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Comparison between woolly rhino forelimbs from Longdan, Northwestern China and Tologoi, Transbaikalian region

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Abstract

The fossil *Coelodonta nihowanensis*, found from the Late Pliocene loess at Longdan in the Linxia Basin (Gansu, China), is the earliest known member of the woolly rhino. The complete skull from Longdan shows that *C. nihowanensis* is a primitive species different from *Coelodonta antiquitatis*. The cranial and dental characters of *C. nihowanensis* are obviously distinct from those of *Coelodonta tologoijensis*, and the former has a smaller body size and more slender limb bones. The associate humerus, radius, and ulna, as well as associate carpals and metacarpals of *C. nihowanensis* found recently from Longdan further show that *C. nihowanensis* has different postcranial features from *C. tologoijensis*, and indicate that they belong to two different species. *C. nihowanensis* is apparently more primitive than *C. tologoijensis*, and the former has better running ability, which is consistent with the chronological distributions of the two woolly rhino species and the evolutionary trend of the genus *Coelodonta*. *C. nihowanensis* may be the ancestral form of *C. tologoijensis*. The woolly rhino originated in northern China, and then dispersed into northern Eurasia. *C. nihowanensis* gradually evolved into *C. tologoijensis*, and finally became *C. antiquitatis*.

1. Introduction

The richest and most widespread rhinoceros during the Quaternary is the woolly rhino (the genus *Coelodonta*). So far no direct ancestral form has been found in pre-Pliocene deposits. The most primitive form, *Coelodonta nihowanensis*, was found only from the Late Pliocene at Longdan in northwestern China (Deng, 2002; Qiu et al., 2004) and Nihewan in northern China (Teilhard de Chardin and Piveteau, 1930). The fossils of the woolly rhino were found widespread from the Late Pleistocene deposits in northern Eurasia. Because the earliest remains of the woolly rhino have been found in East Asia, its Asian origin is beyond any doubt (Kahlke, 1999; Qiu et al., 2004).

The woolly rhino *Coelodonta*, with a fully graviportal skeleton, a thick woolly coat, and enormous tandem horns, was the most famous rhino and one of the best-known Pleistocene animals. However the scarcity of fossil records made its early history still obscure. At the beginning of the 20th century, a milk tooth row with peculiar folds of the woolly rhino on its labial wall was found from Nihewan (Hebei, China), so this specimen was referred to *Coelodonta* cf. *antiquitatis*, clearly belonging to a primitive species of the woolly rhino (Teilhard de Chardin and Piveteau, 1930). This discovery implies that the woolly rhino originated in Asia. Because the material was scarce, they did not establish a new species on the basis of the specimen.

Kahlke (1969, pp. 701–702) stated that he created a new species *Coelodonta nihowanensis* in an announced paper at the VII International Congress of INQUA in 1965, but this paper had not been published up to 1969. Kahlke (1969) restated his opinion and referred the materials of the woolly rhino from the localities Nihewan, Gonghe (Chow and Liu, 1959), Linyi (Chow and Chow, 1959), and Loc. 9 of Zhoukoudian (Teilhard de Chardin, 1936) in China to be in this species. He considered that *C. nihowanensis* has small size and primitive structures. As for the diagnosis of this species, he mentioned only the narrow nasals and some dental differences, without detailed explanation. Qiu et al. (2004) affirmed that *C. nihowanensis* is a valid species according to ICZN, because Kahlke (1969) clearly indicated the fossils of this species and listed complete

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references, although he provided only a few characters and did not give a comprehensive definition for the new species. Chow (1978) established a new subspecies *Coelodonta antiquitatis yenshanensis* for the woolly rhino from Zhoukoudian. Qiu et al. (2004) suggested that only the Nihewan material belongs to *C. nihowanensis*. Deng (2002) and Qiu et al. (2004) described a complete adult skull and mandible and a juvenile skull of *C. nihowanensis* found from Longdan in the Linxia Basin (Gansu, China), which gives a deeper recognition for the characters of this species.

Beljaeva (in Vangengeim et al., 1966) described abundant Early Pleistocene materials from Tologoi site on the Selenga River (Western Transbaikalia), erecting new species *Coelodonta tologoijensis*. Later on this species was discovered in another site Zasuhino 3 (Vangengejm et al., 1990). *C. tologoijensis* can be distinguished from the younger *C. antiquitatis* by less massive body and clearly slender fore and hind limbs, as well as by not high-crowned molars. If the fossils from Tologoi and Nihewan should belong to the same form Kahlke (1999) considered, for priority reasons, the designation *C. tologoijensis* should be used for material from both find complexes. However, because the state of affairs has yet to be examined, the name *C. "nihowanensis"* should qualify for the material from Nihewan.

The skull material found from Longdan has proved that *C. nihowanensis* is different from *C. tologoijensis*, and a preliminary comparison of their limb bones also shows that the two species have obvious differences (Deng, 2006). Recently, we found more material of the forelimb bones of *C. nihowanensis* from Longdan. The new material was recovered from stratigraphically the same position from the lectotype locality of *C. nihowanensis* in Longdan, and displays more slender limb bones and more primitive morphology than *C. tologoijensis*.

Terminology follows Sisson (1953), and the measurements are according to Guérin (1980) and given in mm. Abbreviations used in text and tables: a. = about;

Fig. 1. Right humerus, radius, and ulna (IVPP V 15016) of *Coelodonta nihowanensis* from Longdan in Gansu, China. (1) humerus: posterior view; (2) proximal part of ulna: (a) medial view, (b) anterior view; (3) radius: (a) posterior view, (b) proximal view. Scale bar = 10 cm.

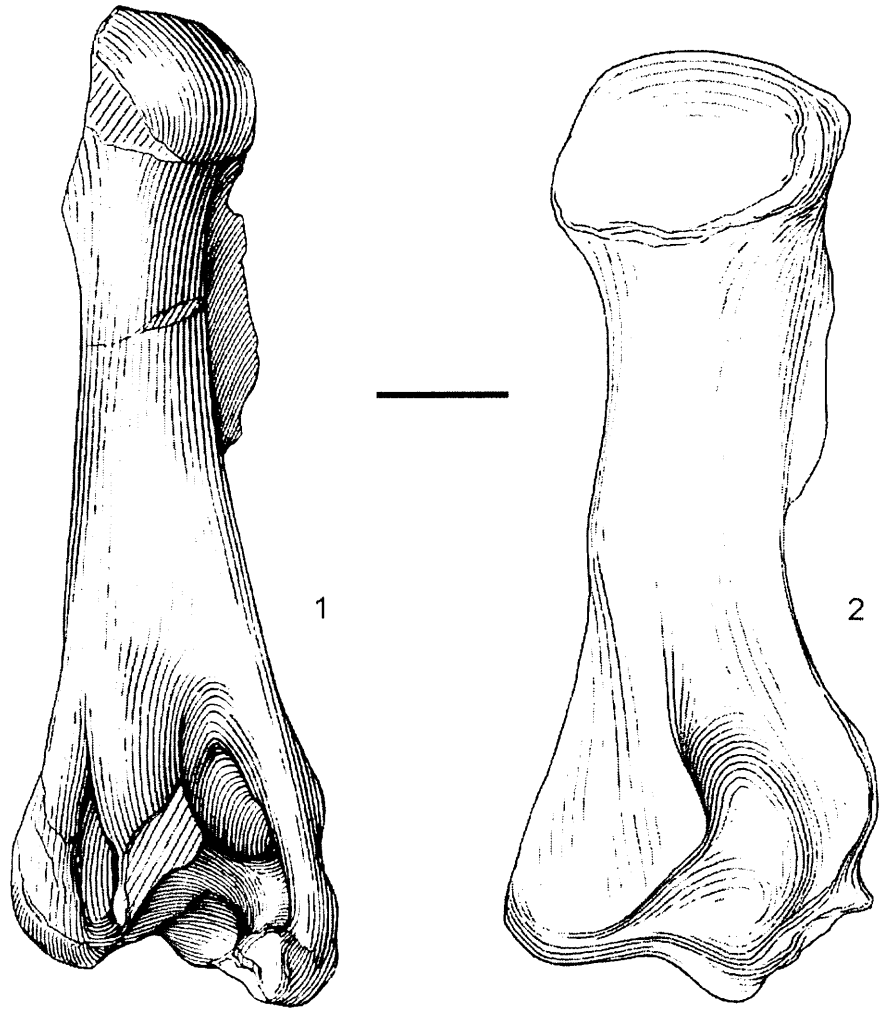

Fig. 2. Comparison between humeri of *Coelodonta nihowanensis* from Longdan, northwestern China and *C. tologoijensis* from Tologoi, Transbaikalia. (1) *C. nihowanensis* (IVPP V 15016); (2) C. *tologoijensis* (after Beljaeva, in Vangengeim et al., 1966, Fig. 48.1). Posterior view. Scale bar = 5 cm.

ant. = anterior; APD = anteroposterior diameter; art. = articular; dis. = distal; *H* = height; IVPP V. specimen prefix of Institute of Vertebrate Paleontology and Paleoanthropology, Beijing: *L* = length; max. = maximal; mid. = middle; min. = minimal; post. = posterior; prox. = proximal; TD = transverse diameter; *W* = width.

2. Description and comparison

The referred specimens of *C. nihowanensis* from Longdan in this paper include IVPP V 15016, right humerus without proximal extremity, radius without distal extremity, and proximal extremity of ulna (Figs. 1, 2(1); Table 1); IVPP V 14967, right carpals and metacarpals (Figs. 3–5; Table 2).

By comparison with *C. tologoijensis*, the humerus, radius, ulna, and carpals of *C. nihowanensis* are markedly smaller in size. No metacarpals of *C. tologoijensis* are found from Tologoi (Beljaeva, in Vangengeim et al., 1966).

Table 1
Measurements of humeri of the woolly rhino from Longdan, Nihewan, and Tologoi

Measures	Longdan	Nihewan	Tologoi
L at head	>393	400	355–365
TD min.	74		76–80
APD at TD min.	78.5		80–98
TD dis.	123	145	133–140
TD dis. art.	95		a. 90–99
TD min./*L* at head	<18.8		20.8–21.4
TD min./TD dis.	60.2		54.2–57.1
TD dis./*L* at head	<31.3	32.9	35.9–37.8
TD dis. art. /TD dis.	77.2		a. 64.3–71.4

So the metacarpals of *C. nihowanensis* are compared with those of *C. antiquitatis* in this paper. The metacarpals of *C. nihowanensis* are much more slender than those of *C. antiquitatis* (Deng, 2006).

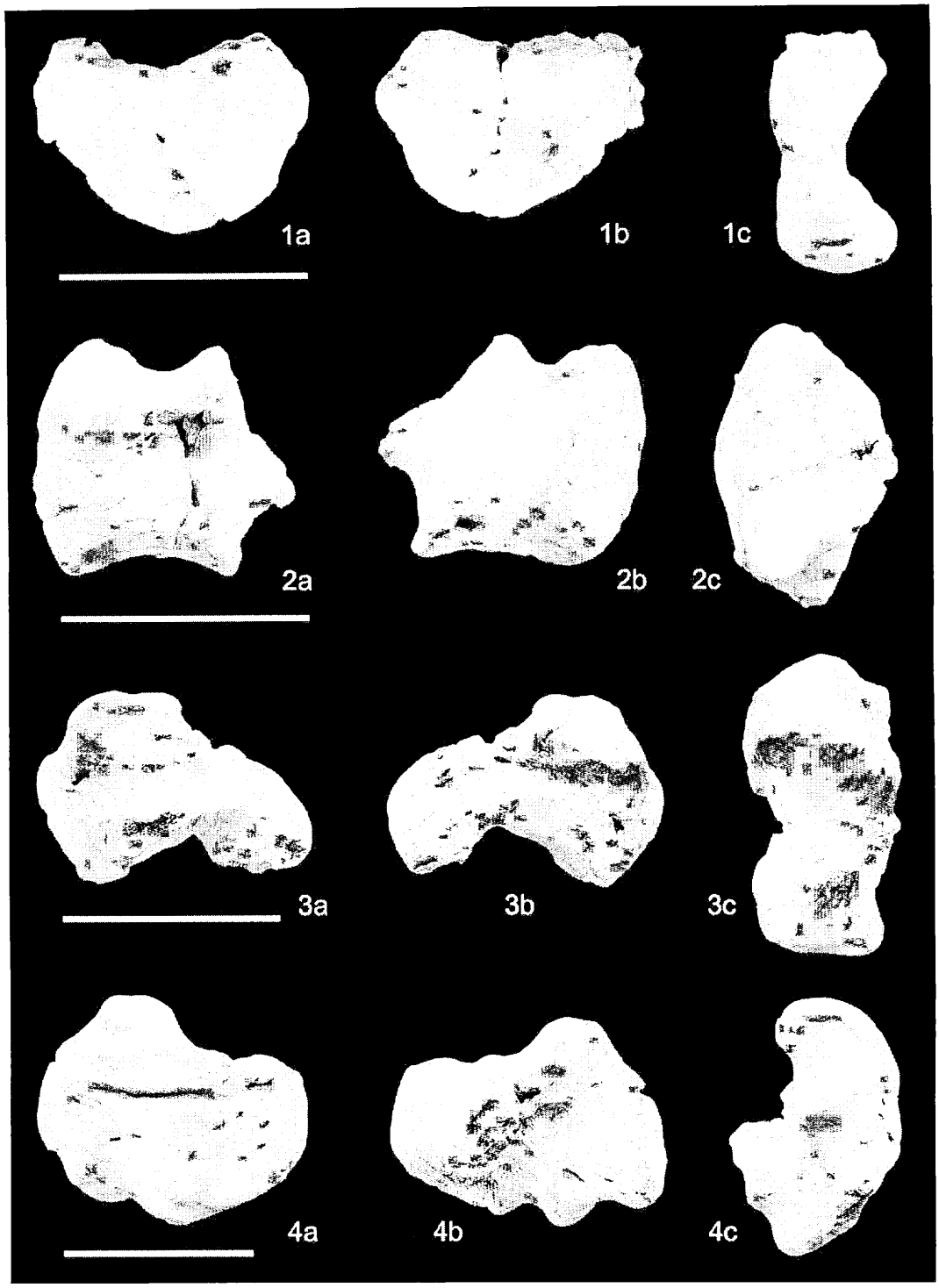

Fig. 3. Right proximal carpals (IVPP V 14967) of *Coelodonta nihowanensis* from Longdan in Gansu, China. (1) pisiform; (2) pyramidal; (3) semilunate; (4) scaphoid; (a) medial view, (b) lateral view, (c) distal view. Scale bars = 5 cm.

2.1. Humerus

The shaft is irregularly cylindrical and has a twisted appearance. The lateral surface is smooth and spirally curved, with high and sharp longitudinal crest (length of about 40 mm) near the posterior margin and above the lateral epicondyle. The medial surface is nearly straight proximo-distally and rounded from side to side. The teres tuberosity is weak. The anterior surface is triangular, wide and smooth proximally, and narrow and roughened distally. The crest of the humerus is thick, rounded, and inclined anteriorly. The deltoid tuberosity is curved

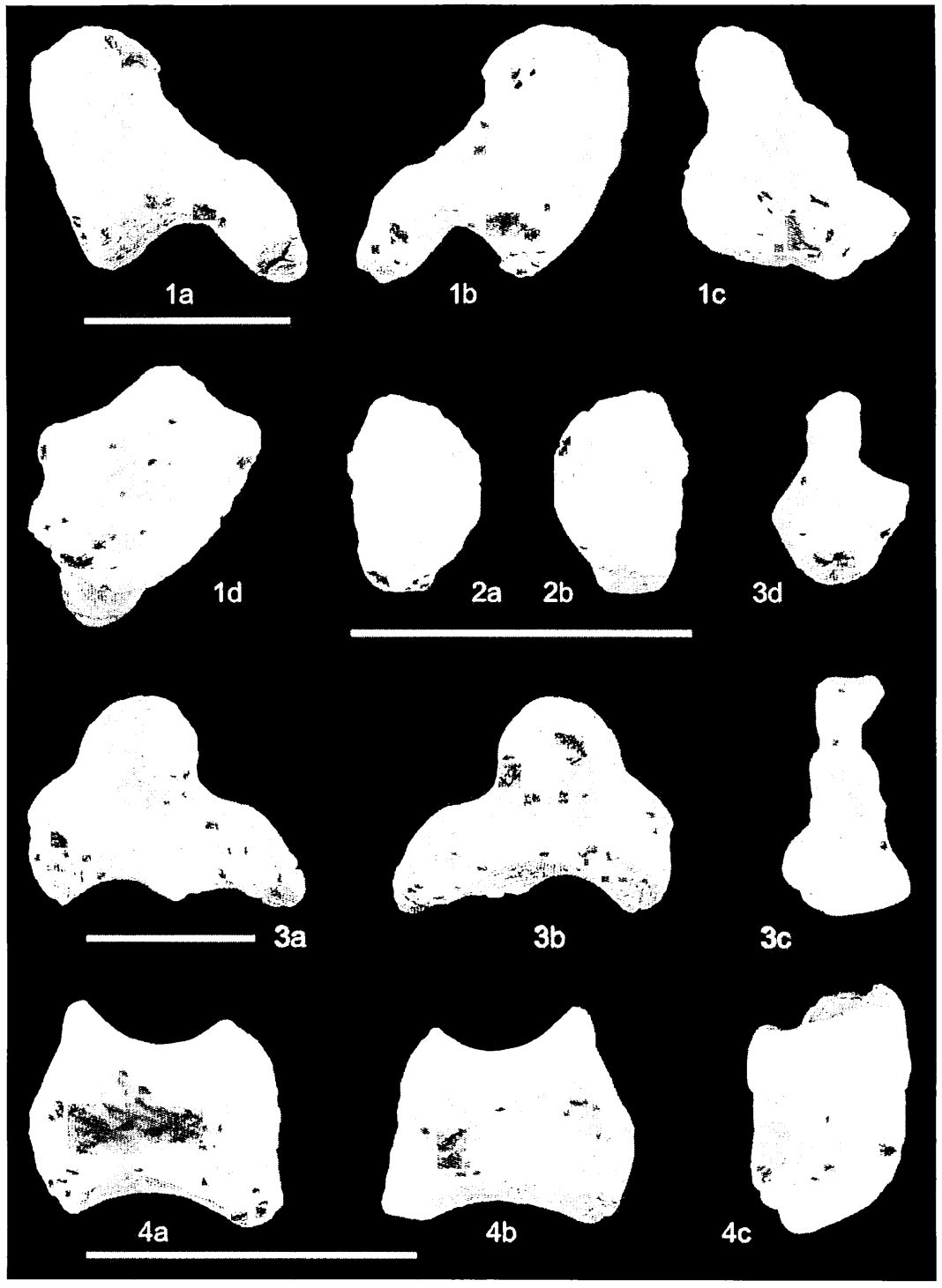

Fig. 4. Right distal carpals (IVPP V 14967) of *Coelodonta nihowanensis* from Longdan in Gansu, China. (1) unciform; (2) trapezium; (3) magnum; (4) trapezoid; (a) medial view, (b) lateral view, (c) proximal view, (d) anterior view. Scale bars = 5 cm.

posteriorly. In the proximal extremity, the head is strongly projected posteriorly, and the articular surface of the head for the scapula is round and convex. In the distal extremity it is inclined latero-distally. The medial condyle is larger, while the lateral condyle is smaller and placed somewhat distally. The coronoid fossa is narrow, deep, and stretched latero-distally. The lateral epicondyle is rugose, slightly curved medially, compressed latero-medially, stretched antero-posteriorly, and projected distally. The lateral ligament depression is wide, deep, and rugose, with a high and thick anterior margin. The lateral part of the medial epicondyle overlaps the olecranon fossa. The olecranon

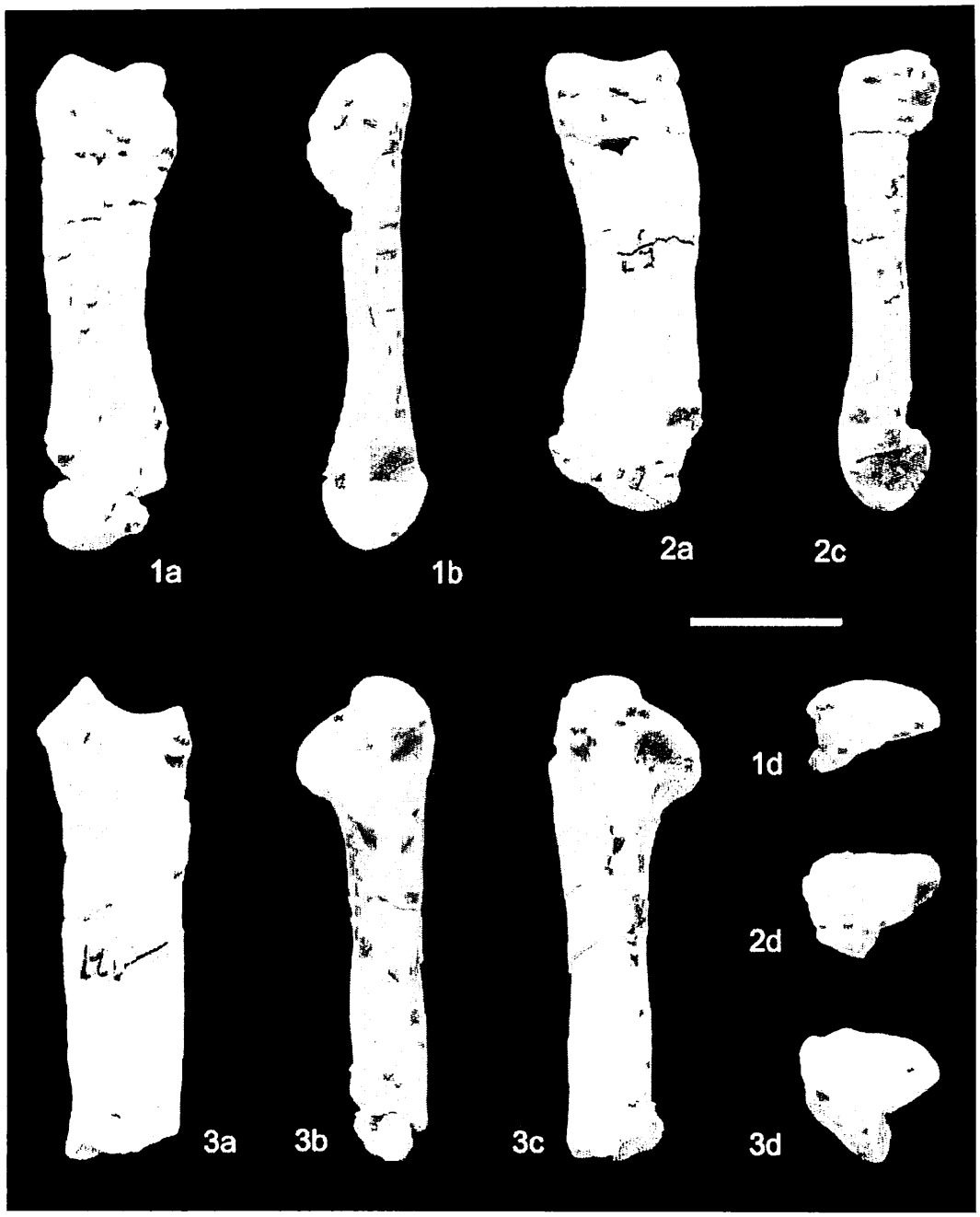

Fig. 5. Right metacarpals (IVPP V 14967) of *Coelodonta nihowanensis* from Longdan in Gansu, China. (1) Mc II; (2) Mc IV; (3) Mc III; (a) anterior view, (b) lateral view, (c) medial view, (d) proximal view; Scale bar = 5 cm.

fossa is large, deep, and inclined latero-distally (Figs. 1(1) and 2(1); Table 1).

The humerus of *C. nihowanensis* is obviously more slender than that of *C. tologoijensis* (Beljaeva, in Vangengeim et al., 1966, Fig. 48.1, Table 46). The distal width of the humerus of *C. nihowanensis* is comparatively narrower than that of *C. tologoijensis*. In *C. nihowanensis*, the olecranic fossa is narrower and higher than it is in *C. tologoijensis*. By comparison, the distal epiphysis is more massive in *C. tologoijensis* than in *C. nihowanensis*, and the distal articular surface is comparatively wider in *C. nihowanensis* than in *C. tologoijensis* (Fig. 2).

2.2. Radius

The shaft is massive and slightly curved posteriorly. The anterior surface is smooth and convex latero-medially. The radial tuberosity is triangular, depressed, and covered with many longitudinal crests. The medial tuberosity is weak, while the lateral tuberosity is more salient. The posterior

Table 2
Measurements of metacarpals of *Coelodonta nihowanensis* and *C. antiquitatis*

Measures	*C. nihowanensis* IVPP V 14967			*C. antiquitatis* Guérin (1980)		
	Mc II	Mc III	Mc IV	Mc II	Mc III	Mc IV
L	164.5	–	154.4	164.18	189.03	151.13
TD prox. max.	46	50.4	43.4	52.93	68.24	53.33
TD prox. art.	34.5	48.7	38.2	48.43	–	–
APD prox.	34	50.5	35	46.95	52.2	44.96
TD mid.	31.5	40	35.4	42.38	56.44	37.58
APD mid.	18	24.5	18.3	27.26	28.71	24.39
TD dis. max.	42	–	–	48.8	65.75	47.91
TD dis. art.	30	–	35	43.5	56.1	45.19
APD dis.	35.4	–	32.5	43.1	50.78	42.26
APD prox./TD prox. max.	73.9	100.2	80.6	88.7	76.5	84.3
APD mid. /TD mid.	57.1	61.3	51.7	64.3	50.9	65.9
TD prox. art./TD prox. max.	75	96.6	88	91.5	–	–
TD. prox. max./*L*	28	–	28.1	32.2	36.1	35.3
TD mid./*L*	19.1	–	22.9	25.8	29.8	24.9
TD dist. art./*L*	18.2	–	22.7	26.5	29.7	29.9

surface is less convex than the anterior one. On the proximal proportion of the posterior surface, the two facets for the ulna are divided by a high, sharp, and laterally declined crest; the lateral facet is triangular, concave, and long proximo-distally, with a strong and tuberculate lateral border, while the medial facet is semicircular, flat, and short. The medial margin is smooth, rounded, and almost straight. The lateral margin is thicker than the medial one and curved medially. The proximal articulate surface for the humerus is concave antero-posteriorly and convex latero-medially. It is divided by a rounded sagittal crest, the posterior end of which is very high and sharp at the posterior border of the proximal surface, into the lateral 1/3 and the medial 2/3. The medial proportion is strongly projected anteriorly (Fig. 1(3)). Measurements: TD prox. = 112; APD prox. = 69; TD mid. = 52.4; APD mid. = 42; TD mid/APD mid = 124.8.

Observed in the materials from Longdan and Nihewan, the radius of *C. nihowanensis* is more slender than that of *C. tologoijensis* (Beljaeva, in Vangengeim et al., 1966, Fig. 48.2, Table 47). By comparison, the proximal extremity in *C. nihowanensis* is comparatively wider than in *C. tologoijensis*. The shaft in *C. nihowanensis* is antero-posteriorly stronger than in *C. tologoijensis*. In *C. nihowanensis*, there is more disproportion between the two sections of the proximal articular surface than there is in *C. tologoijensis*: the medial portion of the articulation, in *C. nihowanensis*, is wider, relative to the lateral portions, than it is in *C. tologoijensis*.

2.3. Ulna

The proximal proportion of the shaft is strongly developed medially. The proximal proportion of the medial margin is thin, tuberculate and declined laterally. The medial surface of the olecranon is concave and smooth, while the lateral surface is less concave and roughened proximally, with a large tuberosity on its postero-proximal proportion to make up an attachment of the lateral head of the triceps. The anterior margin of the olecranon is narrow and smooth, and the anconaeus process is wide, with protruded margins in particular laterally. The semilunar notch is triangular in outline, bifid distally, concave proximo-distally, and convex latero-medially. The medial proportion of the semilunar notch is inclined and strongly projected medially, while the lateral proportion runs parallel to the sagittal plane of the shaft. The synovial fossa is extensive. The distal borders of the semilunar notch contact each other at a 75° angle, which contains a sharp process of the posterior border on the proximal articular surface of the radius (Fig. 1(2)). Measurement: TD prox. art. = 85.

The anterior margin of the olecranon of *C. nihowanensis* is markedly narrower than that of *C. tologoijensis* (Beljaeva, in Vangengeim et al., 1966, Fig. 49, Table 48).

2.4. Pisiform

The pisiform is a medially curved and pentagonal plate. In proximal view, the facet for the radius is slightly concave and right-angled in outline, and the proximal margin is angular and thick. The distal margin is rounded and thin, with a transverse groove separate from the anterior facet for the pyramidal. The lateral surface is flat and rugose, with a wide and shallow horizontal sinew groove, while the medial face is concave, smooth in front, and prominent and rugose behind. The anterior facet for the pyramidal is concave and pentagonal. The free posterior extremity is a thick and rugose tuberosity (Fig. 3(1)). Measurements: $L = 57.3$; W ant. = 24.5; H ant. = 26.4; H post. = 38; W post. = 24.5; W ant./$L = 42.8$; W post./$L = 42.8$; H post./$L = 66.3$; H ant./$L = 46.1$.

By comparison with *C. tologoijensis* (Beljaeva, in Vangengeim et al., 1966, Fig. 51.2, Table 51), the pisiform of *C. nihowanensis* is more compressed latero-medially, and more raised in front but more compressed proximo-distally behind. The proximal margin in *C. nihowanensis* is markedly more concave than that in *C. tologoijensis*.

2.5. Scaphoid

The body is very broad. The proximal surface is deeply concave, with a wide and high posterior border. The distal articular surface in front is divided by a high and sharp transverse crest into two facets for the magnum anteriorly and the trapezoid posteriorly, and it is narrow and rounded behind. The lateral surface bears three facets for the semilunate, two anteriorly and one posteriorly; the antero-proximal facet is narrow, the antero-distal one is semicircular and connected with the distal facet for the magnum, and between the two facets it is broadly excavated and slightly rugose; the posterior facet is long and oval. The medial surface is rugose, with the semicircular medial proportion of the distal facet for the trapezoid. The anterior surface is narrow, convex, and curved laterally, with a wide transverse groove proximally. The posterior surface is strongly tuberculate and obliquely rectangular in outline (Fig. 3(4)). Measurements: $L = 74.5$; $W = 53.5$; $H = 57.2$; L prox. art. = a. 49; W prox. art. = a. 42.5; L dis. art. = 48; W dis. art. = 28.7.

2.6. Semilunate

The body is somewhat wedge shaped, wider in front than behind. In proximal view, the facet for the middle distal facet of the radius is broadly and shallowly saddle shaped, with a marked edge separate from the narrow lateral facet for the ulna. In distal view, the central facet for the unciform is strongly concave, and much wider in front than behind, and it has a rounded transition to the flat and narrow lateral facet for the pyramidal, and a sharp edge separate from the long and concave medial facet for the magnum. In lateral view, there are two flat and semicircular facets for the pyramidal; the proximal one is small and short, while the distal one is large and long; between the two facets it is narrowly and deeply excavated and rugose. In medial view, there are two flat facets for the scaphoid; the proximal one is large and oval, the distal one is small and semicircular, and between the two facets it is narrowly and deeply excavated and strongly rugose. The anterior surface is rectangular and keeled in outline. The posterior surface bears a strong transverse tuberosity on its lower proportion (Fig. 3(3)). Measurements: $L = 69.4$; $W = 40.7$; $H = 49.5$; H ant. = 54; $W/H = 82.2$; $W/L = 58.6$.

The semilunate of *C. nihowanensis* from Longdan is identical to that from Nihewan in outline and size (Teilhard de Chardin and Piveteau, 1930, Pl. II, Fig. 9). The semilunate in *C. nihowanensis* from Longdan is higher than wide, while that in *C. tologoijensis* is wider than high (Beljaeva, in Vangengeim et al., 1966, Fig. 50, Table 49). By comparison with *C. tologoijensis*, the semilunate in *C. nihowanensis* is much more compressed latero-medially and raised proximo-distally. The proximal facet for the radius of *C. nihowanensis* is more concave than that of *C. tologoijensis*. The central excavations on the lateral and medial surfaces of *C. nihowanensis* are deeper than those of *C. tologoijensis*. The anterior surface of *C. nihowanensis* is more convex than that of *C. tologoijensis*.

2.7. Pyramidal

The body is irregular in outline. In proximal view, the facet for the ulna is strongly concave, with a high antero-medial border. In distal view, the facet for the unciform is triangular and concave, but shallower than the proximal facet for the ulna. The lateral surface is slightly rugose, with a prominent and semicircular crest on its posterior border. In medial view, the proximal facet for the semilunate is elongate and contacts the proximal facet for the ulna at a 90° angle; the distal facet for the semilunate is semicircular and contacts the distal facet for the unciform roundly, and between the two facets for the semilunate it is very concave and rugose. The anterior surface is slightly convex and rugose. The posterior surface is strongly concave latero-medially, rugose, and undulate (Fig. 3(2)). Measurements: APD = 37.5; TD = 54.3; $H = 51.2$; $W/H = 106.1$; $W/L = 144.8$.

By comparison with *C. tologoijensis* (Beljaeva, in Vangengeim et al., 1966, Fig. 51.1, Table 50), the pyramidal in *C. nihowanensis* is more compressed antero-posteriorly. The posterior border of the lateral surface in *C. nihowanensis* is semicircular, while that in *C. tologoijensis* is almost straight. The proximal antero-medial border in *C. nihowanensis* is higher than that in *C. tologoijensis*.

2.8. Trapezium

It is a small pea-shaped bone, which is embedded below the scaphoid and behind the trapezoid. It articulates only with the trapezoid. It has a long axis vertically and an apex directed distally. The proximal head is convex, rugose, and rhombic antero-posteriorly in outline. In anterior view, there is a transverse strong prominence in middle. In lateral view, the facet for the trapezoid is olive-shaped proximal-distally, and it occupies the whole lateral surface. The posterior surface is flat, rugose, and narrowly triangular in outline, with a sharp edge separate from the lateral facet. The distal surface is smooth and convex. The medial surface is slightly convex and rugose, with tuberculate distal border (Fig. 4(2)). Measurements: APD = 21; TD = 14.8; $H = 30.1$.

2.9. Trapezoid

The body is cashew shaped. In proximal view, the facet for the scaphoid is widely concave. In distal view, the facet for the Mc II is large, concave, and stretched antero-posteriorly. In lateral view, the facet for the magnum occupies almost the whole lateral surface, and it is rectangular, with curvedly constricted proximal and distal borders and a narrow and long tail distally. In medial view, the posterior facet for the trapezium is triangular, high proximo-distally, and narrow antero-posteriorly, and it connects smoothly with the proximal facet for the scaphoid; its anterior proportion is rugose and depressed, with a small and narrow tuberosity in front. The anterior surface is high proximo-distally and rugose, with a big tuberosity on the distal proportion and a small one on the proximo-medial corner. The posterior surface is irregular in outline, rugose, and tuberculate, with a prominent medial edge and strongly concave lateral half (Fig. 4(4)). Measurements: $L = 40.7$; $W = 25$; $H = 33.8$; $W/H = 74$; $W/L = 61.4$; $L/W = 162.8$.

By comparison with *C. tologoijensis* (Beljaeva, in Vangengeim et al., 1966, Fig. 52, p. 115), the trapezoid of *C. nihowanensis* is more compressed latero-medially and stretched antero-posteriorly. The medial facet for the trapezium in *C. nihowanensis* is wider and inclined posteriorly, while that in *C. tologoijensis* is narrower and inclined anteriorly. The lateral facet for the magnum in *C. nihowanensis* is shorter antero-posteriorly, with a long tail distally, while that in *C. tologoijensis* is longer, without a tail. The lateral half of the posterior surface in *C. nihowanensis* is much more retracted anteriorly than that in *C. tologoijensis*.

2.10. Magnum

It is very irregular in outline, and its posterior proportion is narrow, rugose, and strongly stretched posteriorly, with a well-marked notch behind the proximal process. The proximal articulation has a large and concave medial facet for the scaphoid and a small and flat lateral facet for the unciform in front, and a high medial border and a wide and convex lateral facet for the semilunate behind. In distal view, the facet for Mc III is strongly concave, wide in front, narrow behind, and roundly constricted latero-medially. In lateral view, the anterior facet for the unciform is high proximo-distally, and the other proportion is rugose, tuberculate, and depressed. In medial view, the anterior facet for the scaphoid is strongly concave and high proximo-distally, the central facet for the trapezoid is shallowly concave, with a roundly and deeply constricted posterior border, the distal facet for Mc II is dumbbell shaped and long antero-posteriorly, and the posterior proportion is smooth and curved medially, with the rugose rear-most tuberosity. The anterior surface is a pentagon with a curved distal border, a large and strong latero-distal tuberosity, and a rugose medial half. The free posterior tuberosity is rugose and strong stretched posteriorly (Fig. 4(3)). Measurement: $L = 86.7$; $W = 39.5$; H ant. $= 64.5$; H art. $= 61.4$; H ant. $= 33.5$; W ant./H ant. $= 117.9$.

By comparison with *C. tologoijensis* (Beljaeva, in Vangengeim et al., 1966, Fig. 53.1, p. 115), the anterior surface of the magnum of *C. nihowanensis* is more raised proximo-distally, and the anterior proportion of the proximal facet for the scaphoid is more convex. In anterior view, the borders relative to the trapezoid and Mc II in *C. nihowanensis* have a pointed connection, while those in *C. tologoijensis* have a smooth connection. The proximal facet for the semilunate in *C. nihowanensis* is restricted to the central process, while that in *C. tologoijensis* stretches anteriorly to reach the anterior border of the magnum. The lateral facet for the unciform in *C. nihowanensis* is much broader than that in *C. tologoijensis*.

2.11. Unciform

It is somewhat wedge shaped. In proximal view, the articular surface is divided by a high and rounded central crest into a larger lateral facet for the pyramidal and a smaller medial facet for the semilunate; the crest is inclined latero-posteriorly: the two facets are convex antero-posteriorly and concave latero-medially; and between the anterior articular surface and the posterior tuberosity there is a rugose and semicircular medial depression. In distal view, the facets for Mc IV, Mc III and the magnum are connected smoothly, with a high and sharp anterior border; and the free posterior tuberosity is rugose, compressed proximo-distally, and strongly stretched latero-distally. In lateral view, between the tuberculate anterior surface and the rugose posterior tuberosity it is deeply concave antero-posteriorly. In medial view, the distal facet for Mc III is wide and concave antero-posteriorly, the proximal facet for the magnum is narrow and flat, and between the anterior facet and the posterior tuberosity the proximal proportion is narrow, rugose, depressed, and stretched posterio-distally. The anterior surface is rugose, with a large prominence on the proximo-medial corner. In posterior view, the free tuberosity is oval latero-medially in outline, with a rugose tip (Fig. 4(1)). Measurements: L absolute $= 89$; L anatomic $= 62$; $W = 59.5$; $H = 64$; $W/H = 93$; W/L anatomic $= 96$.

By comparison with *C. tologoijensis* (Beljaeva, in Vangengeim et al., 1966, pp. 115, 117, Fig. 53.2), the unciform of *C. nihowanensis* is slightly more compressed latero-medially; the proximal facet for the pyramidal is broader in *C. nihowanensis*, and the proximal facet for the semilunate is triangular in outline in *C. nihowanensis*, while it is quadrangular in *C. tologoijensis*.

2.12. Mc II

It is straight and prolate. In proximal view, the facet for the trapezoid is concave and strongly stretched

posterio-medially, with a thin posterior process, a high medial edge, and a sharp lateral edge separated from the lateral facet for Mc III. The distal articulation for the first phalanx II is asymmetric and inclined medially, and the sagittal keel is absent anteriorly and weak posteriorly. The lateral trochlea is weak, and the medial one is shallow. The distal lateral fossa is large and deep, while the medial one is small and shallow. In lateral view, the facet for the magnum facet is narrow, stretched antero-posteriorly, and slightly concave at middle, with a small notch at the middle of the lower border, and it is smoothly connected with the oval and flat facet for Mc III. The medial margin of the shaft is slightly curved, with a highly convex distal proportion. The anterior surface of the shaft is smooth and flat, with rugose and projected proximal and distal proportions. In posterior view, there is a vertical crest at the center of the shaft, well developed proximally and disappeared distally (Fig. 5(1); Table 2).

By comparison with *C. antiquitatis* (Borsuk-Bialynicka, 1973, Pl. XVIII; Guérin, 1980, Figs. 95, 96, Table 139), Mc II of *C. nihowanensis* has a thinner proximal extremity, and proportionally much narrower proximal articular surfaces. In *C. nihowanensis*, the proximal articular surface is more concave and more oblique posterio-medially than it is in *C. antiquitatis*. In *C. nihowanensis*, the shaft is straight, whereas it is roundly constricted antero-posteriorly in *C. antiquitatis*. In *C. nihowanensis*, the shaft is obviously thinner antero-posteriorly than it is in *C. antiquitatis*. In *C. nihowanensis*, the distal articular surface is proportionally narrower and more asymmetrical than it is in *C. antiquitatis*.

2.13. Mc III

The distal extremity of the specimen is lost. The shaft is straight and prolate, and the lateral margin is thicker than the medial one. In proximal view, the medial facet for the magnum is large, triangular, very concave latero-medially, strongly stretched posteriorly, visible in anterior view, and separated by a high and sharp crest from the lateral facet for the unciform; the lateral facet for the unciform is small, convex antero-posteriorly, and roundly triangular in outline; and the posterior process is strong and curved laterally. In lateral view, the anterior proximal facet for Mc IV is flat, triangular, and separated by a rounded ridge from the facet for the unciform; the posterior proximal facet for Mc IV is flat, oval, and strongly projected posteriorly; and between them it is rugose and deeply excavated. The lateral margin of the shaft is rugose on the proximal 4/5 and smooth on the distal 1/5, while the medial margin is rugose on the proximal half and smooth on the distal half. In medial view, the proximal facet for Mc II is small, flat, semicircular in outline, and separated from the facet for the magnum by a sharp edge at about 90°. The posterior surface of the shaft has a rough ridge on the medial side proximally, and it is concave from side to side distally (Fig. 5(3); Table 2).

By comparison with *C. antiquitatis* (Borsuk-Bialynicka, 1973, Pl. XVII; Guérin, 1980, Figs. 97, 98, Table 140), Mc III of *C. nihowanensis* has a thicker proximal extremity, and proportionally narrower proximal articular surfaces. The proximal articular surface in *C. nihowanensis* is more concave than it is in *C. antiquitatis*. The crest separating the proximal articular surface from the facet for the unciform is particularly salient and acute in *C. nihowanensis*. In proximal view, by comparison with *C. antiquitatis*, the proximal articular surface in *C. nihowanensis* is more stretched posteriorly and laterally. In *C. nihowanensis*, the proximo-lateral facet for the unciform is broader than it is in *C. antiquitatis*. In lateral view, the anterior facet for Mc IV is triangular, while the posterior facet is oval in *C. nihowanensis*. On the other hand, one facet is rectangular and the other is pentagonal in *C. antiquitatis*. In *C. nihowanensis*, the shaft, in anterior view, is more symmetrical than it is in *C. antiquitatis*; the medial border of the former is flat just under the proximal epiphysis, while that of the latter bulges markedly. In *C. nihowanensis*, the shaft is straight, whereas it is somewhat arched in anterior direction in *C. antiquitatis*. In *C. nihowanensis*, the shaft is much thicker antero-posteriorly than it is in *C. antiquitatis*. In *C. nihowanensis*, the lateral margin of the shaft is straighter than it is in *C. antiquitatis*.

2.14. Mc IV

The shaft is prolate, curved laterally, and wider than that of Mc II. In proximal view, the facet for the unciform is very wide, irregular in outline, and concave latero-medially, with a rounded medial crest separated from the anterior medial facet for Mc III, and the posterior process is short and inclined laterally. The distal articulation for the first phalanx IV is asymmetric and oblique laterally, with an unclear anterior upper border and a steep posterior one. The sagittal keel is absent anteriorly and strong posteriorly. The lateral trochlea is deep, while the medial one is shallow. The medial fossa is semicircular, large, and deep, while the lateral one is absent. The lateral margin of the shaft is thin, smooth, and markedly curved, while the medial one is thick, rugose, and almost straight. In medial view, the anterior proximal facet for Mc III is small and semicircular in outline; the posterior one is flat, oval, displaced posteriorly, and connected with facet for the unciform at the rear-most end; and between them it is a narrow and deep groove. The anterior surface of the shaft is smooth and flat, while the posterior one is rugose and concave from side to side, with a projected medial edge distally (Fig. 5(2); Table 2).

By comparison with *C. antiquitatis* (Borsuk-Bialynicka, 1973, Pl. XVIII; Guérin, 1980, Figs. 99, 100, Table 141), the proximal articular surface of Mc IV of *C. nihowanensis*, in proximal view, has a relatively wider anterior border and, in turn, a shorter medial border. In *C. nihowanensis*, the proximal articular surface is more concave latero-medially and more convex antero-posteriorly than it is in

C. antiquitatis. In *C. nihowanensis*, the shaft is much thinner antero-posteriorly than it is in *C. antiquitatis*. In *C. nihowanensis*, the distal articular surfaces are more asymmetric and more oblique laterally than they are in *C. antiquitatis*. In *C. nihowanensis*, in medial view, the shaft is straighter than it is in *C. antiquitatis*.

3. Discussion

It is generally accepted that *Coelodonta* derived in northern China during the Late Pliocene from some species of the tribe Rhinocerotini and subsequently dispersed to Europe (Chow, 1978; Guérin, 1980). The *Coelodonta* from the Late Pliocene in the Linxia Basin represents the earliest known member of this genus. Because of this earliest known occurrence, the origination of the woolly rhino, distributed widespread in northern Eurasia during the Late Pleistocene, is affirmed in northern China at 2.5 Ma. The presence of *Coelodonta* in Europe and North Asia evidently represents dispersal from northern China. The cranial and dental features of the Eurasian *Coelodonta* indicate that derived varieties of *Coelodonta* already existed in northern China by the end of the Pliocene, and that they dispersed to North Asia and Europe giving rise to several different forms during the Middle Pleistocene and later time (Deng, 2006).

The fossil of *C. nihowanensis* was discovered from the typical loess of the Wucheng Formation at Longdan in the Linxia Basin. The sediment is grayish brown (Munsell color chart: 10 YR 7/4), blocky, well consolidated, without calcareous concretions and visible traces of paleosol layers. Average grain size is 18.89 μm, with those in the 10–50 μm range making about 45% of the total. Total thickness is approximately 90 m. The paleomagnetic dating and stratigraphic sequence show that it is the earliest loess in China, and the time span of its fossiliferous levels is from 2.55 to 2.16 Ma (Qiu et al., 2004). There is no paleosol in the loess at Longdan, which indicated that it represents a different climate from the loess in eastern China. During the sedimentary period of loess, climatic conditions are drier and colder than during paleosol (Liu, 1985). The fossil of *C. nihowanensis* from Linxia occurs above the paleomagnetic boundary of *M/G*. In this period, the polar ice sheets increased rapidly, and the global climate changed markedly. The variation in the global ice volume greatly influenced the deposition of the loess via influences to terrestrial dry degree and winter monsoon strength. The woolly rhino is a typical glacial animal. All known nasal horns of the woolly rhino are laterally flattened and transversely banded. These bands are annual growth zones, and they imply that their steppe was a strongly seasonal environment (Fortelius, 1983). The discovery of the woolly rhino in the Linxia Basin further indicated that the climate was relatively cold at that time, which was the result of the appearance of the Great Glaciation and the uplift of the Tibetan Plateau.

The complete skull found from Longdan proves that *C. nihowanensis* is a species different from *C. antiquitatis* indeed (Deng, 2002; Qiu et al., 2004). Deng (2006) also indicates that the cranial and dental characters of *C. nihowanensis* are obviously distinct from those of *C. tologoijensis*, and the former has more slender limb bones. Actually, Beljaeva (in Vangengeim et al., 1966) has compared the differences of the limb bones between *C. tologoijensis* and *C. nihowanensis* from Nihewan. The forelimb bones of *C. nihowanensis* found recently from Longdan further evidenced that the body size of *C. nihowanensis* is markedly smaller than that of *C. tologoijensis*, and *C. nihowanensis* has different postcranial features compared to *C. tologoijensis*, which indicate that they belong to two different species, respectively.

A strongly limited contact between the semilunate and the magnum in *C. nihowanensis* is connected with the cursorial type of the limb and representing a primitive structure (Osborn, 1929; Borsuk-Bialynicka, 1973). A strong development of the posterior processes of the unciform and magnum makes up an adaptation to fast running (Radinsky, 1965, p. 245). By comparison, these processes in *C. nihowanensis* are more developed than in *C. tologoijensis*, which indicate that the former has faster running than the latter. The above-mentioned features suggest that *C. nihowanensis* is apparently more primitive than *C. tologoijensis*, and the former has the better running ability, which is consistent with the chronological distributions of the two woolly rhino species and the evolutionary trend of the genus *Coelodonta*. As a result, *C. nihowanensis* is the known earliest woolly rhino in the world, and it may be the ancestral form of *C. tologoijensis*. The woolly rhino originated in northern China, and then dispersed to northern Eurasia. *C. nihowanensis* gradually evolved into *C. tologoijensis*, and finally produced *C. antiquitatis*.

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