The palaeoenvironment of the middle Miocene pliopithecid locality in Damiao, Inner Mongolia, China

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ABSTRACT

Damiao, Inner Mongolia, has three main fossil horizons representing the early, middle, and late Miocene. The middle Miocene locality DM01 is the only primate locality from the region and also represents the latest occurrence of pliopithecoids in northern China. The presence of pliopithecoid primates in central Asia after the middle Miocene climatic optimum seems to contradict the general trend of strengthening climatic zonality and increasing aridity. To investigate this enigma, we employ faunal similarity, ecometrics, and stable isotope analysis. Our results support previous inferences concerning the presence of locally humid environments within the increasingly arid surroundings that characterized central Asia. Hypsodonty, estimated mean annual precipitation (MAP), local sedimentology, and large mammal fossils suggest more humid and possibly more forested and wooded environments for the DM01 locality. We compared our results with the adjacent fossil-rich middle Miocene Tunggur localities. However, the small mammal fauna and isotope data are consistent with a mosaic of forest and grassland environment for all Damiao localities. Based on our results, Tunggur may have been too seasonal or not sufficiently humid for pliopithecids. This is supported by the higher mean hypsodonty and lower estimated MAP estimates, as well as slightly higher $\delta^{13}C$ values. We suggest that DM01, the driest known Asian pliopithecid locality, may have been a more humid refugium within a generally drier regional context.

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1. Introduction

Central Inner Mongolia is well known for its fossil-rich Neogene terrestrial deposits that have attracted the attention of palaeontologists since the early 20th century (e.g., Andersson, 1923; Teilhard de Chardin, 1926a, b; Andrews, 1932). However, until the discovery of a pliopithecid primate from the middle Miocene locality of Damiao in 2006, no Miocene primates were known from the region. This is also the latest occurrence of pliopithecoids in Central Asia, excluding the putative *Pliopithecus posthumus* (Schlosser, 1924) from Ertemte, Inner Mongolia (~5−6 mega-

annum [Ma]), the primate status of which has been questioned (e.g., Hürzeler, 1954; Simons, 1972; Simons and Fleagle, 1973; Harrison et al., 1991; Harrison and Gu, 1999; Harrison, 2005) and is not discussed further here. Neither do we discuss other northern Chinese primate localities, such as Tongxin (Ningxia Hui Autonomous Region), Tabenbuluk, nor Yindirte (Gansu Province) that are older than Damiao (late Oligocene to middle Miocene; Bohlin, 1946; Harrison et al., 1991). The particular palaeoecological conditions of pliopithecoids are not yet known, but Eronen and Rook (2004) and Sukselainen et al. (2015) suggest that they preferred humid areas, more humid than other contemporary primate groups. The presence of pliopithecid primates in central Asia after the middle Miocene climatic optimum is particularly interesting since it seems to contradict the general trend of strengthening

climatic zonality and increasing aridity from the early Miocene onwards (Kaakinen et al., 2015). In this study, we investigate why pliopithecids occur at Damiao when they are absent from the similar fossil-rich and intensively collected neighbouring locality of Tunggur (Wang et al., 2003; Zhang et al., 2009), addressing the question using a multi-proxy palaeoecological analysis based on faunal similarity, ecometrics, and stable isotope analysis.

1.1. Environmental context in Eurasia

The Neogene (23–2.6 Ma) of Eurasia can be characterized by three climatically distinct periods: (1) the warm and humid early Miocene (23–17 Ma) with weak seasonality and low temperature gradients and with little variation spatially (Utescher et al., 2000; Mosbrugger et al., 2005; Bruch et al., 2007, 2011); (2) the middle Miocene climatic optimum (17–15 Ma) that was warmer and more humid than the early Miocene (Flower and Kennett, 1994; Fortelius et al., 2002; Böhme, 2003; Bruch et al., 2004; Kaandorp et al., 2005; Liu et al., 2009); and (3) the subsequent cooling that led to a trend towards more arid and open habitats in the late Miocene and Pliocene (Zachos et al., 2001, 2008; Fortelius et al., 2014; Song et al., 2014).

The climate in eastern Asia was dominated by the planetary wind system throughout most of the Miocene, until the latest Miocene when the uplift of the Tibetan Plateau strengthened the regional monsoon system (An et al., 2001; Liu et al., 2009; Passey et al., 2009; Tang et al., 2011, 2013). The climate in China at 17–13.5 Ma was relatively humid, showing no clear pattern of a latitudinal gradient in humidity (Liu et al., 2009). Between 13.5 and 11.1 Ma, the latitudinal climate gradient increased and arid belts appeared in the mid-latitudes (~30–60° N) of Asia, while in the north and south humid conditions continued to prevail (Flower and Kennett, 1994; Liu et al., 2009; Mirzaie Ataabadi et al., 2013). There is no consensus on whether North China was humid during this time (see e.g., Sun et al., 1998; Guo et al., 2002; Sun and Wang, 2005; Liu et al., 2009), but it has been suggested that humid conditions may have occurred locally within a more arid regional environment, such as in riverine corridors (Wang and Zhang, 2011; Kaakinen et al., 2015).

1.2. Pliopithecids

Pliopithecidae was a diverse family that during the Miocene ranged widely throughout Eurasia from the Iberian Peninsula to eastern China. They were also among the first fossil primates to be discovered and described (e.g., Lartet, 1837; Biedermann, 1863; Hofmann, 1893; Ginsburg and Mein, 1980; Ginsburg, 1986; Andrews et al., 1996; Harrison and Gu, 1999; Begun, 2002; Alba et al., 2010; Harrison, 2013). The earliest known occurrence of pliopithecids is from the late early Miocene (~17–18 Ma) of Sihong, Jiangsu, China. These are the two oldest and most primitive genera of pliopithecids, *Dionysopithecus* and *Platodontopithecus* (Li, 1978; Harrison and Gu, 1999; Begun, 2002). More specialized pliopithecines were likely to have originated from these early Asian forms, later dispersing into Europe. Previously, the more derived and late-surviving pliopithecids, the crouzeliines, were thought to have originated from these European forms (Harrison and Gu, 1999; Moyà-Solà et al., 2001; Alba et al., 2010), but new evidence of primitive crouzeliines from Fanchang, east China, implies that they may have originated in Asia prior to arriving in Europe (Harrison, 2013). During the middle Miocene, ~15–12 Ma, pliopithecids are known from several Chinese localities: Laogou, Gansu Province, Junggar Basin, Xinjiang Autonomous Region, Tongxin, Ningxia Hui Autonomous Region, and Damiao, Inner Mongolia (Harrison et al., 1991; Begun, 2002; Deng, 2003; Wu et al., 2003; Zhang and

Harrison, 2008). The latest known occurrence of pliopithecids is also from China, from the late Miocene locality of Shihuiba, Lufeng, Yunnan, where they co-existed with hominoids at ~6.9–6.2 Ma (Dong and Qi, 2013).

The distribution of pliopithecoids as a clade reflects an ecological preference for more persistently humid habitats than those inferred for other contemporary primate clades (Eronen and Rook, 2004; Sukselainen et al., 2015), but not much is known about the ecological preferences of each species. Unlike hominoids, they did not adjust their habitat preferences to the increasingly arid conditions of the Miocene, but effectively remained in their ancestral ecological and climatic niche (Sukselainen et al., 2015). In the late middle Miocene of Asia, pliopithecids are absent from mid-latitudes and are recorded only from north China, at Damiao, Inner Mongolia, ~12.1 Ma (Zhang and Harrison, 2008; Kaakinen et al., 2015).

1.3. Study area

Damiao is located in Siziwang Banner, central Inner Mongolia, ~100 km north of the provincial capital of Hohhot. Following its discovery in 2006, the site was excavated during three field seasons (until 2009). There are three main fossil-bearing horizons with more than 30 mammal localities, the majority of which occur within a few square kilometres ~65 km north of Ulanhua town (Fig. 1). Three of the most productive localities (DM16, DM01, and DM02) are magnetostratigraphically dated to range from early Miocene to earliest late Miocene (Kaakinen et al., 2015). In addition, based on stratigraphy, late Miocene ages can be tentatively inferred for fossils from DM06, DM12, DM13, and DM26, and latest Miocene for the southernmost locality, the so-called "UH Museum". The northernmost locality, DM17, is provisionally considered to be late Eocene in age.

The stratigraphically lowest locality, DM16, is dated to 20–21 Ma and has mainly yielded small mammal remains. The DM16 strata are characterized by red-brown mudstone with thin horizontal laminations and desiccation cracks (Kaakinen et al., 2015). Fossil mammals from the richest locality, DM01, are biochronologically correlated with the late middle Miocene Tunggur fauna and are estimated to be 12.1 Ma (Kaakinen et al., 2015). This locality has more than 30 mammal species, including a pliopithecid primate (Zhang and Harrison, 2008). DM01 fossils come from a 1–1.5 m thick complex of carbonate nodule conglomerate and sandstone beds with distinctive manganese and iron staining. The exposed lateral extent of the locality is ~60 m (Zhang et al., 2012; Kaakinen et al., 2015). The DM02 locality is early late Miocene, with an estimated age of 11.6 Ma, and has produced mainly small mammal teeth that are found in a ~20 cm thick sandstone lying above mudstones (Kaakinen et al., 2015). The depositional setting at Damiao is fluvial in nature with well-drained floodplains (Kaakinen et al., 2015); the large mammal community structure throughout the sequence shows a relatively stable pattern with cervoids predominating (Zhang et al., 2011; Kaakinen et al., 2015). Although the cervoids are not diagnostic of woodland environments, they probably preclude the possibility of exclusively grassland or desert environments for the Damiao sequence.

The Central Asiatic Expedition of the American Museum of Natural History discovered the site of Tunggur in 1928 (Spock, 1929; Andrews, 1932). Subsequent excavations resulted in huge collections of mammalian fossils, including *Platybelodon grangeri*, a shovel-tusked gomphotheriid (Wang et al., 2003, 2013). The Tunggur fauna, also known as the *Platybelodon* fauna, includes all assemblages from the Tunggur Formation and is the most diverse and abundant Chinese middle Miocene mammal assemblage. It is the basis for Tunggurian Land Mammal Stage/Age (LMS) in East
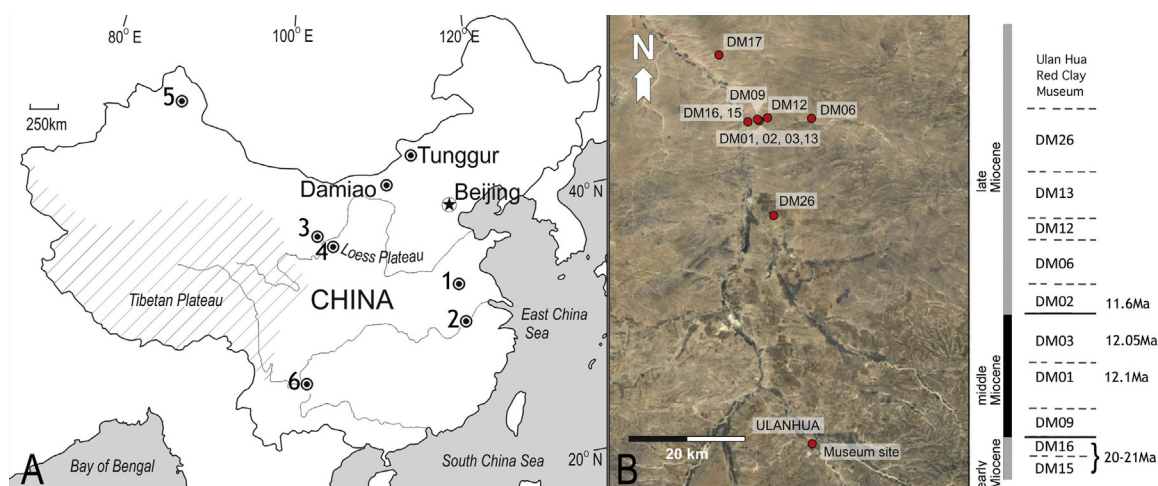
Figure 1. A) Damiao, Tunggur, and other Chinese pliopithecoid localities: (1) Sihong, (2) Fanchang, (3) Hezheng-laogou, (4) Tongxin, (5) Junggar-Tieersihabahe, and (6) Lufeng. B) Damiao localities and their time frame.

Asia spanning from 11.8 Ma to 12.6 Ma (Qiu et al., 2013). The lateral extent of the fossil-bearing sediments in the Tunggur area (Fig. 1) is several hundreds of square kilometres and includes several localities of similar age (e.g., Mandelin Chabu [MC], Aoershun Chaba [AC], Zhunwuguer [ZH], Wolf Camp [WC], Dabuhaer [DA], Platybelodon Quarry [PQ], Moergen, Aletexire [ALU], Huerguolajin [HU], Roadmark 482 [482], Tairum Nor, Tairum Nor middle sandstone [TMS]; Wang et al., 2003). The palaeoenvironment of Tunggur has been investigated using several methods, resulting in somewhat different interpretations. Pollen data from the northeastern part of the Tunggur tableland point to woodland habitats of mixed conifer and broadleaf trees with small areas of shrub/grassland (Dong [1993] in Wang et al., [2003]). Arid grassland or possibly semidesert was suggested by Qiu (1996) based on the small mammal fauna. The large mammals, on the other hand, point to a mixed habitat of woodland and grassland (Colbert, 1939; Wang et al., 2003). Sedimentological analysis suggests small highly alkaline ponds and shallow meandering rivers (Wang et al., 2003). Isotopic analysis of fossil tooth enamel indicates water stressed C3 diets that imply mixed habitats of woodland and C3 grasslands (Zhang et al., 2009). All these palaeoenvironmental proxies suggest a mosaic of different local environments for Tunggur, with grassland and mixed conifer-broadleaf woodland in an area with shallow meandering rivers and alkaline ponds during the dry season, much as in the present-day grasslands of the region (Wang et al., 2003; Zhang et al., 2011).

2. Materials and methods

2.1. Sample

Fossil mammal data for hypsodonty, precipitation, and similarity analysis were downloaded from the New and Old Worlds (NOW) database on 20th October 2014 (Fortelius, 2014; http://www.helsinki.fi/science/now). We included Eurasian localities within the temporal range of 18−7.1 Ma or MN04-MN12 (Mammal Neogene [MN] units following NOW database usage, see also Steininger [1999]). Following Mirzaie Ataabadi (2010), ad hoc MN equivalents (MNEQ) were used instead of traditional MN units to make Eurasian mammal biostratigraphy provisionally uniform. For MNEQ, we used the boundaries of MN units in millions of years to compute a minimum and maximum age estimate for the locality. The assignment to a specific MN unit is based on the locality's temporal range midpoint: when the midpoint falls within the corresponding traditional MN unit's range, and has an equal or shorter duration than the MN unit, it is assigned to it (Mirzaie Ataabadi, 2010). Only localities where both the maximum and the minimum ages fell within the boundaries of the MNEQ-unit were included (MNEQ sensu Mirzaie Ataabadi, 2010).

Tooth samples for isotopic analysis were collected during the 2007 and 2008 field seasons and are held in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) in Beijing. For the analysis, enamel from 79 teeth of large herbivorous fossil and modern mammals was analysed (Table 1). Of these specimens, 52 were perissodactyls (41 rhinos and 11 equids), 25 artiodactyls (15 bovids, four cervids, one giraffid, and a few unidentified ruminants), and two proboscideans (gomphotheriids). The fossil material comes from 12 early to late Miocene localities. The latest Miocene Ulan Hua Red Clay Museum locality is situated near Wulanhua town, ~60 km south of the other Damiao localities. The modern sample consisted of five bovid specimens, including *Bos*, *Ovis*, and *Capra*.

2.2. Hypsodonty and precipitation

As an ecometric proxy for humidity, we used the dental traits of large herbivorous mammals, which have previously been shown to correlate with precipitation and humidity in extant mammals (e.g., Fortelius et al., 2002; Eronen et al., 2010a; Liu et al., 2012). These methods have also been extensively applied to extinct faunal communities (Fortelius et al., 2002, 2003, 2006, 2014; Liu et al., 2009; Eronen et al., 2010a, b; Mirzaie Ataabadi, 2010; Sukselainen et al., 2015). Mean ordinated molar crown height (hypsodonty) is calculated as the ratio of height to length of the second upper or lower molar. It is a measure of dental durability (e.g., Janis and Fortelius, 1988) and it has also been used increasingly as a proxy for humidity. In the NOW database, three classes of hypsodonty are recorded—brachydont, mesodont, and hypsodont. Following the method of Fortelius et al. (2002), these were assigned numerical values 1, 2, and 3 (respectively) and from these ordinated scores, the mean hypsodonty values for large herbivorous mammals (Orders Artiodactyla, Perissodactyla, and Proboscidea) were calculated for each locality. Only localities that fell within one MNEQ unit and had more than one specimen available for hypsodonty scoring were included in the analysis.

Estimated mean annual precipitation (MAP) was calculated using methods of Eronen et al. (2010a, b) and Liu et al. (2012). The method

Table 1
Carbon and oxygen isotope values for Damiao (DM) fossil localities and modern samples.

Sample id	Order	Family	Locality (DM)	Age	δ¹³C ‰PDB	δ¹⁸O ‰PDB
DM.15.113	Artiodactyla	Cervidae	15	Early Miocene	-8.8	-1.9
DM.16.254 rhino	Perissodactyla	Rhinocerotidae	16	Early Miocene	-7.3	-10.4
DM.16.115	Perissodactyla	Rhinocerotidae	16	Early Miocene	-7.4	-9.2
DM.16.291 rhino	Perissodactyla	Rhinocerotidae	16	Early Miocene	-8.1	-9.9
DM.16.294 rhino	Perissodactyla	Rhinocerotidae	16	Early Miocene	-8.1	-11.1
DM.16.255 rhino	Perissodactyla	Rhinocerotidae	16	Early Miocene	-9.1	-9.2
DM.17.186.2	Perissodactyla	Rhinocerotidae	17	Early Miocene	-7.8	-8.6
DM.17.175	Perissodactyla	Rhinocerotidae	17	Early Miocene	-8.4	-7.3
DM.17.174	Perissodactyla	Rhinocerotidae	17	Early Miocene	-8.9	-6.2
DM.17.186.1	Perissodactyla	Rhinocerotidae	17	Early Miocene	-9.0	-8.3
DM.17.176.1	Perissodactyla	Rhinocerotidae	17	Early Miocene	-11.0	-4.4
DM.01.199.1	Perissodactyla	Rhinocerotidae	1	Middle Miocene	-7.2	-5.4
DM.01.196	Artiodactyla	Bovidae	1	Middle Miocene	-8.2	-3.7
DM.01.206	Perissodactyla	Rhinocerotidae	1	Middle Miocene	-8.2	-8.3
DM.01.70	Artiodactyla	Cervidae	1	Middle Miocene	-8.6	-3.8
DM.01.137	Perissodactyla	Rhinocerotidae	1	Middle Miocene	-9.7	-6.1
DM.01.77	Perissodactyla	Rhinocerotidae	1	Middle Miocene	-10.3	-10.1
DM.01.135	Artiodactyla	Cervidae	1	Middle Miocene	-10.7	-11.8
DM.01.198	Perissodactyla	Rhinocerotidae	1	Middle Miocene	-11.0	-8.2
DM.01.91	Perissodactyla	Rhinocerotidae	1	Middle Miocene	-11.1	-10.3
DM.01.99	Perissodactyla	Rhinocerotidae	1	Middle Miocene	-11.3	-10.3
DM.01.197	Perissodactyla	Rhinocerotidae	1	Middle Miocene	-11.3	-9.3
DM.01.207.1	Perissodactyla	Rhinocerotidae	1	Middle Miocene	-11.8	-8.6
DM.01.123	Artiodactyla		1	Middle Miocene	-13.4	-7.2
DM.03.132.2	Artiodactyla		3	Middle Miocene	-7.4	-0.1
DM.03.132.1	Artiodactyla		3	Middle Miocene	-7.9	-7.5
DM.03.128	Artiodactyla	Cervidae	3	Middle Miocene	-10.0	-10.0
DM.03.127.2	Perissodactyla	Rhinocerotidae	3	Middle Miocene	-10.8	-6.0
DM.03.127.1	Perissodactyla	Rhinocerotidae	3	Middle Miocene	-10.9	-9.9
DM.03.130	Artiodactyla		3	Middle Miocene	-11.0	-10.0
DM.03.131	Artiodactyla		3	Middle Miocene	-11.2	-11.2
DM.09.25	Proboscidea	Gomphotheriidae	9	Middle Miocene	-7.5	-5.3
DM.09.27	Proboscidea	Gomphotheriidae	9	Middle Miocene	-9.6	-11.0
DM.02.61	Artiodactyla	Bovidae	2	Late Miocene	-7.3	-2.3
DM.02.48	Artiodactyla	Bovidae	2	Late Miocene	-7.7	-0.0
DM.06.155	Perissodactyla	Rhinocerotidae	6	Late Miocene	-8.4	-8.2
DM.06.153	Perissodactyla	Equidae	6	Late Miocene	-9.8	-8.2
DM.06.139.2	Perissodactyla	Rhinocerotidae	6	Late Miocene	-9.9	-9.5
DM.06.157	Perissodactyla	Equidae	6	Late Miocene	-10.7	-8.4
DM.06.156.1	Perissodactyla	Rhinocerotidae	6	Late Miocene	-11.5	-10.5
DM.06.139.1	Perissodactyla	Rhinocerotidae	6	Late Miocene	-11.6	-7.8
DM.06.156.2	Perissodactyla	Rhinocerotidae	6	Late Miocene	-11.6	-10.9
DM.06.156.3	Perissodactyla	Rhinocerotidae	6	Late Miocene	-11.7	-8.4
DM.06.138	Perissodactyla	Rhinocerotidae	6	Late Miocene	-11.9	-9.7
DM.06.158.1	Perissodactyla	Rhinocerotidae	6	Late Miocene	-12.0	-10.1
DM.12.104	Perissodactyla	Rhinocerotidae	12	Late Miocene	-8.2	-10.6
DM.12.103	Perissodactyla	Rhinocerotidae	12	Late Miocene	-8.4	-7.9
DM.12.100	Perissodactyla	Rhinocerotidae	12	Late Miocene	-8.5	-11.7
DM.12.102	Perissodactyla	Rhinocerotidae	12	Late Miocene	-8.5	-10.2
DM.12.101	Perissodactyla	Rhinocerotidae	12	Late Miocene	-11.1	-5.9
DM.13.37	Perissodactyla	Rhinocerotidae	13	Late Miocene	-8.1	-10.6
DM.13.34	Perissodactyla	Equidae	13	Late Miocene	-8.7	-6.1
DM.13.30	Perissodactyla	Rhinocerotidae	13	Late Miocene	-8.9	-9.6
DM.13.28	Perissodactyla	Equidae	13	Late Miocene	-9.5	-10.6
DM.13.38	Perissodactyla	Rhinocerotidae	13	Late Miocene	-10.7	-8.4
DM.26.BHP-3	Artiodactyla	Bovidae	26	Late Miocene	-7.8	-13.1
DM.26-BHP-2	Perissodactyla	Rhinocerotidae	26	Late Miocene	-8.1	-8.8
DM.26-BHP-6	Perissodactyla	Rhinocerotidae	26	Late Miocene	-8.5	-11.2
DM.26-BHP-7	Artiodactyla	Bovidae	26	Late Miocene	-8.6	-3.1
DM.26-BHP-4	Perissodactyla	Equidae	26	Late Miocene	-9.6	-5.0
DM.26-BHP-1	Perissodactyla	Equidae	26	Late Miocene	-9.9	-8.7
DM.26-BHP-5	Perissodactyla	Equidae	26	Late Miocene	-10.1	-8.4
CN2008-UH-192	Artiodactyla	Bovidae	UH Museum	Late late Miocene	-4.5	-2.4
CN2008-UH-201	Artiodactyla	Bovidae	UH Museum	Late late Miocene	-4.9	-10.8
CN2008-UH-194	Artiodactyla	Giraffidae	UH Museum	Late late Miocene	-6.3	-5.1
CN2008-UH-193	Artiodactyla	Bovidae	UH Museum	Late late Miocene	-6.6	-1.1
CN2008-UH-200	Artiodactyla	Bovidae	UH Museum	Late late Miocene	-6.7	-3.8
CN2008-UH-199	Artiodactyla	Bovidae	UH Museum	Late late Miocene	-6.8	-1.1
CN2008-UH-198	Perissodactyla	Equidae	UH Museum	Late late Miocene	-7.0	-8.4
CN2008-UH-196	Perissodactyla	Equidae	UH Museum	Late late Miocene	-7.0	-9.1
CN2008-UH-197	Perissodactyla	Equidae	UH Museum	Late late Miocene	-7.4	-8.7
CN2008-UH-190	Perissodactyla	Rhinocerotidae	UH Museum	Late late Miocene	-7.6	-7.9
CN2008-UH-191	Perissodactyla	Rhinocerotidae	UH Museum	Late late Miocene	-7.7	-8.2
CN2008-UH-195	Perissodactyla	Equidae	UH Museum	Late late Miocene	-8.2	-8.7

Table 1 (*continued*)

Sample id	Order	Family	Locality (DM)	Age	δ^{13}C ‰PDB	δ^{18}O ‰PDB
CN2008-DM-188	Artiodactyla	Bovidae	Modern	Modern	−5.7	−0.5
CN2008-DM-189	Artiodactyla	Bovidae	Modern	Modern	−6.2	−3.9
CN2008-DM-187	Artiodactyla	Bovidae	Modern	Modern	−6.8	−7.1
CN2008-DM-186	Artiodactyla	Bovidae	Modern	Modern	−8.5	−0.4
CN2008-DM-109	Artiodactyla	Bovidae	Modern	Modern	−8.9	−2.9

of Eronen et al. (2010a) estimates precipitation using a regression tree analysis based on the mean (community-level) molar crown height of large herbivorous mammals. The method of Liu et al. (2012) uses an ordinary least-squares linear regression model to estimate MAP from mean hypsodonty and longitudinal loph count. Both methods show similar trends in the estimated MAP. Since the Eronen et al. (2010a, b) method is more sensitive to small sample size, we focus on the method of Liu et al. (2012). We also note that we are mainly concerned about the relative change in aridity and, therefore, do not focus on absolute precipitation estimates. For the current analysis, we used data from the entire Eurasian continent from the NOW database, but we only discuss the relevant Chinese localities here. Results for both methods are shown in Table 2 for MNEQ06-09 Chinese localities and the Supplementary Online Material (SOM) for all analysed Eurasian localities.

A total of 839 fossil localities were used for the hypsodonty and MAP analysis (SOM). For the purposes of this study, we grouped the localities into four locality types: pliopithecoid localities, hominoid localities, other primate localities (with cercopithecoids, siva-ladapids, tarsiids, lorisids, and/or indeterminate primates), and non-primate localities. The results are shown in graphs and tested using a pairwise Mann−Whitney test.

2.3. Faunal similarity metrics

In paleontological studies, faunal similarity is often used as a measure of faunal provinciality (e.g., Bernor, 1978, 1983; Fortelius et al., 1996; Nargolwalla, 2009). Here we use genus-based faunal resemblance to detect similarities between localities in a geographically and temporally restricted area. Our rationale is that significant differences between contemporaneous faunas may indicate the presence of a barrier between localities, such as water, climate, or vegetation (Simpson, 1940; Middlemiss and Rawson, 1969; Raup and Crick, 1979). Taxonomic presence/absence data from different localities can be used to estimate similarity between fossil localities. Different similarity indices have been employed (see Hammer and Harper [2009] for a review). One of the simplest and oldest is Simpson's index, calculated as M/S, where M is the number of shared taxa and S is the number of taxa in the assemblage with the fewest samples (Simpson, 1943). This method was chosen here since it is insensitive to the size of the sample and ignores absences in the smaller fauna. These qualities are desired for sample sizes that vary and because the Damiao samples are small. Thirteen small mammal and 16 large mammal localities from the middle Miocene and early late Miocene (MNEQ06-09) were analysed. Analyses were run in PAST 3.01 (Hammer et al., 2001) separately for small and large land mammals. (The distinction between 'small' and 'large' land mammals is here purely taxonomic; small mammals included the orders Eulipotyphla, Lagomorpha, and Rodentia, and all other terrestrial orders were considered large mammals.) Chinese localities between MNEQ06 and MNEQ09 that fell within one MNEQ unit were included in the analyses. We follow Eronen et al. (2009) in using genus-level data and including only mammal localities with seven or more genera. Due to the regional focus, we include three Damiao localities that have less than seven

genera of large mammals. This is expected to make our similarity estimates less precise, but is unlikely to bias them systematically. Principal coordinates analysis was used to visualise the Simpson similarity between localities.

2.4. Stable isotope analysis

We use carbon isotope ratios of enamel in herbivorous mammals to show the extent to which their diet was composed of C3 or C4 vegetation. Further, we use oxygen isotope compositions of fossil tooth enamel to reconstruct palaeoclimate (Kohn et al., 1996), especially past aridity (Longinelli, 1984; Fricke et al., 1998; Levin et al., 2006). Plants have distinct ratios of ^{13}C/^{12}C that are preserved in fossil tooth enamel, allowing the study of their past distribution (Koch, 1998; Kohn and Cerling, 2002). Most trees, shrubs, and herbaceous dicots use the C3 photosynthetic pathway, giving forest ecosystems a C3 carbon isotope signature (Passey et al., 2009), while C4 plants are mainly warm season grasses with distributions related to the growing season (rainy season) temperature (Teeri and Stowe, 1976; Tieszen et al., 1979; Young and Young, 1983; Ehleringer et al., 1997). The δ^{13}C values of herbivorous mammal tooth enamel reveal the δ^{13}C value of diet, which in turn sheds light on the environment. For modern mammalian tooth enamel, δ^{13}C values of approximately −9‰ or lower are indicative of a C3-based diet, while δ^{13}C values of about −1‰ or higher indicate a C4-based diet. In water stressed environments, these cut-off values for pure C3 diets are higher in ^{13}C, approximately −8‰ for modern and −7‰ for Miocene fossil samples (the difference between modern and fossil being due to fluctuations in the δ^{13}C of atmospheric CO_2; e.g., Cerling et al., 1997; Passey et al., 2002, 2009), and higher values indicate drier conditions or a small fraction of C4 in the ecosystems.

Fossil tooth enamel from the Damiao localities was sampled by grinding the specimens with a diamond-impregnated drill bit and collecting the resulting powder over weighing paper. Samples were pretreated with 3% H_2O_2 and 0.1 M CH_3COOH buffer solution. Enamel samples were reacted at 90 °C in a common acid bath device (in 100% H_3PO_4) and the resulting CO_2 was analysed on a Finnigan MAT 252 isotope ratio mass spectrometer at the University of Utah. Isotope values were normalised to NBS-19 carbonate reference material (δ^{13}C = 1.95‰ PDB [Pee Dee Belemnite], δ^{18}O = −2.20‰ PDB) or to internal laboratory standards calibrated against NBS-19. The resulting data were tested using a pair-wise Mann-Whitney test to detect possible differences between groups of mammals and different localities (Tables 3−6). Tooth enamel δ^{18}O values are reported as mineral equivalent values using enamel-specific CO_2-mineral fractionation factors (sometimes called phosphoric acid fractionation factors) reported in Passey et al. (2007).

3. Results

3.1. Mean hypsodonty and mean annual precipitation

Although there was variation in sample size between different localities, this did not affect the results significantly as there was no

Table 2
Mean hypsodonty and mean annual precipitations for Chinese MNEQ06-09 localities (sample size refers to the number of taxa per locality with hypsodonty scoring).[a]

ID	Name	LocTYPE	MNEQ	MeanHYP	MAP (Liu et al., 2012)	MAP (Eronen et al., 2010a, b)	Sample size
20625	Jiulongkou	NONPRIM	06	1.22	886.96	1939.00	9
20968	Junggar-Botamoyin	NONPRIM	06	1.00	1241.18	1939.00	8
20969	Junggar-botamoyindong	NONPRIM	06	1.00	596.40	733.10	2
26478	Junggar-chibaerwoyi	NONPRIM	06	1.00	1284.16	733.10	4
20973	Junggar-Ganqikairixi	NONPRIM	06	1.00	882.97	733.10	2
26450	Lantian-koujiacun	NONPRIM	06	1.00	2315.80	733.10	2
24511	Liuhe-lingyanshan	NONPRIM	06	1.00	2029.23	733.10	3
26502	Qaidam-Olongbuluk	NONPRIM	06	1.40	603.58	399.70	5
24220	Tairum Nor	NONPRIM	06	1.40	947.46	399.70	5
24531	Tongxin-dingjiaergou	NONPRIM	06	1.29	1230.95	1405.00	7
24533	Tongxin-jinzuizigou	NONPRIM	06	1.00	2315.80	733.10	2
24535	Tongxin-shataigou	NONPRIM	06	1.00	2315.80	733.10	3
24536	Tongxin-Yehuliquezi	NONPRIM	06	1.00	2315.80	733.10	2
26500	Hezheng-laogou	PLIO	06	1.36	1540.78	1939.00	11
20975	Junggar-Tieersihabahe	PLIO	06	1.00	1599.38	1405.00	6
20624	Tongxin	PLIO	06	1.67	1468.07	399.70	6
24534	Tongxin-maerzuizigou	PLIO	06	1.00	2315.80	733.10	4
23193	Kaiyuan-Xiaolongtan	HOMIN	07/8	1.00	1947.36	1405.00	7
24470	Fangxian	NONPRIM	07/8	1.80	1126.58	399.70	5
26477	Junggar-duolebulejin	NONPRIM	07/8	1.75	1147.18	681.60	8
27063	Junggur_dingshanyanchi	NONPRIM	07/8	1.00	882.97	733.10	3
24499	Lantian-gaopo-64004	NONPRIM	07/8	1.67	894.93	399.70	3
20927	Lantian-gaopo-64008	NONPRIM	07/8	1.50	1250.15	399.70	4
24596	Lanzhou-Quantougou	NONPRIM	07/8	1.00	2029.23	733.10	2
20925	Lintong-lengshuigou	NONPRIM	07/8	1.73	869.97	399.70	11
20978	Minhe-lierbao	NONPRIM	07/8	1.50	1250.15	399.70	4
20985	Minhe-nanhawangou	NONPRIM	07/8	1.50	1250.15	399.70	4
27765	Tunggur-ALU	NONPRIM	07/8	1.57	483.84	399.70	7
27752	Tunggur-DA	NONPRIM	07/8	1.40	775.52	399.70	5
27763	Tunggur-HU	NONPRIM	07/8	1.00	1360.58	1939.00	9
27756	Tunggur-MC	NONPRIM	07/8	1.80	840.01	399.70	5
27761	Tunggur-MOII	NONPRIM	07/8	1.67	894.93	399.70	3
27751	Tunggur-PQ	NONPRIM	07/8	2.00	1044.20	200.90	2
27769	Tunggur-TMS	NONPRIM	07/8	1.00	1885.95	733.10	2
27754	Tunggur-ZH	NONPRIM	07/8	1.50	820.30	399.70	4
27755	Tunggur-AC	NONPRIM	07/8	1.67	1181.50	399.70	3
20621	Tunggur-Moergen	NONPRIM	07/8	1.33	1092.56	1426.00	18
27753	Tunggur-WC	NONPRIM	07/8	1.67	1009.56	399.70	9
24547	Xinan	NONPRIM	07/8	1.50	1078.21	399.70	4
28110	DM01	PLIO	07/8	1.00	1284.16	1405.00	7
28227	DM02	NONPRIM	07/8	1.00	596.40	733.10	6
20628	Amuwusu	NONPRIM	09	1.00	1026.25	733.10	3
24469	Dongxiang-wangji	NONPRIM	09	3.00	202.45	200.90	2
24920	Guonigou	NONPRIM	09	2.57	593.90	200.90	7
24487	Lantian-12	NONPRIM	09	2.00	471.07	200.90	4
20627	Qaidam-Tuosu	NONPRIM	09	2.00	399.43	399.70	11
20631	Wuzhong-ganhegou	NONPRIM	09	1.75	932.25	681.60	4
20632	Zhongning-ganhegou	NONPRIM	09	2.33	906.90	200.90	3

[a] ID = Locality ID as in NOW database; LocTYPE = locality type: HOMIN = locality with hominoids, NONPRIM = locality with no primates, PLIO = locality with pliopithecoids; MNEQ = MN equivalent unit; MeanHYP = mean hypsodonty; MAP = predicted mean annual precipitaiton.

significant correlation between sample size and mean hypsodonty (Spearman's rho = 0.01, p = 0.70). Pliopithecoid localities showed lower and more constant mean hypsodonty values compared to other locality types throughout the studied time interval (Fig. 2). Pairwise Mann-Whitney tests showed that the detected differences in hypsodonty values were significant for all other pairs of locality types except hominoid and non-primate localities (Table 7).

Damiao had markedly lower mean hypsodonty values than most Tunggurian localities, with the exception of Tunggur-TMS and Tunggur-HU, which each had a mean hypsodonty of 1 (Table 2).

Hominoid and pliopithecoid localities both had high estimated MAP, consistently higher than any other locality type (Fig. 3). A pairwise Mann-Whitney test showed that pliopithecoid and hominoid localities cannot be significantly distinguished from each

Table 3
Pair-wise Mann−Whitney test results for δ^{13}C of different groups of large herbivorous mammals (U-values at lower left, p-values at upper right).[a]

U\p-value	Artiodactyla	Proboscidae	Equidae	Rhinocerotidae
Artiodactyla		0.61	0.11	**0.00**
Proboscidae	19.00		0.92	0.37
Equidae	90.50	10.00		0.24
Rhinocerotidae	271.00	25.00	173.00	

[a] Significant values in bold.

Table 4
Pair-wise Mann−Whitney test results for δ^{18}O of different groups of large herbivorous mammals (U-values at lower left, p-values at upper right).[a]

U\ p-value	Artiodactyla	Proboscidae	Equidae	Rhinocerotidae
Artiodactyla		0.25	**0.02**	**0.00**
Proboscidae	12.00		0.92	0.93
Equidae	71.00	10.00		0.27
Rhinocerotidae	234.00	39.00	175.50	

[a] Significant values in bold.

Table 5
Pair-wise Mann-Whitney test results for $\delta^{13}C$ of different localities (number of samples below the locality name; U-values at lower left, *p*-values at upper right).[a]

U\p-value	Modern	Late Miocene						Middle Miocene			Early Miocene	Eocene?
		DM02	DM06	DM12	DM13	DM26	UH	DM01	DM03	DM09	DM16	DM17
	5	2	10	5	5	7	12	13	7	2	5	5
MODERN		0.85	**0.01**	0.30	0.09	0.07	0.71	**0.01**	**0.03**	0.33	0.18	0.33
DM02	4.00		**0.04**	0.08	0.08	0.06	0.32	0.07	0.11	0.70	0.33	0.08
DM06	2.00	0.00		**0.03**	**0.02**	**0.01**	**0.00**	0.17	0.13	0.07	**0.00**	**0.03**
DM12	7.00	0.00	7.00		0.53	0.81	**0.00**	0.24	0.63	0.85	0.09	0.92
DM13	4.00	0.00	6.00	9.00		0.75	**0.00**	0.20	0.33	0.85	0.09	1.00
DM26	6.00	0.00	9.00	15.50	15.00		**0.00**	0.07	0.21	0.66	0.07	1.00
UH	25.00	6.00	0.00	1.00	1.00	2.00		**0.00**	**0.00**	0.12	**0.03**	**0.00**
DM01	7.00	2.00	42.50	20.00	19.00	22.00	6.00		0.58	0.20	**0.02**	0.20
DM03	4.00	1.00	19.00	14.00	11.00	14.00	5.00	38.00		0.31	0.10	0.42
DM09	2.00	1.00	1.00	4.00	4.00	5.00	3.00	5.00	3.00		0.56	0.85
DM16	4.00	2.00	1.00	4.00	4.00	6.00	9.00	8.00	7.00	3.00		0.21
DM17	2.00	0.00	7.00	11.50	12.00	17.00	1.00	19.00	12.00	4.00	6.00	

[a] Significant values in bold.

Table 6
Pair-wise Mann-Whitney test results for $\delta^{18}O$ of different localities (number of samples below the locality name; U-values at lower left, *p*-values at upper right).[a]

U\p-value	Modern	Late Miocene						Middle Miocene			Early Miocene	Eocene?
		DM02	DM06	DM12	DM13	DM26	UH	DM01	DM03	DM09		DM17
	5	2	10	5	5	7	12	13	7	2	5	5
MODERN		0.33	**0.00**	**0.02**	**0.02**	**0.02**	0.07	**0.01**	0.07	0.18	**0.01**	**0.04**
DM02	2.00		**0.04**	0.08	0.08	0.06	0.08	**0.03**	0.11	0.25	0.08	0.08
DM06	0.00	0.00		0.76	0.71	0.92	0.08	0.34	0.73	0.91	0.24	**0.04**
DM12	1.00	0.00	22.00		1.00	0.75	0.13	0.38	0.42	0.85	1.00	0.21
DM13	1.00	0.00	21.50	12.00		0.75	0.13	0.30	0.75	0.85	0.68	0.14
DM26	3.00	0.00	33.50	15.00	15.00		0.22	0.75	1.00	0.88	0.26	0.26
UH	12.00	2.00	33.00	15.00	15.00	27.00		0.29	0.29	0.41	**0.01**	0.96
DM01	6.00	0.00	49.00	23.00	21.50	41.00	58.00		0.97	0.93	0.15	0.32
DM03	6.00	1.00	31.00	12.00	15.00	24.00	29.00	42.00		0.88	0.63	0.33
DM09	1.00	0.00	10.00	4.00	5.00	7.00	7.00	11.00	7.00		0.85	0.85
DM16	0.00	0.00	15.00	12.00	10.00	10.00	4.00	16.00	14.00	4.00		**0.01**
DM17	2.00	0.00	8.00	6.00	5.00	10.00	29.00	20.00	11.00	4.00	0.00	

[a] Significant values in bold.

other. However, all other pairs of localities were significantly different from each other (Table 8). Unlike any other locality type studied, precipitation at pliopithecoid localities was constant throughout their temporal range (Fig. 3).

Closer inspection of the MAP results for Chinese MNEQ06-09 localities revealed that non-primate localities had the widest range, from 200 to 2300 mm. Pliopithecoid localities had the second widest range, between 1300 and 2300 mm. However, only one hominoid locality qualified for the analysis and it had a MAP of about 2000 mm. No cercopithecoid localities qualified for the analyses. The MAP for DM01 is about 1300 mm, which is the lowest of all pliopithecid localities in Asia, but higher than most Tunggur localities and the other two Damiao localities (Table 2).

3.2. Faunal similarity

Results of the faunal similarity analyses are given in Tables 9–12. Tunggurian localities are dominated by grassland adapted small mammals such as Erinaceidae (*Mioechinus*), Dipodidae (*Heterosminthus* and *Protalactaga*), Ochotonidae (*Alloptox*, *Bellatona*, and *Desmatolagus*), and Cricetidae with high crowned teeth (*Gobicricetodon* and *Plesiodipus*). Small mammals in DM01 are similar to Tunggur. Aquatic species in both Tunggur and Damiao are represented by Castoridae. DM01 is most similar to Tunggur localities, especially Tunggur-Moergen. Of primate localities, DM01 was most similar to the Junggar-Tieersihabahe pliopithecid locality from northwestern China when the large mammal fauna was studied.

Small mammals from Junggar-Tieersihabahe were too scarce to allow the locality to be analysed. Principal coordinates analysis plots for small mammals (Fig. 4) showed one group and few outliers, with DM01 grouping closely with Tunggur localities. When large mammal similarity was inspected (Fig. 5), DM01 grouped with DM02 and most Junggar localities, including another pliopithecoid locality, Junggar-Tieersihabahe. Other pliopithecoid localities formed their own group (Tongxin localities and Hezheng-Laogou).

3.3. Isotopes

Early Miocene fossils (11 samples) had $\delta^{13}C$ values ranging from −10.9‰ to −7.3‰, with an average of −8.5 ± 1.0‰ (±values are 1σ [standard deviation]), and $\delta^{18}O$ values ranging between −11.1‰ and −1.9‰ (Fig. 6, Table 1). Middle Miocene localities (22 samples) had lower averages than the early Miocene for carbon and oxygen, −10.0‰ and −7.9‰, respectively. The ranges were also larger, $\delta^{13}C$ from −13.4‰ to −7.2‰ and $\delta^{18}O$ from −11.8‰ to −0.1‰. The average of $\delta^{13}C$ for late Miocene localities (41 samples) was −8.7 ± 1.9‰ with a range from −11.9‰ to −4.5‰. However, the range for late Miocene localities was from −11.9‰ to −7.3‰, with an average of −9.6 ± 1.5‰ when the latest Miocene locality of UH Museum was excluded. $\delta^{18}O$ values ranged between −13.1‰ and −0.0‰, both with and without the latest Miocene locality, however the average was −7.8 ± 3.2‰ with UH Museum and −8.4 ± 2.9‰ without it. The modern sample (five
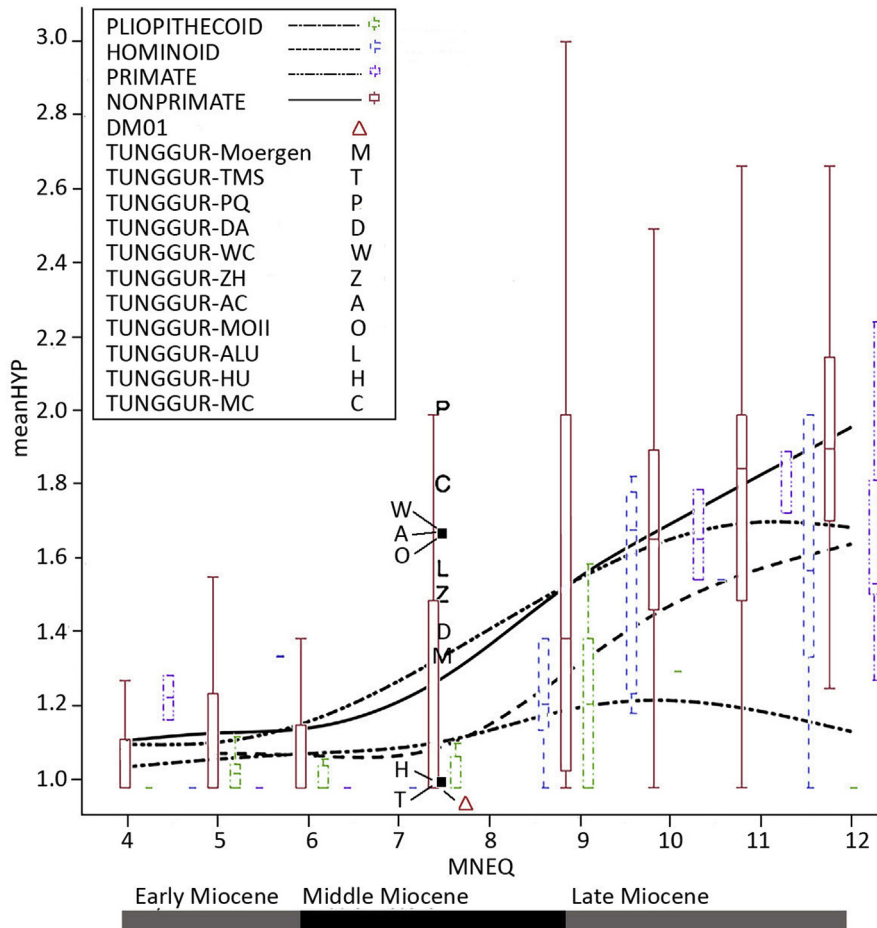
Figure 2. Mean hypsodonty curves from different types of fossil localities at different MNEQ intervals (smoothing spline fit with λ = 10). DM01 and Tunggur localities plotted individually.

specimens) had a range of δ^{13}C between −8.9‰ and −5.7‰, averaging −7.2 ± 1.4‰, and δ^{18}O values between −7.1‰ and −0.4‰, with an average of −3.0 ± 2.8‰. The mean δ^{13}C value for modern mammals was higher than values observed for Miocene localities, although artiodactyls from the latest Miocene UH Museum locality had higher average δ^{13}C than the modern artiodactyl samples. The mean δ^{18}O value for the modern sample was high, but not the highest. The isotope results (Fig. 6) are shown separately for Artiodactyla and Proboscidea, and two families of Perissodactyla (i.e., Equidae and Rhinocerotidae). A pair-wise Mann-Whitney test showed little difference in δ^{13}C values between the groups, with only Artiodactyla and Rhinocerotidae being significantly different from each other (Table 3). δ^{18}O values separated Artiodactyla from both Rhinocerotidae and Equidae with statistical significance (Table 4).

Table 7
Mann–Whitney pair-wise test results for Mean Hypsodonty at different locality types (U-values at lower left, p-values at upper right).[a]

U\ p-value	Cercopithecoid	Hominoid	Non-primate	Pliopithecoid
Cercopithecoid		0.00	0.00	0.00
Hominoid	268.50		0.11	**0.00**
Non-primate	4481.00	10598.00		**0.00**
Pliopithecoid	77.00	823.50	7975.50	

[a] Significant values in bold.

4. Discussion

Situated ~200 km northeast of Damiao, the Tunggur area has several localities that seem to have had similar environmental conditions as the Damiao primate locality, implying suitability for pliopithecids even though no primate fossils have been found (Wang et al., 2003; Zhang et al., 2009). Undersampling is a possibility, though an unlikely explanation for the absence of primate fossils at Tunggur given the large collection of fossils from this site. The Tunggur-Moergen locality in particular seems to have had favourable conditions for pliopithecoids, with the highest combined faunal similarity to Damiao (Tables 9 and 10), similar estimated MAP, and comparable δ^{13}C values (Zhang et al., 2009). However, on average, estimated MAP in Tunggur is lower than in DM01.

During the Miocene, the estimated MAP for different types of localities show a high and stable pattern for pliopithecoid localities with only minor fluctuations through time. Similarly high estimated MAP values for hominoid localities are observed, although towards the end of the Miocene there is clear distinction from the pliopithecoid localities (Fig. 3). Even if pliopithecoid localities cannot be distinguished from hominoid localities with standard statistical significance, it is evident based on our results that hominoid species were more adaptable to the progressively drying Miocene environment. When only Chinese MNEQ06-09 localities are examined, most primate localities are missing from the analysis and meaningful comparisons are not possible. However, several
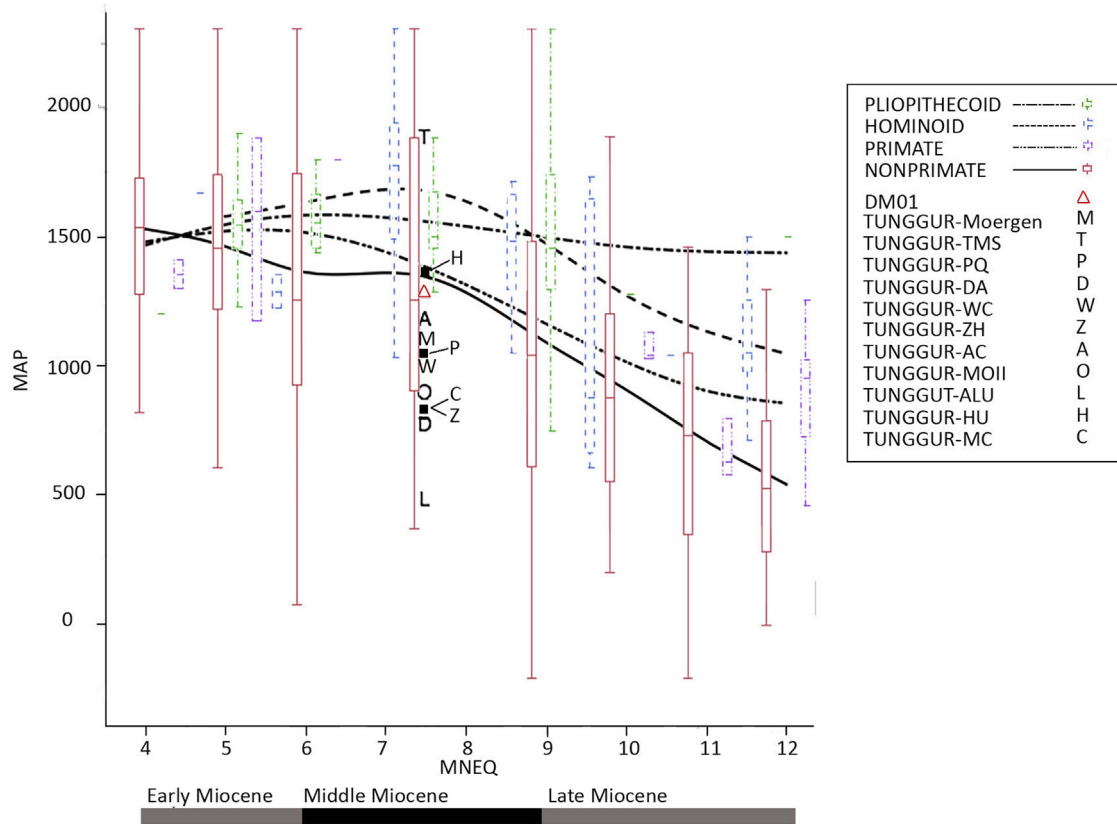
Figure 3. Mean annual precipitation curves from different types of fossil localities at different MNEQ intervals (smoothing spline fit with λ = 10). DM01 and Tunggur localities plotted individually (smoothing spline fit with λ = 10).

Table 8
Mann−Whitney pair-wise test results for predicted mean annual precipitation (MAP) at different locality types (U-values at lower left, *p*-values at upper right).[a]

U\p-value	Cercopithecoid	Hominoid	Non-primate	Pliopithecoid
Cercopithecoid		0.00	0.04	0.00
Hominoid	175.50		**0.00**	0.23
Non-primate	5083.50	8053.00		**0.00**
Pliopithecoid	34.50	1118.00	6983.00	

[a] Significant values in bold.

Table 9
Simpson similarity indices for large mammal faunas from Chinese localities within MNEQ06-09 compared to DM01 locality.

	Locality type[a]	DM01
DM01	PLIO	—
DM02	NONPRIM	1
Hezheng-laogou	PLIO	0.25
Jiulongkou	NONPRIM	0.25
Junggar-Botamoyin	NONPRIM	0.25
Junggar-Tieersihabahe	PLIO	0.5
Tairum Nor	NONPRIM	0.25
Tongxin	PLIO	0.25
Tongxin-dingjiaergou	NONPRIM	0.25
Junggar-duolebulejin	NONPRIM	0.25
Lintong-lengshuigou	NONPRIM	0.25
Tunggur-ALU	NONPRIM	0.5
Tunggur-HU	NONPRIM	0.5
Tunggur-ZH	NONPRIM	0.25
Tunggur-Moergen	NONPRIM	0.75
Tunggur-WC	NONPRIM	0

[a] NONPRIM = locality with no primates, PLIO = locality with pliopithecoids.

Table 10
Simpson similarity indices for small mammal faunas from Chinese localities within MNEQ06-09 compared to DM01 locality.

	Localiy type[a]	DM01
DM01	PLIO	—
DM02	NONPRIM	0.55
Sunite-Chagannuoer	NONPRIM	0.67
Tairum Nor	NONPRIM	0.44
Junggar_dingshanyanchi_XJ20061	NONPRIM	0.46
Junggar_dingshanyanchi	NONPRIM	0.43
Lanzhou-Quantougou	NONPRIM	0.43
Tunggur-482	NONPRIM	0.63
Tunggur-MOII	NONPRIM	0.76
Tunggur-MOV	NONPRIM	0.73
Tunggur-TLR	NONPRIM	0.55
Tunggur-TUR	NONPRIM	0.65
Tunggur-Moergen	NONPRIM	0.82

[a] NONPRIM = locality with no primates, PLIO = locality with pliopithecoids.

pliopithecoid localities are present and it can be seen that DM01 is the driest of them, but still with higher estimated MAP than most Tunggur localities regardless of the method used (Table 2). Nonetheless, both Tunggur-HU and Tunggur-TMS have a similar or higher estimated MAP than DM01, similar to other Chinese pliopithecoid localities. Mean annual precipitation values are estimates with fairly large standard error (see discussion in Eronen et al., [2010a] and Liu et al., [2012]). At regional scales, they are best understood as indicating relative difference between localities, not as absolute estimates of precipitation.

The faunal similarity between DM01 and Tunggur-HU is also high when large mammals are considered, although not as high as between DM01 and Tunggur-Moergen. Tunggur-TMS, on the other

Table 11
Large mammal fauna at Damiao and Tunggur (0 = absence, 1 = presence).

	DM 01	DM16	DM02	Tunggur-ALU	Tunggur-DA	Tunggur-HU	Tunggur-MC	Tunggur-MOII	Tunggur-PQ	Tunggur-TMS	Tunggur-ZH	Tunggur-AC	Tunggur-Moergen	Tunggur-WC
Acerorhinus	0	0	0	1	0	0	1	0	0	1	0	0	1	1
Aelurocyon	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphicyon	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Anchitherium	0	0	0	0	0	1	0	0	0	0	0	1	1	1
Chalicotherium	0	0	0	0	0	1	0	0	0	0	0	0	1	1
Dicrocerus	0	0	0	1	1	1	1	1	0	0	0	0	1	0
Euprox	1	0	1	1	0	1	0	0	0	0	0	0	1	0
Gobicyon	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Hispanotherium	0	0	0	0	0	0	1	0	1	0	0	0	1	1
Kubanochoerus	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Lagomeryx	0	1	0	0	0	1	0	0	0	0	1	0	1	0
Leptarctus	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Listriodon	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Martes	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Melodon	0	0	0	0	0	1	1	0	0	0	1	0	1	0
Metacervulus	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Metailurus	0	0	0	0	0	1	0	0	0	0	0	0	1	1
Micromeryx	1	1	1	0	1	0	0	0	0	0	0	0	1	0
Mionictis	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Palaeotragus	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Percrocuta	0	0	0	1	0	0	0	0	0	0	0	1	1	1
Platybelodon	0	0	0	0	1	1	1	1	1	1	0	1	1	1
Pliopithecus	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Plithocyon	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Pseudarctos	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Sansanosmilus	0	0	0	1	0	0	0	0	1	0	0	0	1	0
Serridentinus	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Stephanocemas	1	1	1	1	1	1	0	0	0	0	1	0	1	0
Sthenictis	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Tungurictis	0	0	0	1	0	1	0	0	0	1	0	0	1	1
Turcocerus	0	0	0	1	1	0	1	1	0	0	1	1	1	1
Zygolophodon	0	0	0	0	0	1	0	0	0	0	0	0	1	0

Table 12
Small mammal fauna at Damiao and Tunggur (0 = presence, 1 = absence).

	DM01	DM16	DM02	Tunggur-482	Tunggur-HU	Tunggur-MOII	Tunggur-MOV	Tunggur-TLR	Tunggur-TUR	Tunggur-AC	Tunggur-Moergen	Tunggur-Tamuqin	Tunggur-WC
Alloptox	0	0	1	1	0	1	1	1	1	0	1	0	0
Anchitheriomys	0	0	0	0	1	0	0	0	0	0	1	0	0
Ansomys	1	0	0	0	0	0	1	0	1	0	1	0	0
Atelerix	0	0	0	0	0	0	0	0	0	0	1	0	0
Atlantoxerus	1	0	0	1	0	1	0	1	1	0	1	0	0
Bellatona	1	0	1	1	0	1	1	1	1	1	1	1	0
Democricetodon	1	0	0	0	0	1	1	0	0	0	1	0	0
Desmanella	1	0	0	0	0	1	0	0	0	0	1	0	0
Desmatolagus	1	0	1	1	0	1	0	1	0	0	1	0	0
Distylomys	0	1	0	0	0	0	0	1	0	0	0	0	0
Eozapus	0	0	1	0	0	0	0	0	0	0	0	0	0
Eucastor	1	0	0	0	0	0	0	0	0	0	0	0	0
Eutamias	1	0	0	0	0	1	1	0	1	0	1	0	0
Gobicricetodon	1	0	1	0	1	1	1	1	1	0	1	1	0
Heterosminthus	1	1	0	1	1	1	1	1	1	0	1	0	1
Hystricops	0	0	0	0	0	0	0	0	0	1	0	0	0
Keramidomys	1	0	0	0	0	1	0	0	1	0	1	0	0
Kherem	0	1	0	0	0	0	0	0	0	0	0	0	0
Leptodontomys	1	0	0	0	0	1	0	0	1	0	1	0	0
Lophocricetus	0	0	1	0	0	0	0	0	0	0	0	0	0
Megacricetodon	0	0	0	1	0	1	1	1	1	0	1	0	0
Metexallerix	0	1	0	0	0	0	0	0	0	0	0	0	0
Microdyromys	1	0	0	0	0	1	0	0	1	0	1	0	0
Mioechinus	1	0	1	1	0	1	1	1	1	0	1	0	0
Mongolosorex	0	0	0	0	0	1	0	0	1	0	1	0	0
Monosaulax	0	0	0	0	1	1	0	0	0	1	0	0	0
Nannocricetus	0	0	1	0	0	0	0	0	0	0	0	0	0
Ochotona	1	0	1	0	0	0	0	0	0	0	0	0	0
Plesiodipus	1	0	0	0	0	1	1	1	1	0	1	1	1
Plesiosminthus	0	1	0	0	0	0	0	0	0	0	0	0	0
Prodistylomys	0	1	0	0	0	0	0	0	0	0	0	0	0
Proscapanus	0	0	0	0	0	1	0	0	1	0	1	0	0
Prosiphneus	1	0	1	0	0	0	0	0	0	0	0	0	0
Protalactaga	1	0	1	1	0	1	1	0	1	0	1	0	0
Pseudotheridomys	0	1	0	0	0	0	0	0	0	0	0	0	0
Quyania	0	0	0	0	0	1	0	0	0	0	1	0	0
Sinodonomys	0	1	0	0	0	0	0	0	0	0	0	0	0
Sinolagomys	0	1	0	0	0	0	0	0	0	0	0	0	0
Sinotamias	0	0	0	0	0	1	0	0	1	0	1	0	0
Steneofiber	1	0	0	0	0	0	0	0	0	0	0	1	0
Tachyoryctoides	0	1	0	0	0	0	0	1	0	0	0	0	0
Trogontherium	0	0	0	0	0	0	0	0	0	0	1	0	0
Yanshuella	0	0	0	0	0	1	0	0	1	0	1	0	0

Figure 4. Principal coordinates analysis plot of faunal similarity based on Simpson index for large mammals.

hand, shares no large mammals with DM01. Small mammals from Tunggur-TMS and Tunggur-HU localities are too scarce to be included in the analyses. Interestingly, comparing MAP estimates of DM01 with the older DM16 and younger DM02 suggests that the area was more humid during pliopithecoid occupancy than before or after. When small mammal similarity data are inspected using principal coordinates analysis, the Damiao pliopithecoid locality groups with the Tunggur localities and the DM02 locality is separated from all localities (Fig. 4). Principal coordinates analysis of large mammal similarity data shows grouping of the two Damiao localities, DM01 and DM02, with most of the Junggar localities, of which one is a pliopithecoid locality, Junggar-Tieersihabahe (Fig. 5). The other Chinese pliopithecoid localities are grouped together, not surprisingly as they are of the same age (MNEQ06) and geographically closely positioned to each other.

Large mammals in Damiao indicate relatively stable environmental conditions through the Miocene, with cervoids the dominant group. This precludes the inference of widespread grassland or desert environments for Damiao localities (Kaakinen et al., 2015). DM01 is dominated by forest and woodland adapted large mammals, like Cervidae (*Stephanocemas* and *Euprox*), Moschidae (*Micromeryx*), Proboscidea (gen. et sp. indet.), and Pliopithecidae (gen. et sp. indet.), indicating a warm and humid environment (Zhang and Harrison, 2008; Wang and Zhang, 2011; Kaakinen et al., 2015).

The small mammals at both Damiao and Tunggur, on the other hand, are dominated by grassland adapted taxa with some castorids indicating the presence of water (Table 12). The occurrence of dipodids and ochotonids together with Sciuridae (*Atlantoxerus*) may indicate a semidesert environment, as suggested for Tunggur (Qiu, 1996). Small mammal remains at Damiao were apparently

accumulated by predators and were deposited in a fluvial environment (Sukselainen et al., 2017). These predators were mainly avian and, even though they are often known to hunt outside their preferred habitats, they rarely forage far (e.g., Hardey et al., 2009 and references therein). This suggests that the Damiao small mammals occupied habitats that were located close to the site of deposition. The taphonomy at Tunggur is not known. However, since predators are one of the main agents of small mammal accumulations (e.g., Andrews and Evans, 1983; Andrews, 1990; Fernandez-Jalvo, 1996; Reed and Denys, 2011), it is likely that predation contributed to the small mammal fossil accumulations at Tunggur as well.

The isotope data from 12 Damiao localities show variation in $\delta^{13}C$ values between −4.5 and −13.4‰, indicating that large herbivorous mammals in Damiao were predominantly feeding on C3 plants or water stressed C3 plants, while no pure C4 diets were consumed, similar to Tunggur (see Zhang et al., 2009). All of the $\delta^{13}C$ values higher than −7‰ are from the latest Miocene locality of UH Museum, suggesting that C4 vegetation was not a significant part of the diet of herbivores at Damiao until the latest Miocene. The presence of C4 vegetation at the latest Miocene UH Museum site also fits the latitudinal profile of northward increasing $\delta^{13}C$ values during the late Miocene (Passey et al., 2009), showing that environments to the north were more open. This is consistent with other studies from central Inner Mongolia (Zhang et al., 2009), where the onset of C4 expansion has been dated to the late Miocene. However, in some cases, the samples reach the higher limits of a pure C3 diet indicating either the presence of a small fraction of C4 vegetation or water stressed conditions with C3 plants displaying higher $\delta^{13}C$ values (Farquhar et al., 1989; Cerling et al., 1997; Wang et al., 2008). Variation between taxa in their
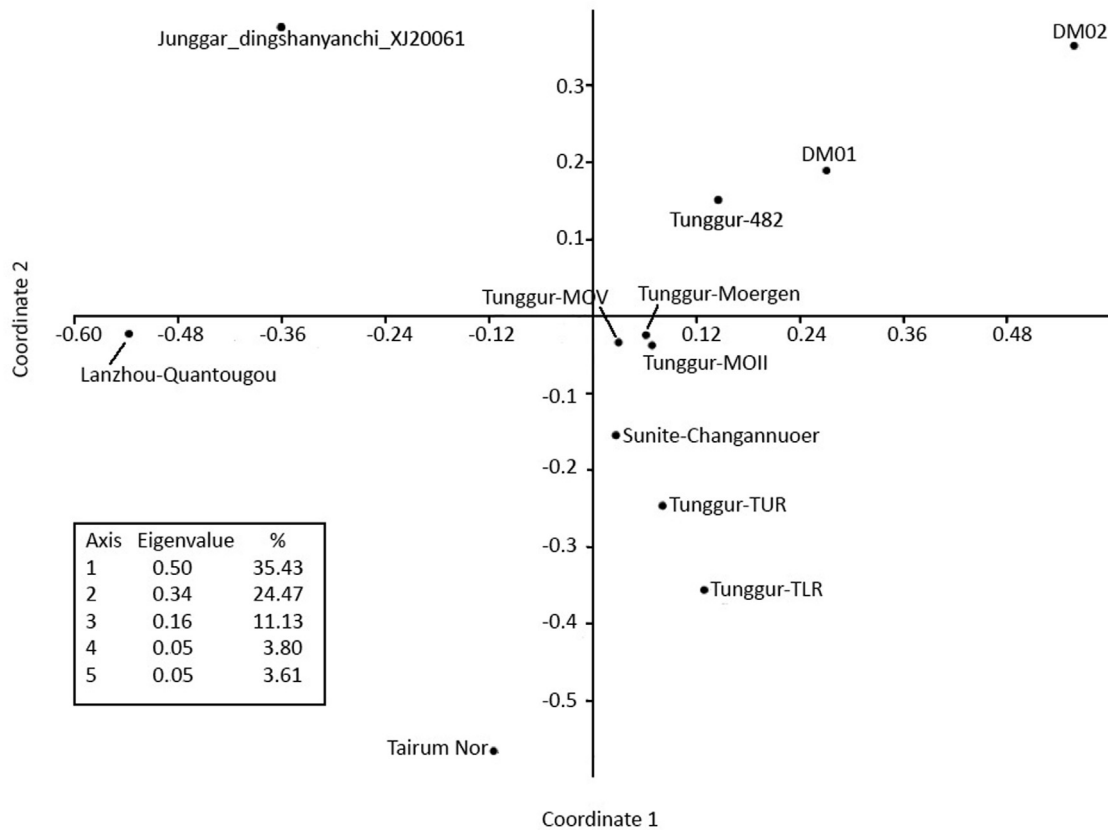
Figure 5. Principal coordinates analysis plot of faunal similarity based on Simpson index for small mammals.

δ^{13}C composition might imply mixed habitats, with lower δ^{13}C values suggesting forests and higher values suggesting grasslands. However, the differences between herbivore groups were not statistically significant, except for Artiodactyla and Rhinocerotidae. As the isotopic signature of most species was similar, this may indicate similar conditions and habitat preferences. Out of all the Damiao localities, the primate-bearing DM01 has the lowest δ^{13}C values, indicating the most humid relative conditions, but likely with locally a mixed habitat indicated by the wide range of δ^{13}C values. However, DM01 is statistically significantly different only from early Miocene DM16, late Miocene UH Museum, and the modern sample (Table 5).

The wide range of δ^{18}O values for DM01 and other middle Miocene localities at Damiao may indicate seasonal aridity, with high values of δ^{18}O indicating more arid conditions and low values suggesting more humid conditions (Sternberg et al., 1989; Quade et al., 1995; Cerling et al., 2004; Feranec and MacFadden, 2006). The highest values of δ^{18}O are seen in Artiodactyla, possibly because they were the most water independent, able to subsist on water in plants in times of seasonal aridity, as are several species today (e.g., Western, 1975; Braun, 1999a, b, c). In oxygen isotopic composition, Artiodactyla are significantly different from both Equidae and Rhinocerotidae, but not Proboscidea, which consists of only two samples (Table 4). Indeed, oxygen isotope data provide the most meaningful information when normalized to contemporaneous meteoric water isotopic compositions, with greater deviations of enamel δ^{18}O relative to meteoric water ($=$ higher absolute values of δ^{18}O) being closely correlated with measures of environmental aridity such as PET $-$ MAP (potential evapotranspiration minus mean annual precipitation; Levin et al., 2006). We do not have estimates of δ^{18}O contemporaneous meteoric water for the different time horizons represented at Damiao, but if we assume

that δ^{18}O was constant through time, we can interpret δ^{18}O values directly as measures of aridity, with higher values indicating more arid conditions. Under this rubric, and restricting the analysis to Artiodactyls with $N \geq 2$ (as there is significant taxon-specific patterning in δ^{18}O data), the more arid intervals are modern, UH Museum (latest Miocene), and DM02 (early late Miocene), whereas the more humid intervals are DM01 and DM03 (middle Miocene), as well as DM26 (late Miocene). These interpretations are preliminary only, and larger and more uniform sample sizes across different taxa at each locality will be necessary for more conclusive estimates of past aridity based on δ^{18}O, as well as independent estimates of δ^{18}O of meteoric water for each locality.

The sedimentological data from the Damiao sequence suggest well-drained floodplains and groundwater evaporation, as evidenced by abundant red-brown fine grained deposits with concentrations of nodular carbonates. Abundant goethite and manganese staining in the stacked carbonate nodule conglomerate at DM01 point to periodic wetting and drying of sediments (cf. Kraus and Hasiotis, 2006), suggesting relatively humid conditions locally. The abraded soil nodule clasts, however, arise from the reworking of underlying overbank deposits, indicating that climate was seasonally dry (cf. Van Itterbeeck et al., 2007; Kaakinen et al., 2015).

The presence of pliopithecoids, a clade that favours humid environments, in central Asia after the middle Miocene climatic optimum seems incompatible with a trend of strengthening of climatic zones and increased aridification at mid-latitudes in wide areas since the early Miocene (Kaakinen et al., 2015). It is, however, consistent with the hypsodonty and estimated MAP values suggesting more humid and possibly more wooded environments for the DM01 pliopithecoid locality. Evidence for warm and humid environments for DM01 also includes the presence of an
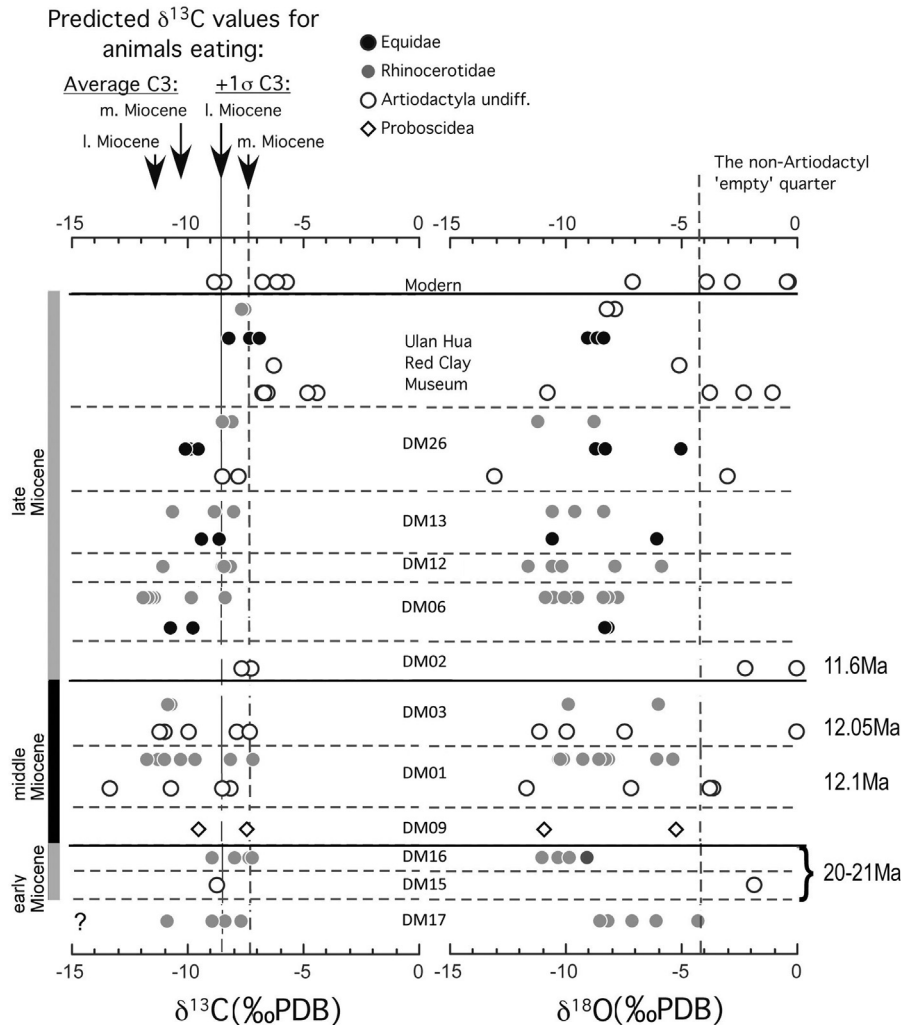
Figure 6. Carbon and oxygen isotope values for Damiao fossil localities and a modern sample. All known palaeomagnetic ages for the individual localities are shown on the right column. (? = Eocene locality). The predicted δ13C values for pure C3 diets (vertical dashed lines in the δ 13C plot) are based on Passey et al. (2002, 2009). The vertical dashed line in the δ 18O plot shows the highest δ 18O value observed for a non-artiodactyl, highlighting the high δ 18O space (right of the dashed line) that is the exclusive domain of artiodactyls.

anchitheriine horse and the cervid *Euprox altus*, as well as the occurrence of abundant goethite and manganese staining commonly attributed to impeded drainage (Kaakinen et al., 2015). Regional interpretation of large mammal proxy data by Liu et al. (2009) supports this scenario by providing evidence of humid areas in the northern parts of China, while a distinctive dry belt developed in the mid-latitudes. The isotopic evidence does not support constantly humid environments, but is compatible with a scenario of a more humid climate with a pronounced dry season or a generally semi-arid habitat with heavily vegetated belts around permanent waterways. Seasonally dry climate may also be inferred from the reworked pedogenic nodules in the DM01 conglomerates (Van Itterbeeck et al., 2007; Kaakinen et al., 2015).

5. Conclusions

Our analyses of the palaeoecology of the late middle Miocene pliopithecoid locality DM01 support previous inferences concerning the presence of locally humid environments within the increasingly arid surroundings that characterized Central Asia. Hypsodonty and estimated MAP, combined with local sedimentology and the species composition of large mammals, suggest more humid and possibly more forested and wooded environments

for DM01. However, the small mammal fauna and isotope data are consistent with a mosaic of forest and grassland environment for all Damiao localities.

Based on the results presented here, Tunggur may have been too seasonal or not sufficiently humid for pliopithecoids. This inference is supported by the higher mean hypsodonty and lower estimated MAP values, as well as the slightly higher δ13C values. We conclude that DM01, the driest known Asian pliopithecoid locality, may have been a more humid refugium within a generally drier regional setting, similar to some of the latest Miocene hominoid localities of western Asia (Kaya et al., 2016; Mirzaie Ataabadi et al., 2016). Although previous research indicates that pliopithecoids favoured humid environments (Eronen and Rook, 2004; Sukselainen et al., 2015), our analyses of the Damiao locality suggest that they could tolerate some level of seasonal dryness.

Supplementary Online Material

Supplementary online material related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2017.03.014.

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