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

Zoltán Csiki[a,1], Mátyás Vremir[b], Stephen L. Brusatte[c,d], and Mark A. Norell[c,d]

[a]Laboratory of Paleontology, Department of Geology and Geophysics, University of Bucharest, 1 N. Bălcescu Boulevard, Bucharest 010041, Romania; [b]Department of Natural Sciences, Transylvanian Museum Society (EME), 2-4 Napoca Street, Cluj-Napoca 400009, Romania; [c]Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024; and [d]Department of Earth and Environmental Sciences, Columbia University, New York, NY 10025

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Islands are noted for the occurrence of aberrant, endemic, and dwarfed taxa (the "island effect"). Late Cretaceous vertebrate assemblages of Romania and elsewhere in Europe are classic examples of island faunas in the fossil record, and are characterized by dwarfed herbivorous dinosaurs and other endemic taxa that are noticeably primitive relative to their mainland contemporaries. Fossils of the predators inhabiting the European paleoislands, however, are exceptionally rare and fragmentary. We describe a new dromaeosaurid theropod, based on an articulated skeleton from the Maastrichtian of Romania, which represents the most complete predatory dinosaur from the middle to Late Cretaceous of Europe. This taxon is characterized by a peculiar body plan, most notably extensive fusion in the hand and distal hindlimb, a highly retroverted pelvis with enlarged femoral muscle attachments, and a pair of hyperextensive pedal claws. However, unlike the island-dwelling herbivorous dinosaurs, its closest relatives are contemporary similar-sized Laurasian taxa, indicating faunal connections between Asia and the European islands late into the Cretaceous. This theropod provides support for the aberrant nature of the Late Cretaceous European island-dwelling dinosaurs, but indicates that predators on these islands were not necessarily small, geographically endemic, or primitive.

Dromaeosauridae | endemic | Europe | island fauna | Theropoda

Islands, both modern and ancient, are notorious for the occurrence of aberrant, endemic, and dwarfed taxa (1, 2). During the Late Cretaceous, an extraordinary time in Earth history characterized by warm temperature and high sea levels, much of Europe was fragmented into numerous small islands (3). The vertebrates inhabiting these islands have long been recognized as peculiar (4, 5). Herbivorous dinosaurs were dwarfed compared to close relatives (5–8) and formed endemic clades that are remarkably primitive relative to contemporaries from other continents, a pattern also seen in lizards, turtles, crocodylians, and mammals (2, 5, 9). As a result, Late Cretaceous assemblages in Romania and elsewhere in Europe are considered prime examples of abnormal island faunas in the fossil record (2).

Little is known, however, about the predators that inhabited these paleoislands, as European Late Cretaceous theropod dinosaurs are represented solely by rare, fragmentary fossils (10). Recent discoveries demonstrate that dromaeosaurids, sickle-clawed relatives of birds, were widely distributed during the Late Cretaceous (11), but their European records are limited to isolated teeth and fragmentary bones that are generally undiagnostic (12). It is unclear, therefore, whether island-dwelling predatory dinosaurs were also dwarfed, primitive, or formed localized clades, or on the contrary, whether the "island effect" was expressed differently, or at all, in these animals.

Here we describe a bizarre new dromaeosaurid, *Balaur bondoc* gen. et. sp. nov. from the Maastrichtian of Romania, which is the most complete and diagnostic nonavialan theropod from the final 60 million years of the Mesozoic in Europe (10). This taxon allows, for the first time, an understanding of the evolution of large carnivores on the European paleoislands. It exhibits a suite of peculiar features, most notably an enlarged pedal digit I, which along with digit II is modified for hyperextension. Nearly 20 additional autapomorphies also characterize this taxon, many of which relate to extensive fusion of elements in the hand and distal hindlimb and enlarged pelvic musculature. This unique dromaeosaurid provides further support for the aberrant nature of island-dwelling dinosaurs, indicates faunal connections between Asia and the European islands late into the Cretaceous, and documents a peculiar, highly autapomorphic body plan previously unknown among theropod dinosaurs.

Systematic Paleontology

Dinosauria Owen, 1842; Theropoda Marsh, 1881; Coelurosauria Huene, 1914; Maniraptora Gauthier, 1986; Dromaeosauridae Matthew and Brown, 1922; *Balaur bondoc* gen. et sp. nov.

Holotype

EME (Transylvanian Museum Society, Dept. of Natural Sciences, Cluj-Napoca, Romania) PV.313, an articulated partial postcranial skeleton of a single individual, including dorsal, sacral, and caudal vertebrae and much of the pectoral and pelvic girdles and limbs (full list of preserved bones in the *SI Appendix*) (Figs. 1 and 2).

Etymology

Balaur, an archaic Romanian term meaning dragon, and *bondoc*, meaning stocky (see *SI Appendix*).

Referred Specimens

FGGUB (Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania) R. 1580 (left humerus), R. 1581 (left ulna), R. 1582–1584 (left manual phalanges), R. 1585 (left metacarpal II) likely from the same individual, approximately 45% larger than the holotype (see *SI Appendix* for details and images).

Horizon and Locality

The type specimen was collected from red floodplain mudstones of the lower-middle part of the Maastrichtian Sebeş Formation (13), exposed at the Sebeş Glod locality near Sebeş, Alba County, Romania, The referred specimens are from pedogenetically modified, dark red, silty mudstones exposed at the Tuştea dinosaur nesting site (14), in the middle part of the Maastrichtian Densuş-Ciula Formation, Haţeg Basin, Hunedoara County, Romania (see *SI Appendix*).

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[1]To whom correspondence should be addressed. E-mail: zoltan.csiki@g.unibuc.ro.

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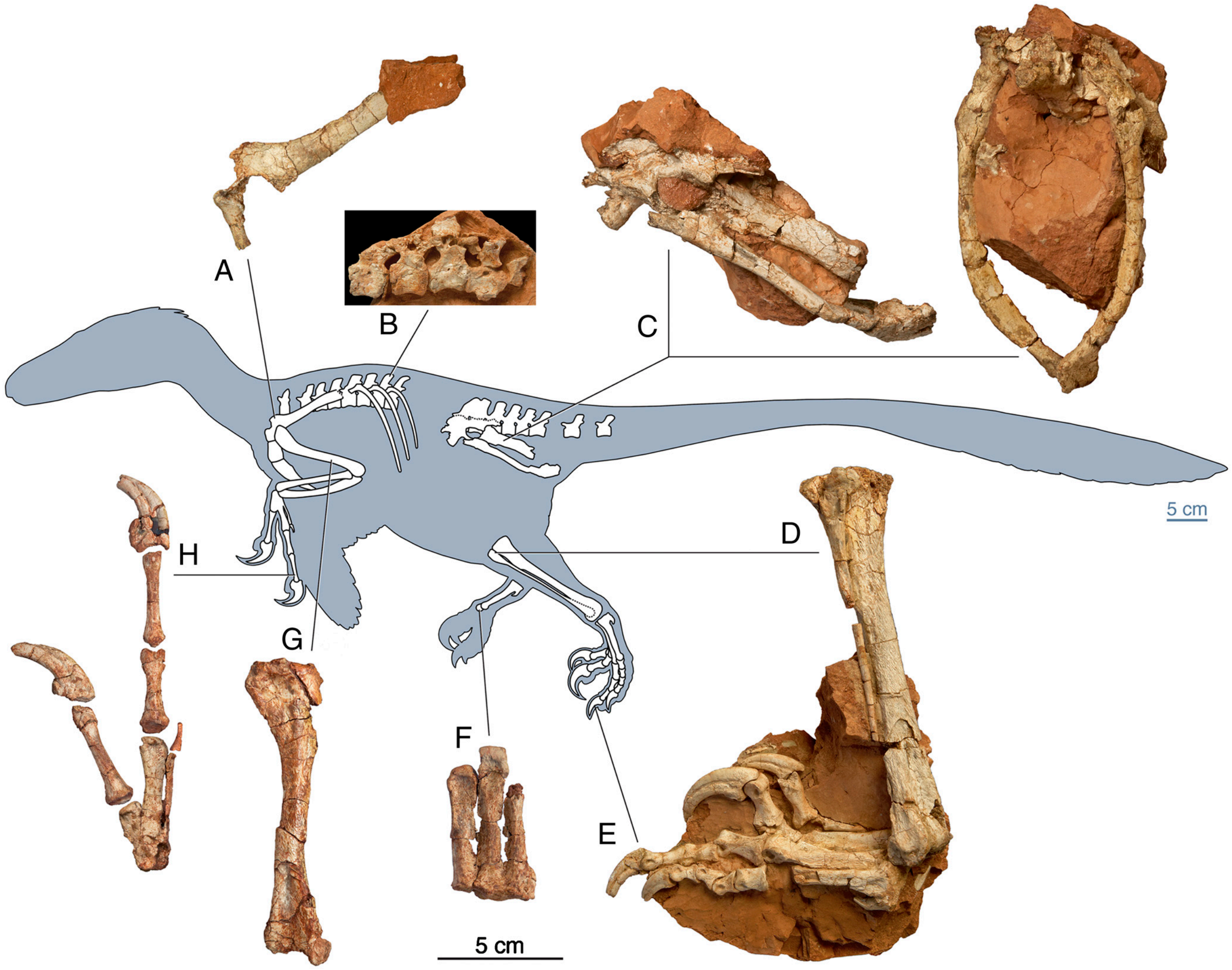

Fig. 1. Skeletal anatomy of *Balaur bondoc*. Reconstruction of the holotype with photos of individual bones. (*A*) Left scapulocoracoid (lateral view). (*B*) Middorsal vertebrae (lateral view). (*C*) Pelvis (left lateral and anterior views). (*D*, *E*) Left hindlimb and pes. (*F*) Right tarsometatarsus (extensor view). (*G*) right humerus (posterior view). (*H*) Right carpometacarpus and manual digits (extensor view). Scale bar at right refers to skeletal reconstruction and at bottom to all bones.

Diagnosis

Dromaeosaurid theropod with the following autapomorphies (asterisk denotes autapomorphies unique among all theropods): hypertrophied coracoid tubercle*; sinuous ridge on lateral surface of distal humerus extends for 1/3 of the length of the bone*; prominent ridge on medial surface of distal half of humerus*; anterior surface of ulna flattened and bisected by longitudinal ridge*; fused carpometacarpus; reduced, splint-like metacarpal III*; mc III contacting mc II distally, buttressed by overhanging ridge on mc II*; distal articular surface not extending onto plantar surfaces of metacarpals I and II; manual ungual II with Y-shaped lateral and medial grooves*; phalanges of manual digit III reduced and digit nonfunctional; extremely retroverted pubes and ischia whose long axes are nearly horizontal*; pubic peduncle laterally everted such that broad cuppedicus fossa faces laterally and dorsally*; pubis reoriented so that lateral surface faces ventrally and pubic tubercle located directly below acetabulum*; ischial obturator tuberosity expressed as enlarged, thin flange that contacts or nearly contacts pubis ventrally*; tarsometatarsus substantially wider (1.5×) than distal tibiotarsus*; fused metatarsus (mt II-V); robust ridges on plantar surfaces of metatarsals II-IV*; metatarsals II and III not ginglymoid; articular region of mts II-III narrower than entire distal end*; first digit of pes functional with enlarged phalanges but vestigial metatarsal I*; and short, hook-like mt V.

Description and Comparisons

The holotype includes no cranial elements but preserves a good representation of the axial and appendicular skeleton. All of the appendicular bones possess an unusual heavily sculptured external surface, which is likely not a diagenetic or a juvenile feature because it is present on all elements of the holotype and the larger referred specimen that was collected at a different site. This texture cannot easily be explained, but is a peculiar feature that is also present on other isolated theropod bones from the Haţeg Basin (see *SI Appendix*). Notably this texture is not present on other vertebrate bones from the same localities.

Dorsal, sacral, and anterior-middle caudal vertebrae are present (Figs. 1 and 2). Pneumatic foramina extend throughout the dorsal column, and broken surfaces reveal extensive internal cavities in the neural arches. The parapophyses of the posterior dorsals project as discrete pedicels and the dorsal neural spines are swollen at their tips, as is characteristic of dromaeosaurids (15, 16). Pneumatic foramina are not present on the sacral and caudal vertebrae.

The ossified sternal plates are separate and the scapula and coracoid are fused, a feature also present in *Velociraptor* (15),

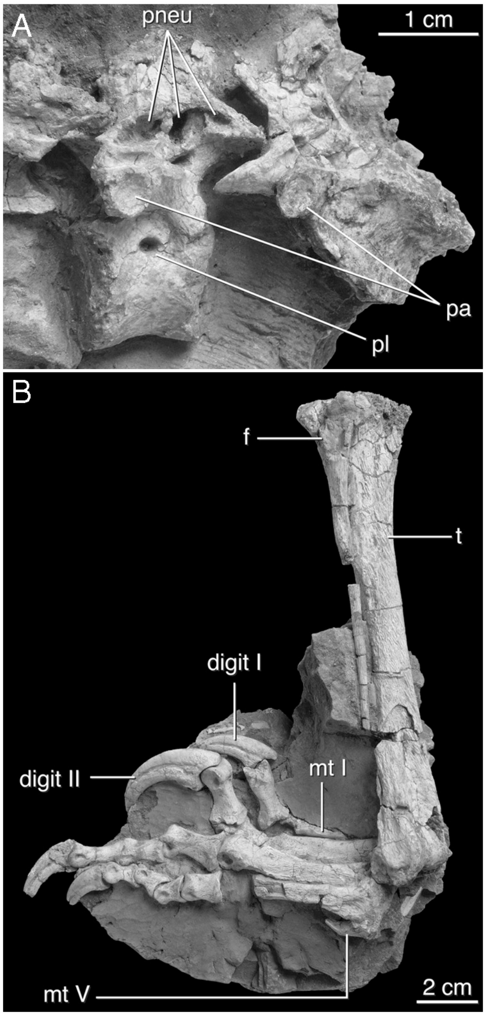

Fig. 2. Unusual skeletal features of *Balaur bondoc*. (*A*) Posterior dorsal vertebrae exhibiting the stalk-like parapophyses characteristic of dromaeosaurids and extensive pneumatic chambers filling the neural arch. (*B*) Left hindlimb, showing the fused tibiotarsus, fused and stout tarsometatarsus, large digit I comprised of enlarged individual phalanges, and hyperextensive capabilities of digits I and II. f, fibula; mt, metatarsal; pa, parapophysis; pl, pneumatic foramina; pneu, pneumatic cavities; t, tibia.

Microraptor (17), and the enigmatic paravian *Pneumatoraptor* from the Santonian of Hungary (18). The coracoid has an extensive ventral process and is inflected medially relative to the scapula, resulting in the “L-shaped” morphology characteristic of paravians (15, 16). The coracoid tubercle is autapomorphically hypertrophied, as it projects anteriorly and laterally as a conical projection that obscures the coracoid foramen in lateral view. The humeral adductor muscles inserting here would have been large. The sigmoidal humerus is marked by a deep groove on the posterior surface distal to the deltopectoral crest, as in *Deinonychus*, *Velociraptor*, and *Linheraptor* (15, 19). Unusually, the radial condyle is located on the anterior surface of the distal humerus, as in therizinosauroids (20) but unique among paravians. The bowed ulna is D-shaped in cross section, due to a flat anterior surface that is bisected by an autapomorphic longitudinal ridge.

The manus is extensively modified relative to other nonavian theropods, especially in the fusion and differential development of the digits (Fig. 1). The carpals and three metacarpals are fused into a “carpometacarpus,” otherwise only present in derived alvarezsauroids, perhaps *Avimimus*, and derived avialians (16, 21). Metacarpals I and II are similar in morphology to those of other dromaeosaurids, although the distal condyles do not extend onto the plantar surface, indicative of more limited manual extension compared to close relatives (22). Digit III is highly autapomorphic and nonfunctional. The metacarpal is a thin splint, only 30% of the mediolateral width of metacarpal II, and contacts metacarpal II both proximally and distally. Phalanx III-1 is reduced to a small nubbin that is much smaller than the phalanges of digits I and II. Other phalanges of digit III are not preserved, but a smoothly convex distal articular surface on phalanx III-1 suggests that additional diminutive phalanges may have been present.

Pelvic bones are fused and the pubis and ischium are so extremely retroverted that they nearly parallel the long axis of the ilium (Fig. 1). In contrast, the pubis in most other paravians, including basal avialans, is oriented at most 45° relative to horizontal (15, 22–24). Extreme retroversion is associated with increased femoral extensor musculature, which attached to a greatly enlarged cuppedicus fossa that extends onto a novel lateral flange on the pubic peduncle. Additionally, the space between the opposing pubes is proportionally wider than in *Velociraptor* and other dromaeosaurids (15, 25), indicative of a more barrel-shaped abdominal and pelvic region. The pubic tubercle is large, faces laterally, and is located directly below the acetabulum, a unique position among dromaeosaurids (and in fact all theropods) that is due to the extreme pubic retroversion. As a result, the tubercle braces the head of the femur ventrally. The lateral surface of the ischium is bisected by a sharp ridge, as in some dromaeosaurids (11), and there is a flange-like obturator tuberosity projecting ventrally, as in *Velociraptor* and *Deinonychus* (25).

The hindlimb exhibits extensive fusion: the tibia and fibula are fused with the proximal tarsals to form a tibiotarsus, the distal tarsals are coossified with the metatarsals, and metatarsals II–V are fused to each other across much of their lengths (Figs. 1 and 2). The latter condition is unique among dromaeosaurids and otherwise seen only in *Avimimus* and derived avialans (16). The stout tarsometatarsus is less than twice as long proximodistally as wide mediolaterally, and is much wider than the tibiotarsus, autapomorphies reflecting a shortened distal leg optimized for strength instead of large stride length (~speed) (26).

The most remarkable feature of the hindlimb is the enlarged and functional first digit, a feature otherwise known only in therizinosauroids and derived avialans among coelurosaurian theropods, which normally have three primary digits (16). Metatarsal I remains a small, wedge-like element that articulates at the midpoint of metatarsal II, as is typical for tridactyl theropods, but the two phalanges of digit I are enlarged, nearly the size of the phalanges of digit II. The second pedal ungual is the largest in the foot and exhibits modifications for extreme extension, as is typical for dromaeosaurids and troodontids (15, 16, 22, 25). However, unlike all other dromaeosaurids, metatarsals II and III are not ginglymoid, and extensor pits are weak on all metatarsals and phalanges, suggesting that extension was limited relative to closely related taxa. Remarkably, digit I is not only large and functional, but also exhibits modifications for hyperextension and its ungual is the second largest in the foot. Digits I and II are articulated and are both preserved in the flexed position that is stereotypical for many deinonychosaur specimens.

Systematics

We added *Balaur bondoc* to the phylogenetic analysis of Turner et al. (16) (see *SI Appendix*), which produced 5,832 most parsimonious trees (length = 880; consistency index = 0.35; retention index = 0.71). The strict consensus of the dromaeosaurid portion of the tree is presented in Fig. 3. *B. bondoc* is recovered as the sister taxon to *Velociraptor*, supported by a fused scapulocoracoid, a cuppedicus fossa rim that is nearly confluent with the acetabular rim, fused distal tarsals, and a muscle attachment flange on metatarsal IV (see *SI Appendix*). This sister taxon

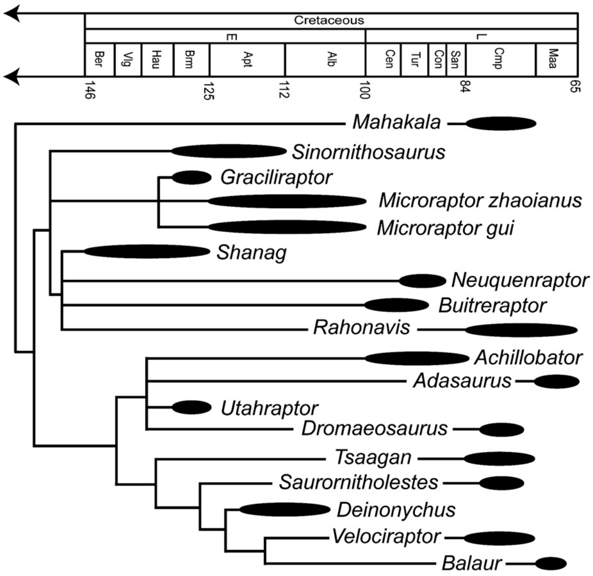

Fig. 3. Phylogenetic relationships and temporal distribution of *Balaur bondoc* and other dromaeosaurids. Strict consensus tree resulting from phylogenetic analysis (5,832 most parsimonious trees of length 880, consistency index = 0.35, retention index = 0.71; see *SI Appendix*), which places *Balaur* as a derived dromaeosaurid closely related to Asian and North American taxa of contemporary or slightly older age. Thick bars represent the finest age resolution for each taxon, not actual duration.

pair is nested within the velociraptorine dromaeosaurids, a clade that also includes *Deinonychus*, *Tsaagan*, and *Saurornitholestes*. This clade, in turn, is deeply nested within Dromaeosauridae, whose internal relationships are well resolved and like those reported in recent studies (16, 27, 28).

Discussion

As the first reasonably complete and well-preserved theropod from the Late Cretaceous of Europe, *Balaur bondoc* is a critical taxon that gives considerable insight into the evolution of dinosaurian predators on the classic European paleoislands. In particular, the discovery helps clarify the biogeographic relationships of Late Cretaceous European dinosaurs, helps illuminate the composition and assembly of the unusual Romanian island faunas, and provides dramatic evidence that dinosaurian predators were probably also subject to the island effect, albeit in different ways than contemporary herbivorous dinosaurs and smaller vertebrates.

It has long been held that the Haţeg Island, and Late Cretaceous Europe in general, supported endemic faunas that arose through lengthy in situ diversification of Late Jurassic—earliest Cretaceous lineages that were stranded in Europe as sea levels rose (5, 9, 18). This hypothesis was supported by the primitive phylogenetic position of many herbivorous dinosaurs, other reptiles, and mammals, which form clades restricted to Late Cretaceous Europe and whose closest non-European relatives are much older taxa (2, 5, 9, 18). However, the closest relatives of *Balaur* are primarily Asian and North American taxa of similar or slightly older age, whereas contemporary (or near nearly so) South American species, and older Laurasian taxa, are placed elsewhere on the phylogeny (Fig. 3). This indicates that faunal interchange between the European archipelago and Asia persisted deep into the Cretaceous, an emerging view supported by recent discoveries of hadrosaurian and ceratopsian dinosaurs (29–33). Thus, the Haţeg Island (and probably the European archipelago, in general) was not solely an endemic refugium for primitive taxa, but its fauna was also shaped by dynamic interchange with the Laurasian mainland.

Although it shares characters with *Velociraptor* and is of the same approximate body size as most other velociraptorine dromaeosaurids, *Balaur* departs markedly from its close relatives in overall morphology and exhibits a previously unknown body plan among derived theropods. The hand is fused, atrophied, and poorly suited for grasping. Unusually, pedal digit I is large and functional, a unique feature among otherwise primarily tridactyl nonavian maniraptorans. In *Balaur*, pedal digit I is highly modified to mimic both the size and hyperextensive capabilities of digit II, resulting in a double set of raptorial claws, perhaps used to disembowel or grasp prey (34). The extra functional digit is associated with numerous modifications of the pelvis and hindlimb, including extensive fusion, a braced articulation between the femur and pelvis, enlarged femoral extensor musculature, and a reinforced and shortened distal hindlimb. Together, these features indicate an animal with hindlimbs optimized for strength and power, with a tetradactyl and hypextensive foot capable of forceful strikes (26).

This novel body plan is a dramatic example of aberrant morphology developed in island-dwelling taxa (1, 2), which is well documented in recently extinct mammals and often develops extremely rapidly, over geologically instantaneous timescales (35–38). Attributing a causal relationship between an island habitat and the unusual morphology of inhabitant taxa is difficult (1, 2). However, given the fact that Late Cretaceous Romania was clearly an island, numerous contemporaries of *Balaur* exhibit dwarfing and other morphological modifications seen in recent island-dwelling taxa (4–8), and the extreme anatomical differences between *Balaur* and its closest relatives, we hypothesize that the aberrant nature of the dromaeosaurid is likely due to the island effect. As such, this is a unique record of an island effect in a nonavian theropod.

More generally, *Balaur* is one of the best examples of an aberrant island-dwelling predator, either extinct or extant. Although the island effect is relatively well documented in numerous herbivores (1, 2), its effect on predators is far from generally accepted (39, 40). Indeed, most island-dwelling mammalian carnivores are morphologically similar to their close relatives and mainland counterparts (41, 42), and differences between the two are often limited to body size (43). The autapomorphic morphology documented in *Balaur* is reminiscent of the highly modified morphology of island herbivores, as well recognized in various mammals (37, 38, 44–47), and represents perhaps the first quality record of an island predator with peculiar anatomical modifications.

Conclusions

In sum, the discovery of *Balaur* enables an updated, and more nuanced, picture of one of the most unusual Mesozoic terrestrial faunas. As a quality record of a Late Cretaceous European theropod, *Balaur* shows that some island-dwelling predatory dinosaurs were aberrant, but in this case not dwarfed or primitive. The highly autapomorphic morphology of *Balaur* is indicative of an endemic taxon, but only in the sense that it is strikingly modified relative to other dromaeosaurids, and not that it is a relictual species stranded in Europe after tens of millions of years of isolation. Endemism of the Late Cretaceous island faunas, therefore, was a result of both extreme morphological transformation and the survival of primitive, ancient lineages.

Materials and Methods

To specify the phylogenetic relationships of *Balaur bondoc*, we added it to the data matrix of Turner et al. (16). The data matrix includes 251 characters scored in 70 ingroup taxa, including 18 dromaeosaurids, and two outgroups (see *SI Appendix*). The matrix was run in TNT; first it was subjected to a "new technology" search, and then all resulting most parsimonious trees were further subjected to a heuristic search using tree bisection and reconnection branch swapping. For further details, see *SI Appendix*.

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