

Sexual Dimorphism in Perissodactyl Rhinocerotid *Chilotherium wimani* from the Late Miocene of the Linxia Basin (Gansu, China)

Authors: Chen, Shaokun, Deng, Tao, Hou, Sukuan, Shi, Qinqin, and Pang, Libo

Source: *Acta Palaeontologica Polonica*, 55(4) : 587-597

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2009.0001>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Sexual dimorphism in perissodactyl rhinocerotid *Chilotherium wimani* from the late Miocene of the Linxia Basin (Gansu, China)

SHAOKUN CHEN, TAO DENG, SUKUAN HOU, QINQIN SHI, and LIBO PANG



Chen, S., Deng, T., Hou, S., Shi, Q., and Pang, L. 2010. Sexual dimorphism in perissodactyl rhinocerotid *Chilotherium wimani* from the late Miocene of the Linxia Basin (Gansu, China). *Acta Palaeontologica Polonica* 55 (4): 587–597.

Sexual dimorphism is reviewed and described in adult skulls of *Chilotherium wimani* from the Linxia Basin. Via the analysis and comparison, several very significant sexually dimorphic features are recognized. Tusks (i2), symphysis and occipital surface are larger in males. Sexual dimorphism in the mandible is significant. The anterior mandibular morphology is more sexually dimorphic than the posterior part. The most clearly dimorphic character is i2 length, and this is consistent with intrasexual competition where males invest large amounts of energy jousting with each other. The molar length, the height and the area of the occipital surface are correlated with body mass, and body mass sexual dimorphism is compared. Society behavior and paleoecology of *C. wimani* are different from most extinct or extant rhinos. M/F ratio indicates that the mortality of young males is higher than females. According to the suite of dimorphic features of the skull of *C. wimani*, the tentative sex discriminant functions are set up in order to identify the gender of the skulls.

Key words: Mammalia, Perissodactyla, *Chilotherium wimani*, sexual dimorphism, statistics, late Miocene, China.

Shaokun Chen [chenshaokun_ivpp@yahoo.com.cn], Chongqing Three Gorges Institute of Paleoanthropology, China Three Gorges Museum, 236 Ren-Min Road, Chongqing 400015, China and Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xi-Zhi-Men-Wai Street, P.O. Box 643, Beijing 100044, China; Tao Deng [dengtao@ivpp.ac.cn], Sukuan Hou [housukuan@gmail.com], Qinqin Shi [shiqin@hotmail.com], and Libo Pang [libopang2002@yahoo.com.cn], Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xi-Zhi-Men-Wai Street, P.O. Box 643, Beijing 100044, China.

Received 7 January 2009, accepted 22 April 2010, available online 27 April 2010.

Introduction

Chilotherium wimani Ringström, 1924 is a middle-sized fossil rhinoceros referred to the subfamily Aceratheriinae, and established on materials from Fugu, Shaanxi, China (Ringström 1924); the morphology of this species is relatively well known. Deng (2001a) described more skulls and mandibles of this species from Fugu, and Deng (2001b, 2002) also discussed the cranial ontogenesis and characters of limb bones of *C. wimani* from the late Miocene, Linxia Basin, Gansu Province. As Deng (2006) remarked, *C. wimani* was the most abundant taxon in the late Miocene “*Hipparion* fauna” of the Linxia Basin and represented a basal form among the known species of *Chilotherium*. The presence of sexual dimorphism in *C. wimani* was observed by Deng (2001b), but only based on two skulls. Plentiful skulls of *C. wimani* were found in the Linxia Basin, and these materials provided us an indispensable sample which allowed us to highlight the sexual dimorphism of *C. wimani* in the late Miocene.

Sexual dimorphism is common among perissodactyls in the fossil record. Gingerich (1981) discovered sexual dimorphism in the Eocene equoid *Hyracotherium*. Radinsky (1963,

1967) found sexual dimorphism in the primitive tapiroids *Homogalax* and *Isectolophus* and the hyracodontid *Hyrachyus*. Coombs (1975) recognized dimorphism in the chalicothere *Moropus*. Fortelius and Kappelman (1993) and Antoine et al. (2004) discussed dimorphism in giant hyracodontid rhinocerotoids.

Sexual dimorphism is variable in living and extinct rhinos. Pocock (1945) and Groves (1982) recognized that *Rhinoceros sondaicus* (the Javan rhino) and *Dicerorhinus sumatrensis* (the Sumatran rhino) have dimorphic incisors, but are not clearly dimorphic in body size or horn size. On the contrary, *Rhinoceros unicornis* (the greater one-horned rhino) is dimorphic in body size and incisor size (Dinerstein 1991a). Owen-Smith (1988) pointed out that *Ceratotherium simum* (the white rhino) is sexually dimorphic in body size and horn size whereas *Diceros bicornis* (the black rhino) is monomorphic. Numerous observations about sexual dimorphism have also been made in Miocene rhinos. Osborn (1898a, b) observed skulls of *Teleoceras fossiger* (late Miocene, North America), *Subhyracodon occidentalis* and *Subhyracodon tridactylum* (Oligocene, North America), and pointed out that these rhinos could be identified to gender on the basis of

the lower tusk morphology. He also found many other dimorphic characters in extinct rhinoceroses: for example nasals and skulls are smaller in females. Dinerstein (1991b) pointed out that male rhinoceros predominantly inflict wounds with the lower incisors (i2) and to a lesser extent with the horn. Mead (2000) concluded that significant sexual dimorphism is evident in *Teleoceras major* (late Miocene, North America) in terms of cranial, mandibular, and post-cranial characters. Mihlbachler (2005) described tusk and body size dimorphism in *Teleoceras proterum* and *Aphelops malacorhinus* (late Miocene, North America). Mihlbachler (2007) discussed the sexual dimorphism and mortality bias in *Menoceras arikarensis* from Agate Springs National Monument, United States (early Miocene).

Sexual dimorphism in two species of the Miocene rhinos in the Linxia Basin, Gansu, China has been noted. Deng (2005) described the sexual dimorphism of Chinese specimens referred to the elasmotheriine *Iranotherium morgani*, in which the male skull is more massive, with a larger nasal horn and stronger zygomas. *Chilotherium wimani*, which will be discussed in this paper, also has been mentioned previously (but based on two skulls only). According to Deng (2001b), the male *C. wimani* has a larger size and stronger build than the female. Many dimensions are larger in males, such as the nasal, supraorbital tubercle and the articular pro-

cesses on the occipital part. Male nasal bones are thicker than in females, and the shape is different where the male has a lentoid section and female a half-lentoid section. The cranial dorsal profile of the male is strongly concave, whereas that of the female is nearly flattened. Deng (2001b) also noted that the cranial dorsal profile becomes more and more concave through ontogeny, and should be a characteristic of the male. The female occipital surface is more quadrate, while the male occipital surface is higher but narrower.

The terminology and morphological variables used in this paper follow those of Heissig (1972, 1999) and Guérin (1980). The measurements are according to Guérin (1980) and are given in mm and area in cm². In addition, we also took other measurements such as the molar row length, the length, width and thickness of i2, maximal and minimal width of symphysis.

Institutional abbreviation.—HMV, Hezheng Paleozoological Museum, Gansu, China.

Other abbreviations.—M, Male; F, Female.

Material and methods

The specimens of *Chilotherium wimani* studied here were collected from different localities in the Linxia Basin (Fig. 1)

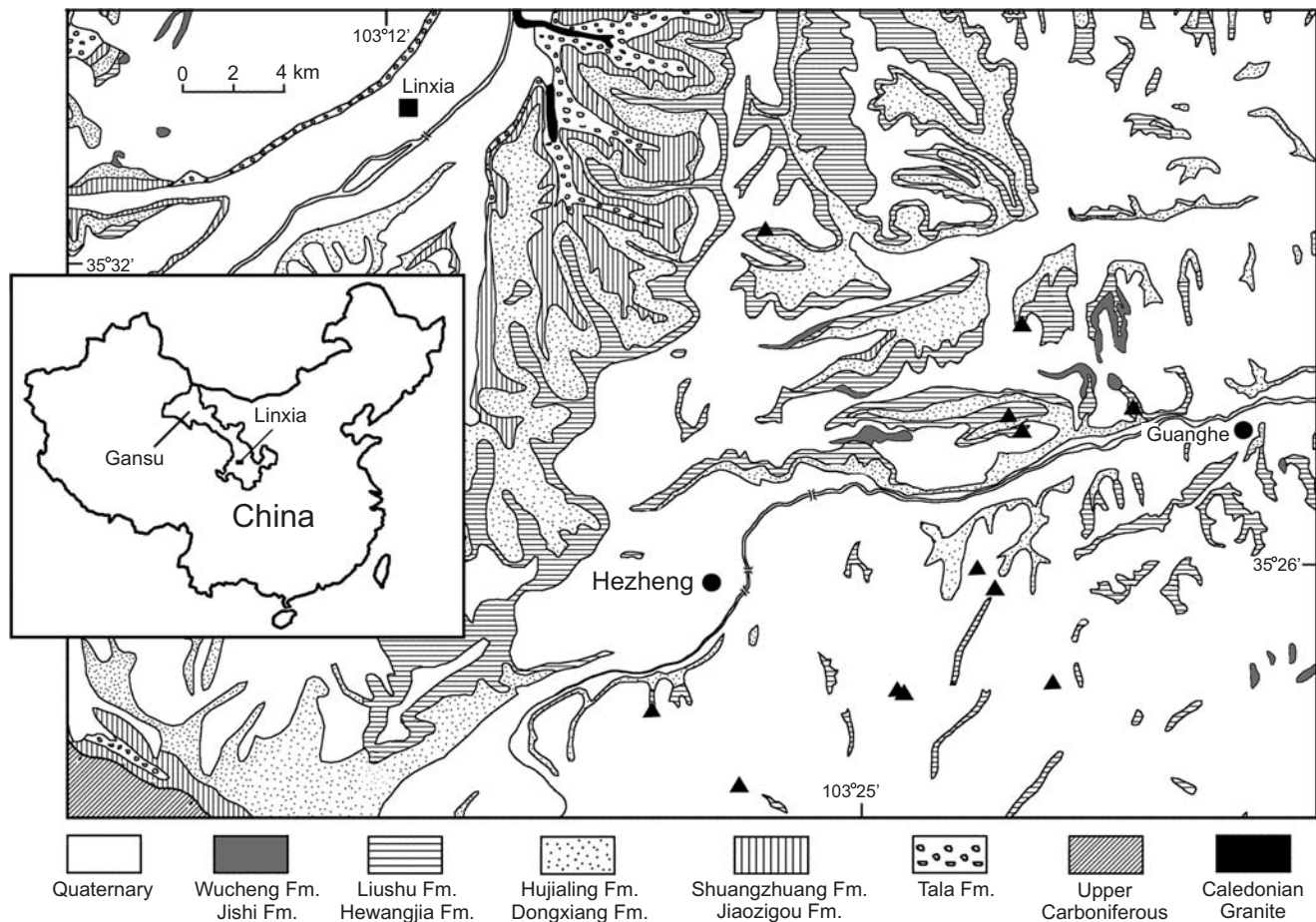


Fig. 1. Map of the Linxia Basin showing the fossil localities (triangles) where *Chilotherium wimani* were found.

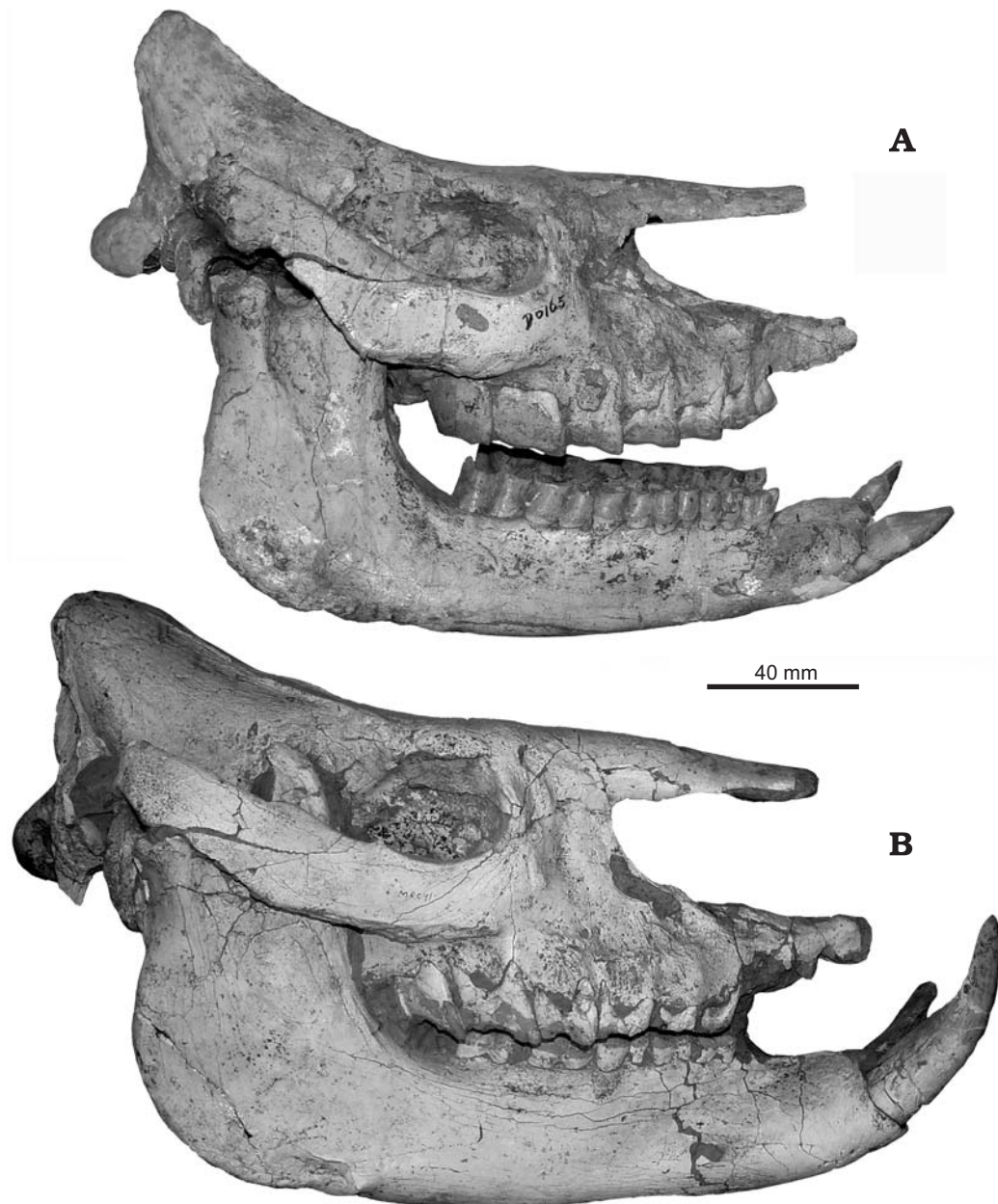


Fig. 2. Skulls of perissodactyl rhinocerotid *Chilotherium wimani* Ringström, 1924 (Liushu Formation, late Miocene, Linxia Basin, Gansu, China) with articulated mandibles. **A.** Female (HMV 1426). **B.** Male (HMV 1451).

and are housed in the Hezheng Paleozoological Museum. They are all from the middle late Miocene. A detailed field correlation indicates that these localities are from the same horizon, i.e., the middle part of the Liushu Formation, within a grey orange or yellow brown silty mudstone or muddy siltstone (Liang and Deng 2005).

Chilotherium wimani could be identified to gender on the basis of lower tusk (i2: Figs. 2, 3). *C. wimani* have lost their incisors, except for the tusk-like i2. The i2 is very well developed, and its cross section is a narrow and round triangle; the left and right incisors diverge from each other in curvature, pointing laterally. The i2 extends outward, upward, and then forward (Deng 2001a). The root of the male i2 is ellipsoidal, while in the female it tends to be round. Kurtén (1969) sug-

gested that, as a common observation, tusks in males were usually better developed than in females among many groups of fossil mammals, which was also pointed in extinct rhinocerotids by Antoine (2002) and by Antoine et al. (2004) in giant rhinocerotids. Muhlbachler (2005) and Prothero (2005) also concluded that the tusks were commonly dimorphic in extinct rhinos.

In our study, all materials were sexed a priori by the tusks, except for one skull in which gender was assumed on the basis of symphyseal morphology. Length, width and thickness of i2 are very significant sexual dimorphic parameters ($p < 0.01$), in which the male/female ratios are 2.02, 1.67, and 1.25. Kurtosis and skewness indicate a slight deviation from a normal distribution, except that the measurement for the



Fig. 3. Tusks (i2) and symphyses of perissodactyl rhinocerotid *Chilotherium wimani* Ringström, 1924 (Liushu Formation, late Miocene, Linxia Basin, Gansu, China). **A.** Female (HMV 1450). **B.** Male (HMV 0746).

width of male i2 is the best normal distribution (Kurt = -0.13, Skew = -0.05). Length, width and thickness data of complete i2 specimens clearly contained “male” and “female” size clusters (Fig. 4A). The length of i2 is the most dimorphic character (Table 1).

Because materials found in the Linxia Basin are lacking the postcranial skeleton and we could not identify the gender without the lower tusks, only measurements of skulls and their articulated mandibles were investigated in order to correlate other cranial characters with sexually dimorphic i2 and mandibular symphysis morphology. In Chinese *C. wimani*, the paired tusks of males are broken or worn at one or both tips in our collection, while tusks of females are always in better condition. Even so, we could still estimate the length of tusks and “sex” these materials easily.

To avoid age-related character variability, only adult specimens with intact structures allowing full measurements to be taken were used (age estimation is based on Liang and Deng 2005 and Hitchins 1978). Seventy-four adult skulls with their articulated mandibles, corresponding to 41 females and 33 males, were measured. Not every measurement was accessible on each skull and mandible, because of factors such as breakage, distortion, and incomplete preparation. For example, only 70 measurements of i2s and symphysis (39 females

and 31 males) were used. Each measurement was taken from one side only (right or left, whichever side is less deformed) on each individual.

For each measurement, we calculated the mean, maximum, minimum, standard deviation, coefficient of variation, kurtosis, skewness, Shapiro-Wilk test and used the two-tailed Student’s *t*-test to test the significance of the dimorphism between male and female (Tables 1–3). Correlations are treated as potentially very significant whenever $p < 0.01$, significant whenever $p < 0.05$ and not significant whenever $p > 0.05$. We also calculated dimorphic ratios (male value/female value) from the mean of each measurement. Occipital surface area was calculated as: $\text{area} = (a+b) \times h/2$, where *a* is width of occipital crest, *b* is width of mastoid processes and *h* is height of occipital surface.

Results

All sexually dimorphic characters in *Chilotherium wimani* are quantitative in nature (Table 2); there are no readily detectable presence/absence (qualitative) characters. As Kurtén (1969) mentioned, qualitative characters are those present in one sex and absent in the other, while quantitative characters, posing

Table 1. Statistic variable for tusks of adult *Chilotherium wimani*. Abbreviations: CV, coefficient of variation; DR, dimorphic ratio (male value/female value); i2L, length of i2 crown; i2T, thickness at base of i2 crown; i2W, width at base of i2 crown; Kurt, kurtosis; *p*, value of the Student’s *t*-test (sig. [2-tailed]); SD, standard deviation; Skew, skewness; SW, value of the Shapiro-Wilk test.

Characters	Sex	Mean	Max	Min	n	SD	CV	Kurt	Skew	SW	<i>p</i>	DR
i2L	male	98.0	118.4	77.8	24	12.86	13.12	-1.19	0.05	0.14	< 0.01	2.02
	female	48.5	70.0	28.6	38	10.06	20.76	-0.44	0.23	0.58		
i2W	male	46.5	57.7	36.3	31	5.03	10.83	-0.13	-0.05	0.83	< 0.01	1.67
	female	27.9	37.9	22.2	39	3.53	12.64	0.76	0.63	0.52		
i2T	male	25.6	30.5	19.2	31	2.89	11.32	-0.68	0.14	0.78	< 0.01	1.25
	female	20.4	24.7	15.5	39	2.23	10.96	-0.56	-0.03	0.62		

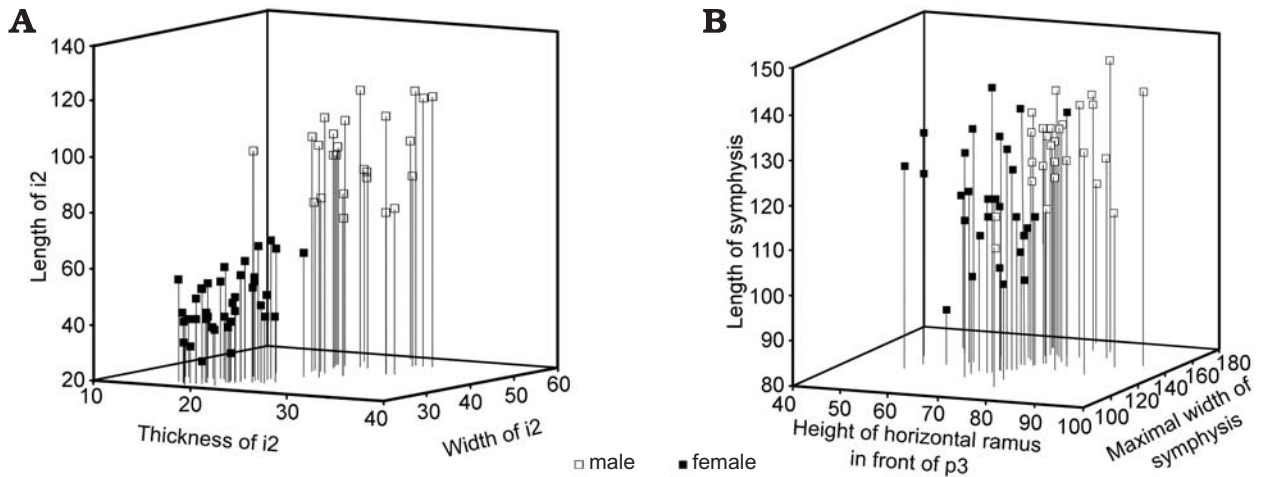


Fig. 4 Sexual dimorphism in tusks (i2s) and symphyses of *Chilotherium wimani*. A. Tusks. B. Symphyses.

Table 2. Sexual dimorphic characters and the morphometric analysis for adult *Chilotherium wimani*. Abbreviations: AWS, maximal width of symphysis; CV, coefficient of variation; DAR, antero-posterior diameter of ascending ramus; DBO, distance between nasal notch and orbit; DNB, distance between nasal tip and bottom of nasal notch; DR, dimorphic ratio (male value/female value); HHp3, height of horizontal ramus in front of p3; HHp4, height of horizontal ramus in front of p4; HOS, height of occipital surface; IWS, minimal width of symphysis; Kurt, kurtosis; LSP, length of symphysis; *p*, value of the Student’s *t*-test (sig. [2-tailed]); SD, standard deviation; Skew, skewness; SW, value of the Shapiro-Wilk test; WLT, width between lacrimal tubercles; WMP, width of mastoid processes; WOC, width of occipital crest; WPC, minimal width between parietal crests; WZA, maximal width between zygomatic arches.

Characters	Sex	Mean	Max	Min	n	SD	CV	Kurt	Skew	SW	<i>p</i>	DR
AWS	male	150.9	175	127.6	30	11.23	7.44	-0.51	0.04	0.80	< 0.01	1.19
	female	126.3	146.5	99.5	38	11.35	8.99	0.18	-0.47	0.42		
IWS	male	103.5	125	85.3	31	9.14	8.84	-0.28	0.1	0.16	< 0.01	1.1
	female	94.3	111.8	76.3	39	8.6	9.12	-0.25	0	0.97		
DNB	male	143	169	124	28	11.19	7.83	-0.27	0.6	0.81	> 0.05	0.97
	female	147.8	164.9	118.3	31	13.71	9.27	-0.71	-0.56	0.14		
DBO	male	63.9	81.1	54.8	29	5.76	9.01	1.43	0.95	0.95	> 0.05	1.04
	female	61.6	77.2	45.2	38	5.98	9.7	0.93	-0.14	0.70		
WOC	male	146.4	170	120.6	26	11.64	7.95	-0.05	-0.06	0.10	> 0.05	1.04
	female	140.4	190	122.5	25	12.91	9.2	7.82	2.15	0.68		
WMP	male	197.2	224	177	22	10.05	5.1	1.03	0.47	0.39	< 0.01	1.06
	female	185.6	205.5	161.8	25	11.87	6.4	-0.37	-0.27	0.31		
WPC	male	40.1	60	15.3	27	11.15	27.78	-0.23	-0.19	0.21	> 0.05	0.91
	female	44.1	66.7	20.3	30	9.51	21.58	0.53	-0.2	0.16		
WLT	male	156.6	182.3	134	28	13.61	8.69	-0.51	0.13	0.16	> 0.05	1.04
	female	151.2	188	124	30	12.55	8.3	1.79	0.49	0.85		
WZA	male	246.4	271	218.8	27	14.24	5.78	-0.92	-0.19	0.59	> 0.05	1.03
	female	239.3	281	151.2	30	24.67	10.31	4.28	-1.3	0.39		
HOS	male	131.3	155	111.6	25	11.93	9.09	-0.85	0.26	0.28	< 0.01	1.07
	female	122.9	132.5	110.4	29	6.71	5.47	-0.78	-0.49	0.72		
HHp3	male	76.9	94.9	65	31	6.83	8.88	0.54	0.44	0.04	< 0.01	1.13
	female	67.2	81.4	51.6	38	7.36	10.95	-0.49	-0.26	0.13		
HHp4	male	78.4	94.6	66.1	31	6.96	8.88	-0.07	0.3	0.11	> 0.05	1.04
	female	75.2	89.4	62	37	7.9	10.51	-0.98	-0.17	0.03		
LSP	male	126.3	145	104.5	28	9.18	7.27	0.04	-0.25	0.90	< 0.01	1.05
	female	118.1	143	92	34	11.72	9.92	-0.36	-0.09	0.99		
DAR	male	143.3	155.4	125	28	8.2	5.72	-0.61	-0.39	0.54	< 0.05	1.03
	female	138.7	159	116	35	8.21	5.92	1.7	-0.5	0.03		

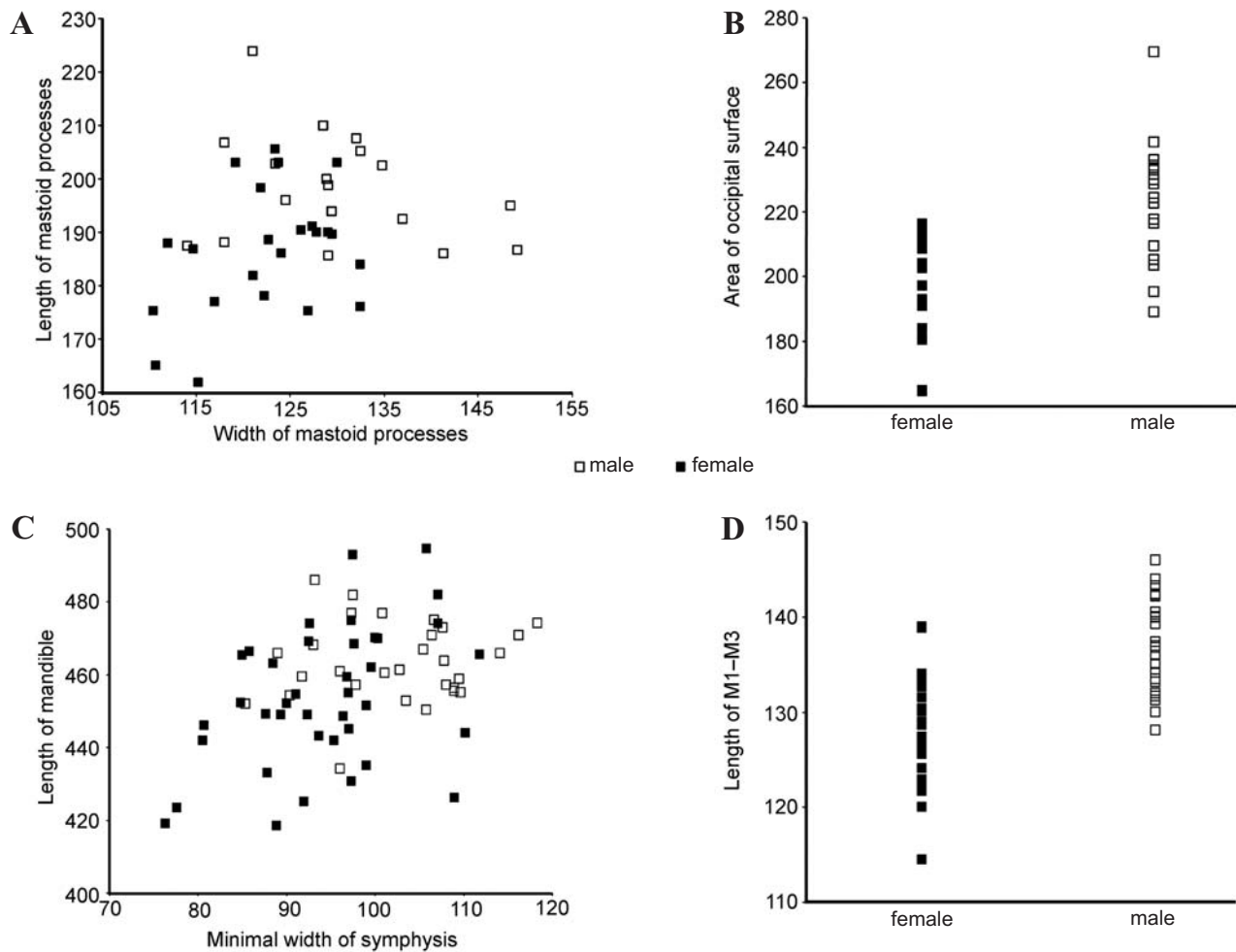


Fig. 5. Sexual dimorphic scatter plots of *Chilotherium wimani*. A. Occipital surface. B. Occipital surface area. C. Mandible. D. Length of upper molar teeth.

serious taxonomic problems for many species or subspecies, differ mainly in size, are much more common and significant in study of fossil materials.

Characteristics of the symphysis are remarkably dimorphic. Sexual dimorphism for length of mandible, maximal and minimal width of symphysis are obvious. For the three measurements, two-tailed student's *t*-test indicates very significant dimorphism ($p < 0.01$), and the M/F ratios are 1.05, 1.19, and 1.10, respectively. Low skewness and kurtosis indicate that the distributions of those measurements are closer to normality than those for tusks. Maximal width of symphysis is the most dimorphic character; height of horizontal ramus in front of p3 is also a very significant sexually dimorphic character ($p < 0.01$). Fig. 4B illustrates the height of horizontal ramus in front of p3, length and maximal width of symphysis, showing the degree of sexual dimorphism in the anterior part of mandible (symphysis).

Via the analysis of the measurements, other very significant sexual dimorphisms are found in *C. wimani*, including the width of mastoid processes ($p < 0.01$) and height of occipital surface ($p < 0.01$) (Fig. 5A). The M/F ratio of the former is 1.06, and the latter 1.07. Skewness and kurtosis indicate these measurements in both genders are not normally

distributed, except the width of mastoid processes of the females. Width of mastoid processes for most males ranges about 190–210 mm, while the females about 170–190 mm. Height of occipital surface for most males ranges about 115–150 mm, while the females about 110–130 mm. The sexual dimorphism in occipital surface area is also very significant (Fig. 5B).

Furthermore, there are some significant dimorphic characters. M/F ratios of antero-posterior diameter of the ascending ramus and length of mandible are 1.02 and 1.03, but both $p < 0.05$. Length of the mandibles for most males ranges about 450–480 mm, while those for females ranges about 420–480 mm. Antero-posterior diameter of ascending ramus for most males ranges about 135–155 mm, while in females the range is 130–150 mm. Skewness and kurtosis indicate better normal distribution, except the antero-posterior diameter of ascending ramus of female. Fig. 5C shows the degree of sexual dimorphic for the posterior part of mandible using minimal width of symphysis and length of mandible.

Mean values of males for distance between nasal notch and orbit, width of occipital crest, width between lacrimal tubercles, maximal width between zygomatic arches and height of horizontal ramus in front of p4 are larger, while dis-

Table 3. Other crano-mandibular morphometric analysis for adult *Chilotherium wimani*. Abbreviations: CHM1, cranial height in front of M1; CHM3, cranial height in front of M3; CHP2, cranial height in front of P2; CV, coefficient of variation; DNO, distance between nasal tip and occipital crest; DNTO, distance between nasal tip and orbit; DOLT, distance between occipital crest and lacrimal tubercle; DOM3, distance between occipital condyle and M3; DON, distance between occipital condyle and nasal tip; DOP, distance between occipital condyle and premaxillary bone; DOPP, distance between occipital crest and postorbital process; DOST, distance between occipital crest and supraorbital tubercle; DR, dimorphic ratio (male value/female value); HBm3, height of horizontal ramus in back of m3; HHm1, height of horizontal ramus in front of m1; HHm2, height of horizontal ramus in front of m2; HHm3, height of horizontal ramus in front of m3; HJC, height of jaw in condyle; HJCP, height of jaw in coronoid process; IWB, minimal width of braincase; Kurt, kurtosis; LM, length of mandible; *p*, value of the Student's *t*-test (sig. [2-tailed]); SD, standard deviation; Skew, skewness; SW, value of the Shapiro-Wilk test; WEO, width between exterior borders of occipital condyles; WFM, width of foramen magnum; WNB, width of nasal base; WPP, width between postorbital processes; WST, width between supraorbital tubercles.

Characters	Sex	Mean	Max	Min	n	SD	CV	Kurt	Skew	SW	<i>p</i>	DR
DOP	male	530.5	558.4	510	23	10.91	2.06	0.44	0.47	0.89	> 0.05	1.00
	female	532.6	589	463	25	23.09	4.34	3.09	-0.61	0.77		
DON	male	515	542	493.1	27	13.3	2.58	-0.48	0.46	0.44	> 0.05	1.00
	female	518.2	562.2	446.6	31	23.83	4.6	1.45	-0.55	0.78		
DNO	male	484.3	503.2	462	28	10.82	2.23	-0.71	0.09	0.10	> 0.05	1.00
	female	483.7	533.5	428.7	31	23.5	4.86	0.1	0.1	0.46		
IWB	male	87.9	102.9	63	30	9.12	10.37	1.05	-1.06	0.06	> 0.05	1.02
	female	86.5	107.6	66.3	38	9.28	10.73	-0.19	0.02	0.22		
DOPP	male	244.7	270	219.3	30	13.15	5.37	-0.77	-0.15	0.19	> 0.05	1.02
	female	242.4	273	143.6	36	21.55	8.89	11.53	-2.58	0.85		
DOST	male	270	294.6	246.9	30	13.15	5.37	-0.51	-0.15	0.59	> 0.05	1.01
	female	269.6	301.1	240.9	36	13.07	4.93	0.11	0.16	0.69		
DOLT	male	307.4	329.4	282.9	30	12.36	4.02	-0.57	-0.08	0.26	> 0.05	1.01
	female	305.7	341.4	270.8	36	15.07	4.93	0.39	0.39	0.86		
DOM3	male	263.8	285.6	232	24	15.14	5.74	-0.49	-0.77	0.48	> 0.05	0.98
	female	270.5	316.9	214.4	34	20.81	7.7	0.89	-0.37	0.95		
DNTO	male	206.2	250	181	27	13.18	6.39	3.33	1.24	0.19	> 0.05	1.00
	female	206.2	231.2	172.9	30	15.12	7.34	-0.51	-0.3	0.89		
WPP	male	136.5	159.6	117	29	10.26	7.52	-0.09	-0.01	0.13	> 0.05	1.00
	female	136.2	177.5	107.4	32	12.67	9.31	2.44	0.63	0.71		
WST	male	153.6	175.4	117	29	10.65	6.93	0.56	-0.52	0.00	> 0.05	1.01
	female	151.9	189	113.7	32	12.89	8.49	2.64	-0.05	0.35		
WNB	male	81.9	96.4	59.9	28	10.39	12.69	-1.08	-0.3	0.55	> 0.05	1.01
	female	81.1	109.3	69.2	32	7.34	9.04	5.6	1.64	0.27		
CHP2	male	137.4	154	110.3	27	10.72	7.8	0.02	-0.54	0.73	> 0.05	1.01
	female	136.3	163.1	110.4	22	11.61	8.51	0.29	0.02	0.65		
CHM1	male	166	194	140.4	27	11.48	6.92	0.4	0.13	0.97	> 0.05	1.00
	female	166.2	202.4	136	31	13.78	8.29	0.48	-0.1	0.67		
CHM3	male	169.9	201	145.5	29	13.28	7.81	0.3	0.58	0.95	> 0.05	0.99
	female	172.2	188	146.3	30	12.04	6.99	-0.63	-0.59	0.45		
WFM	male	40	57.7	32	21	5.96	14.91	2.22	1.2	0.15	> 0.05	0.99
	female	40.6	49.9	31.8	28	4.19	10.31	0.06	0.04	0.30		
WEO	male	113.1	122.9	99	23	6.61	5.84	-1.08	-0.28	0.50	> 0.05	1.01
	female	111.5	135	94.8	30	9.36	8.4	-0.11	0.54	0.02		
LM	male	463.6	486	434.2	29	10.8	2.33	0.61	-0.2	0.48	> 0.05	1.02
	female	454.3	494.6	418.5	40	19.25	4.24	-0.49	0.05	0.71		
HHm1	male	80	103	65	30	8.29	10.37	0.77	0.44	0.19	> 0.05	1.01
	female	79.3	93.9	66.2	35	7.26	9.16	-0.61	-0.11	0.91		
HHm2	male	81.2	106.9	63.4	31	9.2	11.34	0.99	0.5	0.18	> 0.05	1.00
	female	81.5	96.2	68.6	34	6.76	8.29	-0.44	0.22	0.35		
HHm3	male	83.4	99.8	66.2	31	8.32	9.98	-0.52	0.3	0.26	> 0.05	0.99
	female	84.2	99	70.6	32	7.16	8.5	-0.63	-0.02	0.87		
HBm3	male	87.8	101.9	77	26	6.71	7.64	-0.54	0.3	0.46	> 0.05	1.00
	female	87.9	97.1	72	29	5.61	6.38	0.49	-0.47	0.35		
HJC	male	203	252	170.2	29	14.43	7.11	3.85	1.02	0.20	> 0.05	0.99
	female	205.6	234	176.1	38	13.46	6.54	-0.17	0.14	0.09		
HJCP	male	258.6	302.4	225.5	26	16.32	6.31	0.89	0.44	0.86	> 0.05	1.00
	female	257.7	280.8	222	34	13.39	6.54	0.58	-0.57	0.34		

tance between nasal tip and bottom of nasal notch and minimal width between parietal crests are smaller; all of these dimorphisms are not statistically different, however. Particularly, the measurements of minimal width between parietal crests and height of horizontal ramus in front of p4 indicate good M/F ratios (0.91 and 1.04) and normal distributions, but both are not statistically significant ($p > 0.05$) (see Table 2).

Discussion

Sexual selection is generally believed to be the principal cause of sexual dimorphism. The difference between the genders is influenced by the relative investment of the sexes. Dinerstein (1991b) pointed out that rhinoceros males predominantly inflicted wound with the lower incisors (i2), and this fight-related mortality seemed to be prevalent in extant rhino populations. Muhlbachler (1999, 2003) inferred social behaviors for *Teleoceras proterum* and *Aphelops malacorhinus* from attritional fossil assemblages from the Love Bone Bed and Mixon's Bone Bed localities in Florida, United States, and considered the damage of tusks contributing to combat. Based on these inferences, fight-related mortality for male *Chilotherium wimani* was probably one of the causes of death in the Linxia Basin assemblage. The tusks of male *C. wimani* are larger and usually broken and/or more worn than those of the female; the interpretation of these phenomena might be the increased agonistic interactions among the males during sexual combat.

In *C. wimani*, the sexually dimorphic characters of the mandibular bone should be related to the huge tusks in the male and smaller tusks in the female. Robusticity of the mandible in males is plausibly linked to supporting the huge tusks. Deng (2001a) noted that, in dorsal view, the mandibular symphysis became a particularly broad shovel and its posterior border was at the p3 level. The root of i2 influenced the height of horizontal ramus in front of p3 reciprocally, so this was also a very significant sexually dimorphic character. Height of the horizontal ramus in front of p4 is also deeper in males and M/F ratio could be found for this character but it is not significantly dimorphic. Comparing the degree of sexual dimorphism in the tusks (i2s), the shovel symphysis and the posterior part of mandible, the morphological changes associated with a larger i2 in males are the highly sexually dimorphic regions in the mandible; the ascending ramus in the posterior mandible is not as sexually dimorphic.

A robust mandible presumably needs muscularity and a thick ascending ramus. Masseter (from zygomatic arch to ascending ramus), buccinators (from ascending ramus to anguli oris and orbicularis oris) and zygomaticus (from zygomatic arch to anguli oris) in male should be sturdier. Greater size of these muscles is presumed to be reflected in a stronger ascending ramus and zygomatic arch. Antero-posterior diameter of the ascending ramus is significantly larger in male. The mean maximal width between zygomatic arches is larger in males, but not significantly so. Larger maximal width between zygomatic

arches and width of mastoid processes indicate males having wider and more massive skulls. A more powerful neck musculature was probably present to support the massive skull and robust mandible in males.

Body mass should also be dimorphic between sexes in *C. wimani*. Large occipital surface area indicates a massive skull and robust neck, correlated with large body mass. Janis (1990) explained that the height of occipital surface (distance between the base of foramen magnum and the top of the occipital region) showed one of the best correlations with body mass in perissodactyls ($r^2 = 0.971$). However, none of *Chilotherium* body weight has been estimated via the height of occipital surface (in our study, distance between the crest of foramen magnum and the top of the occipital region) or occipital surface area. There is a positive correlation among higher occipital surface, larger occipital surface area and larger body mass. Therefore, it can be assumed that there was sexual dimorphism in body mass to some extent. We measured the length of a sample of upper molars (Fig. 5D), which showed another strong correlation with body mass in all ungulates ($r^2 = 0.92$, Janis 1990). The body mass for both genders of *C. wimani* could be compared through this proxy: males have larger body mass than females, though not highly significant.

In the elasmotheriine *Iranotherium morgani*, as Deng (2005) mentioned, one qualitatively dimorphic character is present: the male has a hemispherical hypertrophy on zygomatic arches while the female has no such structure. Comparing genders of *I. morgani*, Deng (2005) found additional sexually dimorphic characters in the nasal horn boss, the zygomatic arch and the anterior part of the nasals, and considered those differences to be functions of the larger horn boss in the male and the smaller in the female. The nasal horn boss of the male is much rougher and implies a larger horn than that of the female. Prominent rugosities on a rhino's skull are generally considered to be horn bosses, as they are associated with the terminal nasal horn (Qiu and Yan 1982; Ginsburg and Heissig 1989; Antoine, 2002; Deng 2005). The sexually dimorphic characters of the male and female skulls of *I. morgani* show that the male skull is more massive and robust, with a larger nasal horn and stronger zygomas. These features, especially the huge nasal horn, could be used for defense or competition for mating right. *I. morgani* shows higher degrees of sexual dimorphism in these aspects than any of the extant rhinoceros species, but the sexual dimorphism of body mass in *I. morgani* is still unknown.

In *Teleoceras major*, as Mead (2000) mentioned, the most significant dimorphic feature is i2 diameter. Osborn (1898a) already speculated that *Teleoceras* males had larger tusks than females. The width of the mastoid processes, distance between nasal tip and occipital crest, length of mandible, and height of jaw at the condyle are also larger in the male. Mead's (2000) analysis indicates that differences are significant for those characters. Male means are larger in all cranial and mandibular characters that Mead (2000) measured, except the angle of the mandibular symphysis. In

Table 4. Comparison of sexual dimorphism in five species of rhinos.

Feature	<i>Chilotherium wimani</i>	<i>Iranotherium morgani</i>	<i>Teleoceras major</i>	<i>Ceratotherium simum</i>	<i>Rhinoceros unicornis</i>
Tribe	Chilotheriini	Elasmotheriini	Teleoceratini	Dicerotini	Rhinocerotini
Feeding behavior	grazer	grazer	mixed feeder	grazer	mixed feeder
Adult sex ratio	female biased	?	female biased	female biased	female biased
Mating system	polygynous	?polygynous	polygynous	polygynous	polygynous
Life style	herding	?herding	herding	small group	solitary
Environment	steppe	steppe	grassland	savanna	grassland
Sexual dimorphism					
Horn	/	+	–	+	–
Tusk	+	/	+	–	+
Body mass	+	?	+	+	+
Other	occipital surface, mandible, and neck	zygomas	premaxilla, neck, and mandible	neck	neck and upper shoulder muscles

/ character absent; – sexual dimorphism absent; + sexual dimorphism present; ? unknown.

Chilotherium wimani, the sexual dimorphism in the length of the mandible is partially attributable to the enlarged i2 in males. Size-range overlap is evident in all mandibular characters except in i2 diameter in *Teleoceras major*, while in *Chilotherium wimani*, only the length of i2 crown is diagnostic. The sexually dimorphic characters show that *T. major* males have more massive heads than females, and probably, just like *C. wimani*, necks as well. Estimates of body mass, based on non-length long-bone dimensions, suggest an M/F value between 1.13 and 1.23 in *T. major*.

In the extant rhinos, the difference between genders is variable. *Rhinoceros sondaicus* and *Dicerorhinus sumatrensis* have dimorphic characters in incisors rather than in body mass or horn size, while *Diceros bicornis* is monomorphic (Pocock 1945; Groves 1982; Owen-Smith 1988). *Ceratotherium simum* is sexually dimorphic in horn size, body and neck mass (Owen-Smith 1988; Berger 1994), and adult males *C. simum* are estimated to be about 25–43% heavier than females (Owen-Smith 1988). *Rhinoceros unicornis* is dimorphic in incisor size, body mass and neck musculature, and adult male *R. unicornis* can be 1,000 kg heavier than females in captivity but essentially a slightly larger version of females in the wild (Dinerstein 1991a).

As Liang and Deng (2005) demonstrated, the age structure pattern of the *C. wimani* fossils found in the Linxia Basin was consistent with that of a living population, and a natural catastrophe was the likely cause of death. *C. wimani* fossils found in the Linxia Basin were mostly preserved en masse. They are dominant in number of individuals in all sites of the Linxia Basin's late Miocene *Hipparion* fauna, indicating that they are most likely herding mammals. Trivers (1972) surmised that the stronger the dimorphism in a species, the more likely it is to be polygynous, and he thought that was a generally concept in behavioral ecology. Applying this concept to *C. wimani*, the observed degree of sexual dimorphism tends to indicate the presence of polygyny in the Linxia Basin populations.

The cranial and mandibular dimorphism in *C. wimani* approaches that seen in the extinct *Iranotherium morgani* from

China, *T. major* from North American and the extant *C. simum* and *R. unicornis*. In China, *I. morgani* is known from only a few materials (Deng 2005). The extant rhinoceros *R. unicornis* are typically solitary and rarely form small temporary groups, while *C. simum* always form small groups (Sheng 1985) (Table 4). Mead (2000) suggested that ecological analogues rather than closest living relatives may provide the best models for exploring the expected degree of sexual dimorphism in extinct taxa and the ecological affinity of *T. major* was similar to extant *Hippopotamus amphibius* rather than extant rhinoceros species. On the contrary, Muhlbachler (2005) denied the popular belief that *Teleoceras* was ecologically or behaviorally convergent upon *Hippopotamus* or other large herding artiodactyls.

As Mazak (2004) mentioned, the degree of sexual dimorphism is closely related to geographic variation. For example, Asiatic rhino species prefer to reside in alluvial floodplain vegetation of sub-tropical climate where water and green grasses are available all year round. The late Miocene fauna in the Linxia Basin is composed of *Promephitis parvus*, *Parataxidea sinensis*, *Hyaenictitherium wongii*, *Dinocrocuta gigantea*, *Tetralophodon exoletus*, at least five species of *Hipparion*, *Acerorhinus hezhengensis*, *Chilotherium wimani*, *Iranotherium morgani*, *Diceros gansuensis*, *Chalicotherium* sp., *Ancylotherium* sp., *Hezhengia bohlini*, *Cervavitus novorossiae*, *Metacervulus* sp., *Samotherium* sp., *Honanotherium schlosseri*, *Sinotragus* sp., *Palaeotragus* sp., *Gazella* sp., and *Miotragocerus* sp. According to the features of faunal components, *C. wimani* should live in steppes. Analytical results of carbon isotopes of tooth enamel also show a cooling and aridity environment in the north side of the Tibetan Plateau since the middle Miocene (Hou et al. 2006). Sexually dimorphic, large bodied, herding herbivorous mammals, such as gnu (*Connochaetes taurinus*), zebra (*Equus burchellii*) and musk ox (*Ovibos moschatus*), may provide better ecological analogues for *C. wimani*.

In our study, M/F adult ratio is 33:41 = 1:1.24, with minimum collection bias because specimens were collected regardless of sex. Male-male combat is likely to be most intense

in areas where the ratio between breeding-age males and females is close to or exceeds parity with males greatly over-represented (Dinerstein 1991a). Berger (1994) mentioned that evidence from many sexually dimorphic mammals indicated that males experience greater mortality than females. Young male *C. wimani* mortality, just like some living mammals, might have been higher than females. A reason for this might be the presence of competition with adult or the danger from predatory mammals.

From the analysis, it can be found that most non-dimorphic characters are more variable in females than in males. Among the very significant dimorphic characters, only the length of symphysis follows this trend. This might indicate that males tend to invest their energy to develop secondary characteristics utilized in combat; while in female, emphasis is absent and variation exists in most other characters. In these sexually dimorphic mammals, males apparently invest large amounts of energy into competing with other males for mating right or leadership, thus a selective pressure will promote the evolution of dimorphic traits.

C. wimani can be “sexed” easily by the mandible. However, more isolated skulls were found in the Linxia Basin. Even those very significant characters in skulls, like the width of mastoid processes and height of occipital surface, cannot be used to “sex” those skulls, because of the high degree of overlap in these characters between the sexes. According to the morphology of the skull of *C. wimani*, tentative sex discriminant functions are set up by Bayes discriminant analysis in order to identify the gender of the skulls (Table 5). The discriminant functions and its classification results are:

$$Y1 = -332 + 1.741X_1 + 1.771X_2 + 0.461X_3 + 0.327X_4$$

$$Y2 = -371.782 + 1.925X_1 + 1.972X_2 + 0.413X_3 + 0.241X_4$$

X_1 = width between mastoid processes; X_2 = height of occipital face; X_3 = distance between nasal tip and bottom of nasal notch; X_4 = cranial height in front of M1.

When $Y1 > Y2$, the skull should be a female, otherwise be male. In this function, 87.9% of original grouped cases are correctly classified, and 81.8% of cross-validated grouped

Table 5. Classification results of the discriminant functions^{a,b}.

		Sex	Predicted Group Membership		Total
			female	male	
Original	Count	female	14	3	17
		male	1	15	16
	%	female	82.4	17.6	100.0
		male	6.3	93.8	100.0
Cross-validated	Count	female	12	5	17
		male	1	15	16
	%	female	70.6	29.4	100.0
		male	6.3	93.8	100.0

a. 87.9% of original grouped cases correctly classified.

b. 81.8% of cross-validated grouped cases correctly classified.

cases are correctly classified. If these four characters can be measured, we can infer the likely sex of the individual. Although the gender of skulls cannot be identified exactly, the discriminant functions should be a better way and grope to distinguish large samples for paleoecological work.

Acknowledgements

Thanks for staff in Hezheng Paleozoological Museum, especially Shanqin Chen and Wen He. We are grateful to Zhijie Jack Tseng (Natural History Museum of Los Angeles County, California, United States) for his linguistic improvements. Thanks to Kurt Heissig (München, Germany), Pierre-Olivier Antoine (Toulouse, France), and an anonymous referee for their valuable comments. This work is supported by the Knowledge Innovation Program of the Chinese Academy of Sciences (KZCX2-YW-Q09), the National Natural Science Foundation of China (40730210, J0930007), and the Ministry of Science and Technology of China (2006CB806400).

References

- Antoine, P.-O. 2002. Phylogénie et évolution des Elasmotheriinae (Mammalia, Rhinocerotidae). *Mémoires du Muséum National d'Histoire Naturelle, Paris* 188: 1–359.
- Antoine, P.-O., Shah, S.M.I., Cheema, I.U., Crochet J.-Y., de Franceschi, D., Marivaux, L., Métais, G., and Welcomme, J.L. 2004. New remains of the baluchither *Paraceratherium bugtiense* (Pilgrim, 1910) from the late/latest Oligocene of the Bugti Hills, Baluchistan, Pakistan. *Journal of Asian Earth Sciences* 24: 71–77. <http://dx.doi.org/10.1016/j.jaes.2003.09.005>
- Berger, J. 1994. Science, conservation, and black rhinos. *Journal of Mammalogy* 75: 298–308. <http://dx.doi.org/10.2307/1382548>
- Coombs, M.C. 1975. Sexual dimorphism in chalicotheres (Mammalia, Perissodactyla). *Systematic Zoology* 24: 55–62. <http://dx.doi.org/10.2307/2412697>
- Deng, T. 2001a. New materials of *Chilotherium wimani* (Perissodactyla, Rhinocerotidae) from the late Miocene of Fugu, Shaanxi. *Vertebrata Palasiatica* 39: 129–138.
- Deng, T. 2001b. Cranial ontogenesis of *Chilotherium wimani* (Perissodactyla, Rhinocerotidae). In: T. Deng and Y. Wang (eds.), *Proceedings of the Eighth Annual Meeting of the Chinese Society of Vertebrate Paleontology*, 101–112. China Ocean Press, Beijing.
- Deng, T. 2002. Limb bones of *Chilotherium wimani* (Perissodactyla, Rhinocerotidae) from the late Miocene of the Linxia Basin in Gansu, China. *Vertebrata Palasiatica* 40: 305–316.
- Deng, T. 2005. New discovery of *Iranotherium morgani* (Perissodactyla, Rhinocerotidae) from the late Miocene of the Linxia Basin in Gansu, China, and its sexual dimorphism. *Journal of Vertebrate Paleontology* 25: 442–450. [http://dx.doi.org/10.1671/0272-4634\(2005\)025%5B0442: NDOIMP%5D2.0.CO;2](http://dx.doi.org/10.1671/0272-4634(2005)025%5B0442: NDOIMP%5D2.0.CO;2)
- Deng, T. 2006. Neogene rhinoceroses of the Linxia Basin (Gansu, China). *Courier Forschungsinstitut Senckenberg* 256: 43–56.
- Dinerstein, E. 1991a. Effects of *Rhinoceros unicornis* on riverine forest structure in lowland Nepal. *Journal of Wildlife Management* 55: 401–411. <http://dx.doi.org/10.2307/3808968>
- Dinerstein, E. 1991b. Sexual dimorphism in the greater one-horned rhinoceros (*Rhinoceros unicornis*). *Journal of Mammalogy* 72: 45–457. <http://dx.doi.org/10.2307/1382127>
- Fortelius, M. and Kappelman, J. 1993. The largest land mammal ever imagined. *Zoological Journal of the Linnean Society* 108: 85–101. <http://dx.doi.org/10.1111/j.1096-3642.1993.tb02560.x>
- Gingerich, P.D. 1981. Variation, sexual dimorphism, and social structure in

- the early Eocene horse *Hyracotherium* (Mammalia, Perissodactyla). *Paleobiology* 7: 443–455.
- Ginsburg, L. and Heissig, K. 1989. *Hoploaceratherium*, a new generic name for “*Aceratherium*” *tetradactylum*. In: D.R. Prothero and R.M. Schoch (eds.), *The Evolution of Perissodactyla*, 418–421. Oxford University Press, Oxford.
- Groves, P. 1982. The skulls of Asian rhinoceroses: wild and captive. *Zoo Biology* 1: 251–261. <http://dx.doi.org/10.1002/zoo.1430010309>
- Guérin, C. 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale: comparaison avec les espèces actuelles. *Documents du Laboratoire de Géologie de l'Université de Lyon, Sciences de la Terre* 79: 1–1184.
- Heissig, K. 1972. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan, 5. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-Schichten. *Bayerische Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse, Abhandlungen, Neue Folge* 152: 1–112.
- Heissig, K. 1999. Family Rhinocerotidae. In G. E. Rössner and K. Heissig (eds.), *The Miocene Land Mammals of Europe*, 175–188. Verlag Dr. Friedrich Pfeil, München, Germany.
- Hitchins, P.M. 1978. Age determination of the black rhinoceros (*Diceros bicornis* Linn.) in Zululand. *South African Journal of Wildlife Research* 8: 71–80.
- Hou, S.K., Deng, T., and Wang, Y. 2006. Stable carbon isotopic evidence of tooth enamel for the late Neogene habitats of the *Hipparion* fauna in China. In W. Dong (ed.), *Proceedings of the Tenth Annual Meeting of the Chinese Society of Vertebrate Paleontology*, 85–94. China Ocean Press, Beijing.
- Janis, M.C. 1990. Correlation of cranial and dental variables with body size in ungulates and macropodoids. In: J. Damuth and B.J. MacFadden (eds.), *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, 255–299. Cambridge University Press, Cambridge.
- Kurtén, B. 1969. Sexual dimorphism in fossil mammals. In: G.E.G. Westermann (ed.), *Sexual Dimorphism in Fossil Metazoa and Taxonomic Implications*. International Union of Geological Sciences, Series A1: 226–233. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Liang, Z. and Deng, T. 2005. Age structure and habitat of the rhinoceros *Chilotherium* during the late Miocene in the Linxia Basin, Gansu, China. *Vertebrata Palasiatica* 43: 219–230.
- Mazak, J.H. 2004. On the sexual dimorphism in the skull of the tiger. *Mammalian Biology* 69: 392–400. <http://dx.doi.org/10.1078/1616-5047-00161>
- Mead, J.A. 2000. Sexual dimorphism and paleoecology in *Teleoceras*, a North American Miocene rhinoceros. *Paleobiology* 26: 689–706. [http://dx.doi.org/10.1666/0094-8373\(2000\)026%3C0689:SDAPIT%3E2.0.CO;2](http://dx.doi.org/10.1666/0094-8373(2000)026%3C0689:SDAPIT%3E2.0.CO;2)
- Mihlbachler, M.C. 1999. Population structure and implications for social behavior in Miocene Florida rhinoceroses. *Journal of Vertebrate Paleontology* 19: 64A.
- Mihlbachler, M.C. 2003. Demography of late Miocene rhinoceroses (*Teleoceras proterum* and *Aphelops malacorhinus*) from Florida: linking mortality and sociality in fossil assemblages. *Paleobiology* 29: 412–428. [http://dx.doi.org/10.1666/0094-8373\(2003\)029%3C0412:DOLMRT%3E2.0.CO;2](http://dx.doi.org/10.1666/0094-8373(2003)029%3C0412:DOLMRT%3E2.0.CO;2)
- Mihlbachler, M.C. 2005. Linking sexual dimorphism and sociality in rhinoceroses: insights from *Teleoceras proterum* and *Aphelops malacorhinus* from the late Miocene of Florida. *Bulletin of the Florida Museum of Natural History* 45: 495–520.
- Mihlbachler, M.C. 2007. Sexual dimorphism and mortality bias in a small Miocene North American rhino, *Menoceras arikarensis*: Insights into the coevolution of sexual dimorphism and sociality in rhinos. *Journal of Mammalian Evolution* 14: 217–238. <http://dx.doi.org/10.1007/s10914-007-9048-4>
- Osborn, H.F. 1898a. A complete skeleton of *Teleoceras fossiger*. Notes upon the growth and sexual characters of this species. *Bulletin of the American Museum of Natural History* 10: 51–59.
- Osborn, H.F. 1898b. The extinct rhinoceroses. *Memoirs of the American Museum of Natural History* 1 (3): 75–164.
- Owen-Smith, R.N. 1988. *Megaherbivores: the Influence of Very Large Body Size on Ecology*. 369 pp. Cambridge University Press, Cambridge.
- Pocock, R.I. 1945. A sexual difference in the skulls of Asiatic rhinoceroses. *Proceedings of the Zoological Society of London* 115: 319–322.
- Prothero, D.R. 2005. *The Evolution of North American Rhinoceroses*. 228 pp. Cambridge University Press, Cambridge.
- Qiu, Z. and Yan, D. 1982. A horned *Chilotherium* skull from Yushe, Shansi. *Vertebrata Palasiatica* 20: 122–132.
- Radinsky, L. 1963. Origin and early evolution of North American Tapiroidea. *Peabody Museum of Natural History Bulletin* 17: 1–106.
- Radinsky, L. 1967. *Hyrachyus*, *Chasmotherium*, and the early evolution of helaletid tapiroids. *American Museum Novitates* 2313: 1–23.
- Ringström, T. 1924. Nashörner der *Hipparion*-fauna Nord-Chinas. *Palaeontologia Sinica, Series C* 1 (4): 1–159.
- Sheng, H.L. 1985. Perissodactyla and Artiodactyla [in Chinese]. In: H.L. Sheng, P.C. Wang, H.J. Lu, and L.B. Zhu (eds.), *Introduction to Mammalogy*, 211–247. East China Normal University Press, Shanghai.
- Trivers, R.L. 1972. Parental investment and sexual selection. In: B. Campbell (ed.), *Sexual Selection and the Descent of Man, 1871–1971*, 136–179. Aldine Press, Chicago.