Fig. 1 J and K). Just as with the femora, the left ilium (Fig. 1 M) and proximal ulna (Fig. 1 N) are of generalized cimolodontan build. The ulna has a robust olecranon process rising above the vertically divided, relatively deep semilunar notch. The ilium is slender and elongate. The nearly intact femora, along with the skull, show that *Litovoi* was similar in body proportions to other multituberculates (26, 27), but fairly large (ca. 166 g) compared with most other Late Cretaceous species (*SI Appendix, Table S1*). It was not, however, substantially larger or smaller than its mainland contemporaries, so it cannot be considered an island dwarf or an abnormally large island taxon.

Systematics

To test the phylogenetic relationships of *Litovoi*, we added it to a large dataset of multituberculates and other mammals, which we analyzed with parsimony and Bayesian techniques (*Materials and Methods*). Our phylogenetic analysis places *Litovoi* within Cimolodonta (Fig. 3A), and together with *Kogaionon* and *Barbatodon* into a monophyletic Kogaionidae united by a suite of synapomorphies (*SI Appendix, Part E2 and Fig. S10*). This analysis reinforces the hypothesis that kogaionids are a specialized endemic European clade (15, 17). We interpret this endemism as related to their island habitat (Fig. 4A).

Brain Evolution

We compared the brain size and proportions of *Litovoi* to 533 other mammals and close nonmammaliaform cynodont kin (Fig. 3C and *SI Appendix, Fig. S11*). *Litovoi* has a substantially lower brain-to-body size ratio than other multituberculates, and surprisingly clusters with a variety of much more primitive, distantly related nonmammaliaform cynodonts and basal mammaliaforms

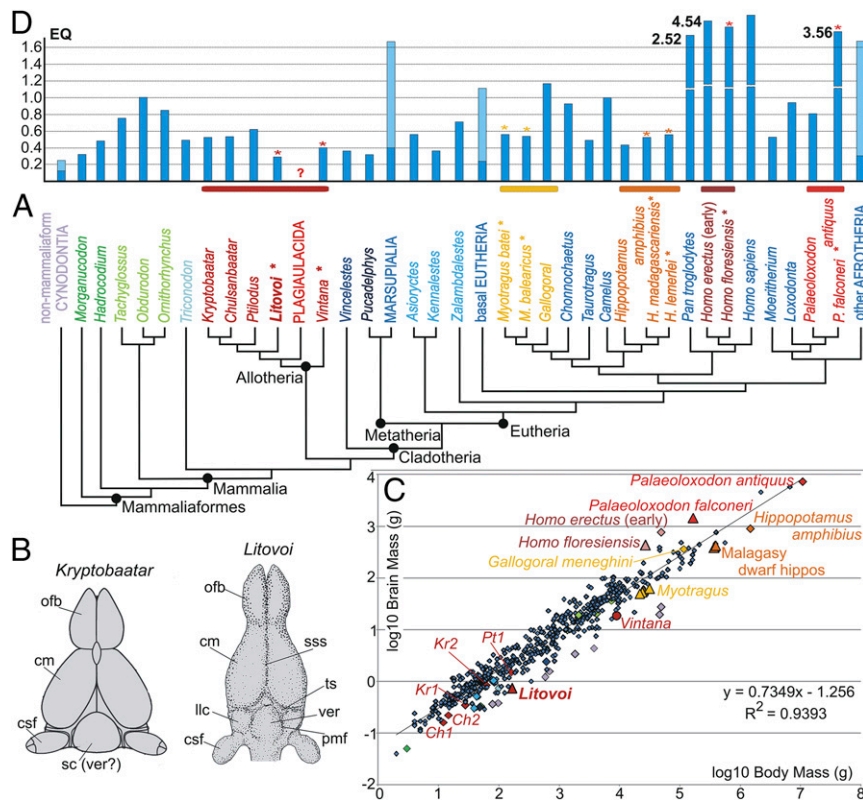


Fig. 3. Details of relative brain development in *Litovoi*, interpreted from its digital endocast. (A) Phylogenetic position of *Litovoi*, based on the integration of a simplified version of strict consensus tree of 110 most parsimonious trees recovered in our phylogenetic analysis into a consensus tree showing wider mammaliaform relationships (see details in *Materials and Methods* and *SI Appendix, Parts D and E* and *Fig. S10*); insular taxa are marked by *. (B) Comparison of brain structure between *Kryptobaatar dashzevegi* and *Litovoi*, emphasizing reinterpretation of the hindbrain structure, which in *Litovoi* is more similar to the typical therian pattern than interpreted previously in multituberculates (*SI Appendix, Figs. S7–S9*). Abbreviations: cm, cerebrum; csf, cast of subarcuate fossa (for parafoolculus); llc, lateral lobe of cerebellum; ofb, olfactory bulb; pmf, paramedian fissure; sc, superior (longitudinal) sagittal sinus; ts, transverse dural venous sinus; ver, vermis. (C) Graph plotting brain mass (\log_{10} BrainMass) of selected derived cynodontians relative to their body mass (\log_{10} Body Mass). Color coding of taxa as in *Fig. 3A*; red symbols mark allotherians: Chu, *Chulsanbaatar*; Kr, *Kryptobaatar*; Pt, *Ptilodus*; triangles mark insular taxa (see *SI Appendix, Figs. S11–S14* for more details, and *Materials and Methods* and *SI Appendix* for estimation methods, data sources and references). (D) EQ value plots for the taxa represented in *Fig. 3A*; clades with insular members marked by horizontal segments, insular taxa marked by *; dark and light blue in suprageneric taxa (i.e., nonmammaliaform Cynodontia, Marsupialia, Eutheria, and Afrotheria) represent minimum and maximum EQ values in the sample. Note that high (>2) EQ values are not to scale, values added for easy comparisons.

(*SI Appendix, Figs. S11–S14*). Its encephalization quotient (EQ) is also low, at 36–60% of the EQ of other multituberculates (*SI Appendix, Table S1*), comparable to that of nonmammaliaform cynodonts and below the 0.5 value long considered a threshold of mammals (28). The olfactory bulbs, however, are larger (relative to brain size) than they are in nearly every other mammaliaform in our sample, and at least 50% larger in proportional size than in other multituberculates, which have generally larger olfactory bulbs than other mammals (17, 22, 28) (*SI Appendix, Fig. S15*). Similarly, the parafoolculi are the largest (relative to brain size) of any mammaliaform in our dataset, and exceed those of other multituberculates, otherwise characterized among mammals by relatively large subarcuate fossae housing the cerebellar parafoolculi (28, 29), by ~50% (*SI Appendix, Fig. S16*). The proportionally small brain (relative to its body size) and proportionally large olfactory bulbs and parafoolculi (especially compared with brain size) are not retained mammaliaform plesiomorphies, as the conditions of *Litovoi* are highly modified relative to adjacent nodes on the phylogeny, and most importantly, to other multituberculates (*Fig. 3A* and *D*).

Discussion

Litovoi exhibits an array of unusual features relative to other Mesozoic mammals, particularly closely related mainland multituberculates. These include the autapomorphically domed skull

and a highly unusual brain, which is so small relative to body size that it not only is significantly smaller compared with other multituberculates, but falls within the range of much more primitive nonmammalian cynodonts and basal mammaliaforms (*Fig. 3*). According to our dataset, it has one of the smallest encephalization quotients of any advanced mammaliaform, living or extinct (*Fig. 3* and *SI Appendix, Table S7*). Nonetheless, *Litovoi* possesses enormous olfactory bulbs and parafoolculi, relative to both other multituberculates and mammaliaforms in general, indicating that not all regions of the brain were tiny, and that it likely had particularly sharp sense of smell and keen eye movement control, and possibly efficient hearing.

We hypothesize that the atypical brain of *Litovoi* is related to its island habitat. It is difficult to conclusively demonstrate that certain features are causally related to insularity, but three lines of evidence support our hypothesis. First, *Litovoi* lived on an ancient island, as demonstrated by clear geological evidence (10–12), and is found alongside a bevy of other vertebrates, particularly dinosaurs, that exhibit peculiar anatomical features that have been interpreted as insularity-related modifications (10–13). Second, *Litovoi*—and possibly other kogaionids, judging by their narrow skull roofs (*Fig. 4B* and *C* and *SI Appendix, Fig. S8*)—underwent a reduction in brain size relative to the continental multituberculates that bracket them on the phylogeny. Third,

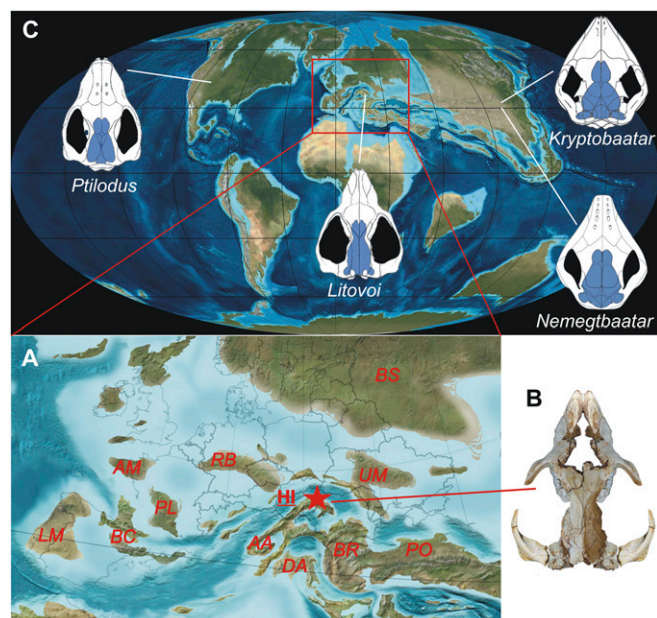


Fig. 4. Paleogeographic setting of *Litovoi*. (A) Location of the Hațeg Island (HI), place of discovery for *Litovoi*, within the Late Cretaceous European Archipelago. Abbreviations: AA, Austroalpine Landmass; AM, Armorican Massif; BC, Basque-Catalonian Landmass; BR, Balkans-Rhodope Landmass; BS, Baltic Shield; DA, Dalmatian-Adriatic Landmass; LM, Lusitanian Massif; PL, Provençal Landmass; PO, Pontides orogenic chain; RB, Rhenish-Bohemian Landmass; UM, Ukrainian Massif. (B) Reconstruction of the skull of *Litovoi* in dorsal view (SI Appendix, Figs. S7 and S8). (C) Comparison between skull and brain shape of *Litovoi*, an insular multituberculata, and those of Late Cretaceous Mongolian (*Kryptobaatar*, *Nemegetbaatar*) and Paleocene North American (*Ptilodus*) mainland multituberculates (skull outlines not at the same scale; see SI Appendix, Figs. S7 and S8 for details and references). Paleogeographic maps, courtesy of Ron Blakey (deeptimemaps.com).

there is strong evidence from more recent insular mammals that extreme changes in neurosensory anatomy and biology often occur after a lineage is implanted on an island. In fact, some of the odd features of *Litovoi* parallel cases in Cenozoic and more recent insular mammals (5, 6), most remarkably the Plio-Pleistocene bovid *Myotragus* (3), where a small brain has been explained as an adaptation for reducing metabolic rate and diverting energy investment from development of expensive neural tissue toward other needs in a resource-limited environment (3, 4). However, *Litovoi* stands out from almost all small-brained insular mammals—save the island-dwelling giant Minorcan rabbit *Nuralagus* (30)—in that its tiny brain is not related to a reduction in body size, as it is one of the relatively large Cretaceous multituberculates (31) (SI Appendix, Table S1).

In *Litovoi*, it is particularly intriguing that brain atrophy was selective. Although the brain itself is abnormally small, certain regions of the brain are enlarged. In particular, the olfactory bulbs (associated with the sense of smell) and paraflocculi (involved in balance and oculomotor activities) remain disproportionately well developed, both relative to the rest of the brain and the body (SI Appendix, Figs. S15 and S16). This indicates that keen senses and motor control were still important to *Litovoi* despite the constraints that forced its brain reduction, perhaps because it was nocturnal (17), and/or because it shared its environment with a variety of small predators (11).

The discovery of *Litovoi* demonstrates that Mesozoic mammals altered their anatomy and biology when isolated on islands, similar in some ways to Cenozoic insular placentals, but different in detail. Another Mesozoic mammal, the recently described large-bodied, big-eyed, keen-smelling Cretaceous gondwanatherian *Vintana*

(32), also exhibits some parallels with *Litovoi*, notably a small brain and enlarged olfactory bulbs (33). The strange characteristics of *Vintana* were interpreted as products of the isolation of Madagascar as Gondwana fragmented during the Cretaceous (32), not explicitly as island-related modifications. However, we hypothesize that similar evolutionary phenomena may have been in operation, although Madagascar was much larger (ca. 7×) than *Litovoi*'s Transylvanian island (12).

Thus, in summary, the ability to adapt to insular and resource-limited environments developed early in mammalian history, in species more basal than therian mammals and long before celebrated examples from Mediterranean islands (3, 5, 7). Furthermore, insularity-related modifications may have been a common characteristic of Mesozoic mammals sequestered on small islands and peripheral isolates of fragmenting continents. It was not only dinosaurs whose anatomy and biology were reshaped by these unusual habitats, as has long been recognized (10), but mammals too.

Conclusions

The previously undiscovered kogaionid species *Litovoi tholoecephalos* provides a glimpse at an island-living mammal from the Mesozoic. It has features that we interpret as related to its isolated habitat, particularly a narrow brain that is proportionally much smaller than those of other mammals, including mainland multituberculates and other Mesozoic and more modern species, but with proportionally enlarged regions for olfactory and oculomotor processing. Our phylogenetic analyses unite the kogaionids based on a suite of derived morphologies, establishing them as a diverse clade of endemic European species that locally survived the end-Cretaceous mass extinction. Brain size reduction, in concert with increased sensory acuity but without marked body size change, appears to be a novel expression of the island effect in mammals (3–9) and evidence that Mesozoic mammals were capable of being shaped by insularity.

Materials and Methods

CT-Scan and Imaging. The cranium was scanned using an X-ray computed tomography scanner (GE Phoenix v|tome|x s 240 CT Scanner) at the Microscopy and Imaging Facility, American Museum of Natural History. The energy settings were 150 kV and 0.16 mA, and a total of 1,500 slices with interslice sampling distance of 0.0233 mm were obtained, resulting in a 9.3-GB dataset that was used for segmentation and 3D reconstruction of the digital model. Segmentation of the scan data, endocast construction, and volume measurements were made with VG Studio Max 3.0. (see details in SI Appendix, Part B4).

Plotting Methods. The data plots in Fig. 3 C and D and SI Appendix, Figs. S11–S16 were constructed using a large sample of mammaliaforms, based primarily on the database of Hoffmann et al. (ref. 33 and references therein) employed in their study of the endocranial morphology of the Late Cretaceous Malagasy gondwanatherian *Vintana* (32), a member of the sister group of Multituberculata. Their database comprises two sets: one of 517 extinct and extant derived cynodonts, most of them members of Mammaliaformes, with endocranial volume and body mass data; and a smaller sample of 163 extinct and extant mammaliaforms for which olfactory bulb values were also reported.

We expanded the first dataset of Hoffmann et al. (ref. 33; SI Appendix, Table S7) to include a larger number of individuals for multituberculates for which relevant measurements are available (*Chulsanbaatar*, *Kryptobaatar*, and *Ptilodus*; SI Appendix), to establish the range of possible individual variation. Their body size and EQ were estimated using the same methods as for *Litovoi* (SI Appendix, Part C) instead of being simply taken from literature. Besides multituberculates, we also added other mammalian taxa (both extinct and extant), particularly island-dwelling species together with their close mainland relative with reported body and brain size estimates (SI Appendix, Part D). Body mass estimate for *Vincelestes neuquenianus* was corrected from Hoffmann et al. (33), based on Macrini et al. (34). Our brain size-EQ dataset includes 533 taxa (some represented by multiple specimens), with 8 nonmammaliaform cynodontians and 525 mammaliaforms.

Multituberculates are represented by four taxa and a total of eight specimens (see full details in *SI Appendix*).

We also expanded the second, smaller database with olfactory bulb volume data (OB database) from Hoffmann et al. (33), especially by adding multituberculates as well as basal eutherians, for a total of 168 mammaliaform taxa (for sources, see *SI Appendix, Part D* and *Table S8*). To assess the relative development of the subarcuate fossae (i.e., paraflocculi; *SI Appendix, Fig. S16*), less commonly reported in publications, we added *Litovoi* to a dataset gathered by Macrini (25) (*SI Appendix, Table S9*).

To account for the incompletely preserved posteriormost part of the braincase in *Litovoi*, the three datasets also include a sensitivity estimate in which its digitally measured endocranial volume is increased by 5% (considered to represent a maximum amount of endocranial volume that may be missing) and its body size estimate is increased by adding 0.1 mm to skull length (*SI Appendix, Parts B and C*). These revised data were not plotted in Fig. 3 and *SI Appendix, Figs. S10–S15*, as their locally marginally higher values do not alter our main conclusions: that *Litovoi* has significantly reduced its endocranial volume, but retained relatively large olfactory bulbs and subarcuate fossae, compared with all other multituberculates and most other mammaliaforms in our sample.

Phylogenetic Analyses. Our phylogenetic analysis utilizes a dataset that broadly samples multituberculates, which is built on a data matrix that one of us (J.M.) has been iteratively building with colleagues (35, 36). This dataset, in turn, has sampled taxa and characters from several previous studies (see refs. 35 and 36, and *SI Appendix, Part D* for more source details).

Our dataset includes 46 taxa scored for 107 characters (*SI Appendix, Parts D and E*). We expanded the most recent iterations of the dataset (see details

in *SI Appendix, Part D*) by adding two taxa: *Barbatodon transylvanicus* and *Litovoi*, which, together with *Kogaionon unguereanui*, are represented by the best preserved and most complete specimens among kogaionids. We also added five new characters and modified some character states from previous studies (details in *SI Appendix, Part D2*).

Phylogenetic analyses were conducted using parsimony in PAUP* (Version 4.0a152) (37) and likelihood-based Bayesian inference in MrBayes 3.2.4 (38, 39). For Bayesian analyses, we used the Mk model for discrete morphological data (40), with a gamma parameter for rate variation. Fig. 3A is based on the results of our phylogenetic analyses (*SI Appendix, Fig. S10*) concerning the position of the Kogaionidae (including *Litovoi*) within Multituberculata, integrated into a simplified version of a consensus of mammaliaform phylogenetic relationships. See full details of the phylogenetic analyses in *SI Appendix, Parts D and E*.

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