Original Article

Hip heights of the gigantic theropod dinosaurs
Deinocheirus mirificus and *Therizinosaurus cheloniformis*, and implications for museum mounting and paleoecology

Senter Phil[1] and Robins H. James[2]

[1] *Department of Natural Sciences, Fayetteville State University, 1200 Murchison Road, Fayetteville, North Carolina 28303, U.S.A., psenter@uncfsu.edu*
[2] *Department of Biology, Southeast Missouri State University, One University Plaza, Cape Girardeau, Missouri 63701, U.S.A., jhrobins@semo.edu*

Abstract：The gigantic theropod dinosaurs *Deinocheirus mirificus* and *Therizinosaurus cheloniformis*, from the Upper Cretaceous Nemegt Formation of Mongolia, are known only from bones of the forelimb and pectoral girdle. They possess the longest known forelimbs among theropods. To determine whether the lengths of forelimb elements have predictive value for the length of the hindlimb(HL = length of femur + tibia + metatarsal III), we computed Spearman's Rank Correlation Coefficients for HL versus various forelimb bones in ornithomimosaurs, theropods in general, and bipedal dinosaurs in general. We found that scapular length and humeral length correlate well(> 90%) with HL in all three samples, but lengths of the radius and second metacarpal do not. Using regressions of scapular length ✕ HL and humeral length ✕ HL we find that HL is 3323.14 - 3646.50 mm for *D. mirificus* and 3001.10 for *T. cheloniformis*. These two animals have the highest HL in the dinosaur fauna of the Nemegt Formation, and *D. mirificus* has the highest HL of any theropod. Contemporaneous tyrannosaurids could bite no higher than their bellies and thighs, and other contemporaneous predators were too small to have preyed upon them. If *D. mirificus* and *T. cheloniformis* were browsers and contemporaneous herbivores cropped vegetation with the neck in the osteologically neutral position, these two theropods would have competed for foliage only with each other.

Key Words：*Deinocheirus, Therizinosaurus*, Theropoda, Dinosauria, Nemegt Formation

Introduction

One of the goals of paleontology is to reconstruct the ancient world in as much detail as possible. This is made difficult by the high frequency of incomplete skeletons in the fossil record. Two cases in point are the theropod dinosaurs *Deinocheirus mirificus* and *Therizinosaurus cheloniformis*, neither of which is known from a complete skeleton(Fig. 1). These two animals are of interest for several reasons that are related to gigantic size. First, they possess the longest known forelimbs among bipedal dinosaurs. Second, they are the largest theropods in their fauna, that of the Upper Cretaceous Nemegt Formation of Mongolia. Third, each is the largest member of the group of theropods to which it belongs: Ornithomimosauria in the case of *D. mirificus* and Therizinosauroidea in the case of *T. cheloniformis*(Senter, 2007a; Zanno et al., 2009). The combined lengths of the humerus, radius, second metacarpal, and phalanges of the second finger are 2.36 m for *D. mirificus* and 2.40 m for *T. cheloniformis*(Osmólska and Roniewicz, 1970; Barsbold, 1976).

Unfortunately, in each of these two giants the skeleton beyond the forelimb is largely unknown. Known material of *D. mirificus* includes only left and right forelimbs, scapulae, and coracoids, and a few scraps of the axial skeleton, all from one individual(Osmólska and Roniewicz, 1970). Known material of *T. cheloniformis* includes only a right forelimb(without the phalanges of the first and third fingers), coracoid, and scapula with most of the scapular blade missing, all from one individual(Barsbold, 1976). A partial hindlimb was referred to *Therizinosaurus*(Perle, 1982), but that referral is uncertain because the two specimens have no overlapping parts to confirm generic or specific identity.

Casts of the pectoral girdles and forelimbs of *D. mirificus* are commercially available(e.g. at www.dinocasts.com), and a mount of these bones makes an impressive museum display(Fig. 1), especially if mounted next to the forelimb skeletons or complete skeletons of smaller ornithomimosaurs. It would be particularly impressive to be able to mount the *D. mirificus* forelimbs at the height that they occupied in the live animal. Articulated skeletons of theropods and other bipedal dinosaurs show that the tip of the scapula is approximately level with the acetabulum when the vertebral column is horizontal(Fig. 2), and Carpenter(2002)argues convincingly that the scapular blade in theropods was oriented about 60° from the horizontal in life. Therefore, if acetabular height can be determined, cast scapulae of *D. mirificus* can be mounted at approximately the height
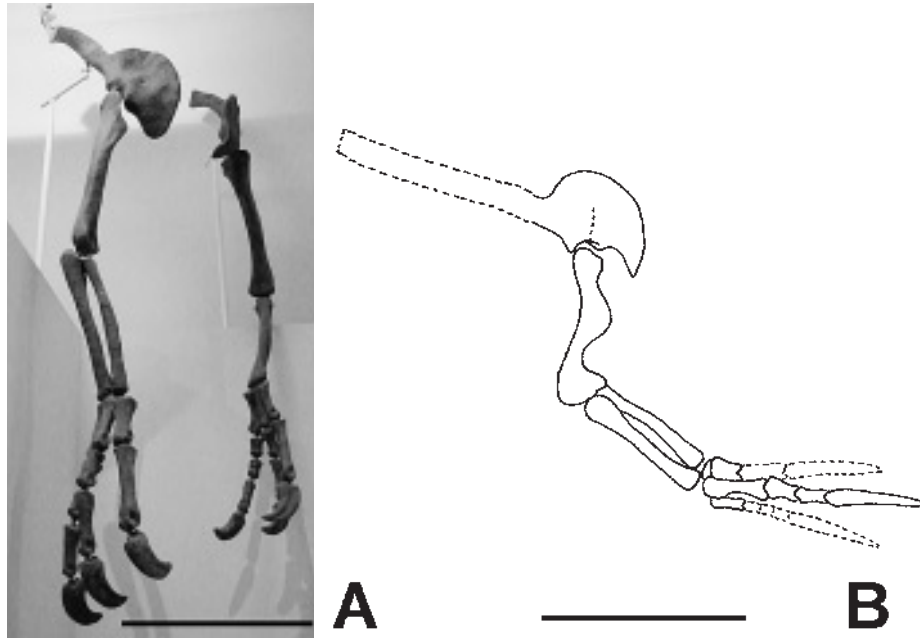
Fig. 1　Known material of *Deinocheirus mirificus* and *Therizinosaurus cheloniformis*. A. *D. mirificus*（mounted cast）. B. *T. cheloniformis*（after Barsbold, 1976）. Scale bars = 1 m.
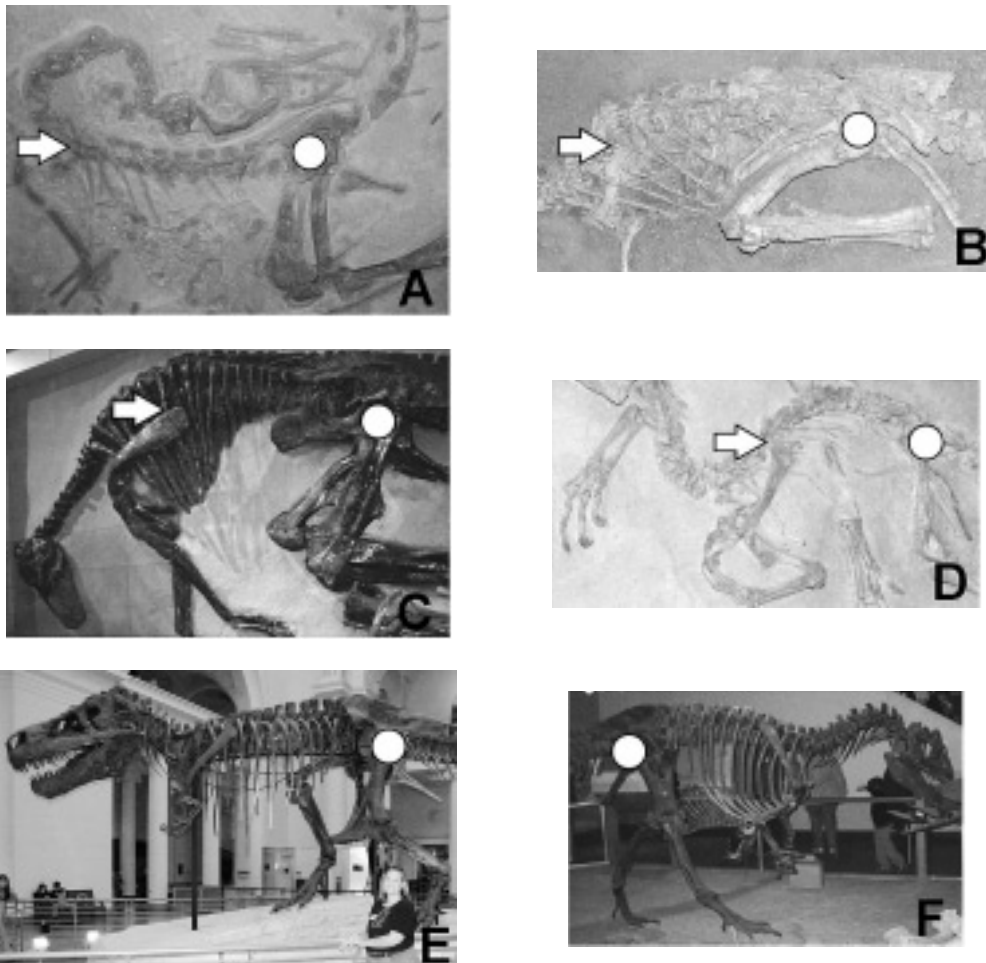

Fig. 2　Articulated skeletons of bipedal dinosaurs（A - D）, showing that the acetabulum（white circle）is approximately level with the tip of the scapular blade（arrow）if the vertebral column is horizontal, and mounted theropod skeletons, showing that the acetabulum is approximately level with the mouth in short-necked theropods. A. The theropod *Compsognathus longipes*（cast）. B. The theropod *Coelophysis bauri*. C. The hadrosaurid ornithopod *Edmontosaurus* sp. D. The heterodontosaurid ornithischian *Heterodontosaurus tucki*（cast）. E. The theropod *Tyrannosaurus rex*. F. The theropod *Allosaurus fragilis*.
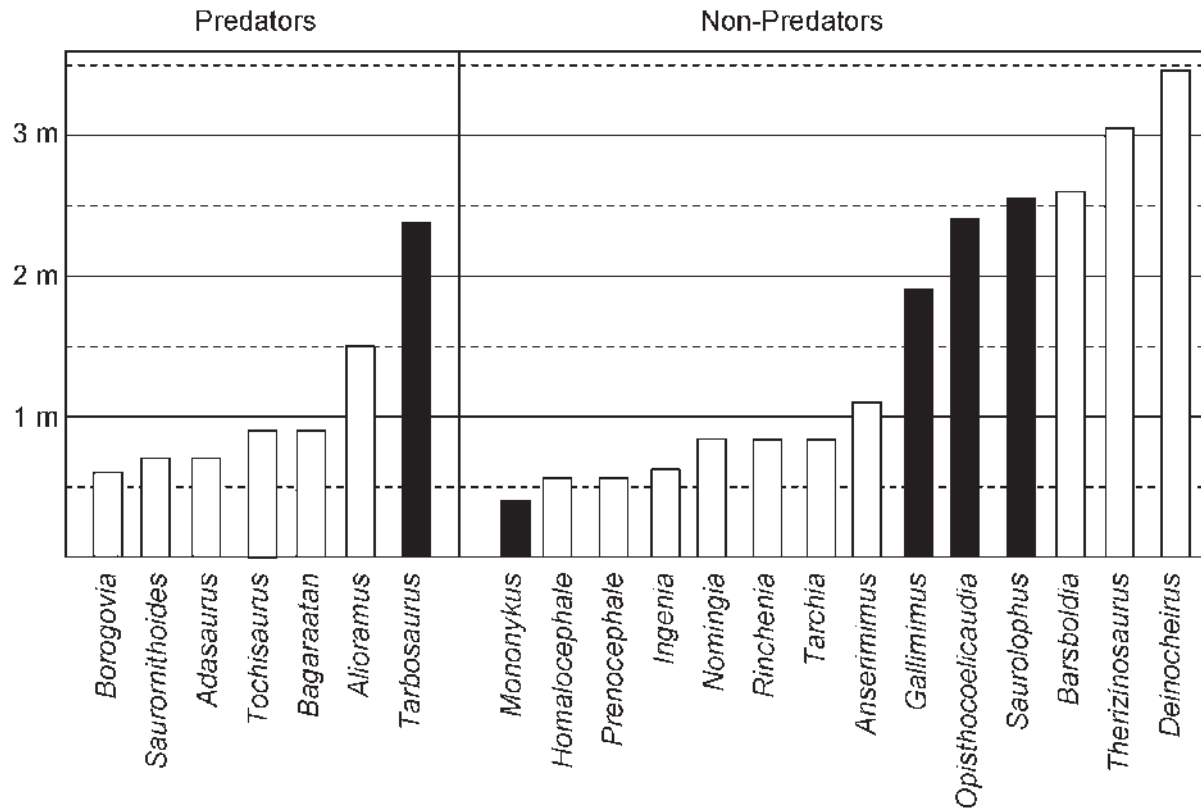
Fig.3   HL（length of femur + tibia + metatarsal II）of dinosaurs from the Nemegt Formation（Upper Cretaceous）of Mongolia（from data in Table 5）.   White bars: estimated HL.   Black bars: known HL.

that they occupied in life and angled so that the forelimbs are also at the correct height.

Determination of acetabular height also has paleoecological implications.   The height of an animal has bearing on its ability to resist predation, because it influences the ability of a predator with a mouth at a particular height to inflict a bite at a given body region.   In addition, the height of a herbivore influences its ability to avoid competition for foliage with contemporaneous herbivores.   This has relevance to *D. mirificus* and *T. cheloniformis* because recent phylogenetic studies（Senter, 2007a; Zanno et al., 2009）show that both *D. mirificus* and *T. cheloniformis* are phylogenetically bracketed by taxa that exhibit specializations for herbivory（Kobayashi et al., 1999; Barrett, 2005; Kirkland et al., 2005; Zanno et al., 2009）.   It is therefore most parsimonious to reconstruct the diets of these two animals as herbivorous.

Because of the implications for museum mounts and paleoecology, we became interested in discovering whether skeletal dimensions outside the forelimb could be determined for *D. mirificus* and *T. cheloniformis*, given only the dimensions of their forelimbs.   In particular, we focused on the length of the hindlimb without the phalanges（femur + tibia + metatarsal III）, hereafter abbreviated HL, a proxy for acetabular height.

Abbreviations

AM, Albany Museum, Grahamstown, South Africa.   AMNH, American Museum of Natural History, New York City, New York, USA.   CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada.   GI, Geological Institute, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia.   IRSNB, Institut Royal de Sciences Naturelles de Belgique, Brussels, Belgium.   IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.   JME, Jura-Museum Eichstätt, Eichstätt, Germany.   LVP, Laboratory of Vertebrate Paleontology, Geological Survey of China, Beijing, China.   LH, Long Hao Geologic Paleontologic Research Center, Hohhot, China.   LV, Museum of Lufeng Dinosaurs, Lufeng, China.   MNHN, Musée National d'Histoire Naturelle, Paris, France.   NCSM, North Carolina State Museum of Natural Sciences, Raleigh, North Carolina, USA.   QG, Queen Victoria Museum, Salisbury, United Kingdom.   ROM, Royal Ontario Museum, Toronto, Ontario, Canada.   SAM, South African Museum, Cape Town, South Africa.   SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.   UA, Université d'Antananarivo, Antananarivo, Madagascar.   UCMP, University of California Museum of Paleontology, Berkeley, California, USA.   USNM, United States National Museum, Washington, D.C., USA.   ZPAL, Paleobiological Institute of the Polish Academy of Sciences, Warsaw, Poland.   ZDM, Zigong Dinosaur Museum, Zigong, China.

Methods

We first sought to determine whether the lengths of pectoral and forelimb bones（scapula, humerus, radius, and metacarpal II）are correlated highly enough with HL.   For this we used the literature to collect data on bone lengths from all bipedal dinosaur taxa for which HL and the length of at least one of the

Table 1　Appendicular bone lengths（mm）in bipedal dinosaurs.　HL = hindlimb length（length of femur + tibia + metatarsal III）.

Taxon 　Specimen	Scapula Information source	Humerus	Radius	Metacarpal II	HL
Deinocheirus mirificus 　ZPAL MgD-1/6	1190 Osmólska and Roniewicz (1970)	938	630	230	–
Therizinosaurus 　*cheloniformis* 　GI 100/15	– Barsbold (1976)	760	550.4	286.8	–
	Other Ornithomimosauria				
Gallimimus bullatus 　GI DPS 100/11	450 Osmólska et al. (1972)	530	350	115	1935
Ornithomimus edmontonicus 　ROM 851	260 Russell (1972)	276	–	100	1220
Sinornithomimus dongi 　IVPP V 1197-10	204 Kobayashi and Lü (2003)	212	145	54.7	883
Struthiomimus altus 　AMNH 5339	350 Russell (1972)	310	228	103	1380
Struthiomimus altus 　AMNH 5257	375 Russell (1972)	360	263	113	1455
	Other Therizinosauroidea				
Neimongosaurus yangi 　LH V0001	– Zhang et al. (2001)	222	180	–	755
	Other Theropoda				
Acrocanthosaurus atokensis 　NCSM 14345	970 Currie and Carpenter (2000)	370	220	116	2587
Allosaurus fragilis 　USNM 4734	652 Gilmore (1920)	310	222	122	1867
Bambiraptor feinbergorum 　AMNH FR 30556	85 Burnham (2004)	105	85	47.8	362
Caudipteryx zoui 　IVPP V 12430	80 Zhou et al. (2000)	69	56	28	446
Coelophysis bauri 　AMNH 7224	124 Colbert (1989) and A. Hungerbuehler, pers. comm. (2008)	134	82	39.7	549
Coelophysis rhodesiensis 　QG/1	– Raath (1969)	100	61	26	563
Compsognathus longipes 　MNHN CNJ 79	51.2 Peyer (2006)	56.3	41	27.3	319.4
Dilong paradoxus 　IVPP V 14243	69 Xu et al. (2004)	96	–	–	501
Dilophosaurus wetherilli 　UCMP 37302	375 Welles (1984)	270	192	105	1387
Gorgosaurus libratus 　CMN FV 2120	876 Lambe (1917)	324	156	98	2634
Juravenator starki 　JME Sch 200	42 Göhlich and Chiappe (2006)	27	19.3	11.5	144.1
Nqwebasaurus thwazi 　AM 6040	64.7 de Klerk et al. (2000)	58.5	44.2	26.5	331.4
Rahonavis ostromi 　UA 8656	82.2 Forster et al. (1998)	–	126.9	–	255.8
Segisaurus halli 　UCMP 32101	93 Camp (1936)	–	–	–	404
Sinraptor dongi 　IVPP V 10600	755 Currie and Zhao (1993)	–	–	–	2062
Tyrannosaurus rex 　AMNH 973	950 Osborn (1906)	–	–	–	2580
	Non-theropods				
Agilisaurus louderbacki 　ZDM 6011	82 Peng (1992)	97	85	–	509.5
Edmontosaurus annectens 　USNM 2414	900 Brown (1913)	610	620	250	2590
Heterodontosaurus tucki 　SAM K1332	86.9 Santa Luca (1980)	82.3	57	23.3	324.9
Mantellisaurus atherfeldensis 　IRSNB 1551	600 Norman (1986)	440	345	115	1740
Iguanodon bernissartensis 　IRSNB 1534	920 Norman (1986)	820	530	145	2260
Jingshanosaurus xinwaensis 　LV 003	844 Zhang and Yang (1994)	430	262	105	2912
Kritosaurus incurvimanus 　ROM 4614	776 Parks (1920)	630	555	185	2351
Lufengosaurus huenei 　LVP-GSC V15	400 Young (1941)	320	181	56	1131
Ouranosaurus nigeriensis 　GDF 300	620 Taquet (1976)	555	416	110	1930
Parksosaurus warreni 　ROM 804	230 Galton (1974)	218	128	–	743
Plateosaurus engelhardti 　SMNS 13200	500 von Huene (1926)	400	240	100	1420
Saurolophus osborni 　AMNH 5220	970 Brown (1913)	500	600	245	2540
Stegoceras validum 　University of Alberta 2	128 Gilmore (1924)	88	49	–	545
Thescelosaurus neglectus 　USNM 7760	186 Gilmore (1915)	–	149	34	782

Table 2　Spearman's Rank Correlation Coefficients between HL（femur length + tibia length + metatarsal III length）and each pectoral and forelimb element.　See text for descriptions of group membership

Group	Scapula	Humerus	Radius	Metacarpal II
All Group	0.957 (n = 34)	0.918 (n = 31)	0.873 (n = 32)	0.860 (n = 27)
Non-theropod Group	0.938 (n = 14)	0.813 (n = 13)	0.895 (n = 14)	0.800 (n = 11)
Theropod Group	0.907 (n = 15)	0.951 (n = 13)	0.786 (n = 13)	0.764 (n = 11)
Ornithomimosaur Group	1.000 (n = 5)	1.000 (n = 5)	1.000 (n = 5)	1.000 (n = 5)

Table 3　Simple linear regression results and predicted HL（femur length + tibia length + metatarsal III length）of *Deinocheirus mirificus* and *Therizinosaurus cheloniformis*.　The regression equations follow the standard B + MX = Predicted Y.

Taxon	Forelimb element	B	MX	Predicted Y
D. mirificus	scapula	251.63 mm	2.5811 × 1190 mm	3323.14 mm
	humerus	245.49 mm	3.6258 × 938 mm	3646.50 mm
	mean			3484.82 mm
T. cheloniformis	humerus	245.49 mm	3.6258 × 760 mm	3001.10 mm

pectoral and forelimb bones listed above had been published by the end of 2008（Table 1）.　We omitted alvarezsaurids from our sample because their forelimbs exhibit extreme reduction that could throw off the results of this analysis（Perle et al., 1994）. We also omitted juveniles.　We computed Spearman's Rank Correlation Coefficients for four groups within our sample of 44 bipedal dinosaurs.　We named these groups the All Group （entire sample without *D. mirificus* and *T. cheloniformis*; n = 36）, the Non-theropod Group（all the non-theropods in the sample; n = 14）, the Theropod Group（all theropods in the sample except *D. mirificus* and *T. cheloniformis*; n = 17）, and the Ornithomimosaur Group（all ornithomimosaurs in the sample except *D. mirificus*; n = 5）.　We used Spearman's Rank Correlations because they are non-parametric tests for association between two variables that are appropriate when the exact functional relationships between pairs of variables are unknown（Sokal and Rohlf, 1994; Zar, 1996）.

Forelimb elements with the highest correlations were retained forward into simple linear regressions with HL to predict HL in *Deinocheirus* and *Therizinosaurus*.　Prediction of an unknown value for an individual on the y-axis in a simple linear regression assumes that the range of known values on the x-axis encompasses the x-axis value for the unknown individual（Sokal and Rohlf, 1995; Zar, 1996）.　We violated that assumption in the estimate of HL of *D. mirificus*, but we were operating within the constraints imposed by the enormous forelimb size of *D. mirificus* and the paucity of available fossil material for the largest bipedal dinosaurian taxa.　Because of the great lengths of limb bones in *Iguanodon bernissartensis*, we did not violate the assumption in the estimate of HL for *T. cheloniformis*.

The correlations between lengths of forelimb elements and HL for the four groups are presented in Table 2.　The highest correlations are those for scapular length × HL and humeral length × HL.　Those correlations are highest（100%）for the Ornithomimosaur Group but are still high（> 90%）for the Theropod Group and the All Group.　Because the correlations are so high in the All Group and because it is the group with the largest sample size, we used the All Group to compute regressions to predict HL in *D. mirificus* and *T. cheloniformis*.

Results

Estimated HL is 3323.14 - 3646.50 mm for *D. mirificus*.　It is 3001.10 mm for *T. cheloniformis*（Table 3）.

Discussion

Sample sizes used here are small, and it is possible that with larger sample sizes our results may have differed somewhat. Part of the reason for the small sample sizes is a lack of bipedal dinosaur skeletons for which the lengths of all the bones used here（scapula, humerus, metacarpal II, femur, tibia, metatarsal III） have been reported.　In some cases a skeleton is missing one or more of these bones.　In others, all six bones are present but the length of at least one was not reported.　In others, the scapula is fused to the coracoid, and an estimate of the length of the scapula alone was not reported.

Table 4   HL （femur + tibia + metatarsal III） in mm for gigantic theropods. e, estimated. The estimate for *Spinosaurus aegyptiacus* has a large margin of error, because it is based on specimens without limb bones.

Taxon	Hindlimb length	Information source
Acrocanthosaurus atokensis	2654e	Senter (2007b)
Carcharodontosaurus		
saharicus	2876e	Senter (2007b)
Giganotosaurus carolinensis	3142e	Senter (2007b)
Saurophaganax maximus	2493e	Senter (2007b)
Spinosaurus aegyptiacus	3200e	dal Sasso et al. (2005, fig. 5)
Tyrannosaurus rex	3224	Brochu (2002)
Tyrannotitan chubutensis	3075	Novas et al. (2005)

Despite this, our results provide reasonable enough estimates of HL in *D. mirificus* and *T. cheloniformis* to draw useful inferences regarding the mounting of casts and regarding the ecology of these animals within the Nemegt community. HL equals acetabular height when the femur, tibia, and metatarsus are in line with each other, perpendicular to the ground. However, in extant animals the knee and ankle are usually somewhat bent during standing and during most or all phases of the step cycle. Therefore, rather than mounting the scapula of *Deinocheirus* with its tip－which is level with the acetabulum in bipedal dinosaurs（Fig. 2）－at 3.323 to 3647 m, museum personnel should position the tip of the scapula somewhat less than this height from the floor. As Carpenter's（2002）work indicates, the long axis of the scapular blade should be slanted at $60°$ from the horizontal to ensure that the forelimbs hang at the correct height.

D. mirificus and *T. cheloniformis* are among the tallest theropods known（Table 4）. In fact, if our estimates are correct, *D. mirificus* is the tallest known theropod. The great height of these two species has implications for their standing as prey items. Nemegt predators of the families *Dromaeosauridae* and *Troodontidae* stood less than one meter tall at the hips（Table 5）. It is therefore difficult to imagine that they posed a threat to *D. mirificus* and *T. cheloniformis*, each of which exceeded three meters in HL. Among Nemegt predators, only the tyrannosaurids exceeded one meter in HL, and of these only *Tarbosaurus bataar* exceeded two meters. Even so, HL is one-third again that of *T. bataar* in *D. mirificus* and *T. cheloniformis*. The mouth in short-necked theropods is approximately the height of the acetabulum（Fig. 2）. A large *T. bataar* would therefore have only been able to bite no higher than the belly or thigh of a standing adult *D. mirificus* or *T. cheloniformis*. The latter would have towered over the predator, which would have been at a convenient height for the intended prey to defend itself by employing the huge, heavy manual claws that are characteristic of both *D. mirificus* and *T. cheloniformis*（Fig. 1）.

D. mirificus and *T. cheloniformis* are the tallest of the known Nemegt dinosaurs. Because none of their contemporaries even approached their hip heights（Table 5）, they were tall enough to forage at a much greater heights than other Nemegt herbivores. If they were browsers, the extra height afforded to their mouths by the presumable possession of the S-curved neck that is typical of theropods placed their mouths high above those of contemporaneous herbivores. This would have provided vertical stratification of foraging, enabling them to avoid competition for plant food with contemporaries other than each other. On the other hand, if *D. mirificus* and *T. cheloniformis* grazed, they would have competed with contemporary grazers, regardless of their great height.

If the contemporaneous sauropods browsed, and if they did so with their necks raised, then they may have competed for browse with *D. mirificus* and *T. cheloniformis*. However, it is likely that sauropods foraged with their necks horizontal or nearly so. In the osteologically neutral pose（ONP）, the pose at which the cervical zygapophyses best fit each other, the neck is nearly horizontal or is held so that the head approaches the ground, not only in sauropods（Stevens and Parrish, 2005a, b）but also in extant animals for which the ONP is known: rabbits and chickens（Taylor et al., 2009）. While extant animals tend to habitually keep the cervical column much more hyperextended than the ONP most of the time（Taylor et al., 2009）, rabbits and chickens orally apprehend food with the neck in a pose that approaches or achieves the ONP（personal observation by P.S., 2009）. Giraffes are often used as extant analogs of sauropods; giraffes tend to keep their necks horizontal when cropping vegetation, although they often keep their necks elevated at other times（Simmons and Scheepers, 1996; personal observation by P.S., 2009）. Therefore, there is no reason to infer that sauropods cropped vegetation with their necks raised.

In sauropods the base of the neck is approximately the height of the acetabulum, so a sauropod feeding with its neck horizontal would have had its head at acetabular height. In the Nemegt sauropod *Opisthocoelicaudia skarzynskii* this height is 2.405 m（Borsuk-Bialynicka, 1977）. In the Nemegt sauropod *Nemegtosaurus mongoliensis* this height is difficult to estimate, because the species is known only from a skull, and skull dimensions correlate poorly with limb

Table 5 HL（femur + tibia + metatarsal III）in mm for dinosaurs of the Nemegt Formation. e, estimate （missing element lengths estimated based on proportions in close relatives）.

Taxon	HL	Information source
Theropoda: Alvarezsauridae		
Mononykus olecranus	357.4	Perle et al. (1994)
Theropoda: Dromaeosauridae		
Adasaurus mongoliensis	700–800e	unpublished photos
Theropoda: Oviraptorosauria		
Ingenia yanshini	600–700e	Barsbold 91986)
Nomingia gobiensis	700–800e	Barsbold et al. (2000)
Rinchenia mongoliensis	700–1000e	Barsbold (1986)
Theropoda: Ornithomimosauria		
Anserimimus planinychus	1100–1200e	Barsbold (1988)
Deinocheirus mirificus	3323–3647e	this paper
Gallimimus bullatus	1935	Osmólska et al. (1972)
Theropoda: Therizinosauroidea		
Therizinosaurus		
cheloniformis	3001.1e	this paper
Theropoda: Troodontidae		
Borogovia gracilicrus	500–700e	Osmólska (1987)
Saurornithoides junior	700–900e	Barsbold (1974)
Tochisaurus nemegtensis	900–1000e	Kurzanov and Osmólska (1991)
Theropoda: Tyrannosauridae		
Alioramus remotus	1000–2000e	Kurzanov (1976)
Bagaraatan ostromi	900–1000e	Osmólska (1996)
Tarbosaurus bataar	2360	Maleev (1974)
Sauropoda		
Nemegtosaurus mongoliensis	2123e	(Nowiński, 1971; see Discussion)
Opisthocoelicaudia		
skarzynskii	2405	Borsuk-Bialynicka (1977)
Ornithopoda		
Barsboldia sicinskii	2600–2700e	Maryańska and Osmólska (1981)
Saurolophus angustirostris	2530	Maryańska and Osmólska (1984)
Pachycephalosauria		
Homalocephale calathoceros	500–600e	Maryańska and Osmólska (1974)
Prenocephale prenes	500–600e	Maryańska and Osmólska (1974)
Ankylosauria		
Tarchia gigantea	750–800e	Maleev (1956)

dimensions in sauropods. The size of the specimen's skull is close to that of the sauropod *Dicraeosaurus hansemanni*, in which HL is approximately 2.123 m（Senter, 2007b）. The skull is much larger than those of specimens of the sauropods *Euhelopus zdanskii* and *Shunosaurus lii* with HL of 1.700 （estimated）and 2.057 m, respectively（Wiman, 1929; Zhang, 1988; Senter, 2007b）. The skull is much smaller than those of

specimens of the sauropods *Camarasaurus grandis* and *Jobaria tiguidensis* with HL of 2.638 and 3.180 m, respectively. Although caution should be exercised with any estimate of sauropod hinglimb length based on skull dimensions, these numbers are consistent with the possibility that in *N. mongoliensis* HL was close to that of *D. hansemanni*, more than those of *E. zdanskyi* and *S. lii*, and less than those of *C.*

grandis and *J. tiguidensis*. If so, *N. mongoliensis* with a horizontal neck did not compete for browse with *D. mirificus* and *T. cheloniformis*.

While the lengths of the scapula and humerus in dinosaurs correlate well with HL, the lengths of the radius and metacarpal II do not. This shows that there is greater variation across Dinosauria in the relative lengths of the antebrachium and hand than in the relative lengths of the scapula and humerus.

Acknowledgements

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