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DIETARY ADAPTATIONS AND PALAEOECOLOGY OF LOPHIALETIDAE (MAMMALIA, TAPIROIDEA) FROM THE EOCENE OF THE ERLIAN BASIN, CHINA: COMBINED EVIDENCE FROM MESOWEAR AND STABLE ISOTOPE ANALYSES

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Abstract: Lophialetidae is an extinct group of endemic Asiatic tapiroids that are widely distributed in the Eocene sediments of Asia. *Schlosseria magister* and *Lophialetes expeditus* are the most abundant species in this family. However, their dietary and ecological characteristics are largely unknown. For the first time, we reconstruct the palaeodiet and habitat of these two lophialetids using a combination of mesowear and stable carbon isotope analysis of fossil teeth excavated from the Erlian Basin, China. Mesowear analysis (n = 141) suggests that the dietary structure of *S. magister* and *L. expeditus* shifted from less to more abrasive diets from ~52 to ~42 Ma. Stable carbon isotope analysis (n = 137) suggests that the habitats of *S. magister* and *L. expeditus* became drier and/or more open through time. The dietary shifts of the two lophialetids are consistent with evident changes in habitat. The changes in the diet and habitat were probably related to global climate change during that time period. The gradual drop in global temperatures during the early–middle Eocene led to a drier and more open terrestrial ecosystem in the Erlian Basin, probably resulting in changes in floral composition of the environment inhabited by *S. magister* and *L. expeditus*. Hence, herbivores highly susceptible to vegetation modification had to develop new resource exploitation strategies to adapt to these changes. *Schlosseria magister*, considered to be the sister-group of *L. expeditus* and with a low level of ecological flexibility, was unable to adapt to the habitat changes finally becoming extinct at ~45 Ma.

Key words: Inner Mongolia, ungulate, palaeodiet, palaeoecology, mesowear, stable carbon isotope.

RECONSTRUCTING the palaeodiet of extinct animals is a significant aspect in the study of vertebrate palaeontology. It aids in understanding the ecology of a certain geological time period, and identifying the habitat of extinct species. Meanwhile, it can reveal the dietary adaptation and foraging behaviour of fossil groups in the process of evolution, thus providing significant information for elucidating the relationship between the evolution of terrestrial mammals and palaeoenvironmental changes (Fortelius & Solounias 2000; Kaiser *et al.* 2000; Schulz *et al.* 2007; Solounias *et al.* 2010; DeMiguel *et al.* 2011; Strani *et al.* 2018). In order to obtain palaeodiet information for various fossil groups, a variety of dietary analysis methods have been proposed and applied, including dental wear analysis (e.g. Fortelius & Solounias 2000; Kaiser *et al.* 2000; Solounias & Semprebon 2002), stable carbon and oxygen isotope analyses (e.g. Cerling *et al.* 1997; Wang *et al.* 2008*a*; Zazzo *et al.* 2010;), hypsodonty index analysis (e.g. Janis 1988; Jernvall & Fortelius 2002; Damuth & Janis 2011), premaxillary shape analysis (e.g.

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Solounias *et al.* 1988; Solounias & Moelleken 1994; Dompierre & Churcher 1996), masticatory morphology analysis (e.g. Solounias *et al.* 1995; Solounias & Moelleken 1999) and dental calculus analysis (e.g. Power *et al.* 2015; Chen *et al.* 2018). In general, multi-proxy approaches (using two or three analytical techniques) are frequently used to reconstruct the palaeodiet of a species, to obtain more reliable and detailed dietary information. For specific research materials (fossil teeth), multi-proxy approaches combining dental wear (including microwear and mesowear) analysis and stable isotope analysis has been used widely in the past few years (e.g. Rivals *et al.* 2014; Kubo *et al.* 2015; Jones & Desantis 2017).

The Mongolian Plateau has attracted the interest of many palaeontologists and geologists, as one of the most significant regions in the world for Palaeogene vertebrate palaeontological and stratigraphical research (Wang *et al.* 2010). The Palaeogene Asian Land Mammal Ages (ALMA) are based mainly on the mammalian faunas discovered in this region (particularly the Erlian Basin), because of well-exposed Palaeogene strata and abundant mammalian fossils (Wang *et al.* 2010, 2019). The Eocene mammalian faunas of the Erlian Basin are dominated by diverse perissodactyls (Tapiroidea, Rhinocerotoidea, Brontotheriidae and Chalicotherioidea) (Tong *et al.* 1995; Wang *et al.* 2007; Bai *et al.* 2018). A large number of academic papers and monographs based on the abundant fossils from the Erlian Basin have contributed to our knowledge of the perissodactyls (Matthew & Granger 1926; Radinsky 1965; Qi 1987; Wang *et al.* 2008*b*, 2010; Bai *et al.* 2017, 2018). However, most previous research has concentrated on their morphology and biostratigraphy, and there has been a lack of studies related to palaeodiet, palaeoecology and palaeoclimate in the area. Based on analyses of the fossil mammal assemblages in the eastern Erlian Basin and other regions, Wang *et al.* (2010) suggested that the mammalian evolutionary pattern in the early Palaeogene appeared to be directly influenced by global environmental changes during that time. It is widely accepted that mammalian evolution on the Mongolian Plateau corresponded to and coevolved with global environmental changes represented by the mammalian fauna turnover (Meng & McKenna 1998; Wang *et al.* 2010). Global climate changes forced a turnover of the terrestrial flora, resulting in changes in faunal habitat. However, given the poor conditions of preservation, there is no palaeoecological evidence (e.g. palynology or palaeobotany) to test whether or not there was a floral turnover caused by global or regional environmental change during that period, and if that turnover impacted mammalian faunas.

Lophialetidae are endemic Asiatic tapiroids that were distributed widely in Asia during the Eocene (Matthew & Granger 1926; Radinsky 1965). Two extinct species, *Schlosseria magister* and *Lophialetes expeditus*, are the most abundant in this family with holotypes discovered in the Erlian Basin (Matthew & Granger 1926; Radinsky 1965). Our recent stratigraphic investigation confirms that the presence of *S. magister* at Huheboerhe is restricted to the Arshanto Formation (AS), and *L. expeditus* is present only in the Irdin Manha Formation (IM), suggesting that they can be used as index fossils (Li 2009; Li & Wang 2010). Traditionally, the two species are considered to be browsers on the basis of their brachydont cheek teeth, and were thought to inhabit dense forest. However, there is no convincing evidence to support this hypothesis.

In this study, we aim to reconstruct the diets and habitats of the two most abundant lophialetids *S. magister* and *L. expeditus* uncovered in the Huheboerhe area of the Erlian Basin, Inner Mongolia. We combined dental mesowear analysis and stable carbon isotope analysis to reconstruct and compare the diets and habitats of these two species and to address the following questions: (1) what are the dietary traits and habitats of *S. magister* and *L. expeditus*; (2) how did *S. magister* and *L. expeditus* adapt to the changing environment during the early–middle Eocene; and (3) what was the impact of global climate change on the diets and ecology of *S. magister* and *L. expeditus*?

GEOLOGICAL SETTING

The Erlian Basin (42°–44°N, 110°–114°E) is located in central Inner Mongolia, near the border of China and Mongolia (Fig. 1) (Jiang 1983; Wang *et al.* 2012*a*). Palaeogene deposits are well exposed in the Erlian Basin. Recently, Wang *et al.* (2010, 2012*a*, 2019) provided improved chronological data for several formations based on comprehensive investigations and comparisons between the new data and previous studies and archives. In the eastern part of the Erlian Basin, exposures of the lower Palaeogene are subdivided into three lithological units in ascending order: the Nomogen Formation (NM) mainly consisting of sandstones, muddy sandstones and sandy mudstones; the Arshanto Formation (AS) composed of red mudstones and siltstones; and the Irdin Manha Formation (IM) consisting of white sandy mudstones, sandstones and conglomerates (Meng *et al.* 2007; Wang *et al.* 2010). In the Huheboerhe area, these formations have been well-documented in a composite section that is based on four sections measured in the area (Fig. 2) (Meng *et al.* 2007; Wang *et al.* 2012*a*). Moreover, at least 12 mammal-bearing horizons are identified, including 4 in the Nomogen Formation (NM-1 to NM-4), six in the Arshanto Formation (AS-1 to AS-6), and two in the Irdin Manha Formation (IM-1 and IM-2) (Fig. 2) (Wang *et al.* 2010, 2012*a*), which are correlated to four Asian Palaeogene Land Mammal Ages (Gashatan,

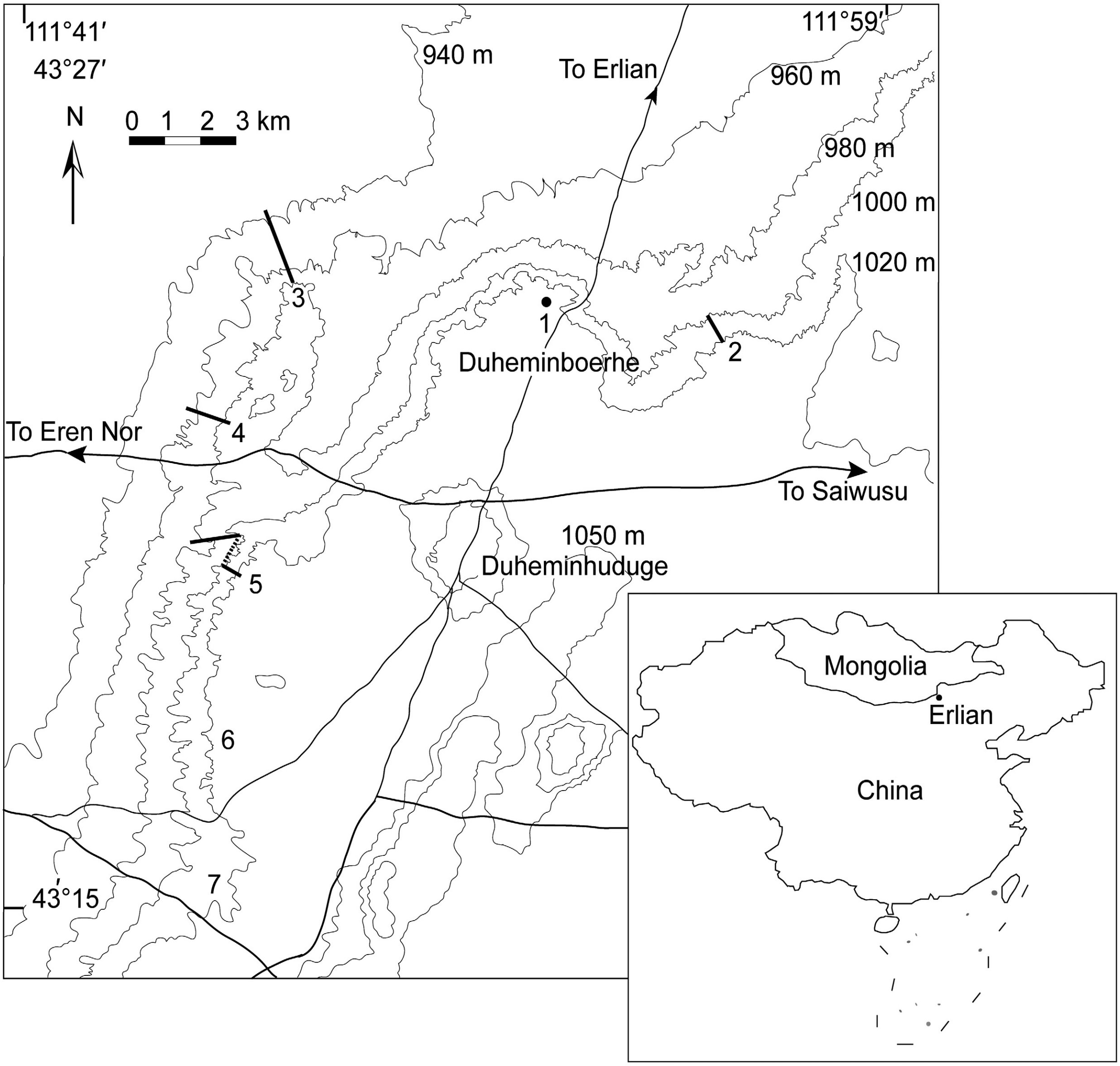

FIG. 1. Map showing the location and stratigraphic sections in the Huheboerhe area in the Erlian Basin, Nei Mongol (modified from Bai *et al.* 2017). 1, presumed location of Camp Margetts; 2, Daoteyin Obo (5 miles east of Camp Margetts); 3, Nuhetingboerhe (6 miles west of Camp Margetts); 4, Wulanboerhe; 5, Huheboerhe (7 miles south-west-by-west (235°) of Camp Margetts); 6, Chaganboerhe (10 miles south-west of Camp Margetts); 7, Jibuqilehasha.

Bumbanian, Arshantan and Irdinmanhan) (Wang *et al.* 2010). Wang *et al.* (2010, 2019) deduced the time frame for several formations including the temporal ranges of related land mammal ages according to the recent palaeomagnetic results in the Huheboerhe area and other related areas. Estimated numerical ages for the base of Irdin Manha Formation and Arshanto Formation are ~45 and ~52 Ma respectively (Fig. 2). The Arshanto Formation is early Eocene and middle Eocene, and the Irdin Manha Formation is middle Eocene in age.

MATERIAL AND METHOD

The Palaeogene deposits in the Huheboerhe area are rich in fossils of mammals, and a large number of specimens have been collected with detailed stratigraphical record during the field investigation in recent decades. The materials analysed in this study are fossil teeth of *S. magister* and *L. expeditus* unearthed from the Huheboerhe area of the Erlian Basin, Inner Mongolia. Unbroken upper second molars were selected for mesowear analysis.

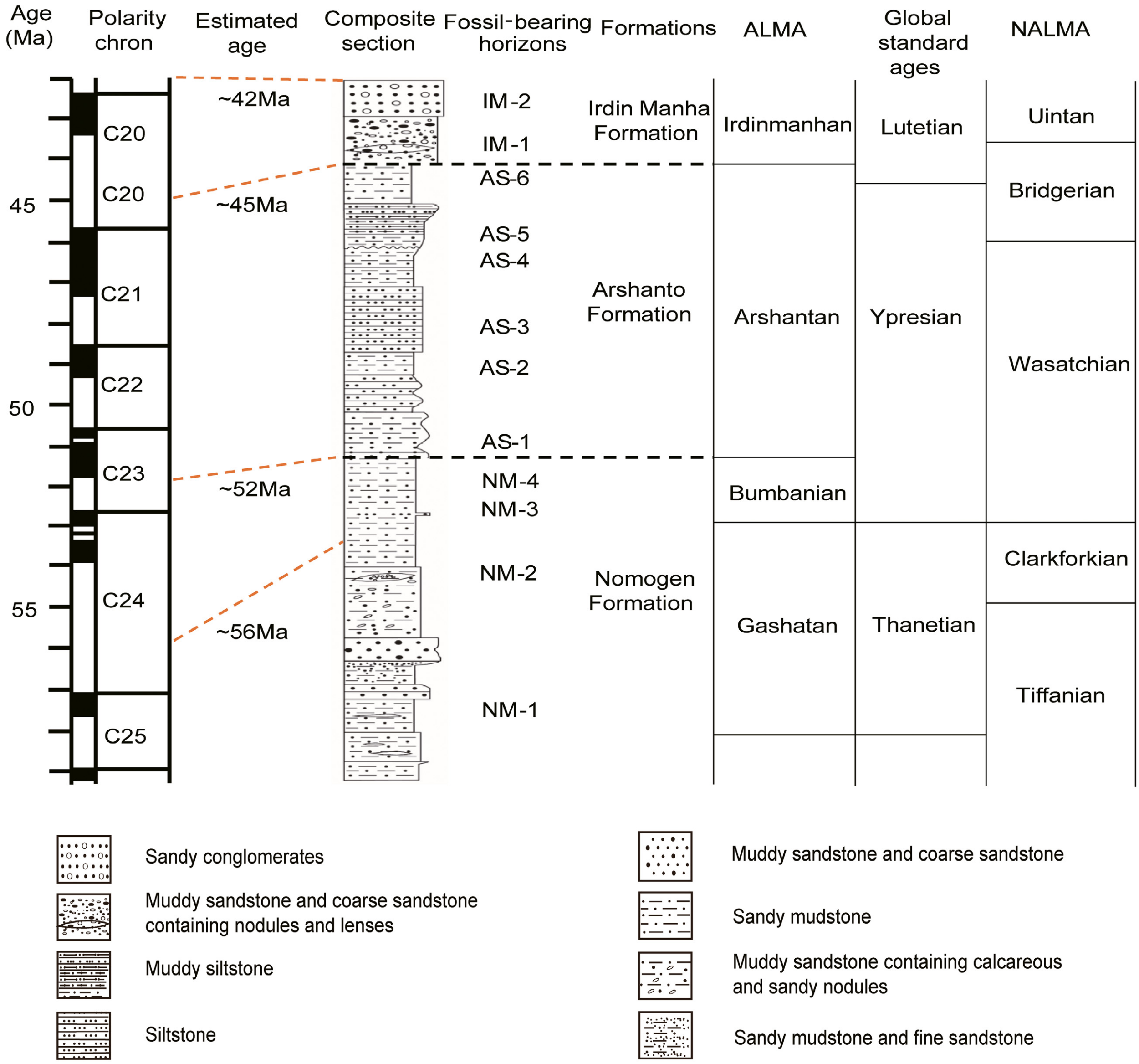

FIG. 2. Palaeogene stratigraphy, palaeomagnetic polarities, mammalian horizons and their correlation in the eastern Erlian Basin, China (modified from Wang *et al.* 2010, 2019). *Abbreviations*: ALMA, Asian Land Mammal Ages; NALMA, North American Land Mammal Age. Colour online.

Identifiable tooth fragments and some complete molars were selected for stable isotope analysis. Premolars and third molars were examined whenever possible to reduce the effects of pre-weaning diet on the δ^{13}C of the tooth enamel. Additional teeth from the same individual were excluded to the greatest possible extent to ensure that every tooth represents a different individual. The teeth covered by sandstone or mudstone were cleaned in a laboratory at the Institute of Vertebrate Palaeontology and Palaeoanthropology (IVPP), Chinese Academy of Sciences.

Tooth mesowear analysis

Mesowear analysis is a quantitative, robust and convenient method to reconstruct palaeodiet (Fortelius & Solounias 2000; Kaiser & Solounias 2003). It is based on the physical properties of ungulate foods as reflected in the relative amounts of attritive and abrasive wear that they cause on occlusal surface enamel (Fortelius & Solounias 2000; Rivals *et al.* 2007). Mesowear is observed and scored from the buccal side of upper molars, preferably the paracone of M2 (Fortelius & Solounias 2000; Rivals & Lister 2016).

Herbivorous mammals with low abrasion (high attrition) diets (e.g. browsers) usually maintain high relief and sharpened apices. Mammals with high abrasion (low attrition) diets (e.g. grazers) result in low relief occlusal surfaces, and blunted cusp apices. The diet of grazers consists of grasses containing more abrasive biogenic silica in the form of phytoliths as compared to tree leaves, resulting in heavy wear on a tooth (Fortelius & Solounias 2000; Saarinen *et al.* 2015; Cammidge 2017). It is important to note that low statured plants, or the parts of plants close to the ground, also are highly abrasive because exogeneous grits/sediments are included more often in the diet of mammals consuming these plants (Saarinen *et al.* 2015; Cammidge 2017). Moreover, dust and grit are more likely to adhere to plants growing in open and/or dry environments than those growing in closed and/or wet environments. Grazers and/or species in open habitats may ingest more abrasive matter than browsers and/or species in closed habitats. Teeth of mixed feeders having diets between grazers and browsers often exhibit moderate relief and rounded buccal cusp apices. Compared with dental microwear, which relates only to the last few meals, mesowear is more likely to reflect diet over an extended period of the individual's life (Danowitz *et al.* 2016). The time period can range approximately from weeks to years and is related to the overall rate of dental wear (Damuth & Janis 2011). When selecting the materials that could reflect the real diet of extinct species, as far as possible, unworn teeth (very young individuals), extremely worn teeth (very old individuals) and those with broken or damaged cusp apices should be excluded from mesowear analysis (Fortelius & Solounias 2000; Rivals & Lister 2016). Cusp sharpness is sensitive to ontogenetic age among young individuals (who have not yet developed substantial wear facets) and among dentally senescent individuals (Rivals & Lister 2016). However, for intermediate age groups which typically include the majority of individuals in a fossil collection, mesowear has been found to be less sensitive to age and more strongly related to diet (Rivals *et al.* 2007, Rivals & Lister 2016). Therefore, this method can offer a quantitative, robust and rapid estimation of the physical properties of ungulate foods, and has been applied widely to fossil teeth for palaeodietary reconstruction, and for palaeoecological and palaeoenvironmental analysis (Mihlbachler *et al.* 2011; Gong 2017).

We used the standard method introduced by Fortelius & Solounias (2000) to measure and evaluate the cusp shape and cusp relief (occlusal relief). Cusp shape is categorized as sharp (Fig. 3A), round (Fig. 3B), or blunt according to the referenced model. Cusp relief (Fig. 3C) is classified as high or low according to the cut off value provided by Fortelius & Solounias (2000). We used the following method to calculate mesowear score (Croft & Weinstein 2008): (1) 0 for an individual with high occlusal relief and sharp cusps; (2) 1 for an individual with high occlusal relief and round cusps; (3) 2 for an individual with low occlusal relief and round cusp; (4) 2.5 for an individual with low occlusal relief and sharp cusps; (5) 3 for an individual with high or low occlusal relief and blunt cusp. The study by Fortelius & Solounias (2000) suggested that the ideal sample size for mesowear analysis is between 10 and 30. However, the available sample size from the first and sixth fossil horizons of the Arshanto Formation is less than 10. Ultimately, we analysed 141 upper M2 for mesowear (*S. magister* from AS2, n = 40; *S. magister* from AS3, n = 13; *S. magister* from AS4, n = 10; *S. magister* from AS5, n = 31; *L. expeditus*, n = 47). The detailed mesowear data of individual sample are presented in Gong *et al.* (2019, appendix A).

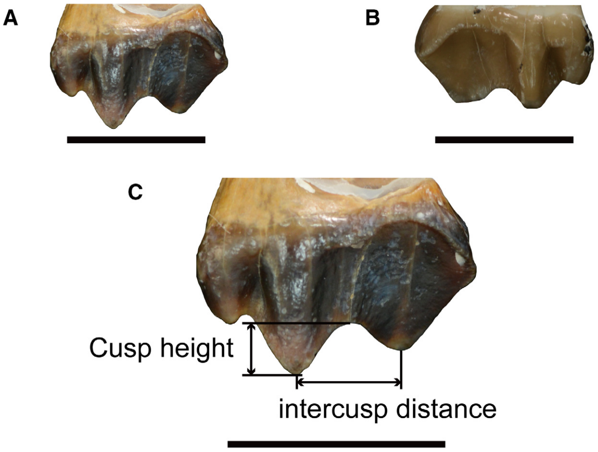

FIG. 3. Mesowear variables of *Schlosseria magister* (buccal view). Cusp shape was scored subjectively based on comparisons with extant mammals as: A, sharp; B, round. C, occlusal relief was measured as cusp height divided by intercusp distance. Scale bar represents 1 cm. Colour online.

Stable carbon isotope analysis

Stable carbon isotope analysis of fossil tooth enamel has been established as a valuable and robust tool for reconstructing palaeodiet of extinct ungulates and inferring palaeoecological information in terrestrial ecosystems (e.g. Koch 1998; Kohn & Cerling 2002; Wang *et al.* 2012*b*; Stacklyn *et al.* 2017; Bowman *et al.* 2017; Sun *et al.* 2019). Tooth enamel consists of apatite crystals which are densely packed and more resistant to diagenetic alteration. Therefore, it is considered to be the most suitable material for palaeodietary and palaeoecological reconstruction by stable isotopic analysis (Kolodny *et al.* 1983; Shemesh *et al.* 1988; Quade *et al.* 1992; Wang & Cerling 1994; Lecuyer *et al.*1999). According to the different photosynthetic pathways for carbon fixation (e.g. C_3 pathway and C_4 pathway) of terrestrial plants, most plants are typically categorized into C_3 plants (trees, forbs, most shrubs and cool season grasses) and C_4 plants (mostly warm-season grasses). Plants that utilize these two different photosynthetic pathways have very different stable carbon isotopic compositions. Modern C_3 plants have $\delta^{13}C$ values of $-20‰$ to $-35‰$, with an average of $-27‰$; and C_4 plants have $\delta^{13}C$ values ranging from $-9‰$ to $-17‰$, averaging $-13‰$ (O'Leary 1988; Farquhar *et al.* 1989; Cerling *et al.* 1997, 2004). The carbon isotope difference between C_3 plants and C_4 plants will be transferred into the tissues (e.g. bone and tooth enamel) of animals with further isotopic fractionation through the food chain (Wang *et al.* 2008*c*). Previous studies of modern mammals with known diet suggested that tooth enamel (structural carbonate in hydroxyapatite) is enriched in the heavy carbon isotope ^{13}C by ~13–14‰ relative to the diet (Lee-Thorp & van der Merwe 1987; Lee-Thorp *et al.* 1989; Wang *et al.* 1994; Cerling *et al.* 1997; Cerling & Harris 1999). Large ruminant mammals have a higher enrichment factor ($\varepsilon^*_{\text{enamel}-\text{diet}} = 14.1 \pm 0.5‰$) (Cerling & Harris, 1999; Stacklyn *et al.* 2017). Non-ruminant mammals have lower enrichment factors of ~13‰, which is probably due to physiological differences between ruminant and non-ruminant (Passey *et al.* 2005; Stacklyn *et al.* 2017). In the modern world, mammals feeding on C_3 vegetation typically have enamel-$\delta^{13}C$ values of about $-13‰$. Mammals consuming C_4 vegetation have $\delta^{13}C$ values of about + 1‰, and mixed feeders (feeding on both C_3 and C_4 vegetation) have $\delta^{13}C$ values between these two extremes (Lee-Thorp *et al.* 1989; Cerling *et al.* 1997; Wang *et al.* 2008*a*). Therefore, the dietary information and niche partitioning of herbivores can be revealed through comparison of the $\delta^{13}C$ values of structural carbonate in their tooth enamel. The carbon isotopic composition of tooth enamel also can provide valuable insights into the mammal's habitat (e.g. Farquhar *et al.* 1989; Cerling & Harris 1999; Codron *et al.* 2005). Plants growing under water-stressed conditions or low atmospheric partial pressure of CO_2 (pCO_2), or in relatively open environments where more evaporation occurs, have higher $\delta^{13}C$ values (above the average value of $-27‰$). Plants growing under closed canopies or in dense forests have more negative $\delta^{13}C$ values resulting from the influence of soil respiration and light limitation (Schleser & Jayasekera 1985; Sternberg *et al.* 1989; van der Merwe & Medina 1989). Furthermore, the $\delta^{13}C$ values of atmospheric CO_2 (the carbon source for terrestrial plants) has changed over time (Tipple *et al.* 2010), affecting the $\delta^{13}C$ values of plants and their consumers. The past changes in the carbon isotope composition of atmospheric CO_2 must be accounted for in order to compare the reconstructed palaeodiet $\delta^{13}C$ values with the $\delta^{13}C$ values of modern plants (Bowman *et al.* 2017).

A total of 137 molars (including a few tooth fragments) were selected for stable carbon analysis in this study (*S. magister* from AS1, n = 16; *S. magister* from AS2, n = 14; *S. magister* from AS3, n = 26; *S. magister* from AS4, n = 25; *S. magister* from AS5, n = 23; *S. magister* from AS6, n = 5; *L. expeditus* from IM, n = 28). The results of the stable carbon isotope analyses of the samples are presented in Gong *et al.* (2019, appendix B). We took a bulk enamel sample from every individual by drilling along the growth axis of the tooth. No serial enamel samples were taken in this study because the teeth of *S. magister* and *L. expeditus* are small with a very thin enamel layer, and are thus not suitable for serial sampling (by drilling).

The enamel samples then were prepared following a treatment procedure described by Wang & Deng (2005). The enamel carbonate powders were soaked in 5% reagent sodium hypochlorite (NaClO) overnight at room temperature to remove any possible organic contaminants. After that, the samples were cleaned with distilled water four or five times using centrifugation to remove the remaining NaClO. The powder was then treated with 1 M acetic acid overnight to remove non-structural carbonate, and then cleaned with distilled water and freeze-dried (Wang & Deng 2005). Then, ~2–3 mg of the enamel powder was weighed into a reaction vial and baked for a few hours in a drying oven set to ~60°C to remove moisture absorbed onto the powder. Caps and septa were screwed onto the vials immediately. After flushing the vials with pure He, the enamel samples were reacted with 100% phosphoric acid at 25°C for about 72 h to produce CO_2, and the carbon isotopic ratios of the CO_2 were measured using a Gas Bench II Auto-Carbonate device connected to a Thermo-Finnigan MAT Delta Plus XP stable isotope ratio mass spectrometer (IRMS) at Florida State University. Three standards were run for every 15 samples. Results were calibrated (two-point calibration method) by different carbonate standards and reported in standard delta (δ) notation as $\delta^{13}C$ value in reference to the international carbonate standard VPDB (Vienna Pee Dee Belemnite). The analytical precision (based on repeated analyses of standards including NBS-19 and our lab standards MERK, Roy-cc and MB-cc, which were processed with each batch of samples) is $\pm 0.1‰$ (1σ) or better.

RESULTS

Mesowear analysis results

We obtained the original measurement data of every individual of *S. magister* and *L. expeditus* (Gong *et al.* 2019, appendix A). The ratio of cusp height to intercusp distance was greater than 0.1 for all teeth. Therefore, the occlusal relief of every tooth is categorized as high according to the standard introduced by Fortelius & Solounias (2000). Table 1 compiles summary mesowear data including average mesowear scores, percentages of individuals with different cusp types (sharp and blunt), and high occlusal relief. As a comparative dataset for dietary classification, we use 27 'typical' extant species which have been shown to provide reliable dietary data without controversy in both mesowear and microwear analyses (Solounias & Semprebon 2002).

For the 27 typical modern ungulates, there are range separations of mesowear scores according to different type of diet (Fig. 4). The browsers have the mesowear scores of 0–0.5, with an average of 0.2. The mixed feeders have mesowear scores of 0.3–0.8, with an average of 0.6, and the grazers have mesowear scores of 1.0–2.7, with an average of 1.7. A one-way ANOVA was significant ($p < 0.0001$).

The scores of *S. magister* from AS2, AS3 and AS4 (0.3, 0.4 and 0.5) fall into the overlapping area between browsers and mixed feeders. It suggests that *S. magister* from AS2, AS3 and AS4 were either browsers or mixed feeders. The scores of *S. magister* from AS5 (0.6) are all within the range of mixed feeders while scores of *L. expeditus* (1.2) fall into the range of grazers. It suggests that *S. magister* from AS5 were typical mixed feeders, and *L. expeditus* from IM were grazers.

The discriminant function analyses (DFA) of the 27 typical modern ungulates dataset resulted in two canonical discriminant functions. The first function was highly significant ($p > 0.001$, Wilks' lambda) and responsible for 99.2% of the original variable information. The variable 'percentage of individuals with sharp cusps' had the greatest influence on this function (loading = 0.746). The other three variables had relatively lower loadings (high loading = 0.221; blunt loading = −0.188; mesowear score loading = −0.412). A plot of these two functions (Fig. 5) illustrates good separation of modern taxa along the *x*-axis (function 1) and little separation along the *y*-axis (function 2).

Schlosseria magister specimens from AS2 are classified as browsers, and the *S. magister* specimens from other fossil horizons (AS3, AS4 and AS5) and *L. expeditus* are classified as mixed feeders. The posterior classification probabilities are mostly high (0.95 for *S. magister* from AS3; 1 for *S. magister* from AS4, AS5; 1 for *L. expeditus*), except for specimens of *S. magister* from AS2 (0.54). Conditional probabilities ranged widely from 0.09 (*S. magister* from AS2) to 0.95 (*S. magister* from AS4). The scores on discriminant function 1 (DF1) for *S. magister* decrease progressively from AS2 to AS5. *Lophialetes expeditus* had the lowest score on discriminant function 1 that plotted to the left of the mixed feeders range (Fig. 5).

Hierarchical cluster analysis (HCA) of the typical ungulate dataset produced three main clusters: two of grazers and one of mixed feeders and browsers (Fig. 6). The non-grazer cluster includes two subclusters: one of browsers; and one of mixed feeders. The mixed feeder subcluster includes all mixed feeder species among the 27 modern ungulates of known diet, and the browser subcluster includes all of the browser species among the 27

TABLE 1. The dental mesowear data of 27 'typical' modern ungulates, *Schlosseria magister* and *Lophialetes expeditus*.

Species	N	MS	% sharp	% blunt	% high	Diet
Aepyceros melampus	17	0.6	35.2	0	100	M
Alcelaphus buselaphus	76	1.5	3.2	28	57	G
Alces alces	30	0	100	0	100	B
Bison bison	15	2.7	0	73.3	0	G
Carpicornis sumatraensis	22	0.7	45.4	4.5	100	M
Ceratotherium simum	26	2.3	0	28	0	G
Cervus canadensis	19	0.5	47.3	0	100	M
Connochaetes taurinus	52	1.5	15.3	28.8	55	G
Damaliscus lunatus	5	2	20	20	20	G
Dicerorhinus sumatrensis	5	0.2	80	0	100	B
Diceros bicornis	34	0.1	94.1	0	100	B
Equus burchelli	122	2.3	27	33.6	0	G
Equus grevyi	29	2.2	34.4	24.1	0	G
Eudorcas thomsonii	146	0.6	55.4	1.3	88	M
Giraffa camelopardalis	61	0.3	73.7	0	94	B
Hippotragus equinus	26	1.1	3.8	0	85	G
Hippotragus niger	20	1.3	0	15	85	G
Kobus ellipsiprymnus	22	1	0	0	96	G
Nanger granti	18	0.6	50	0	88	M
Odocoileus hemionus	33	0.5	72.7	0	100	B
Odocoileus virginianus	18	0.1	88.8	0	100	B
Okapia johnstoni	8	0.1	87.5	0	100	B
Ovibos moschatus	52	0.8	57.6	0	81	M
Redunca redunca	77	1.1	6.4	2.5	91	G
Rhinoceros sondaicus	5	0	100	0	100	B
Taurotragus oryx	14	0.3	50	0	100	M
Tragelaphus scriptus	47	0.5	51	0	100	M
Schlosseria magister (AS2)	40	0.3	67.5	0	100	
Schlosseria magister (AS3)	13	0.4	61.5	0	100	
Schlosseria magister (AS4)	10	0.5	50	0	100	
Schlosseria magister (AS5)	31	0.6	41.9	0	100	
Lophialetes expeditus (IM)	47	1.2	32.6	26.1	100	

Data of 27 modern ungulates from Croft & Weinstein (2008).
N, sample size; MS, mesowear score; % sharp, the percentage of individuals with sharp cusps; %blunt, the percentage of individuals with blunt cusps; %H, the percentage of individuals with high cusp relief; M, mixed feeder; G, grazer; B, browser.

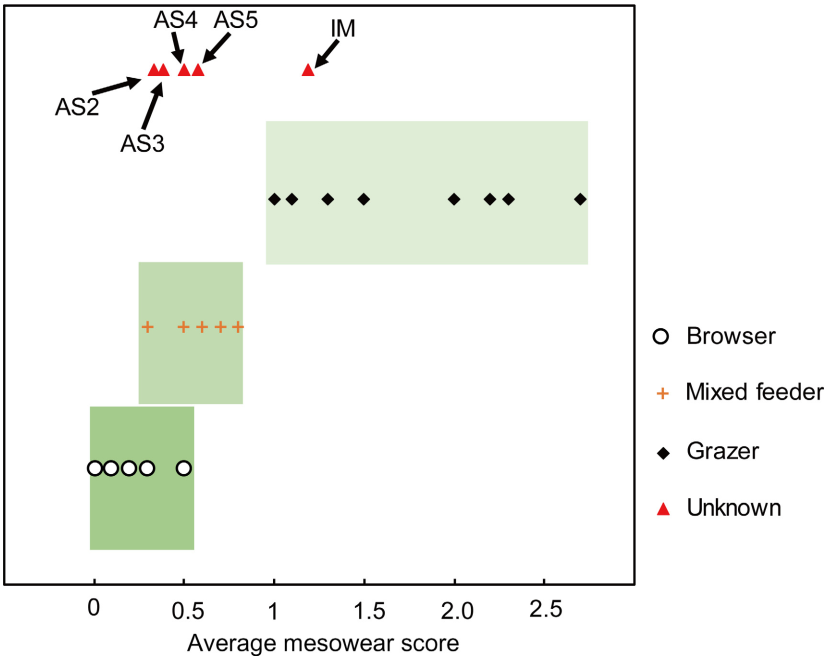

FIG. 4. Distribution of the average mesowear scores for 27 typical modern ungulates of known diet and two lophialetids (*Schlosseria magister* and *Lophialetes expeditus*, shown as solid triangles) from different fossil-bearing horizons. Colour online.

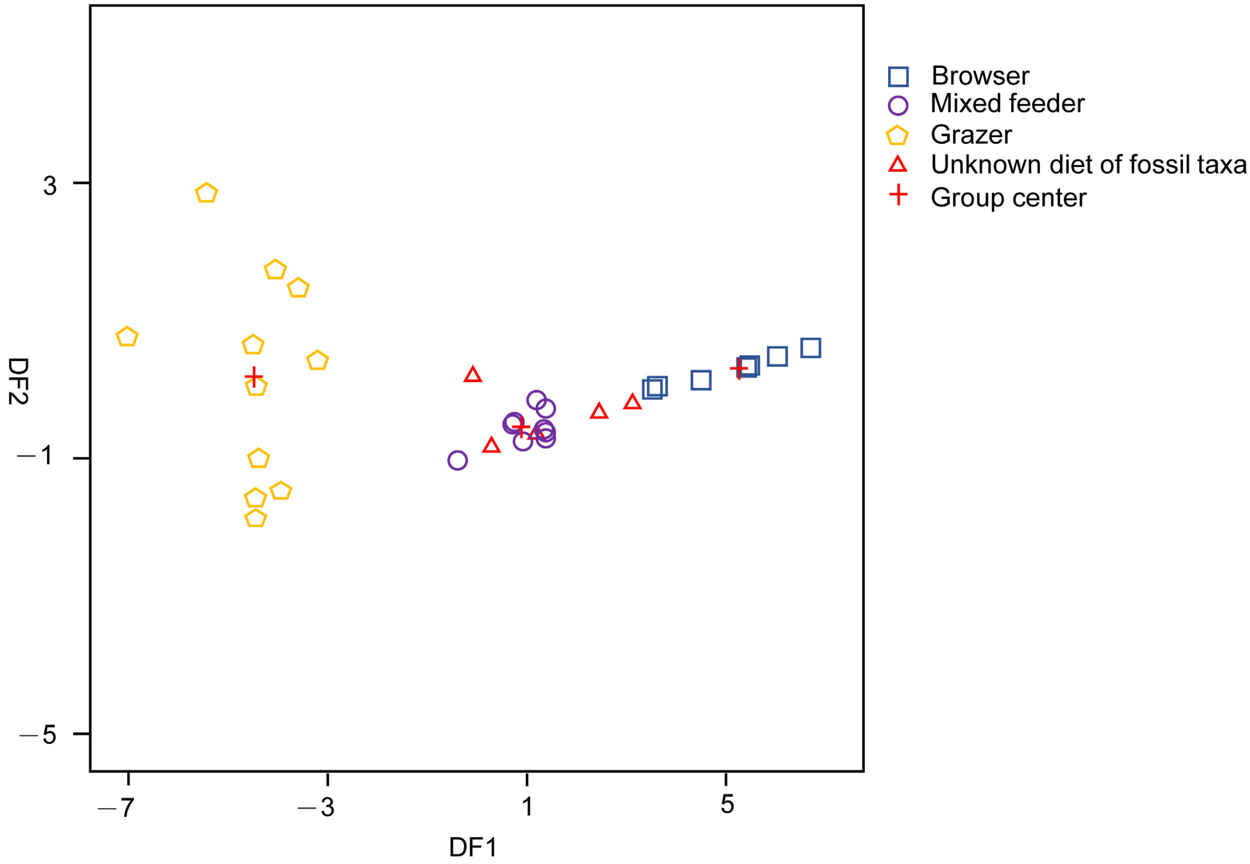

FIG. 5. Predicted diets of modern grazers (pentagons), mixed feeders (circles), browsers (squares) and fossil taxa (*Schlosseria magister* and *Lophialetes expeditus*) with unknown diet (triangles) based on a dietary discriminant function analysis of 27 typical modern ungulates of known diet. Only the first function (DF1) was significant. Colour online.

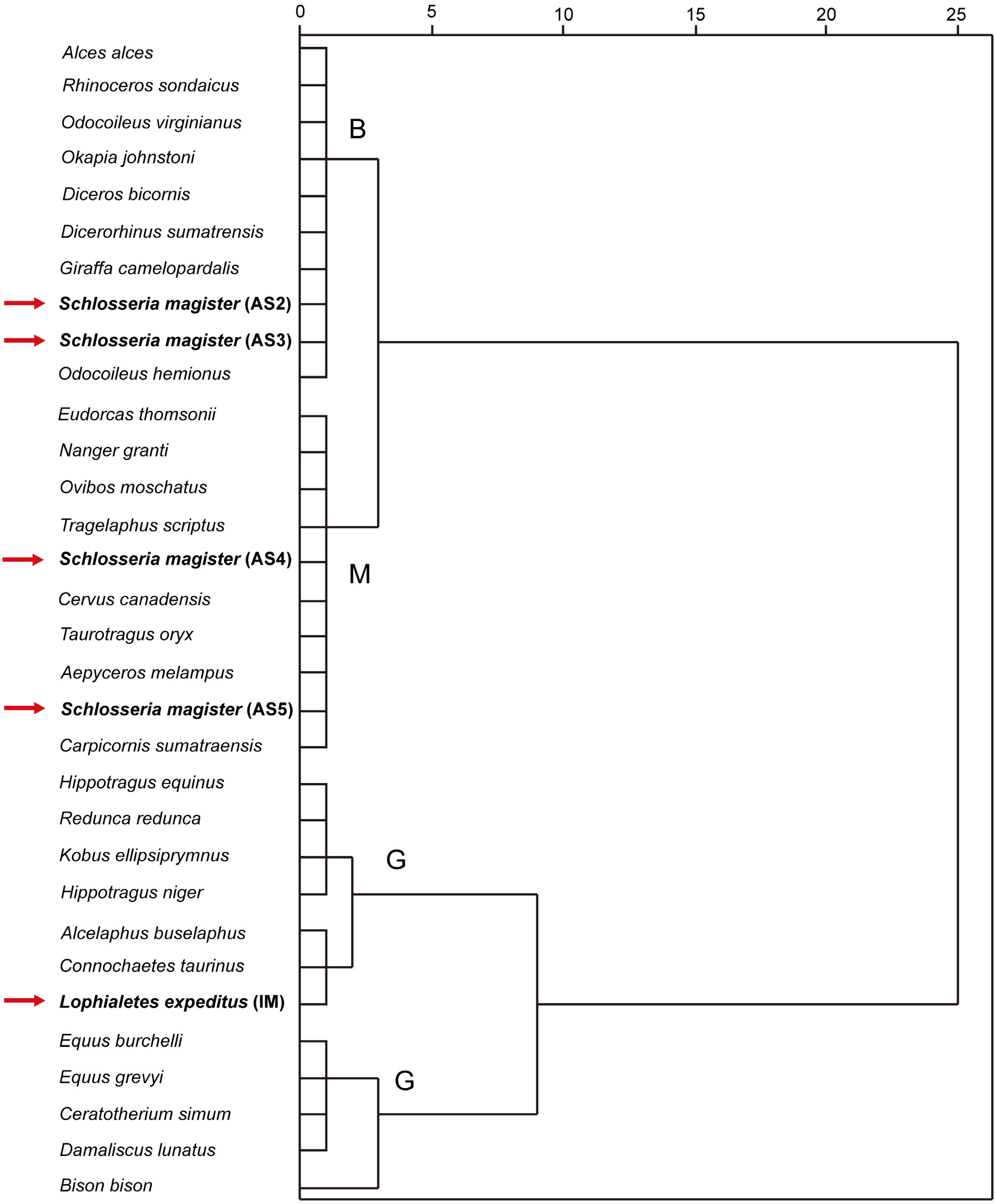

FIG. 6. Dendrogram based hierarchical cluster analysis of 27 typical modern ungulates of known diet and two lophialetids (*Schlosseria magister* and *Lophialetes expeditus*) from different fossil-bearing horizons. Clusters of grazers (G), mixed feeders (M), and browsers (B) are indicated at their base. Colour online.

modern ungulates. Among the 27 typical modern ungulates, *Schlosseria magister* from AS2 and AS3 clustered with browser subcluster, and *S. magister* from AS4 and AS5 clustered with the mixed feeder subcluster. And *Lophialetes expeditus* from IM clustered with grazer cluster.

Stable carbon isotope analysis results

The results of carbon stable isotope composition are summarized in Table 2.

Enamel δ^{13}C values of *S. magister* from the Huheboerhe area range from −7.5 to −13‰, with a mean of −10.1 ± 1.1‰ ($n = 109$), and enamel δ^{13}C values of *L. expeditus* range from −7.5 to −10.8‰, with an average of −8.6 ± 0.7‰ ($n = 28$). The isotopic variations in *S. magister* and *L. expeditus* reflect differences in their diets and habitats. Using an enrichment factor ($silon^{*}_{\mathrm{diet-enamel}}$) value of 13‰ for both *S. magister* and *L. expeditus* (non-ruminants) and the enamel δ^{13}C values, we reconstructed the diet-δ^{13}C values of these two Eocene species from the fossil-bearing horizons as follows.

For *S. magister* from AS1, the δ^{13}C values of enamel samples range from −9.0 to −12.9‰, with an average of −10.8 ± 1.0‰. This gives a reconstructed diet-δ^{13}C of −23.8 ± 1.0‰, ranging from −22.0 to −25.9‰. For *S. magister* from AS2, the δ^{13}C values of enamel samples range from −7.9 to −12.4‰, with an average of −10.7 ± 1.2‰. This yields a reconstructed diet-δ^{13}C of −23.7 ± 1.2‰, ranging from −20.9 to −25.4‰. For *S. magister* from AS3, the δ^{13}C values of enamel samples range from −7.5 to −13.0‰, with an average of −10.3 ± 1.2‰. This gives a reconstructed diet-δ^{13}C of −23.3 ± 1.2‰, ranging from −20.5 to −26.0‰. For *S. magister* from AS4, the δ^{13}C values of enamel samples range from −7.7 to −11.1‰, with an average of −9.6 ± 0.8‰. This gives a reconstructed diet-δ^{13}C of −22.6 ± 0.8‰, ranging from −20.7 to −24.1‰. For *S. magister* from AS5, the δ^{13}C values of enamel samples range from −8.1 to −11.0‰, with an average of −9.7 ± 1.0‰. This gives a reconstructed diet-δ^{13}C of −22.7 ± 1.0‰, ranging from −21.1 to −24.0‰. For *S. magister* from AS6, the δ^{13}C values of enamel samples range from −8.5 to −11.8‰, with an average of −9.8 ± 1.7‰. This gives a reconstructed diet-δ^{13}C of −22.8 ± 1.7‰, ranging from −21.5 to −24.8‰. For *L. expeditus* from IM, the δ^{13}C values of enamel samples range from −7.5 to −10.8‰, with an average of −8.6 ± 0.7‰. This gives a reconstructed diet-δ^{13}C of −21.6 ± 0.7‰, ranging from −20.5 to −23.8‰.

Geochemical evidence indicates that the δ^{13}C values of atmospheric CO_2 have changed significantly over geological time (e.g. Tipple *et al.* 2010), affecting the δ^{13}C values of plants and ultimately tooth enamel of herbivores (e.g. Bowman *et al.* 2017). Proxy records suggest that the δ^{13}C of atmospheric CO_2 during the early–middle Eocene time period represented by our samples ranged from −5.45‰ to −6.09‰, with an average of −6.0 ± 0.1‰ (Fig. 7A; Tipple *et al.* 2010). That was about 2‰ higher than the present-day atmospheric CO_2 δ^{13}C value of −8‰ (Kohn 2010; Tipple *et al.* 2010). Thus, a correction factor of −2‰ needs to be added to the above reconstructed diet δ^{13}C values to make them directly comparable to modern plants or diet δ^{13}C values.

DISCUSSION

Mesowear features and dietary traits

The DFA and HCA of the tooth mesowear data on *S. magister* from AS2 to AS5 and *L. expeditus* from IM presented here provide the first evidence for the dietary habits of lophialetids from the Eocene of Erlian Basin, Inner Mongolia, China. The results from these statistical analyses show dietary traits with a clear tendency toward more abrasive from *S. magister* (AS) to *L. expeditus* (IM).

By comparing the mesowear scores, both DFA and HCA suggest browsing diets or browse-dominated mixed

TABLE 2. Summary of results of carbon isotope analyses of tooth enamel samples of *Schlosseria magister* and *Lophialetes expeditus* from Huheboerhe area of the Erlian Basin, Inner Mongolia.

Species	Fossil-bearing horizon	Average δ^{13}C (‰ vs VPDB)	Range of diet-δ^{13}C (‰ vs VPDB)	Average diet-δ^{13}C (‰ vs VPDB)	Standard deviation (±1σ)	No. of samples/ individuals
S. magister	AS1	−10.8	−22.0 to −25.9	−23.8	1.0	16
S. magister	AS2	−10.7	−20.9 to −25.4	−23.7	1.2	14
S. magister	AS3	−10.3	−20.5 to −26.0	−23.3	1.2	26
S. magister	AS4	−9.6	−20.7 to −24.1	−22.6	0.8	25
S. magister	AS5	−9.7	−21.1 to −24.0	−22.7	1.0	23
S. magister	AS6	−9.8	−21.5 to −24.8	−22.8	1.7	5
L. expeditus	IM	−8.6	−20.5 to −23.8	−21.6	0.7	28

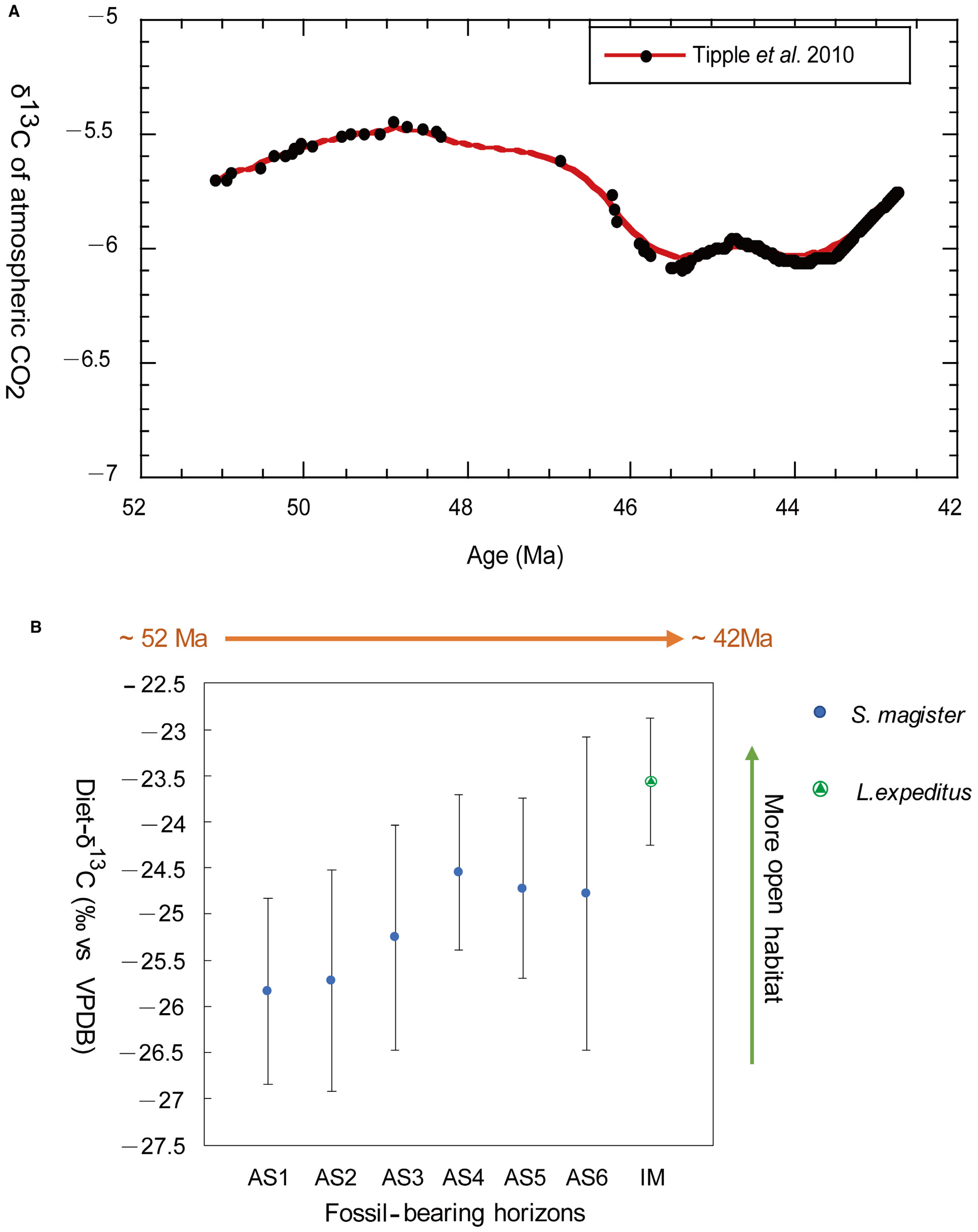

FIG. 7. A, change in δ^{13}C values of atmospheric CO_2 during the early–middle Eocene time period (data from Tipple *et al.* 2010). B, plot of reconstructed mean diet-δ^{13}C values of *Schlosseria magister* and *Lophialetes expeditus* found from Huheboerhe area of the Erlian Basin, Inner Mongolia, China; each point represents the reconstructed mean diet-δ^{13}C values of one species; error bar indicates 1σ from the mean. Colour online.

feeding dietary traits for *S. magister* from AS2 and AS3, typical mixed feeding dietary traits for *S. magister* from AS4 to AS5, and grazing diet or graze-dominated mixed feeding dietary traits for *L. expeditus* from IM. It is important to note that the dietary types of fossils are more complicated than that of extant mammals because we know very little about the palaeoecological and palaeoclimatic context of the extinct animals. Therefore, when interpreting the mesowear data, other factors also should be considered. *S. magister* from AS2 have low mesowear scores (0.3) and a high percentage of individuals with sharp cusps (67.5%) consistent with the features of typical extant browsers. DFA assigns the *S. magister* from AS2 to the browsing group, and HCA allocates it to the mixed feeder cluster. In addition, *S. magister* has low-crowned molars with shearing crests, suggesting a possible browsing diet. Taking the above factors into account, *S. magister* specimens from AS2 were most likely to have been browsers feeding on soft leaves, tender twigs, and/or other less abrasive plant materials. For *S. magister* from AS3, DFA indicates a mixed feeding diet, and HCA indicates a browsing diet. Moreover, the mesowear score of *S. magister* from AS3 falls into the overlapping area between browsers and mixed feeders. Taken together, the above data suggest that *S. magister* individuals from AS3 were probably browse-dominated mixed feeders that consumed a higher percentage of less abrasive plant material, such as soft leaves. For *S. magister* fossils from AS4 and AS5, both DFA and HCA show that they were mixed feeders. Given the general understanding of mixed feeders, they were herbivores eating both leaves and grasses. However, mesowear analysis only determines whether the level of abrasion and tooth wear features on the occlusal surface of molars are similar to those of extant mixed feeders. In other words, the mixed feeders are those that consume both soft plants parts (e.g. leaves, fruits, tender twigs and tender grasses) and more abrasive items (e.g. stiff branches, harsh grasses, fruit with hard covers or seeds, soil and grit). The mesowear analysis suggests that the dietary composition of *S. magister* gradually changed from AS2 to AS5, with increasing amounts of abrasive items consumed by *S. magister* over time. As there was no significant change in the body size of *S. magister* over that time, we assume that the quantity of food consumed by individuals from different fossil horizons was very similar. Thus, a change in the dietary composition of *S. magister* is the most plausible explanation for the differences in the mesowear data. As noted above, the mesowear data indicate that *S. magister* fossils from AS4 and AS5 have typical mixed feeding dietary traits, with more abrasive items in their diet than *S. magister* specimens from AS2 and AS3. The mesower features of *L. expeditus* teeth from IM, which include a high mesowear score (1.2), a low percentage of individuals with sharp cusps (32.6%) and high percentage of individuals with blunt cusps (26.1%), are consistent with those of typical extant grazers. DFA assigns the *L. expeditus* fossils to the mixed feeders group, and HCA places that species in the grazer cluster. Moreover, dental morphological analysis reveals larger sized and much higher lophodont teeth in *Lophialetes* than in *Schlosseria*, as well as a greater degree of molarization of the premolars. This molarization indicates that *Lophialetes* had a greater ability to consume a more abrasive diet than that of *Schlosseria*. Based on the above analysis, it is most likely that *L. expeditus* was a grazer, consuming harsh vegetation or other abrasive items.

Stable carbon isotopes, diet and habitat change

Enamel samples from *S. magister* and *L. expeditus* exhibit significant stable carbon isotopic variations (Table 2). The reconstructed diet-$\delta^{13}C$ values range from $-20.5‰$ to $-26‰$ with the highest $\delta^{13}C$ value found in both *L. expeditus* and *S. magister* from AS3 and the lowest in *S. magister* teeth from AS3. Considering that the $\delta^{13}C$ value of atmospheric CO_2 during the early–middle Eocene represented by our samples was about 2‰ higher than that of the modern atmosphere (Tipple *et al.* 2010), 2‰ should be deducted from the reconstructed diet-$\delta^{13}C$ value of *S. magister* and *L. expeditus* to make it directly comparable to a diet-$\delta^{13}C$ value found in modern terrestrial-plant ecosystems. That is, the reconstructed diet-$\delta^{13}C$ values range from $-20.5‰$ to $-26‰$ for *S. magister* and *L. expeditus* individuals should be equivalent to a modern diet-$\delta^{13}C$ values of $\sim -22.5‰$ to $-28‰$, which is within the range observed for modern C_3 plants. This indicates that these early–middle Eocene lophialetids ate pure C_3 vegetation and lived in a habitat dominated by C_3 plants. The *S. magister* specimens from AS1 to AS3 have a large range of $\delta^{13}C$ variation (with $\Delta\delta^{13}C$ value 3.9‰, 4.5‰ and 5.5‰ respectively) and *S. magister* and *L. expeditus* teeth from other fossil horizons have a relatively small range of $\delta^{13}C$ variation (about 3‰). This variation implies that the *S. magister* individuals from AS1 to AS3 had wider dietary range and more dietary flexibility, and *S. magister* and *L. expeditus* from other fossil horizons had a more specialized diet.

Previous research indicated that modern C_3 vegetation has a considerable range in $\delta^{13}C$ values ($-20‰$ to $-35‰$). Compared to the average $\delta^{13}C$ value of about $-27‰$, water-stressed ecosystems have higher $\delta^{13}C$ (as high as $-20‰$), and plants growing in the understory of the closed canopies of dense forests have more negative $\delta^{13}C$ values (as low as $-35‰$) (Farquhar *et al.* 1989; van der Merwe & Medina 1989; Ehleringer *et al.* 1991; Ehleringer & Monson 1993; Cerling *et al.* 1997). The reconstructed average diet-$\delta^{13}C$ values for *S. magister* and

L. expeditus range from −21.6‰ to −23.8‰, equivalent to modern diet-δ^{13}C values of ~−24‰ to −26‰, which are significantly higher than −27‰. This result indicates that *S. magister* and *L. expeditus* did not live in a dense forest with a closed canopy. On the contrary, water-stressed ecosystems or relatively open environments where more evaporation occurs were most likely to be the habitats of *S. magister* and *L. expeditus* during the early–middle Eocene. We found that the reconstructed mean diet-δ^{13}C values of *S. magister* and *L. expeditus* displayed an overall increasing trend from AS1 to IM (Fig. 7B). Only the diet-δ^{13}C values of *S. magister* fossils from AS5 and AS6 deviate slightly (by ~0.1‰) from this overall trend, probably reflecting the slight decrease in the δ^{13}C of atmospheric CO_2 at around 44–45 Ma (Tipple *et al.* 2010). This general increasing trend, which is opposite to the trend in the reconstructed δ^{13}C of atmospheric CO_2 for the same time interval (Fig. 7A; Tipple *et al.* 2010), indicates that the habitats of *S. magister* and *L. expeditus* became more open and/or drier as a whole over time. Moreover, the diet-δ^{13}C value of *L. expeditus* was 1.2‰ higher than that of *S. magister* from AS6, and at least 1‰ higher than that of *S. magister* from the other older fossil horizons. These data suggest that the habitat of *L. expeditus* had become significantly drier and more open than that of its earlier relatives. However, Ni *et al.* (2007, 2010) reported a new omomyid euprimate (*Baataromomys ulaanus*) from Bumbanian strata at Wulanboerhe and a new primate (*Tarkops mckennai*) from the Irdin Manha Formation in the Erlian Basin. The occurrence of these primates suggests that forested habitats must have been present, at least sporadically, in the Erlian Basin during the early–middle Eocene. The large range of variation in the reconstructed diet-δ^{13}C values (from −20.5‰ to −26‰, equivalent to modern values of −22.5‰ to −28‰) for *S. magister* and *L. expeditus* individuals suggest that the basin had diverse habitats ranging from forest (perhaps riparian forest) to more open and drier habitats. Therefore, the *S. magister* and *L. expeditus* individuals probably lived in edge zone of a forest or a relatively open area where the forest (or woodland) canopies were broken.

Implications for palaeoecology and palaeoclimate

Deep-sea oxygen isotope records (Zachos *et al.* 2001) reveal a trend of decreasing global temperatures (from ~12 to ~8°C) during the period when the *S. magister* and *L. expeditus* lived (~52 to ~42 Ma). A significant but complicated question is whether the global temperature changes had an effect on the habitats and diet of *S. magister* and *L. expeditus* during the early–middle Eocene of the Erlian Basin. Here, we compare the temporal changes of dietary composition and diet-δ^{13}C values with the deep-sea temperature record as shown in Figure 8 in order to address this question.

From the underlying Arshanto Formation to the upper Irdin Manha Formation, our mesowear data show that *S. magister* and *L. expeditus* changed from browser to grazer as their diet became more abrasive, and the diet-δ^{13}C values increased from −23.8‰ to −21.6‰, which cannot be explained by changes in the δ^{13}C values of atmospheric CO_2 (Fig. 7A), indicating a shift to a more open

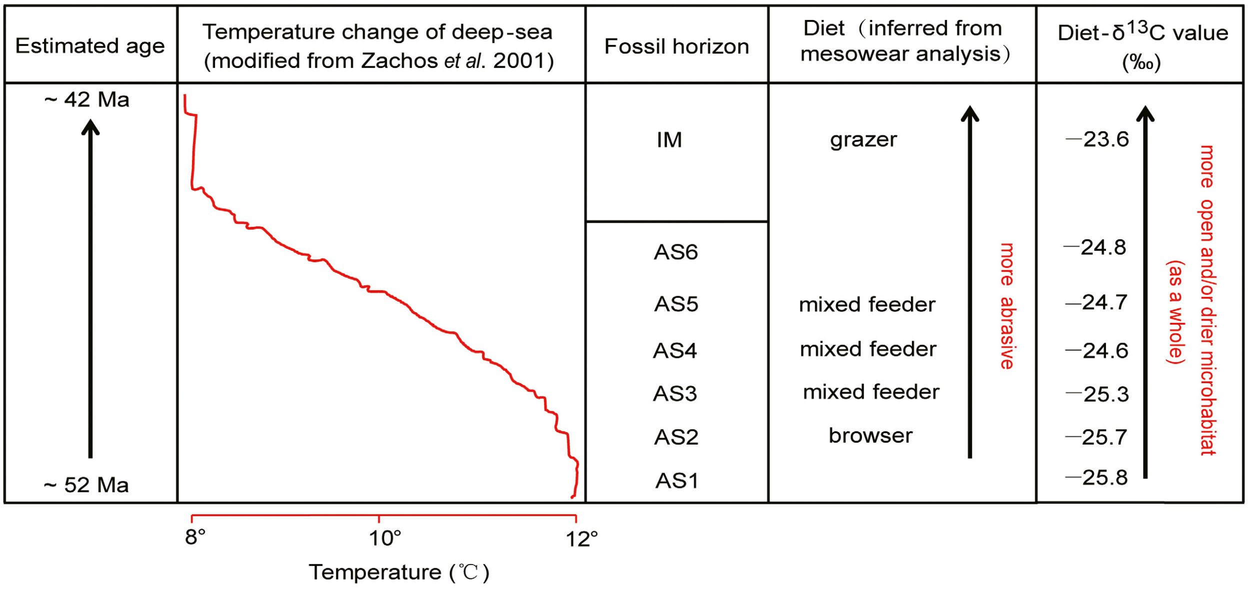

FIG. 8. Comparison of dietary change, habitat change and global climatic change. Colour online.

TABLE 3. Statistical significance of differences in mean carbon isotopic compositions of *Schlosseria magister* and *Lophialetes expeditus* from different fossil-bearing horizons (or different ages) as determined by two-tailed t-tests.

Sample	Mean difference (‰)	df	t	p	Significant difference at 95% confidence interval?
S. magister (AS1) vs *S. magister* (AS2)	0.1	28	−0.275	0.786	No
S. magister (AS2) vs *S. magister* (AS3)	0.4	38	−1.153	0.256	No
S. magister (AS3) vs *S. magister* (AS4)	0.7	49	−2.394	0.021	**Yes**
S. magister (AS4) vs *S. magister* (AS5)	0.1	46	0.646	0.521	No
S. magister (AS5) vs *S. magister* (AS6)	0.1	26	0.069	0.946	No
S. magister (AS6) vs *L. expeditus* (IM)	1.2	31	−2.740	0.010	**Yes**

and/or drier habitat. The drying trend (a process tending to drier conditions but not necessarily to an arid climate type) from ~52 to ~42 Ma in the study area as indicated by the increasing diet-$\delta^{13}C$ values corresponds to a decreasing trend in global temperatures (Fig. 8). This suggests that the change in diet and habitat of the two lophialetids was most likely to have been caused by global climate change during this period as documented by deep-sea sediment $\delta^{18}O$ records (Zachos *et al.* 2001). Therefore, global climate change probably had an important impact on mammalian evolution. Our mesowear and stable carbon isotope data suggest that the gradual drop in global temperatures following the Early Eocene Climatic Optimum (from ~52 to ~42 Ma) led to a progressively drier and/or more open terrestrial ecosystem, with related changes in floral composition and density in the Huheboerhe area of the Erlian Basin. In a relatively open environment like a woodland (or a low-density forest) with plenty of sunlight and limited shade, lophialetids had to adjust their diet by consuming more abrasive items and different plants in order to adapt to the ecological/environmental change. That change is because more exogenous hard materials like soil and grit were ingested with plant materials in more open habitats, resulting in higher incidences of abrasive mesowear features (Kaiser & Schulz 2006). Thus, the more abrasive diet of lophialetids was probably a response to change in habitat or ecology.

Fossils of *S. magister* and *L. expeditus* are only known from the Arshanto and Irdin Manha formations, respectively. Previous studies (e.g. Matthew & Granger 1926; Radinsky 1965) suggested that *S. magister* was probably the ancestral form of *L. expeditus*. The change in habitat probably was the significant driving force in the evolution from *S. magister* to *L. expeditus*. Mesowear documents the dietary shifts of lophialetids during a drying climate. There were three distinct dietary shifts. One happened between *S. magister* from AS2 (browser) and *S. magister* from AS3 (browse-dominated mixed feeder). Another shift happened between *S. magister* from AS3 (browse-dominated mixed feeder) and *S. magister* from AS4 (typical mixed feeder); and the last happened between *S. magister* from AS5 (typical mixed feeder) and *L. expeditus* from IM (grazer). Moreover, there are two conspicuous variations in mean diet-$\delta^{13}C$ values determined by two-tailed t-tests (Table 3) that happened between AS3 and AS4 ($\Delta\delta^{13}C = 0.7‰$, $p < 0.05$), and between AS6 and IM ($\Delta\delta^{13}C = 1.2‰$, $p < 0.05$). Assuming that same species living in the same area would have a similar diet under similar ecological conditions, the very close average diet-$\delta^{13}C$ values between AS1 ($\delta^{13}C = -23.8‰$) and AS2 ($\delta^{13}C = -23.7‰$) indicates that *S. magister* from these fossil horizons probably had similar diets and habitats. The reconstructed diet-$\delta^{13}C$ values also suggest that the diets and habitats of *S. magister* from AS5 ($\delta^{13}C = -22.7‰$) and AS6 ($\delta^{13}C = -22.8‰$) were very similar. Therefore, we consider the *S. magister* individuals from AS1 as browsers, and *S. magister* fossils from AS6 as mixed feeders. The dietary shifts of the two lophialetids inferred from mesowear are consistent with the changes in habitat as documented by the stable carbon isotope data (Fig. 8; Table 3). This implies that the changes in habitat were probably the driving factor in the dietary shifts of these two lophialetids. With the habitat getting drier and/or more open, *S. magister* was unable to adapt to such a dramatic change in ecological environment and became extinct after AS1 (~45 Ma). Meanwhile, *L. expeditus*, with a stronger dietary adaptability, evolved from *S. magister* and was able to survive in a drier and more open habitat.

CONCLUSIONS

Combining both stable isotope analysis and mesowear analysis, we have drawn the following conclusions and inferences:

1. *Schlosseria magister* individuals from AS2 were browsers and *S. magister* fossils from AS3 were probably browse-dominated mixed feeders. *S. magister* specimens from AS4 and AS5 were typical mixed feeders. *S. magister* fossils from AS1 had a diet/habitat similar to their counterparts from AS2, and were probably browsers. *S. magister* fossils from AS6 had a diet/habitat similar to those from AS5, probably mixed

feeders. *Lophialetes expeditus* individuals from IM were grazers. The food ingested by *S. magister* and *L. expeditus* became more abrasive from AS1 to IM.

2. All of the reconstructed diet-$\delta^{13}C$ values fall within the range for C_3 plants, indicating that both *S. magister* and *L. expeditus* ate C_3 vegetation and lived in an environment dominated by C_3 plants. This result is consistent with previous studies (Cerling *et al.* 1993, 1997) suggesting that the expansion of C_4 plants happened in the late Miocene and terrestrial ecosystems were dominated by C_3 plants prior to the late Miocene. No substantial evidence so far demonstrate that C_4 plants existed in Erlian Basin in the early–middle Eocene. Our data show that the habitats of *S. magister* and *L. expeditus* progressively became more open and/or drier from AS1 (~52 Ma) to IM (~42 Ma). Taking the occurrence of early–middle Eocene primate fossils in the Huheboerhe area into account, *S. magister* and *L. expeditus* probably inhabited a relatively open forest environment like a woodland (or a low-density forest).
3. It appears that global climate change (global deep-sea temperature declining from ~52 to ~42 Ma) was a major driving factor for the changes in diet and habitat of *S. magister* and *L. expeditus*. In response to declining global temperature from ~52 to ~42 Ma, local ecosystems in the Huheboerhe area in the Erlian Basin became more open and drier. *S. magister* and *L. expeditus*, adapted to the changing ecosystem (habitat) through changes their diet (by consuming more abrasive items). The dietary shifts of the two lophialetids inferred from mesowear are consistent with the evident changes in habitat revealed by the enamel carbon isotope data. Therefore, the dietary shift was probably related to the palaeoecological change during the early–middle Eocene in the Huheboerhe area, Erlian Basin. *Lophialetes expeditus*, which was the sister-group of *S. magister* and had strong dietary adaptability, was able to survive in a drier and more open ecological environment. *S. magister* was unable to adapt to such a changing habitat and became extinct after AS1 (~45 Ma).

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DATA ARCHIVING STATEMENT

Supplementary data (Appendix A, B) for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.j77qp27

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