

## ***Aniksosaurus darwini* gen. et sp. nov., a new coelurosaurian theropod from the Early Late Cretaceous of Central Patagonia, Argentina**

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**Abstract:** The theropod dinosaur *Aniksosaurus darwini* gen. et sp. nov. has been recovered from the Upper Cretaceous, Bajo Barreal Formation, of Central Patagonia. *Aniksosaurus darwini* gen. et sp. nov. was a small tetanurine, approximately 2 meters long. *Aniksosaurus* exhibits several unique traits (e.g., cranial cervical vertebrae with dorsoventrally deep neural arches, provided with a pair of cavities at their cranial surfaces; neural canal wide; cranial caudals with ventral sagittal keel, and transverse processes triangular-shaped in dorsal view; manual ungual phalanges robust; ilium with extremely expanded brevis shelf; femur with deep notch for M. Iliotrochantericus; metatarsal and digit IV of pes transversely narrow). Available postcranial bones of *Aniksosaurus* exhibit derived features of Coelurosauria (e.g., ilium with well developed cupped fossa; femur with anterior trochanter proximally projected, almost reaching the level of the articular head; greater trochanter craniocaudally expanded; femoral head rectangular-shaped in cranial aspect; and fibular shaft craniocaudally narrow), as well as characteristics suggesting that the new Patagonian taxon is more derived than some basal coelurosaurians such as compsognathids, *Ornitholestes*, and coelurids. Comparisons with maniraptoriforms (a clade including Ornithomimosauria, Tyrannosauridae, Oviraptorosauria, Alvarezsauridae and Paraves) support that *Aniksosaurus* is less derived than these theropods. In sum, *Aniksosaurus* is here considered as a Late Cretaceous survivor of a basal coelurosaurian radiation.

**Key words:** coelurosaurian, Late Cretaceous, Patagonia, Argentina.

The fossil record of coelurosaurian theropods from South America has considerably increased in the last 15 years. Currently, remains of seven named species of non-avian coelurosaurians have been recovered from different Cretaceous localities of Argentina and Brazil. They are members of a variety of lineages including, among the most conspicuous, the compsognathid *Mirischia asymmetrica* (Naish *et al.*, 2004), and the maniraptoriform *Santanaraptor placidus* (Kellner, 1999, 2001), both from the ?Albian Santana Formation of NE Brazil, the alvarezsaurids *Alvarezsaurus calvoi* and *Patagonykus puertai* (Bonaparte, 1991; Novas, 1996, 1997), possible oviraptorosaurs from NW Argentina (Frankfurt & Chiappe, 1999), derived maniraptorans of unknown affiliation from the Maastrichtian Marilia Formation (Novas *et al.*, 2005), and the dromaeosaurids *Neuquenraptor argentinus* (Novas & Pol, 2005), *Unenlagia comahuensis* (Novas & Puerta, 1997; Novas, 2003), *Buitreraptor gonzalezorum* (Makovicky *et al.*, 2005), and possibly also *Unquillosaurus ceibali* (Novas & Agnolín, 2004). We add to this

list of coelurosaurians a new predatory dinosaur, *Aniksosaurus darwini* gen. et sp. nov., from the Cenomanian Bajo Barreal Formation of central Patagonia (Fig. 1).

The new taxon is known from postcranial remains belonging to at least to five specimens that were recovered from a single fossil locality. The discovery was made by personnel of the Laboratorio de Paleovertebrados of the Universidad Nacional de la Patagonia «San Juan Bosco» (UNPSJB) in the context of the project «Los vertebrados del Grupo Chubut: características y evolución-primer etapa», conducted by the senior author. The new theropod was briefly described by Martínez & Novas (1997) who preliminarily interpreted it as a basal coelurosaurian resembling the Late Jurassic *Ornitholestes hermanni* from North America (Osborn, 1917; Carpenter *et al.*, 2005).

**Institutional abbreviations:** AMNH, American Museum of Natural History, New York; MACN, Museo Argentino de Ciencias Naturales «B. Rivadavia», Buenos Aires; MCZ, Museum of

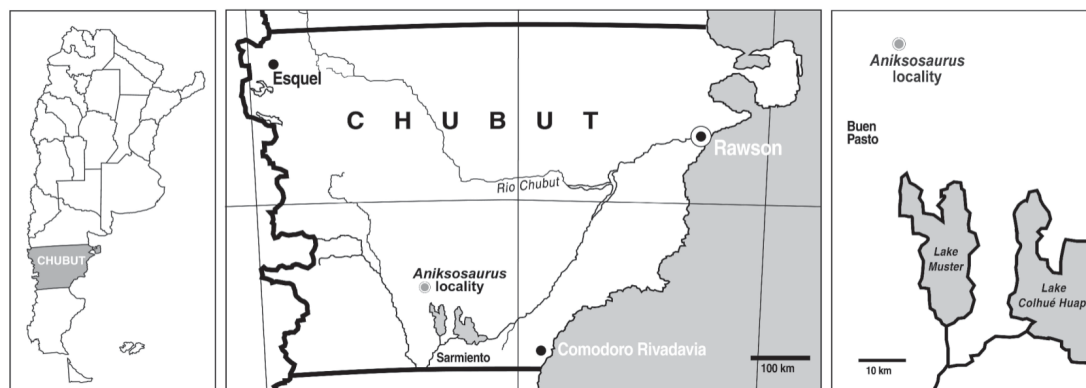


Fig. 1. Geographic location of the Estancia «Laguna Palacios», Chubut Province, central Patagonia, Argentina, where the remains of *Aniksosaurus darwini* gen. et sp. nov. were found.

Comparative Zoology, Cambridge; **MDT-PV**, Museo Desiderio Torres -Paleovertebrados, Sarmiento, Chubut, Argentina; **MOR**, Museum of the Rockies, Bozeman; **NMC**, Canadian Museum of Nature, Ottawa; **YPM**, Yale Peabody Museum, New Haven.

#### MATERIALS AND METHODS

*Studied specimens:* The following specimens were studied: *Allosaurus fragilis* (AMNH 5767), *Deinonychus antirrhopus* (AMNH 3015, MCZ 4371, YPM 5205, 5206, 5236), *Ornitholestes hermani* (AMNH 619), and *Piatnitzkysaurus floresi* (MACN-CH 895).

*Terms of anatomical orientation:* We follow terms employed in avian anatomy (Clark, 1993). «Cranial» and «caudal» are used here in place of «anterior» and «posterior», respectively.

*Systematic nomenclature:* Coelurosauria includes extant birds and all theropods sharing a more recent common ancestor with extant birds than with *Allosaurus* (Holtz et al., 2004).

*Collected material of Aniksosaurus darwini:* The material referred to this taxon was recovered from a single quarry four meters long, two meters wide and one meter thick. The recovered bones includes five tibiae of the right side, thus indicating that the fossil assemblage is made up, at least, by five different specimens. We interpret that they belong to a single species for the following reasons: 1) all the bones correspond to small animals of approximately the same size; 2) at least some bones (e.g., femur, tibia and foot of the holotype specimen, MDT-PV 1/48) were preserved in articulation; 3) duplicate hindlimb elements (e.g., femur, tibia, metatarsals, and pedal phalanges) are anatomically identical to the holotype; 4) available bones exhibit theropod, tetanurine and coelurosaurian synapomorphies

(these derived features are listed in the text below); and, 5) there is no evidence of any other dinosaurian taxon preserved in the quarry. However, with the exception of the holotype specimen (consisting of an articulated right hindlimb), the majority of the bones were found disarticulated, thus we avoid the identification of discrete specimens composed of more than a single bone. For this reason, we confer consecutive numbers to the isolated skeletal elements found in the quarry.

The fossil-bearing tuff is pure and shows no indication of transport (J. C. Sciutto, pers. comm.). Therefore, we tentatively interpret that the taphonomic association of different individuals of *Aniksosaurus darwini* as evidence of gregarious behavior in this theropod species.

Interestingly, there are some differences among the various long bones of *Aniksosaurus*, that mainly concern the robustness of the humerus, the proportion (i.e., area and depth) of the fossa for the insertion of the M. ischiofemoratus (Hutchinson, 2001) on the femur, and the relative size of the crista fibularis of tibia.

On femur MDT-PV1/23 there are tooth marks of small size (3 mm wide), arranged in opposing rows that were probably left by a small scavenging vertebrate.

#### SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842  
SAURISCHIA Seeley, 1887  
THEROPODA Marsh, 1881  
TETANURAE Gauthier, 1986  
COELUROSURIA Huene, 1920

#### *Aniksosaurus*, gen. nov.

*Etymology.* From Greek *aniksi*, «spring», referring to September 21<sup>st</sup> (i.e., the beginning of

the spring in the Southern Hemisphere), the day when the theropod was found; and Greek *saurus*, «lizard».

*Type species.* *Aniksosaurus darwini*, sp. nov.

*Known distribution.* Upper Cretaceous, Central Patagonia, South America.

*Diagnosis.* As for the type and only known species.

***Aniksosaurus darwini*, sp. nov.**

(Figs. 2-13, Table 1-2)

*Holotype.* MDT-PV 1/48. Articulated right hindlimb including femur, fibula, tibia and foot.

*Hypodigm.* Associated material collected at the site where the holotype was discovered: cervical vertebra (MDT-PV 1/14); two dorsal vertebrae (1/6, 1/18); proximal caudal vertebra (1/32); mid-caudal vertebra (1/13); six indeterminate vertebrae (1/7, 1/8, 1/9, 1/15, 1/47, 1/52); three indeterminate neural arches (1/21, 1/30, 1/46); three left humeri (1/29, 1/37, 1/42); two right humeri (1/16, 1/36); left ulna (1/17); manual ungual phalanx (1/40); three left ilia (1/24, 1/33, 1/35); right ilium (1/5); left ischium (1/41); two left femora (1/23, 1/26); two right femora (1/3, 1/27); three left tibiae (1/1, 1/22, 1/34); four right tibiae (1/2, 1/10, 1/28, 1/44); two indeterminate metatarsi (1/4, 1/45); indeterminate phalanx (1/43); and several indeterminate fragments (1/11, 1/12, 1/19, 1/20, 1/25, 1/31, 1/38, 1/39).

*Locality and Horizon.* Laguna Palacios ranch, approximately 30 km north of Buen Pasto, in south-central Chubut Province, 280 km west of Comodoro Rivadavia, Argentina (Fig. 1). The specimens come from a level of volcanic tuff at the upper part of the Lower Member of the Bajo Barreal Formation. The Bajo Barreal Fm. is widely exposed in the southeastern corner of the Argentinian Province of Chubut, central Patagonia. The age of the Bajo Barreal Formation has recently been under dispute, although most authors agree that it falls within the Late Cretaceous. Based on palynological studies of equivalent units, Archangelsky *et al.* (1994) assigned a Late Albian-Cenomanian age to the Lower Bajo Barreal Fm. Recently obtained radiometric Ar-Ar dating ages from tuffs and ignimbrites of the Bajo Barreal Fm. provide ages between 91 and 95.8 Ma (Bridge *et al.*, 2000), a range of ages corresponding to Cenomanian-Turonian. This unit has yielded remains of abelisaurid theropods (*e.g.*, *Xenotarsosaurus bonapartei* and other abelisaurid remains; Martínez *et al.*, 1986; Martínez *et al.*, 1993; Lamanna *et al.*, 2002; Martínez *et al.*, 2004), and a large theropod with hypertrophied pedal un-

gual phalanges resembling *Megaraptor namunhuaiquii* (Martínez *et al.*, 1999). Sauropods found in the same levels include remains of a diplodocimorph (Sciutto & Martínez, 1994), a nearly complete skull and partial cervical series of a yet unnamed basal titanosaurian (Martínez, 1998b, 1999), remains referred to the basal titanosaur *Andesaurus* sp. (Calvo & Bonaparte, 1991; Powell *et al.*, 1989), most of postcranial skeleton of the early titanosaurian *Epachthosaurus sciuttoi* (Martínez *et al.*, 1989, 2004; Powell, 1990), and Titanosaurinae remains (Powell, 1986; Sciutto & Martínez, 1994). A basal igua-nodontian ornithopod, *Notohypsilophodon comodorensis* has also been described from the Bajo Barreal Fm (Martínez, 1998a).

*Diagnosis.* Small theropod with the following autapomorphies: cervical vertebrae with the neural arch pedicels unusually deep (*i.e.*, 2.5 times the height of the centrum); wide neural canal on cervical vertebrae; cranial caudals with ventral sagittal keel; manual ungual phalanges robust; iliac brevis shelf lateroventrally expanded; caudolateral surface of proximal femur with strong depression and rugosities presumably for the attachment for *M. ischiotrochantericus*; metatarsal IV and its correspondent digit transversely narrow.

*Etymology.* In honor of the great naturalist Charles Darwin, who visited Patagonia in 1832-1833, inspiring him to reach clearer interpretations of the evolution of life that changed human thought forever.

## DESCRIPTION

*Aniksosaurus* was a small, albeit robust theropod with an estimated body length of 2 meters and 70 centimeters tall at the level of the pelvic girdle. Following methods explained by Heinrich *et al.* (1993) for estimation of body weight based on measurements from available femora, the body weight of the preserved specimens ranged between 65 through 40 kilograms (G.Casal, pers.comm.). Available specimens of *Aniksosaurus* appear to correspond to adult individuals, as suggested by fusion between neural arches and centra of recovered caudal vertebrae.

### Vertebral column and ribs

Five incompletely preserved vertebrae (*i.e.*, a cervical, a fragmentary dorsal, and three caudals) form the basis of the following description. Also, some fragmentary remains of ribs have been recovered. The available **cervical vertebra** (Fig. 2) preserves the caudal section of the neural arch and the vertebral centrum. It resembles cervical

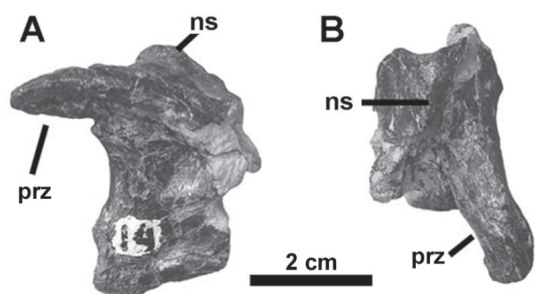


Fig. 2. *Aniksosaurus darwini* gen. et sp. nov. Cervical vertebra (MDT-PV 1/14) in lateral (A), and dorsal (B) views. Abbreviations: ns, neural spine; prz, prezygapophysis.

9 of *Allosaurus* (Madsen, 1976) and the first dorsal of *Deinonychus* (labeled as «cervico-dorsal» in Ostrom, 1969) in the height of the neural arch, bearing epiphyses of small size, a craniocaudally short neural spine, and presence of an excavation on the lateral surface of neural arch. The neural spine of this vertebra is incomplete, but it seems to have been craniocaudally short and dorsoventrally low. Caudal to the neural spine, a large and deep postspinal cavity is present. The postzygapophyses are robust and with lateroventrally oriented and transversely wide articular facets. The epiphyses are represented by small, elliptical rugosities on the dorsal face of the postzygapophyses. The caudal surface of the neural arch exhibits, above the neural canal, a deep pneumatic excavation. The neural canal equals the diameter of the caudal centrum surface. Such features of the cervical vertebra of *Aniksosaurus* differ from those of *Allosaurus* and *Deinonychus*, for example, in which the centrum is transversely wider and inversely the neural canal is smaller in size. The centrum looks proportionally reduced (in transverse diameter). It is slightly excavated laterally and lacking of ventral keel. It is internally hollow, with a thin sagittal wall dividing the centrum into two internal cavities. The available cervical of *Aniksosaurus* differs from those of abelisauroid theropods (e.g., *Ilokelesia*, *Laeviusuchus*) in that the postzygapophyses are closer to the midline than in the latter taxa (in which the neural arch is notably wider transversely), and the epiphyses are small, in contrast with the well-developed ones of abelisauroids. Finally, *Aniksosaurus* lacks the wide pneumatic cavities that are present caudal to the diapophysis as occurs among abelisauroid theropods (e.g., *Ilokelesia*).

Three **caudal vertebrae** have been recovered. One of them (MDT-PV 1/32; Fig. 3) resembles

caudal 4 of *Allosaurus* (Madsen, 1976). The neural spine is high, vertically oriented and rectangular-shaped in side view and placed on the caudal half of the neural arch. Deep, but narrow pre- and post-spinal cavities are present at the base of the neural spine. The prezygapophyses are short and robust. The transverse processes are triangular in dorsal aspect and oriented at an angle of  $40^\circ$  with respect to the axial plane. The centrum is amphicoelous, transversally narrow, V-shaped in cross-section, with a sharp ventral keel. Another caudal (MDT-PV 1/13, Fig. 4) resembles caudal 19 of *Allosaurus* (Madsen, 1976) in the proportionally long and low centrum and reduction and distal placement of the neural spine. The latter structure is craniocaudally short and the prezygapophyses slightly surpass the cranial margin of the centrum. The transverse processes are well developed and caudally projected, with their bases located on the caudal half of the neural arch. The centrum has traces of a ventral longitudinal groove.

#### Forelimb

**Humerus.** This bone (Fig.5A-C) is sigmoid in lateral view, as in *Allosaurus* (Madsen, 1976) and *Piatnitzkysaurus* (Bonaparte, 1986). Unfortunately, any of the five available humeri is complete, so the length of the most complete humerus (MDT-PV 1/16) is estimated to be around 13 cm. The humerus is a robust element, especially towards the extremities, being subcircular in cross-section at mid-shaft. The robustness of this bone clearly distinguishes from the considerably more slender and elongate humeri of *Ornitholestes* and *Coelurus* (Carpenter *et al.*, 2005). Albeit the extremities of the available humeri of *Aniksosaurus* are not entirely preserved, a «twisting» along the longitudinal axis of shaft is apparent: as observed from one of its ends, the angle resulting from the intersection of both proximal and distal transverse axes is around  $50^\circ$ , an angling similar to that of *Piatnitzkysaurus floresi* (MACN-CH 865). The deltopectoral crest is not complete on any of the available humeri, but the preserved portions show that it was well developed. The crest is transversely thick and cranially oriented, as usual in non-avian theropods. Its distal end is bulky and rounded. The lateral surface of the deltopectoral crest shows a weak muscle scar. The humeral shaft bears a large depression on its caudolateral surface for a muscle attachment. Another, but weaker, muscle scar extends diagonally across the caudal face of humerus, distal to the mid-shaft. The distal end of the humerus is cranially bowed; on its cranial surface there are traces of an intercondylar depression. The hu-

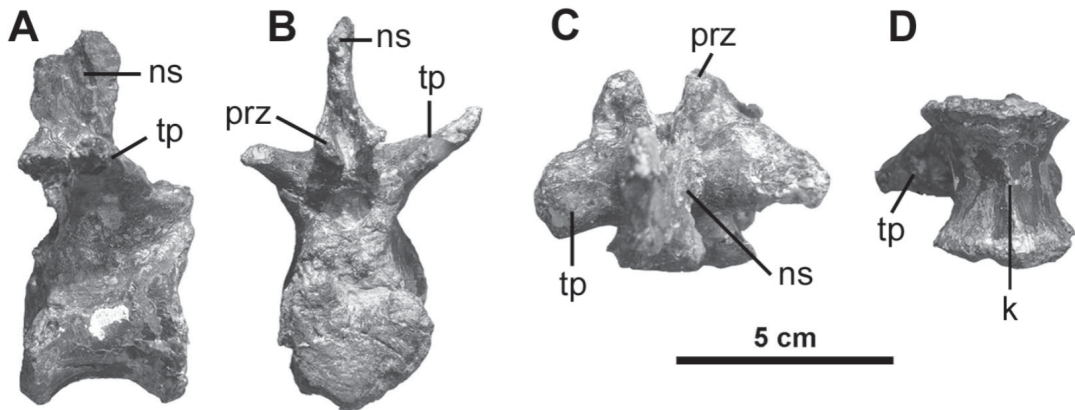


Fig. 3. *Aniksosaurus darwini* gen. et sp. nov. Proximal caudal vertebra in lateral (C), dorsal (D), and ventral (F) views. Abbreviations: k, ventral keel; ns, neural spine; prz, prezygapophysis; tp, transverse processes.

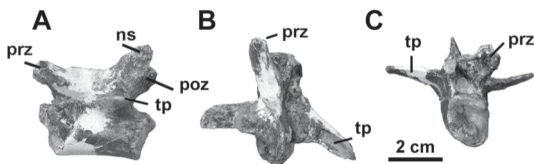


Fig. 4. *Aniksosaurus darwini* gen. et sp. nov. Distal caudal vertebra in lateral (A), dorsal (B) and cranial (C) views. Abbreviations: ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tp, transverse processes.

merus of *Aniksosaurus* is clearly distinguishable from these of abelisauroid theropods (e.g., *Masiakasaurus*, *Carnotaurus*, *Aucasaurus*), in which the dectopectoral crest is poorly developed and the humeral shaft is straight in both cranial and lateral views (Novas et al., 2006).

The only available **ulna** (MDT-PV 1/17) belongs to a left forelimb. The proximal end of the ulna is incomplete, lacking the olecranon process and the articular surface for the humerus. The ulna was found no more than 25 cm away from two of the available humeri (MDT-PV 1/16 and 1/29). Although it is not unreasonable that these forelimb bones may belong to the same individual, the ulna looks proportionally elongate compared to any of the available humeri: our best estimate of the ulna to humerus length ratio is 80%, a condition resembling that of the derived maniraptoran *Deinonychus* (Ostrom, 1969), in contrast to basal tetanurans in which the ulna is shorter with respect to the humerus. The ulna of *Aniksosaurus* seems more gracile than those of

*Allosaurus* and *Piatnitzkysaurus*, but it is more robust in comparison with that of *Ornitholestes* and *Coelurus* (Carpenter et al., 2005). The ulna of *Aniksosaurus* is craniocaudally expanded and has a convex medial surface. The lateral tuberosity delimits the depression for articulation with the proximal end of radius. The ulnar shaft is curved (i.e., caudally convex), albeit it does not form the continuous convexity as observed in derived coelurosaurids (e.g., dromaeosaurids, troodontids), but a change in curvature exists on both proximal and distal ends, resembling basal tetanurans (e.g., *Allosaurus*, *Piatnitzkysaurus*). Notably, the caudal margin of the shaft is sharp, a condition resembling that of *Megaraptor* (Novas, 1998; Calvo et al., 2004), but different from the transversely rounded caudal surface seen in most theropods (e.g., *Piatnitzkysaurus*, *Deinonychus*, birds). The ulna thins distally, but expands again transversely and craniocaudally at its distalmost end. As a result, a planar surface extends across the cranial surface of the distal half of the bone. The distal articular surface of the bone is elliptical, with the longest axis transversely oriented, in contrast with the rounded distal end of coelophysids (Colbert, 1989; Raath, 1977), and the craniocaudally expanded articular surface of *Allosaurus*, dromaeosaurids (e.g., *Saurornitholestes* MOR 660) and ornithomimids. In this sense, the ulna of *Aniksosaurus* resembles the ulna of troodontids in its transversely expanded distal end (*Troodon?* NMC 12.433). Although the forearm is not well documented among basal abelisauroids, both ulna and radius are extremely short in Abelisauridae (e.g., *Carnotaurus*, *Aucasaurus*), in sharp contrast to

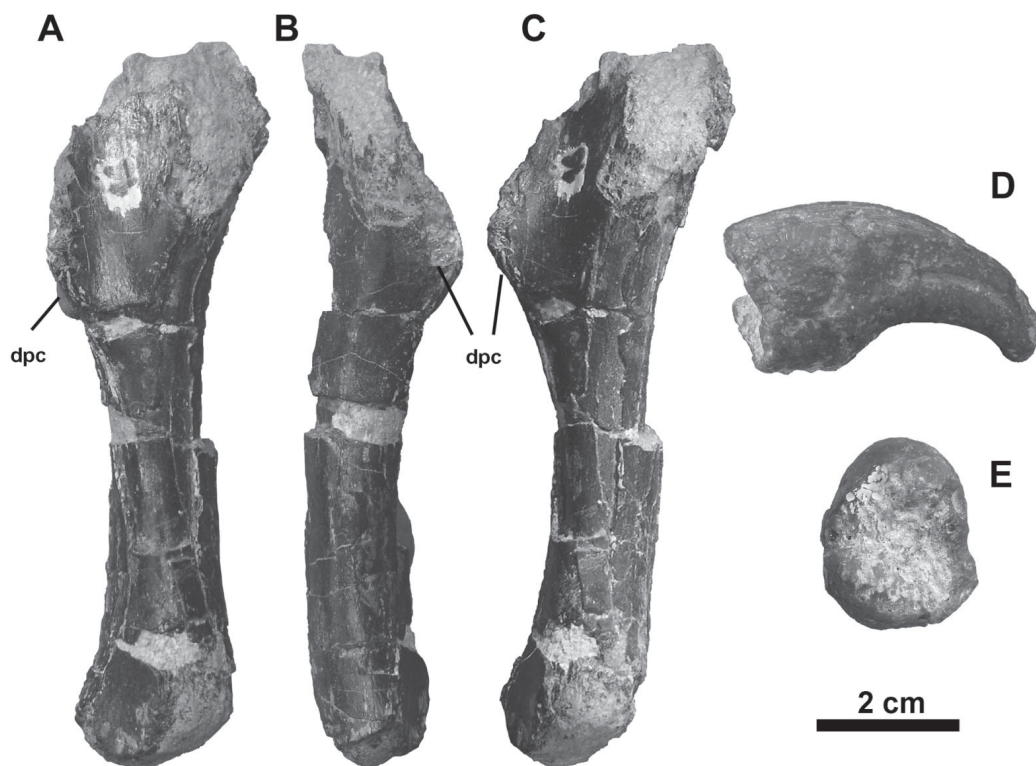


Fig. 5. *Aniksosaurus darwini* gen. et sp. nov. A-C, right humerus (MDT-PV 1/16) in cranial (A), lateral (B) and medial (C) views. D,E, manual ungual phalanx (MDT-PV 1/40) in side (D) and proximal (E) views. Abbreviations: dpc, deltopectoral crest.

the more conservative proportions described for *Aniksosaurus*.

A **manual ungual phalanx**, lacking part of its proximal end, is preserved (MDT-PV 1/40; Fig. 5D,E). This ungual probably belongs to digit I of the manus, based on its remarkable curvature, transverse thickness, axial symmetry, and relative proportions with respect to the available humeri and ulna. However, the ungual cannot be confidently assigned to the left or to the right hand. The ungual phalanx is strongly curved in lateral view, and looks big with respect to the preserved humeri and ulna, thus suggesting that *Aniksosaurus* was a large-clawed animal. Proximally, the ungual phalanx is oval in cross section. The flexor tubercle is prominent and rounded in ventral view.

#### Pelvic girdle

The pelvic girdle of *Aniksosaurus* is represented by four incomplete ilia and an isolated ischium, but none of the pubes has been recovered.

**Ilium.** The iliac blades are broken off, excepting for some portions of the preacetabular wing. However, most of pubic and ischiadic peduncles, acetabular rim, and postacetabular wing are available, thus offering relevant information about iliac anatomy. The craniolaterally excavated pubic peduncle of one of the ilia (Fig. 6) demonstrates that a widely developed cuppedicus fossa was present, and part of its external boundary ridge is represented by a horizontal crest on the lateral surface of the preacetabular wing. The presence of a cuppedicus fossa on the ilium of *Aniksosaurus* constitutes a synapomorphy of Coelurosauria, as it is seen in most of its members (e.g., *Ornitholestes*, *Tyrannosaurus*, Ornithomimidae, *Deinonychus*), being absent in basal tetanurines (e.g., *Allosaurus*) and abelisauroids. The acetabulum is proportionally low, with a faint and slightly laterally projecting supracetabular crest. Thus, the acetabular roof is transversely narrow, a condition differing from that of basal Theropoda (e.g., *Coelophysus*, *Elaphrosaurus*, *Allosaurus*) in which the supracetabular crest is

Table 1. Measurements (in millimeters) of selected bones of *Aniksosaurus darwini* gen. et sp. nov. The asterisk (\*) indicate that the bone is incomplete or deformed.

<b>Cervical vertebra</b>		MDT-PV 1/14				
Centrum height at the cranial articular surface		12				
Height of the neural arch up to the spine base		23				
Height of the neural canal		10				
<b>Anterior caudal vertebra</b>		MDT-PV 1/32				
Centrum length		34				
Centrum width		33				
Centrum height		37				
Total height		80				
<b>Middle caudal vertebra</b>		MDT-PV 1/13				
Centrum length		40				
Length of the neural arch		38				
Total height		17*				
<b>Humeri</b>		MDT-PV 1/16	MDT-PV 1/37	MDT-PV 1/29	MDT-PV 1/42	
Length		110*	?	?	?	
Width of deltopectoral crest		26	29*	?	22	
Distal width		30*	?	?	?	
Least shaft diameter		15	14	13	13	
<b>Ulna</b>		MDT-PV 1/17				
Length		110*				
Proximal width		25				
Least shaft diameter		10				
<b>Manual ungual phalanx</b>		MDT-PV 1/40				
Length		44				
Greatest width		16				
Proximal height		24				
<b>Ilia</b>		MDT-PV 1/33	MDT-PV 1/24			
length		165*	160*			
<b>Femora</b>		MDT-PV 1/3	MDT-PV 1/23	MDT-PV 1/27	MDT-PV 1/26	
Length		247	204*	204*	240*	
Least shaft diameter		27	21	27	29	
Proximal width		60	?	?	?	
<b>Ischium</b>		MDT-PV 1/41				
Preserved length		75				
Probable length		160				
<b>Tibiae</b>		MDT-PV	MDT-PV	MDT-PV	MDT-PV	MDT-PV
		1/1	1/2	1/10	1/22	1/28
length		?	245*	?	270*	?
least width		17	21	18	22	20
						1/34
						250
						19

laterally prominent, and is similar to the more derived condition of coelurosaurs in which this crest is reduced. Moreover, the supracetabular crest of *Aniksosaurus* is less well developed than in the basal maniraptoran *Ornitholestes*. The pubic peduncle of ilium is craniocaudally elongate and has a triangular cross-section, as is usual in Tetanurae. The ischiadic peduncle is smaller, and part of the antitrochanter is discernible on one of the ilia (MDT-PV 35). The antitrochanter is craniocaudally convex and placed more laterally than the pubic peduncle. The postacetabular blade

is craniocaudally elongate, and its lateral surface is convex, reflecting the existence of a well developed ventral fossa for the *M. caudifemoralis brevis*. The brevis fossa expands transversely towards the rear, depicting a paddle-shaped contour in ventral view. The brevis fossa is bounded laterally by a prominent and markedly expanded brevis shelf, which is quadrangular in lateral view (Fig. 6A). The brevis fossa is also limited by a medial shelf (which articulates with the sacral ribs), extending parallel to the brevis shelf, although it is less well developed than the latter structure.

Table 2. Measurements (in millimeters) of holotype specimen of *Aniksosaurus darwini* gen. et sp. nov. The asterisk (\*) indicate that the bone is incomplete or deformed.

	Length	Least width of shaft
Femur	204*	20
Tibia	245*	23
Fibula	225*	4
Mtt II	98	10
Mtt III	124	10
Mtt IV	105	9
Ph I-1	16	
Ph I-2	15	
Ph II-1	31	
Ph II-2	21	
Ph III-1	33	
Ph III-2	30	
Ph IV-1	22	
Ph IV-2	16	
Ph IV-3	15	

**Ischium.** This bone (MDT-PV 1/41) lacks a good part of its cranial border and almost all the distal part of the shaft. The preserved portions of ischium indicate this bone was long and slender, transversely flattened and slightly curved medially. The acetabular surface is represented by a proximal emargination, being caudally bounded by an enlarged, transversely thick iliac peduncle. The rest of the preserved ischium indicates that the obturator process and pubic peduncle (both broken) appear to have been plate-like. The shaft is transversely almost flattened, with its external surface convex.

### Hindlimb

**Femur.** Five femora have been recovered from the quarry, the best preserved of which is MDT-PV 1/3 (Fig. 7). The femur of *Aniksosaurus* is stout, closely resembling the proportions of *Allosaurus* (Gilmore, 1920; Madsen, 1976). The femoral head is transversely elongate and craniomedially projected. The anterior trochanter is wing-shaped and separated from the greater trochanter by a deep cleft, which is narrower than that on the femur of *Allosaurus*. The anterior trochanter is more proximally projected than in *Allosaurus*, reaching a level slightly ventral to the greater trochanter. The anterior trochanter has a marked bulge (accessory trochanter; Hutchinson, 2001) at the base of its cranial margin, as it is seen in *Tyrannosaurus*, for example. The greater trochanter is similar to

those of *Tyrannosaurus* and Ornithomimidae (Osmólska et al., 1972) in being craniocaudally expanded, constituting a derived coelurosaurian condition different from that of *Allosaurus* and more basal theropods (e.g., abelisauroids, coelophysoids) in which the greater trochanter is craniocaudally narrower. Distal to the greater trochanter, there is a small but deep elliptical depression near the caudal margin of the lateral surface of femur, which may represent the site of insertion of the M. ischiotrochantericus (Fig. 7B, istr; Hutchinson, 2001). This feature does not seem as well-developed in smaller specimens. The elliptical depression mentioned above is present, but less marked, in *Piatnitzkysaurus* and probably in *Ceratosaurus* (Gilmore, 1920) and *Tyrannosaurus* (Osborn, 1906).

The fourth trochanter is not complete on any of the femora, but the information taken together from several specimens indicates that it was not prominent, although it was proximodistally very extensive reaching the middle of the shaft. There is a marked muscular trace on the medial surface of the femoral shaft, immediately cranial to the fourth trochanter. This depression is deep and semicircular in contour, and corresponds to the insertion of the M. caudifemoralis longus (e.g., Hutchinson, 2001). This depression is as deep as in *Allosaurus* (Madsen, 1976), *Sinraptor* (Currie & Zhao, 1993), and *Gorgosaurus* (Lambe, 1914), thus contrasting with the condition present in adult specimens of derived coelurosaurs (e.g., ornithomimids, oviraptorans, dromaeosaurids) in which such depression is almost absent.

The femoral shaft is curved in lateral view and triangular in transverse section with the apex projecting cranially. A nutrient foramen perforates the proximal third of the shaft on its cranial surface, as in *Allosaurus*. A sharp and rugose ridge extends along the craniomedial edge of the distal shaft, bounding the adductor fossa present on the medial surface of the femoral shaft. However, the adductor fossa is not as deep as in other theropods such as *Allosaurus*, *Sinraptor*, *Tyrannosaurus* and *Gallimimus*, for example.

Distally, the femur is transversely wide, with well-defined articular condyles. The extensor groove is weakly defined on the craniodistal surface of the femur, a condition that differs from that of *Piatnitzkysaurus*, *Sinraptor*, *Allosaurus* or *Tyrannosaurus* in which this groove is deep. The tibial condyle is transversally narrow, proximodistally low and craniocaudally wide, with a flattened distal articular surface. The fibular condyle is conical, craniocaudally short, and more distally projected than the tibial condyle.



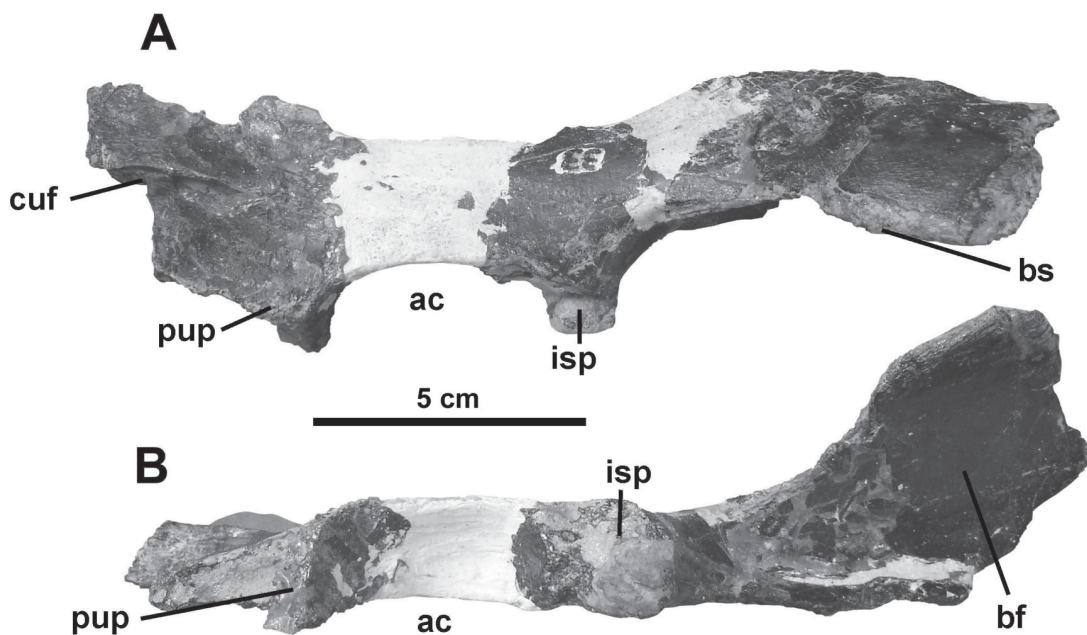


Fig. 6. *Aniksosaurus darwini* gen. et sp. nov. Left ilium in lateral (A) and ventral (B) views. Abbreviations: ac, acetabulum; bf, brevis fossa; bs, brevis shelf; cuf, fossa cuppedicus; isp, ischiadic peduncle; pup, pubic peduncle.

The ectocondylar tuberosity, although incomplete in all the femora, is triangular in cross-section, being proximodistally high and transversely narrow. Between the ectocondylar tuber and the tibial condyle there is a deep, wide, and triangular popliteal fossa, with a weak circular depression in its proximal portion. The shape of this fossa and the presence of the circular depression at its proximal portion are similar to the condition in *Allosaurus*. The fibular condyle is proximodistally high, approximately the same height caudally as the ectocondylar tuberosity. The lateral surface of the fibular condyle has a number of well-marked striations similar to those in *Allosaurus*.

**Tibia.** Seven tibiae are available. The tibia is long and slender, and based on the holotype specimen (MDT-PV 1/50; Fig.8), it is longer (by approximately 20%) than the respective femur. However, the tibia of *Aniksosaurus* is notably more robust and proportionally shorter than in *Coelurus* (Carpenter *et al.*, 2005), in which this bone is slender and considerably more elongate respect to femur length. The cnemial crest of the tibia of *Aniksosaurus* looks prominent, but its incomplete state in all of the available tibiae precludes comparisons of its development (*e.g.*, degree of cranial and proximal projection) to other theropods. The fibular crest is represented by a

sharp, longitudinally extensive and laterally directed flange, restricted to the proximal third of the tibia, being intermediate in lateral outgrowth between the robust and conspicuous one of *Allosaurus* and the less marked of *Deinonychus*. A foramen is present on the lateral face of the shaft, distal to the fibular crest. The tibial shaft is almost straight in lateral view, but slightly curved (*i.e.*, laterally convex) in cranial aspect. Most of the cranial surface of the shaft is flattened, and along its outer side there is a distinct facet for articulation with the fibula. The fibular crest is connected with the outer malleolus of distal tibia through a sharp lateral margin.

Distally, the end of the tibia is moderately expanded transversely and it is not flared medially and laterally to the degree observed in *Allosaurus*, for example. The distal end is craniocaudally compressed and triangular in distal view. The depression for reception of the ascending process of astragalus is craniocaudally shallow and describes a proximodistally high and transversely wide subtriangular contour, indicative that this part of the astragalus (not preserved) was scale-like and well developed. *Aniksosaurus* differs from *Allosaurus* in that the flange that abuts against the proximal edge of the ascending process of astragalus is almost absent. Moreover, the internal border of the ar-

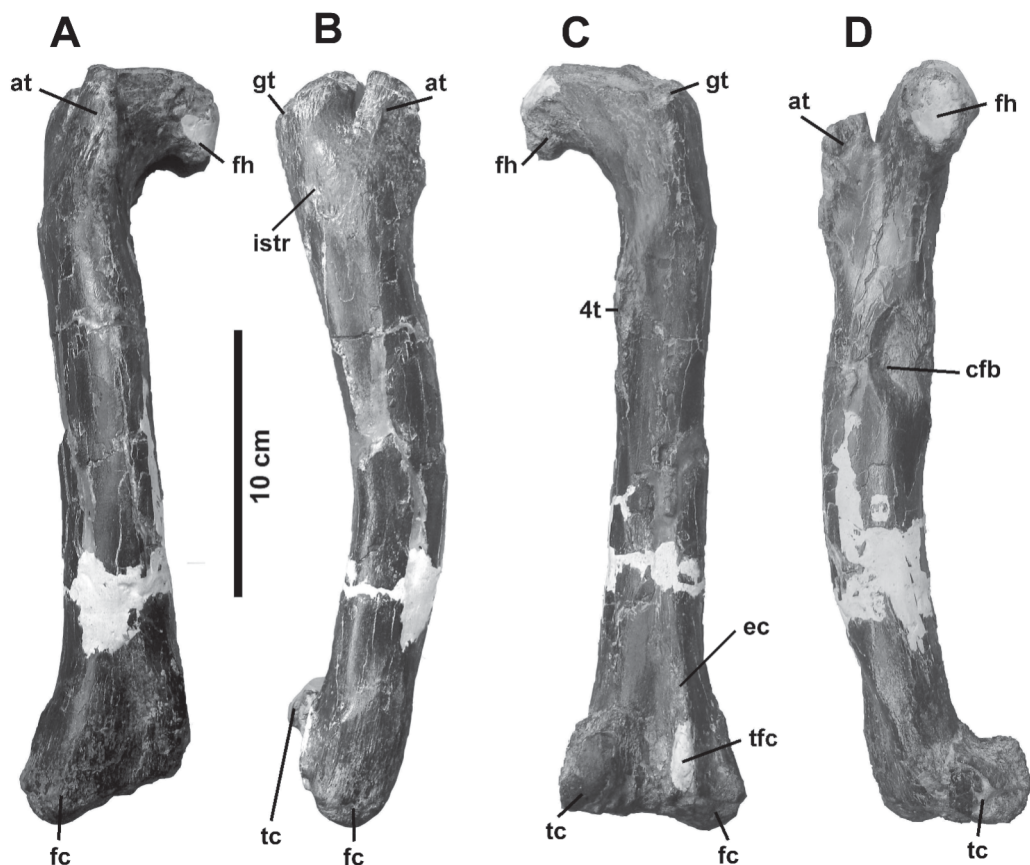


Fig. 7. *Aniksosaurus darwini* gen. et sp. nov. Right femur in cranial (A), lateral (B), caudal (C) and medial (D) views. Abbreviations: at, anterior trochanter; cfb, insertion of *M. caudifemoralis brevis*; ec, ectocondylar tuberosity; fc, fibular condyle; 4t, fourth trochanter; gt, greater trochanter; istr, insertion of *M. ischiotrochantericus*; tc, tibial condyle.

ticular facet for reception of the ascending astragalar process approaches the medial edge of the inner malleolus more closely than in *Allosaurus*, indicating that the ascending process of astragalus in *Aniksosaurus* was transversely wider than in basal theropods (e.g., *Allosaurus*, *Sinraptor*).

The lateral malleolus of the distal tibia is more prominent than the medial one, and exhibits a transversely convex cranial facet for articulation with the distal extremity of fibula. In distal view, the tibia depicts a subtriangular contour, with concave both cranial and caudal margins and the outer malleolus curved and projected caudally.

**Fibula.** Only the right fibula (MDT-PV 1/49) of the holotype has been preserved. It is proximally incomplete and its shaft is somewhat deformed. It is a very long and thin bone, much more slender than in *Allosaurus*, being similar

to that of coelurosaurian theropods (e.g., *Coelurus*, *Gallimimus*; Rauhut, 2003). Its proximal region is craniocaudally expanded and medially excavated, but state of preservation avoids to estimate its depth and extension. Unlike other theropods, a «biceps tubercle» (i.e., the site of insertion of the *M. iliofibularis*) is not obvious. The distal expansion of the fibula for articulation with the tarsus is reduced, also indicating a reduced fibular facet on both calcaneum and astragalus.

**Metatarsals and phalanges.** A well-preserved, articulated right foot is available (MDT-PV 1/51; Fig. 9). The proximal and distal ends of metatarsals I, III and IV are slightly eroded, and the unguis phalanx of digit 2 and the three distal phalanges of digit 3 are not preserved. The foot is approximately symmetrical, with metatarsal III being the longest and metatarsals II and IV virtually equal in length. Metatarsal III

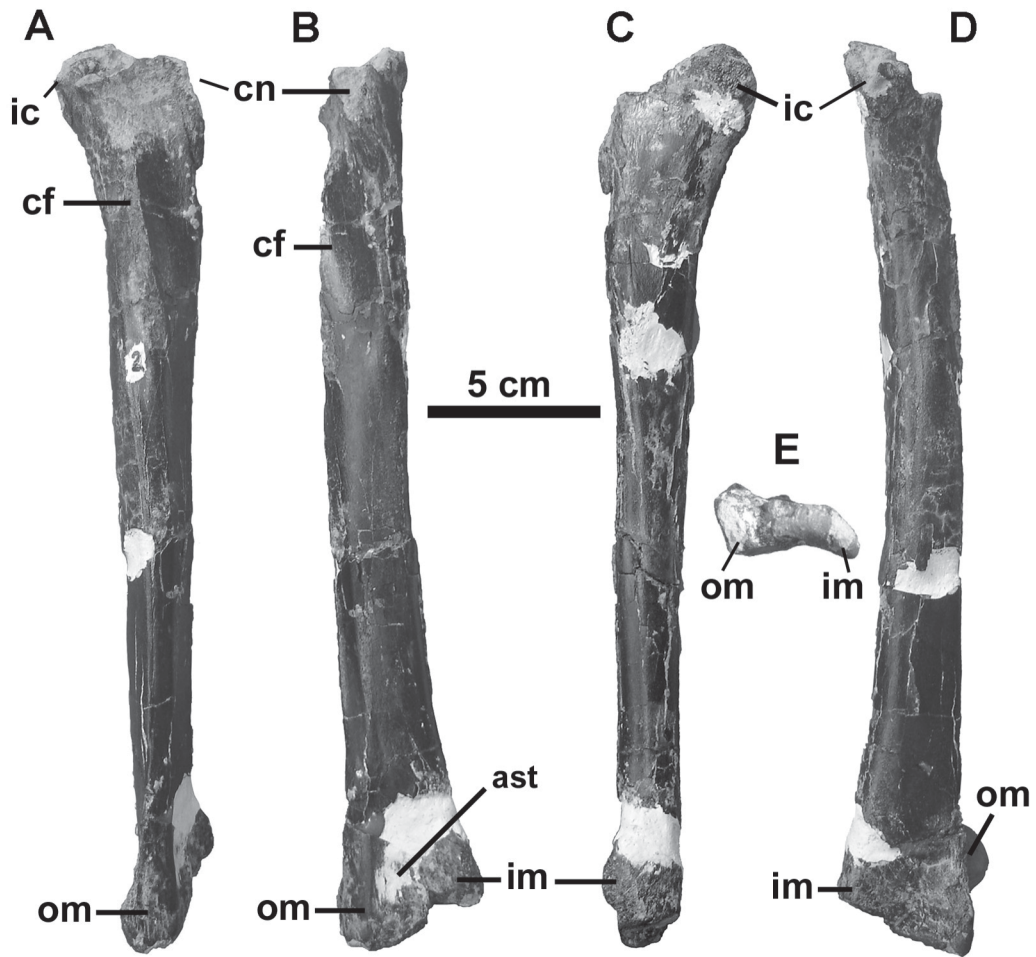


Fig. 8. *Aniksosaurus darwini* gen. et sp. nov. Right tibia (MDT-PV 1/50) in lateral (A), cranial (B), medial (C), caudal (D) and distal (E) views. Abbreviations: ast, astragalar depression; cf, crista fibularis; cn, cnemial crest; ic, inner condyle of proximal tibia; im, inner malleolus; om, outer malleolus.

roughly represents 50% of tibial length (ratio based on measurements of the holotype specimen). The metatarsals are proportionally robust and subcylindrical in cross-section. In general, the foot of *Aniksosaurus* looks more robust than in *Ornitholestes* (Carpenter *et al.*, 2005), especially the pedal phalanges which in the later taxon are longer and more slender than in the Patagonian taxon. The same observation also applies for *Coelurus* (Carpenter *et al.*, 2005) which exhibits very elongate metatarsals, even more than in *Ornitholestes*.

A fragment of **metatarsal I** has been preserved attached to the caudolateral half of metatarsal II. Metatarsal I exhibits a ginglymoid distal articulation with a deep wide lateral ligament pit. **Metatarsal II** is straight in cranial

view, becoming transversely broader towards the distal end. It is mediolaterally compressed along the proximal half, but subtriangular in cross-section distally. It is sigmoid (*i.e.*, caudal convexity) in side view. The distal articulation is partially damaged, but it is documented the presence of a deep medial ligament pit. **Metatarsal III** is straight in cranial view and its shaft becomes transversely broader towards its distal extremity. Its proximal end is craniocaudally expanded, thus forming triangular surfaces for the articulation with the proximal extremities of both metatarsal II and IV. As seen in proximal aspect, the contour of metatarsal III is tear-shaped, being transversely wider cranially than caudally. However, this metatarsal apparently lacks the «hour-glass» shape present among basal tetra-

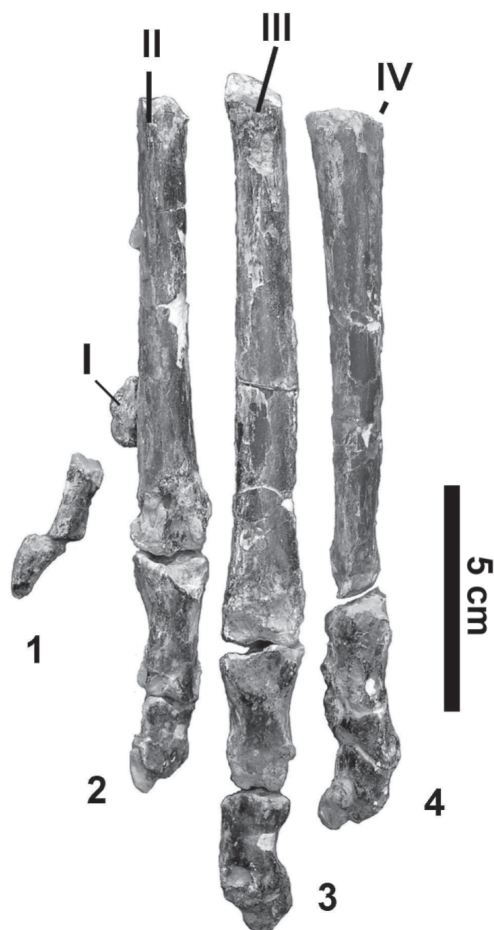


Fig. 9. *Aniksosaurus darwini* gen. et sp. nov. Right foot in cranial view. Abbreviations: 1-4, digits 1 to 4; I-IV, metatarsals I to IV.

nurans (e.g., *Piatnitzkysaurus*, *Sinraptor*, *Allosaurus*, *Ornitholestes*, *Tanycolagreus*). The cranial surface of metatarsal III is transversely convex on its proximally third, becoming flat on the rest of the bone. The medial and lateral surfaces of metatarsal III are nearly flat, but the medial surface for articulation with metatarsal II is slightly grooved longitudinally, thus sharply distinguishing from the caudal surface of metatarsal III. Moreover, the medial facet for metatarsal II exhibits a well defined distal margin, thus clearly separating from the medial surface of distal ginglymoid. The caudal surface of metatarsal II is almost flat, except for its distal third, which is slightly notched both medially and laterally. Such medial and lateral concavities create the room for the distal articulations of metatarsals II and IV, respectively, when the metatarsals are articulated. As a result, the caudal surface of

metatarsal III describes a slight longitudinal ridge between the aforementioned concavities. Such construction of metatarsal III differs from that of *Allosaurus* (Madsen, 1976). In contrast, the metatarsal III of *Aniksosaurus* resembles (albeit it is not identical to) the condition present among derived coelurosaurians (e.g., *Neuquenraptor*). Finally, in contrast to *Allosaurus*, *Megaraptor*, and *Fukuiraptor*, in which the caudal surface of distal articulation is strongly excavated and bounded by a pair of longitudinal ridges, in *Aniksosaurus* this surface is almost flat. The distal articulation of metatarsal III has a wide cranial excavation for extensor ligament, as well as deep collateral ligament pits.

**Metatarsal IV** is nearly straight in cranial view. In proximal view it has a subtriangular outline with a caudomedial projection for articulation with metatarsal III, that is similar to but less developed than those present in *Piatnitzkysaurus*, *Sinraptor*, *Allosaurus* and *Ornitholestes*. The caudal surface of metatarsal IV is almost flat, especially over its proximal two thirds. The distal half of the medial face of the shaft is marked by a diagonal groove directed caudodistally. The distal third of the bone thins transversely, roughly representing half the transverse width of metatarsal III. This condition differs from the other tetanurans (e.g., *Allosaurus*, *Sinraptor*, *Gallimimus*, *Ornitholestes*, *Deinonychus*, *Sinornithoides*) in which the distal end of metatarsal IV is unreduced.

**Pedal phalanges.** The proximal phalanges are longer than the distal phalanges. All of the proximal phalanges have their distal ends slightly craniocaudally and transversely expanded. Ventrally the phalanges are quite flat, more than in *Allosaurus*, *Sinraptor* or *Deinonychus*. The ungual phalanx of digit 1 is subtriangular and lateromedially compressed with a lateral groove. There is no groove on the medial surface.

#### CHARACTER ANALYSIS

*Aniksosaurus* distinguishes from other theropods by the following combination of features:

1) **Caudal cervicals with elevated neural arch pedicles.** The base of the neural arch in the caudal cervical vertebrae is not dorsoventrally higher than the vertebral centrum in Ceratosauria, *Allosaurus*, Tyrannosauridae, *Gallimimus*, *Ornitholestes* and *Deinonychus*. In *Aniksosaurus*, however, the base of the neural arch is 2.5 times the height of the centrum.

2) **Wide neural canal on caudal cervical vertebrae.** In *Aniksosaurus* the neural canal is

wide and elliptical, with a vertical longest axis of the ellipse being dorsoventrally oriented. The neural canal is proportionally small in relation to the vertebral centrum and the base of the neural arch in *Sinraptor*, *Allosaurus*, *Gallimimus*, and *Deinonychus*, for example. The neural canal is also large in *Coelurus* (Carpenter *et al.*, 2005) and *Avimimus* (Kurzanov, 1987) although it is not elliptical but square. Whether this feature of *Aniksosaurus* was related with allometric changes during ontogeny remains unknown.

3) **Cranial caudals with saggital ventral keel.** There is a longitudinal ventral groove on the cranial caudal centra of many theropods: *Dilophosaurus*, *Ceratosaurus*, *Carnotaurus*, *Torvosaurus*, *Piatnitzkysaurus*, *Sinraptor*, *Allosaurus*, *Gallimimus*, *Ornitholestes*, *Coelurus*, *Deinonychus* and Alvarezsauridae (Bonaparte, 1991; Bonaparte *et al.*, 1990; Britt, 1991; Carpenter *et al.*, 2005; Currie & Zhao, 1993; Madsen, 1976; Novas 1997; Osmólska *et al.*, 1972; Ostrom, 1969). In this context, the single saggital keel present in the proximal caudals of *Aniksosaurus* is tentatively interpreted as an autapomorphic feature of this taxon, pending on more information about the distribution of this character within Tetanurae.

4) **Robust manual unguals.** In most theropods, the manual ungual phalanges are strongly compressed transversely. The height to width ratio of the articular surface of the manual ungual phalanges is 1.54 for *Tarbosaurus*, 1.58 for *Dilophosaurus*, 1.6 for *Sinraptor*, 1.83 for *Allosaurus* and 2.34 for *Deinonychus* (Maleev, 1955; Welles, 1984; Currie & Zhao, 1993; Gilmore, 1920; Ostrom, 1969). Conversely, the ratio in *Aniksosaurus* is 1.1, thus demonstrating the presence of manual unguals of heavy construction, which look large when compared with any of the preserved long bones (*e.g.*, humeri, ulna, femora, tibiae) of this taxon. In contrast, the manus of *Coelurus* (Carpenter *et al.*, 2005) and *Tanycolagreus* (Carpenter *et al.*, 2005) are delicate and slender, in sharp contrast with the robust construction of the manus of *Aniksosaurus* inferred on the basis of its ponderous ungual. The robust condition of the ungual phalanges of *Aniksosaurus* remembers some ornithomimids and alvarezsaurids, in which the height to width ratio is lower than 1.5 (P. Makovicky, pers. comm). However, manual unguals of these two derived coelurosaurian clades are not trenchant and curved as in *Aniksosaurus*.

5) **Brevis shelf of the ilium extremely expanded and projected lateroventrally.** In theropods, the brevis shelf is a well developed ridge oriented ventrolaterally, serving as exter-

nal boundary of the brevis fossa. In ventral view the brevis fossa is rectangular-shaped, even in *Ceratosaurus* (Gilmore, 1920) and abelisaurids (*e.g.*, *Carnotaurus*; Bonaparte *et al.*, 1990) in which the brevis shelf is well developed. Moderately expanded brevis shelves are documented in *Dilophosaurus*, *Piatnitzkysaurus*, *Allosaurus*, *Sinraptor*, and basal coelurosaurians such as *Ornitholestes*, *Tyrannosaurus* and *Ornithomimus* (in some derived maniraptorans, such as the dromaeosaurid *Deinonychus*, a wing-like brevis shelf is absent on the caudolateral portion of the ilium; Novas, 1996). *Aniksosaurus* clearly distinguishes from theropods mentioned above in that the caudal half of brevis shelf is strongly projected outside, thus resulting in a fan-shaped expansion in ventral view. Interestingly, the condition described for *Aniksosaurus* is reminiscent of that in the alvarezsaurid *Shuuuuaia deserti* (Chiappe *et al.*, 2002) as well as the flightless Cretaceous bird *Patagopteryx deferraris* (Alvarenga & Bonaparte, 1992).

6) **Caudolateral surface of proximal femur with strong depression and rugosities presumably for the attachment for M. ischiotrochantericus.** On the caudolateral surface of proximal femur, *Aniksosaurus* has a strong semilunar bulge, delimiting a well-marked depression on some femora, which presumably served for the attachment of the M. ischiotrochantericus (Hutchinson, 2001). On the contrary, such depression is absent in ceratosaurians (*e.g.*, *Ceratosaurus*, *Carnotaurus*, *Xenotarsosaurus*), basal tetanurans (*e.g.*, *Piatnitzkysaurus*, *Allosaurus*), and coelurosaurians (*e.g.*, *Tyrannosaurus*, *Gallimimus*, *Deinonychus*).

7) **Metatarsal IV and its digit transversely narrow.** In most theropods, the distal end of the metatarsal IV is less expanded transversely than those of metatarsals II and III. Nevertheless, the distal reduction of metatarsal IV is much more marked in *Aniksosaurus* than in other theropods. The ratio of the distal width of metatarsal III with respect to the distal width of metatarsal IV is 1.57 in *Dilophosaurus*, 1.37 in *Allosaurus*, 1.16 in *Sinraptor*, 0.85 in *Gallimimus*, and 1.14 in *Deinonychus* (Welles, 1984; Gilmore, 1920; Currie & Zhao, 1993; Osmólska *et al.*, 1972; Ostrom, 1969). In *Aniksosaurus*, the ratio is 2.14. In congruence with the reduction of metatarsal IV, its correspondent digit is also constricted transversely, but without loss of phalanges: phalanx 2 of digit 4 in *Aniksosaurus* has a transverse width of 9 mm, representing 75% of the thickness of phalanx 2 of digit 2 (12 mm) and slightly less than 70% of phalanx 2 of digit 3 (13 mm). In contrast, digit 4 is equal or subequal to digit 2 in

transverse width in *Dilophosaurus*, *Allosaurus* and *Deinonychus*. Digit 4 is lateromedially thicker than digit 2 in *Sinraptor* and *Gallimimus*. Digit 4 is also thicker than digit 3 in the troodontid *Borogovia* (Osmólska, 1987). The condition described above for *Aniksosaurus* resembles that of ceratosaurians (e.g., *Ceratosaurus*, abelisauroids), in which metatarsal III and its digit is transversely wider than metatarsals II and IV and their digits, condition that may have evolved convergently in *Aniksosaurus* and ceratosaurians.

## DISCUSSION

*Aniksosaurus* was discovered in the same formation where several remains of abelisauroid theropods have been found (e.g., *Xenotarsosaurus bonapartei*, as well as an isolated maxilla and vertebrae referred to *Abelisauridae* indet.; Martínez *et al.*, 1986, 2004; Lammana *et al.*, 2002). Although it is appropriate to ask if *Aniksosaurus* is a member of this group of dinosaurs, we did not identify abelisauroid synapomorphies in any of the preserved elements of *Aniksosaurus* (excepting for the narrow proportions of metatarsal IV and its digit). Moreover, comparisons with well known taxa of Abelisauroida such as *Carnotaurus* (Bonaparte *et al.*, 1990) and *Masiakasaurus* (Carrano *et al.*, 2002) clearly demonstrate important distinctions with *Aniksosaurus*, including: 1) humerus with well defined deltopectoral crest (different from the atrophied one of abelisauroids), 2) manual unguals stoutly constructed (being distinct from the slender and reduced manual unguals of abelisauroids), 3) ilium with well developed cuppedicus fossa (which is absent among abelisauroid theropods), 4) femur with proximally projected anterior trochanter, almost reaching the level of the articular head (contrasting with the less well projected anterior trochanter present among abelisauroids), 5) greater trochanter craniocaudally expanded (different from the craniocaudally narrow one plesiomorphically retained by abelisauroids), 6) femoral head rectangular in cranial aspect (in contrast with abelisauroids in which the femoral head is bulbous and craniomedially oriented), 7) trochanteric shelf represented by a faint rugosity (different from the prominent ridge that is characteristic of abelisauroids), and 8) fibular shaft craniocaudally narrow (instead of the wider shaft retained in abelisauroids).

The anatomical characteristics enumerated above not only justify the allocation of *Aniksosaurus* outside of Abelisauroida, but also support the referral of *Aniksosaurus* within Coelu-

rosauria. For example, a transversely wide cuppedicus fossa, an anterior trochanter placed level with the greater trochanter, a reduced fourth trochanter, a poorly developed adductor fossa on the distal femur, and a reduced fibula are features shared by Compsognathids, coelurids, ornithomimids, tyrannosaurids and paravians. In this context, the narrowing of metatarsal IV and its digit documented in the coelurosaurian *Aniksosaurus* is better interpreted as convergently evolved also in ceratosaurian theropods.

Elucidation of the phylogenetic position of *Aniksosaurus* among Coelurosauria is difficult to assert, mainly due to the lack of preservation of important portions of the skeleton, including the skull, manual bones and tarsus. At least, available information supports that the new Patagonian taxon is not a member of the Maniraptoriformes (*sensu* Holtz, 2000), a coelurosaurian subclade including Ornithomimosauria, Tyrannosauridae, Oviraptorosauria, Alvarezsauridae and Paraves, because the Patagonian taxon retains the following plesiomorphies: distal tibia with astragalar surface proportionally low, and insertion of the M. caudifemoralis longus extensive and deep.

*Aniksosaurus* exhibits limb bones that resemble the robust proportions seen in the basal tetanuran *Allosaurus*, for example, rather than the gracile and elongate ones of most coelurosaurians (e.g., *Ornitholestes*, *Coelurus*, *Tanycolagreus*, ornithomimosaurians, oviraptorosaurians, paravians). Although the phylogenetic significance of such limb bone proportions in theropod dinosaurs requires further exploration, the robustness of *Aniksosaurus* may support its basal position among coelurosaurians.

Assuming that *Aniksosaurus* is a basal coelurosaur, it is required to examine briefly its relationships with other representatives: *Aniksosaurus* resembles the compsognathid *Sinosauropteryx* (Currie & Chen, 2001) and the bizarre coelurosaur *Nqwebasaurus* (De Klerk *et al.*, 2000), in the robust construction of the humerus and manual unguals, although other basal tetanurans (as for example, *Allosaurus*, *Piatnitzkysaurus*, *Torvosaurus*) also exhibit proportionally shortened humeri and manual unguals of ponderous construction. Moreover, no distinctive features of Compsognathidae are identified in the Patagonian taxon, thus reference of *Aniksosaurus* to this coelurosaurian clade is untenable. Besides, no unique features are shared by *Aniksosaurus* with *Ornitholestes* and Coeluridae (including *Coelurus* and *Tanycolagreus*).

Some features of *Aniksosaurus* look highly derived for a basal coelurosaurian, including a

strongly reduced supracetabular crest (a condition that is shared with tyrannosaurids, oviraptorosaurians and paravians), and absence of a medial adductor fossa on the distal femur (derived condition shared with oviraptorosaurians, alvarezsaurids and paravians). However, the remaining available bones of *Aniksosaurus* do not exhibit synapomorphies of paravians or tyrannosaurids, so the condition mentioned above for the supracetabular crest and distal femur may represent independent acquisitions with respect to derived coelurosaurians.

In proximal view it is observed that metatarsal III of *Aniksosaurus* is not constricted (*i.e.*, hourglass shaped) as in the basal tetanurans *Sinraptor* (Currie & Zhao, 1993) and *Allosaurus* (Gilmore, 1920) and the basal coelurosaurians *Ornitholestes* and *Tanycolagreus* (Carpenter *et al.*, 2005). In contrast, the proximal extremity of metatarsal III of *Aniksosaurus* lacks the caudomedial hook that wraps metatarsal II caudally. Although *Aniksosaurus* seems more derived than some basal coelurosaurians (*e.g.*, *Ornitholestes*, *Tanycolagreus*; Carpenter *et al.*, 2005) with regard to the construction of the proximal metatarsus, it does not show, however, the derived pattern of arctometatarsalian theropods (*e.g.*, ornithomimids, tyrannosaurids, elmsaurids and troodontids; Holtz, 1994). In particular, *Aniksosaurus* is less derived than dromaeosaurids (*e.g.*, *Deinonychus*; Ostrom, 1969) in which metatarsal III is proximally compressed and the facets for articulation with metatarsal II and IV are parallel and perpendicular with respect to the transverse plane.

In sum, available information indicates that *Aniksosaurus* occupies a basal position within Coelurosauria, looking more derived than compsognathids, coelurids and *Ornitholestes*, although less derived than Maniraptoriformes. In this context, the new South American taxon is relevant, because it may represent a Late Cretaceous survivor of a poorly documented basal coelurosaurian radiation.

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