Hands, Feet, and Behaviour in Pinacosaurus (Dinosauria: Ankylosauridae)

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Hands, feet, and behaviour in *Pinacosaurus* (Dinosauria: Ankylosauridae)

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Structure of the manus and pes has long been a source of confusion in ankylosaurs, owing to the imperfect preservation or complete lack of these parts of the skeletons in most specimens, and the fact that many species appear to have undergone a reduction in numbers of digits and phalanges. New specimens of *Pinacosaurus* from Alag Teeg in Mongolia confirm that the phalangeal formula of the manus is 2-3-3-3-2. However, there are only three toes in the pes, which has a phalangeal formula of X-3-3/4-3/4-X. Importantly, the number of phalanges in the third and fourth pedal digits can vary between either three or four per digit, even within the same specimen. The Alag Teeg site has yielded as many as a hundred skeletons of the ankylosaur *Pinacosaurus*, most of which were immature when they died. Each skeleton is preserved in an upright standing position, with the bones of the lower limbs often in articulation. The remainder of the skeleton, including the upper parts of the limbs, is generally disarticulated and somewhat scattered. Based on the presence of large numbers of juvenile *Pinacosaurus* specimens at Alag Teeg, as well as other Djadokhta-age sites (Ukhaa Tolgod in Mongolia, Bayan Mandahu in China), it seems juvenile *Pinacosaurus* were probably gregarious.

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Introduction

Many ankylosaur specimens have been recovered from Asia over the past eighty years (Maryańska 1971, 1977; Tumanova 1983, 1985, 1993; Barrett et al. 1998; Godefroit et al. 1999; Vickaryous et al. 2001; Xu et al. 2001; Hill et al. 2003). They have been assigned to numerous genera (Tumanova 2000), some of which have multiple species, although none is better represented than *Pinacosaurus grangeri* Gilmore, 1933. In spite of the large number of specimens that have been collected, there are still many details of anatomy that are poorly understood in this and other ankylosaurs.

Pinacosaurus grangeri of the Djadokhta Formation was described originally by Gilmore (1933). The holotype (AMNH 6523) consists of most of the skull and jaws, and a few scattered bones and osteoderms from Bayan Zag (= Bayn Dzak, Shabarak Usu, the Flaming Cliffs, Fig. 1). Most specimens of *Pinacosaurus* collected by the Soviet (1946–1949), Polish-Mongolian (1965–1971) and Soviet-Mongolian/Russian-Mongolian (1969–present) expeditions were also from this site (Maleev 1954; Maryańska 1977). Next to *Proto-*

ceratops andrewsi, *Pinacosaurus grangeri* is the most frequently recovered articulated dinosaur at Bayan Zag (Watabe and Suzuki 2000a).

Ukhaa Tolgod is a Djadokhta-age site that is best known for its remarkable diversity of small theropods (Dashzeveg et al. 1995), although *Pinacosaurus grangeri* is common at this locality as well (Hill et al. 2003).

A second species—*Pinacosaurus ninghsiensis* Young, 1935—was recovered in Djadokhta-age beds from Ningxia in China, but is considered by most workers to be a junior synonym of *Pinacosaurus grangeri* (Maryańska 1977; Coombs and Maryańska 1990; Vickaryous et al. 2004).

The Canada-China Dinosaur Project worked in 1987, 1988, and 1990 at Bayan Mandahu (Fig. 1), a Djadokhta-age site in Inner Mongolia (Jerzykiewicz et al. 1993). Amongst the many specimens recovered were twelve skeletons of juvenile *Pinacosaurus* from a single site (Currie 1991; Burns et al. 2010). Additionally, they found a second site (Site 63) with two juvenile *Pinacosaurus* (field numbers IVPP 050790-1a, 050790-1b). The Chinese-Belgian expeditions (Godefroit et al. 1999) have since recovered more specimens

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Fig. 1. Map of Mongolia and adjacent regions of China and Russian showing the relative positions of the four sites (Alag Teeg, Bayan Zag and Ukhaa Tolgod in Mongolia, Bayan Mandahu in China) where *Pinacosaurus* skeletons have been found.

from Bayan Mandahu, which have been identified as a new species (*Pinacosaurus mephistocephalus*). The holotype of this species (IMM 96BM3/1) is a virtually complete skull and skeleton that is almost double the length of any of the juveniles. However, it was still apparently immature because it lacks appreciable body armour and has only the first stages of development of a tail club. Although the skull has been described (Godefroit et al. 1999), the postcranial skeleton awaits detailed description. Parts of both front limbs are evident tucked underneath the body in the prepared specimen, but none of the foot bones can be seen.

An atypical Djadokhta-age site is Alag Teeg, located close to Tögrögiin Shiree (= Toogreek, Tugrig, Tukriken Shire, Tugrugyin Shireh) and Bayan Zag. It was discovered in 1969 by the Soviet-Mongolian Paleontological Expedition, who excavated specimens there in 1969 and 1970 (Tverdochlebov and Zybin 1974). Rather than typical redbeds deposited under arid conditions, the lowermost beds at Alag Teeg show a fluvial influence (Fastovsky 2000; Hasegawa et al. 2009). Hadrosaurs, which are extremely rare in most Djadokhta-age sites, are relatively common at Alag Teeg, whereas *Protoceratops andrewsi* is rare. However, the most common dinosaur at Alag Teeg is *Pinacosaurus*. Thirty specimens of this dinosaur were found at Alag Teeg in 1969 by the Joint Soviet-Mongolian Paleontological Expedition (Tverdochlebov and Zybin 1974; Maryańska 1977; Fastovsky and Watabe 2000), which subsequently used a bulldozer to expose the fossiliferous level. The majority of articulated and partially articulated skeletons were apparently about two meters long. The skeletons have neither been catalogued nor described in detail, and it is not even clear whether more than a representative sample was collected. Tverdochlebov and Zybin (1974) pointed out that the specimens were buried upright in normal life positions in the mudstone-rich lower section at Alag Teeg, which they interpreted as either a swamp or a dry lakebed. The presence of desiccation cracks suggested to them that the animals may have concentrated in drying ponds during a drought. They also proposed that the ankylosaurs might have become mired during flooding, but felt this scenario was less likely. Similarly, Hasegawa et al. (2009) interpreted the mudstone level as deposition in ephemeral ponds or lakes at the highest flood stages.

Table 1. Phalangeal formulae, where they are known, of thyreophorans. "0" indicates that there are no phalanges, but that there is the remnant of a metapodial. "X" indicates that there are no metapodials or phalanges.

Genus	Specimen	Manus	Pes	Source
Scelidosaurus	BMNH R1111		2-3-4-5-0	Owen 1863; Norman et al. 2004
Huayangosaurus	ZDM T7001		X-2-3-3-0	Galton and Upchurch 2004
Kentrosaurus	MNHB Ki 112		X-2-2-2-X	Galton 1982; Galton and Upchurch 2004
Stegosaurus	USNM 4280, 4937	2-2?-2?-1-0	X-2?-3?-2-X	Gilmore 1914
Stegosaurus	USNM 4937, 7401	2-2-2-2-?1	X-2-2-2-X	Galton and Upchurch 2004
Dracopelta	IGM 3	?-3-4-2+-?		Pereda-Suberbiola et al. 2005
Euoplocephalus	AMNH 5266		X-3-4-4-X	this paper
Euoplocephalus	ROM 784		X-3-4-4-X	Coombs 1986
Euoplocephalus	ROM 833		X-3-4-3+-X	Coombs 1986
Liaoningosaurus	IVPP V12560	2-3-3-2-0?	0-3-4-5-0	Xu et al. 2001
Niobrarasaurus	MU 650 VP		2-3-4-4-X	Carpenter et al. 1995
Nodosaurus	YPM 1815		2-3-4-5-X	Carpenter and Kirkland 1998
Panoplosaurus	CMN 2759	?-3-3-3-?	Unknown	this paper
Peloroplites	CEUM, paratypes	2-?3-3-?-?	Unknown	Carpenter et al. 2008
Pinacosaurus	various	2-3-3-3-?2	X-3-3/4-4/3/4-X	this paper
Saichania	MPC 100/151	5 digits	unknown	Maryańska 1977
Sauropelta	AMNH 3032, 3016	2-3-4?-3?-2?	2-3-4-4/5?-0	Ostrom 1970; Carpenter 1984
Shamosaurus		5 digits		Vickaryous et al. 2004
Talarurus	PIN 557-3	2-3-3-3-2	unknown (Maryańska 1977)	Maleev 1956; Maryańska 1977
Tarchia	PIN 551-29	unknown	4 digits	Tumanova 2000
Zhejiangosaurus	ZMNH M8718	unknown	X-3-4?-5?-X	Lu et al. 2007

The Mongolian-Japanese Joint Paleontological Expedition visited Alag Teeg annually from 1993 to 1998 (Watabe and Suzuki 2000a), and in 1995 and 1996 collected many skeletons of young individuals of *Pinacosaurus* from what they referred to as a mass-burial site (Fastovsky and Watabe 2000). In 1995 alone, they recovered more than twenty juvenile *Pinacosaurus* skeletons (Suzuki and Watabe 2000b), and by 1996 the number of individuals had climbed to more than thirty (Watabe and Suzuki 2000b). It is possible that some of these are the same specimens that had been uncovered by the Russian expedition in 1969. Fastovsky (2000) briefly described the sedimentology of Alag Teeg, and interpreted the lower mudstone beds in which the ankylosaurs are found as the floodplain of a braided system.

In 2001, 2003, 2004, 2005, and 2006, the "Dinosaurs of the Gobi" (Nomadic Expeditions) trip led by the authors visited Alag Teeg. There they found the remains of more than forty juvenile specimens of *Pinacosaurus* that had died upright in life positions. Unfortunately, the tops of most of the bodies had been removed by erosion and by previous collecting activity. Within the friable red silty mudstone, forelimbs and hindlimbs were found articulated in anatomical position. Multiple specimens of the manus and pes were collected to address several questions associated with the anatomy of these regions of ankylosaurs. Furthermore, they provide additional information on the minimum number of individuals preserved.

Alag Teeg is only 35 km WNW of Bayan Zag (Fig. 1), where the type specimen of *Pinacosaurus grangeri* was collected. One would expect that the *Pinacosaurus* species represented at Alag Teeg is probably *Pinacosaurus grangeri*. However, one of the juvenile skulls (MPC 100/1344) has strongly developed jugal horns similar to those of *Pinacosaurus mephistocephalus*. The left jugal horn protrudes more than 3.5 cm from the skull, which is itself only 16 cm long. The beds at Alag Teeg are stratigraphically lower than those of Tögrögiin Shiree and Bayan Zag (Dashzeveg et al. 2005) and were laid down in a different depositional environment. Hasegawa et al. (2009) have recently proposed the name Alagteeg Formation for these lower beds, and chose a type section within 200 m of the main concentration of ankylosaurs. Given its lower stratigraphic position, it is quite possible that the Alag Teeg *Pinacosaurus* is a different species than the specimens recovered from geographically close sites like Bayan Zag.

The manus is not known in most genera of ankylosaurs (Coombs and Maryańska 1990; Christiansen 1997a; Vickaryous et al. 2004), and the pes (Christiansen 1997b) is poorly documented (Table 1). Pereda-Suberbiola et al. (2005) gave an overview of the manus and pes in the Ankylosauria, and predicted (based on the counts of primitive ornithischians, stegosaurs and ankylosaurs) that the basal thyreophoran manual phalangeal formula would be 2-3-4-3-2(or 3?) and that the primitive pedal phalangeal formula would be 2-3-4-5-0.

More than a dozen partial and complete specimens of *Pinacosaurus* were collected at Bayan Mandahu in China, and the majority of specimens were found in life position with the limbs tucked underneath the body (Figs. 2, 3). Not all of these

Fig. 2. Ankylosaurid dinosaur *Pinacosaurus* from Upper Cretaceous of Bayan Mandahu, China (all specimens in IVPP). Oblique photograph of the Canada-China Dinosaur Project quarry in 1990 at Bayan Mandahu, China. The articulated skeletons are lettered from A to F, and these letters correspond to those in the quarry diagram (Fig. 3).

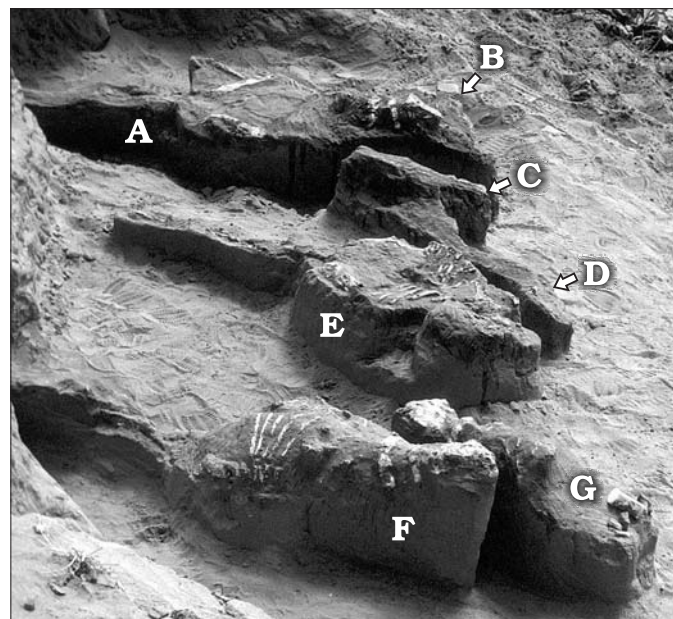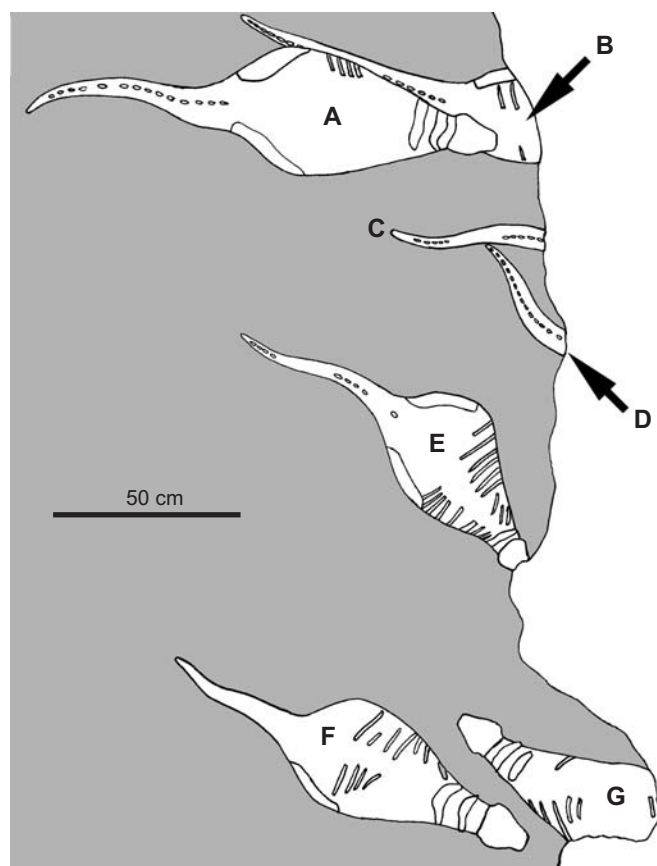Fig. 3. Ankylosaurid dinosaur *Pinacosaurus* from Upper Cretaceous of Bayan Mandahu, China (all specimens in IVPP). Quarry diagram showing the alignment of juvenile skeletons, all of which were upright with limbs positioned underneath their bodies.

Table 2. Limb bone measurements (in mm) of *Pinacosaurus* from Alag Teeg. Abbreviations: DW, distal width; PW, proximal width; SW, shaft width (smallest transverse diameter).

Bone	Number	Length	PW	SW	DW
Scapula	MPC 100/1332	160	–	44	64
Scapula	MPC 100/1333	345	–	100	106
Coracoid	MPC 100/1332	84	73H	–	–
Humerus, left	MPC 100/1310	152	67	27	66
Humerus, both	MPC 100/1333	260	120	45	128
Humerus, right	MPC 100/1335	115	–	–	–
Humerus, left	MPC 100/1344	126	64	25.5	58
Humerus, left	MPC 100/1346	132	51+	24	60.6
Radius, left	MPC 100/1310	98	32	–	34
Radius, distal end of right	MPC 100/1314	–	–	–	34
Radius, right	MPC 100/1323	83.5	28.5	13.4	28.7
Radius, left	MPC 100/1326	87.5	29.5	13	25.6
Radius, right	MPC 100/1330	–	–	14	31
Radius, left	MPC 100/1333	165	71	30	71
Radius, left	MPC 100/1335	82	26	–	27
Radius, right	MPC 100/1335	72	–	12.5	27
Ulna with olecranon, left	MPC 100/1310	104	47	21	26
Ulna, distal end of right	MPC 100/1314	–	–	–	24
Ulna with olecranon,	MPC 100/1319	94.3	45.3	15.2	23.3
Ulna with olecranon, right	MPC 100/1322	103	48	14	26
Ulna with olecranon, right	MPC 100/1323	92	46	13	24
Ulna with olecranon, left	MPC 100/1326	95.2	45.6	16	23
Ulna, right	MPC 100/1330	–	–	15	21
Ulna with olecranon, left	MPC 100/1333	180	102	36	51
Ulna with olecranon, left	MPC 100/1335	93	36	12	19
Ulna with olecranon, right	MPC 100/1335	–	–	14	17
Femur, right	MPC 100/1322	198	74	36	66
Femur, left	MPC 100/1322	197	74	35.5	64.6
Femur, right	MPC 100/1322	192	70	34.8	65.6
Femur, left	MPC 100/1334	200	71.5	31	67
Tibia, right	MPC 100/1308	–	–	–	79
Tibia, left	MPC 100/1308	–	–	–	83
Tibia, right	MPC 100/1316	–	–	–	69
Tibia, left	MPC 100/1316	–	–	–	67
Tibia, right	MPC 100/1320	–	–	–	63.6
Tibia, left	MPC 100/1323	–	–	–	66.6
Tibia, left	MPC 100/1327	152	56	27	57
Tibia, left	MPC 100/1334	141	72	26	74
Fibula, left	MPC 100/1308	–	–	–	28
Fibula, right	MPC 100/1316	–	–	–	28
Fibula, left	MPC 100/1316	–	–	–	26
Fibula, right	MPC 100/1320	–	–	–	21
Fibula, left	MPC 100/1334	–	–	12	27

specimens have been prepared, and those that have been prepared are exposed only in dorsal and lateral views. Consequently, the Bayan Mandahu specimens provide no information at this time about the anatomy of the limbs of *Pinacosaurus*. In *Pinacosaurus grangeri*, the phalangeal formula of the manus has been estimated (Maryańska 1977) but previously has not been confirmed by specimens. The manus is pentadactyl in *P. mephistocephalus* but the phalangeal formula is not known (Godefroit et al. 1999). The pedal phalan-

geal formula of *Pinacosaurus* is less certain, and as it turns out, even the estimated number of digits (Maryańska 1977; Coombs and Maryańska 1990; Fastovsky and Weishampel 1996; Tumanova 2000) is incorrect. Knowing the correct composition of the foot of *Pinacosaurus* is important for the determination of its relationships to other ankylosaurids (Carpenter 2001), and in the identification of footprints (Ishigaki 1999; McCrea et al. 2001).

The majority of specimens from Alag Teeg were preserved in life position with the limbs tucked underneath them, and the bodies would have protected the limbs from above. This explains why the specimens collected by the Dinosaurs of the Gobi expeditions include a disproportionate number of hands and feet, often associated with propodial and epipodial elements (Table 2). It is not clear at this time whether the upper parts of the bodies of the Alag Teeg specimens were removed before burial during the Cretaceous, were destroyed by erosion, were removed by collecting parties, or were generally lost because of a combination of all these factors. Some were clearly exposed long enough before burial for the bones to disarticulate, although they often remain in association. The sedimentology and taphonomy of the site will be considered in another paper.

The spellings of Mongolian geographic and stratigraphic names follow those of Benton et al. (2000), and the chronostratigraphic framework is from Jerzykiewicz and Russell (1991). Phalangeal formulae are designated in the manner outlined by Padian (1992).

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CEUM, Prehistoric Museum, College of Eastern Utah, Price, Utah, USA; CMN, Canadian Museum of Nature, Ottawa, Canada; IMM, Inner Mongolia Museum, Hohhot, People's Republic of China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China: MPC, Paleontological Center of the Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; ROM, Royal Ontario Museum, Toronto, Canada; ZMNH, Zhejiang Museum of Natural History, Zhejiang, China; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Material studied

MPC 100/1307. Right tarsals, metatarsals, phalanges (Field number PJC2001.7).

MPC 100/1308. Right and left distal ends of tibiae plus tarsals, metatarsals and phalanges of a single individual (Field number PJC2003.45, Ank K).

MPC 100/1309. Pedal phalanges IV-1, IV-2, IV-4 (left foot) (Field number PJC2003.46).

MPC 100/1310. Left arm including humerus, radius, ulna, one carpal, five metacarpals, five proximal phalanges (Field number PJC2003.49, Ank D).

MPC 100/1311. Tibia, fibula, two tarsals, three left pedal phalanges (Field number PJC2003.54, Ank B).

MPC 100/1312. Pieces of numerous pedal phalanges (Field number PJC2003.55, Ank I).

MPC 100/1313. Pedal phalanges III-2, IV-1, IV-3 (Field number PJC2003.56, Ank I).

MPC 100/1314. Distal ends of the right radius and ulna, plus most of the hand (Field number PJC2003.58, Ank E).

MPC 100/1315. Nine manual phalanges from a small individual, and four manual phalanges from an adult were found on the same spot (Field number PJC2003.59, Ank H).

MPC 100/1316. Distal ends of tibiae and fibulae plus both feet of a single individual (Field number PJC2003.60, Ank F).

MPC 100/1317. Manual phalanx ?V-2 (right hand) plus other fragments (Field number PJC2003.62, Ank N).

MPC 100/1318. Manual phalanges I-1, II-1, III-1, ?V-2 (right hand) (Field number PJC2003.63, Ank A).

MPC 100/1319. Left pes (Field number PJC2003.48, Ank L).

MPC 100/1320. Distal ends of tibia and fibula plus right foot (Field number PJC2003.61, Ank G).

MPC 100/1321. Skull and assorted bones (Field number PJC2004.12, Ank T).

MPC 100/1322. Two individuals mixed with two quadrates, coracoid, right ulna, ischium, three femora (Field number PJC2004.13, Ank S).

MPC 100/1323. Right ulna, hand and two feet from the same individual. Might be same individual as 100/1326. (Field number PJC2004.14, Ank R).

MPC 100/1324. Osteoderms, eight vertebrae, coracoid, etc. (possibly of either MPC 100/1325 or MPC 100/1326). (Field number PJC2004.15, Ank Q).

MPC 100/1325. Right hand (possibly the same individual as MPC 100/1326). (Field number PJC2004.16, Ank P).

MPC 100/1326. Forearm, hand, and associated tail. (Field number PJC2004.17, Ank O).

MPC 100/1327. Left tibia and foot (Field number PJC2003.50, Ank D).

MPC 100/1328. Left foot (Field number PJC2003.57, Ank M).

MPC 100/1329. Vertebral centra, manual ungual, left foot, right metatarsals and phalanges (PJC2005.25, Ank U).

MPC 100/1330. Neck plates, vertebrae and hand (PJC2005.26, Ank V).

MPC 100/1331. Complete right foot (PJC2005.27, Ank W).

MPC 100/1332. Scapula, coracoid, ribs (PJC2005.28, Ank X).

MPC 100/1333. Ilia, both humeri, radius and ulna, both hands, one foot of a large individual (PJC2005.29, Ank Y).

MPC 100/1334. Tibia, fibula, distal tarsal, two metatarsals, phalanges. Second individual with small fibulae (PJC2005.30, Ank Z).

MPC 100/1335. Skull, two arms and leg (PJC2005.31, Ank AA).

MPC 100/1336. Osteoderms (PJC2005.32, Ank BB).

MPC 100/1337. Right manus (PJC2006.161, map coordinates X21.6, Y102.1).

MPC 100/1338. Partial manus (PJC2006.141, map coordinates X5.0, Y95.7).

MPC 100/1339. Left tibia, fibula and foot (PJC2006.142, map coordinates X6.3, Y96.5). Right tibia, fibula and foot (PJC2006.143, map coordinates X6.5, Y96.3). Left radius, ulna and hand (PJC2006.144, map coordinates X6.5, Y96.9). Right ulna, radius and hand (PJC2006.146, map coordinates X6.8, Y96.7).

MPC 100/1340. Right radius, distal ulna and hand (PJC2006.145, map coordinates X6.8, Y96.3).

MPC 100/1341. Distal ends of right radius and ulna, manus (PJC2006.147, map coordinates X20.5, Y101.6).

MPC 100/1342. Left tibia, fibula, pes (PJC2006.148, map coordinates X22.9, Y100.3).

MPC 100/1343. Left partial femur, tibia, fibula, foot (PJC2006.149, map coordinates X23.0, Y100.6), and right foot (PJC2006.151, map coordinates X23.0, Y101.0).

MPC 100/1344. Skull and cervical vertebrae (PJC2006.152, map coordinates X27.1, Y98.0), second cervical ring (PJC2006.154, map coordinates X27.4, Y98.2), articulated string of dorsal vertebrae (PJC2006.150, map coordinates X27.2, Y97.5), scapula (PJC2006.155, map coordinates X27.2, Y97.4), right humerus (PJC2006.153, map coordinates X27.3, Y97.5), right femur (PJC2006.156, map coordinates X27.9, Y97.8), left femur (PJC2006.157, map coordinates X27.4, Y98.0), tail (PJC2006.159, map coordinates X27.6, Y97.2).

MPC 100/1345. Cervical half-ring (PJC2006.158, map coordinates X27.5, Y100.2) and thoracic rib (map coordinates X27.6, Y100.2).

MPC 100/1346. PJC2006.160. Coracoid and right humerus from close to Ank Z.

MPC 100/1347. PJC 2006.162. Right frontal from close to baseline near MPC 100/1344 (but clearly not the same individual).

Description of the limbs of *Pinacosaurus*

Ontogenetic changes in ankylosaur limb proportions are not well understood, so all specimens were measured (Tables 2–5). The morphologies of the major limb bones of ankylosaurs have been well-described and illustrated (Coombs 1986), and therefore only specific characters are described in this paper. However, there is considerable confusion about the numbers of digits in the manus and pes.

Forelimb.—The humerus (Fig. 4A) has been used to distinguish *Pinacosaurus* species (Godefroit et al. 1999). The *Pinacosaurus* humeri from Alag Teeg are similar to those described as *Pinacosaurus mephistocephalus*. The bone is short and robust, expanded strongly proximally and distally,

Table 3. Length measurements (in mm) of metacarpal and manual phalanges of ankylosaurs. **A**. Pinacosaurus specimens from Alag Teeg and Bayan Zag (final column, Maryańska 1977). **B**. Other ankylosaurs, including *Pinacosaurus mephistocephalus* (IMM 96BM3/1) from Godefroit et al. (1999).

A

Element	MPC 100/1310	MPC 100/1314	MPC 100/1315	MPC 100/1315 adult	MPC 100/1317	MPC 100/1318	MPC 100/1323	MPC 100/1325	MPC 100/1326
Right/Left	L	R	R		R	R	R	R	
McI	37.9	28.1	–	–	–	–	29.3	34.9	
McII	33.5	28.5	–	–	–	–	28.9	32.8	
McIII	37.4	29.9	–	–	–	–	30.2	33.6	
McIV	33.8	26.6	–	–	–	–	28.8	31.9	
McV	30.7	14+	–	–	–	–	24.3	26.5	27.7
I-1	13.7	9.2	–	15	–	11.8	9.9	12.6	
I-2	–	11.8	12+	17	–	–	13.3	–	
II-1	11.2	9.1	8.5	18	–	10.9	8.6	10.5	
II-2	–	–	3.3	–	–	–	–	2.5	
II-3	–	11.4	10+	–	–	–	–	12.6	
III-1	10.3	7.9	9.8	–	–	8.8	8.5	11.0	
III-2	–	2.6	3.3	–	–	–	4.5	–	
III-3	–	7.4	–	–	–	–	9.7	11.1	
IV-1	12.4	10.2	10.8	11	–	–	10.0	12.3	
IV-2	–	–	4.0	–	–	–	1.5	3.9	
IV-3	–	–	–	–	–	–	–	5.0	
V-1	11.3	–	11.4	–	–	–	8.8	10.1	11.0
V-2	–	–	–	–	8.8	9.9		–	
V-3	–	–	–	–	–	–		–	

B

Element	MPC 100/1333	MPC 100/1333	MPC 100/1335	MPC 100/1335	MgD-II/9	IMM 96BM3/1	CMN 2759
Right/Left	R	L	L	R			L
McI	55	55		28.8	34	42	–
McII	52	53	33	28	35	39	99
McIII	54	51	35	25	37	38	115
McIV	53	53			ca. 33	34	114
McV	38	40				27	–
I-1	19	18		9			–
I-2	20			13			–
II-1	14	14		9			49
II-2	6	5		3.3			7
II-3							56
III-1	14	14					28
III-2	4			4.5			25
III-3	14	14		7.5			53
IV-1		4		5			27
IV-2				4.2			25
IV-3							45
V-1							–
V-2							–
V-3							–

and has a robust head flanked by a strong medial process and large deltopectoral crest. In both MPC 100/1344 and MPC 100/1346, the deltopectoral crests extend 68 mm (more than half the length) down the shaft. This is the only postcranial character evident from the specimens examined to suggest that the Alag Teeg *Pinacosaurus* might be *P. mephisto-cephalus* rather than *P. grangeri*. However, study of a wider range of material may ultimately show that this character is ontogenetically controlled and is of no use in distinguishing species. It is beyond the scope of this paper to determine whether or not *P. grangeri* and *P. mephistocephalus* are distinct. Although there are a few characters suggesting the Aleg Teeg material can be diagnosed as the latter, the dominance of the former in nearby sites suggests one should be
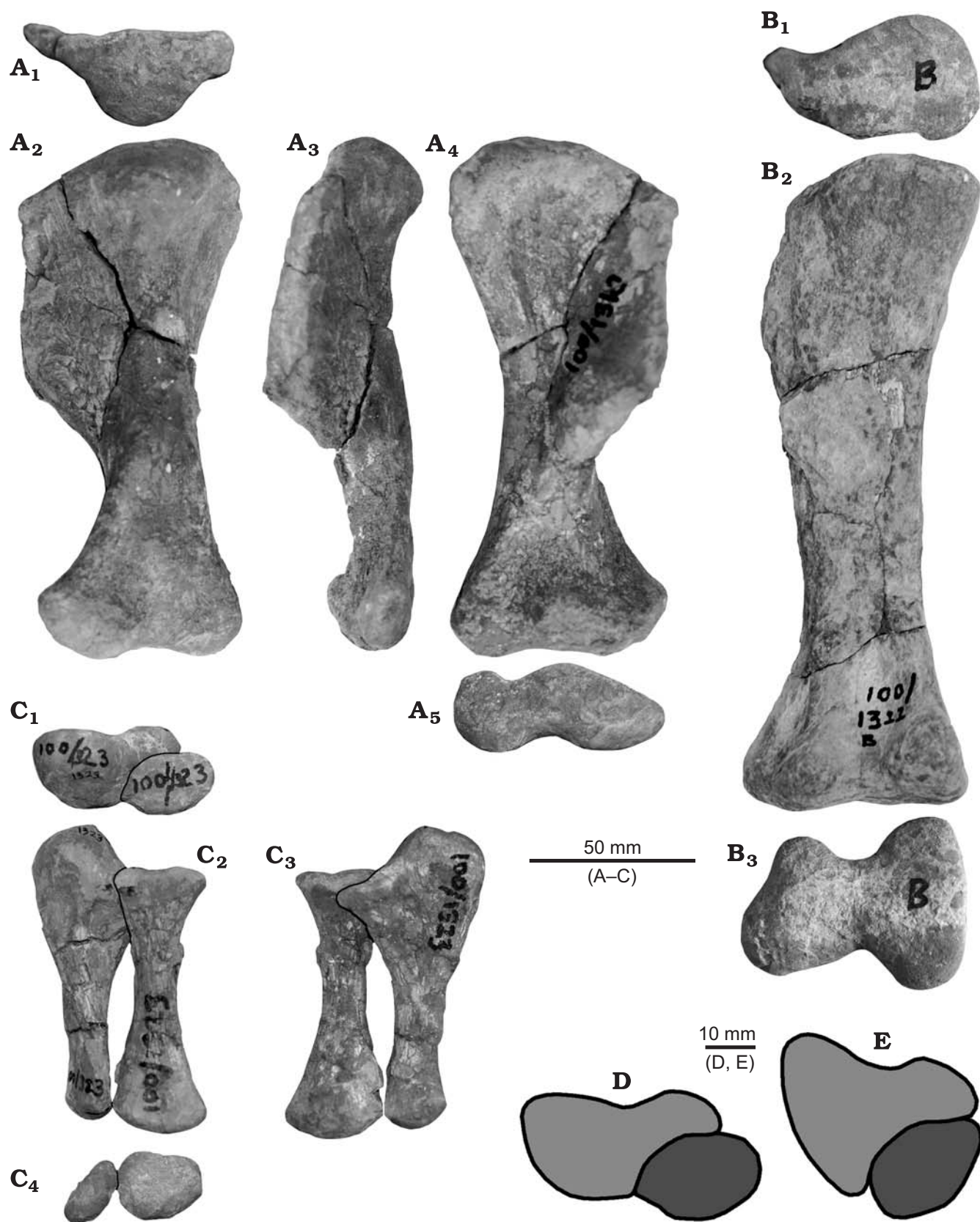
Fig. 4. Ankylosaurid dinosaur *Pinacosaurus*, limb elements from the Alagteeg Formation (Upper Cretaceous) of Alag Teeg, Mongolia. **A**. Humerus (MPC 100/1310) in proximal (A_1), dorsal (A_2), lateral (A_3), ventral (A_4), and distal (A_5) views. **B**. Femur (MPC 100/1322) in proximal (B_1), posterior (B_2), and distal (B_3) views. **C**. Radius, ulna (MPC 100/1323) in proximal (C_1), medial (C_2), lateral (C_3), and distal (C_4) views. Comparison of outlines of proximal ends of ulna (light gray) and radius (dark gray) of MPC 100/1323 (**D**) and reversed image of MPC 100/1326 (**E**).

Table 4. Measurements (in mm) of tarsal elements of *Pinacosaurus* from Alag Teeg. Identifications are tentative (see text) for the three tarsals of each ankle. Because the orientations of these bones are uncertain, length, width and depth measurements represent the three major dimensions of each of the bones, and are arranged from greatest (length) to least (depth) size. All measurements are in mm.

Number	Tarsal	Length	Width	Depth
MPC 100/1307	calcaneum	28.5	24.4	9.8
MPC 100/1307	distal tarsal	16.3	11.5	6.4
MPC 100/1307	astragalus			12.1
MPC 100/1308	calcaneum	23.5	20.5	7.2
MPC 100/1308	distal tarsal, right	12.5	9.4	4.9
MPC 100/1308	distal tarsal, left	10.2	8.0	4.6
MPC 100/1308	astragalus	23.5	18.3	15.3
MPC 100/1316	calcaneum	24.5	23.1	5.6
MPC 100/1316	distal tarsal	16.2	12.4	5.6
MPC 100/1316	astragalus			9.4
MPC 100/1320	calcaneum	19.9	17.4	6.9
MPC 100/1320	distal tarsal	15.2	9.5	5.5
MPC 100/1320	astragalus	21.7	17.3	11.9
MPC 100/1323	distal tarsal	8.3	5.7	3.4
MPC 100/1323	astragalus	18.5	14.4	4.5
MPC 100/1331	calcaneum	23	22	8
MPC 100/1331	distal tarsal	19	11	6
MPC 100/1331	astragalus	20	18.5	9
MPC 100/1334	calcaneum	24	18	12
MPC 100/1334	distal tarsal	17	14	7
MPC 100/1334	astragalus	27	22	5
MPC 100/1339	calcaneum	24.6	25.2	7.9
MPC 100/1339	distal tarsal	15.8	13.1	5.8
MPC 100/1339	astragalus	25.3	17.4	9.8
MPC 100/1343	calcaneum	22.4	22.5	8.0
MPC 100/1343	distal tarsal	10.9	7.5	4.6
MPC 100/1343	astragalus	26.4	19	14.1

cautious with identifications. Consequently, the Aleg Teeg material will be simply referred to as *Pinacosaurus* for the rest of this paper.

A small round carpal bone found amongst the scattered phalanges of MPC 100/1310 has a diameter of 4.5 mm. If Maleev (1954) is correct in his identification of the single carpal in PIN 614 as an intermedium, then this is probably the second specimen known for any Mongolian ankylosaur (Maryańska 1977). Maryańska (1977) also described two possible sesamoid bones at the distal articulations of metacarpals I and II.

None of the hands collected (Table 3) is complete, but they preserve complementary parts and suggest that the normal phalangeal formula was 2-3-3-3-2, as proposed by Maryańska (1977). MPC 100/1358 preserves the first four metacarpals plus the proximal part of the fifth (Fig. 5), complete digits I and III, and partial digits II and IV. MPC 100/1310 (Fig. 6) includes nine manual phalanges of a small individual. MPC 100/1315 includes nine manual phalanges of a small individual.

Whereas they vary greatly in shaft diameter, the first four metacarpals (Figs. 5, 6) are almost the same length (Table 3). The lengths increase marginally from metacarpal I through III,

diminish marginally in metacarpal IV, and markedly in metacarpal V. In each case, the first metacarpal is the widest of the five and the fifth is the narrowest. For example, the minimum shaft width of the first metacarpal of MPC 100/1341 is 12 mm, whereas it is only 8.5 mm in the fifth. The metacarpals form a tightly integrated arch in proximal view (Figs. 5A, 6A), and as preserved *in situ* it is evident that they would have been held almost vertically in the living animals as in stegosaurs and sauropods (Senter 2010). The shapes and outlines of the metacarpals are somewhat variable although certain tendencies are evident. The proximal articular surfaces of the first and fifth metacarpals tend to be quadrilateral in outline, the second and third tend to be triangular, and the fourth is usually twice as long anteroposteriorly compared with the mediolateral width. In general, the proximal articular surface areas of metacarpals I, II, and III are more massive, and metacarpals IV and V
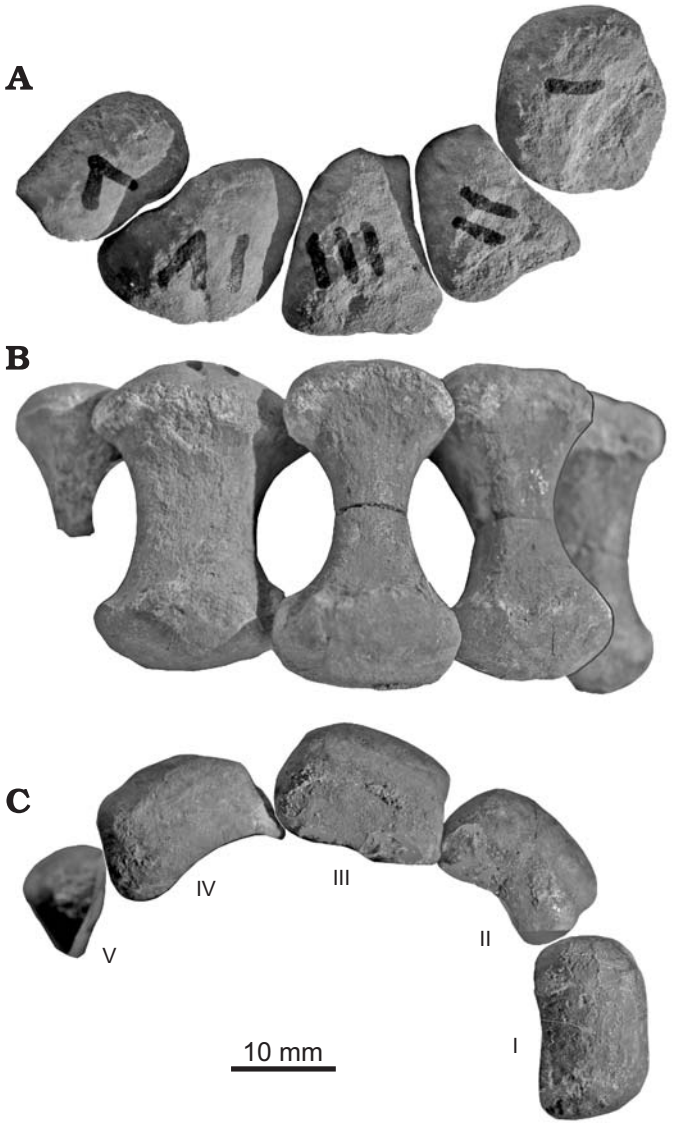

Fig. 5. Ankylosaurid dinosaurs *Pinacosaurus* (MPC 100/1358) from the Alagteeg Formation (Upper Cretaceous) of Alag Teeg, Mongolia. Right metacarpus in proximal (**A**), anterior (**B**), and distal (**C**) views. Fifth metacarpal is incomplete distally.

Table 5. Length measurements (in mm) of metatarsal and pedal phalanges of *Pinacosaurus* specimens from Alag Teeg. Metatarsal lengths are the maximum measurements taken from the proximoposterior edge to the distal end of the bone.

Number	R/L	MtII	MtIII	MtIV	II-1	II-2	II-3	III-1	III-2	III-3	III-4	IV-1	IV-2	IV-3	IV-4
MPC 100/1307	R	51.3	53.5	48.6	22.1	10.6	–	18.4	9.9	–	–	15.2	9.4	4.8	26.4
MPC 100/1308	R	52.4	52.3	47.4	20.2	9.6	31.3	17.8	8.3	–	23+	13.4	6.5	4.4	20+
MPC 100/1308	L	50.8	51.9	48.3	20.9	8.6+	31.5	18.2	8.4	–	22+	14.8	7.4	3.6	28.5
MPC 100/1309	L	–	–	–	–	–	–	–	–	–	–	15.8	9.2	–	14+
MPC 100/1311	?	–	–	–	19.1	–	–	18.3	–	–	–	–	–	4.2	–
MPC 100/1312	R	–	–	–	–	8	–	–	–	–	–	–	–	–	–
MPC 100/1313	?	–	–	–	–	9.9	–	–	–	–	–	15.2	–	3.3	–
MPC 100/1316	R	47.6	48.6	42.8	20.5	7.5	27.7	17.4	10	–	28	17.2	7.6	4.4	23.8
MPC 100/1316	L	45.6	45.5+	30+	18.2	8.8	28.9	18.1	10.4	–	–	17.4	7.7	–	26.1
MPC 100/1319	L	48	48	42	24	9	–	20	11	–	19+	19	8	4	24+
MPC 100/1320	L	42.3	43.3	40.2	18.2	8.3	24.4	14.9	8.6	–	25.2	13.3	5.3	–	24.4
MPC 100/1323	R	40.1	41.8	39.4	18.3	6.9	24.5	16.2	8.5	–	26.4	13.8	6.3	4.3	21.1
MPC 100/1323	L	40.5	41.7	39.4	20.5	7.9	22.4	16.3	7.7	–	17+	13.8	5.5	2.7	–
MPC 100/1327	L	–	–	–	22.8	9.4	25+	19.3	10.3	–	20+	–	–	–	–
MPC 100/1328	L	27.1	27.5	27.4	15.3	–	–	–	5.3	–	24.9	10.5	–	–	–
MPC 100/1329	L	–	–	–	16	7	26	14	7	–	29	12	6	3	18
MPC 100/1331	R	45	47	45	19	9	25	18	8	2.5	24	15	7	5	24
MPC 100/1334	L	43	44	38	17	6	22+								

smaller. The proximal articular surfaces fit together such that when they are assembled, the distal articular surfaces are flush with the substrate, forming a smooth, radiating arch.

The distal end of the first phalanx of manual digit one (I-1) is weakly ginglymoid, which is true of all ankylosaur phalanges that directly support an ungual. The distal condyles of the first phalanx of each of digits II, III and IV (Fig. 6) are strongly separated (Maryańska 1977). The distal ends of these phalanges flare medially and laterally, so that the distal end of each phalanx is wider than its proximal end. The degree of distal divergence appears to trend from moderate in I-1 until it almost bifurcates in IV-1. Phalanges II-2, III-2 and IV-2 are narrow but curved plates of bone that occupy the concavities between the distal condyles of the first phalanges. In MPC 100/1314, the distal end of III-2 provides a shallowly ginglymoid distal articulation for the ungual. In contrast, the disk-like III-2 of MPC 100/1315 has a strongly ginglymoid distal end, which suggests that in this specimen there may possibly have been one more disk-like phalanx (III-3) between it and the ungual. The phalanges in any one digit diminish rapidly in size distally as a result of this morphologic arrangement.

A complete fifth manual digit has not been recovered, despite the fact that more than a dozen articulated hands were collected. Eleven of the mani recovered each have a single phalanx associated with the fifth metacarpal, although the two bones are not in articulation in ten of those specimens. The first phalanx was found articulated with the distal end of the fifth metacarpal in MPC 100/1339. Although considerably narrower than the first phalanges of the other manual digits, V-1 is similar in overall shape, being mediolaterally wide (13 mm proximally) and dorsoventrally shallow (5.5 mm) relative to its proximodistal length (12 mm). Phalanx V-1 does not continue the pronounced bifurcation trend as found in the other first phalanges of the manus. Instead, there

is a single eminence on the medial side of the distal condyle, with the lateral side being simple and flat. Most other phalanges associated with the fifth digit are comparatively more cubical; for example, specimen MPC 100/1341 has a non-terminal phalanx from the digit V with almost equal dimensions (mediolateral width, 9 mm; proximodistal length, 9 mm; dorsoventral thickness, 7 mm), and a rounded cross-section. It is presently unknown which phalanx (second or third) these columnar phalanges represent.

Hooflike unguals are present on the first three manual digits, the largest on the first digit, and the smallest on the third. A small, complete, disarticulated ungual was found associated with MPC 100/1337. This element matches well the distal articulation of the only other phalanx of the fifth digit. The proximal articular surface of this ungual is crescentic and forms an
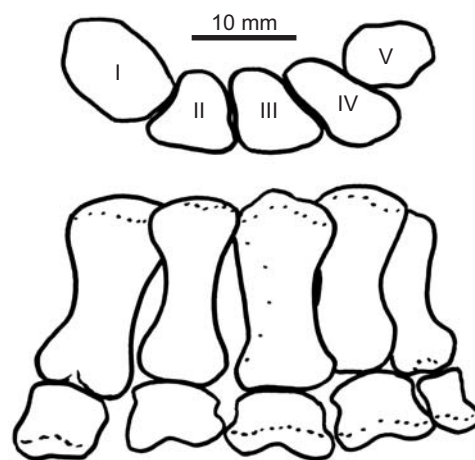

Fig. 6. Ankylosaurid dinosaur *Pinacosaurus grangeri* Gilmore, 1933 (MPC 100/1310) from the Alagteeg Formation (Upper Cretaceous) of Alag Teeg, Mongolia. Outline of left metacarpus and proximal phalanges in proximal (**A**) and anterior (**B**) views.
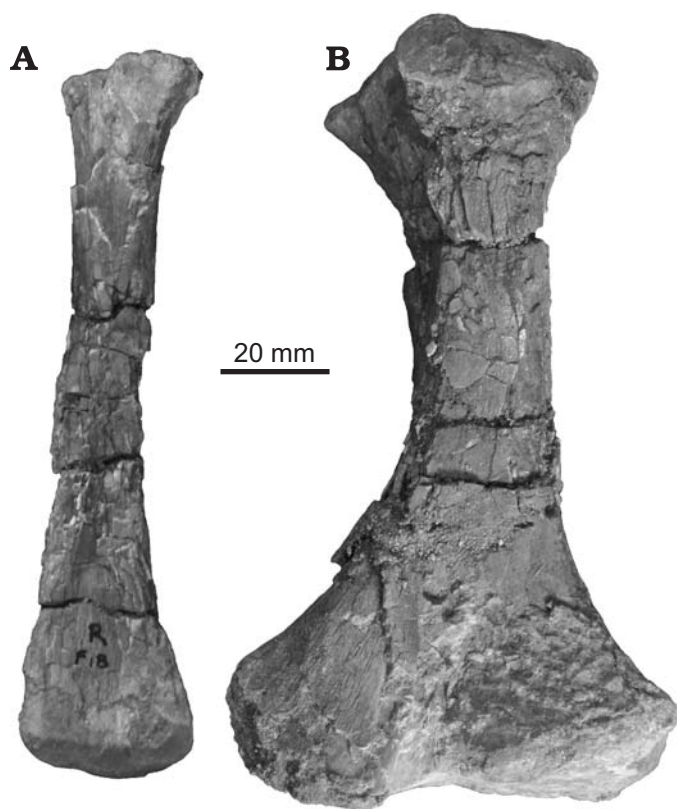
Fig. 7. Ankylosaurid dinosaur *Pinacosaurus* (MPC 100/1339) from the Alagteeg Formation (Upper Cretaceous) of Alag Teeg, Mongolia. Right fibula (**A**) and tibia (**B**) in anterior view.
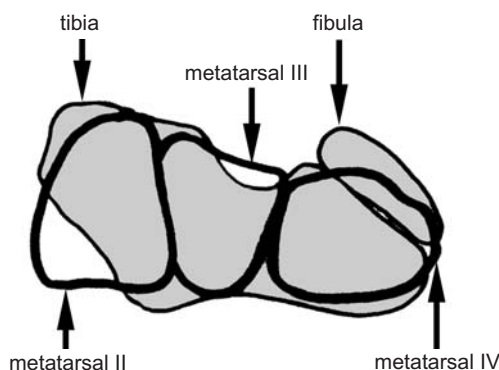

Fig. 8. Ankylosaurid dinosaur *Pinacosaurus* (MPC 100/1308) from the Alagteeg Formation (Upper Cretaceous) of Alag Teeg, Mongolia. Outlines of distal ends of tibia and fibula (grey infilling) overlain by outlines of the proximal ends of the metatarsals. Anterior is towards the top.

obtuse angle with the longitudinal axis of the flattened hoof-like body of the ungual. The ungual therefore splays laterally from the central axis of the digit, which is an unlikely arrangement if it belonged to any of the digits other than the fifth.

Hindlimb.—The tibiae of MPC 100/1339 (Fig. 7) and MPC 100/1308 (Fig. 8) expand distally to form two distinct condylar regions separated by an anterior sulcus. The medial articular region is an anteroposteriorly broad, almost flat, anteromedially sloping surface that articulates directly with metatarsal II. Close conformation of the distal end of the tibia and the

proximal end of the metatarsal suggests that intervening cartilaginous tarsals would have been highly reduced or entirely absent. The lateral articular surface of the tibia is narrow anteroposteriorly but is more strongly convex than the medial articular surface. The anterior margin of the lateral articular surface is relatively straight and faces anterolaterally to make contact with the distal end of the fibula. Together, the fibula and the lateral articular surface of the tibia contact the convex dorsal surface of the proximal tarsal.

There are three ossified tarsals (Figs. 9, 10B), all of which are central or lateral in position. The largest, most robust element was proximal in position in all articulated specimens. The concave dorsal surface of this tarsal articulates with the fibula dorsally and the tibia posteriorly, and is therefore considered to be a calcaneum. Coombs (1986) identified a similar element in AMNH 5266 as a calcaneum. The anteromedial and ventral surfaces articulate with the epipodials. The largest dimension is the anteromedial-posterolateral width, followed by the dorsoventral length, and the medial to anterolateral thickness is the smallest dimension.

The widest element represents a much-reduced astragalus based on its placement in articulated specimens, on the distal articular surface of the tibia, in the concavity between the lateral and medial distal condyles. It is a curved element, proximally concave where it lies underneath and articulates with the concavity of the tibia, and distally convex where it articulates with the epipodials. They roughly match the shape of the tarsal identified as an astragalus in AMNH 5266 by Coombs (1986), who compared it with AMNH 5404 in which the astragalus is fused to the tibia (Coombs 1979).

The smallest tarsal (MPC 100/1308) is a well rounded element that lacks any finished bone, and is nested above the contact between the third and fourth metatarsals. In MPC 100/1343, the element was found in articulation with the distal surface of the astragalus. In MPC 100/1307 and 100/1331, the same element is not convex on all surfaces. The presumed posterior surface is shallowly concave, as is one of the sides, which also has a small surface of finished bone. Based on its position in *Pinacosaurus*, it is most likely distal tarsal III.

The anatomy of the ankylosaur pes (Coombs and Maryańska 1990; Christiansen 1997b) is undocumented for most ankylosaurs (Table 1). Maleev (1954) identified three toes in a specimen of "*Syrmosaurus viminicaudus*" (PIN 614), currently recognized as *Pinacosaurus grangeri* (Maryańska 1977), and suggested a phalangeal formula of X-3-3-3?-X. The pes of each of the newly-collected *Pinacosaurus* has three digits (Table 5). Previous descriptions had suggested either three (Maleev 1954) or four (Maryańska 1977) toes were present. The four-digit hypothesis was primarily based on a specimen with a damaged left foot (ZPAL MgD-II/9) that appears to demonstrate four metatarsals, although it only has enough phalanges for three digits. To date, most review papers have accepted that *Pinacosaurus* has four toes (Coombs and Maryańska 1990; Glut 1997; Tumanova 2000; Ford and Kirkland 2001). Interestingly, this assumption has since been transferred to *Tarchia gigantea* (Coombs and Maryańska 1990), al-
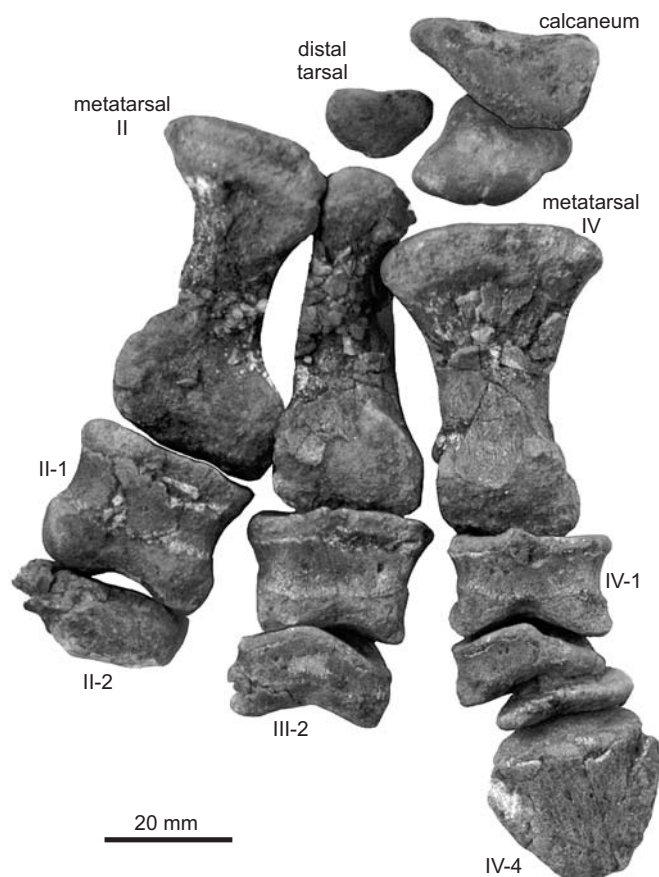
Fig. 9. Ankylosaurid dinosaur *Pinacosaurus* (MPC 100/1307) from the Alagteeg Formation (Upper Cretaceous) of Alag Teeg, Mongolia. Right tarsus, metatarsus and digits in ventral view.

though no specimens have been described that demonstrate the number of pedal digits. The only ankylosaurid in which the foot is well-known is *Euoplocephalus tutus*, which has three toes (Coombs 1986; Penkalski 2001).

Metatarsal III is longer than the second metatarsal, which in turn is longer than the fourth (Table 5). The proximal articulation of the second metatarsal is inclined toward the anterior face of the bone, forming an acute angle of about 120° with the longitudinal shaft of the bone. This angle is almost perpendicular in the third metatarsal, and is perpendicular in metatarsal IV. When in articulation, the combined proximal articular surface is more horizontal medially, and more vertical laterally. This would correspond to the surface articulating with the distal articular surface of the tibia/ astragalus medially, and more the anterior surface of the tibia/fibula/calcaneum laterally. The distal ends of the second and fourth metatarsals are shallowly convex, whereas that of the third is slightly ginglymoid.

The most medial of the three digits in the pes of *Pinacosaurus* has three phalanges, indicating that it is unlikely to be the first digit, which primitively has only two phalanges. This suggests that the three digits are the second, third and fourth, a pattern corroborated by the morphology of the pes of nodosaurids such as *Sauropelta* (e.g., AMNH 3016). *Sauropelta*

has four digits in the pes but is relatively primitive for an ankylosaur in that it retains a reduced fifth metatarsal.

The second to fourth toes of MPC 100/1308 are respectively 61.5, 56.4, and 54.3 mm in length. The second toe is also the thickest, and bears the largest of the three bluntly-tipped, hoof-like pedal unguals. Phalangeal length decreases progressively in the following order: II-3, III-3, IV-4, II-1, III-1, IV-1, II-2, III-2, IV-2, and IV-3. The interphalangeal joints are all ginglymoid, although are only shallowly so between II-2 and II-3, and between IV-3 and IV-4, and lack the conspicuous bifurcation seen in the manus.
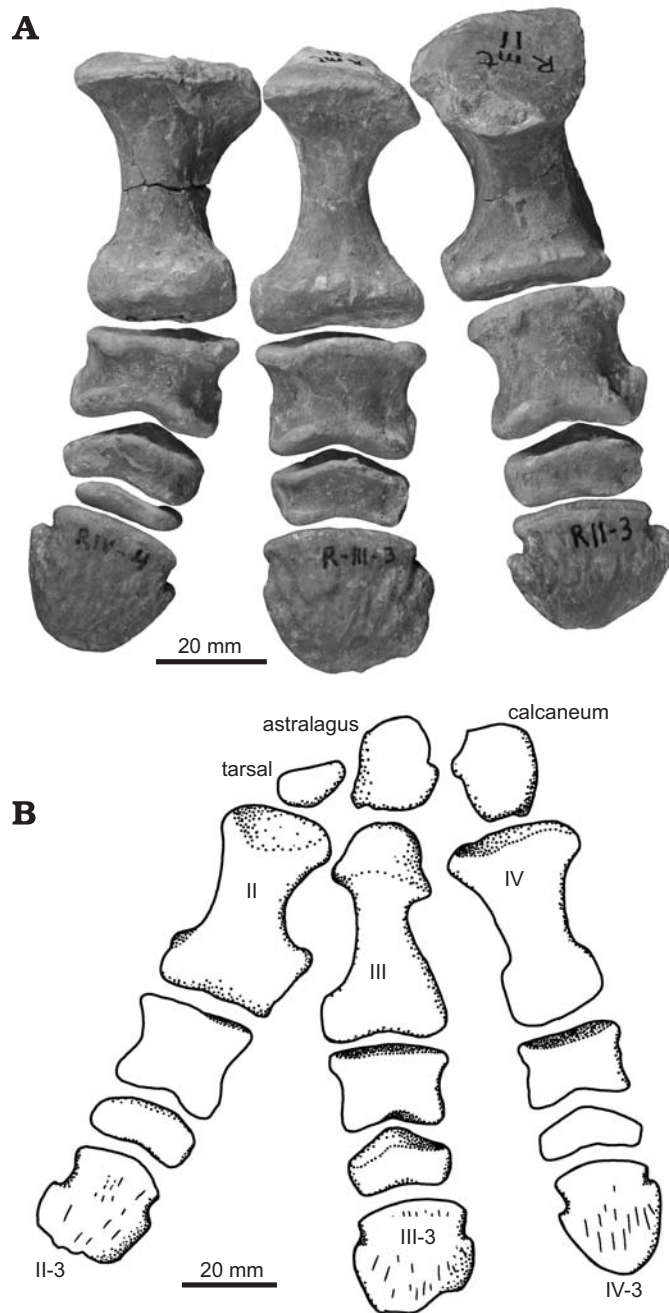

Fig. 10. Ankylosaurid dinosaur *Pinacosaurus* from the Alagteeg Formation (Upper Cretaceous) of Alag Teeg, Mongolia. **A**. MPC 100/1339, right foot. **B**. Dorsal view of MPC 100/1320 (left tarsals, metatarsals and phalanges).
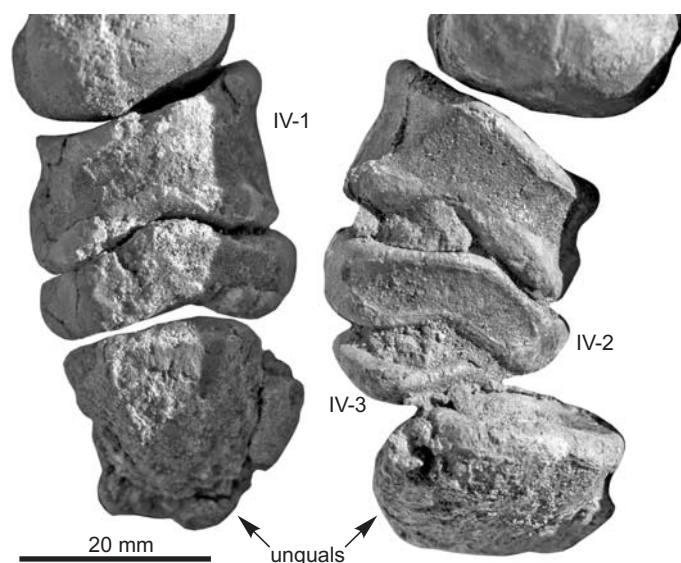
doi:10.4202/app.2010.0055

Fig. 11. Ankylosaurid dinosaur *Pinacosaurus* (MPC 100/1316) from the Alagteeg Formation (Upper Cretaceous) of Alag Teeg, Mongolia. Left (to the left) and right fourth digits of the feet of a single individual showing different phalangeal counts.

Each of the third and fourth digits has lost a single phalanx, and the phalangeal formula in the majority of specimens (6 of 10 specimens, Table 5) is 0-3-3-4-0. Two specimens (MPC 100/1331, 100/1342) retain the full complement of four phalanges in the third digit, although III-3 is small in comparison with the other phalanges. Some articulated specimens (MPC 100/1309, left pes of 100/1316, 100/1320) lack phalanx IV-3. Furthermore, in MPC 100/1316 (Fig. 11), IV-3 is present in the right but not the left pes.

Discussion

Lesothosaurus diagnosticus (Thulborn 1972; Sereno 1991) may be a basal thyreophoran, and its pentadactyl manus and a tetradactyl pes likely represent the plesiomorphic condition (Butler et al. 2008). A similar phalangeal count is common to *Heterodontosaurus tucki*, Norman et al. 2004 (a basal ornithischian outside Ornithopoda, Butler et al. 2008) and basal neoceratopsians (*Protoceratops andrewsi*, Dodson et al. 2004). Among more proximate outgroups to Ankylosauria (other thyreophorans), the phalangeal count of the manus is unknown. The pes of *Scelidosaurus harrisonii* (Owen 1863; Norman et al. 2004) and reportedly *Scutellosaurus lawleri* (Colbert 1981) each has four digits, while that of stegosaurs is reduced to three (Galton and Upchurch 2004).

As in *Pinacosaurus mephistocephalus* (Godefroit et al. 1999), the manus of the *Pinacosaurus* specimens from Alag Teeg retain the primitive pentadactyl condition. A five-digit manus is also known for several other ankylosaurs, including the ankylosaurids *Saichania chulsanensis* (phalangeal count unknown; Maryańska 1977) and *Talarurus plicatospineus*

(2-3-3?-3?-2; Maleev 1956; Maryańska 1977), and the nodosaurid *Sauropelta edwardsorum* (tentatively 2-3-4?-3?-2?; Ostrom 1970). Although the phalangeal count is unknown, *Edmontonia rugosidens* has been described as having either a tetradactyl (Carpenter 1990) or a pentadactyl (Coombs and Maryańska 1990) manus. A four-digit manus is also described for the enigmatic ankylosaur *Liaoningosaurus paradoxus* (2-3-3-2-0?; Xu et al. 2001). The exact phalangeal count remains unclear for most ankylosaurs, owing to the rarity of articulated specimens. A specimen of *Dracopelta zbyszewskii* has a phalangeal formula of ?-3-4-2+-? (Pereda-Suberbiola et al. 2005). Three digits of the hand were discovered with the holotype of *Panoplosaurus mirus* (CMN 2759). Although the three fingers were initially identified as I, II, and III (Lambe 1919; Sternberg 1921; Carpenter 1990), re-examination of the specimen shows that each of the three digits has 3 phalanges, and that they are therefore more likely to be digits II, III, and IV. This opens to question which side of the body they are from. The associated humerus is from the left side. Fingers seem to be on wrong side as mounted in plaster in a drawer of the CMN, which suggests that the order of the fingers has been reversed.

The foot of *Pinacosaurus* is clearly tridactyl as in *Euoplocephalus* and *Liaoningosaurus*. However, of the two specimens of *Euoplocephalus* illustrated by Coombs (1986), AMNH 5266 was illustrated as having five phalanges, and ROM 784 (the type of *Dyoplosaurus acutosquameus*) has only four phalanges. However, upon detailed investigation of the individual phalangeal elements of AMNH 5266, it is evident that some of the phalanges had been mis-identified, and the phalangeal count is the same as that of ROM 784 (X-3-4-4-X). The phalangeal formula of the pes in *Euoplocephalus* is X-3-4-4/5-X, compared with X-3-3/4-3/4-X in *Pinacosaurus*. This suggests that in the reduction of numbers of phalanges, *Pinacosaurus* is more derived than *Euoplocephalus* and *Liaoningosaurus*. Furthermore, each penultimate phalanx is relatively smaller in *Pinacosaurus* than in *Euoplocephalus*, and only fills the gap between the articular condyles of the antepenultimate phalanx. The condition of the penultimate phalanx in *Liaoningosaurus* is presently unclear.

Among other ankylosaurs, the number of pedal digits is four in the nodosaurids *Sauropelta* (reportedly 2-3-4-4/5-0; Ostrom 1970), *Nodosaurus textillis* (2-3-4-5-0; Carpenter and Kirkland 1998) and *Niobrarasaurus colelii* (2-3-4-4-0; Carpenter et al. 1995), although a fifth metatarsal is present in *Sauropelta*. McCrea et al. (2001) have referred Early Cretaceous footprints with five fingers and four toes to Nodosauridae. Four pedal digits have been reported for the ankylosaurids *Tarchia gigantea* (phalangeal count unknown; Tumanova 2000) and *Talarurus*. The pes of the latter has alternatively been reconstructed as either 2-3-4-5-0 (Maleev 1956) or 2-3-4-4-0 (Maryańska 1977), although it is acknowledged by both authors that the specimen is a composite of what appears to be multiple individuals. Ishigaki (1999) reported the presence of quadrupedal tracks of ankylosaurids from Mongolia, but did not describe them.

As in many ankylosaurs, including *Dracopelta* (Pereda-Suberbiola et al. 2005), *Sauropelta* (Ostrom 1970), and *Euoplocephalus* (Coombs 1986), the longest components of the digits in *Pinacosaurus* are the unguals (most distal) and first (most proximal) phalanges. It is also worth noting that while the longest first manual phalanges in subadult *Pinacosaurus* are I-1 and IV-1, followed by V-1, and finally II-1 and III-1, the reverse is true for the adult specimen from the same site (MPC 100/1315): II-1 is the longest, followed by I-1, and finally IV-1 (digits III and V are not represented; see Table 5). Pereda-Suberbiola et al. (2005) report that II-1 and III-1 are the longest proximal manual phalanges in *Dracopelta* and *Sauropelta*. In the pes, the longest proximal digit of *Pinacosaurus* is II-1, similar to the conditions in *Nodosaurus* and *Euoplocephalus*. In *Niobrarasaurus*, II-1, III-1, and IV-1 are all reportedly about the same length.

The present work documents unequivocal evidence of variation in phalangeal formulae of *Pinacosaurus*, based on the examination of multiple articulated specimens from a single locality. Previously, such variation has been identified for *Euoplocephalus* (Coombs, 1986) and has since been revoked (Arbour et al. 2009). However, in that instance the material was collected from two different stratigraphic horizons (ROM 784 from the Dinosaur Park Formation; AMNH 5266 from the Horseshoe Canyon Formation) and localities, with at least one of the two specimens (AMNH 5226) partially disarticulated, leaving the interpretation of intraspecific phalangeal loss open to question. Variation in phalangeal formulae is known for a variety of modern taxa, including amphibians (Alberch and Gale 1985; Shubin et al. 1995; Pacces Zaffaroni et al. 1992), turtles (Minx 1992; Crumly and Sánchez-Villagra 2004), squamates (Pregill et al. 1986; Greer 1987, 1991), and at least one bird (the domestic fowl, *Gallus gallus;* Hogg 1980). Among extant tetrapods, phalangeal loss usually involves digits I, IV, and V (Minx 1992). Interestingly, in *Pinacosaurus* phalangeal reduction involves both digits III and IV.

Relationships

Study of the manus and pes of *Pinacosaurus* has identified a number of characters that may help refine our understanding of the relationships of this dinosaur to other ankylosaurids. The number of pedal digits is shared with *Euoplocephalus*, and this suggests that there were only three digits in the pes of other ankylosaurids as well. Even though *Talarurus* was originally reported as having four digits (Maleev 1954), the exact number is unknown (Maryańska 1977). Recent phylogenetic analyses have recovered *Pinacosaurus* as either a basal (Hill et al. 2003; Parsons and Parsons 2009; Burns et al. 2010) or derived (Coombs and Maryańska 1990; Kirkland 1998; Carpenter 2001; Vickaryous et al. 2004) ankylosaurine ankylosaurid. Given the observed variation, even within a single individual, phalangeal formulae may prove to be unreliable phylogenetic characters for ankylosaurs (see also Minx 1992). In addition, the presence of a tridactyl pes in both deeply nested ankylosaurids (*Pinacosaurus* and *Euoplocephalus*) and the morphologically disparate *Liaoningosaurus* indicates that this condition has evolved independently at least twice in ankylosaurs. In comparison with *Euoplocephalus*, which has a pedal phalangeal formula of X-3-4-4/5-X, *Pinacosaurus* (X-3-3/4-3/4-X) shows a tendency toward more reduction of numbers of phalanges in both digits III and IV. Furthermore, even when *Pinacosaurus* has the same phalangeal count as *Euoplocephalus*, the penultimate phalanx is reduced to a proximodistally reduced thin, mediolaterally narrow plate of bone that is nested between the distal condyles of the antepenultimate phalanx. In contrast, the third phalanx in the third digit and the penultimate phalanx in the fourth digit are wide enough to be continuous with the lateral and medial margins of the antepenultimate phalanges, and are relatively longer proximodistally. The reduction and/or loss of distal phalanges in the pes of *Pinacosaurus* suggest it is more derived than *Euoplocephalus*. This presumably can be used, with discretion, to refine the phylogenetic relationships of ankylosaurines once further information is known about pes structure in the other taxa.

Taphonomy

In contrast to North America, where ankylosaurs are often preserved upside down (Sternberg 1970), Asian ankylosaurs tend to be found upright with their limbs in standing position. Presumably, the North American specimens were transported by fluvial systems and rolled over in water. In contrast, Asian ankylosaurs are hypothesized to have been buried *in situ* and have not been transported. The upright, standing positions of most of the specimens suggest rapid burial, possibly in sandstorms (Currie 1989; Jerzykiewicz et al. 1993). The fact that the limbs of the *Pinacosaurus* specimens of Alag Teeg are found in a muddy facies suggests that these animals may have been mired in mud when they died.

The localized concentrations of articulated skeletons of juvenile *Pinacosaurus* at Bayan Mandahu (Currie 1989), Alag Teeg and Ukhaa Tolgod strongly suggest that this dinosaur was gregarious when immature. The close proximity of the specimens in life positions in monodominant assemblages (Figs. 2, 3, 12) provides even stronger evidence for gregarious behaviour in ankylosaurs than the bonebeds used to infer social structure in other dinosaurs. These include prosauropods (Huene 1928; Sander 1992; Hungerbühler 1998), sauropods (Coombs 1975, 1990; Coria 1994; Myers 2004; Sander et al. 2006), stegosaurs (Hennig 1925), ornithopods (Horner and Makela 1979; Hooker 1987; Norman 1987; Winkler et al. 1988, 1997; Forster 1990; Rogers 1990; Varricchio and Horner 1993; Derstler 1995; Ryan et al. 1995; Hanna et al. 1999; Godefroit et al. 2000; Lauters et al. 2008) and ceratopsians (Currie 1981; Currie and Dodson 1984; Sampson 1995; Ryan et al. 2001; Wolfe et al. 2004; Eberth and Getty 2005; Currie et al. 2008; Mathews et al. 2009; Eberth et al. 2010). It cannot be determined whether herding was a normal behavioural pattern
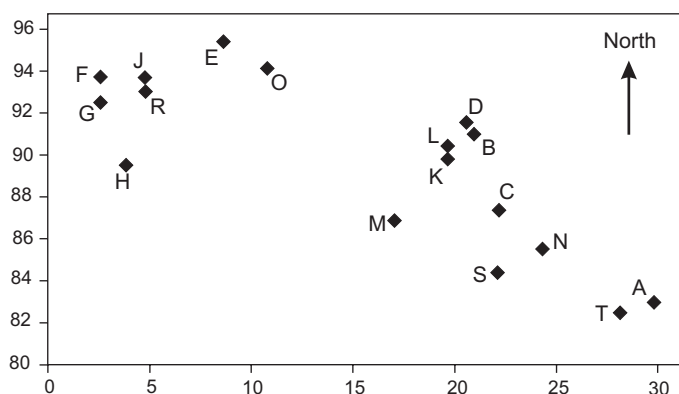
Fig. 12. Distribution of some of the *Pinacosaurus* specimens in most concentrated section at Alag Teeg, Alagteeg Formation (Upper Cretaceous), Mongolia. Lettering of individuals was assigned in the order of discovery and excavation, and each corresponds to a specimen listed under the "Material Studied" section. For example "A" on the drawing corresponds to "Ank A", which is MPC 100/1318. Units are in meters.

for juvenile *Pinacosaurus*, or if it only occurred under certain stressed conditions, such as drought. Nevertheless, the fact that there are concentrations of *Pinacosaurus* at every major Djadokhta-aged locality except for Tögrögiin Shiree suggests that their clustering behaviour was not uncommon. The presence of a dozen two-metre long *Pinacosaurus* at Bayan Mandahu and more than thirty individuals of the same size at Alag Teeg is curious for its absence of both smaller and larger animals. It is possible that larger, stronger, more mature individuals were able to escape whatever catastrophes befell these animals. However, that does not explain the absence of smaller, younger animals.

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