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Female preference promotes asynchronous sex evolution in Elephantiformes

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Abstract Sexually dimorphic characters are usually thought to enhance copulatory success by intraspecific competition; for example, larger body size and stronger tusks are sexually dimorphic characters in fossil and extant male proboscideans. Here, we show that some sexually dimorphic characters in fossil Elephantiformes, the largest group of proboscideans, are strongly correlated with the evolution of this group rather than direct sexual competition. In Miocene *Platybelodon grangeri* and *Gomphotherium angustidens*, males tended to initially possess evolutionarily more derived characters than females, and females then evolved similar variation. This phenomenon may have occurred as a result of female preference. During the early evolutionary stage (thriving stage) of Elephantiformes, sexual selection pressure promoted development of more prominent derived characters in males than females. However, during their late evolutionary stage (declining stage), sexual selection pressure seems to have weakened; thus, the asynchrony between the two sexes diminished. This new discovery may help explain a common mechanism of large ungulate evolution and extinction, because substantial sexual dimorphism is often displayed in thriving groups, such as Cervidae and Bovidae, in contrast to little sexual dimorphism in declining groups, such as extant taxa of Equidae, Rhinoceridae, and Giraffidae.

Key words Elephantiformes, sexual dimorphism, female preference, evolution

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1 Introduction

Since Darwin, sexual selection has been considered the key factor that influences secondary sexually dimorphic character development within a species (Darwin, 1874; Fisher, 1930; Andersson, 1994). As a result, these characters are thought to improve male copulatory success by intraspecific competition. However, the relationship between sexual dimorphism

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and evolution is not fully understood. For example, in Elephantiformes Tassy, 1988, sexual dimorphism has been observed in Oligocene *Phiomia*, Miocene *Platybelodon grangeri*, *Gomphotherium angustidens*, ?*Stegotetrabelodon* sp. (Matsumoto, 1924; Osborn and Granger, 1932; Lambert, 1992; Tassy, 1996, 2013; Bibi et al., 2012; Wang et al., 2013), and extant elephants (Nowak, 1999; Roth and Shoshani, 1988; Kurt et al., 1995; Douglas-Hamilton et al., 2006; Lee and Poole, 2011). In *G. angustidens* there is sexual dimorphism not only of body size and tusk characteristics but also of other characters that have not been fully understood (Tassy, 1996, 2013). Furthermore, in large ungulates, substantial sexual dimorphism is often exhibited in early evolutionary stage (thriving) groups, such as Cervidae and Bovidae; however, little sexual dimorphism in late evolutionary stage (declining) groups, such as extant taxa of Equidae, Rhinoceridae, and Giraffidae. Therefore, the mechanism underlying sexual dimorphism and evolution in this group should be studied further.

Recently, a population of fossil *P. grangeri* was discovered from the Middle Miocene Zengjia locality, Guanghe County, Gansu Province, China (Fig. 1). This population included a large number of crania and mandibles (Wang et al., 2013), and therefore provided a good model to study sexual dimorphism in Miocene Elephantiformes and evaluate the relationship between elephantiforme sexual dimorphism and evolution.

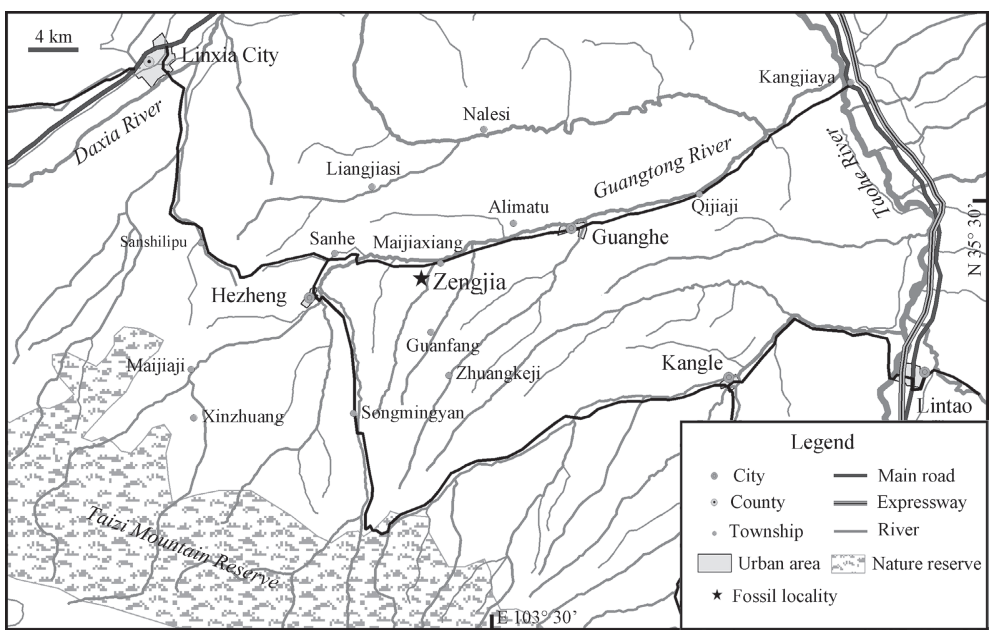

Fig. 1 Map showing the Zengjia locality (N 35°26'23.1", E 103°26'37.6", H 2150 m) yielding the population of *Platybelodon grangeri*

Institutional abbreviations AMNH, American Museum of Natural History, New York, USA; BPV, Beijing Natural History Museum, Beijing, China; HMV, Paleozoological Museum, Hezheng, Gansu, China; MNHN, Muséum National d'Histoire Naturelle, Paris, France.

2 Materials and methods

Specimens All of the *Platybelodon grangeri* specimens from the Zengjia locality are housed in HMV, and a total of 32 specimens were analyzed: HMV 0014–0020, 0022–0039, 0042, 0043, 0939, 0940, 1836, 1841, and 1842. The ontogenetic ages of the specimens range from Dental Age XVIII to XXI (Tassy, 2013), which means all of the specimens were adults (as determined based on functioning m3 and/or M3) with similar ontogenetic ages. *P. grangeri* from Tunggur are AMNH 26408, 26460, 26462, 26469, 26472, and 26490 (Dental Ages from XVIII to XX). These specimens are from the *Platybelodon* Quarry and Wolf Camp localities because they were found in the same horizon (Wang et al., 2003). *Loxodonta africana* specimens are four adult females (AMNH 32732, 42469, 51949, and 88404) and four adult males (AMNH 32734, 39083, 51939, and 113819). Two *Gomphotherium angustidens* crania are MNHN Si37 (male, Dental Age XIX) and MNHN SEP185 (female, Dental Age XXI). An adult skull with an associated mandible (probably a male) of *Platybelodon danovi* is BPV 2000 (Dental Age XX). All of the specimens belong to the museum collections and are open to scientific research.

Locality and age All of the *P. grangeri* specimens that were considered part of the same population were collected from the Zengjia locality (N 35°26′23.1″, E 103°26′37.6″, H 2150 m, No. LX200002, Fig. 1) of the Linxia Basin, Gansu Province, China. The fossil bearing strata belong to the Middle Miocene Hujialiang Formation, which consists of grayish-yellow fine conglomerates and sandstone rocks, which indicate fluvial strata (Deng et al., 2013). The fauna is also composed of a typical Middle Miocene mammalian community, including *Castor* sp., *Alloptox* sp., *Pseudaelurus* sp., *Gomphotherium* cf. *G. subtapiroideum*, *G. wimani*, *Zygolophodon* cf. *Z. gobiensis*, *Chalicotherium* sp., *Anchitherium gobiensis*, *Hispanotherium matritense*, *Listriodon* sp., *Kubanochoerus* sp., and Cervidae indet. (Deng et al., 2013).

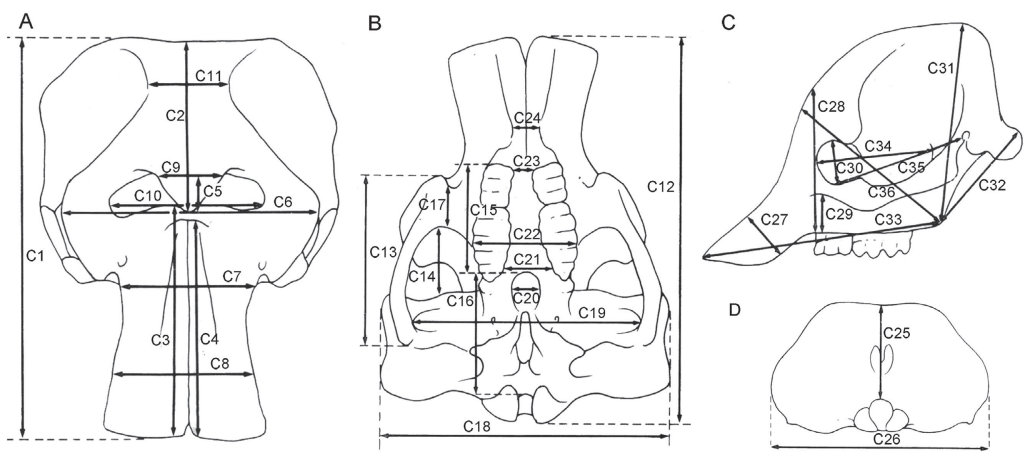

Fig. 2 The cranial measurements of Elephantiformes, after Tassy (1996: fig. 11.1, slightly revised), not scaled
A. dorsal view; B. ventral view; C. lateral view; D. posterior view

Measurements Cranial and mandibular measurements of elephantiforme specimens were based on those described by Tassy (2013); a total of 36 cranial measurements (Fig. 2, indicated by "C") and 24 mandibular measurements (Fig. 3, indicated by "M") were taken. There was one minor change to the measurement protocol: M1 was taken from the anterior border of the incisive alveolus instead of from the lower tusk, which we did not analyze in the present article, to the mandibular condyles.

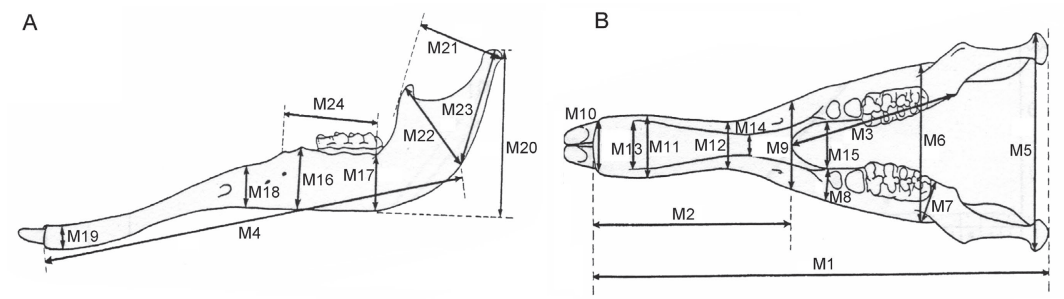

Fig. 3 The mandibular measurements of Elephantiformes in lateral (A) and dorsal (B) views
After Tassy (1996: fig. 11.1, slightly revised), not scaled

Measurement inclusion In multivariate sex assessment, measurements that reflect little sexual dimorphism and have substantial variation may affect the results. Therefore, the only measurements used in analysis are those for which the coefficient of variation is less than 15. The included measurements consist of a total of 21 cranial measurements, C1–4, 6–8, 10–12, 14, 15, 18, 19, 22, 30, 31, and 33–36, and 18 mandibular measurements, M1–10, 12, 13, 17, 20–24.

Data prediction and modification In the multivariate sex assessment analysis, a complete data set is ideal but not available because of the incompleteness of specimens. Therefore, we used a linear regression method (Wang and Deng, 2010) to predict the missing measurements.

For the analyzed material, some measurements were questionable because of substantial deformation or unreliable restoration. In these cases, the questionable data were considered missing. Then, the data were weighted based on the mean of the raw data and the predicted data. The weighted measurement values were calculated as follows:

$$w = \exp(-|p - m|/0.0098p), \quad \text{eq. (1)}$$

where w is the weight, p is the predicted datum, and m is the original measured value ($1 - w$ is assigned as the weight for predicted data). Complete pseudo data sets were constructed using this procedure.

Data normalization We estimated the total length, or size factor (SF), of each specimen based on the C1 and M1 values. In the complete pseudo data set, data were divided by each SF to produce a size-normalized pseudo (SNP) data set to obtain shape information. Then, the SNP data set was logarithmically transformed, because each measurement was of equal importance for morphological discrimination and should be analyzed on the same scale. The following formula was used:

$$X_i = \ln(M_i/<M>), \qquad \text{eq. (2)}$$

where M_i was an SNP value of a certain measurement of specimen i and $<M>$ was the mean of the SNP values for all specimens. This new data set was defined as the size-normalized logarithmic pseudo (SNLP) data set for multivariate analyses.

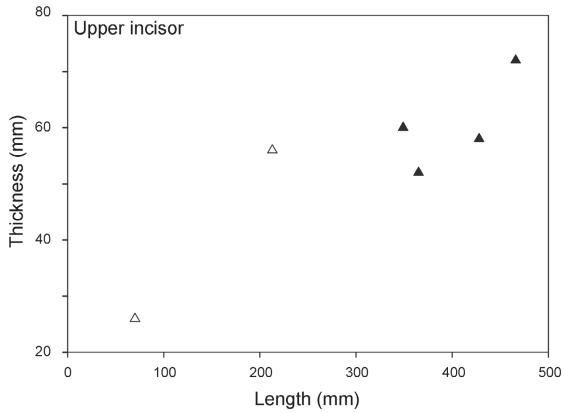

Fig. 4 Bivariate scatter plot of upper tusks in male and female *Platybelodon grangeri*
Solid triangles, male; open triangles, female

Sex assessment Before sex assessment, only the length of upper incisor could be directly used for sexual discrimination (< *ca*. 300 mm for females and > *ca*. 300 mm for males, Fig. 4). These typical adult crania were first selected to form the SNLP data sets (males and females were considered two different groups) and examined by principal component analysis (PCA). The resulting principal components (PCs), of which the cumulative variance contribution rate exceeded 95%, were selected as new variables for Fisher's discriminant function analysis (DFA), and the first discriminant function (DF1) was calculated. Then, the remaining crania of uncertain sex were examined using the DF1 (Appendix 1) and we preliminarily determined the sex for each cranium. Then, these crania were divided into two groups based on inferred sex, and two more SNLP data sets were constructed then re-examined in a new PCA–DFA cycle. If a cranium clustered into the opposite sex group in DFA, we changed the cranium's sex assignment and began another PCA–DFA cycle. Cycles did not stop until the data clustered appropriately based on sex assignment. After several PCA–DFA cycles, an optimal sex assessment was obtained for each cranium.

No sex assignment was proposed based on mandibular characters or measurements. The specimens with long symphyses were considered male, because some were associated with male crania (HMV 0939 and 0940). Consequently, those mandibles with short symphyses were considered female. The same PCA–DFA cycles were performed on the mandibles as on the crania until all of the mandibles had optimal sex assessments.

Univariate analyses Univariate analyses were carried out on individual characters in both sexes. Only the originally measured or modified values were used in analyses, and those specimens missing original measurements were not included. For each measurement (including M3 and m3 measurements), the mean, standard deviation (s.d.), coefficient of variation (c.v.), and maximal and minimal values were calculated. Two-tailed Student's t-tests were performed between the two sexes, and p-values less than 0.05 were considered significant.

Bivariate scatter plots and histograms DF1 from the last PCA–DFA cycle and normalized length from crania and mandibles, length and width from M3 and m3, and length and maximal width of mandibular symphyses were depicted in bivariate scatter plots; the 95% confidential eclipses for both sexes were calculated and also included in the plots. C2/C1, C34/

C31, and M11/M2 measurements of each specimen were calculated and their statistics were performed. The mean + s.d. of the results were shown in histograms. Two-tailed Student's t-tests were performed between the two groups, and p-values less than 0.2 were considered significant.

Simpson's ratio diagrams The formula for Simpson's ratio is as follows:

$$r = \ln(m/s), \qquad \text{eq. (3)}$$

where m is a measured value in an object group, s is the corresponding value in the standard group, and r is the resultant Simpson's ratio. Both m and s are available from individual specimens and the mean of the specimens. Simpson's ratio diagrams were used to compare both sexes of *Platybelodon grangeri*, *Gomphotherium angustidens*, and *Loxodonta africana*.

3 Results

The results show that there is significant sexual dimorphism in the population of fossil *P. grangeri* (Figs. 5A, B, and Appendix 1). In addition to larger and more robust upper tusks, which are beneficial for direct combat, other craniomandibular sexually dimorphic characters in males include: 1) a higher-arched but shorter temporal fossa (C34/C31); 2) more posteriorly positioned nasal bones, which indicates a more developed trunk (C2/C1) (Figs. 6A, B, and I); and 3) a longer mandibular symphysis (M11/M2) (Figs. 6C, D, I, and Fig. 7). The p-values of C34/C31 (0.1775) and C2/C1 (0.1233) indicate that these ratios are significant because they are under the significance level of 0.2. This relatively high significance level is acceptable for two reasons. First, male and female individuals are in the same population of the same species. Therefore, the measurement ratios should not substantially differ. Second, the sample size is relatively small. However, the p-value of M11/M2 (0.0058) is under the significance level of 0.05 (as in the univariate analysis); this is important because we used symphysis length to initially determine sex.

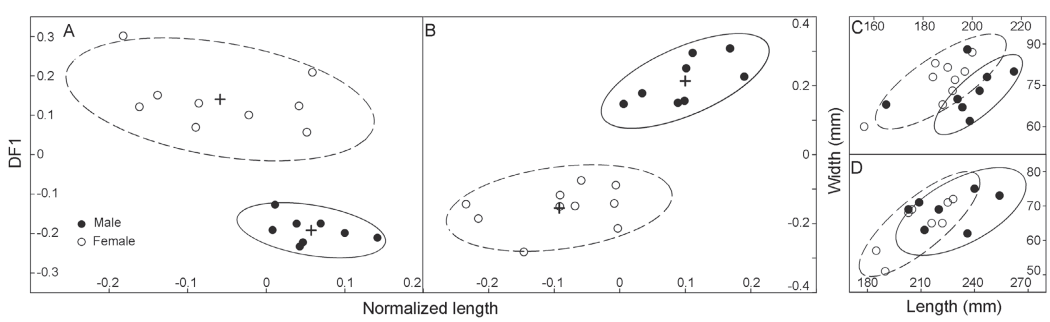

Fig. 5 Bivariate scatter plots showing sexual dimorphism in *Platybelodon grangeri* from the Zengjia locality
Cranium (A) and mandible (B) are examined in PCA–DFA cycles for sex-assessment and the final results are shown in normalized length–DF1 plane. As a result of sex-assessment, measurements from M3 (C) and m3 (D) are also shown on length–width plane. Two sexes are represented by solid (male) and open cycles (female), respectively, with 95% confidential ellipses denoting their distributions (solid-lined ellipses for male and dash-lined ellipses for female)

In addition to the above craniomandibular sexually dimorphic characters, males also possess narrower and longer M3 and m3. Note that the molar measurements, which were not used for sex assessment, are independent variables; thus, this is an independent verification of our sex assessment (Figs. 5C and D). In the Simpson's ratio diagrams, the slopes of C1 & C2, C31 & C34, and M2 & M11 differ between male and female *P. grangeri*, which also indicates sexual dimorphism in these characters (Fig. 8). However, Student's t-tests for single measurements primarily produce large, non-significant p-values (Tables 1 and 2), which indicates a relatively large amount of overlap in variation of these characters between the two sexes. These sexually dimorphic characters are often obscured by difficulty in sex determination and the incompleteness of specimens unless more elaborate methods are used, such as the one presented in this article.

The above sexually dimorphic characters were also observed in *P. grangeri* from

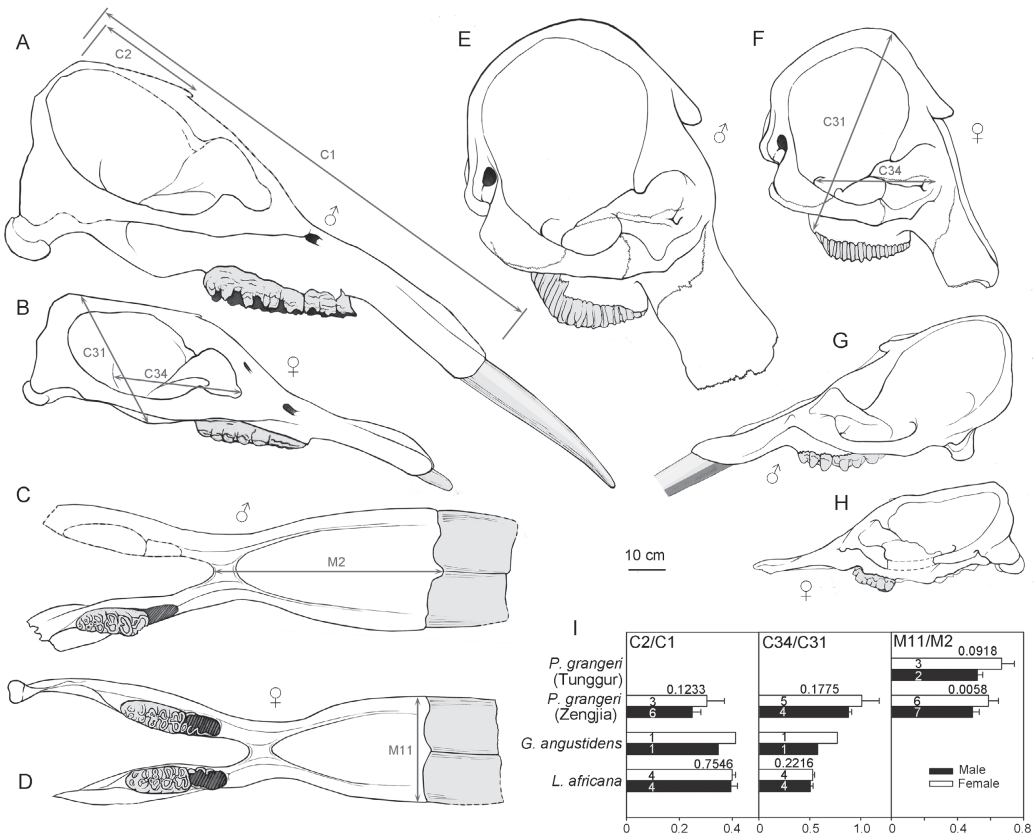

Fig. 6 Sketches showing sexual dimorphism in crania (A, B, E–H) and mandibles (C, D) of *Platybelodon grangeri* (A–D), *Loxodonta africana* (E, F), and *Gomphotherium angustidens* (G, H)

A. HMV 0940; B. HMV 0023; C. HMV 0031; D. HMV 0042; E. AMNH 51939; F. AMNH 88404; G. MNHN Si37; H. MNHN SEP185; I. histograms show sexual dimorphism in three evolutionary significant characters (C2/C1, C34/C31, M11/M2) with the form mean + s.d. ♂, male; ♀, female

Measurements are illustrated on the sketches. The number in each bar represents the sample size n and the number near each pair of bars represents the p-value of the t-test

Tunggur. In a female cranium (AMNH 26462), the upper border of the nostril aperture is located in line with postorbital processes (Osborn and Granger, 1932). In contrast, a possible male (AMNH 26480) has more posteriorly positioned nostril aperture, although the incisors

Table 1 Univariate analyses between male and female crania in *Platybelodon grangeri* (mm)

measurements	sex	n	max	min	mean	s.d.	c.v.	p-value
C1	male	8	1107	968	1018.5	46.8	4.6	0.045
	female	7	1060	800	933.3	97.2	10.4	
C2	male	8	288	227	258.4	25.4	9.8	0.081
	female	7	334	255	287.7	34.6	12.0	
C3	male	6	877	689	766.8	70.1	9.1	0.491
	female	3	778	695	734.3	41.7	5.7	
C4	male	8	829	635	721.4	62.3	8.6	0.021
	female	8	725	560	637.9	66.4	10.4	
C6	male	6	494	452	476.0	14.3	3.0	0.347
	female	9	568	378	446.3	72.7	16.3	
C7	male	7	297	207	246.7	36.5	14.8	0.321
	female	8	266	194	230.9	22.1	9.6	
C8	male	8	210	173	190.4	12.5	6.6	0.107
	female	8	215	135	173.5	24.8	14.3	
C10	male	8	345	225	282.6	38.1	13.5	0.949
	female	8	362	232	284.0	46.5	16.4	
C11	male	7	266	205	237.0	22.7	9.6	0.217
	female	9	272	157	216.0	37.9	17.5	
C12	male	8	1136	952	1049.0	69.2	6.6	0.323
	female	5	1105	858	1002.0	95.2	9.5	
C14	male	6	317	253	285.0	27.0	9.5	0.456
	female	5	304	220	270.8	33.6	12.4	
C15	male	7	363	236	303.4	41.2	13.6	0.112
	female	6	373	313	335.8	21.5	6.4	
C18	male	8	591	442	524.5	50.7	9.7	0.235
	female	5	544	450	490.8	39.8	8.1	
C19	male	6	466	404	440.0	24.6	5.6	0.402
	female	4	464	362	419.0	51.0	12.2	
C22	male	8	272	212	244.5	21.5	8.8	0.425
	female	9	270	212	236.6	18.5	7.8	
C30	male	6	120	67	100.8	18.8	18.6	0.118
	female	6	135	100	116.7	12.7	10.9	
C31	male	6	456	388	424.8	22.5	5.3	0.277
	female	7	455	334	400.1	48.3	12.1	
C33	male	8	805	645	723.1	52.6	7.3	0.092
	female	8	750	570	670.3	63.9	9.5	
C34	male	8	450	344	393.9	39.0	9.9	0.904
	female	6	417	358	391.7	22.5	5.8	
C35	male	8	418	382	403.5	11.6	2.9	0.762
	female	7	469	343	398.4	44.8	11.3	
C36	male	6	427	320	370.2	40.4	10.9	0.420
	female	5	443	360	390.4	38.4	9.8	
length of M3	male	8	217	165	197.3	14.9	7.56	0.156
	female	9	200	156	187.2	12.8	6.84	
width of M3	male	8	88	62	73.3	8.36	11.4	0.450
	female	9	87	60	76.4	8.28	10.8	

Note: Measurements see Fig. 2.

Table 2 Univariate analyses between male and female mandibles in *Platybelodon grangeri* (mm)

measurements	sex	n	max	min	mean	s.d.	c.v.	p-value
M1	male	7	1630	1356	1489.9	98.2	6.6	0.003
	female	5	1344	1066	1256.0	113.1	9.0	
M2	male	8	853	598	722.1	81.3	11.3	0.036
	female	6	688	490	623.2	71.9	11.5	
M3	male	8	530	452	496.3	26.4	5.3	0.005
	female	8	470	355	439.3	41.0	9.3	
M4	male	8	1494	1206	1378.9	98.1	7.1	0.001
	female	7	1287	944	1128.7	130.1	11.5	
M5	male	5	455	343	406.6	43.2	10.6	0.919
	female	5	464	352	409.6	47.2	11.5	
M6	male	8	403	299	355.5	41.3	11.6	0.546
	female	10	401	301	344.9	31.6	9.2	
M7	male	7	106	81	95.6	9.5	9.9	0.883
	female	10	117	78	96.5	14.4	14.9	
M8	male	7	75	51	65.9	8.9	13.5	0.482
	female	10	73	61	68.1	3.7	5.4	
M9	male	8	200	155	180.0	15.5	8.6	0.847
	female	10	205	152	181.5	16.7	9.2	
M11	male	7	364	329	343.1	11.5	3.4	0.255
	female	6	415	286	364.3	45.3	12.4	
M12	male	8	176	153	166.9	9.5	5.7	0.696
	female	9	191	151	164.8	11.9	7.2	
M13	male	8	375	250	302.6	47.1	15.6	0.833
	female	6	366	243	307.8	41.4	13.5	
M17	male	8	144	106	131.9	13.0	9.8	0.323
	female	8	156	92	123.0	20.8	16.9	
M20	male	4	374	320	346.8	22.5	6.5	0.236
	female	5	374	250	312.8	47.9	15.3	
M21	male	5	288	247	273.2	16.8	6.2	0.090
	female	5	264	185	241.6	32.5	13.5	
M22	male	5	289	201	259.2	34.4	13.3	0.445
	female	5	284	210	242.2	32.5	13.4	
M23	male	5	300	259	280.0	15.9	5.7	0.126
	female	6	311	181	244.3	44.6	18.3	
M24	male	8	397	260	327.1	46.3	14.2	0.279
	female	9	347	264	306.9	26.5	8.6	
length of m3	male	7	254	203	224.86	18.8	8.36	0.107
	female	8	228	185	209.25	16.14	7.71	
width of m3	male	7	75	62	68.857	4.845	7.04	0.228
	female	8	72	51	64.75	7.265	11.2	

Note: Measurements see Fig. 3.

were broken. There are also two types of mandibular symphyses, short and long, which may represent females and males, respectively (Fig. 7). However, juvenile individuals exhibit width/length ratios that are intermediate between adult males and females (Fig. 7). Furthermore, these sexually dimorphic characters were also observed in Middle Miocene *G. angustidens*. In male crania, the temporal fossa is higher but short, and the nasal bones are more posteriorly positioned (Figs. 6G, H, I, and Fig. 8; Tassy, 1996: fig. 11.4).

Sexual dimorphism in ancestral *Phiomia serridens* and derived *Loxodonta africana* has also been studied (Matsumoto, 1924; Roth and Shoshani, 1988; Lee and Poole, 2011).

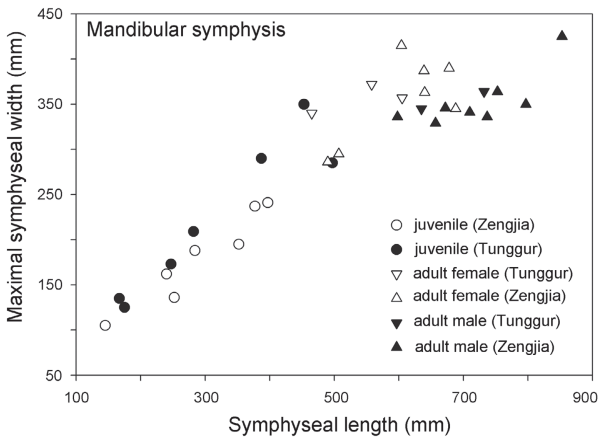

Fig. 7 Bivariate scatter plot of length vs. maximal width of mandibular symphysis in *Platybelodon grangeri*
♂, male; ♀, female

In *P. serridens*, there appears to have sexual dimorphism with regard to size but only have slight sexual dimorphism with regard to symphyseal morphology. For instance, *P.* "*osborni*" Matsumoto, 1922 differs from *P.* "*wintoni*" (Andrews, 1905) in more posteriorly positioned proximal edge of mandibular symphysis (Matsumoto, 1924). However, these two species now have been considered junior synonyms of *P. serridens* (Shoshani and Tassy, 1996: appendix C2). However, in extant *L. africana*, although size difference is still prominent (Roth and Shoshani, 1988; Lee and Poole, 2011), the high-arched cranium, extremely posteriorly positioned nostril aperture, and stout mandibles are highly homomorphic in both sexes (Figs. 6E, F). In the Simpson's ratio diagram, the shapes of polylines that represent the two sexes of *L. africana* are almost identical, which means that individuals of the two sexes display highly similar cranial shapes (Fig. 8).

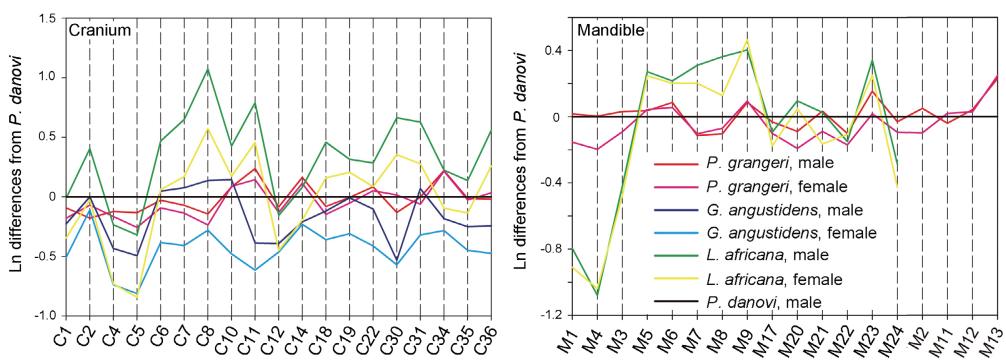

Fig. 8 Simpson's ratio diagrams showing the cranial and madibular sexual dimorphsim between two sexes in Elephantiformes
A skull of *Platybelodon danovi* (BPV 2000) is shown as the standard (the black lines)
Measurements see Figs. 2 and 3

4 Discussion

We analyzed sexual dimorphism in four different elephantiforme taxa covering its entire known evolutionary range (Oligocene *Phiomia*, Miocene *Gomphotherium*, *Platybelodon*, and extant *Loxodonta*). These taxa are closely related and represent key nodes in the evolution of Elephantiformes. Previous phylogenetic analyses revealed that *Phiomia* is the sister group

of all other taxa of Elephantiformes, except the contemporary *Palaeomastodon* (Shoshani and Tassy, 2005; Gheerbrant and Tassy, 2009). Therefore, *Phiomia* is an ideal primitive elephantiforme model. *Gomphotherium* is considered the most important representative of the group trilophodont gomphotheres s. s., which is derived from *Phiomia* and sister to Elephantoidea; thus, *Gomphotherium* represents an intermediate stage between primitive *Phiomia* and derived elephants. *Platybelodon* (a member of Amebelodontinae), which is also derived from *Phiomia*, is a close relative of trilophodont gomphotheres s. s. and includes the group trilophodont gomphotheres s. l.. Moreover, as one of the two representatives of extant elephant genera, *Loxodonta* is representative of elephantiforme terminal taxa.

Many sexually dimorphic characters differ among these taxa. However, larger and stronger upper tusks in males were observed in all taxa. These sexually dimorphic characters are clearly associated with male social behavior, such as combat. However, it is difficult to interpret the role of other sexually dimorphic characters in sexual competition, such as C34/C31, C2/C1, M11/M2, and length/width of M3 and m3 in *Platybelodon* and the sexually dimorphic characters C34/C31 and C2/C1 in *Gomphotherium*. Nevertheless, these characters have strong evolutionary significance in Elephantiformes (Andrews, 1906; Maglio, 1972). The nostril aperture is anterior to the orbit in *Phiomia*, the same level as the orbit in *Gomphotherium* and *Platybelodon*, and posterior to the orbit in *Loxodonta*, which indicates gradual elongation of the trunk in the evolutionary history of Elephantiformes. The brain case is flat and anteroposteriorly elongated in *Phiomia*, slightly arched and shortened in *Gomphotherium* and *Platybelodon*, and strongly arched and shortened in *Loxodonta*; this represents gradual vertical orientation of m. temporalis, which indicates that masticatory function shifted from grinding shearing to horizontal shearing (Maglio, 1972). Therefore, an arched brain case and posteriorly positioned nostril aperture are derived characters in Elephantiformes. Furthermore, the mandibular symphysis is short in *Phiomia* but long in *Platybelodon*, and m3 and M3 are wide in *Phiomia* but narrow in *Platybelodon* (narrowness of m3 and M3 is a diagnostic feature in Amebelodontinae; Tassy, 1986). Therefore, at least in Amebelodontinae, a long symphysis and narrow m3 and M3 are derived characters.

Based on the sexual dimorphism analysis, we can draw two conclusions. First, four evolutionarily significant characters were sexually dimorphic in Miocene *Gomphotherium* or *Platybelodon* and perhaps other members of the trilophodont gomphotheres s. l. group, but were not sexually dimorphic in the primitive taxon *Phiomia* and terminal taxon *Loxodonta*. Second, in *Gomphotherium*, *Platybelodon*, and perhaps other members of the trilophodont gomphotheres s. l. group, if a character was sexually dimorphic, males always possessed evolutionary more derived character states than females. This issue is of interest with regard to elephantiforme evolutionary history, because the two sexes show asynchronous evolution. This asynchrony might have evolved in primitive *Phiomia*, become exaggerated in the Miocene trilophodont gomphotheres, and ceased in extant elephants. It appears as though character variation in males slightly preceded similar variation in females, and eventually the females evolved similar character variation (Fig. 9). However, at present, it is not entirely clear why

this phenomenon occurred.

It is difficult to determine the mechanism underlying the production of the sexually asynchronous morphological variations in the evolution of Elephantiformes at genetic and ontogenetic levels. We hypothesize that this asynchrony may reflect female preference; that is, in the evolution of a sex-related character in a group, female choice plays a key role (Fisher, 1930; Anderson, 1994). For example, in a population of *Gomphotherium* or *Platybelodon*, genetic variation (possibly sex-linked gene(s)) produces variation in a sexually dimorphic character, such as trunk length variation in males. The individuals with a longer-than-average trunk, which was determined when there was a more posteriorly positioned nostril aperture (values less than C2/C1), were more attractive to females; this could be because a longer trunk enhances survival of both the males and their offsprings. Similar cases could also be made for the characters C34/C31 and M11/M2 . Therefore, this sexual selection pressure may have promoted the prevalence of the sex-linked allele or alleles that code for a longer trunk in the population and produced the sexual dimorphism we observed in *Gomphotherium* and *Platybelodon*.

This "runaway selection" process (Fisher, 1930) represents the first step of the asynchronous sex evolution; the derived male character variation slightly preceded similar variation in females. Because the newly developed character in males was also advantageous in females, the longer trunk allele(s) were gradually fixed as non-sex-linked gene(s). Finally, as determined by similar C2/C1 values for both sexes, extant female Elephantiformes also have longer trunks, as can be observed in extant *Loxodonta*. Moreover, sexual selection pressure also weakened, and it was not necessary for males to have longer trunks than females. This process represents the second step of the asynchronous sex evolution: the females evolved similar traits to those of the males. This two-step hypothesis is plausible for explaining the sexual asynchrony observed in elephantiforme evolution and describing the development of this newly derived character within Elephantiformes.

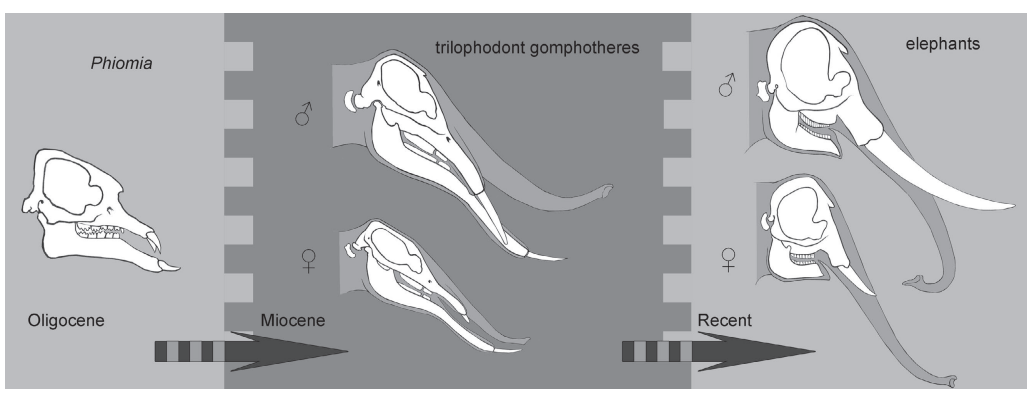

Fig. 9 Schematics showing asynchronous evolution between two sexes in Elephantiformes
The gray scales in the background represent relatively greater (relatively darker) or smaller (relatively lighter) sexual-dimorphism, not to scale. ♂, male; ♀, female. Sketches of *Phiomia* after Andrews (1906)

This asynchronous sex evolution in Elephantiformes appears to be correlated with thriving and declining groups. Miocene *Gomphotherium* and *Platybelodon* show more prominent sexual dimorphism than primitive *Phiomia* and terminal *Loxodonta*. The Miocene is a thriving period for Elephantiformes, who had a broad geological distribution and diverse taxa; in contrast, there are only three extant species of elephants, which are confined to tropical areas in Asia and Africa (Shoshani and Tassy, 1996). One possible reason for this correlation with asynchronous sex evolution is that females became less selective of these traits in males and sexual selection pressure consequently decreased, which led to extant elephantiforme females and males possessing similar derived characters. For example, females seem very picky in copulation and often refuse to mate with males they dislike (Douglas-Hamilton et al., 2006). Furthermore, relationships between sexual dimorphism and evolution were also observed in other groups of large ungulates. For example, thriving groups, such as Cervidae and Bovidae, often exhibit substantial sexual dimorphism, whereas declining groups, such as extant members of Equidae, Rhinoceridae, and Giraffidae (Janis, 1982), often exhibit little sexual dimorphism. However, some extinct taxa of Equidae and Rhinoceridae, such as *Hyracotherium* and *Chilotherium*, have strong sexual dimorphism during their thriving period (Gingerich, 1981; Chen et al., 2010).

The patterns observed in this study may be related to the relationship between male competition and female preference. As Darwin (1874) and Fisher (1930) have discussed, both factors contribute to animals' mating behaviors. In most cases (especially in the thriving groups), the two factors do not contradict each other. A male elephant does compete and defeat competitors to gain copulatory priority, because female elephants are often attracted to and want to mate with the winner. However, in some cases (appears more frequently being in declining groups), even the winner in male competitions may not successfully attract females. A previous study showed that female elephants may refuse males' mating attempts (Douglas-Hamilton et al., 2006). As in humans, males can attract females by various direct or indirect competitions with other males, but the ultimate decision is often up to the female.

The second issue is that the variation in males is less than that in females. The 95% confidential eclipses of females take up a larger area in Fig. 5A, B, and most standard deviations from female measurements are greater than those of male measurements (Tables 1 and 2). This phenomenon has also been noticed in other larger ungulates, such as extant *Equus hemionus* and fossil *Chilotherium wimani* (Chen et al., 2010; Wang, 2010), and even observed in some birds, reptiles, anurans, and invertebrates (Johnston, 1966; Stamps and Gon III, 1983). This phenomenon could occur if males are opportunists and would be willing to mate with a wide range of females, however females are picky because of their greater sexual investment in fewer gametes (Fisher, 1930; Anderson, 1994). This mechanism may also have been involved in the observed asynchronous sex evolution and would be helpful for preserving potential variation in the genomes of the species to maintain evolutionary potential, which facilitates rapid response to dramatic environmental changes.

5 Conclusions

In this paper, we studied sexual dimorphism in a fossil population of *Platybelodon grangeri* from the Middle Miocene Zengjia locality in China. In this population, males possess larger and stronger upper tusks than females. However, several other morphological characters also slightly differ between the sexes, and males have: 1) slightly more arched brain cases, 2) slightly more posteriorly positioned nostril apertures; 3) longer mandibular symphyses; and 4) narrower m3 and M3. The slightly more arched brain cases and slightly more posteriorly positioned nostril apertures are also observed in Miocene *Gomphotherium* but not in primitive *Phiomia* and terminal *Loxodonta*. By comparing these data with previously determined elephantiforme evolutionary data, we observed asynchronous evolution between males and females. In the thriving period of Elephantiformes, males possessed more derived characters than females; however, in the declining period, females and males possessed similar derived characters. This type of asynchronous sex evolution should be studied further because it might also have occurred in other large ungulates.

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雌性偏好促进象型类的性别异时进化

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摘要：性双型的特征通常被认为产生于种内争夺交配优先权的斗争。例如，现生和化石的雄性长鼻类动物具有较大的体型和较粗壮的上门齿。本研究阐释了如下现象：化石象型类动物(Elephantiformes, 长鼻类的主要类群)一些性双型特征与其进化历史具有相关性，而与性别竞争并非直接相关。在中新世的葛氏铲齿象(*Platybelodon grangeri*)和狭齿嵌齿象(*Gomphotherium angustidens*)中，雄性比雌性倾向于具有进化中更进步的特征，如同雄性在进化中领先雌性一步。这种现象可能与雌性偏好的机制相耦合。在象型类动物进化的早期(繁荣期)，性别选择压促使雄性比雌性产生更加显著的进步特征；然而，在它们进化的晚期(衰退期)，性别选择压似乎减弱，性别的异时进化也减少。这种新的发现或许在大型有蹄类的演化过程中有一定的普遍意义，因为那些繁荣的类群中通常性双型显著，如鹿科和牛科；而衰落的类群中通常性双型不显著。

关键词：长鼻类，性双型，雌性偏好，进化

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Appendix 1 The weighs of cranial and mandibular measurements in final DFA

Cranium			Mandible		
measurements	values for normalization	weighs in DFA	measurements	values for normalization	weighs in DFA
C1	961.104	0.015	M1	1347.978	0.183
C2	0.288	0.379	M2	0.486	−0.263
C3	0.739	−0.013	M3	0.345	−0.116
C4	0.700	−0.050	M4	0.911	0.330
C6	0.478	0.259	M5	0.296	−0.448
C7	0.250	−0.180	M6	0.262	0.102
C8	0.190	−0.117	M7	0.073	0.114
C10	0.296	0.468	M8	0.050	−0.102
C11	0.236	−0.290	M9	0.136	−0.252
C12	1.026	0.050	M11	0.263	−0.404
C14	0.290	−0.030	M12	0.123	−0.155
C15	0.343	0.410	M13	0.224	−0.184
C18	0.516	−0.236	M17	0.094	0.226
C19	0.439	0.010	M20	0.242	−0.307
C22	0.252	−0.062	M21	0.187	−0.071
C30	0.120	0.251	M22	0.183	−0.111
C31	0.431	−0.295	M23	0.192	0.048
C33	0.722	0.032	M24	0.234	−0.301
C34	0.407	0.015			
C35	0.412	0.036			
C36	0.399	0.232			
threshold = −0.089 male < −0.089; female > −0.089			threshold = 0.021 male > 0.021; female > −0.021		

Note: Here we demonstrate the procedure for determining the sex of a specimen based on the table. Note that the table is only suitable for *Platybelodon grangeri* from the Zengjia locality. Firstly, the missing and questionable data should be predicted or modified as shown in Materials and methods section, forming a pseudo data vector for all the measurements of the specimen. Secondly, each pseudo datum is divided by measurement C1 (for cranium) or M1 (for mandible), except C1 or M1 itself, forming SNP data; and each SNP datum is again divided by the corresponding value for normalization listed in the column two (for cranium) or column five (for mandible), taking the natural logarithm, and forming the SNLP data. Thirdly, each SNLP datum is multiplied by the corresponding weights listed in the column three (for cranium) or column six (for mandible), and then sum them up. Finally, compare the sum to the thresholds in the bottom of the table for determination of the sex for the specimen.