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Original Article

Pedal function in deinonychosaurs（Dinosauria：Theropoda）：a comparative study

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Abstract：Members of the Cretaceous theropod clade Deinonychosauria have a highly modified second toe with an enlarged, recurved ungual. Here I present the first comparative study of pedal function in deinonychosaurs and other theropods to test hypotheses of function for this toe. I manually manipulated bones and casts to determine pedal range of motion in the non-deinonychosaurian theropods *Dilophosaurus*, *Allosaurus*, *Mononykus*, and *Chirostenotes*; and the deinonychosaurs *Troodon*, *Neuquenraptor*, *Rahonavis*, *Bambiraptor*, *Deinonychus*, and *Dromaeosaurus*. I also used movies of walking bird feet for comparison. The results of the study show that：(1) contrary to previous suggestions, the distodorsal eminence of pedal phalanx II-1 of deinonychosaurs is not correlated with greater hyperextensibility of phalanx II-2 than in other theropods；(2) the proximoplantar process of phalanx II-2 of deinonychosaurs limits flexion, as previously suggested (3) movement of the second toe is sub-orthal in dromaeosaurids, the toe remains adducted (angled toward the animal's midline) through hyperextension and flexion in *Troodon*, and in other theropods the second and fourth toes diverge during hyperextension and converge during flexion；(4) pedal phalanx I-1 is immobile in *Chirostenotes* and the examined deinonychosaurs but has a wide range of motion in other theropods；(5) contrary to a previous suggestion, the hallux of *Rahonavis* was not retroverted；(6) range of motion in the second toe is consistent with opening tough insect nests in dromaeosaurids but not *Troodon*；(7) the deinonychosaurian second toe was hyperextended, not flexed, during locomotion.

Key Words：Dromaeosauridae, Troodontidae, Theropoda, functional morphology, hindlimb

Introduction

The theropod dinosaur clade Deinonychosauria includes the Cretaceous families Dromaeosauridae and Troodontidae, in both of which the second toe is highly modified (Sereno, 1998; Makovicky and Norell, 2004; Norell and Makovicky, 2004). Each phalanx of the second toe exhibits an unusual feature. The distal end of the proximal phalanx exhibits a dorsal eminence, the proximoplantar articular surface of the second phalanx is extended into a prominent process, and the ungual phalanx is enlarged and recurved (Makovicky and Norell, 2004; Norell and Makovicky, 2004) (Fig. 1).

Functional interpretations of each feature have appeared in the literature, but most have not been tested experimentally. The distodorsal eminence of phalanx II-1 has been interpreted as a feature allowing extreme hyperextension (Ostrom, 1969; Paul, 1988). Articulated troodontid skeletons with the joint hyperextended (Russell and Dong, 1993; Xu and Norell, 2004; Xu and Wang, 2004) and published illustrations of the range of motion in the second toe of the dromaeosaurids *Deinonychus* (Ostrom, 1969) and *Bambiraptor* (Burnham et al., 1997) show that hyperextensibility is present at this joint in deinonychosaurs. However, to demonstrate that the distodorsal eminence is the feature that permits hyperextensibility, one must show that hyperextensibility is absent at this joint in theropods that lack the eminence. To date, no study has done this.

The proximoplantar process of the second phalanx has been interpreted as a bony stop, limiting flexion (Ostrom, 1969). Flexion is limited at that joint in *Deinonychus* (Ostrom, 1969) and *Bambiraptor* (Burnham et al., 1997). However, to demonstrate that the proximoplantar process is the feature that limits flexion, one must show that greater ability to flex at this joint is present in theropods that lack the process. To date, no study has done this.

The enlarged, recurved ungual has been interpreted as a weapon for disemboweling prey with large slashes (Ostrom, 1969; Adams, 1987), a weapon for delivering small punctures (Carpenter, 2002; Manning et al., 2006), and a digging tool (Colbert and Russell, 1969). An experimental test of the first two hypotheses confirms that the claw is more likely to have made small punctures than disemboweling slashes (Manning et al., 2006), but the digging hypothesis has not been tested.

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Other functional issues relating to deinonychosaurian feet also deserve study. For example, Ostrom (1969, 1990) and Paul (1988) suggested that the second toe of deinonychosaurs was kept in a hyperextended position when not in use, to keep the claw clear of the ground, so as to avoid wear. That is a plausible suggestion, and articulated specimens show that the toe was hyperextended when at rest (Russell and Dong, 1993; Norell and Makovicky, 1999; Xu and Norell, 2004). However, so far no study has tested whether a strongly flexed position would not be equally capable of keeping the claw clear of the ground during locomotion. While it is clear that the toe was capable of achieving a hyperextended position (Ostrom, 1969; Burnham et al., 1997), it is worth asking whether a strongly flexed position would have been feasible during locomotion, a question that has not been posed in the literature before now.

Another issue deserving study is the range of motion in the toe in three dimensions. Osmólska (1982) suggested that the ginglymoid distal end of the second metatarsal of dromaeosaurids resulted in greater restriction of mediolateral movement of the toe than in troodontids, which lack the ginglymus. That is a plausible and testable suggestion, but so far it has not been tested.

An issue with implications for character scoring in phylogenetic data matrices, is the orientation of the hallux in deinonychosaurian feet. The hallux of *Rahonavis*—which was at first considered a bird (Forster et al., 1998) but is now thought to be a dromaeosaurid (Makovicky et al., 2005; Senter, 2007; Turner et al., 2007)—has been thought to be retroverted, as in birds, due to its orientation relative to the rest of the foot as found in situ (Forster et al., 1998). However, the foot was found only in loose articulation (Forster et al., 1998), and it is possible that the toe had rotated about its long axis postmortem, as is the case with the retroverted distal phalanges of the third toe of a specimen of the dromaeosaurid *Microraptor*, in which the plantar surface of the ungual faces cranially (Hwang et al., 2002, fig. 30). Other, better articulated dromaeosaurid feet exhibit an unretroverted hallux (Norell and Makovicky, 1997; Xu et al., 2000), so it would be an interesting example of convergent evolution between birds and a dromaeosaurid if the hallux of *Rahonavis* were retroverted. However, so far no one has put together the bones of the foot of *Rahonavis*, which are now free of the matrix, to determine how they fit.

With the exception of the experimental study by Manning et al. (2006), discussion of pedal function in deinonychosaurs has been theoretical, with no testing of hypotheses. Also, studies comparing deinonychosaurian pedal function to that of other dinosaurs have not yet been done. Here, I report such a study in which functional hypotheses are tested.

Abbreviations

AMNH, American Museum of Natural History, New York City, New York, USA. CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada. GI, Mongolian Institute of Geology, Ulaan Baatar, Mongolia. IVPP, Insistute of Vertebrate Paleontology and Paleoanthropology, Beijing, China. MCF, Museo Carmen Funes, Plaza Huincul, Provincia de Neuquén, Argentina. UA, Université d' Antananarivo, Antananarivo, Madagascar. UCMP, University of California Museum of Paleontology, Berkeley, California, USA. YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

Materials and Methods

Specimens Examined

I examined toe motion in the troodontid *Troodon formosus*; the dromaeosaurids *Neuquenraptor argentinus*, *Rahonavis ostromi*, *Bambiraptor feinbergi*, *Deinonychus antirrhopus*, and *Dromaeosaurus albertensis*; and four non-deinonychosaurian theropods: the coelophysoid *Dilophosaurus wetherilli*, the allosauroid *Allosaurus fragilis*, the alvarezsaurid *Mononykus olecranus*, and the oviraptorosaur *Chirostenotes pergracilis*. The phylogenetic relationships among these taxa are shown in Fig. 2. For the study of *T. formosus* I used casts of the right second toe and distal metatarsus of CMN FV 12340, the phalanges of the left and right second toes of CMN FV 1650, and the phalanges

Figure 1 Casts of phalanges of the second toe of a non-deinonychosaurian theropod (*Mononykus olecranus*) and a deinonychosaur (*Deinonychus antirrhopus*), with indications of distodorsal eminence (left arrow) and proximoplantar process (right arrow). Not to scale. A. *Mononykus olecranus*. B. *Deinonychus antirrhopus*.

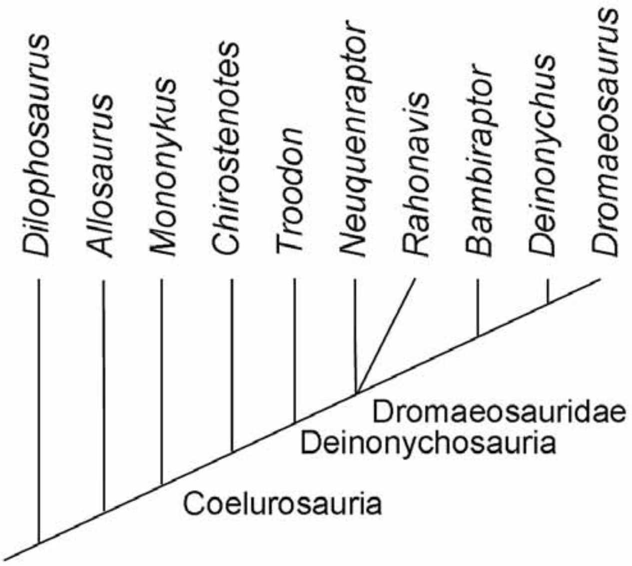


Figure 2 Phylogenetic relationships among the theropods examined in this study, after Senter (2007).

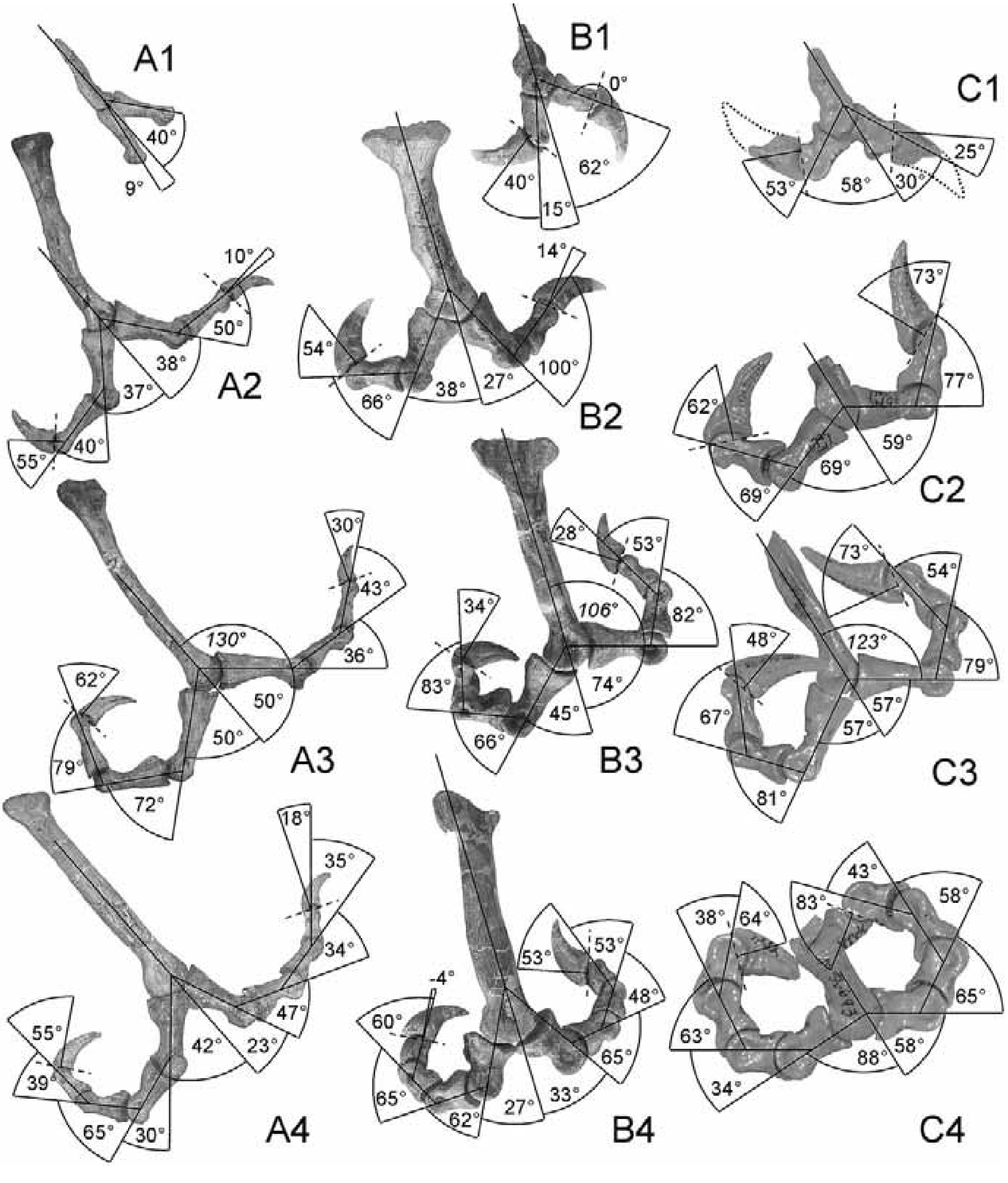


Figure 3 Range of motion in theropod left toes in medial view (reversed right toes in D and G), with metatarsals oriented as if the cranial edge of the metatarsus is at the maximum forward excursion with phalanx III-1 horizontal, as in walking birds immediately before the foot is lifted off the ground (position estimated in E—I). Not to scale. Italicized numbers represent angle made between metatarsus and the ground with the third digit in maximum hyperextension (angle determined by distal end of metatarsal III for specimens in which the bone is has experienced diagenetic sagittal bending, e. g. in *Dilophosaurus wetherilli*). A. *Dilophosaurus wetherilli*. B. *Allosaurus fragilis*. C. *Mononykus olecranus*. D. *Chirostenotes pergracilis*. E. *Troodon formosus* (CMN FV 12340). F. *Troodon formosus* (CMN FV 1650). G. *Troodon formosus* (CMN FV 1650). H. *Troodon formosus* (CMN FV 8539). I. *Neuquenraptor argentinus*. J. *Rahonavis ostromi*. K. *Bambiraptor feinbergi*. L. *Deinonychus antirrhopus*. M. *Dromaeosaurus albertensis*. Number next to each letter in the figure indicates the number of the digit (for example, for *Dilophosaurus wetherilli* A1 indicates the first toe and A2 indicates the second toe). In J4, angle between metatarsal IV and phalanx IV-1 estimated (proximal end of phalanx is missing), based on morphology of articular surface of metatarsal IV.

of the left second and third toes of CMN FV 8539. For *N. argentinus* a colleague (see Acknowledgements) used casts of the second toe and the non-ungual phalanges of the third toe of the left foot of MCF PVPH 77. For *R. ostromi* I used casts of the left foot (missing phalanges III-4, IV-4, IV-5, and the proximal end of IV-1) of UA 8656. For *Bambiraptor feinbergi* I used casts of the complete left foot of AMNH FR 30556. For *D. antirrhopus* I used casts of the left foot (missing only metatarsal I) of YPM 5205. For *D. albertensis* I used bones of the left second toe (missing the ungual) of AMNH 5356. For *D. wetherilli* I used bones of the left foot of UCMP 37302, which is missing only the first ungual. For *A. fragilis* I used bones of the complete left foot of AMNH 680. For *M. olecranus* I used casts of the left foot of GI N 107/6, of which all elements are represented, but metatarsals II and IV are represented only by the proximal and distal extremities, and metatarsal III is represented only by the distal extremity. For *C. pergracilis* I used casts of the complete right foot of CMN FV 8538.

Methods and Hypotheses

For several functional hypotheses (listed below), I used manual manipulation of bones or casts to test predictions regarding range of motion. As in previous studies of theropod hands, I used the limits of joint surfaces as indicators of the limits of motion (Osmólska and Roniewicz, 1969; Galton, 1971; Gishlick, 2001; Carpenter, 2002; Senter, 2005; Senter and Parrish, 2005; Senter and Robins, 2005). This method involves the assumption that at a given joint the articular surface of the distal bone will reach but not pass beyond the edge of the articular surface of the proximal bone. I did not adjust measurements of motion at joints to account for the influence of soft tissues. This is because its influence is expected to be minimal or zero. In birds, range of motion as measured with bare bones has been found to approximate the range of motion found with fully-fleshed individuals (Hutson, 2007). The same is not true for alligators (Hutson, 2007), but this is because the articular cartilages capping the limb bones of alligators are shaped differently from the bony

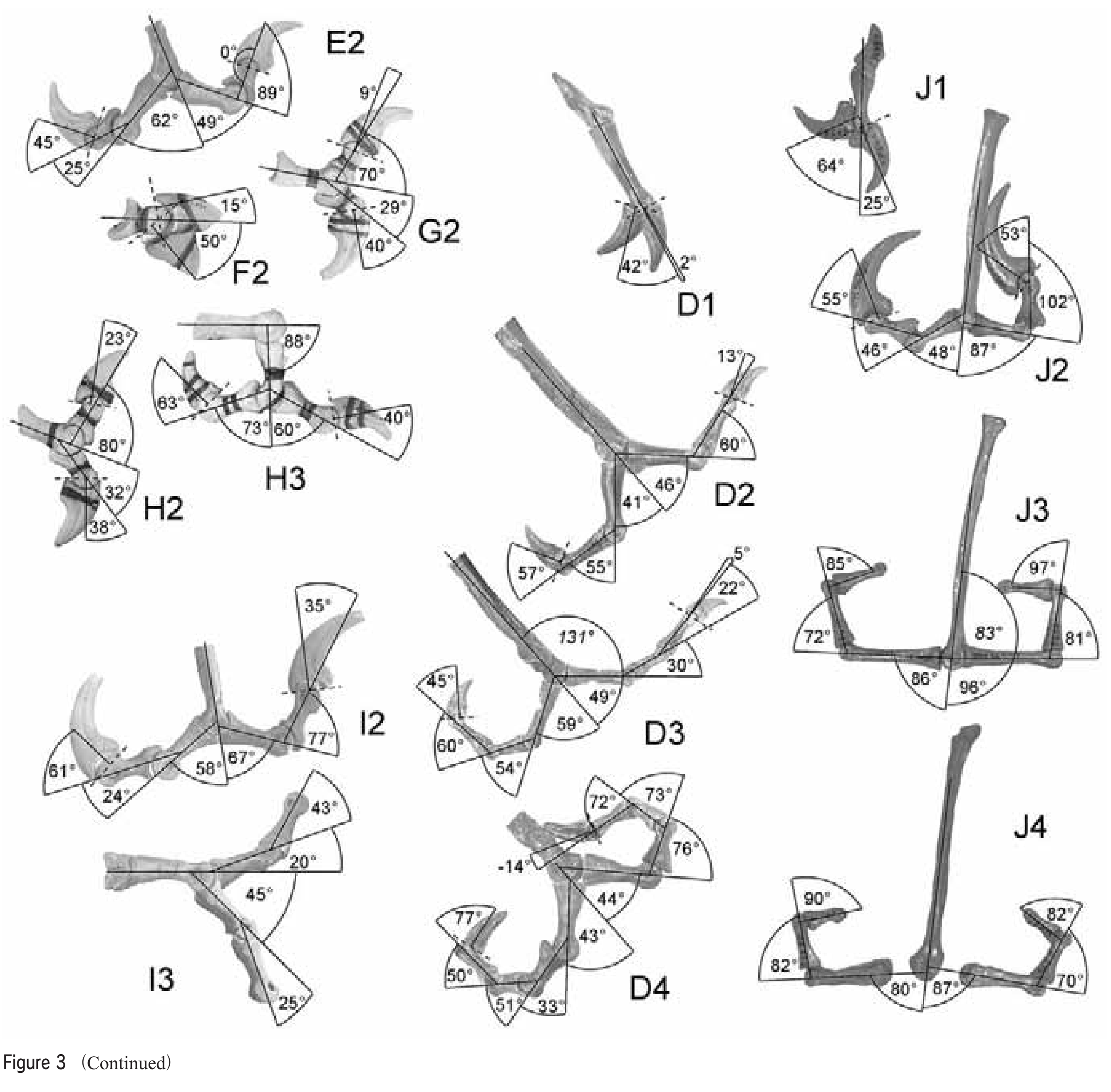


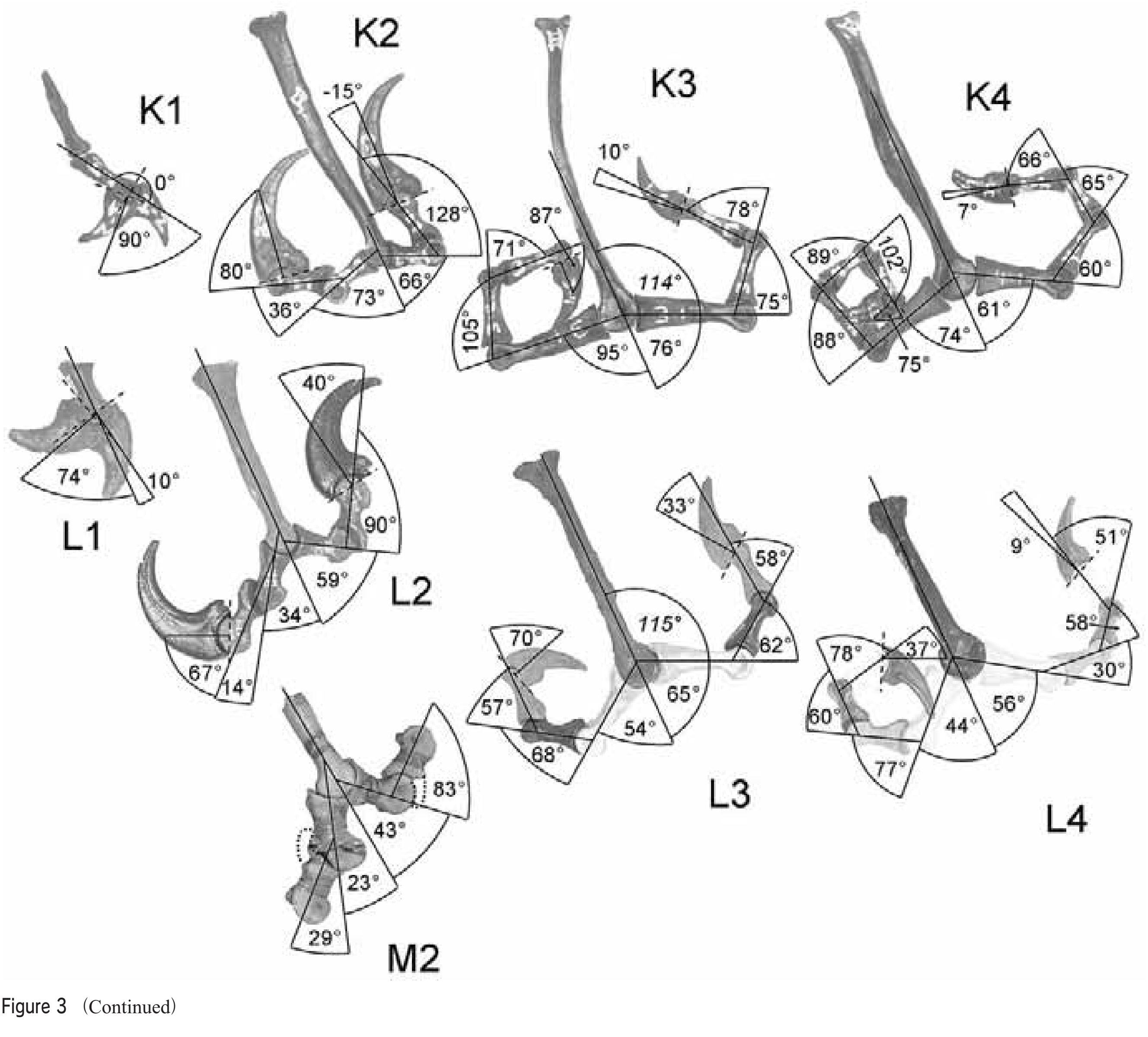
Figure 3 (Continued)

surfaces that they cap, whereas the contours of the articular cartilages match those of the underlying bony surfaces in bird limbs (personal observation). The tight fit between the foot bones of theropods examined in this study indicates that the contours of their articular cartilages must have matched those of the underlying bony surfaces, as in birds. The range of motion found with bare bones should therefore approximate that found in the fleshed-out animal, as is the case with birds (Hutson, 2007).

In two cases, range of motion was estimated. For the metatarsophalangeal joint of the fourth toe of *Rahonavis*, in which the proximal surface of phalanx IV-1 is missing, I used the morphology of the distal articular surface of metatarsal IV to estimate range of motion. For the first interphalangeal joint of the second toe of *Dromaeosaurus*, in which the proximoplantar process of phalanx II-2 is missing, I estimated range of flexion based on the relative size of the process in other dromaeosaurids.

To determine ranges of digital flexion and hyperextension I posed each toe lateral-side down on a sheet of foam rubber, with small foam rubber blocks used for extra support as necessary. Three exceptions are *Neuquenraptor*, casts of which were posed by sticking them together with putty, and *Rahonavis* and *Mononykus*, casts of which were held together by scotch tape applied to the lateral side during posing. I digitally superimposed photos of each toe in full flexion and full hyperextension and used a protractor to measure the arc through which each phalanx could move (Fig. 3). Each non-ungual phalanx was considered to be oriented at 0° to the next proximal element if the long axes of the two elements were collinear. An ungual phalanx was considered to be oriented at 0° to the next proximal element if a line connecting the tips of the dorsal and palmar lips of the proximal articular surface of the ungual (broken line in Fig. 3) was perpendicular to the long axis of the penultimate phalanx (Fig. 3).

To examine three-dimensional range of motion, bony elements were fastened together with plastic-coated wire twists (for larger specimens) or thin, steel wire (for casts of smaller specimens) or putty (*Neuquenraptor*) (Fig. 4, 5). I used scotch tape to hold casts of some metatarsals together. For all but *Dilophosaurus*, *Allosaurus*, and *Neuquenraptor* I posed each foot with the metatarsus perpendicular to a tabletop, with parts of the foot supported as needed by horizontal bars that were clamped to chemistry ring stands (for larger specimens) or loops of thin,



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steel wire (for smaller specimens). *Neuquenraptor* casts were posed with the metatarsus horizontal, clamped to the tabletop, with the phalanges over the edge of the table. The foot bones of *Dilophosaurus* and *Allosaurus* were too heavy to suspend, so I rested their metatarsi on foam rubber sheets and supported partially flexed and partially hyperextended proximal phalanges on blocks of foam rubber or horizontal bars that were clamped to chemistry ring stands.

I used osteological manipulations, as described above, to test the following hypotheses. (1) The distodorsal eminence of pedal phalanx II-1 of deinonychosaurs allows more hyperextension than in other theropods. (2) The proximoplantar process of pedal phalanx II-2 of deinonychosaurs limits flexion more than in other theropods. (3) Mediolateral movement of the dromaeosaurid second toe is more restricted than in troodontids and other theropods. (4) Range of motion in deinonychosaurian toes differs from that of other theropods in ways not addressed by the hypotheses above. (5) The hallux of *Rahonavis* is retroverted. (6) The deinonychosaurian second toe could be used for hook-and-pull digging. (7) The deinonychosaurian second toe was held in hyperextension during locomotion.

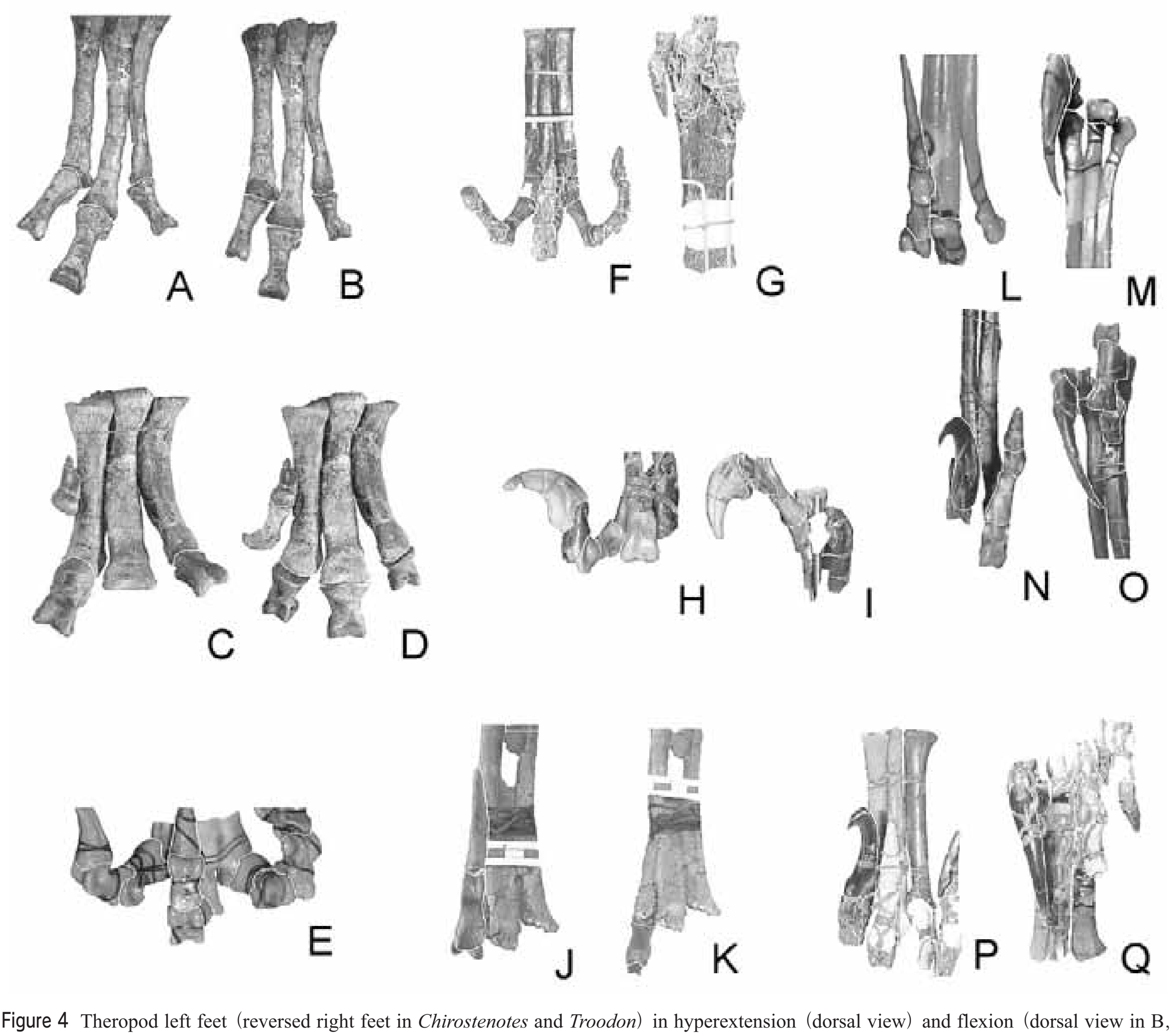


Figure 4 Theropod left feet (reversed right feet in *Chirostenotes* and *Troodon*) in hyperextension (dorsal view) and flexion (dorsal view in B, D, and K; plantar view in the others). Medial is to the viewer's left. Not to scale. A. *Dilophosaurus wetherilli*, hyperextension of proximal phalanges of second through fourth toes. B. *D. wetherilli*, flexion of proximal phalanges of second through fourth toes. C. *Allosaurus fragilis*, hyperextension of proximal phalanges of second and fourth toes. D. *A. fragilis*, flexion of first toe and proximal phalanges of second through fourth toes. E. *Mononykus olecranus*, hyperextension of second through fourth toes. F. *Chirostenotes pergracilis*, hyperextension of second through fourth toes. G. *C. pergracilis*, flexion of second through fourth toes. H. *Troodon formosus*, hyperextension of second toe. I. *T. formosus*, flexion of second toe. J. *Neuquenraptor argentinus*, hyperextension of second toe. K. *N. argentinus*, flexion of second toe. L. *Rahonavis ostromi*, hyperextension of second toe and proximal phalanx of third toe. M. *R. ostromi*, flexion of second toe and proximal phalanx of third toe. N. *Bambiraptor feinbergi*, hyperextension of second and third toes (fourth metatarsal not shown). O. *B. feinbergi*, flexion of second and third toes (fourth metatarsal not shown). P. *Deinonychus antirrhopus*, hyperextension of second through fourth toes. Q. *D. antirrhopus*, flexion of second through fourth toes.

Results

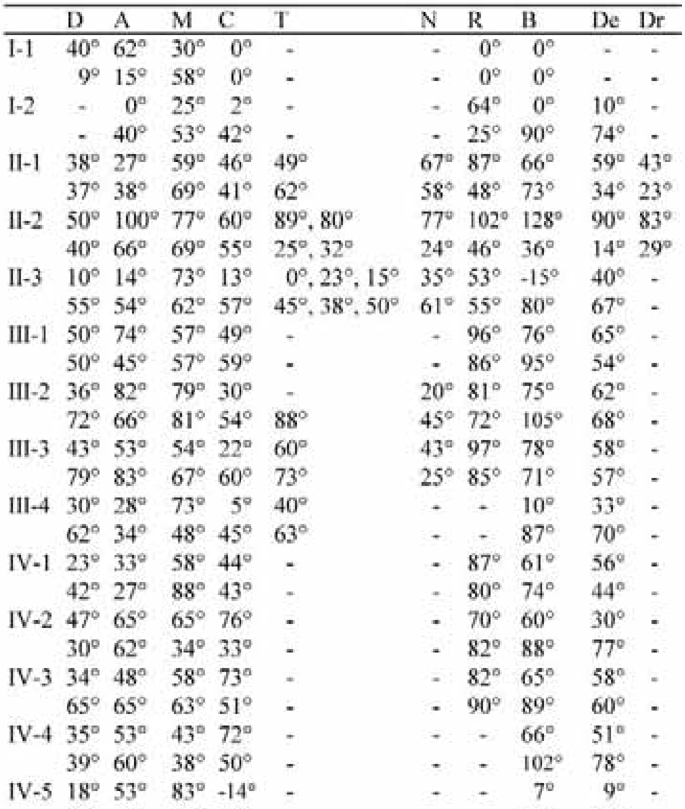
Range of Hyperextension of the Second Phalanx

The range of hyperextension of pedal phalanx II-2 is 70° - 128° in deinonychosaurs （Fig. 3E－L） （Table 1）. It is 60° in *Chirostenotes*, an oviraptorosaur in which the pedal phalanx II-1 exhibits a distodorsal eminence as in deinonychosaurs （Fig. 3D）. Among theropods without the eminence, the range of hyperextension is 50° in *Dilophosaurus*, 100° in *Allosaurus*, and 77° in *Mononykus* （Fig. 3A－C）（Table 1）. There is therefore broad overlap between ranges of hyperextension between theropods with the eminence those without. This shows that the presence or absence of the eminence does not correlate with the range of hyperextension.

Range of Flexion of the Second Phalanx

The range of flexion in the second phalanx is 14° - 36° in deinonychosaurs in which a proximoplantar process is present on phalanx II-2 （Fig. 3E－I, K－M） （Table1）. It is 46° in *Rahonavis*, a deinonychosaur that has a small, plantar keel distal to the proximal extremity of the phalanx instead of a proximally extensive process （Fig. 3J）. It is 40° - 69° in non-deinonychosaurs （Fig. 3A－D）（Table 1）. The proximoplantar process is therefore associated with reduced ability to flex at the joint.

Table 1 Ranges of hyperextension （top numbers） and flexion （bottom numbers） of theropod pedal phalanges.
A＝*Allosaurus*, B＝*Bambiraptor*, C＝*Chirostenotes*, D＝*Dilophosaurus*, De＝*Deinonychus*, Dr＝*Dromaeosaurus*, M＝*Mononykus*, N＝*Neuquenraptor*, R＝*Rahonavis*, T＝*Troodon*.



	D	A	M	C	T	N	R	B	De	Dr
I-1	40°	62°	30°	0°	-	-	0°	0°	-	-
	9°	15°	58°	0°	-	-	0°	0°	-	-
I-2	-	0°	25°	2°	-	-	64°	0°	10°	-
	-	40°	53°	42°	-	-	25°	90°	74°	-
II-1	38°	27°	59°	46°	49°	67°	87°	66°	59°	43°
	37°	38°	69°	41°	62°	58°	48°	73°	34°	23°
II-2	50°	100°	77°	60°	89°, 80°	77°	102°	128°	90°	83°
	40°	66°	69°	55°	25°, 32°	24°	46°	36°	14°	29°
II-3	10°	14°	73°	13°	0°, 23°, 15°	35°	53°	-15°	40°	-
	55°	54°	62°	57°	45°, 38°, 50°	61°	55°	80°	67°	-
III-1	50°	74°	57°	49°	-	-	96°	76°	65°	-
	50°	45°	57°	59°	-	-	86°	95°	54°	-
III-2	36°	82°	79°	30°	-	20°	81°	75°	62°	-
	72°	66°	81°	54°	88°	45°	72°	105°	68°	-
III-3	43°	53°	54°	22°	60°	43°	97°	78°	58°	-
	79°	83°	67°	60°	73°	25°	85°	71°	57°	-
III-4	30°	28°	73°	5°	40°	-	-	10°	33°	-
	62°	34°	48°	45°	63°	-	-	87°	70°	-
IV-1	23°	33°	58°	44°	-	-	87°	61°	56°	-
	42°	27°	88°	43°	-	-	80°	74°	44°	-
IV-2	47°	65°	65°	76°	-	-	70°	60°	30°	-
	30°	62°	34°	33°	-	-	82°	88°	77°	-
IV-3	34°	48°	58°	73°	-	-	82°	65°	58°	-
	65°	65°	63°	51°	-	-	90°	89°	60°	-
IV-4	35°	53°	43°	72°	-	-	-	66°	51°	-
	39°	60°	38°	50°	-	-	-	102°	78°	-
IV-5	18°	53°	83°	-14°	-	-	-	7°	9°	-
	55°	-4°	64°	77°	-	-	-	75°	37°	-

Pedal Range of Motion in Three Dimensions

In all taxa examined, each interphalangeal joint allows motion only in one plane. With one exception, for all metatarsophalangeal joints of the taxa examined at which both the metatarsal and the proximal phalanx are known, the phalangeal articular surface of each metatarsal is too narrow to allow adduction （movement toward the animal's midline） and abduction （movement away from the animal's midline）. This is true even for non-ginglymoid metatarsals. The exception is the fourth metatarsal of *Chirostenotes*, which is sufficiently wider than the proximal phalanx to allow the fourth toe to be adducted and abducted.

In non-deinonychosaurs, the toes spread apart during hyperextension and converge during flexion （Fig. 4A－G, 5A－E）. Flexion of the whole foot could not be illustrated in *Mononykus* due to problems with posing the casts, but manual manipulation shows that in *Mononykus* full pedal flexion results in tight convergence of the second and fourth toes so that their unguals nearly touch, while the third toe protrudes further cranially than in *Chirostenotes* and its ungual remains markedly cranial to those of the second and fourth toes. In *Troodon* the second toe remains adducted （angled toward the animal's midline） through hyperextension and flexion （Fig. 4H－I, 5F－G）. In dromaeosaurids－including *Dromaeosaurus*, which is not illustrated due to problems with posing the specimen－motion of the second toe is sub-orthal in hyperextension and flexion （Fig. 4J－Q, 5H－O）. However, this lack of medial movement of the toe is not due to the ginglymoid shape but is due to the orientation of the phalangeal surface of the second metatarsal.

Other Differences in Range of Motion Between Theropod Taxa

The first metatarsophalangeal joint of *Dilophosaurus*, *Allosaurus*, and *Mononykus* is rounded, allowing a large range of motion（Fig. 3A-C; Table 1）. However, the joint surface is subplanar in *Chirostenotes* and the examined deinonychosaurs, allowing no motion （Fig 3D, J, K; Table 1）. No other trends in range of motion among the taxa examined here, other than those that are mentioned above, are discernible from the results.

Hallucal Orientation

The lateral articular surface of the first metatarsal of *Rahonavis* is flat and fits the medial surface, but not the posterior surface, of the second metatarsal. With the first and second metatarsals correctly articulated, the hallux is unretroverted （Fig 6）. Because the shaft of the first metatarsal is not twisted, this result is consistent with the results of the study of Middleton（2001）, who found that the degree of twisting of the shaft of the first metatarsal is related to the degree of hallucal retroversion in birds. The apparent retroversion of the hallux of *Rahonavis* as found in situ （Forster et al., 1998） is therefore an artifact of postmortem displacement, as in at least one specimen of *Microraptor* （Hwang et al., 2002）.

Test of the Hook-and-pull Digging Hypothesis

Hook-and-pull digging, in which one finger is used to create and enlarge an opening, requires enlargement of the claw of the digging finger. In extant hook-and-pull diggers (pangolins and anteaters), the finger with the enlarged claw is drawn to the palm through the substrate while the palm rests on the substrate, so that the claw tip meets the palm (Hildebrand, 1985). The functional equivalent of this for a deinonychosaurian foot is for the digit with the enlarged claw to be drawn through the substrate to the sole while the ball of the foot rests on the substrate. The hypothesis that deinonychosaurs used the second toe for hook-and-pull digging to open tough insect nests therefore predicts that one digit has an enlarged claw and has sufficient range of motion to press the tip of the claw against the sole. This hypothesis is falsified for *Troodon*, in which permanent adduction of the second toe prevents the claw from being pressed against the sole.

The horny claw on a dromaeosaurid ungual extends beyond the tip of the ungual for a distance of about 50% of the length along the outer curve of the ungual (Xu et al., 2000; Ji et al., 2001; Czerkas et al., 2002). Given this, it is readily apparent from Fig. 3J and Fig. 3K that the range of motion in the second toe allows the claw to be pressed to the sole in *Rahonavis* and *Bambiraptor*. The range of motion in the second toe also allows the claw to be pressed to the sole in *Neuquenraptor* and *Deinonychus*. This is not readily apparent from Fig. 3I and 3L, but in both cases the ungual looks shorter than it really is, because its tip is missing. Once the tip of the ungual is restored and one takes into account the further extension of the horny claw and the extent to which the flesh of the foot extended beyond the plantar surface of the metatarsus, it is evident that the claw can be pressed to the sole in *Neuquenraptor* and *Deinonychus*. The ungual is unknown in *Dromaeosaurus*, but the range of flexion in the second toe resembles that of *Deinonychus*; if its ungual also resembled that of *Deinonychus* in relative size and curvature, then the claw could be pressed to the sole in *Dromaeosaurus*.

Movement of Bird Feet During Walking, and Position of Deinonychosaurian Second Toe During Locomotion

The movies revealed that in extant birds the angle between the dorsal (cranial) surface of the metatarsus is greatest when the foot first contacts the ground and is smallest immediately before the foot leaves the ground; that is, the metatarsus at its most horizontal at the beginning of the step and is at its most vertical at the end of the step (Fig. 7; Table 2). The foot

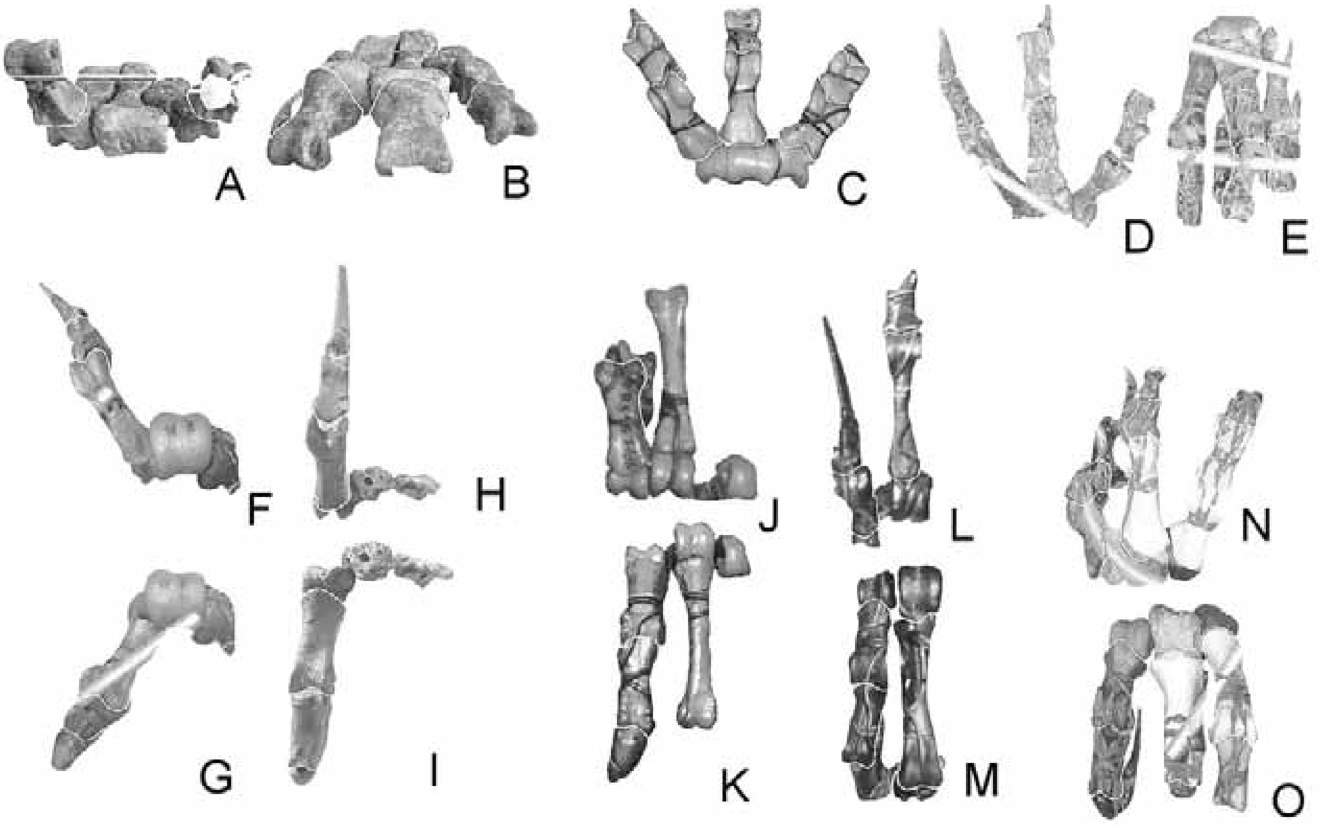


Figure 5 Theropod left feet (reversed right feet *Chirostenotes* and *Troodon*) in hyperextension and flexion from viewpoint of distal end of metatarsus. Medial is to the viewer's left. Not to scale. A. *Allosaurus fragilis*, hyperextension of proximal phalanges of second and fourth toes. B. *A. fragilis*, flexion of first toe and proximal phalanges of second through fourth toes. C. *Mononykus olecranus*, hyperextension of second through fourth toes. D. *Chirostenotes pergracilis*, hyperextension of second through fourth toes. E. *C. pergracilis*, flexion of second through fourth toes. F. *Troodon formosus*, hyperextension of second toe. G. *T. formosus*, flexion of second toe. H. *Neuquenraptor argentinus*, hyperextension of second toe. I. *N. argentinus*, flexion of second toe. J. *Rahonavis ostromi*, hyperextension of second toe and proximal phalanx of third toe. K. *R. ostromi*, flexion of second toe and proximal phalanx of third toe. L. *Bambiraptor feinbergi*, hyperextension of second and third toes (fourth metatarsal not shown). M. *B. feinbergi*, flexion of second and third toes (fourth metatarsal not shown). N. *Deinonychus antirrhopus*, hyperextension of second through fourth toes. O. *D. antirrhopus*, flexion of second through fourth toes.

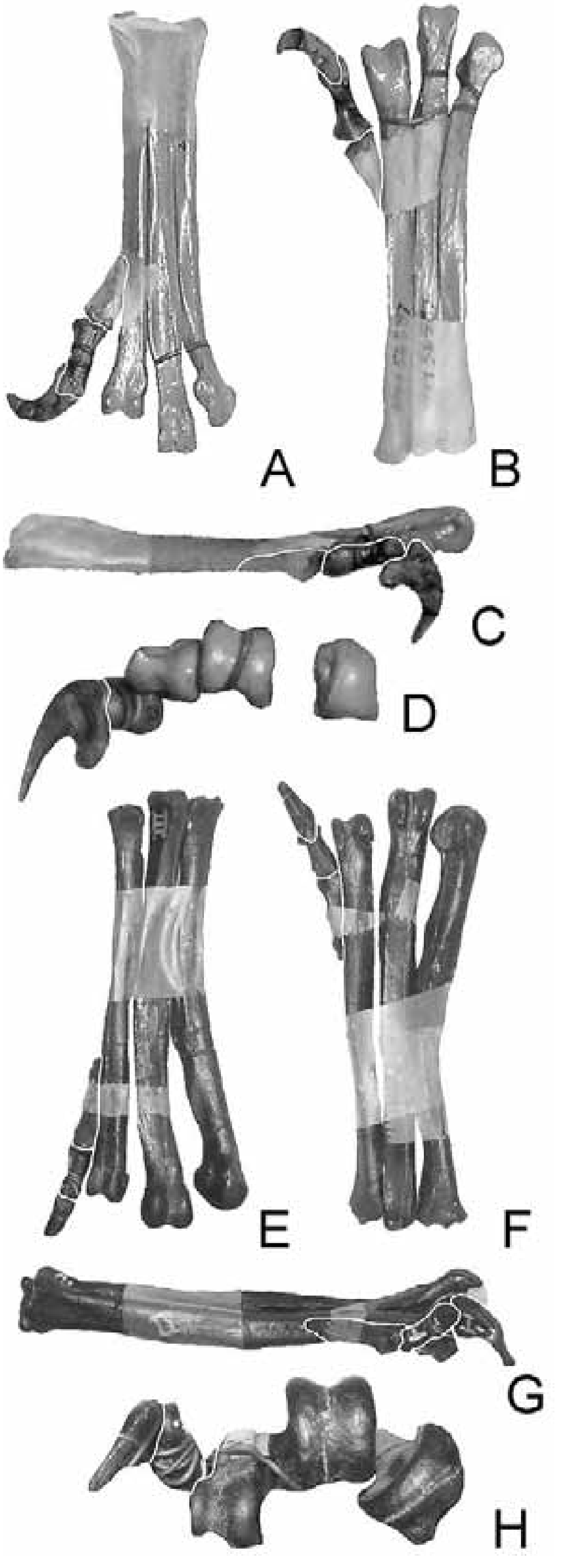


Figure 6 Articulated metatarsus and first toe of *Rahonavis*, with the same of *Bambiraptor* for comparison, showing lack of retroversion of the first toe of *Rahonavis*. （A－D） metatarsus and first toe of *Rahonavis* in dorsal（A）, plantar（B）, medial（C）, and distal（D）views. （E－H）metatarsus and first toe of *Bambiraptor* in dorsal（E）, plantar（F）, medial（G）, and distal（H） views. Note that postmortem warping of the metatarsal shafts of *Bambiraptor* prevents correct alignment of their distal ends （H）.

approaches the ground with all toes extended, and first contact with the ground is made simultaneously by all four toes. For a brief instant the ball of the foot （distal end of metatarsus） and the pad beneath the proximal phalanx of each toe remain barely clear of the ground while all other sub-phalangeal pads contact the ground simultaneously （Fig. 7A）. Then the ball of the foot and all sub-phalangeal pads are pressed to the ground, with the cranial surface of the metatarsus at a very obtuse angle to the ground （Fig. 7B）. As the body of the bird passes over the foot, the metatarsus swings through an arc such that its cranial surface makes a less obtuse angle to the ground （7. 6C）, and then the foot is lifted. The ball of the foot and the most proximal sub-phalangeal pad of each toe are lifted first, while all other sub-phalangeal pads remain in contact with the ground （Fig. 7D）. This lasts only a brief instant, after which all other pads are lifted off the ground simultaneously.

At all points of the avian step cycle during which the toes contact the ground, the third toe is either entirely horizontal （pressed to the substrate） or nearly so. Even at the points during which the proximal sub-phalangeal pad is off the ground while the other pads contact the ground, the proximal phalanx is very nearly horizontal and is only very barely clear of the ground （Fig. 7A, D）.

Under the assumption that deinonychosaurian feet moved in a manner similar to that of bird feet, we can use the above information to constrain the position of the deinonychosaurian second toe relative to the ground during the step cycle. The toe had to occupy such a position as to keep the claw off the ground during all parts of the step cycle at which the foot contacted the ground, even as the angle between the metatarsus and the substrate changed during the step. Because the third toe is horizontal

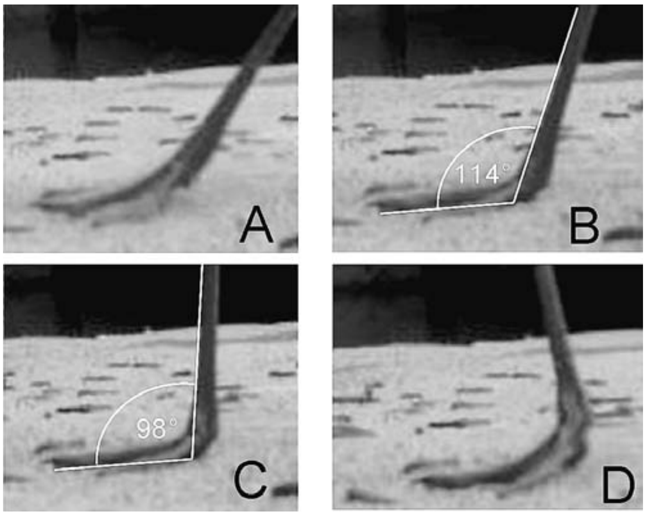


Figure 7 Four phases of the step cycle of a Black-necked Stilt （*Himantropus mexicanus*）. A. contact with the ground is first made simultaneously by all sub-phalangeal pads of the foot except those of the proximal phalanges. B. the ball of the foot （distal metatarsus） and all sub-phalangeal pads contact the ground； labeled angle represents angle A1 of Table 1. C. the ball of the foot and all sub-phalangeal pads remain in contact with the ground while the metatarsus rotates forward； labeled angle represents angle A2 of Table 2. D. the ball of the foot and the proximal sub-phalangeal pad of each toe are lifted, while the rest of the pads remain in contact with the ground； the rest of the pads will then be lifted simultaneously.

while the foot is in contact with the ground, the most vertical possible orientation of the metatarsus is the angle between the metatarsus and phalanx III-1 when the latter is at full hyperextension. The toes in Fig. 3 are oriented so that the fully hyperextended phalanx III-1 is horizontal; the orientation of the metatarsus in Fig. 3 therefore represents the most vertical possible orientation of the metatarsus while the foot is in contact with the ground. As shown in Fig. 3, hyperextension of the second toe with the metatarsus thus oriented keeps the claw of the second toe clear of the ground, while flexion of the second toe is too limited to allow any part of the second toe to clear the ground. Therefore, to keep the claw of the deinonychosaurian second toe clear of the ground when not in use, it must have been held in hyperextension, not flexion.

I did not examine running birds, but during the parts of the step cycle when the foot contacts the ground, the orientation of the avian foot relative to the ground and to the rest of the hindlimb is virtually the same whether a bird is walking or running (Muybridge, 1957). If the same was true for deinonychosaurs, then the second toe was held in hyperextension, not flexion, during both walking and running.

Discussion

Conferral of hyperextensibility is the only previously proposed functional explanation for the deinonychosaurian distodorsal eminence of phalanx II-1 (Ostrom, 1969; Paul, 1988). The results here indicate that while the eminence did not impede hyperextensibility, neither did it confer hyperextensibility. The range of hyperextensibility was instead determined by how far the distal articular surface continued up the dorsal surface of the phalanx. A different functional explanation is therefore needed for the distodorsal eminence. I propose that the eminence increased the mechanical advantage of the toe. The eminence increases the moment arm about the center of rotation of phalanx II-2, and a greater moment arm confers greater mechanical advantage (Kardong, 1998).

One effect of the reduced range of flexion in pedal phalanx II-2 of dromaeosaurids that have the proximoplantar process of phalanx II-2 is that it prevented the claw from puncturing the sole—except in Bambiraptor, in which the range of flexion of phalanx II-1 is greater than in other theropods. In *Troodon* the toe avoided puncturing the sole by remaining adducted during flexion (Fig. 4, 5). It is therefore possible that the potential to accidentally wound themselves in the foot was an important enough selective factor to influence the evolution of the proximoplantar process in deinonychosaurs.

Another effect of the proximoplantar process is that, because it is wrapped around the distal surface of phalanx II-1 during hyperextension, it serves as a bony stop that prevents phalanx II-2 from becoming dislocated by moving proximally over the dorsal surface of phalanx II-1. Such protection would have been of greater importance to theropods that kept that digit in extreme hyperextension than in those that did not, hence its appearance

Table 2 Angle between dorsal (cranial) surface of metatarsus and substrate during footfalls in walking birds. A1 = angle between metatarsus and substrate when foot first contacts ground, A2 = angle between metatarsus and substrate immediately before foot leaves ground. n = number of footfalls examined.

Taxon	A1 range	A1 mean	A2 range	A2 mean
Aratinga solstitialis (Psittaciformes, Psittacidae)	—	142° (n = 1)	—	106° (n = 1)
Ardeotis kori (Gruiformes, Otitidae)	110° - 123°	116° (n = 13)	74° - 87°	82° (n = 12)
Cairina moschata (Anseriformes, Anatidae)	114° - 154°	130° (n = 19)	90° - 124°	105° (n = 18)
Dendrocygna viduata (Anseriformes, Anatidae)	113° - 133°	124° (n = 12)	94° - 116°	108° (n = 12)
Grus canadensis (Gruiformes, Gruidae)	102° - 118°	108° (n = 3)	—	92° (n = 1)
Himantropus mexicanus (Charadriiformes, Recurvirostridae)	114° - 122°	117° (n = 4)	98° - 107°	104° (n = 3)
Larus atricilla (Charadriiformes, Laridae)	121° - 145°	134° (n = 4)	—	98° (n = 1)
Phoeniconaias minor (Ciconiiformes, Phoenicopteridae)	114° - 130°	121° (n = 13)	82° - 109°	97° (n = 8)
Platalea alba (Ciconiiformes, Threskionidae)	—	141° (n = 1)	—	136° (n = 1)
Quiscalus mexicanus (Passeriformes, Icteridae)	142° - 148°	145° (n = 4)	90° - 106°	97° (n = 4)

only in deinonychosaurs. It is possible, of course, that selection pressure influencing the evolution of the process came from both the potential for foot-wounding and the potential for dislocation, not just one or the other.

It is noteworthy that the strong canting of the phalangeal articular surface of the second metatarsal of *Troodon* keeps the second toe adducted (angled toward the animal's midline) throughout its arc of movement. The phalangeal articular surface of the second metatarsal of the troodontid *Saurornithoides mongoliensis* is also strongly canted, and the second toe is held in an adducted, hyperextended position in an articulated specimen (Currie and Peng, 1993). However, the canting is weaker in more basal troodontids such as *Mei long* (in which the canting is almost absent) and *Sinornithoides dongi*; in articulated specimens of both taxa the second toes are hyperextended but not adducted (Russell and Dong, 1993; Xu and Norell, 2004). The orientation of the distal end of the second metatarsal in basal troodontids therefore resembles the dromaeosaurid condition rather than the typical theropod condition or the condition in *Troodon*. The range of motion in the second toes of *Troodon*, as found here, should therefore not be interpreted as representative of troodontids in general. From a functional standpoint the switch to permanent adduction of the second toe in derived troodontids is enigmatic, and I am aware of no hypothesis that explains it.

Chirostenotes, an oviraptorosaur, is more closely related to deinonychosaurs than are the other taxa examined here (Fig. 2). It is therefore possible that the subplanar articular surface at the first metatarsophalangeal joint—present in *Chirostenotes* and deinonychosaurs but absent in the other examined theropods—is a synapomorphy of Oviraptorosauria and Deinonychosauria. However, inclusion of that character in a phylogenetic analysis, which is beyond the scope of this paper, is needed to confirm or falsify that hypothesis.

Colbert and Russell (1969) hypothesized that the enlarged claw of the deinonychosaurian second toe was a digging tool, but they did not specify the type or purpose of the digging. Vertebrates employ three different types of digging with their limbs: humeral-rotation digging, scratch-digging, and hook-and-pull digging (Hildebrand, 1985). Humeral-rotation digging is employed by moles, some frogs, and some amphisbaenians to construct subterranean burrows; it involves moving dirt posteriorly by alternate movements of wide palms through the frontal (coronal) plane from in front of the face toward the flanks (Reed, 1951; Gans, 1974; Emerson, 1976; Hildebrand, 1985). Scratch-digging, for which many mammals use the forelimbs (Hildebrand, 1974) and for which birds use the hindlimbs (personal observation), is used to make depressions in the ground or to construct burrows; it involves parasagittal limb movements to move dirt posteriorly (Hildebrand, 1985). Hook-and-pull digging, employed by anteaters and pangolins to crack into tough insect nests, involves flexion of a single digit with an enlarged claw to puncture a surface and then enlarge the opening (Hildebrand, 1985). It is unlikely that deinonychosaurs used the claw of the second toe for humeral-rotation digging or scratch digging. The former is implausible, and for the latter deinonychosaurs are more likely to have used the unmodified third and fourth toes, because scratch-digging does not require enlargement of an ungual. However, the hypothesis that the second toe was used for hook-and-pull digging is plausible, because that form of digging does require enlargement of the claw of one digit, such as is found in deinonychosaurian feet.

The results of this study show that pedal range of motion in Dromaeosauridae did not preclude hook-and-pull digging with the second toe to crack into tough insect nests. However, just because an animal *can* perform an action does not necessarily mean that it *will*. Also, even if dromaeosaurids did crack into insect nests, it does not necessarily mean that they were mainly insectivorous. Large vertebrates often dwell in termite nests (Estes, 1991; Branch, 1998), so excavation of such nests could have been done to apprehend vertebrate prey. It stretches the imagination to think that *Deinonychus* and *Neuquenraptor*, with femoral lengths of 336 mm and over 180 mm respectively (Ostrom, 1976; Novas and Pol, 2005), subsisted on insects. On the other hand, *Rahonavis* and *Bambiraptor*—with respective femoral lengths of 88 mm and 118 mm (Forster et al., 1998; Burnham, 2004)—were small enough for at least partial insectivory. The shape of the claw is also worth considering. The claws of the nest-cracking fingers of extant pangolins and anteaters are relatively straight, as is that of the presumed nest-cracking theropod *Mononykus* (Senter, 2005). While the results here show that the range of motion in the second toes of dromaeosaurids did not preclude nest-cracking, it remains to be seen whether the strong curvature of the ungual of the deinonychosaurian second toe was conducive to such activity. It is important to note that if the deinonychosaurian toe was used for nest-cracking, that does not preclude other functions for the toe, such as the dispatching of prey. A single structure can have multiple functions.

The finding that the deinonychosaurian second toe was held in extension, not flexion, when not in use is consistent with observations of walking and standing birds. All toes remain extended during locomotion and standing in birds, and it stands to reason that the same would be true of theropods. Because the toes would be extended anyway, no special, extra muscular exertion would be required to keep the deinonychosaurian second toe extended during walking or standing, whereas such exertion would be necessary to keep one toe flexed while the others are extended.

The second toe of dromaeosaurids is generally considered a predatory weapon (Ostrom, 1969, 1990; Paul, 1988; Carpenter,

Figure 8 Right foot of standing Sandhill Crane (*Grus canadensis*) in posterolateral view, showing recurved claw of second toe. The claw is used to wound opponents.

1998). A specimen of the dromaeosaurid *Velociraptor mongoliensis* with its foot at the throat of a ceratopsian, *Protoceratops andrewsi*, appears to confirm the use of the claw as a weapon (Carpenter, 1998; Holtz, 2003), although it is unclear whether the claw was being used for offense or defense in that specimen. There is disagreement as to the use of the second toe of troodontids. Paul (1988) opined that it was used in predation, while Osmólska (1982) and Osmólska and Barsbold (1990) disagreed, arguing that the slender hindlimb bones and the lack of ginglymoid metatarsophalangeal joints in troodontids suggested less capability for forceful movements of the toe than in dromaeosaurids. However, extant emus and cassowaries kick each other during intraspecific fights (Davies, 2002); their metatarsophalangeal joints are only very shallowly ginglymoid, and their metatarsi are more slender than those of troodontids. My own personal observations of the troodontid *Sinovenator changii* (IVPP V 12615) and casts of the troodontids *Sinornithoides youngi* (IVPP V 9612) and *Troodon formosus* (CMN FV 8539) show that in each case the transverse width of the metatarsus at midshaft is greater than one tenth the length of the metatarsus. The midshaft transverse width is less than one tenth the length of the metatarsus in the Emu (*Dromaius novaehollandiae*: AMNH 1708) and the Double-wattled Cassowary (*Casuarius casuarius*: AMNH 963). The Sandhill Crane has a metatarsus that is more slender even than those of emus and cassowaries, and it too kicks vigorously during agonistic encounters (C. Atherton, personal communication, 2006). Therefore, the slenderness of the troodontid metatarsus and its lack of ginglymoid surfaces did not preclude the use of the second toe as a weapon.

The second toe is modified as a weapon both in cassowaries and in the Sandhill Crane. In the former its ungual and claw are enlarged, although not recurved (Davies, 2002). In the latter the claw is strongly recurved, and its tip is protected from wear by rotation of the toe about its long axis so that the claw lies upon its side when the foot contacts the ground (Fig. 8). A zookeeper who has had the misfortune to be kicked and wounded by both a Sandhill Crane and an Emu notes that in both cases the wounding toe was the second toe (C. Atherton, personal communication, 2006), even though its claw is unmodified in the Emu. This suggests that the second toe is in the best position to make contact with a victim during a kick by an animal with a birdlike foot. If that is correct, it is no accident that the second toe is the one that has been convergently modified in cranes, cassowaries, and deinonychosaurs. A kinematic test of that hypothesis is beyond the scope of this study but may be a worthwhile direction for future research. Lastly, one should note that deinonychosaurs did not necessarily use the second toe against prey alone (or at all); they may have used it to attack each other as ratites and cranes do.

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デイノニコサウルス類（恐竜上目：獣脚亜目）における趾骨の比較機能形態学的研究

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要旨：白亜紀の獣脚類であるデイノニコサウルス類は大型でカーブした末節骨を備えた特徴的な第二趾をもつ．本論文はデイノニコサウルス類と他の獣脚類における趾骨の機能に関する最初の比較検討である．本研究ではデイノニコサウルス類（*Troodon, Neuquenraptor, Rahonavis, Bambiraptor, Deinonychus, Dromaeosaurus*）及び他の獣脚類（*Dilophosaurus, Allosaurus, Mononykus, Chirostenotes*）について実際に骨格及びレプリカ標本を動かすことによって趾骨の可動領域の検討を行った．また比較のため現生鳥類の歩行様式の検討も行った．その結果以下のことが示唆された．(1) これまでの研究結果とは異なり，デイノニコサウルス類における第二趾第一趾骨の遠位の背隆起は他の獣脚類ほど第二趾第二趾骨の過伸展性とは関連しない．(2) これまでの研究結果のように，デイノニコサウルス類の第二趾第二趾骨の近位の底突起は趾骨の屈曲を制限する．(3) ドロマエオサウルス類では第二趾はほぼ上下に動く．また*Troodon*では過伸展時から屈曲時まで趾骨は正中に対して内転した状態を保つ．他の獣脚類では第二及び第四趾は過伸展時には外転し，屈曲時には内転する．(4) 第一趾第一趾骨は*Chirostenotes*及び検討したデイノニコサウルス類では可動しないが，他の獣脚類では広い可動域を持つ．(5) これまでの研究結果とは異なり，*Rahonavis*の第一趾は後方を向いていない．(6) ドロマエオサウルス類では，第二趾の可動範囲は頑丈な昆虫類の巣を破壊する動きに関連しているが，*Troodon*ではそうではない．(7) デイノニコサウルス類の第二趾は，歩行時には屈曲状態ではなく，過伸展状態にある．

キーワード：ドロマエオサウルス科，トロオドン科，獣脚亜目，機能形態，後脚