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Dinevenator, a New Genus of Troodontid Dinosaur from the Late Cretaceous of New Mexico

Steven E. Jasinski [1,2,*] and Robert M. Sullivan [1]

[1] New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, NM 87104, USA
[2] Department of Environmental Science and Sustainability, Harrisburg University, 326 Market Street, Harrisburg, PA 17101, USA
* Correspondence: sejasinski@gmail.com

Abstract

An isolated left frontal from the Upper Cretaceous (upper Campanian) strata of the San Juan Basin in northwestern New Mexico, USA, was originally identified as a species of the dromaeosaurid (Theropoda: Dromaeosauridae) *Saurornitholestes* ("*S.*" *robustus*) and was subsequently identified as a troodontid (Troodontidae). A reassessment of this holotype specimen shows its distinct nature among troodontids and is here named *Dinevenator*, gen. nov. *Dinevenator robustus* differs from other troodontids, including the thick-skulled species *Xenovenator espinosai* from the upper Campanian Cerro del Pueblo Formation, Coahuila, Mexico. These differences include: dorsoventrally thick and robust frontals; frontals thicker posteriorly; relatively flat frontals, lacking a well-developed parasagittal trough and sagittal ridge; a posteromedial nasal projection between the frontals that is wider than long; a more laterally oriented posterior portion of the lateral endocranial wall; and a mediolaterally wider anteromedial portion of the frontal that houses the orbital fossa. A phylogenetic analysis was also run based on a modified dataset, recovering *Dinevenator robustus* in a clade of robust troodontins (Troodontini) as the basal-most taxon and as the sister taxon to (*Albertavenator curriei* + *Xenovenator espinosai*). The recognition of a distinct, large, robust-skulled troodontid also increases the known diversity of theropod dinosaurs from the southern United States and provides further evidence for dinosaurs that are unique to the Kirtlandian faunas of New Mexico during the Late Cretaceous.

Keywords: Troodontidae; Cretaceous; Campanian; Kirtlandian; New Mexico; Maniraptora; Theropoda; Dinosauria; Laramidia; evolution

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1. Introduction

Sullivan [1] reported on an isolated left frontal (SMP VP-1955) from the De-na-zin Member of the Kirtland Formation, San Juan Basin, New Mexico, USA. He made this the holotype of a new species (*Saurornitholestes robustus*) in the belief that it represented a robust species of the dromaeosaurid *Saurornitholestes*. Turner et al. [2], while reviewing Dromaeosauridae, determined that SMP VP-1955 did not have synapomorphies of the family and considered it a nomen dubium. Subsequently, Evans et al. [3] reidentified this taxon as belonging to Troodontidae but still considered it to be a nomen dubium. A recent paper by Rivera-Sylva et al. [4] reevaluated this specimen and concluded the species was valid and not a nomen dubium. Moreover, they demonstrated it was closely related to the new troodontid *Xenovenator espinosai*, from the Cerro Del Pueblo Formation, Coahuila,

Mexico, based, in part, on having relatively thick frontals, and questionably referred it to the genus *Xenovenator*, as *Xenovenator*(?) *robustus*. Here we redescribe and reevaluate this species and place it in *Dinevenator* gen. nov., distinguishing it from *Xenovenator* and other troodontids, particularly North American taxa.

Institutional abbreviations—CPC, Colección Paleontológica de Coahuila, Museo del Desierto, Saltillo, Coahuila, Mexico; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; SMP, State Museum of Pennsylvania, Harrisburg, Pennsylvania, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Alberta, Canada; UMNH, Natural History Museum of Utah (formerly Utah Museum of Natural History), Salt Lake City, Utah, USA.

2. Materials and Methods

Within the current study, we follow the terminology of Evans et al. [5], except where noted. Regarding anatomical directions, we utilize anterior and posterior, rather than cranial or rostral and caudal, respectively.

A phylogenetic analysis was conducted on *Dinevenator robustus* to determine its phylogenetic relationships. The analysis was run on a modified dataset from Rivera-Sylva et al. [4]. No new characters or taxa were added, so the analysis was still run on 118 characters and 32 operational taxonomic units (OTUs). However, scores were reviewed, and several were changed, including those of *Albertavenator curriei* and *Dinevenator robustus*. For *A. curriei*, changes were made to character 2 → changed to state 2, and character 13 → 1. For *D. robustus*, changes were made to character 5 → state 1; character 7 → 0; character 10 → 0; character 11 → 0; and character 14 → 0. Analyses were run in the program Tree Analysis Using New Technology (TNT version 1.5; see [6,7]). The dataset was subjected to a traditional search using Wagner trees with a random seed of 10 and 9999 replicates (number of additional sequences) (with default parameters for the swapping algorithm of tree bisection-reconnection [TBR] of 10 trees to save per replication). The matrix was subjected to 9999 replicates of random addition sequences, with minimum branch lengths set to collapse. Tree statistics reported here include the consistency index (CI) and retention index (RI). The full data matrix, with the updated scores, is available in the Supplementary Material for this article.

Nomenclatural Act

This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix 'http://zoobank.org/'. The LSID for this publication is urn:lsid:zoobank.org:pub:50CD3906-D122-41E2-9CA3-220C86A581B2.

3. Geological Setting

SMP VP-1955, the holotype of *Dinevenator robustus* (Sullivan), was collected from the De-na-zin Member of the Kirtland Formation, in the San Juan Basin of northwestern New Mexico, USA. The De-na-zin Member is lithologically distinct from the underlying upper Campanian Hunter Wash and Farmington members of the Kirtland Formation and the disconformable overlying upper Maastrichtian Naashoibito Member of the Ojo Alamo Formation (Figure 1). *Dinevenator robustus* [1] is part of the Willow Wash local fauna of Williamson and Sullivan [8] and Sullivan and Lucas [9,10], which is latest Kirtlandian age.

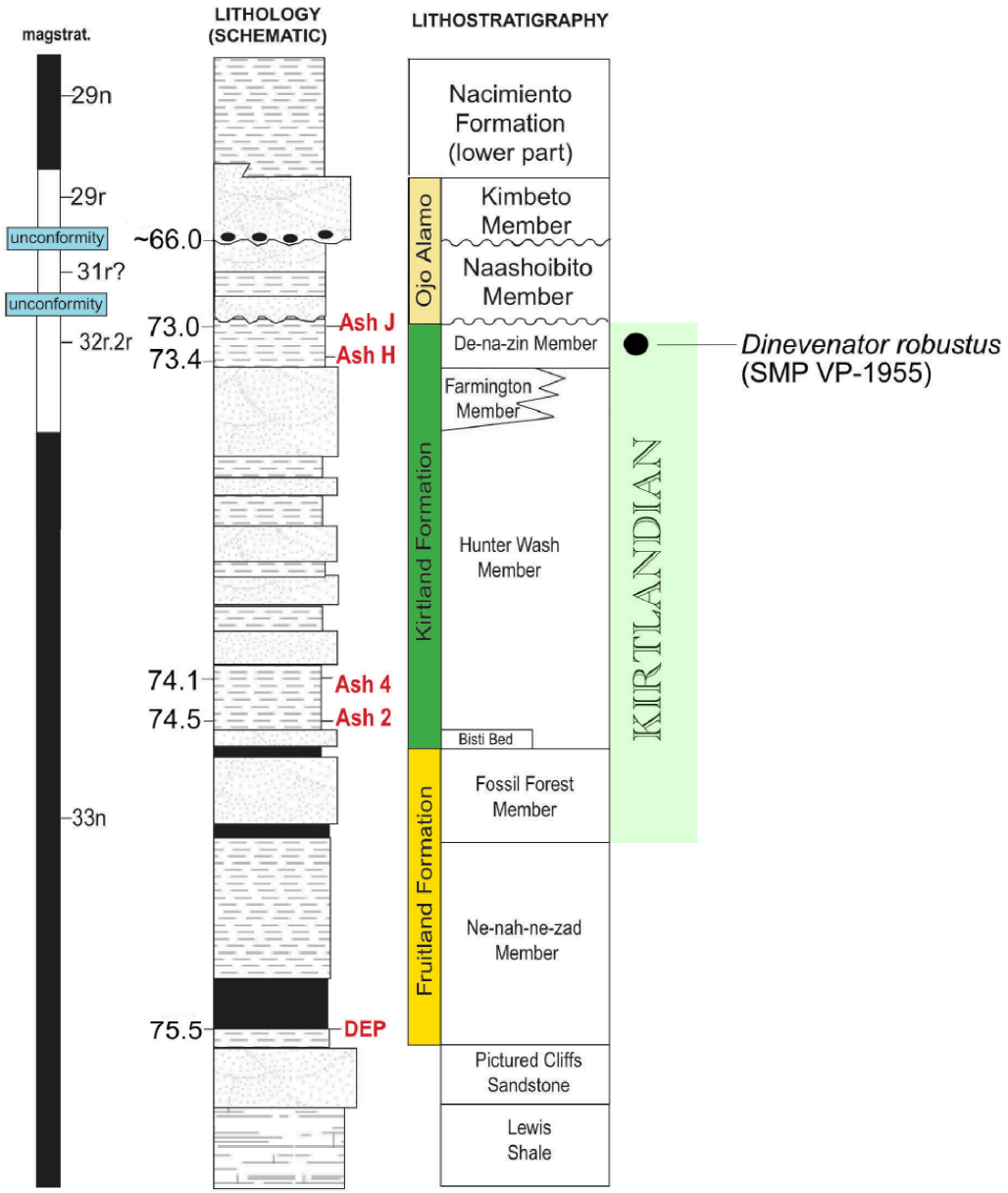

Figure 1. Generalized stratigraphic section showing where the holotype (SMP VP-1955) of *Dinevenator robustus* (Sullivan, 2006) [1] was recovered. Stratigraphic section modified from Jasinski and Sullivan [11]: (figure 5). Abbreviations: magstrat., magnetostratigraphy; n, normal; r, reversed.

4. Results

4.1. Systematic Paleontology

Dinosauria—Owen, 1842 [12]
Saurischia—Seeley, 1888 [13]
Theropoda—Marsh, 1881 [14]
Troodontidae—Gilmore, 1924 [15]
Troodontinae—van der Reest and Currie, 2017 [16]
Troodontini—Rivera-Sylva et al., 2026 [4]
Dinevenator—gen. nov.
ZooBank urn:lsid:zoobank.org:act:2764BDD0-4580-4635-9C86-ED0B08668A4D.

Etymology. The genus name is derived from the Navajo word *Diné*, in reference to the people of the Navajo Nation, and from the Latin root *venat*, meaning hunt; here referring to the Latin word *venator*, meaning hunter.

Type species. *Saurornitholestes robustus* Sullivan, 2006 [1]; San Juan Basin, New Mexico, USA, late Campanian: Kirtlandian land-vertebrate age (LVA), Late Cretaceous.

Diagnosis. Same as for species.

Horizon/Age. De-na-zin Member, Kirtland Formation; upper Campanian (Kirtlandian LVA), ~73.4–73.0 Ma.

Comments. Previously considered a species of the dromaeosaurid *Saurornitholestes* (Dromaeosauridae) by Sullivan [1].

Revised description. See below.

Dinevenator robustus (Sullivan, 2006 [1]).

Saurornitholestes robustus Sullivan, 2006 [1]: (p. 253, figure 1).
Saurornitholestes robustus Sullivan, 2006 [1]; Evans et al., 2014 [3]: (p. 730, figure 1E–H).
"Saurornitholestes" robustus nomen dubium, Sullivan, 2006 [1]; Evans et al., 2014 [3]: (p. 731).
Xenovenator(?) *robustus* (Sullivan, 2006 [1]); Rivera-Sylva et al., 2026 [4]: (p. 15).
X. [*enovenator*] *robustus* (Sullivan, 2006 [1]); Rivera-Sylva et al., 2026 [4]: (pp. 16, 18).

NEW SYNONYMY

Figures 2 and 3.

Holotype. SMP VP-1955, nearly complete left frontal.

Revised diagnosis. A member of Troodontidae based on a shallow lateral wall defining the fossae for the olfactory system, the exclusion of the supratemporal fossa from the dorsal surface of the frontal, and a raised orbital rim (as discussed by Evans et al. [3]). Distinguished by the following suite of characters (* = autapomorphy): (1) dorsoventrally thick frontals; (2) frontals thicker posteriorly versus anteriorly *; (3) nearly flat frontals, lacking a well-developed parasagittal trough and sagittal ridge, consequently the dorsolateral surface for the orbital rim is robust but only slightly raised; (4) posteromedial nasal projection between the frontals that is wider than long *; (5) no overlap of the nasal onto the frontal anteromedially; (6) more laterally oriented posterior portion of the lateral endocranial wall of the frontal; (7) mediolaterally wider anteromedial portion of the frontal that houses the orbital fossa (olfactory bulb impression) when viewed ventrally (shared with *Xenovenator espinosai*); and (8) lacks transverse ventral ridge separating the cerebral and olfactory fossae (as noted by Rivera-Sylva et al. [4]: p. 26).

4.2. Description

SMP VP-1955 (holotype) is a nearly complete left frontal (Figure 2). The dorsal surface of the specimen is slightly weathered. The postorbital process in the posterolateral portion of the frontal is broken and missing. Due to the breakage, the posterior portion of the lateral endocranial wall in the region of the cerebral fossa (cerebral hemisphere surface) is also missing. There is also slight breakage anterolateral to the orbital rim, although this is not extensive, and little is likely missing.

The frontal has a maximum anteroposterior length of 62 mm. The maximum preserved mediolateral width, measured posteriorly at the level of the postorbital process, is 30.7 mm.

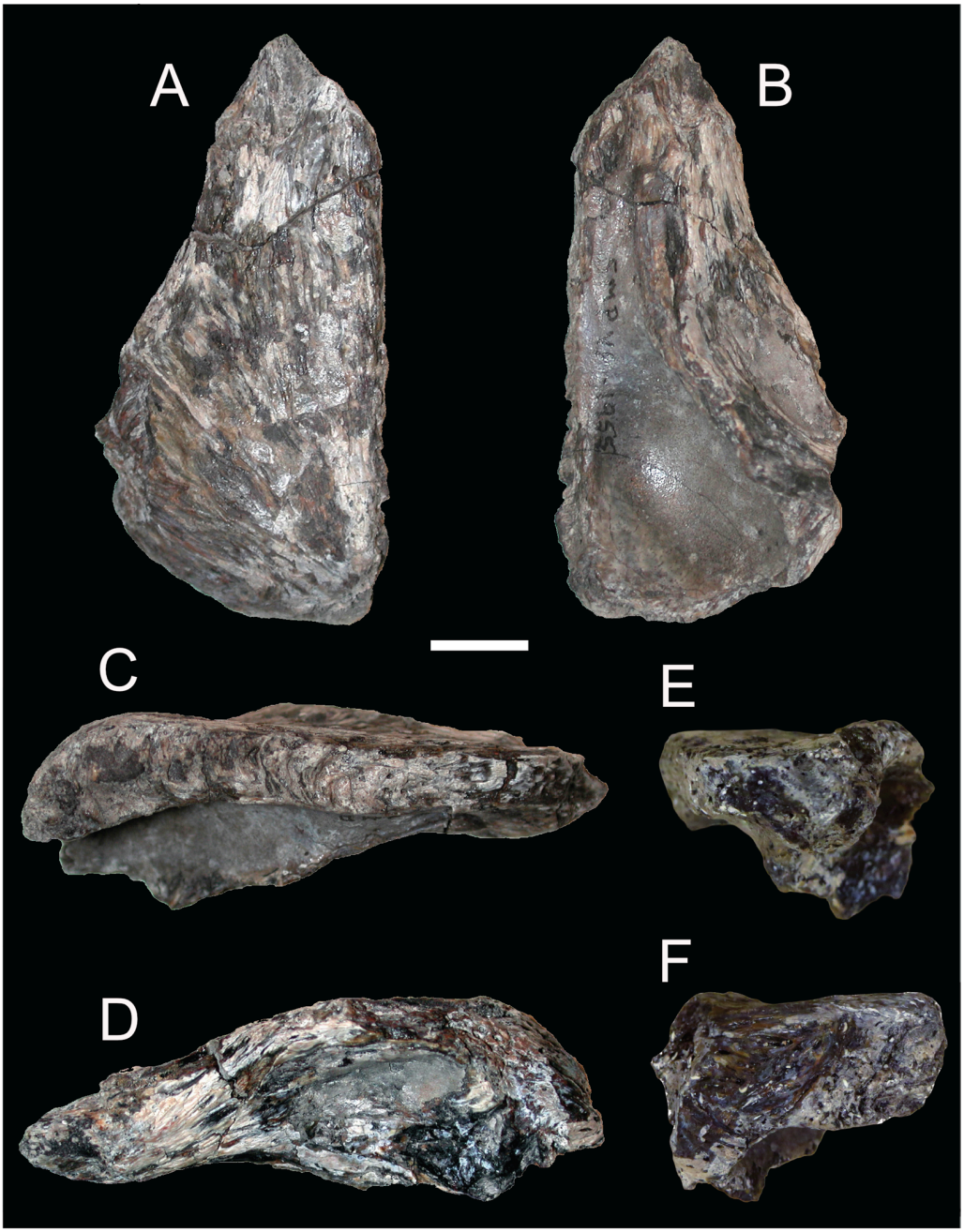

Figure 2. *Dinevenator robustus* (Sullivan, 2006) [1], SMP VP-1955 (holotype), left frontal. (**A**) Dorsal view; (**B**) ventral view; (**C**) medial view; (**D**) lateral view; (**E**) anterior view; and (**F**) posterior view. See Figure 3 for landmark features. Bar scale equals 1 cm.

The dorsal surface is well preserved, with only slight weathering that does not cause changes to the resulting preserved morphology nor result in features that would not be present in the original bone. Dorsally, the frontal is mostly flat, with the anterior portion slightly lower than the posterior portion. There is a slight, inconspicuous depression, or parasagittal trough, between the sagittal suture (interfrontal suture of Evans et al. [5], van der Reest and Currie [16], Cullen et al. [17]), Varrichio et al. [18], and Rivera-Sylva et al. [4], among others) and the orbital rim (Figure 3C). This differs from the distinct depression or trough seen in *Troodon formosus*/*Stenonychosaurus inequalis*/*Latenivenatrix mcmasterae* [16–18], which results in a prominent sagittal ridge concomitant with the sagittal suture in these taxa. While the mediodorsal surface is flat, the lateral edge, corresponding with the dorsal orbital rim, is slightly raised. The nasal facet, where the nasal contacts the

frontal, is oval and situated anterolaterally (Figures 2A and 3A). The anteromedial edge of the frontal is angled anterolaterally-posteromedially, suggesting the medial projection of both nasals (posteromedial process of the nasals) extends between the anterior ends of the frontals (see Figure 4). Anterolaterally, there is a small facet for the lacrimal-frontal contact (Figures 2A and 3A), which results in a sharply angled L-shape posterolaterally, a feature shared with *Xenovenator espinosai* [4]. Posteriorly, there is no distinct supratemporal ridge as the posterior portion gently angles ventrally, making up the anterior wall of the supratemporal fenestra. This morphology suggests the supratemporal fossae may have been slightly larger in diameter than in other North American troodontids (Figures 2A and 3A), but would have also had a gentler curvature to the anterior border of the fenestra, blending into the dorsal flattened portion of the frontal. This generally conforms with the strong anterior displacement of the supratemporal fossae and postorbital processes as described by Rivera-Sylva et al. [4], albeit likely not to the same extent mentioned in their study. There is no interfrontal (anterior) process of the parietals.

The ventral side of SMP VP-1955 is better preserved than the dorsal side. The ventral surface is largely made up of the lateral endocranial wall and the cerebral fossa (Figures 2B and 3B). The lateral endocranial wall, a prominent feature of the ventral side of the frontal, makes up the dorsal and dorsomedial portion of the orbit and is robust. It is semi-circular, with the anterior portion directed anteroposteriorly (sagittally), while the posterior portion is curved posterolaterally. There is a distinct and deep depression posteriorly on this wall, here referred to as the orbital roof depression. The cerebral fossa is large, deep, and sub-oval. The olfactory fossa (olfactory bulb impression) is incipient and oval, located anteromedially. The olfactory tract between these two features is relatively mediolaterally thin, but only slightly thinner than the olfactory fossa portion anterior to it. The olfactory tract is also thicker as a gentle convexity compared to the concavities for the cerebral and olfactory fossae. Similar to the dorsal surface, the nasal facet is oval and positioned anteriorly, with the lacrimal buttress immediately lateral to it; both are unbroken surfaces. As noted by Rivera-Sylva et al. [4], there is no transverse ridge separating the cerebral and olfactory fossae.

Medially, the most significant feature is the depth of the sagittal suture, sometimes called the interfrontal, frontal-frontal, or midline suture (Figures 2C and 3C). It is robust and thick, being twice as thick posteriorly (10 mm) as anteriorly (5 mm). The raised orbital rim can be seen in the medial view, particularly as the medial portion of the dorsal surface is flat. The surface of the sagittal suture is largely made up of curved ridges, with the rounded portions directed posteriorly. Viewed medially, the posteroventral portion of the lateral endocranial wall is incomplete. The posterior angle, making up part of the supratemporal fossa, is also present in medial view, although the thickened and robust posteromedial portions of the frontal give this region of the frontal a slightly bulbous appearance.

Laterally, SMP VP-1955 has a slightly raised orbital rim and lateral endocranial wall (Figures 2D and 3D). The orbital roof depression is clearly visible posterolaterally on the lateral endocranial (or orbital) wall. A small portion of the raised orbital rim is broken posteriorly, but the remaining portion of the rim is complete (see Figure 3A). The orbital rim is robust, and its dorsal rise is prominent in lateral view. The frontal becomes slightly thinner anteriorly but remains robust. The posteroventral break of the lateral endocranial wall is also evident. The posterior portion is gently rounded, making up part of the anterior border of the supratemporal fossa.

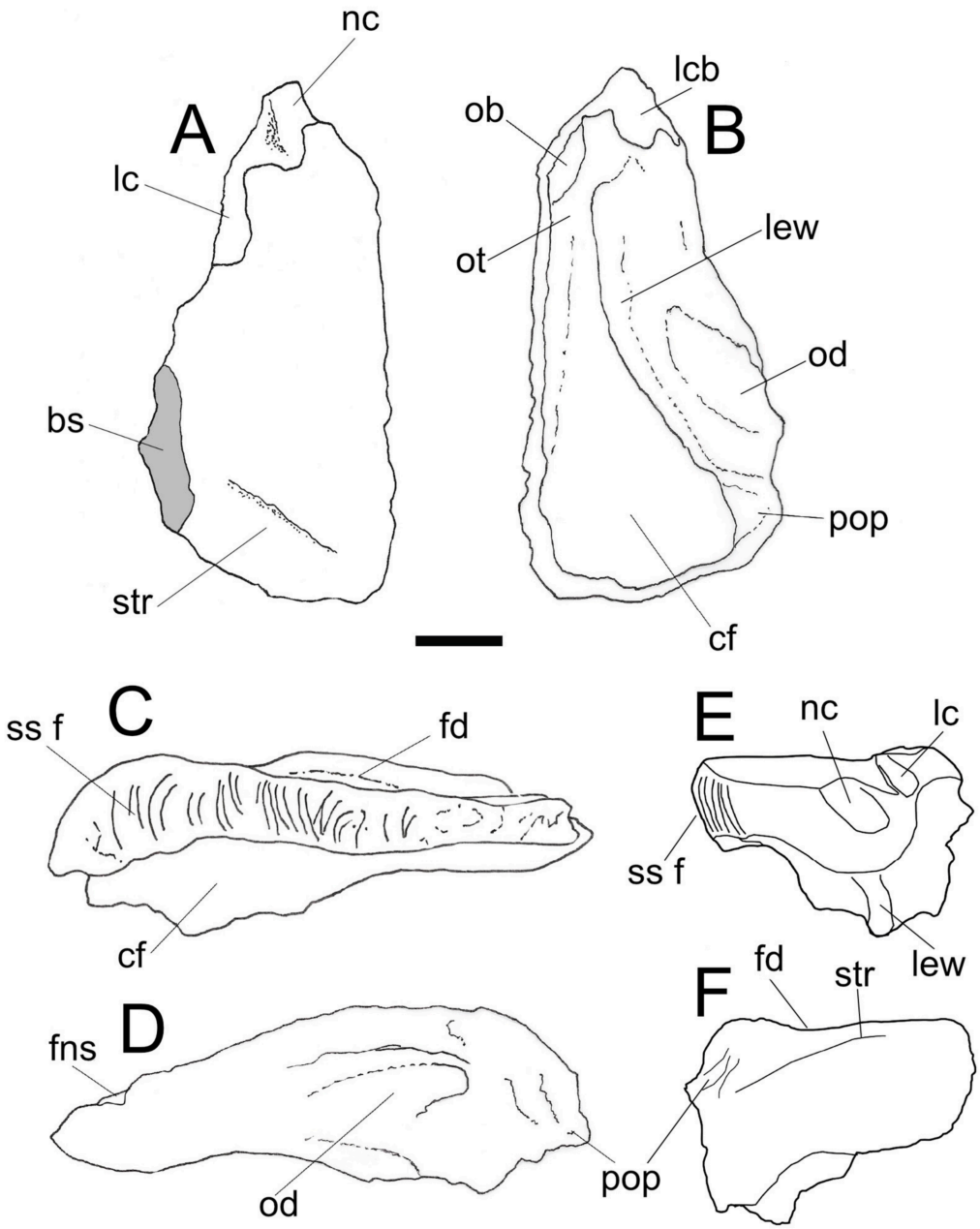

Figure 3. *Dinevenator robustus* (Sullivan, 2006) [1], SMP VP-1955 (holotype), left frontal, line drawing. (**A**) Dorsal view; (**B**) ventral view; (**C**) medial view; (**D**) lateral view; (**E**) anterior view; and (**F**) posterior view. Abbreviations: bs, broken surface; cf, cerebral fossa; fd, frontal depression; fns, frontonasal suture; lc, lacrimal contact; lcb, lacrimal buttress; lew, lateral endocranial wall; nc, nasal contact; ob, olfactory bulb impression (olfactory fossa); od, orbital roof depression; ot, olfactory tract; pop, postorbital process; ss f, frontal sutural surface; str, supratemporal ridge. Bar scale equals 1 cm.

Anteriorly, the dorsolateral portion of the frontal that corresponds with the nasal facet is angled anteroventrally. The ventrolateral portion that corresponds with the lacrimal buttress is less well preserved, but clearly preserves this contact surface. Anteromedially, the frontal is flat, with remnants of sutures where the nasal would have projected posteromedially between the frontals.

Posteriorly, the thickened posteromedial portion of the frontal contacts the parietal, suggesting a thickened parietal as well. While the postorbital process is incomplete in SMP VP-1955, the preserved portions suggest the frontal becomes thinner in this region. The smaller portion of the frontal that makes up the anterior edge of the supratemporal fossa is

also more clearly visible in this view. There is a small indentation on the posterior edge of the specimen (Figures 2B and 3B), but this is due to breakage.

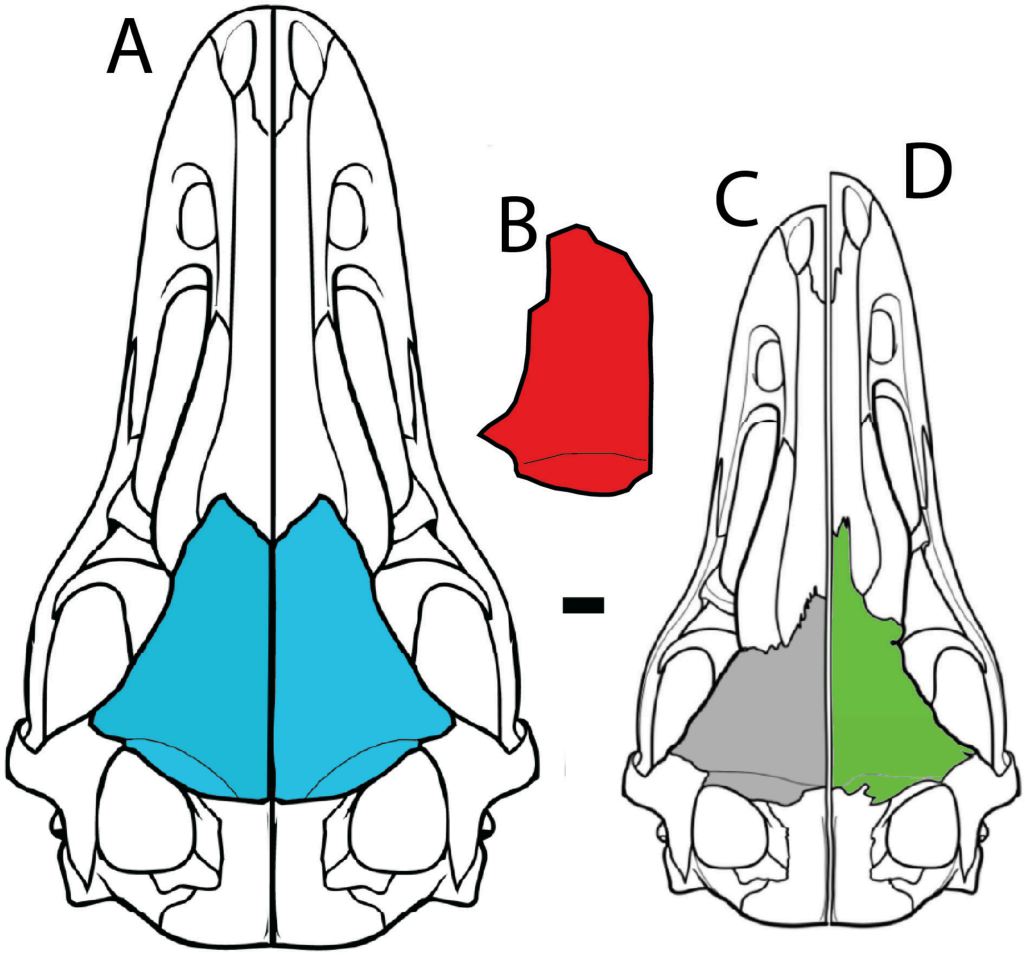

Figure 4. Dorsal reconstruction of the skull of (**A**) *Dinevenator robustus* (Sullivan, 2006 [1]; [SMP VP-1955]) highlighting the frontal shape relative to that of (**B**) *Xenovenator espinosai* (CPC 2976), (**C**) *Albertavenator curriei* (TMP 1993.105.0001), and (**D**) *Stenonychosaurus ("Troodon") inequalis* (TMP 1993.036.0086 and TMP 1986.049.0010). Note: frontals highlighted in (**A**) blue, (**B**) red, (**C**) grey, and (**D**) green). Figure (**A**,**C**,**D**) modified from Evans et al. [5]: (figure 4). Bar scale equals 1 cm.

4.3. Remarks and Comparisons

Dinevenator robustus (SMP VP-1955), a large, robust troodontid, is morphologically most similar to *Albertavenator curriei* and *Xenovenator espinosai*. Therefore, we focus our comparisons on those two taxa, rather than the more gracile forms, like *Troodon formosus*, a taxon that may be the senior synonym of *Stenonychosaurus inequalis* (contra '*inaequalis*' usage by Osmólska [19]; Rivera-Sylva et al. [4]) according to Varricchio et al. [18], and *Latenivenatrix mcmasterae*, which may be conspecific with *S. inequalis* [17], and hence, *Troodon formosus* (see Varricchio et al. [18], for full discussion; see also Fan et al. [20]).

Dinevenator robustus (SMP VP-1955) is a large troodontid based on the size of the frontal (see Figure 4). At 62 mm long, it is larger than *A. curriei* and comparable to some of the larger individuals of *S. inequalis* (UALVP 52611) as noted by Cullen et al. [17] and Varricchio et al. [18], and the unnamed Kaiparowits troodontid (UMNH VP16303) as figured by Zanno et al. [21]: (figure 22.11).

Aguillón-Martinez and Rivera-Sylva [22] described a braincase that was more recently named *Xenovenator espinosai*, a new 'thick-skulled' troodontid from the late Campanian

Cerro del Pueblo Formation of Coahuila, Mexico [4]. In their new description, Rivera-Sylva et al. [4] described several similarities and differences with *Dinevenator robustus*. Similarities included: 'an L-shaped frontal–lacrimal contact, thickening of the frontals, and strong anterior displacement of the supratemporal fossae and postorbital processes' [4]: (p. 15). We agree with the former two similarities. The supposed strong anterior displacement of the supratemporal fossae and postorbital processes is not as apparent, particularly compared with the placement of these features in several other troodontid taxa (e.g., *Albertavenator curriei*, *Latenivenatrix mcmasterae*, *Stenonychosaurus inequalis*, *Troodon formosus*), e.g., [5,16–18]. These troodontids have a distinct ridge, sometimes called the supratemporal ridge on the frontal: While *D. robustus* and *X. espinosai* have a gentle curvature to this border of the supratemporal fossa, this does suggest the 'supratemporal ridge,' while gently curved, is slightly anteriorly located on the frontal, but not to a significant degree, and not to the same degree as in *Xenovenator espinosai*. We note here that Rivera-Sylva et al. [4] significantly used the referred frontal (CPC 2976) for comparing *D. robustus* and *X. espinosai*.

Most troodontids have a small posteromedial projection of the nasals between the anterior end of the frontals, including *Latenivenatrix mcmasterae*, *Stenonychosaurus inequalis*, *Troodon formosus*, and the unnamed Kaiparowits troodontid, e.g., [5,16–18,21,23]. *Albertavenator curriei* and *Xenovenator espinosai* also have a small interfrontal projection of the nasals, e.g., [4,5], although they are slightly more conspicuous than the gracile forms, particularly *X. espinosai*. Distinct from these is the pronounced, wide posteromedial projection of the nasals between the frontals in *Dinevenator robustus*, particularly between the two anterior-most projections of the frontals (Figure 4). The posterior nasal projection has a maximum length of 13 mm and maximum width between the anterior-most frontal projections of 21 mm.

Posteriorly, some troodontids have an interfrontal (anterior) process of the parietal that splits the posteromedial edges of the frontals. This is present in *Albertavenator curriei* [5] and *Xenovenator espinosai* [4]. It is also present in *Troodon formosus*, *Stenonychosaurus inequalis*, and *Latenivenatrix mcmasterae*, and the unnamed Kaiparowits troodontid, although it tends to be anteroposteriorly short but wide in these more gracile forms; see [16–18,21]. *Dinevenator robustus* lacks an interfrontal (anterior) process of the parietal. However, there may be interspecific variation in this feature [5]. As mentioned above, there is slight breakage posteriorly on the frontal of *D. robustus* (SMP VP-1955); however, this occurs posterolaterally where there is a slight indentation near where the supratemporal fossa would be. This is likely due to the thin nature of the bone in this region, but would not affect the lack of an interfrontal (anterior) process of the parietal in *Dinevenator robustus*.

As noted by Evans et al. [3], the raised orbital rim is a common feature among troodontids. A domed, or what is probably more properly considered a convex, dorsal surface of the frontal is present in *Xenovenator espinosai*, unlike the parasagittal trough/depression and prominent sagittal ridge seen in other North American troodontids (e.g., *Albertavenator curriei*, *Latenivenatrix mcmasterae*, *Stenonychosaurus inequalis*, *Troodon formosus*). This parasagittal depression is less prominent in *Dinevenator robustus*; consequently, the orbital rim is less pronounced and there is no sagittal ridge (Figures 2A and 3A).

While *D. robustus* has a sub-oval nasal facet on the frontal, other North American troodontids tend to have a sub-triangular nasal facet that is sharply pointed posteriorly. As mentioned by Rivera-Sylva et al. [4], the L-shaped lacrimal facet is only shared with *X. espinosai*. The lacrimal buttress on the ventral surface in *Dinevenator robustus* is positioned anteriorly, particularly compared to other North American troodontids (e.g., *A. curriei*, *L. mcmasterae*, *S. inequalis*, *T. formosus*, unnamed Kaiparowits troodontid), where it lies more laterally and posteriorly. The lack of a sharper supratemporal ridge on the frontal, resulting in a gentle curve on the posterior portion of the frontal, appears to be shared among the

robust North American troodontids, with *D. robustus* the least conspicuous among the three species (i.e., compared to *A. curriei* and *X. espinosai*).

The semi-circular lateral endocranial wall (see Figures 2 and 3) is sagittally oriented anteriorly before the posterior portion flares out, angling posterolaterally in SMP VP-1955. The midlength portion of the wall pinches more in other troodontids, leading to a more constricted and mediolaterally thinner olfactory tract. The lateral endocranial wall is also more laterally situated in *D. robustus* (Figures 2B and 3B) than other North American troodontids, although it is more similar to *X. espinosai* and *A. curriei* (i.e., other robust North American troodontids) than other species. In particular, *S. inequalis* and *L. mcmasterae* have the wall situated more medially, especially where it curves closest to the midline between the olfactory and cerebral fossae, resulting in a much thinner olfactory tract. This more lateral placement of the wall in *D. robustus* results in a wider area for the olfactory and cerebral fossae. The olfactory fossa is less concave than in other troodontids, but the more lateral position of the lateral endocranial wall likely means it was still wider than in other troodontids. The external depression on the posterior portion of the lateral endocranial wall (Figures 2B,D and 3B,D) is also present in *T. formosus*, *S. inequalis*, and possibly *L. mcmasterae*, but is inconspicuous or absent in *A. curriei* and *X. espinosai*. *Dinevenator robustus* lacks a transverse ventral ridge between the olfactory and cerebral fossae, further distinguishing it from *X. espinosai* [4], including the referred specimen CPC 2976. The holotype (CPC 2973) does not clearly show this feature [4,22], but that may be due to the articulated nature of the specimen. The gentler convexity present between these two fossae in *D. robustus* is more like the condition in other North American troodontids.

The deep sagittal suture of the frontal in *D. robustus* (Figures 2C and 3C) is like *A. curriei* and *X. espinosai* [4,5]. This is distinct from the thinner, more gracile morphology present in the other North American troodontids like *L. mcmasterae*, *S. inequalis*, *T. formosus*, and the unnamed Kaiparowits troodontid, e.g., [16–18,21,23]. Among these troodontids with thickened, more robust frontals, the sagittal suture of *A. curriei* remains relatively uniformly thick [5], while it is thicker anteriorly in *X. espinosai* [4], and thicker posteriorly in *D. robustus*.

As mentioned above, the raised orbital rim of *D. robustus* (Figures 2D and 3D) is a common feature among troodontids, e.g., [3]. The robust, thickened orbital rim is also more robust than in other troodontids. The gracile North American troodontids (*L. mcmasterae*, *S. inequalis*, and *T. formosus*) all have thin, gracile orbital rims. Among the other robust North American troodontids, *A. curriei* and *X. espinosai* are less robust than *D. robustus*, even if they are more so than the gracile forms.

We also note here that Sullivan [1], when naming '*Saurornitholestes*' *robustus* from SMP VP-1955, noted comparisons with SMP VP-1270, which he earlier referred to as the dromaeosaurid *Saurornitholestes langstoni* [24]. After SMP VP-1955 was re-assessed as a troodontid by Evans et al. [3], Jasinski [25] re-assessed VP-1270 and named it a distinct dromaeosaurid species, *S. sullivani*. Differences between these two specimens and species were stated by Jasinski [25], and do not need to be restated here.

5. Phylogenetic Results

Phylogenetic analyses were conducted to investigate the interrelationships of troodontines, focusing on troodontins and *Dinevenator robustus* in particular. The analysis was run on a modified dataset from Rivera-Sylva et al. [4], the latest phylogenetic analysis conducted on troodontids. The actual analysis was run on only a subset of the full Rivera-Sylva et al. [4] dataset, particularly the troodontins, with *Archaeopteryx lithographica* as the outgroup. In this way, we utilized the same outgroup as Rivera-Sylva et al. [4], while focusing on the intrarelationships within Troodontini. This meant that the resulting analysis

was conducted using 8 operational taxonomic units (OTUs) and 118 characters, and these results can be compared with those of Rivera-Sylva et al. [4] (Figure 5). Upon re-evaluation of the characters from the Rivera-Sylva et al. [4] dataset, several scores were changed, including those of *Albertavenator curriei* and *Dinevenator robustus* (see Section 2 above).

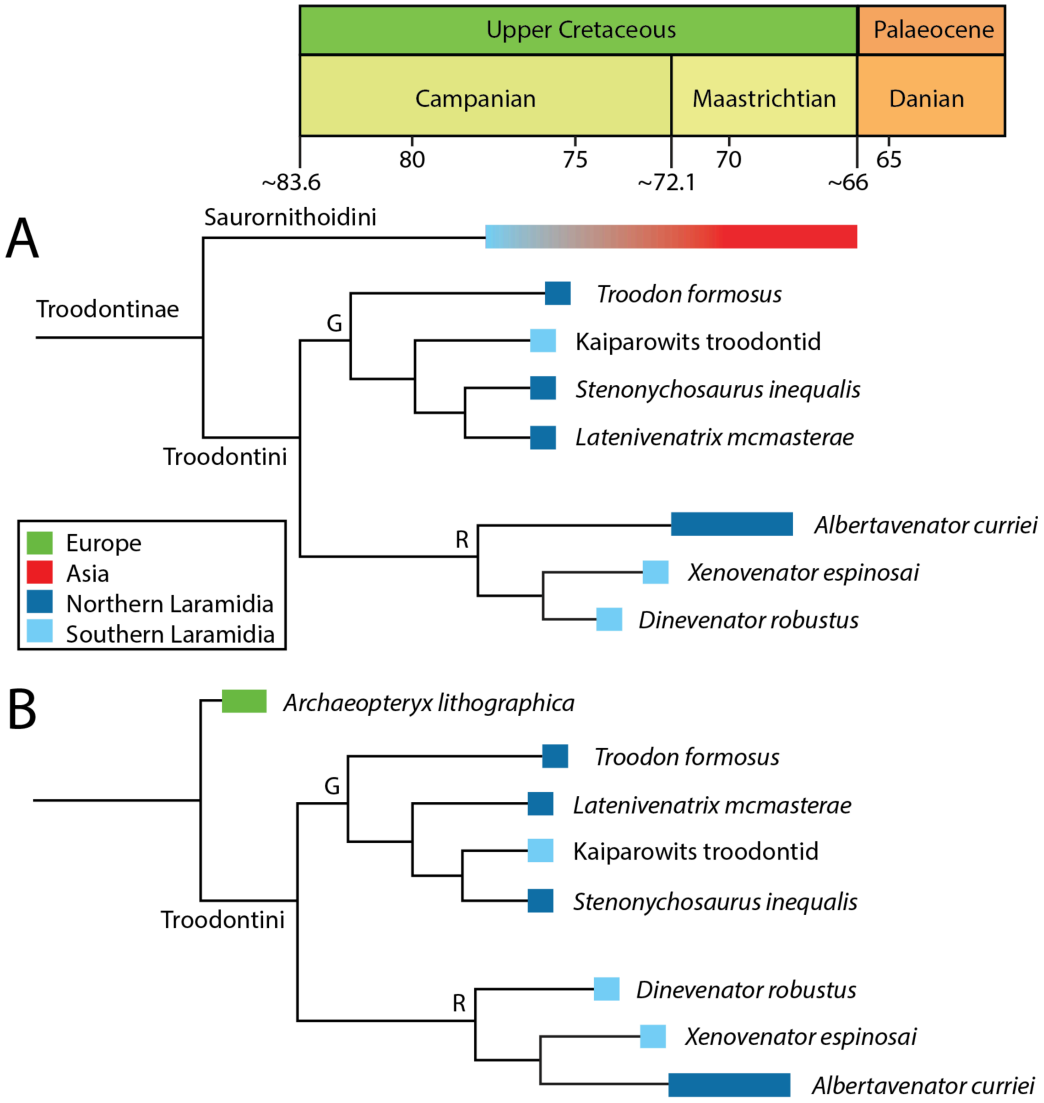

Figure 5. Phylogenetic trees highlighting the evolutionary relationships of *Dinevenator robustus* among Troodontinae. (**A**) Modified phylogenetic tree of Rivera-Sylva et al. [4]: (figure 11), resulting in a robust troodontin clade of (*Albertavenator curriei* + (*Xenovenator espionosai* + *Dinevenator robustus*)). (**B**) Strict consensus tree from the phylogenetic analysis performed in this study, resulting in a robust troodontin clade of (*Dinevenator robustus* + (*Albertavenator curriei* + *Xenovenator espinosai*)). Abbreviations: G, gracile forms clade; R, robust forms clade.

Maximum parsimony analyses were run in the program Tree Analysis Using New Technology (TNT version 1.5; see [6,7]). All characters were left unweighted, and a branch-and-bound search was used with minimum branch lengths set to collapse. This analysis resulted in a consistency index (CI) of 0.955, a retention index (RI) of 0.733, and a tree length of 88 steps (Figure 5B). *Talos sampsoni*, known from the Upper Campanian Kaiparowits Formation of Utah [26], has been recently recovered as a saurornithoidin, so it was not included here in the smaller analysis. However, when the full dataset was run (see Supplementary Material), it was recovered in a group with other saurornithoidins, including *Saurornithoides mongoliensis*, *Borogovia gracilicrus*, and *Zanabazar junior*.

The main analysis resulted in a clade of robust troodontins (*Dinevenator robustus* + (*Xenovenator espinosai* + *Albertavenator curriei*)). The sister clade to this, a group of more gracile troodontins, is (*Troodon formosus* + (*Latenivenatrix mcmasterae* + (Kaiparowits Formation troodontin + *Stenonychosaurus inequalis*)) (Figure 5B). These results are similar to those of Rivera-Sylva et al. [4]: (figure 11), although the Kaiparowits Formation troodontin is found to be more derived as the sister to *S. inequalis*, and *A. curriei* is found as more derived as the sister taxon to *X. espinosai* rather than *D. robustus*.

The full analysis, with all OTUs included, still recovers a robust troodontin clade, although the three taxa are recovered in a polytomy (see Supplementary Material). The gracile North American troodontins are recovered in a polytomy with the robust North American troodontin clade.

6. Discussion

Currie [27] (p. 52) noted that "the frontal is one of the more useful isolated bones of theropods as there is only a single pair in any individual, they tend to be found relatively frequently, and they are diagnostic at the species level." This has been supported by several theropod species being named based on distinct frontals, e.g., [5,16,25,28,29], lending credence to the fact that the distinct frontal of *Dinevenator robustus* is diagnostic of a unique species.

6.1. Troodontid Systematics

Since the establishment of *Troodon formosus* [30], early studies mistakenly considered "troodontids" to be pachycephalosaurids based on similarity in tooth morphology, e.g., [15,31–35]. However, Sternberg [36] recognized the tooth morphology of *Troodon* as distinct from dome-headed taxa like *Stegoceras* and *Pachycephalosaurus* and found that *Troodon* affinities instead lay with Theropoda. Recent studies on troodontids have largely been concerned with the description of new species and specimens and their phylogenetic systematics. North American troodontids, in particular, have been difficult to assess due to their rarity, lack of corresponding elements between specimens, and their overall incomplete nature, e.g., [3–5,16–18,21–23,26,27,37–49], thus leading to disagreements among workers as to the synonymy and validity of certain taxa. Despite these multiple studies, and others, troodontid phylogeny remains one of, if not the least resolved of the paravian groups [50].

In the most recent phylogenetic analysis on troodontid systematics, Rivera-Sylva et al. [4]: (figure 11) recovered Troodontinae, of van der Reest and Currie [16], using a different character matrix, but did not recover the same topology. Rivera-Sylva et al. [4] further recovered subclades within Troodontinae, which they identified as Saurornithoidini and Troodontini, the latter of which included all large-bodied North American troodontids (e.g., *Troodon*, *Stenonychosaurus*, *Latenivenatrix*, *Albertavenator*, and *Xenovenator*). We note that they also recovered *Xenovenator*(?) *robustus* within this clade. We largely agree with their analysis, particularly as they include several characters focused on the morphology of the frontal, and utilize their resulting phylogenetic tree here (Figure 5A). However, some of their characters are scored incorrectly for *robustus*, and changing these affects the resulting topology (Figure 5B).

Dinevenator robustus (="*Xenovenator*(?) *robustus*") was recovered by Rivera-Sylva et al. [4]: (figure 11) in a clade as (*Albertavenator curriei* + (*Xenovenator espinosai* + *Xenovenator*(?) *robustus*)). This clade, a subclade of Troodontini, represents a clade of robust-skulled North American troodontids (Figure 5), distinct from the other subclade of troodontins which represent the more gracile North American troodontids from the Late Cretaceous.

This clade of robust-skulled troodontids has its temporally oldest members inhabiting southern Laramidia. The youngest member also happens to be the only member from

northern Laramidia (i.e., *Albertavenator curriei*). The presence of a robust troodontid in northern Laramidia, and an unnamed gracile troodontid from the Kaiparowits Formation (UMNH VP 16303) in Utah in southern Laramidia, see [21], potentially suggests migration between the two regions during the Campanian. Even specimens from farther north in Alaska [44] suggest more gracile troodontids were present, rather than more robust forms. Additionally, it is also clear that the gracile forms are older than the robust forms (Figure 5; see also [51]). It is more likely that the gracile forms are more ancestral for North American troodontids, and robust forms evolved later. This may suggest the current phylogenetic relationships are being influenced by convergent evolution rather than consistent immigration between the regions during the Campanian. However, we note that the relative paucity of North American troodontid fossils makes this difficult to currently test, and it is possible that both clades were present in both regions throughout the last part of the Cretaceous. Regardless, it is apparent that more information is needed to definitively determine the evolutionary relationships of Troodontidae.

As noted above, changing several of the character scores results in a different phylogeny (Figure 5B). The placements of *Latenivenatrix mcmasterae* and the unnamed Kaiparowits Formation troodontin change between the two analyses among gracile troodontins, but our focus is on the different phylogenetic placement of *Dinevenator robustus*. Rather than the sister taxon to *Xenovenator espinosai*, it is now recovered as sister to (*Xenovenator espinosai* + *Albertavenator curriei*). This moves the oldest member of the robust troodontins to the basal-most position within the clade. It also suggests *robustus* and *espinosai* are not sister taxa, strengthening the idea that *robustus* is not a species within *Xenovenator*. The full analysis also recovered the robust troodontin clade, although the three OTUs listed here were recovered in a polytomy (see Supplementary Material). Regardless of the different topology within the clade, it is better to maintain separate genera for these three species.

6.2. San Juan Basin Troodontids

The San Juan Basin of New Mexico is important for our understanding of Late Cretaceous vertebrates, particularly among fossil localities in southern North America. While the north (e.g., Alberta, Montana, North Dakota) has been more intensely collected, areas to the south (e.g., New Mexico, Texas, Utah, Mexico) have historically seen less collecting, although this has increased significantly over the past three decades, especially in New Mexico. Recent collecting efforts have greatly expanded our understanding of the vertebrate fossils of the San Juan Basin and aided in our understanding of the Late Cretaceous in North America, particularly of New Mexico and the southern United States. While troodontids have previously been reported from the San Juan Basin [25,52–60], these have been based exclusively on teeth. Aside from the original description of SMP VP-1955 [1], the only other troodontid specimen reported from the same unit (De-na-zin Member of the Kirtland Formation) is a single tooth (NMMNH P-68395) mentioned and figured by Williamson and Brusatte [59]: (figure 7E–J), which they identified as Troodontidae indeterminate.

The presence of a unique, robust-skulled troodontid in the late Campanian of the San Juan Basin further supports its unique vertebrate assemblage (Willow Wash local fauna), and from the Kirtlandian in general. This assemblage has shown connections with dinosaurs from the north, south, east, and Asia. These connections suggest numerous migratory events during the Late Cretaceous, which is not unexpected, particularly as the Western Interior Seaway was receding, providing further opportunities for dinosaurs to traverse between these regions; see [61].

7. Conclusions

SMP VP-1955 is found to be diagnostic, and allows recognition of *Dinevenator*, gen. nov., establishing the valid species *D. robustus*. This unique species is diagnosed based on features of the holotype frontal, including its robust and thick nature, morphology of the sagittal suture, shape of the nasal facet, shape and size of the posterior portion of the nasal, and placement of the lateral endocranial wall, among other things. An updated phylogenetic analysis places it in a clade of robust North American troodontins, but not sister to *Xenovenator espinosai*. Recognition of a distinct, large, robust, thick-skulled troodontid adds to the unique nature of the ancient ecosystems of the San Juan Basin. Different dinosaur groups show closer relationships with species from various other geographic regions, implying a complex interplay between species and systems during the Late Cretaceous of North America.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fossils4030021/s1, I. Character list for the character taxon matrix; II. Character score data matrix; III. Strict consensus tree of full phylogenetic analysis; IV. Figure S1. Life reconstruction of *Dinevenator robustus*, ~73 million years ago in what is today northwestern New Mexico, USA. This is the ancient landscape of the De-na-zin Member of the Kirtland Formation, with *Dinevenator robustus* preying on the multituberculate mammal *Mesodma*. Artwork by Sergey Krasovkiy.

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Abbreviations

Institutional abbreviations. **CPC**, Colección Paleontológica de Coahuila, Museo del Desierto, Saltillo, Coahuila, Mexico; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; **SMP**, State Museum of Pennsylvania, Harrisburg, Pennsylvania, USA; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UALVP**, University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Alberta, Canada; **UMNH**, Natural History Museum of Utah (formerly Utah Museum of Natural History), Salt Lake City, Utah, USA.

Anatomical abbreviations. **cf**, cerebral fossa; **fd**, frontal depression; **fns**, frontonasal suture; **lcb**, lacrimal buttress; **lew**, lateral endocranial wall; **ob**, olfactory bulb impression (olfactory fossa); **od**, orbital roof depression; **ot**, olfactory tract; **pop**, postorbital process; **ss f**, frontal sutural surface; **str**, supratemporal ridge.

Phylogenetic abbreviations. **G**, gracile forms clade; **R**, robust forms clade.

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