

A microraptorine (Dinosauria–Dromaeosauridae) from the Late Cretaceous of North America

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Edited by James P. Kennett, University of California, Santa Barbara, CA, and approved January 30, 2009 (received for review November 17, 2008)

The fossil assemblages of the Late Cretaceous of North America are dominated by large-bodied dinosaur species. Associated skeletons of small dinosaurs are exceedingly rare, and small (<10 kg) carnivorous theropods have not previously been reported from these beds. Here, we describe a small dromaeosaurid from the 75-million-year-old Dinosaur Park Formation of Alberta, Canada. *Hesperonychus elizabethae* gen. et sp. nov. is represented by a pelvic girdle from an animal weighing ≈1,900 g. Despite its size, the pubes and ilia are coossified, indicating that the animal was somatically mature. This is the smallest carnivorous, nonavian dinosaur known from North America. Phylogenetic analysis of *Hesperonychus* reveals that it is not closely related to previously described North American dromaeosaurids. Instead, *Hesperonychus* is a member of the dromaeosaurid clade Microraptorinae, a group containing the 4-winged *Microraptor* and the feathered *Sinornithosaurus*, both from the Lower Cretaceous Jehol Group of China. *Hesperonychus* is the youngest known member of this lineage, extending the temporal range of the clade by 45 million years, and it is the first microraptorine known from North America, providing further evidence for an affinity between the dinosaur faunas of North America and Asia. Study of fossil collections from the Dinosaur Park and Oldman formations of Alberta has revealed numerous isolated bones of small, basal dromaeosaurids, which are tentatively referred to *Hesperonychus*. These fossils suggest that small dromaeosaurids were a significant component of the carnivore community in this Late Cretaceous biota.

Campanian | Dinosaur Park Formation | microraptorinae | theropoda

The vast majority of known nonavian dinosaurs are medium- and large-bodied forms, ranging in size from tens to thousands of kilograms (1). This pattern is especially evident in the Late Cretaceous of North America (2–8). Here, large-bodied (>1,000 kg) dinosaurs dominate fossil assemblages in terms of number of skeletons (2, 3, 7) and number of species (4–6, 8). Small-bodied (<10 kg) carnivorous dinosaurs have not previously been described from these assemblages.

Until now, the smallest carnivorous dinosaur known from the Late Cretaceous of North America was the dromaeosaurid *Saurornitholestes langstoni*, which weighed ≈10 kg [see *Dinosaur Mass Data and Equations* in supporting information (SI) Appendix]. Other animals are unlikely to have filled the small-carnivore niche. The alvarezsaurid theropod *Albertonykus* (9, 10) appears to have been a specialized insectivore (10) rather than a carnivore in the strict sense, and the stegodont marsupials were highly specialized durophages (11, 12) that may have fed on aquatic invertebrates rather than terrestrial prey.

The apparent absence of small, endothermic (or, in the case of dinosaurs, presumably endothermic) carnivores in these Late Cretaceous ecosystems is remarkable: In modern, mammal-dominated terrestrial communities, small-bodied animals outnumber large-bodied animals, both in terms of the number of individuals in a given area (13, 14) and number of species (15, 16). That dinosaurs might have left the small-carnivore niche vacant in North America is still more perplexing when one considers that many small carnivorous dinosaurs are known from

Europe, Asia, and Gondwana (17–28). This raises the question of whether small-bodied, endothermic carnivores were truly rare in these assemblages, or whether our picture of these ecosystems is incomplete.

Recently, study of museum collections resulted in the identification of a specimen of a previously unknown dinosaur from the Upper Cretaceous (upper Campanian) Dinosaur Park Formation (29) of Alberta, Canada. The specimen was collected in 1982 but lay unstudied for 25 years. Preparation of the fossil revealed that it represents a new genus of the clade Dromaeosauridae, a group of birdlike, carnivorous theropods (30).

This animal, *Hesperonychus elizabethae*, gen. et sp. nov., is almost an order of magnitude smaller than any other carnivorous dinosaur known from the Dinosaur Park Formation (see *Dinosaur Mass Data and Equations* in SI Appendix) or any North American Cretaceous assemblage. This find demonstrates that in the Late Cretaceous of North America, dromaeosaurids exploited the small-carnivore niche.

Surprisingly, *Hesperonychus* does not appear to be related to previously known North American dromaeosaurids, such as *Dromaeosaurus albertensis* (31) and *Saurornitholestes langstoni* (32). Instead, it shares features with the Microraptorinae, a clade of small, basal dromaeosaurids that includes the feathered *Sinornithosaurus* and the bizarre “4-winged” *Microraptor*, both from the Lower Cretaceous Jehol Group of China (20–22, 24).

Systematic Paleontology

Systematics are as follows: Theropoda Marsh, 1881; Coelurosauria von Huene, 1914; Maniraptora Gauthier, 1986; Dromaeosauridae Matthew and Brown, 1922; Microraptorinae Senter et al., 2004; *Hesperonychus elizabethae* gen. et sp. nov.

Holotype

UALVP (University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton) 48778, a partial pelvic girdle comprising the pubes and ilia (Fig. 1).

Referred Material

A number of isolated pedal phalanges are tentatively referred to *Hesperonychus* (see *Specimen Data* in SI Appendix and Fig. 2). Phalanx II-1 is represented by TMP (Royal Tyrrell Museum of Palaeontology, Drumheller, AB, Canada) 1989.116.65, TMP 1966.19.22, and UALVP 50687. Phalanx II-2 is represented by TMP 1992.36.61 and TMP 1983.67.7. Phalanx II-3 is represented by TMP 1979.10.6, TMP 1980.16.1880, TMP 1990.107.15, TMP 1995.092.0009, TMP 2000.12.100, and UALVP 50686.

Author contributions: N.R.L. designed research; N.R.L. and P.J.C. performed research; N.R.L. analyzed data; and N.R.L. and P.J.C. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/cgi/content/full/0811664106DCSupplemental.

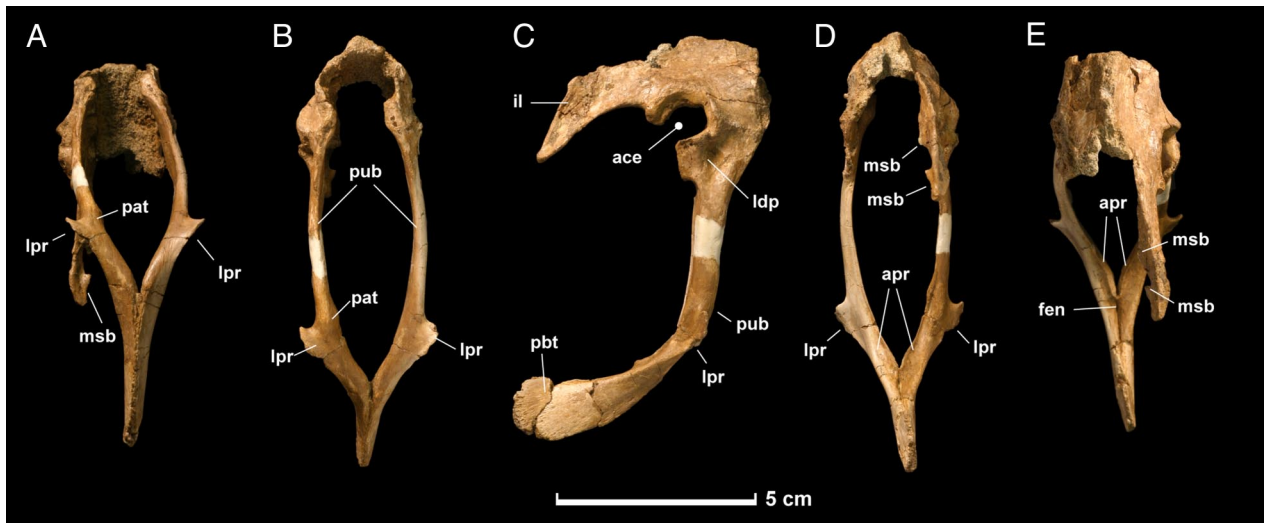


Fig. 1. Holotype pelvic girdle (UALVP 48778) of *Hesperonychus elizabethae* from the late Campanian Dinosaur Park Formation of Alberta, Canada. (A) Ventral view. (B) Anterior view. (C) Right lateral view. (D) Posterior view. (E) Dorsal view. ace, acetabulum; apr, pubic apron; fen, fenestra; il, ilium; ldp, lateral depression; lpr, lateral process; msb, medial shelf of brevis fossa; pat, pathology; pbt, pubic boot; pub, pubis.

Etymology

The name *Hesperonychus* derives from *hesperus* (Latin, west) and *onychos* (Greek, claw). The specific epithet *elizabethae* honors the late Dr. Elizabeth Nicholls, who discovered the holotype.

Horizon and Locality

The holotype was collected from exposures of the Dinosaur Park Formation located on the south side of the Red Deer River, ≈ 20 km east of Dinosaur Provincial Park, Alberta. The Dinosaur Park Formation was deposited during the middle of the late Campanian, between 76.5 and 74.8 Ma (29). Referred material was collected from Dinosaur Provincial Park and surrounding badlands and other locations in southern Alberta, including Devil's Coulee, Manyberries, Onefour, Irvine, and Sandy Point (*Specimen Data* in *SI Appendix*); all are within 200 km of the type locality. All specimens for which precise stratigraphic data are available come from a narrow chronostratigraphic interval that encompasses the Dinosaur Park Formation and coeval beds of the uppermost Oldman Formation (*Specimen Data* in *SI Appendix*). This interval represents no more than 1.7 million years of time (29).

Diagnosis

Small dromaeosaurid characterized by the following autapomorphies: pubic peduncle of ilium with medial surface deeply excavated; posterior wing of ilium with medial shelf split to form anterior and posterior processes; lateral tubercles of pubis wing-like and curving anteriorly; pubis with fossa on lateral surface ventral to acetabulum; pubic apron shifted onto posterior surface of pubis; pubic symphysis teardrop-shaped in lateral view; ischiadic process of pubis reduced to a narrow lamina.

Description and Comparisons

Hesperonychus is a remarkably small theropod. By using a regression of pubis length against body mass, the holotype is estimated to have weighed $\approx 1,900$ g, approximately half the weight of a domestic cat. Despite the small size of the animal, the pubes and ilia are completely fused to each other, indicating that the animal was somatically mature.

The pubic peduncle of the ilium is long anteroposteriorly and has a deep fossa medially, which extends onto the medial surface of the pubis. The lateral surface of the pubic peduncle is convex, with no trace of a cuppedicus fossa. The ilia are strongly inclined

medially and may have contacted each other dorsally along the midline. Unlike the situation in *Velociraptor*, in which the ilia diverge posteriorly and the dorsal margin is laterally everted (30, 33, 34), the posterior alae of the ilia would have been approximately parallel, and the postacetabular blade projects vertically. As in basal paravians (23, 35–37), the posterior wing of the ilium is tapered and curved ventrally in lateral view. Along the dorsal edge of the posterior ala, there is a distinct tubercle, a common maniraptoran feature (36). The brevis shelf projects ventrolaterally away from the posterior blade of the ilium. Medially, the medial shelf of the brevis fossa is split into separate anterior and posterior processes, a condition unique to *Hesperonychus*. The acetabulum is similar to those of other dromaeosaurids in that it lacks a prominent supracetabular crest (30, 36). However, anteriorly, the contribution of the ilium to the acetabulum is broad, and the anterior rim projects strongly laterally, as it does in *Unenlagia* (36). The medial opening of the acetabulum is partially closed, as it is in other Dromaeosauridae (36). The acetabulum opens dorsolaterally rather than laterally, as is the case in *Velociraptor* (38), suggesting the ability to partially abduct the hindlimbs. This morphology is of interest in light of proposals that *Microaptor gui* abducted its feathered hindlimbs to function as airfoils (24).

As in many other paravians (20, 23, 24, 30, 33–35, 37), the pubic shaft projects posteroventrally. The proximal end of the pubis has a distinct scar on its anterior surface, in the same position as the large tubercle found in *Velociraptor* (33). The proximal end also bears a deep depression on its lateral surface, just ventral and anterior to the acetabulum. The ischiadic peduncle of the pubis is mediolaterally compressed and its contact with the ischium is reduced to a thin blade of bone. The distal shaft of the pubis sharply curves posteriorly, as it does in the Jehol dromaeosaurids *Microaptor* (24) and *Sinornithosaurus* (20); *Unenlagia* shows a similar curvature but it is more weakly developed (35). Proximally, the shaft of the pubis is mediolaterally compressed. Unlike the condition in *Velociraptor*, where the distal shaft of the pubis is anteroposteriorly flattened (33, 34), the distal shaft is subcircular in section. The right pubic shaft has an unusual swelling not seen on the left, apparently representing a well-healed fracture. On the lateral surface of each pubic shaft, there is a distinct process, as in other microraptorines (20–22, 24). However, in the new taxon, these processes are larger, winglike, and curve anteriorly. The laminae that form the

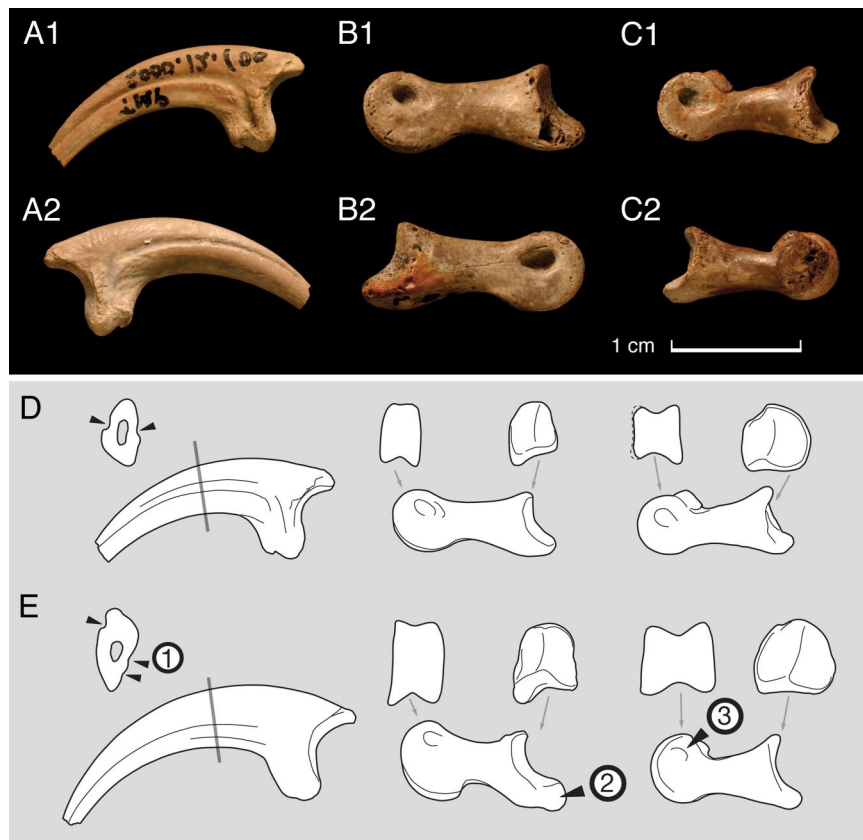


Fig. 2. Pedal phalanges, cf. *Hesperonychus*. (A) Pedal phalanx II-3 (TMP 2000.12.100), from Dinosaur Provincial Park, Canada (reversed from left) in medial (A1) and lateral (A2) views. (B) Right pedal phalanx II-2 (TMP 1983.67.7) in medial (B1) and lateral (B2) views. (C) Right pedal phalanx II-1 (1989.116.65) in medial (C1) and lateral (C2) views. (D and E) cf. *Hesperonychus* specimens (D) compared with *Saurornitholestes langstoni* (E), a typical member of the Eudromaeosauria. Derived features characterizing the Eudromaeosauria include (1) paired grooves on the medial surface of the ungual that are shifted ventrally relative to the lateral groove; (2) phalanx II-2 with an elongate heel of the proximal articular surface, and (3) phalanx II-1 with strong dorsal projection of the distal articular surface. Absence of these eudromaeosaur features indicates that these fossils are from a basal dromaeosaur, rather than juveniles of *Saurornitholestes* or *Dromaeosaurus*.

pubic apron are greatly reduced, and their midline contact is all but lost, resulting in a deep, broad pelvic canal. Unusually, these laminae are located on the posterior surface of the shaft rather than on the medial surface, as is the case in other deinonychosaurs (21–23, 30, 33–35). At their ends, the pubes fuse to form a symphysis. No distinct anterior or posterior processes are present. Instead, the symphysis is spatulate in lateral view, as in other microraptorines (20, 24).

In addition to the holotype, numerous small pedal phalanges have been recovered from the Dinosaur Park and Oldman formations (Fig. 2 A–C), which are tentatively referred to *Hesperonychus*.

Phalanx II-1, the proximal phalanx, is long and slender, as in basal deinonychosaurs (20–24, 39) (Fig. 2C). Its distal articular surface is broad and spool-shaped in distal view (Fig. 2D), as in other dromaeosaurids (30). However, in medial view, the distal articular surface is weakly expanded and subcircular (Fig. 2D). In contrast, the distal articular surface is dorsally extended in Eudromaeosauria (Fig. 2E). The proximal articular surface has a small medial cotyle.

Phalanx II-2, the penultimate phalanx, resembles those of basal deinonychosaurs (20–22, 39) in being relatively long and gracile, with a short proximal articular heel and weak expansion of the proximal and distal articular surfaces (Fig. 2B). In ventral view, the heel is triangular, as in *Sinovenator* and saurornitholestines. Ventrally, the flexor tendon groove is only weakly

developed, in contrast to the condition in saurornitholestines, in which this groove is prominent.

Phalanx II-3, the ungual phalanx (Fig. 2A), resembles the sickle claw of basal dromaeosaurids such as *Rahonavis* (39) and microraptorines (20, 22). In cross-section, the claw is broad for its depth; the medial surface is almost flat, and the lateral surface is highly convex (Fig. 2D), resulting in a semilunate cross-section. A similar cross-section occurs in *Rahonavis* UA (University of Antananarivo, Antananarivo, Madagascar) 8656 and the troodontid *Sinovenator* IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, Peoples Republic of China) V12615. In contrast, derived dromaeosaurids (Eudromaeosauria), including *Saurornitholestes* (Fig. 2E), *Velociraptor* (33, 34), *Deinonychus* (40), and *Utahraptor* (41), have a more blade-like claw. Phalanx II-3 is also distinguished by the more symmetrical arrangement of the vascular grooves. In Eudromaeosauria, the lateral groove is shifted toward the dorsal edge of the claw, and the medial groove is shifted ventrally (40, 41) This asymmetry is only weakly developed in the ungual phalanges of the new taxon (Fig. 2), although it is developed to a greater degree than in troodontids. Eudromaeosauridae also exhibit an accessory vascular groove on the medial surface of pedal ungual II, which is absent from the fossils described here (Fig. 2).

The linear dimensions of the referred specimens range from 71% to 105% of the dimensions of the corresponding elements in the microraptorine *Sinornithosaurus millennii* (IVPP V12811), whereas the pubis of the holotype is 80% of the length of the

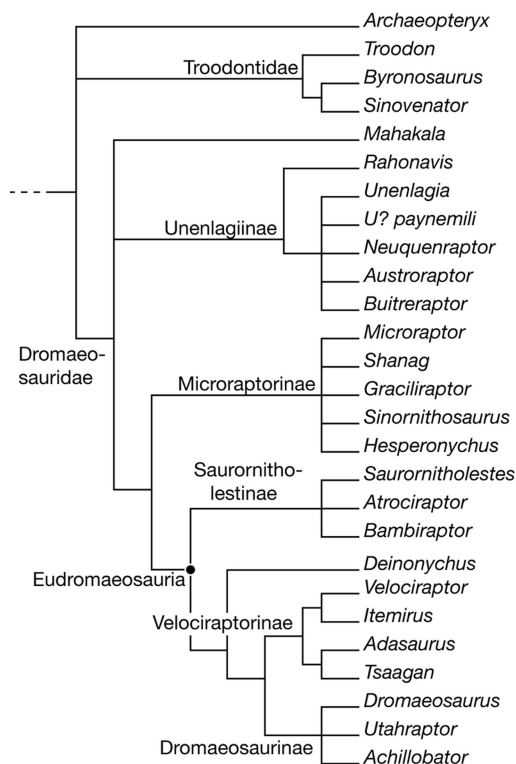


Fig. 3. Strict consensus of 5,292 most parsimonious trees resulting from phylogenetic analysis of 23 in-group taxa, 4 out-group taxa, and 114 characters. *H. elizabethae* was found to be part of the clade Microraptorinae. Tree length = 223, consistency index = 0.5430, retention index = 0.6930, rescaled consistency index = 0.3791.

pubis in IVPP V12811 (see *Specimen Data* in *SI Appendix*). Thus, the referred elements and the holotype of *Hesperonychus* belong to individuals of comparable size. The pedal phalanges are virtually identical to the pedal phalanges of digit II in *Sinornithosaurus* and *Microraptor*. However, they lack features found in the Eudromaeosauria, indicating that they do not represent juveniles of *Saurornitholestes langstoni* or *Dromaeosaurus albertensis*, the eudromaeosaurs known from the Dinosaur Park assemblage (31, 32). As described above, the second pedal digit of Eudromaeosauria is characterized by numerous derived characters (blade-like ungual with asymmetrically arranged vascular grooves; elongate proximal articular heel of phalanx II-2; dorsally extended medial condyle of phalanx II-1) that are conspicuously absent in these specimens (Fig. 2 *D* and *E*). The presence of these synapomorphies in a juvenile eudromaeosaur, the holotype of *Bambiraptor feinbergorum* (42), demonstrates that the absence of such features cannot be explained as the result of ontogenetic changes in morphology. For these reasons, we interpret the referred specimens as coming from a small-bodied basal dromaeosaur. In the absence of an associated skeleton, referral to *Hesperonychus* must be considered tentative, but this identification is consistent with the available evidence.

Systematics

Phylogenetic analysis places *Hesperonychus* in the dromaeosaurid clade Microraptorinae (Fig. 3). Referral of *Hesperonychus* to the Microraptorinae is supported by the presence of a lateral process of the pubis, strong posterior curvature of the pubic shaft, and a spatulate pubic foot.

This study agrees with previous studies in recovering the clades Microraptorinae, Velociraptorinae, Dromaeosaurinae, and Unenlagiinae (26–28, 43, 44), although the membership of

some of these clades differs in our analysis. *Shanag ashile*, for instance, was found to belong to the Microraptorinae, and *Adasaurus mongoliensis* was found to be a member of the Velociraptorinae (Fig. 3). Another result of this study is the recovery of a clade containing 3 taxa from the Campanian of North America: *Saurornitholestes langstoni*, *Atrociraptor marshalli*, and *Bambiraptor feinbergorum*. This clade is here named Saurornitholestinae. *Bambiraptor* has been referred to the Microraptorinae in some studies (43), but our analysis shows that it is not a member of this clade. Although *Bambiraptor* resembles microraptorines in having a curved pubis, this resemblance is superficial: It is the pubic symphysis that is curved, not the pubic shaft (as is the case in Microraptorinae). Rather, the animal shares derived features with *Saurornitholestes* (prominent depression caudal to the accessory antorbital fenestra, ridge on the medial surface of the ischium). *Saurornitholestes* was found to be the sister taxon of a clade consisting of Velociraptorinae, Dromaeosaurinae, and *Deinonychus* (Fig. 3). These taxa and the Saurornitholestinae form a monophyletic group (26–28, 30, 43, 44) of derived dromaeosaurids, here termed Eudromaeosauria.

Discussion and Conclusions

The recognition of *Hesperonychus* results in a remarkable extension of the temporal range of the Microraptorinae. Previously, the geologically youngest known microraptorines came from the Jiufotang Formation of northeastern China's Jehol Group (24) (≈ 120 Ma) (45). The discovery of *Hesperonychus* in the Dinosaur Park Formation (≈ 75 Ma) (29) therefore extends the range of the clade by ≈ 45 million years, more than half the length of the Cretaceous. It remains unknown whether *Hesperonychus* represents the persistence of a 4-winged morphology, as seen in *Microraptor gui* (24), or a flightless form, such as *Sinornithosaurus* (20). The latter seems more likely in light of the fact that *Hesperonychus* approached *Sinornithosaurus* in size. Surprisingly, there appears to have been little evolution in body size in the Microraptorinae during their long history. The discovery of *Hesperonychus* indicates that microraptorines continued to exploit the small predator niche for at least 50 million years, whereas the Eudromaeosauria continued to exploit the medium- and large-bodied predator niche over the same span of time (27). In this respect, the evolution of the Dromaeosauridae appears to have been surprisingly conservative.

Additionally, *Hesperonychus* is the first definitive member of the Microraptorinae known from North America. This results in a geographic range extension for the clade, and provides further evidence of an affinity between the dinosaur faunas of North America and Asia (46, 47).

The discovery of *Hesperonychus* also alters our understanding of the predator community in the Late Cretaceous of North America. It now appears that North American carnivorous dinosaurs ranged widely in body size, from <2 kg to many tonnes, >4 orders of magnitude (Fig. 4). The large difference in size between *Hesperonychus* and other, contemporary dromaeosaurids is consistent with the suggestion that dinosaurian predators were highly segregated in terms of body size so as to reduce competition for prey (48).

Despite the absence of associated skeletons, *Hesperonychus* may have been a relatively common animal in the Dinosaur Park fauna. The most common element, phalanx II-3, is represented by at least 10 specimens in the TMP collections. For the same element, *Saurornitholestes* is known from ≈ 30 isolated specimens; only 2 *Dromaeosaurus* specimens have been recognized. Therefore, considering that the small bones of *Hesperonychus* have a low preservation potential and that their size makes them easy to overlook in the field, fossils of this microraptorine are relatively common. It remains to be seen whether microraptorine

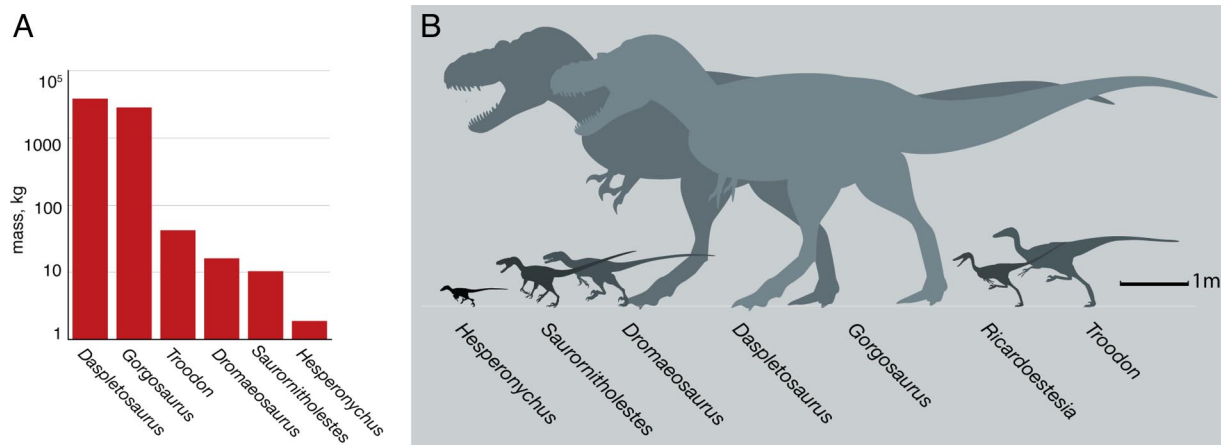


Fig. 4. Size of *H. elizabethae* and other carnivorous dinosaurs from the Dinosaur Park assemblage of Alberta. (A) Comparison of body mass of *H. elizabethae* and other carnivorous dinosaurs (a mass estimate is not given for *Ricardoestesia*, which is known only from teeth and dentaries). (B) Relative size of *Hesperonychus* and other predatory dinosaurs from the assemblage.

elements will be recognized in other North American fossil assemblages.

Whereas *Hesperonychus* is diminutive when compared with contemporary theropods, by the standards of Mesozoic mammals it was a relatively large animal. The metatherian *Eodelphis cutleri* is perhaps the largest mammal in the Dinosaur Park assemblage, but it weighed just 600 g (49). Ironically, therefore, our discovery of a small theropod in the assemblage actually emphasizes the lack of substantial overlap in body size between dinosaurs and mammals in this fauna. The patterns seen in the Dinosaur Park assemblage are therefore consistent with the conventional wisdom that dinosaurian predation and competition limited the evolution of large body size in Mesozoic mammals, the existence of uncommon “giant” taxa such as Gobiconodontidae (50) notwithstanding. Relatively few Mesozoic mammals approached or exceeded 500–5,000 g (51), the size of the smallest nonavian dinosaurs, and few if any nonavian dinosaurs were <100 grams (24), the size of the average Mesozoic mammal (51). However, one could also argue that nonavian dinosaurs were precluded from evolving small body size by mammalian competition. Such interpretations are not mutually exclusive.

That the existence of *Hesperonychus* remained undetected until now, >100 years after the discovery of the Dinosaur Park Formation assemblage, underscores the degree to which preservational and collecting biases alter our picture of dinosaur-dominated faunas. The Late Cretaceous of the Western Interior boasts one of the world’s richest and most intensively studied Mesozoic terrestrial fossil assemblages, but skeletons of small vertebrates are vanishingly rare (2, 3, 7). In contrast, isolated microfossils document the presence of a rich fauna of small, terrestrial vertebrates. This fauna included amphibians, squamates, birds, mammals (52–58), and, as shown here, small dromaeosaurids. Only a small percentage of these taxa are known from associated remains, demonstrating the existence of a strong taphonomic bias against the preservation of small

vertebrate skeletons (2, 3, 59). Historically, this problem has been compounded by a collecting bias that has favored the recovery of large, relatively complete dinosaur skeletons. The existence of similar biases in other fossil assemblages has doubtless served to obscure the diversity, abundance, and ecological importance of the small-bodied members of the Dinosauria.

Materials and Methods

Mass was estimated for *Hesperonychus* by regressing mass estimates for *Archaeopteryx* and dromaeosaurids against pubis length by using ordinary least-squares (OLS) regression (see *Dinosaur Mass Data and Equations* in *SI Appendix*) to generate an allometric equation. Systematics of *Hesperonychus* were established by coding the holotype into a morphological data matrix (see *Data Matrix* in *SI Appendix*) of 114 characters (*Taxa and Characters* in *SI Appendix*) with 23 in-group taxa. The matrix includes previously published (26–28, 36, 43, 44, 60, 61) and heretofore unpublished characters. Four out-group taxa were used to polarize the characters. Out-group taxa used were the troodontids *Troodon*, *Byronosaurus*, and *Sinovenator* and the basal avian *Archaeopteryx*. Phylogenetic analysis was performed in PAUP* version 4b10 in branch and bound search mode. Five characters were ordered, and all characters were equally weighted. Tree statistics were calculated with uninformative characters excluded.

ACKNOWLEDGMENTS. We thank Clive Coy for his skillful preparation of the holotype. For discussions, we thank David Evans, Mark Norell, Anthony Russell, Jessica Theodor, Alan Turner, Xu Xing, and the University of Calgary Vertebrate Morphology Research Group. We also thank the anonymous reviewers whose suggestions have greatly improved this manuscript. We appreciate the assistance of James Gardner (Royal Tyrrell Museum of Palaeontology, Drumheller, AB, Canada), Farish Jenkins (Museum of Comparative Zoology, Cambridge, MA), Walter Joyce (Yale Peabody Museum, New Haven, CT), Scott Hartman (Wyoming Dinosaur Center, Thermopolis, WY), Mark Norell (American Museum of Natural History, New York), Ken Stadtman (Brigham Young University, Provo, UT), Brandon Strilisky (TMP), and Xing Xu (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, Peoples Republic of China) for specimen access and T. Miyashita (University of Alberta Laboratory for Vertebrate Paleontology, Edmonton) for assistance with collections. This work was supported by a National Science Foundation Graduate Research Fellowship, the Alberta Ingenuity Graduate Studentship, the University of Calgary Dean’s Entry Grant (to N.R.L.), and Natural Sciences and Engineering Research Council Discovery Grant 203091-02 (to P.J.C.).

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