



High frequency of arthropod herbivore damage in the Miocene Huaitoutala flora from the Qaidam Basin, northern Tibetan Plateau

Qijia Li ^a, Weiyudong Deng ^b, Torsten Wappler ^c, Torsten Utescher ^d, Natalia Maslova ^e, Yusheng (Christopher) Liu ^f, Hui Jia ^g, Chengyu Song ^a, Tao Su ^b, Cheng Quan ^{a,*}

^a School of Earth Science and Resources, Chang'an University, Xi'an 710054, China

^b Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China

^c Hessisches Landesmuseum Darmstadt, 64283 Darmstadt, Germany

^d Senckenberg Research Institute and Natural Museum, 53115 Frankfurt am Main, Germany

^e Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow 117647, Russia

^f Department of Earth & Environmental Sciences, University of Missouri-Kansas City, Kansas City, MO 64110, United States of America

^g School of Earth Sciences and Engineering, Xi'an Shiyou University, Xi'an 710065, China

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ABSTRACT

Plant–arthropod interaction offers insight into the evolution of terrestrial ecosystems in the geological past. In this study, leaf fossils with arthropod traces, collected from the Miocene Huaitoutala flora, Qaidam Basin, northern Tibetan Plateau, were studied to provide direct evidence of plant–arthropod interactions on the Tibetan Plateau. The results show a total of 36 damage types belonging to eight different functional feeding groups, classified on 303 out of 433 leaf specimens with a damage frequency of 70%. Compared to other Miocene fossil floras worldwide, the Huaitoutala flora represents a relatively high frequency and diversity of damage. It indicates that, apart from climatic factors, the influence of local niche and biotic factors might have contributed to the intensive plant–arthropod interactions observed at that time, suggesting that the Miocene ecosystem hereof was not as barren as previously thought.

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1. Introduction

Plants and arthropods are major components of Earth's terrestrial biodiversity (Möller et al., 2017; Calatayud et al., 2018). In the terrestrial ecosystems, plants often provide food resources and nesting locations and shelters for arthropods (Schoonhoven et al., 2006). Meanwhile, arthropods can promote pollination and dispersal (Coley and Kursar, 2014; Mishra et al., 2015). Therefore, due to their constructed complex and intricate trophic network, plant–arthropod interactions play a vital role in the maintenance and evolution of terrestrial ecosystems (Ma et al., 2020). Although records of arthropod damage on plants are relatively well documented worldwide (e.g., Labandeira and Currano, 2013), there are still gaps in our knowledge for certain time intervals regarding the origin and diversification of these ecologically critical plant–arthropod associations (e.g., Labandeira, 2013a, 2013b). To date, the data originates overwhelmingly from Europe and North America, but the representation of relevant studies is highly patchy through time (Pinheiro et al., 2016). In the geological past, leaf fossils with arthropod

traces offer a unique opportunity to explore plant–arthropod interactions (Labandeira and Currano, 2013; Cariglino, 2018; Kodrul et al., 2018). Particularly, an increasing number of paleoecologists are trying to explore plant–arthropod interactions, especially during the geological periods of ecological transitions based on arthropod damaged leaf fossils (Wilf and Labandeira, 1999; Wilf et al., 2006; Currano et al., 2008, 2010; Donovan et al., 2016).

During the Miocene, most species and genera of extant plants and animals have emerged (Cronquist, 1978; Cantalapiedra et al., 2015; Ding et al., 2020), and its ecological framework closely resembles that of the present-day (Deng et al., 2019). Correspondingly, Miocene arthropod damage diversity and host specificity patterns were similar to current conditions (Diéguez et al., 1996; Waggoner and Poteet, 1996; Waggoner, 1999; Erwin and Schick, 2007; Adroit et al., 2016; Möller et al., 2017). Hence, the study of plant–arthropod interactions in this period could provide a perspective for reconstructing the basic features of Miocene ecosystems, and offers a frame to understand ecosystems of present day or in the future. However, systematic surveys of plant–arthropod interactions in Miocene floras are still rare, especially as exemplified by the insufficient materials from the mid-latitudes of Asia, making it difficult to explore the global ecosystem overall (Prokop et al., 2010; Paik et al., 2012; Knor et al., 2012, 2013, 2015; Khan et al.,

* Corresponding author.

E-mail address: quan@chd.edu.cn (C. Quan).

2014, 2015; Möller et al., 2017; Zhang et al., 2018; Robledo et al., 2018; Ma et al., 2020; Adroit et al., 2021; Gandolfo and Zamaloa, 2021). Therefore, new data of arthropod herbivory from additional Miocene mid-latitude paleo-floras could promote understanding of the evolution of global terrestrial ecosystems.

We recently found many leaf fossils with multiple arthropod lesions from the Miocene of Huaitoutala, Qaidam Basin, northern Tibetan Plateau, in which the fossil leaves with numerous arthropod damages are well-preserved. The plant–arthropod interactions from the Miocene Huaitoutala flora were studied quantitatively based on detailed descriptions of arthropod damage. Furthermore, based on statistical analyses and comparison with plant–arthropod interactions data from other Miocene sites worldwide, this study also discussed the causes of damage frequency and diversity patterns in the Miocene mid-latitude Huaitoutala flora.

2. Geological background

The Qaidam Basin, an isolated inland basin since the Paleocene, is infilled with Cenozoic deposits attaining a thickness of over 10,000 m. The Cenozoic strata within the Qaidam Basin have been subdivided into six units, ascendingly including Lulehe, Xia Ganchaigou, Shang Ganchaigou, Xia Youshashan, Shang Youshashan, Shizigou, and Qigequan formations (Wang et al., 2007). The plant fossils studied here were collected from the lower to middle part of the Shang Youshashan Formation, outcropping at Huaitoutala town of Delingha City in Qinghai Province, China (37°14'32"N, 96°44'9"E, Fig. 1A). The fossil plants were collected from a layer at ~900 m in the section of Huaitoutala (Fig. 1), from which the flourishing mammal fauna of Oloubuluke was reported, collected from depth levels from ~500 m to 1600 m. Based on detailed paleomagnetic studies (Fang et al., 2007),

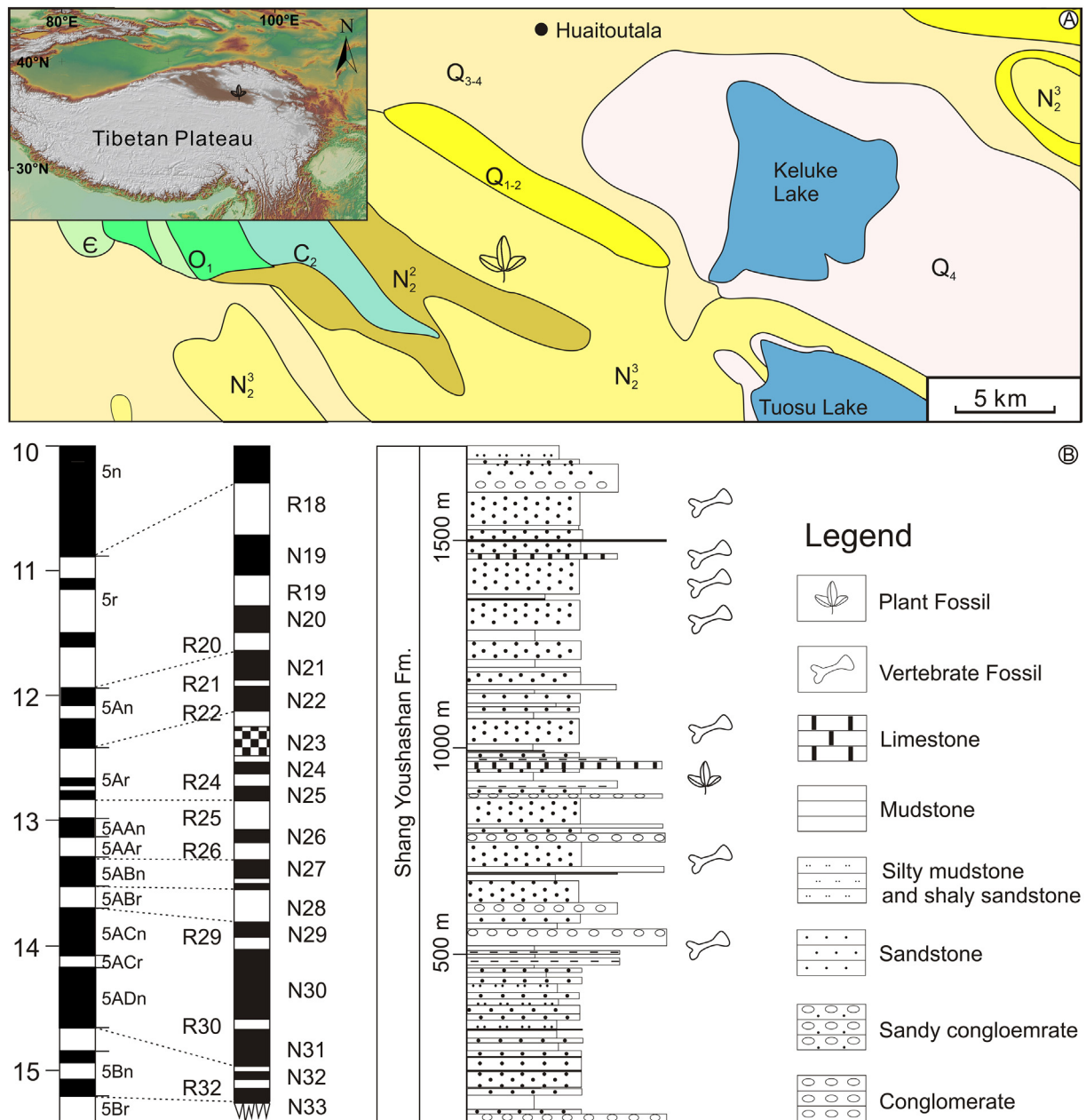


Fig. 1. Geological setting of the fossil locality. A. Maps showing the fossil location; B. The stratigraphic section is related to fossils, showing the magnetostratigraphic correlation, the chronology, and the lithology of the studied section.

the layer that contained the presently studied plant fossils (Fig. 1B) corresponds to 5Ar of the geomagnetic polarity time scale (GPTS; Cande and Kent, 1995). Linear interpolation between the thickness of the strata and age yields an age of ~12.7 Ma for this flora (Fig. 1).

3. Materials and methods

A total of 573 specimens, including 531 leaf fossils, were collected between 2019 to 2020. Under the prefix HT0001–0573 for specimen numbers, all specimens are stored at the School of Earth Science and Resources, Chang'an University, Xi'an, China. In this study, 479 leaf fossils were analyzed, while samples with more than two thirds of the leaf area missing were excluded. All leaf fossils were examined and photographed using a digital single-lens reflex camera (Nikon D50) and a stereoscope microscope (Olympus SZ61). According to leaf characteristics such as general shape and venation, each specimens was assigned to given morphotype except for 75 poorly preserved specimens. A morphotype is a designation given to a group of specimens that are morphologically distinct from all other specimens but not yet identifiable to a specific taxon. In Total, 17 morphotypes were classified in the Huaitoutala flora. For leaf fossils, well-preserved specimen were chosen to reconstruct the leaf mass per area (LMA). Detailed paleo-LMA was estimated based on the method by Royer et al. (2007).

Macrofossils were examined carefully for the presence or absence of damage types described in Labandeira et al. (2007) and Wappler et al. (2012). All insect damage types (DTs) were classified into different functional feeding groups (FFG) based on Labandeira et al. (2007), such as hole feeding (HF), margin feeding (MF), skeletonization (S), surface feeding (SF), piercing and sucking (P&S), galling (G), mining (M) and oviposition (O). Besides, for each DT, a host specificity index (HS) was described by Labandeira et al. (2007), which estimates the degree of host specialization, i.e., generalized interactions (HS = 1), intermediate interactions (HS = 2), and specialized interactions (HS = 3). Paleo-latitude data to analyze was obtained from the Ocean Drilling Stratigraphic Network (ODSN, <https://www.odsn.de/>). The relationships between the percentages of damaged leaves, the number of FFGs and paleo-latitude were explored by linear regression analysis. All data statistics and plots were performed by using OriginPro 2021 software (OriginLab, Northampton, MA, USA).

4. Results

The majority of plant specimens collected in the study area were angiosperms except for some rhizome fossils of *Equisetum*. Among 479 studied leaves, 46 specimens, belonging to Cyperaceae, Poaceae and Typhaceae, are monocotyledonous angiosperms. In this plant–arthropod interaction study, a total of 433 dicotyledonous samples, grouped into 17 leaf morphotypes, are observed (Appendix A). The most abundant morphotype (M10) includes 198 samples.

Traces of arthropod damage was present on 70% of the examined 433 dicotyledonous leaves. 65% of the damaged leaf specimens have a single DT, while 15% of damaged leaves possess no less than two DTs (Appendix B). This leads to 303 damaged dicot leaves displaying 471 separate records of damage. All these damaged records were categorized into 36 distinct damage types (DTs, Plates I–III), which were assignable to 8 functional feeding groups (FFGs), i.e., hole feeding, margin feeding, skeletonization, surface feeding, piercing & sucking, oviposition, mining, and galling (Appendix B). Besides, according to the host specificity analyses, 84% are generalist interactions, 11% are intermediate interactions, and 5% are specialized interactions. Detailed information on specimen numbers, leaf morphotypes, and associated DTs and FFGs from the Huaitoutala flora are compiled in Appendix B. Besides, all the Asian Miocene floras with arthropod damage data for comparison with the Huaitoutala flora are compiled in Appendix C. The relationships between paleo-latitude and the percentages of damaged leaves, the number of FFGs are shown in Fig. 2. The percentage of damaged leaves reflected

increasing trend with the increase of paleo-latitude ($R^2 = 0.90$, $P < 0.01$; Fig. 2A and B), while there is no distinct correlation between the number of FFGs and paleo-latitude ($R^2 = 0.01$, $P > 0.05$; Fig. 2C).

4.1. Hole feeding

DTs information: DT001 (53 occurrences, Plate I, 1), DT002 (39 occurrences, Plate I, 2), DT003 (39 occurrences, Plate I, 3), DT005 (30 occurrences, Plate I, 4), DT007 (15 occurrences, Plate I, 5), DT010 (1 occurrences, Plate I, 5), DT057 (2 occurrences, F Plate I, 6), and DT064 (2 occurrences, Plate I, 7).

Hole feeding, as one type of external feeding, is featured by perforations of the leaf with reaction tissue surrounding the damage without reaching the margin of the lamina. Detailed DT classification in hole feeding is often based on hole size, shape, position, the extent of development of plant response tissue, etc.

In the Huaitoutala flora, hole feeding (181 occurrences) is very common represented by 8 damage types. The most frequently observed damage is DT001, which is described as small-sized circular holes (Plate I, 1). Besides, both DT002 characterized by medium-sized circular perforations (Plate I, 2) and DT003 identified by similar-sized but polylobate holes (Plate I, 3) are also dominant. DT005 described as large-sized, polylobate perforations (Plate I, 4), and DT007 (Plate I, 5), Labandeira et al. (2007) described as curvilinear to rectilinear elongate holes that lack parallel sides, are followed. More than three polygonal or irregular holes arranged at the divergence point of secondaries from primary veins (DT057, Plate I, 6) or linearly lodged at the leaf margin (DT064, Plate I, 7) are rare. In addition, the least common hole damage type is DT010, which is identified by an excised tissue loop attaching a loosely central disc (Plate I, 5). For the host specificity, DT001, DT002, DT005, and DT007 belong to generalized damage with no host preference (HS = 1), while DT010, DT057, and DT064 with intermediate host specificity (HS = 2).

Host plants: morphotype 3; morphotype 4; morphotype 7; morphotype 8; morphotype 10; morphotype 11; morphotype 12; morphotype 16.

4.2. Margin feeding

DTs information: DT012 (46 occurrences, Plate I, 8), DT013 (3 occurrences, Plate I, 9), DT014 (6 occurrences, Plate I, 10), DT015 (1 occurrences, Plate I, 11), DT142 (2 occurrences, Plate I, 12).

Margin feeding is the excision and consumption of all tissues along the leaf edge. Detailed DTs division in margin feeding is often based on excision shape, angle, position, the extent of development of plant response tissue, etc.

In the Huaitoutala flora, 58 occurrences related to 5 DTs are assigned to margin feeding damage. Within 5 types of margin feeding, DT012 (Plate I, 8) showing isolated and circular leaf margin feeding was predominant, followed by DT014 (Plate I, 10), possessing the excision extending to midvein. As a kind of margin feeding, the apex feeding DT013 (Plate I, 9) was infrequent in the Huaitoutala flora. DT142 (Plate I, 12), a kind of cusped margin feeding, possessing a broad rim of reaction tissue, was also very rare in this flora. Besides, DT015 (Plate I, 11), described as a deeply trenched excision, was recorded with only one occurrence. These five DTs were assigned to generalized (DT012, DT013, DT014), intermediate (DT015) and specialized (DT142) levels of herbivore specificity, respectively.

Host plants: morphotype 4; morphotype 7; morphotype 8; morphotype 10; morphotype 11; morphotype 14; morphotype 17.

4.3. Skeletonization feeding

DTs information: DT016 (24 occurrences, Plate II, 1), DT017 (1 occurrences, Plate II, 2), DT020 (1 occurrences, Plate II, 3), DT021 (3 occurrences, Plate II, 4), DT024 (1 occurrences, Plate II, 5).

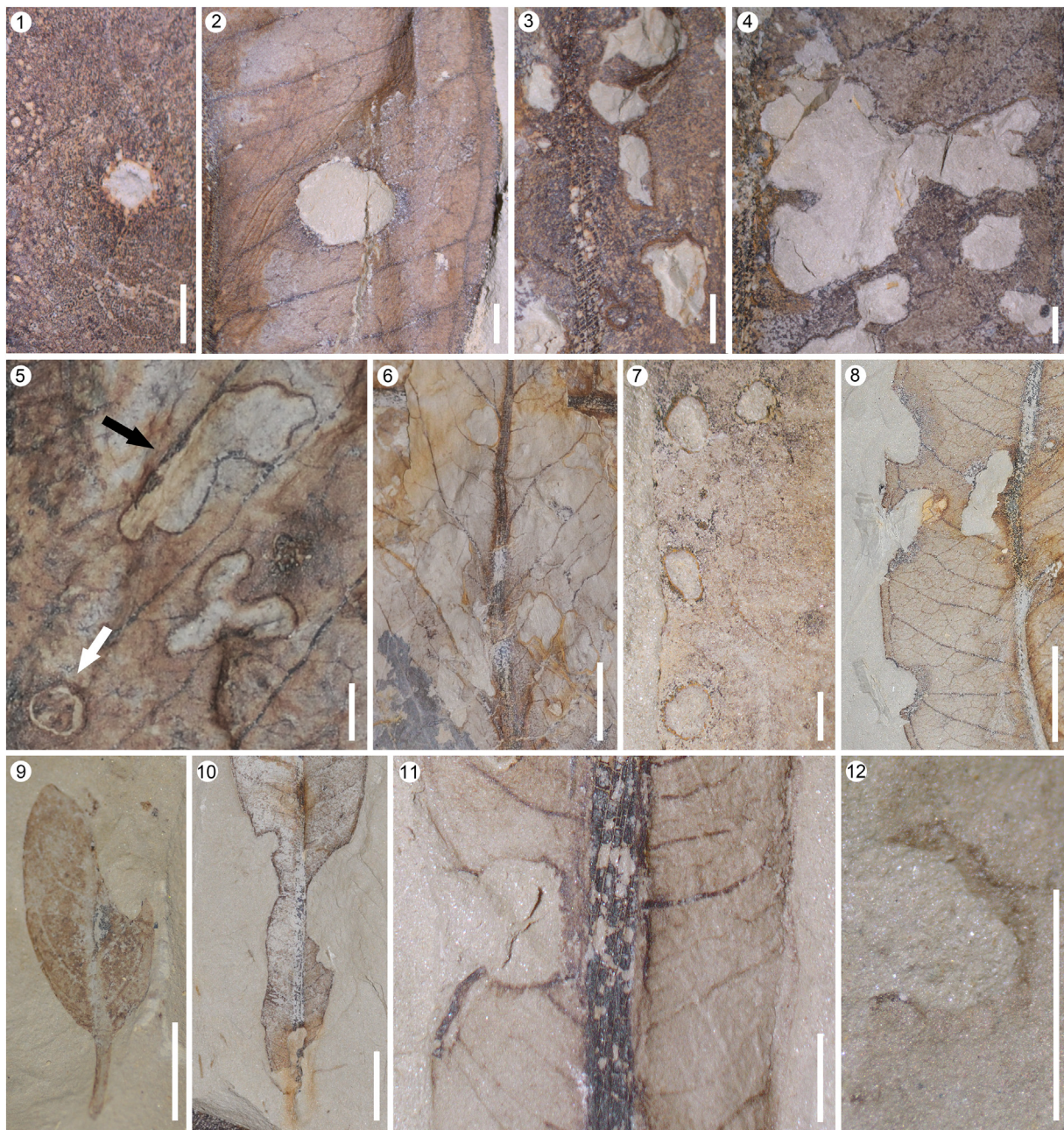


Plate I. Representative hole-feeding and margin-feeding traces on leaves of the middle Miocene Huaitoutala flora. 1–7. hole-feeding traces; 8–12. margin-feeding traces. 1. DT001, scale bar = 5 mm; 2. DT002, scale bar = 5 mm; 3. DT003, scale bar = 5 mm; 4. DT005, scale bar = 5 mm; 5. DT007 (black arrow) and DT010 (white arrow), scale bar = 1 mm; 6. DT057, scale bar = 5 mm; 7. DT064, scale bar = 1 mm; 8. DT012, scale bar = 5 mm; 9. DT013, scale bar = 5 mm; 10. DT014, scale bar = 5 mm; 11. DT015, scale bar = 1 mm; 12. DT142, scale bar = 1 mm.

Skeletonization is the consumption of the complete thickness of intercostal leaf tissues but leaving one or more orders of veins intact. Further DT classifications within skeletonization are often based on skeletonization area shape, position, residual orders of the vein, the extent of development of plant response tissue, etc.

In the Huaitoutala flora, skeletonization is represented by DT016, DT017, DT020, DT021, and DT024. DT016 (Plate II, 1), showing a weakly developed reaction rim, is the most abundant skeletonization DT at Huaitoutala. By comparison, DT017 (Plate II, 2), possessing a strongly developed reaction rim, was examined with only one occurrence. Besides, DT020 (Plate II, 3) described as elongate, curvilinear to rectilinear skeletonization area and DT024 (Plate II, 5) identified by ovoidal to circular skeletonization area were also recorded with only one occurrence

separately. The distinctive DT021 (Plate II, 4) had three occurrences, represented by the removal of highest vein orders and absence of broad swaths of interveinal tissue. For the host specificity, DT016, DT017 represent generalized damage with no host preference (HS = 1) and DT020, DT021, and DT024 with intermediate host specificity (HS = 2).

Host plants: morphotype 4; morphotype 7; morphotype 8; morphotype 10; morphotype 11; morphotype 15; morphotype 16.

4.4. Surface feeding

DTs information: DT029 (9 occurrences, Plate II, 6), DT030 (3 occurrences, Plate II, 7), DT031 (3 occurrences, Plate II, 8).

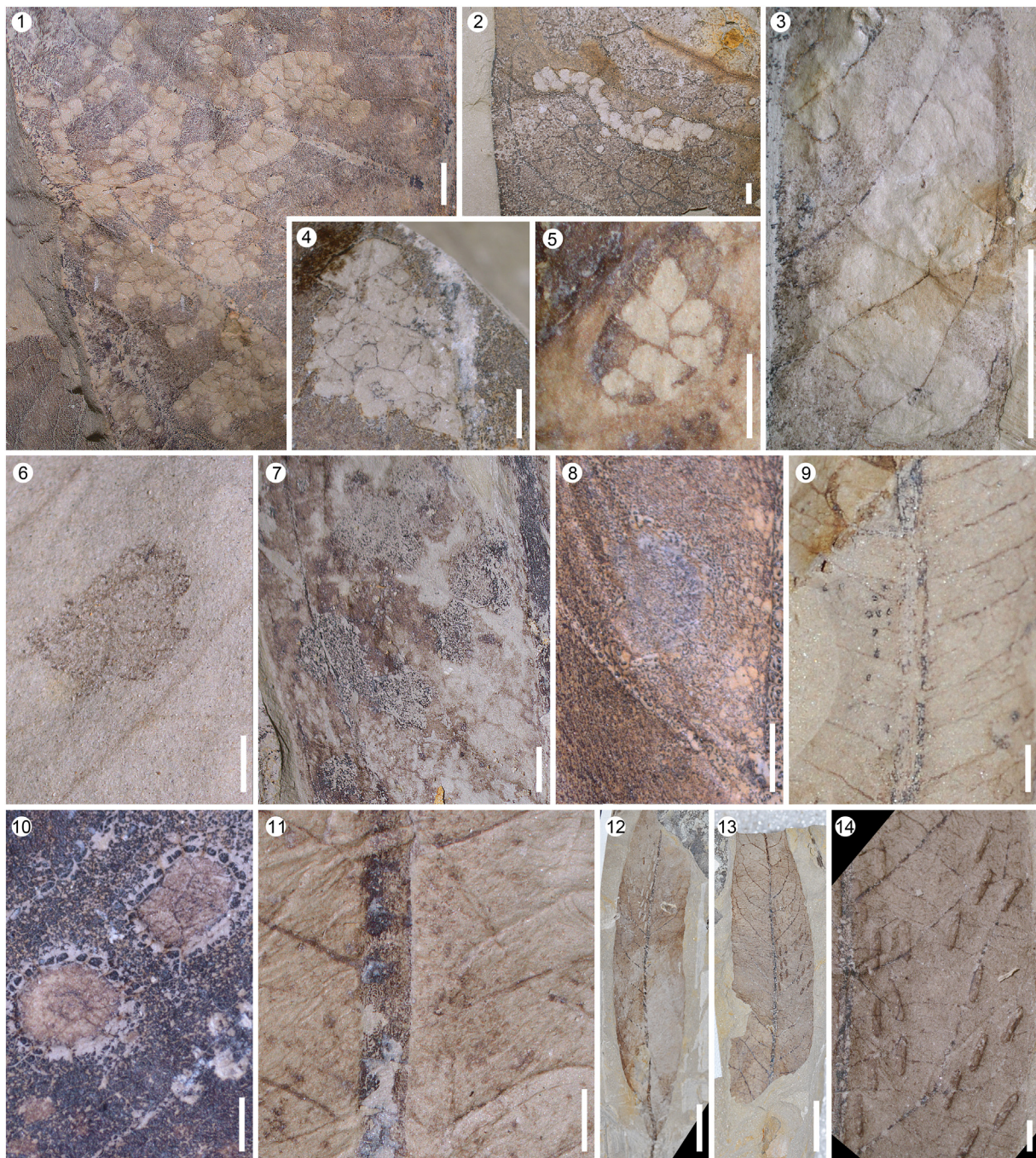


Plate II. Representative skeletonization, surface-feeding, piercing & sucking and oviposition traces on leaves of the middle Miocene Huaitoutala flora. 1–5. skeletonization traces; 6–8. surface-feeding traces; 9–11. piercing & sucking traces; 12–14. oviposition traces. 1. DT016, scale bar = 1 mm; 2. DT017, scale bar = 1 mm; 3. DT020, scale bar = 5 mm; 4. DT021, scale bar = 1 mm; 5. DT024, scale bar = 1 mm; 6. DT029, scale bar = 1 mm; 7. DT030, scale bar = 1 mm; 8. DT031, scale bar = 1 mm; 9–10. DT046, scale bar = 1 mm; 11. DT168, scale bar = 1 mm; 12–13. DT054, scale bar = 10 mm; 14. DT054, enlargement of M, scale bar = 1 mm.

Surface feeding, as one subgroup of external foliage feeding, is described by abraded or scraping damage of one or more tissue layers from a plant-organ surface without removing the whole layers. Detailed DT divisions in surface feeding are often based on surface abrasion shape, position, the extent of development of plant response tissue, etc.

In the present materials, surface feeding is the least common external feeding damage observed on dicot fossils from Huaitoutala occurring 15 times with three different DTs. The most frequent type of surface feeding was determined as DT029, possessing abrasion of varied sizes and shapes without well-developed reaction rims (Plate II, 6). By contrast to the weak or absent reaction rims of DT029 (Plate II, 6), DT030 (Plate II, 7) expresses strong reaction-rim development.

Meanwhile, the difference between DT030 (Plate II, 7) and DT031 (Plate II, 8) is abrasion shape, with the former shows a polylobate shape while the latter shows a circular to ellipsoidal shape. However, differently from DT029, both DT030 and DT031 were very rare in this flora. All these 3 DTs were divided into generalized levels of herbivore specificity.

Host plants: morphotype 4; morphotype 10; morphotype 11.

4.5. Piercing and sucking

DTs information: DT046 (7 occurrences, Plate II, 9,10), DT168 (1 occurrence, Plate II, 11).

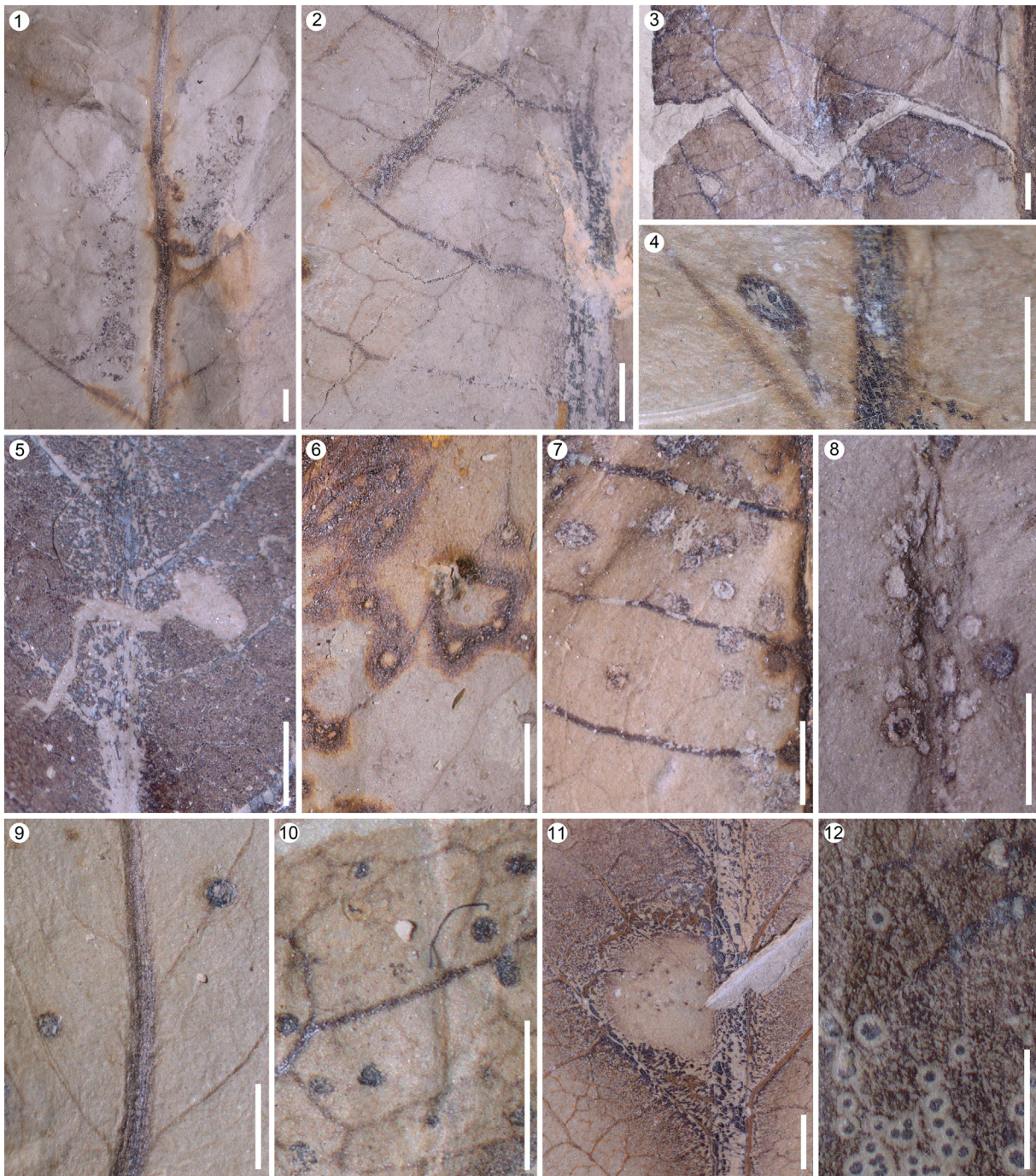


Plate III. Representative mining and galling traces on leaves of the middle Miocene Huaitoutala flora. 1–5. mining traces; 6–12. galling traces. 1. DT037; 2. DT040. 3; DT105; 4. DT171; 5. DT176; 6. DT011; 7. DT032; 8. DT033; 9. DT034; 10. DT080; 11. DT120; 12. DT144. scale bar = 1 mm.

Some arthropods, for example, aphids and scale insects, possess very specialized stylet-like mouthparts to penetrate plant organs and suck the nutritious sap. The penetrative puncturing damage caused by such kinds of herbivores is known as piercing and sucking. The internal division of piercing and sucking is often based on puncture shape, pattern, size, and position, etc.

In the Huaitoutala flora, there are two different types of piercing and sucking, i.e., DT046 and DT168. Most common are circular, centrally depressed punctures with less than 2 mm diameter (DT046, [Plate II](#), 9,10). DT168 can be identified by rounded, ~0.5 mm scales, including earlier waxy instars along or covering the main veins ([Plate II](#), 11). It is the least common piercing and sucking damage type at Huaitoutala. For

the host specificity, both DT046 and DT168 represent specialized host specificity (HS = 3).

Host plants: morphotype 7; morphotype 10.

4.6. Oviposition

DTs information: DT054 (2 occurrences, [Plate II](#), 12–14).

Oviposition damage is caused by the egg-laying process of female insects. In other words, oviposition only represents the response of egg insertion into plant tissues, although it is classified as a kind of FFGs. Detailed DT division in oviposition is often based on oviposition scars

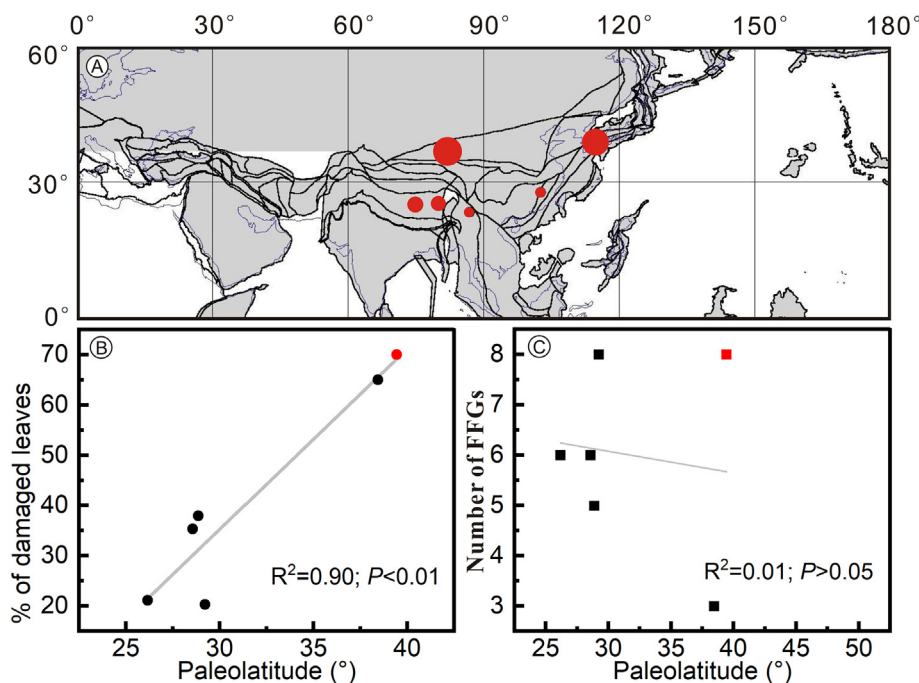


Fig. 2. Latitudinal distribution of damage frequency and diversity in the Miocene. A. map of Miocene sites with arthropod-damaged fossils. The size of red dots represents the actual percentage of damage frequency. B. Latitudinal pattern of damage frequency. The red dot represents the percentage of damage frequency from the Huaitoutala flora. C. Latitudinal pattern of damage diversity. The red dot represents the number of FFGs of the Huaitoutala flora. Detailed fossil site information can be found in Appendix C. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

shape, amount, position, orientation, the appearance of reaction rims, etc.

Only one type of oviposition (DT054, Plate II, 12–14) with two occurrences was recorded in the Huaitoutala flora. The distinctive oviposition DT054 is identified by more than 20 ovoidal scars, 1.0–1.5 mm long, arranged into multiple, subparallel rows (Plate II, 14), representing a very specialized interaction (HS = 3).

Host plants: morphotype 4.

4.7. Mining feeding

DTs information: DT037 (2 occurrences, Plate III, 1), DT040 (2 occurrences, Plate III, 2), DT105 (1 occurrences, Plate III, 3), DT171 (1 occurrences, Plate III, 4), DT176 (1 occurrences, Plate III, 5).

Leaf mining is a specialized feeding habit in which the larva feeds within host-plant leaf tissue while the epidermis remains intact. Therefore, like piercing and sucking, mining is also one subgroup of endophytic feedings. Detailed DTs in mining were defined by their pathway and extension of frass, position on the plant organ, the shape of the terminal chamber, occurrence patterns of coprolites, etc.

In the Huaitoutala flora, seven occurrences related to 5 DTs are assigned to mining traces. It means there is no dominant type among the 5 identified mine types. DT037 (Plate III, 1), a blotch mine with two occurrences, is characterized by an overall ellipsoidal shape with frass-laden serpentine internal space. Differing from occurrence patterns of coprolites within DT037, DT040 is filled with solid frass in the entire mine. Meanwhile, DT040 (Plate III, 2), shows a semi-linear trajectory with an enlarged terminal and also occurred in 2 records of the present flora. In addition, in each case, DT105, DT171, and DT176 appeared only once, and all of them had their own diagnostic criteria. For example, DT105 (Plate III, 3) was described as a serpentine non-frass mine with a parallel side. DT171 (Plate III, 4) was represented by a small frass-filled mine with a circular terminal chamber, while DT176 (Plate III, 5) was identified by a 3 mm long mine with a short linear early phase and a sharply expanded terminal phase. For the host

specificity, all DTs, including DT037, DT040, DT105, DT171, and DT176, represent specialized host specificity (HS = 3).

Host plants: morphotype 7; morphotype 10; morphotype 11.

4.8. Gall ing feeding

DTs information: DT011 (125 occurrences, Plate III, 6), DT032 (22 occurrences, Plate III, 7), DT033 (5 occurrences, Plate III, 8), DT034 (10 occurrences, Plate III, 9), DT080 (1 occurrence, Plate III, 10), DT120 (3 occurrences, Plate III, 11), DT144 (4 occurrences, Plate III, 12).

As one of types of endophytic feeding, galls are anomalous hypertrophic, differentiated and hyperplastic cells and tissues induced by parasitic or pathogenic organisms which can invade host-plant tissues and secrete substances. Detailed DT division in galling is often based on galls size, shape, position, the extent of development of plant response tissue, three-dimensional structures, etc.

Along with hole feeding, galling is the most common damage examined on leaves from the Huaitoutala records, including 170 occurrences with seven different DTs. Most common are circular to polylobate galls with less than 4 mm in longest dimension, possessing an unhardened central tissue and surrounded by a wide rim of thick area (DT011, Plate III, 6). DT032 (Plate III, 7), followed by 22 occurrences, described as small circular galls occurring on the interveinal areas. By contrast, DT033 with five occurrences often occurs on primary veins (Plate III, 8), and DT034 with ten records occurs on secondary veins of the leaf (Plate III, 9). DT144 has four occurrences and is identified by its fused galls with dark inner core and surrounding smooth surface and circular margins (Plate III, 12). Besides, the semicircular, ~2.5 mm diameter galls with a woody outer rim attached to the primary vein (Plate III, 11) were assigned to DT120 with three occurrences. DT080 (Plate III, 10), characterized by hemispherical, thoroughly carbonized galls with ~0.3 mm diameter avoiding primaries and secondaries, was examined only in one occurrence. These galling DTs provide a range of host-plant specialization, from generalized (DT011) to intermediate (DT032, DT034, DT080, DT120, DT144), to specialized (DT034) feeding behaviors.

Host plants: morphotype 4; morphotype 7; morphotype 8; morphotype 9; morphotype 10; morphotype 11; morphotype 16.

5. Discussion

At present, plant–arthropod associations from many Cenozoic floras have been reported, which have provided important information for the understanding of plant–arthropod interaction and paleoecology/paleoclimate conditions (e.g., Wilf and Labandeira, 1999; Wilf, 2008; Wappler, 2010; Su et al., 2015; Adroit et al., 2016; Currano et al., 2019; Deng et al., 2020; Robledo et al., 2020). However, compared to most previous works on Cenozoic floras, a much higher percentage of arthropod-damaged leaves (70%) was observed in the Miocene of Huaitoutala. For example, the Eocene Luckenau Clay Complex flora of central Germany contains ca. 6.1% damaged leaves (Müller et al., 2018), while the Miocene Lingang flora, southern China, includes 21% (Zhang et al., 2018). Moreover, the fact of 36 varied DTs belonging to 8 FFGs further indicates a high damage diversity, namely hole feeding, margin feeding, skeletonization, surface feeding, oviposition, piercing & sucking, leaf mining, and galling. Both these exceptional facts raise the question of why there was such a high percentage of leaves with traces of herbivory in the Miocene Huaitoutala flora.

Many factors had a significant influence on herbivory, including both biotic and abiotic ones (Adams et al., 2010; Currano et al., 2011; Wappler et al., 2012; Leckey and Smith, 2017; Müller et al., 2018; Loughnan and Williams, 2019; Ma et al., 2020). By comparing to the published data from other paleofloras, insights could be gained to interpret the unique pattern and intensity of arthropod damage in the Huaitoutala flora.

For abiotic factors, a latitudinal difference in arthropod damage frequency and diversity was found in both modern- and paleo-floras (Coley and Barone, 1996; Adams and Zhang, 2009; Adams et al., 2010; Zhang et al., 2011; Coley and Kursar, 2014; Liu et al., 2020). The effects of latitudinal gradients are comprehensive by containing various climatic impacts especially related to temperature (Wilf and Labandeira, 1999; Currano et al., 2010). Besides, previous studies suggest that carbon dioxide (CO₂) concentration might affect arthropod herbivory by influencing C/N ratios and photosynthesis rates (i.e., Wappler et al., 2012; DeLucia et al., 2012). Therefore, to eliminate the effects of CO₂, all the Asian Miocene floras with arthropod damage data are selected for comparison with the Huaitoutala flora under consideration of latitudinal gradients, based on the resolution of geological dating and data availability (Appendix C). The results show that there is a strong positive correlation between latitude and damage frequency ($R^2 = 0.90$, $P < 0.01$; Fig. 2A and B), but no obvious relationship between number of FFGs and latitude ($R^2 = 0.01$, $P > 0.05$; Fig. 2C).

In modern floras, most studies display an increase in the diversity and intensity of herbivory with lower latitude (Coley and Barone, 1996; Adams et al., 2010; Zhang et al., 2011). A similar result was also found in a study on Permian plant–arthropod interactions (Liu et al., 2020). However, the present consequence of the Asian Miocene latitude–damage frequency relationship does not support the above viewpoint of modern and Permian latitude–damage studies. In fact, although increased herbivory with decreased latitude seems intuitively reasonable because of more stable and favorable climate conditions at a lower latitude, there are some previous studies showing different latitude–herbivory patterns, i.e., uncorrelation (Andrew and Hughes, 2005; Loughnan and Williams, 2019), or even positive correlation (Adams and Zhang, 2009), like in the present study.

Independently studying herbivory–latitude patterns within different climatic zones might provide further explanations. In terms of modern temperature zones, within some species, less folivory in warm lower latitudes than cool higher latitudes was reported (Adams and Zhang, 2009). However, in sub-tropical to tropical forests, herbivore diversity and rates of herbivory increase with decreased latitude (Coley and Barone, 1996). This is explained as a result of varied temperatures

along the latitudinal gradient (Coley and Barone, 1996; Adams et al., 2010). Similarly, when only considering low-latitude Miocene floras such as the Toupai flora (Ma et al., 2020), Arunachal Pradesh flora (Khan et al., 2014), Darjeeling flora (Khan et al., 2015), Lincang flora (Zhang et al., 2018), the result also shows that the damage frequency is positively correlated with the mean annual temperature and the coldest month mean temperature (Ma et al., 2020; Appendix C). At present, although there are no reconstructed climate data available from the selected Miocene floras in the mid-latitudes, i.e., the Geumgwangdong flora and Huaitoutala flora, the Miocene latitude–herbivory pattern still provide part of the explanation for the unexpected high damage frequency from the Huaitoutala flora. Moreover, the number of FFGs is not correlated with latitude (Fig. 2C), perhaps because other factors confound the relationship.

In addition to latitude, local habitat is also an important abiotic factor. Comparing to other Miocene floras, the damage frequency and diversity of the Huaitoutala flora are similar to that of the Hindon Maar flora (Möller et al., 2017) and Geumgwangdong flora (Paik et al., 2012). Habitat analysis shows that both the Hindon Maar and Geumgwangdong floral sites represent isolated volcanogenic lakes, surrounded by zonal vegetation on fertile volcanic soil (Paik et al., 2012; Möller et al., 2017). Favorable growth conditions, including fertile soil, could promote the flourishing and diversity of the host plants, which have a positive relationship with herbivory (Wappler et al., 2012; Möller et al., 2017). However, based on sedimentological and mammal data, the Huaitoutala flora developed in a freshwater lakeside. The inferred habitat reflects the flora related to a lake surrounded by forest (Wang et al., 2007). Several plants of swampy habit, for example, reeds and *Equisetum*, developed at the borders of the water bodies near the lakeshore. At the same time, a forest habitat existed at a close distance to the lake as indicated by mammals (i.e., *Lagomeryx* and *Stephanocemas*), preferring forest (Wang et al., 2007). It seems that although all these three floras show high damage frequency, the reasons are different in terms of habitat factors.

As most studies observed, the higher level of damage diversity and frequency from most functional feeding groups (FFGs) connected obviously with a warmer and more humid environment. While the microenvironment hypothesis suggests that gall makers produce galls to resist harsh environment. Therefore, it often shows the opposite response due to galls' lower resistance against pathogens (Labandeira and Prevec, 2014; Labandeira, 2021) and parasitoids (Schachat et al., 2019). However, it seems contradictory that the Huaitoutala flora exhibits a high frequency of DTs either from galling or other functional feedings. In the Huaitoutala floras, besides hole feeding, the high frequency of galling substantially contributes to the rich leaf damage in the Huaitoutala flora. A similar proportional composition of FFGs is also found in the Lincang flora (Zhang et al., 2018). Nevertheless, differing from suitable habitat in Lincang flora, considering the near-lake habitat, the high frequency, and diversity galling observed in the Huaitoutala flora might indicate different environmental stress (Fernandes and Price, 1992; Price et al., 1998; Müller et al., 2018).

Notably, the damage type identification accepted here was based on a catalog of damage types on plant fossils published by Labandeira et al. (2007). In this catalog, microscopic round or oval plaques, tubercles, and dots, 1 mm or less in diameter, occasionally with the pits, on fossil plants are interpreted as galls caused by insects (e.g., Labandeira et al., 2007; Donovan et al., 2016). It is assumed that such galls are produced by insects, however, they can also be initiated by small mites (Knor et al., 2013). Moreover, this type of damage is macromorphologically very similar to that caused by endophytic micromycetes (e.g., Maslova et al., 2018, 2021). For example, it cannot be ruled out that DTs 034, 080, and 144 (Plate III, 9, 10, 12) represent substances that could also be produced by fungi. Moreover, the final result of the plant responses might be integrated. Arthropods can be carriers of fungal spores, bacteria, or viruses, which cause secondary damage to areas that insects first attacked (e.g., Rohfritsch, 2008; Kobune et al., 2012). The Huaitoutala

flora developed in the lakeshore might also provide a high air humidity to produce galls by fungi. Whereas DTs 034, 080, and 144 just contribute a little for high damage frequency in the Huaitoutala flora.

The dominant type of galling in the Huaitoutala flora is DT011, which is interpreted as a generalized type of feeding on plant hosts, although galling often represents highly specialized feeding. The richness of DT011 with a low value of host specificity might imply that the Miocene Huaitoutala flora suffered from the environmental or nutritional stress. In general, three hypotheses, i.e., “Hydric stress hypothesis,” “Nutritional stress hypothesis,” and “Plant species richness hypothesis”, are used to explain the richness and abundance of galling (Julião et al., 2018). For example, galling richness under humid conditions is lower than under relatively dry conditions due to the high activity of fungi in the moist environment. The test by Price et al. (1998) based on 280 samples of local species of galling herbivorous arthropods from 14 countries also shows a reduced richness in the wet tropics and cool temperate regions. This means harsh environment stress, especially water stress is strong relative to the richness of galling.

For the Huaitoutala section, evidence based on geochemical proxies and fossils (Wang et al., 2007; Zhuang et al., 2011, 2014; Bao et al., 2019; Fu et al., 2022) suggests a relatively warm and humid climate during ca. 15.3–12 Ma, including ~12.7 Ma of the present flora. Even though, the location of the present flora near the lake may still cause physiological dryness of plant hosts due to the oxygen limitation in roots and sustaining wind presence, like those in the modern ecosystem (Parent et al., 2008). Previous studies also suggest physiologically relevant stresses on the host plants rather than the humid environment could increase the richness and frequency of galls (Price et al., 1998). Besides, the high diversity and frequency of galling in the Huaitoutala flora might be related to the diversity of host species. It is supported by the phenomenon that total 7 leaf morphotypes in the Huaitoutala flora suffer the damage of DT011 (Appendix B). Meanwhile, sedimentological evidence indicate a rapid intensified aridity in Huaitoutala ca. 12.6 Ma (Bao et al., 2019). This process of aridification is also suggested by mammal data (Wang et al., 2007). The drying and cooling of the climate could lead to the succession of plants. Therefore, the late successional forests, temperature and host abundance also tends to cause the nutritional stress, which favors the prevalence of galling (Fernandes and Price, 1991; Adroit et al., 2016). Moreover, the modern global galling pattern suggests the peak of galling species richness on the latitudinal gradient was between 25 to 38°N or S (Price et al., 1998). The paleolatitude of the Huaitoutala site was located in 39°N, close to the peak range of modern galling richness.

Besides abiotic factors, biotic factors may also influence the damage frequency and diversity, such as differences in species composition, herbivory preference, and leaf trait characters (Curran et al., 2011; Adroit et al., 2018; Loughnan and Williams, 2019). For host differences, among all 17 leaf morphotypes in the Huaitoutala flora, no arthropod traces have been found associated with leaf morphotypes 1, 2, 3, 6, and 13 (Appendix B). The damage frequencies in the four most common morphotypes (morphotype 7, 8, 10, and 11) vary from 49% to 95%. In addition, cosmopolitan species, such as *Salix* found in the present flora, tend to have a higher background level in the diversity of herbivorous arthropods (Cornell, 1985). Therefore, host diversity might be an important factor affecting the damage frequency. In the Huaitoutala flora, the dominant functional feeding groups are hole feeding and galling, and 87% of damage types belong to generalized damage with no host preference. Herbivores consuming multiple host plant taxa, in some ways, could alleviate competition (Coley and Kursar, 2014). In turn, arthropods in the present flora may be highly competitive, resulting in a high damage frequency. However, as mentioned above, different leaf morphotypes suffer from different arthropod damage intensity. It means that such kinds of arthropods might have a bias in host selection. It may be due to the differences in leaf traits. In general, “slow-return” species with high LMA are typically associated with greater thickness, lower nutritious and higher amounts of secondary metabolites (Coley,

1983; Wright et al., 2004; Royer et al., 2007). And leaves possessing all of these characteristic often have relatively low damage by arthropods (Mithöfer and Boland, 2012). In other word, there is a negative correlation between LMA and damage frequency (Royer et al., 2007). In the Huaitoutala flora, the average LMA of M10, the most abundant morphotype including 198 samples, is 89 g/m². This value is far less than the upper bound of the transition between “fast return” species and predominately “slow-return” species (129 g/m²; Wright et al., 2004). The relatively low paleo-LMA value of M10 might be associated with high damaged frequency (Royer et al., 2007). Regarding leaf richness, the present flora is dominated by thin-leaved taxa (Plates I–III, Appendix A). This may be one of the important factors for the high damage frequency.

6. Conclusion

1) Plant–arthropod interactions are examined based on arthropod damaged leaf fossils from the Miocene Huaitoutala site. For the recovered leaf fossils, eight principal functional feeding groups of 36 damage types among 17 dicot leaf morphotypes are categorized, indicating a wide range of feeding guilds, suggesting an ecosystem of prosperity.

2) Compared to other Miocene floras, the Miocene Huaitoutala flora represents an unexpectedly high frequency of arthropod-damaged leaves ca. 70%. The results indicate that, apart from climatic factors, biotic factors and local niche influence may have played important roles in explaining the plant–arthropod interactions.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2021.104569>.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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