Research

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A case of long-term herbivory: specialized feeding trace on *Parrotia* (Hamamelidaceae) plant species

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Interactions between plants and insects evolved during millions of years of coevolution and maintain the trophic balance of terrestrial ecosystems. Documenting insect damage types (DT) on fossil leaves is essential for understanding the evolution of plant–insect interactions and for understanding the effects of major environmental changes on ecosystem structure. However, research focusing on palaeoherbivory is still sparse and only a tiny fraction of fossil leaf collections have been analysed. This study documents a type of insect damage found exclusively on the leaves of *Parrotia* species (Hamamelidaceae). This DT was identified on *Parrotia* leaves from Willershausen (Germany, Pliocene) and from Shanwang (China, Miocene) and on their respective endemic modern relatives: *Parrotia perisca* in the Hyrcanian forests (Iran) and *Parrotia subaequalis* in the Yixing forest (China). Our study demonstrates that this insect DT persisted over at least 15 Myr spanning eastern Asia to western Europe. Against expectations, more examples of this type of herbivory were identified on the fossil leaves than on the modern examples. This mismatch may suggest a decline of this specialized plant–insect interaction owing to the contraction of *Parrotia* populations in Eurasia during the late Cenozoic. However, the continuous presence of this DT demonstrates a robust and long-term plant–herbivore association, and provides new evidence for a shared biogeographic history of the two host plants.

1. Introduction

An ecosystem is a set of abiotic environmental conditions with communities of organisms living and interacting therein. Interactions between organisms contribute to a fragile equilibrium within ecosystems [1–3], and this balance can be drastically disturbed by modern human activities [4–6]. Global environmental change is expected to affect plant–insect associations in various ways, as insects play significant roles such as herbivores [7] and pollinators for crop production [8]. These interactions are the result of millions of years of evolution [9–11]. Plant–herbivore interactions are of particular importance for terrestrial food webs that sustain biodiversity and ecosystem balance [12–14]. Variation in the style and quantity of herbivory depends mostly on abiotic parameters, primarily climatic conditions [9,15–17]. Consequently, it is not surprising that many studies have measured significant changes in the patterns of herbivory on fossil leaves through geological time as environmental conditions have changed [16,18–25].

Recent research has been carried out on some late Cenozoic floras from Europe using standardized damage type (DT) nomenclature. This research includes work on the famous Lagerstätte of Willershausen in Germany [26]. During the identification of herbivory traces on fossil leaves of Willerhsausen (i.e. 8073 fossil specimens analysed), an insect DT was recorded exclusively on fossil leaves similar to *Parrotia persica* (DC.) C. A. Mey. These leaves were the most abundant within the fossil assemblage [26,27] and hosted many examples of this specific insect feeding trace [26]. Parallel to this study, another investigation was conducted mostly on modern leaves of *P. persica* from the Hyrcanian forest region [28]. During this study, herbivory traces similar to those on the fossils were observed on living *P. persica* at Aliabad-e Katul, Pasand and Molla Kala in Iran (figure 1). Lastly, within the framework of another project on fossil plants from the Lagerstätte of Shanwang (Miocene), north-east China [31,32], around 1300 leaves were studied and the same insect feeding trace was identified on just one *Parrotia* leaf.

This study describes the type of the plant–herbivore interaction found exclusively on leaves of the two known *Parrotia* species. In addition to the fossil and modern materials mentioned previously, some modern leaves of *Parrotia subaequalis* were also measured in the Yixing forest (China), where one of the small endemic populations of *P. subaequalis* still exists [33]. We discuss how such external leaf feeding remained unchanged for 15 Myr across Eurasia, in the face of major environmental changes. Finally, we discuss how this discovery provides new perspectives on the evolution of plant–insect interactions.

2. Material and methods

2.1. Fossil record of *Parrotia*

Parrotia was present in East Asia and possibly North America during the Eocene and seemed to spread to western Eurasia across Central Asia during the Oligocene [34]. During the early Oligocene the genus was present in Kazakhstan from where it disappeared during the Miocene [35]. *Parrotia pristina* (Ettingshausen) Stur and *Parrotia fagifolia* (Göppert) Heer were described from Europe. These names were also used for Palaeogene and Neogene leaf fossils of East Asia [36,37]. In addition, *Fothergilla* Hu & Chaney [38] was described from the early to middle Miocene Shanwang flora of China. Based on the morphological similarity with the extant *Shaniodendron subaequalis* (=*Parrotia subaequalis*), *Fothergilla virburnifolia* was later transferred to *Shaniodendron viburnifolium* (Hu and Chaney) Wang & Li [39]. In Europe and Kazakhstan, fossils assigned to *Parrotia* are commonly called *P. pristina* (*P. fagifolia* being a junior synonym). In East Asia, the nomenclature is somewhat unclear: *S. viburnifolium* should be treated as *Parrotia virburnifolia* based on the current taxonomic treatment of *Shaniodendron* as a synonym of *Parrotia* [40]. At the same time, this name competes with the earlier name *P. pristina*, which also has been used for East Asian fossils. For practical reasons, in this study we refer to the European fossils as *P. pristina* and to the East Asian examples, as *P. viburnifolia*.

2.2. *Parrotia persica* (DC.) C. A. Mey

Parrotia perisca is a deciduous tree 8–25 m tall [41]. The leaves are oblong to obovate, up to 15 cm long and 6 cm wide, with 5–8 pairs of secondary veins [27,41,42]. Nowadays, *P. persica* exists only in the Hyrcanian forest south of the Caspian Sea (Iran, Azerbaijan). The leaf shape of *P. persica* is very consistent despite there being size variability in leaves throughout the Hyrcanian forest owing to variable local abiotic
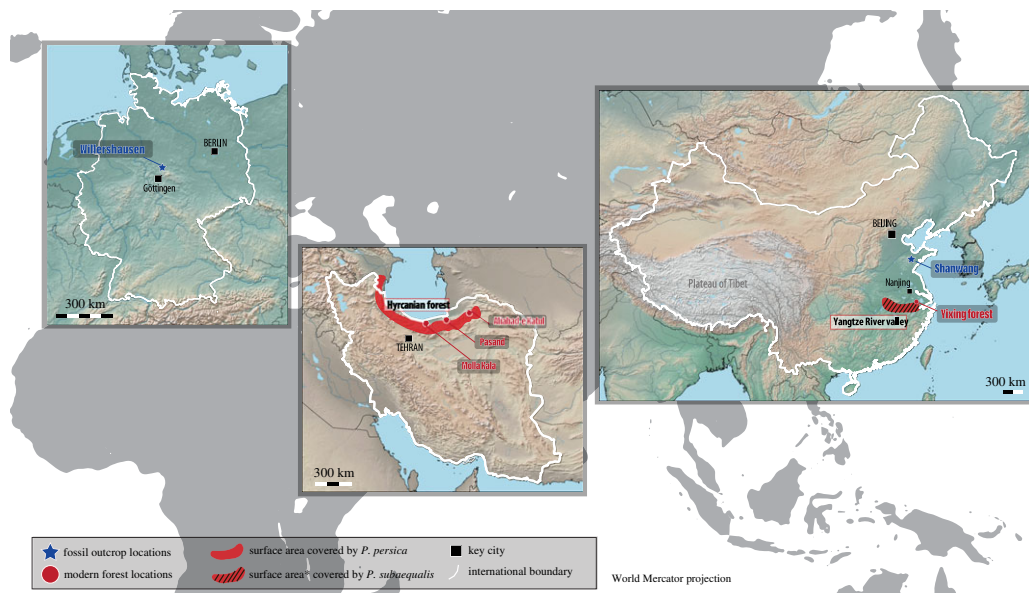
Figure 1. Eurasian locations including both fossil and modern occurrences of *Parrotia* that contain examples of the damage type DT297. The distribution for *P. subaequalis* in China has been drawn in one large area for clarity. In reality, the distribution of *P. subaequalis* in the Yangtze River valley is very fragmented, only small isolated populations occur in the valley. More details are provided by Geng *et al.* [29] and Li & Zhang [30].

conditions [43]. *Parrotia persica* is an Arcto-Tertiary relict species [34]. Its close fossil relatives were very common in European forests during the Neogene [42,44–50]. In this study, fossil leaves from Willershausen (Pliocene) in Germany and modern leaves from the Hyrcanian forest in northern Iran were studied comparatively (figure 1).

2.2.1. Willershausen, 3 Ma, Germany

Willershausen is a Lagerstätte in the centre of Germany, close to Göttingen (figure 1). It is a lacustrine clay pit containing more than 130 fossil plant species including many leaves of *Zelkova zelkovifolia*, *Carpinus orientalis* Mill., *Carya minor* Schenk and *P. pristina* [27,48,51] the last of these is the most abundant in the fossil plant assemblage of Willershausen [26]. The palaeoforest represented by this fossil leaf assemblage is dated around 3 Ma; MN 16/17 [34,52]. Adroit *et al.* [26], analysed 8073 leaf specimens of which 517 were attributed to a fossil relative of *Parrotia*.

2.2.2. Hyrcanian forest, modern, northern Iran

In terms of plant species richness, the Hyrcanian forest region (figure 1) is considered a good modern analogue of the European forests of the late Cenozoic [42,53], such as that represented by the Willershausen Lagerstätte. The Hyrcanian forest region is a refuge for several extant Arcto-Tertiary plant species that are endemic to this area (such as *P. persica*) [34,42,54,55]. This forest extends from Golestan National Park (northeastern Iran) to eastern Azerbaijan, and is bordered by the Caspian Sea to the north and the Alborz mountains to the south, encompassing 1.85 million ha [56]. Adroit *et al.* [28] collected and analysed 2160 leaves of *P. persica* and observed additional leaves from other species (such as *Zelkova carpinifolia* (Pall.) K. Koch, *Quercus castaneifolia* C. A. Mey, *Acer cappadocicum* Gled.), which commonly co-occur with *Parrotia*.

2.3. *Parrotia subaequalis* (H. T. Chang) R. M. Hao and H. T .Wei

Similar to its sibling species [57,58], *P. subaequalis* is a large shrub or small tree, 5–10 m tall [57]. Rarely, it reaches up to 20 m tall with pruning and staking, as evident in a village on Qingliang Peak, Linan, China. Leaf blades of *P. subaequalis* are mostly broad-obovate or elliptic, 4–6.5 cm long, and 2–4.5 cm wide, and thinly leathery [59]. *Parrotia subaequalis* is a Cenozoic relic plant species endemic to eastern China [29].

Fossil specimens from Miocene strata indicate the former distribution of *Parrotia* in Shanwang, Shandong Province, northeastern Central China [60,61] and in Huadian, Jilin Province, northeastern China [62]. Its population size severely decreased during Quaternary glaciations [63]; the modern species has a narrow and scattered distribution on Mt Qinling-Dabie and Mt Tianmu (China). *Parrotia subaequalis* was described from Yixing, Jiangsu province as *Hamamelis subaequalis* H. T. Chang and later transferred to the monotypic genus *Shaniodendron* [64]. Subsequently, flower morphology [60] and a molecular phylogenetic study [58] suggested that *Shaniodendron* should be included within *Parrotia* resulting in the name *P. subaequalis*. The modern leaves of *P. subaequalis* came from the Yixing forest in eastern China (figure 1).

2.3.1. Shanwang, 18–15 Ma, China

Shanwang is a Lagerstätte [31] containing a diverse assemblage of organisms dominated by angiosperms [31,32]. It is located in northeastern China, in Shandong province (figure 1).

According to various dating methods, the Shanwang deposit is early—middle Miocene [65], i.e. 18–15 Ma [31,66–69]. Both pollen and fossil leaf studies indicate the presence of *Quercus*, *Pterocarya*, *Ulmus*, *Populus*, *Fraxinus*, *Carpinus* and *Betula* [70]. They represent an evergreen broad-leaved and mixed deciduous forest [70]. The fossil collection from this deposit is stored in the Nanjing Institute of Geology and Palaeontology (Nanjing, China) and includes 1298 leaves, of which 40 are attributed to *Parrotia*.

2.3.2. Yixing forest, modern, eastern China

The modern Yangtze River valley is an appropriate environmental analogue of the Shanwang Miocene site, although the Shanwang palaeoforest may have experienced lower annual temperatures including possibly colder summers and lower seasonality in rainfall. Yixing Forest Farm, located in the Yangtze River valley (figure 1), is one of the most significant state-owned forest farms in southwestern Jiangsu Province, covering 34 km², with 97% forest coverage. This farm is set in the region of Mt Yili, which is geographically a low-altitude hilly terrain forming the eastern extension of Mt Qinlin-Dabie [71]. There is a small population of *P. subaequalis* trees in the central part of Yixing Forest Farm, with three eminent old trees and around 20 mature individuals. Other small populations occur within and around the farm [29]. In the field, 41 leaves of *P. subaequalis* were sampled.

2.4. Observations

All the specimens were studied with a stereomicroscope (Leica EZ4) and a transmitted light microscope (Zeiss AXIO Zoom V.16). They were photographed with a Lumix GX8 mounted on a copy stand. The fossil leaves from the various collections were sampled many years ago and described in previous works. No additional sampling was attempted, as the fossil collections are large enough and because, nowadays, collecting in Willershausen (Germany) and Shanwang (China) is forbidden. All the modern leaves were sampled from the ground (litter) in the Hyrcanian forest region (Iran) and Yixing forest (China). Leaves from the litter are more representative for plant–insect interactions as herbivory is not homogeneously distributed throughout the tree and the whole spectrum of leaf DTs is best captured when leaves from all parts of the tree including the canopy are considered [72–75]. Moreover, to collect a fallen leaf from the litter means collecting after the whole lifespan of this leaf, and then no more herbivory can happen. Lastly, the leaves from the litter represent at least a part of the taphonomy process. For those reasons, the leaf litter is better for the standardization of samples for the whole study.

2.5. Terminology

Currently, the main reference to identify and classify the plant–insect interactions in the fossil record is the '*Guide to Insect (and Other) Damage Types on Compressed Plant Fossils*' [76]. This guide subdivides herbivory traces on leaves into seven functional feeding groups (FFGs): hole feeding, margin feeding, skeletonization, surface feeding, mining, piercing and sucking and galling. For each FFG, numerous DTs are recognized. For each of these DTs, a host specificity index (HS) is assigned that distinguishes between generalist and specialist damage [77]. The determination of this HS index is based on diverse parameters, such as its geographical distribution, plant species diversity affected by the damage, damage quantity, shape variations, among others factors (more details in [25,70]).

2.6. Deposition of fossil specimens

Fossil *P. persica* leaves from Willershausen (Germany) analysed in this study are all deposited at the Geoscience Centre of the University of Göttingen (GZG.W collection). The fossil leaves of *P. viburnifolia* (labelled as *P. subaequalis* in the collection) belong to the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (China).

2.7. Measurements

With the help of photography and the software IMAGEJ, each leaf was measured following several parameters, such as length, width and surface area of the leaf blade. Where possible, the width of the petiole was also measured in order to determine the leaf mass per area (LMA) for each specimen. LMA is an index that corresponds to the relationship between the thickness and the density of the leaf [78,79]. Thereafter, the specific damage on each *Parrotia* leaves was recorded and described, and the measurements of the surface area of the damage, the length and the width at three different positions along the damage, and the number of holes, were compared between the two *Parrotia* species and both fossil and modern leaves. Basic statistical tests based on the averages of measurements (Shapiro, Fisher and Wilcoxon) were made in addition to these morphological comparisons.

3. Results

At Willershausen, 32 leaves of *P. pristina* had the DT DT297 and we counted 143 occurrences in total. In general, one leaf can include more than one damage occurrence (figure 2). In Shanwang, four leaves of the species *P. viburnifolia* (= *P. subaequalis* fossil relative) had 13 occurrences of this specific DT. In all of the fossil collections, no leaves from other species had DT297. In the modern Hyrcanian forest, despite the large amount of *P. persica* leaves collected, only six had this DT, and in a low quantity as only seven occurrences in total were recognized. In the Yixing forest, damage abundance is even lower; only four occurrences on two leaves of *P. subaequalis* were identified.

Overall, 167 damage occurrences were observed in this study among 43 leaves of *Parrotia* species (figure 2). A large majority of them were observed on *P. pristina* from Willershausen (85%) and then 7% on *P. viburnifolia* from Shanwang. The modern samples of *Parrotia* spp. (i.e. *P. persica* and *P. subaequalis* together) represent 8% of our observations.

3.1. Morphological description

The average of the damage measurements has been calculated by counting all the occurrences from all the leaves, but it must be noted that fossil *Parrotia* leaves from Willershausen are the most representative in terms of the size variability for this specific damage (figure 3). This is certainly a consequence of the large quantity of specimens analysed. Nevertheless, we split and compared the average of damage sizes per locality (then per *Parrotia* species) (figure 3).

The damage trace is a curved skeletonization subdivided in a row of several holes. This long, curved chain of small holes usually is less than 1 cm long. However, some of the specimens can reach 1.5 cm in length, but this is quite rare. Individual holes are commonly rectangular with rounded corners. The length of each hole never exceeds more than 1 mm and the width of each hole, i.e. the width of the damage, is around 0.6 mm. There is no variation of the width along the course of the damage. On average, the surface area of the damage is 4.1 mm^2 (±1.4) with a length of 5.4 mm (±1.3) and a global width of 0.6 mm (±0.08). The number of holes can vary from 3 to 12, but in most cases it is 5–8.
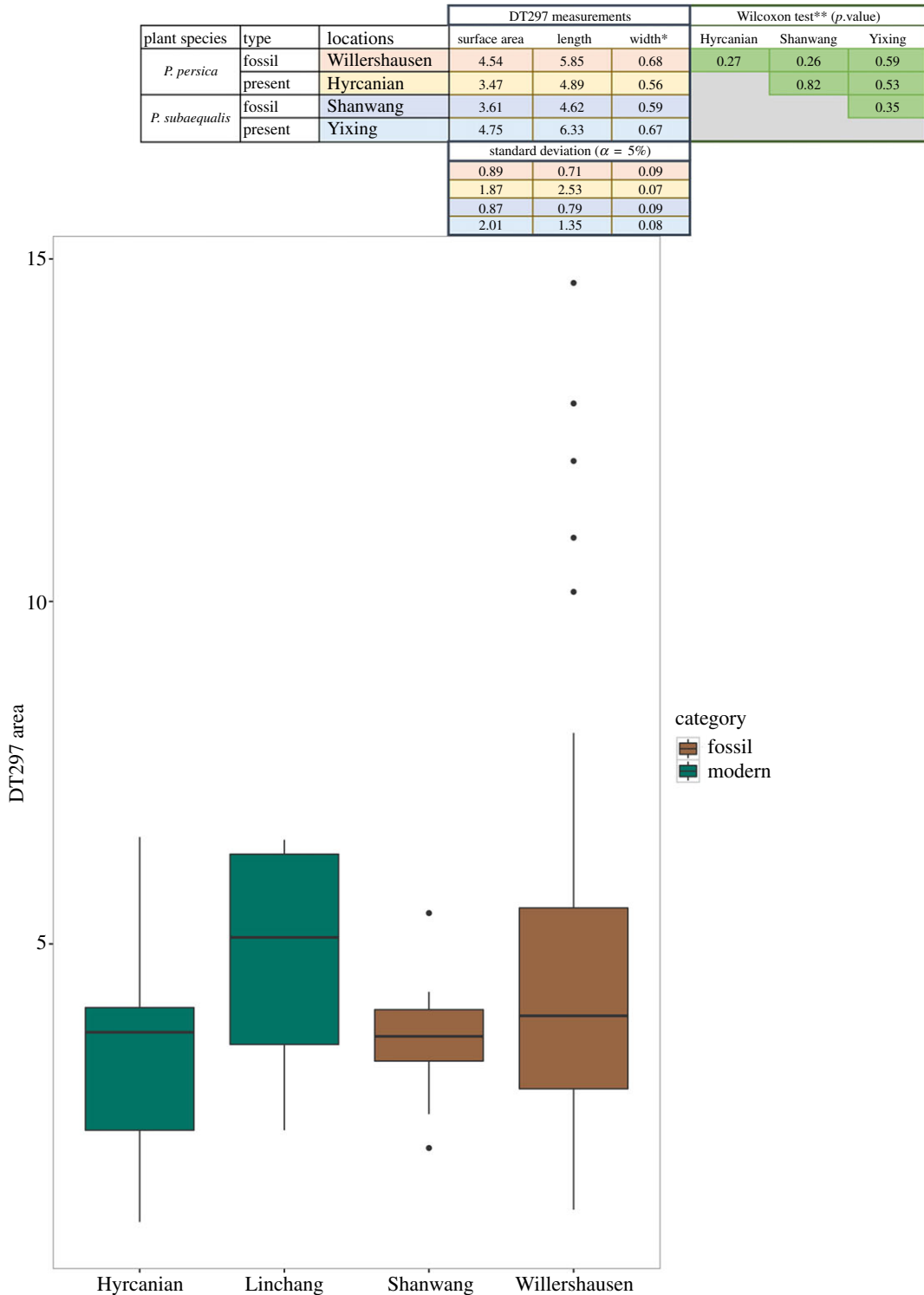
The small lines that separate individual holes from each other are very thin, commonly inconspicuous or missing. Although these lines are indistinct, it is possible to infer their existence by carefully observing the internal borders of the damage. In some cases, the small lines are missing along longer portions of the damage (figure 2, C2). The margin of the damage is marked by black edges. This black scar is a typical reaction from the leaf after being attacked by insect feeding and makes it possible to distinguish a herbivory trace made by an insect during the leaf's lifespan from a detritivorous trace made after abscission [76,77]. Overall, the path of the damage is not affected by the leaf venation. However, we noted that the damage usually follows a secondary vein instead of removing it. Exceptionally, we
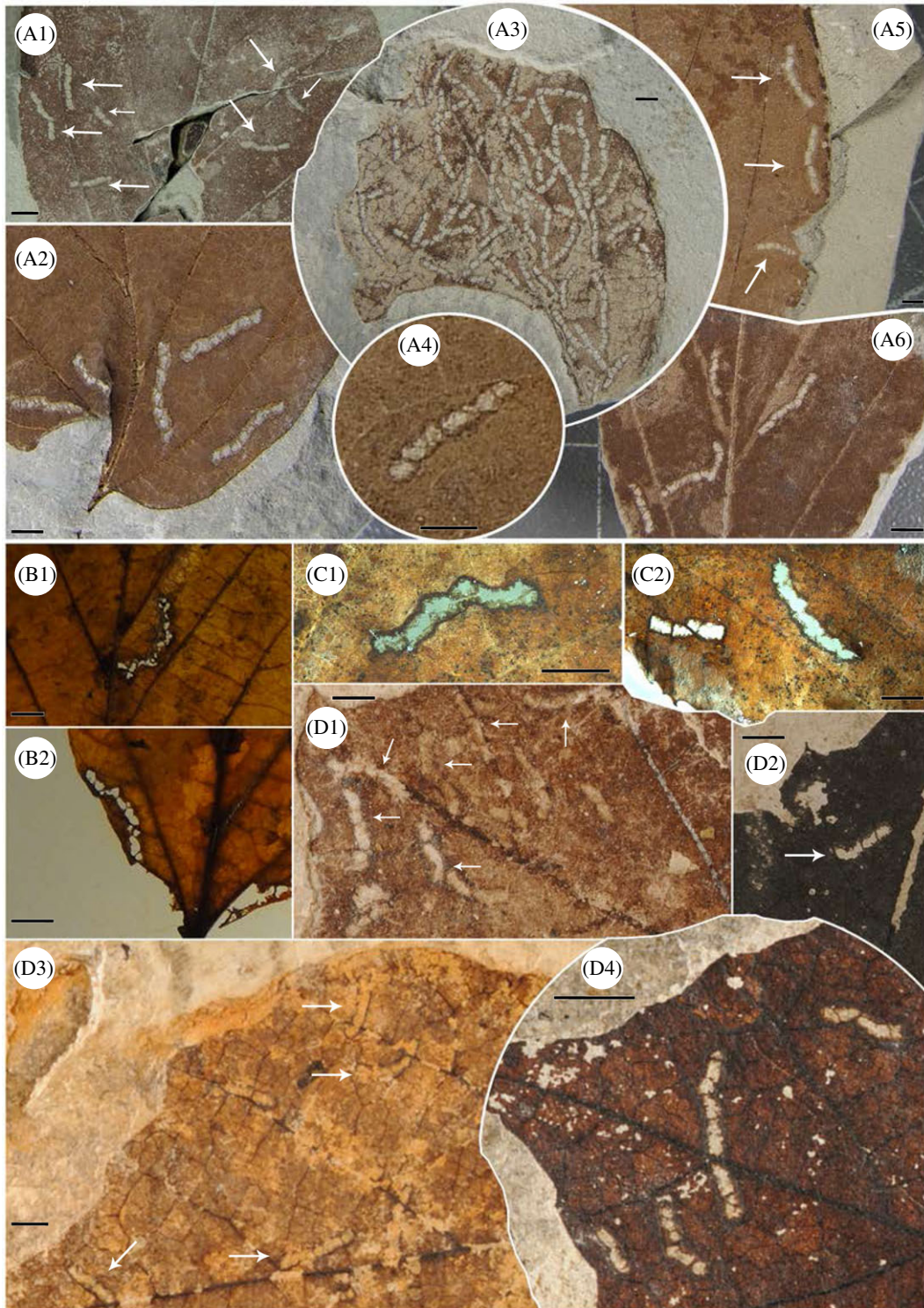
Figure 2. Damage type DT297 on every type of leaf attributed to *Parrotia*. A1–A6 Fossil specimens of *P. pristina* from the Pliocene of Willershausen, Germany. The material is deposited in the Geoscience Centre, University of Göttingen (GZG), Germany. B1–B2 Modern specimens of *P. persica* from the Hyrcanian forest (northern Iran), more details are provided by Adroit *et al*. [28]. C1–C2 Modern leaves of *P. subaequalis* from the Yixing forest, Yangtze River area, eastern China. D1–D4 Fossil specimens of *S. subaequalis* (= synonym of *P. subaequalis*) from the mid-Miocene of Shanwang, China. The material is deposited in the collection belonging to the Nanjing Institute of Geology and Palaeontology (NIGPAS), China. Black bars represent 2.5 mm.

noted that damage crosses over the primary vein (figure 2, D4) but without removing the vein. There is usually more than one damage example per leaf blade; a single example of damage per leaf is rare. We also observed some cases in which the entire leaf blade was covered by this damage (figure 2, A3).

plant species	type	locations	DT297 measurements			Wilcoxon test** (*p*.value)		
			surface area	length	width*	Hyrcanian	Shanwang	Yixing
P. persica	fossil	Willershausen	4.54	5.85	0.68	0.27	0.26	0.59
	present	Hyrcanian	3.47	4.89	0.56		0.82	0.53
P. subaequalis	fossil	Shanwang	3.61	4.62	0.59			0.35
	present	Yixing	4.75	6.33	0.67			
			standard deviation ($\alpha = 5\%$)					
			0.89	0.71	0.09			
			1.87	2.53	0.07			
			0.87	0.79	0.09			
			2.01	1.35	0.08			

Figure 3. Box-plots based on the comparison of the average area of DT297 per locality. Green boxes represent modern leaves, brown boxes denote fossil leaves. The upper table provides all measurements made on DT297. A Wilcoxon test comparison has been made on the measurements and the results concerning surface area comparison between each location are presented on the right. Surface area has been chosen as it directly includes the length and width. There is no significant difference between values from these sites ($\alpha = 1\%$).

3.2. Host plant

Based on the fossil record, there is little doubt that DT297 is exclusively found on *Parrotia* species. Investigations of fossil leaves from Willershausen were based on around 8000 fossil specimens representing more than 130 plant species/morphotypes. The Shanwang collection consists of around 1300 leaf specimens and includes more than 100 morphotypes.

3.3. The specimen reference of DT297

This DT was originally described as a trace fossil *Phagophytichnus catellarius* ichnosp. nov. by Straus [51]. The fossil specimen of *P. pristina* from which *Ph. catellarius* was described belongs to the Willershausen fossil collection from Göttingen. We photographed in high resolution the sample used for the holotype of this DT (electronic material supplementary, S1). The holotype is labelled GZG.W no. 10626 and is located in the Willershausen plant macrofossil collection at Göttingen University, Germany.

3.4. Classification

The classification of this DT follows the rules and terminology of the *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils* [76]. This damage is now designated: DT297.

4. Discussion

First and foremost, it is important to mention that there is no difference in terms of leaf thickness between the two extant *Parrotia* species or between fossil and modern leaves, as estimated by LMA (electronic material supplementary, S2) based on the method from Royer *et al*. [79]. LMA can be correlated with climatic factors [80–82], leaf nutrient availability [83,84] and, furthermore, can affect herbivory patterns observable on the leaf blade [78,85].

4.1. DT297: a new classification for this specialist insect damage trace

Our observations demonstrate that modern *P. persica* and *P. subaequalis* bear the same insect feeding trace (DT297). Morphological descriptions are consistent and statistical assessments support this observation. Indeed, measurements of the surface area, length and the width of this DT between the *Parrotia* species and between fossil and modern specimens do not reveal any significant differences ($\alpha = 0.1$) (figure 3). The statistics may be quite weak owing to the small number of measurements on modern leaves. However, as the statistics did not demonstrate any significant variations of measurements, our results indicate little size variation of the damage.

The DT DT297 (figure 4) is new for the '*Guide to Insect (and Other) Damage Types on Compressed Plant Fossils*' [76] and will be will be considered for the next version of that guide and classified into the 'skeletonization' FFG.

This herbivory trace is exclusively found on *Parrotia* for at least 15 Myr. Indeed, it is important to note that the outcrops mentioned in this study are not the only ones which have been investigated for the present study. Several fossil localities in Eurasia of Cenozoic age have also been investigated but lacked any trace of this DT [20,23,28,75,86–89], either on *Parrotia* leaves or on any other plant species. Such assemblages include the fossil leaves of *Parrotia* from Berga and Bernasso documented by Adroit *et al*. [26]. Further, the method of identification of DTs in the leaf fossil record [76] has now been used for more than 10 years in numerous studies throughout the world and through all geological time periods [18,21,24,25,90–92], and none mentioned feeding traces equivalent to DT297. Hence, DT297 can be considered a highly specialized term of skeletonization with a host specificity index of 3 (HS = 3).

4.2. Specialist herbivory pattern for 15 Myr in Eurasia

DT297 provides direct evidence of the continuous relationship between a plant and a herbivore. So far, this is the most ancient herbivory trace specifically identified and still distinctive in the modern flora on the same plant genus. This specific damage has never changed in terms of plant host association or morphological characteristics (shape, size). It has been distinguished from western Europe to eastern Asia over at least 15 Myr; a long period of time and a large geographical area characterized by marked environmental differences.

The warm climate during the Middle Miocene Climatic Optimum (17–15 Ma) [93], followed by progressive cooling during the Middle Miocene Climate Transition (15–13 Ma) [94], and the onset of glacial–interglacial cycles from the Middle Pleistocene Transition (1.2–0.7 Ma) onwards [95] occurred between the first known traces of DT297 and the present. In addition, orogenesis was extremely important in Eurasia, especially with the rise of the Tibet-Qinghai Plateau [96–98], which formed a barrier between eastern Asia (*P. subaequalis*) and the Caucasus—Europe (*P. persica*) during this interval.

Figure 4. Artistic representation of both *Parrotia persica* (left) and *Parrotia subaequalis* (right) bearing the damage type DT297. The illustration was produced by Mr Dinghua Yang from the Nanjing Institute of Geology and Palaeontology, Nanjing, China.

DT297 represents remarkable stasis in a feeding strategy. Numerous studies have demonstrated shifts in herbivory during various geological events [16,23,99,100]. Those herbivory changes are mostly caused by climate variations impacting insect physiology [101–105] and, in some cases, by interruptions of gene exchange between plant and insect species [106,107] created by the emergence of new landforms.

Although the specific damage on *Parrotia* over (at least) 15 Myr can be used to reconstruct the trophic relationships of *Parrotia* in its environment, it is very difficult to determine the insect causing this damage. Straus [51] suggested that this trace fossil could have been produced by Chrysomelidae larvae. Based on our comparisons with known insect feeding from the literature we suggest that DT297 could have been caused by insects belonging to subfamily Galerucinae/Alticinae, probably by *Altica* which was widely distributed in Eurasia from at least the Eocene [108–110]. Both subfamilies are recorded in the Yangtze River valley and the Hyrcanian forest region with some endemic species of these regions [111–116].

The present specific damage shared between *P. subaequalis* and *P. persica* which are today completely isolated from each other, provides direct evidence that they occupied a common ecological niche, which is today separated by vicariance into two geographical areas [117]. The congenerity of the *Parrotia* species between eastern Asia and Caucasus is still not clear based on previous studies and has led some to assign the Asian taxon to *S. subaequalis* (= *P. subaequalis*) for some researchers [39,64]. However, Li *et al.* [118] used internal transcribed spacers from the nuclear gene of Hamamelidaceae and found support for *Parrotia* and *Shaniodendron* as a monophyletic group [118,119]. Additional studies based on the chloroplast gene 'matK' segregated *Parrotia* and *Shaniodendron* as distinct taxa [120,121]. A recent study even describes the whole chloroplast genome of *P. subaequalis* [122]. However, chloroplast markers usually do not reconstruct taxonomic but biogeographic relationships [123–127]. Thus DT297 can contribute to better understanding of the shared biogeographic history of the two host lineages in western Eurasia and eastern Asia and supports the accordance of lineages between these *Parrotia* species presented in this study.

In a continuous coevolution between insect attack and plant defence strategies [128,129], it is difficult to explain why such a specific herbivory mode has never changed over 15 Myr. One hypothesis is that this insect damage can be mutualistic in some cases. Although this is debated within the scientific community, Agrawal [130] demonstrated, based on plant fitness, that certain types of insect feeding could represent mutualistic interactions between the insect and the plant. Moreover, a recent meta-analysis of

hundreds of scientific publications [131] about the 'overcompensation' for insect herbivory also supports this hypothesis. However, to focus only on plant fitness is insufficient to discuss mutualism as a whole, because mutualism also implies an evolutionary history of the plant–animal interaction [132], in which a specific feeding trace, such as DT297, can be considered as a direct evidence.

4.3. DT297 more common in the fossil record than on modern leaves

We observed many more examples of DT297 on fossil than on modern leaves. The most striking difference is seen in *P. persica* and its fossil relative *P. pristina*, as we observed around 500 fossil specimens from Willershausen [26] versus more than 2300 modern specimens in its modern range in the Hyrcanian forest [133], and yet the large majority of DT297 has been observed on the fossil leaves (electronic supplementary material, S3). This is also true for the Chinese fossil leaf assemblages, which recorded almost 10 times more occurrences of DT297 than the modern *P. subaequalis* leaves from the Yixing forest area (electronic supplementary material, S3). This unexpected pattern can be explained in various ways.

These significant differences in occurrence could indicate an ecological change for this specialist plant–insect interaction. The populations of insects specialized on *Parrotia* could have significantly decreased during the last 15 Myr until they became relictual in the Hyrcanian and Yixing forests. The large climatic changes during the Miocene [93,134,135] and the introduction of glacial–interglacial cycles in the Quaternary [52,95] had a huge impact on numerous plant species' populations and their distributions [55,136–138], including *Parrotia* [139–141]. However, there are some examples of insect species that survived the glacial–interglacial cycles and recolonized the same area, such as the arctic–alpine insect species *Arcynopteryx dichroa* in the Central European highlands [142].

Sampling biases might also have caused the marked differences of occurrences between fossil and modern leaves. The modern leaves sampled represent only 1 or 2 years of leaf shedding, whereas fossil leaves may represent many years of leaf production and hence environmental variation, such as dry or wet years. Fossil leaves from Shanwang were recovered from several layers (19 sub-units in total) of diatomaceous sedimentary rocks [143] and represent a maximum of 3 Myr of elapsed time [31,66,69]. At Willershausen, fossils were collected from a clay pit and fossils from various layers were mixed. Based on lithological differences and contrasting fossil preservation, it is certain that the leaves from this outcrop represent many years of deposition [144,145]. Plant–insect interactions can significantly change from 1 year to another owing to a multitude of factors, such as climate seasonality [146–149]. Thus, insect feeding observed in the fossil record is generally more representative of the global herbivory pattern on *Parrotia* taxa than the observations made on modern leaf litter.

Only increased sampling efforts for *Parrotia* leaves from modern sites and fossil assemblages will enable better characterization of this differences in DT occurrences. Accordingly, one of the main objectives of our study was to thoroughly describe the specific DT DT297 in order to provide a basis for more comprehensive investigations in the future.

5. Conclusion

This study highlights and describes a long-term mode of herbivory, expressed as a skeletonization, which is exclusively represented on *Parrotia* species. We corroborate the damage (DT297) affinity to *Parrotia* taxa, for at least 15 Myr, and document this likeness relationship by providing structural similarities and detailed measurements supported by statistics. This specific DT provides direct evidence, quite rare in palaeoecology, of a long-term relationship between a plant species and its herbivore. DT297 is currently the most specific long-term herbivory trace identifiable on the same modern plant lineage. Henceforth, in order to better understand this interaction, fieldwork should be made in the Hyrcanian and/or Yixing forests in order to directly observe the insect species causing this distinct damage form.

The continuous presence of this DT over 15 Myr demonstrates a robust and long-term plant–herbivore association, and provides new evidence for a shared biogeographic history of the two host plants. This may have implications for improved understanding of phylogenetic relationships between the western Eurasian and East Asian host plant species.

References

1. Brooker RW, Callaghan TV. 1998 The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* **81**, 196–207. (doi:10.2307/3546481)

2. May RM. 1975 Stability in ecosystems: some comments. In *Unifying concepts in ecology: report of the plenary sessions of the first international congress of ecology, the Hague, the Netherlands, September 8–14, 1974* (eds WH van Dobben, RH Lowe-McConnell), pp. 161–168. Dordrecht, The Netherlands: Springer.

3. Tschirhart J. 2000 General equilibrium of an ecosystem. *J. Theor. Biol.* **203**, 13–32. (doi:10.1006/jtbi.1999.1058)

4. Heller NE, Zavaleta ES. 2009 Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biol. Conserv.* **142**, 14–32. (doi:10.1016/j.biocon.2008.10.006)

5. IPCC. (ed). 2007 *Climate change 2007: the physical science basis: contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change.* Cambridge, UK: Cambridge University Press.

6. Turner BLI, Clark WC, Kates RW, Richards JF, Mathews JT, Meyer WB. 1990 *The earth was formed by human action: global and regional changes in the past 300 years.* Cambridge, UK: Cambridge University Press.

7. Hillstrom ML, Lindroth RL. 2008 Elevated atmospheric carbon dioxide and ozone alter forest insect abundance and community composition: carbon dioxide and ozone alter forest insect communities. *Insect Conserv. Divers.* **1**, 233–241. (doi:10.1111/j.1752-4598.2008.00031.x)

8. Goulson D, Nicholls E, Botías C, Rotheray EL. 2015 Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* **347**, 1255957. (doi:10.1126/science.1255957)

9. Coley PD, Barone JA. 1996 Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* **27**, 305–335. (doi:10.1146/annurev.ecolsys.27.1.305)

10. Grimaldi D. 1999 The co-radiations of pollinating insects and angiosperms in the cretaceous. *Ann. MO. Bot. Gard.* **86**, 373–406. (doi:10.2307/2666181)

11. McGhee GR. 2011 *Convergent evolution: limited forms most beautiful.* Cambridge, MA: MIT Press.

12. Forister ML *et al.* 2015 The global distribution of diet breadth in insect herbivores. *Proc. Natl Acad. Sci. USA* **112**, 442–447. (doi:10.1073/pnas.1423042112)

13. Lewinsohn TM, Novotny V, Basset Y. 2005 Insects on plants: diversity of herbivore assemblages revisited. *Ann. Rev. Ecol. Evol. Syst.* **36**, 597–620. (doi:10.1146/annurev.ecolsys.36.091704.175520)

14. Nyman T. 2010 To speciate, or not to speciate? Resource heterogeneity, the subjectivity of similarity, and the macroevolutionary consequences of niche-width shifts in plant-feeding insects. *Biol. Rev.* **85**, 393–411. (doi:10.1111/j.1469-185X.2009.00109.x)

15. Coley PD, Aide TM. 1991 Comparisons of herbivory and plant defenses in temperate and tropical broad-leaved forests. In *Plant-animal interactions: evolutionary ecology in tropical and temperate regions* (eds PW Price, TM Lewinsohn, GW Fernandes), pp. 25–49. New York, NY: Woodruff W. Benson.

16. Currano ED, Labandeira CC, Wilf P. 2010 Fossil insect folivory tracks paleotemperature for six million years. *Ecol. Monogr.* **80**, 547–567. (doi:10.1890/09-2138.1)

17. Zvereva EL, Kozlov MV. 2006 Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: a metaanalysis. *Glob. Change Biol.* **12**, 27–41. (doi:10.1111/j.1365-2486.2005.01086.x)

18. Currano ED, Labandeira CC, Wilf P. 2009 Dynamics of plant-insect interactions during late Paleocene and early Eocene environmental perturbations in the Bighorn Basin, Wyoming, USA. *Clim. Biot. Events Paleogene* **9**, 44–46.

19. Labandeira C. 2006 The four phases of plant-arthropod associations in deep time. *Geol. Acta* **4**, 409.

20. Labandeira CC, Kustatscher E, Wappler T. 2016 Floral assemblages and patterns of insect herbivory during the Permian to Triassic of Northeastern Italy. *PLoS ONE* **11**, e0165205. (doi:10.1371/journal.pone.0165205)

21. Labandeira CC, Dilcher DL, Davis DR, Wagner DL. 1994 Ninety-seven million years of angiosperm-insect association: paleobiological insights into the meaning of coevolution. *Proc. Natl Acad. Sci. USA* **91**, 12 278–12 282. (doi:10.1073/pnas.91.25.12278)

22. Wappler T. 2010 Insect herbivory close to the Oligocene–Miocene transition: a quantitative analysis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **292**, 540–550. (doi:10.1016/j.palaeo.2010.04.029)

23. Wappler T, Currano ED, Wilf P, Rust J, Labandeira CC. 2009 No post-Cretaceous ecosystem depression in European forests? Rich insect-feeding damage on diverse middle Palaeocene plants, Menat, France. *Proc. R. Soc. B* **276**, 4271–4277. (doi:10.1098/rspb.2009.1255)

24. Wilf P. 2008 Insect-damaged fossil leaves record food web response to ancient climate change and extinction. *New Phytol.* **178**, 486–502. (doi:10.1111/j.1469-8137.2008.02395.x)

25. Wilf P, Labandeira CC, Johnson KR, Coley PD, Cutter AD. 2001 Insect herbivory, plant defense, and early Cenozoic climate change. *Proc. Natl Acad. Sci. USA* **98**, 6221–6226. (doi:10.1073/pnas.111069498)

26. Adroit B, Girard V, Kunzmann L, Terral J-F, Wappler T. 2018 Plant-insect interactions patterns in three European paleoforests of the late-Neogene-early-Quaternary. *PeerJ* **6**, 24. (doi:10.7717/peerj.5075)

27. Knobloch E. 1998 Der pliozäne laubwald Laubwald von willershausen Willershausen am harz Harz (Mitteleuropa). *Doc. Nat.* **120**, 1–302. (doi:10.1002/fedr.4921100505)

28. Adroit B, Malekhosseini M, Girard V, Abedi M, Rajaei H, Terral J-F, Wappler T. 2018 Changes in pattern of plant-insect interactions on the Persian ironwood (*Parrotia persica*, Hamamelidaceae) over the last 3 million years. *Rev. Palaeobot. Palynol.* **258**, 22–35. (doi:10.1016/j.revpalbo.2018.06.007)

29. Geng Q, Yao Z, Yang J, He J, Wang D, Wang Z, Liu H. 2015 Effect of Yangtze River on

population genetic structure of the relict plant *Parrotia subaequalis* in eastern China. *Ecol. Evol.* **5**, 4617–4627. (doi:10.1002/ece3.1734)

30. Li W, Zhang G-F. 2015 Population structure and spatial pattern of the endemic and endangered subtropical tree *Parrotia subaequalis* (Hamamelidaceae). *Flora Morphol. Dist. Funct. Ecol. Plants* **212**, 10–18. (doi:10.1016/j.flora. 2015.02.002)

31. Yang H, Yang S. 1994 The Shanwang fossil biota in eastern China: a Miocene Konservat-Lagerstätte in lacustrine deposits. *Lethaia* **27**, 345–354. (doi:10.1111/j.1502-3931.1994. tb01585.x)

32. Zhang J-F, Sun B, Zhang X-Y. 1994 *Sedimentary geology of shanwang basin*. Beijing, China: Science Press.

33. Hao RM, Wei HT. 1998 A new combination of Hamamelidaceae. *Acta Phytotaxon. Sin.* **36**, 80.

34. Mai DH. 1995 *Tertiäre Vegetationsgeschichte Europas: Methoden und Ergebnisse*. Stuttgart, Germany: Fischer. See https://books.google.de/ books?id=wTvwAAAAMAAJ.

35. Zhilin SG. 1989 History of the development of the temperate forest flora in Kazakhstan, U.S.S.R. from the Oligocene to the Early Miocene. *Bot. Rev.* **55**, 205–330. (doi:10.1007/ BF02858522)

36. Tanai T. 1967 On the Hamamelidaceae from the Paleogene of Hokkaido, Japan. *Trans. Proc. Palaeontol. Soc. Jpn* **66**, 56–62.

37. Pavlyutkin BI, Yabe A, Golozoubov VV, Simanenko LF. 2016 Miocene floral changes in the Circum-Japan Sea areas—their implications in the climatic changes and the time of Japan Sea opening. *Mem. Natl. Mus. Nat. Sci. Tokyo* **51**, 109–123.

38. Hu HH, Chaney RW. 1940 *A miocene floare from Shantung province, China*, pp. 1–147. Washington, DC: Carnegie Institute of Washington Publication.

39. Wang X-Q, Li H-M. 2000 Discovery of another living fossil - Shaniodendron subaequale (H.T.Chang) Deng *et al*. in China - Clearing up paleobotanists' a long-term doubt. *Acta Palaeontol. Sin.* **39**, 308–317.

40. Wu ZY, Raven PH, Hong DY. 2003 *Flora of China. Vol. 9 (pittosporaceae through connaraceae)*. Beijing, China: Science Press and Missouri Botanical Garden Press, St. Louis.

41. Coombes AJ, Debreczy Z. 2015 *The book of leaves*. Brighton, UK: Ivy Press. See https:// books.google.de/books?id=UvENswEACAAJ

42. Leroy SA, Roiron P. 1996 Latest Pliocene pollen and leaf floras from Bernasso palaeolake (Escandorgue Massif, Hérault, France). *Rev. Palaeobot. Palynol.* **94**, 295–328. (doi:10.1016/ S0034-6667(96)00016-4)

43. Yosefzadeh H, Tabari M, Akbarinia M, Akbarian MR, Bussotti F. 2010 Morphological plasticity of *Parrotia persica* leaves in eastern Hyrcanian forests (Iran) is related to altitude. *Nord. J. Bot.* **28**, 344–349. (doi:10.1111/j.1756-1051.2009. 00451.x)

44. Bachmann GH, Ehling BC, Eichner R, Schwab M. 2008 *Geologie von Sachsen-Anhalt*. Stuttgart, Germany: Schweizerbart Science Publishers.

45. Boulter MC, Hubbard RNLB, Kvaček Z. 1993 A comparison of intuitive and objective

interpretations of Miocene plant assemblages from north Bohemia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **101**, 81–96. (doi:10. 1016/0031-0182(93)90153-A)

46. Buzek C. 1971 *Tertiary flora of the northern part of the petipsy area (North-Bohemian Basin)*. Stuttgart, Germany: Schweizerbart Science Publishers. See http://www.schweizerbart.de// publications/detail/isbn/9783510991037/ Rozpravy_Buzek_Tertiary_Flora_Bd_36.

47. Denk T, Güner TH, Kvaček Z, Bouchal JM. 2017 The early Miocene flora of Güvem (Central Anatolia, Turkey): a window into early Neogene vegetation and environments in the Eastern Mediterranean. *Acta Palaeobot.* **57**, 237–338. (doi:10.1515/acpa-2017-0011)

48. Ferguson DK, Knobloch E. 1998 A fresh look at the rich assemblage from the Pliocene sink-hole of Willershausen, Germany. *Rev. Palaeobot. Palynol.* **101**, 271–286. (doi:10.1016/S0034-6667(97)00078-X)

49. Macaluso L, Martinetto E, Vigna B, Bertini A, Cilia A, Teodoridis V, Kvaček Z. 2018 Palaeofloral and stratigraphic context of a new fossil forest from the Pliocene of NW Italy. *Rev. Palaeobot. Palynol.* **248**, 15–33. (doi:10.1016/j.revpalbo. 2017.08.005)

50. Martinetto E. 2003 Leaves of terrestrial plants from the Pliocene shallow marine and transitional deposits of Asti (Piedmont, NW Italy). *Boll. Soc. Paleontol. Itatiana* **42**, 75–11.

51. Straus A. 1977 Gallen, Minen und andere Fraßspuren im Pliozän von Willershausen am Harz. *Verh. Bot. Ver. Prov. Brandenburg* **113**, 41–80.

52. Hilgen FJ. 1991 Astronomical calibration of Gauss to Matuyama sapropels in the Mediterranean and implication for the geomagnetic polarity timescale. *Earth Planet. Sci. Lett.* **104**, 226–244. (doi:10.1016/0012-821X(91)90206-W)

53. Suc J-P. 1978 Analyse pollinique de dépôts Plio-Pléistocènes du sud du massif basaltique de l'Escandorgue (Site de Bernasso, Lunas, Hérault, France). *Pollen Spores* **20**, 497–512.

54. Akhani H, Ziegler H. 2002 Photosynthetic pathways and habitats of grasses in Golestan National Park (NE Iran), with an emphasis on the C4-grass dominated rock communities. *Phytocoenologia* **32**, 455–501. (doi:10.1127/ 0340-269X/2002/0032-0455)

55. Arpe K, Leroy SAG. 2007 The Caspian Sea level forced by the atmospheric circulation, as observed and modelled. *Quat. Int.* **173–174**, 144–152. (doi:10.1016/j.quaint.2007.03.008)

56. Talebi KS, Sajedi T, Pourhashemi M. 2014 *Forests of Iran*. Dordrecht, The Netherlands: Springer.

57. Li H, Yue C, Zhang Y, Shao S, Yu L. 2012 Advance of research on *Parrotia subaequalis* (in Chinese). *J. Zhejiang For. Sci. Technol.* **32**, 79–84.

58. Li J-H, Bogle AL, Klein AS. 1997 Close relationship between *Shaniodendron* and *Parrotia* (Hamamelidaceae), evidence from ITS sequences of nuclear ribosomal DNA. *J. System. Evol.* **35**, 481–483.

59. Fang Y, Jin Y, Deng M, Yang Q, Li B. 1997 Macroscopic and microscopic structure of *Parrotia*

subaequalis leaves and its systemic significance (in Chinese). *Plant Resour. Environ.* **3**, 36–42.

60. Yang Q. 1994 Preliminary report on the study of *Shaniodendron subaequalis* (in Chinese). *J. Jiangsu For. Sci. Technol.* **1**, 14–18.

61. Zhou Z, Momohara A. 2005 Fossil history of some endemic seed plants of East Asia and its phytogeographical significance (in Chinese). *J. Plant Classif. Resour.* **27**, 449–470.

62. Manchester SR, Chen Z, Geng B, Tao J. 2005 Middle Eocene flora of Huadian, Jilin Province, Northeastern China. *Acta Palaeobot.* **45**, 3–26.

63. Yao Z, Wang Z, Yan C, Dong Z, Xu W, Wei N, An S. 2010 The photosynthesis response to different light intensity for the endangered plant *Parrotia subaequalis* (in Chinese). *J. Nanjing For. Univ.* **34**, 83–88.

64. Deng MB, Wei HT, Wang XQ. 1992 *Shaniodendron subaequale* (H.T. Chang) M.B. Deng, H.T. Wei & X.Q. Wang. *Acta Phytotaxon. Sin.* **30**, 59–61.

65. Gradstein F, Ogg JG, Smith AG, Bleeker W, Lourens LJ. 2004 A new Geologic time scale, with special reference to Precambrian and Neogene. *Episodes* **27**, 83–100. (doi:10.18814/ epiiugs/2004/v27i2/002)

66. He H, Deng C, Pan Y, Deng T, Luo Z, Sun J, Zhu R. 2011 New 40Ar/39Ar dating results from the Shanwang Basin, eastern China: constraints on the age of the Shanwang Formation and associated biota. *Phys. Earth Planet. Inter.* **187**, 66–75. (doi:10.1016/j.pepi.2011.05.002)

67. Liang M-M, Bruch A, Collinson M, Mosbrugger V, Li C-S, Sun Q-G, Hilton J. 2003 Testing the climatic estimates from different palaeobotanical methods: an example from the Middle Miocene Shanwang flora of China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **198**, 279–301. (doi:10.1016/S0031-0182(03)00471-1)

68. Qiu Z. 1989 The Chinese Neogene mammalian biochronology: its correlation with the European neogene mammalian zonation. In *European neogene mammal chronology* (eds EH Lindsay, V Fahlbusch, P Mein), pp. 527–556. Boston, MA: Springer.

69. Sun Q, Collinson ME, Li C-S, Wang Y, Beerling DJ. 2002 Quantitative reconstruction of palaeoclimate from the Middle Miocene Shanwang flora, eastern China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **180**, 315–329. (doi:10.1016/S0031-0182(01)00433-3)

70. Liu G, Leopold EB. 1992 Paleoecology of a Miocene flora from the Shanwang formation, Shandong province, northern East China. *Palynology* **16**, 187–212. (doi:10.1080/ 01916122.1992.9989412)

71. Zhao J. 2008 Qinling East Extension and Jiangsu Natural Environment (in Chinese). *Jiangsu Geol.* **1**, 79.

72. Cornelissen T, Stiling P. 2005 Sex-biased herbivory: a meta-analysis of the effects of gender on plant-herbivore interactions. *Oikos* **111**, 488–500. (doi:10.1111/j.1600-0706.2005. 14075.x)

73. Leckey EH, Smith DM, Nufio CR, Fornash KF. 2014 Oak-insect herbivore interactions along a temperature and precipitation gradient. *Acta Oecol.* **61**, 1–8. (doi:10.1016/j.actao.2014. 08.001)

74. Reynolds BC, Crossley Jr DA. 1997 Spatial variation in herbivory by forest canopy arthropods along an elevation gradient. *Environ. Entomol.* **26**, 1232–1239. (doi:10.1093/ee/26.6.1232)

75. Su T, Adams JM, Wappler T, Yong-Jiang H, Jacques FMB, Liu Y-S, Zhou Z-K. 2015 Resilience of plant-insect interactions in an oak lineage through Quaternary climate change. *Paleobiology* **41**, 174–186. (doi:10.1017/pab.2014.11)

76. Labandeira CC, Wilf P, Johnson KR, Marsh F. 2007 *Guide to insect (and other) damage types on compressed plant fossils*. Washington, DC: Smithsonian Institution, National Museum of Natural History, Department of Paleobiology.

77. Labandeira CC. 2002 The history of associations between plants and animals. In *Plant-animal interactions: an evolutionary approach* (eds CM Herrera, O Pellmyr), pp. 26–74, 248–261. London, UK: Blackwell Science.

78. de la Riva EG, Olmo M, Poorter H, Ubera JL, Villar R. 2016 Leaf mass per area (LMA) and its relationship with leaf structure and anatomy in 34 mediterranean woody species along a water availability gradient. *PLoS ONE* **11**, e0148788. (doi:10.1371/journal.pone.0148788)

79. Royer DL et al. 2007 Fossil leaf economics quantified: calibration, Eocene case study, and implications. *Paleobiology* **33**, 574–589. (doi:10.1666/07001.1)

80. Givnish T. 2002 Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fenn.* **36**, 703–743. (doi:10.14214/sf.535)

81. Ishida A, Diloksumpun S, Ladpala P, Staporn D, Panuthai S, Gamo M, Yazaki K, Ishizuka M, Puangchit L. 2006 Contrasting seasonal leaf habits of canopy trees between tropical dry-deciduous and evergreen forests in Thailand. *Tree Physiol.* **26**, 643–656. (doi:10.1093/treephys/26.5.643)

82. Prior LD, Bowman DMJS, Eamus D. 2004 Seasonal differences in leaf attributes in Australian tropical tree species: family and habitat comparisons. *Funct. Ecol.* **18**, 707–718. (doi:10.1111/j.0269-8463.2004.00885.x)

83. Fonseca CR, Overton JM, Collins B, Westoby M. 2000 Shifts in trait-combinations along rainfall and phosphorus gradients. *J. Ecol.* **88**, 964–977. (doi:10.1046/j.1365-2745.2000.00506.x)

84. McDonald PG, Fonseca CR, Overton JM, Westoby M. 2003 Leaf-size divergence along rainfall and soil-nutrient gradients: is the method of size reduction common among clades? *Funct. Ecol.* **17**, 50–57. (doi:10.1046/j.1365-2435.2003.00698.x)

85. Currano ED, Wilf P, Wing SL, Labandeira CC, Lovelock EC, Royer DL. 2008 Sharply increased insect herbivory during the Paleocene–Eocene Thermal Maximum. *Proc. Natl Acad. Sci. USA* **105**, 1960–1964. (doi:10.1073/pnas.0708646105)

86. Gunkel S, Wappler T. 2015 Plant-insect interactions in the upper Oligocene of Enspel (Westerwald, Germany), including an extended mathematical framework for rarefaction. *Palaeobiodiversity Palaeoenvironments* **95**, 55–75. (doi:10.1007/s12549-014-0176-6)

87. Knor S, Prokop J, Kvaček Z, Janovský Z, Wappler T. 2012 Plant–arthropod associations from the Early Miocene of the Most Basin in North Bohemia—Palaeoecological and palaeoclimatological implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **321–322**, 102–112. (doi:10.1016/j.palaeo.2012.01.023)

88. Kunzmann L, Moraweck K, Müller C, Schröder I, Wappler T, Grein M, Roth-Nebelsick A. 2019 A Paleogene leaf flora (Profen, Sachsen-Anhalt, Germany) and its potentials for palaeoecological and palaeoclimate reconstructions. *Flora* **254**, 71–87. (doi:10.1016/j.flora.2018.11.005)

89. Wappler T, Grímsson F. 2016 Before the 'Big Chill': patterns of plant-insect associations from the Neogene of Iceland. *Glob. Planet. Change* **142**, 73–86. (doi:10.1016/j.gloplacha.2016.05.003)

90. Dong J, Sun B, Mao T, Yan D, Liu C, Wang Z, Jin P. 2018 Liquidambar (Altingiaceae) and associated insect herbivory from the Miocene of southeastern China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **497**, 11–24. (doi:10.1016/j.palaeo.2018.02.001)

91. Ma F-J, Ling C-C, Ou-Yang M-S, Yang G-M, Shen X-P, Wang Q-J. 2020 Plant–insect interactions from the Miocene (Burdigalian–Langhian) of Jiangxi, China. *Rev. Palaeobot. Palynol.* **275**, 104176. (doi:10.1016/j.revpalbo.2020.104176)

92. McDonald CM, Francis JE, Compton SGA, Haywood A, Ashworth AC, Hinojosa LF, Smellie J. 2007 *Herbivory in Antarctic fossil forests: evolutionary and palaeoclimatic significance*. Lincoln, NE: University of Nebraska.

93. Böhme M. 2003 The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **195**, 389–401. (doi:10.1016/S0031-0182(03)00367-5)

94. Frigola A, Prange M, Schulz M. 2018 Boundary conditions for the Middle Miocene Climate Transition (MMCT v1.0). *Geosci. Model Dev.* **11**, 1607–1626. (doi:10.5194/gmd-11-1607-2018)

95. Clark PU, Archer D, Pollard D, Blum JD, Rial JA, Brovkin V, Mix AC, Pisias NG, Roy M. 2006 The middle Pleistocene transition: characteristics, mechanisms, and implications for long-term changes in atmospheric pCO2. *Quat. Sci. Rev.* **25**, 3150–3184. (doi:10.1016/j.quascirev.2006.07.008)

96. Kutzbach JE, Prell WL, Ruddiman WmF. 1993 Sensitivity of Eurasian Climate to surface uplift of the Tibetan Plateau. *J. Geol.* **101**, 177–190. (doi:10.1086/648215)

97. Zhisheng A, Kutzbach JE, Prell WL, Porter SC. 2001 Evolution of Asian monsoons and phased uplift of the Himalaya–Tibetan plateau since Late Miocene times. *Nature* **411**, 62–66. (doi:10.1038/35075035)

98. Bartholomé E, Belward AS. 2005 GLC2000: a new approach to global land cover mapping from Earth observation data. *Int. J. Remote Sens.* **26**, 1959–1977. (doi:10.1080/01431160412331291297)

99. Adams JM, Brusa A, Soyeong A, Ainuddin AN. 2010 Present-day testing of a paleoecological pattern: is there really a latitudinal difference in leaf-feeding insect-damage diversity? *Rev. Palaeobot. Palynol.* **162**, 63–70. (doi:10.1016/j.revpalbo.2010.05.004)

100. Wilf P, Johnson KR, Cúneo NR, Smith ME, Singer BS, Gandolfo MA. 2005 Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. *Am. Nat.* **165**, 634–650. (doi:10.1086/430055)

101. Chown SL, Gaston KJ. 2010 Body size variation in insects: a macroecological perspective. *Biol. Rev.* **85**, 139–169. (doi:10.1111/j.1469-185X.2009.00097.x)

102. Clapham ME, Karr JA. 2012 Environmental and biotic controls on the evolutionary history of insect body size. *Proc. Natl Acad. Sci. USA* **109**, 10 927–10 930. (doi:10.1073/pnas.1204026109)

103. Harrison JF, Kaiser A, VandenBrooks JM. 2010 Atmospheric oxygen level and the evolution of insect body size. *Proc. R. Soc. B* **277**, 1937–1946. (doi:10.1098/rspb.2010.0001)

104. Schmidt-Nielsen K, Knut S-N. 1984 *Scaling: why is animal size so important?* Cambridge, UK: Cambridge University Press.

105. Siemann E, Tilman D, Haarstad J. 1996 Insect species diversity, abundance and body size relationships. *Nature* **380**, 704–706. (doi:10.1038/380704a0)

106. Maron JL, Agrawal AA, Schemske DW. 2019 Plant–herbivore coevolution and plant speciation. *Ecology* **100**, e02704. (doi:10.1002/ecy.2704)

107. Stenberg JA, Witzell J, Ericson L. 2006 Tall herb herbivory resistance reflects historic exposure to leaf beetles in a boreal archipelago age-gradient. *Oecologia* **148**, 414–425. (doi:10.1007/s00442-006-0390-7)

108. Nadein KS, Perkovsky EE. 2019 Small and common: the oldest tropical Chrysomelidae (Insecta: Coleoptera) from the lower Eocene Cambay amber of India. *Alcheringa: Australas. J. Palaeontol.* **43**, 597–611. (doi:10.1080/03115518.2019.1622780)

109. Jolivet P, Petitpierre E, Hsiao TH. 2012 *Biology of chrysomelidae*. Berlin, Germany: Springer Science & Business Media.

110. Bukejs A, Konstantinov A. 2013 New genus of flea beetle (Coleoptera: Chrysomelidae: Galerucinae: Alticini) from the Upper Eocene Baltic amber. *Insecta Mundi* **306**, 1–5.

111. Shumilovskikh LS et al. 2016 Landscape evolution and agro-sylvo-pastoral activities on the Gorgan Plain (NE Iran) in the last 6000 years. *Holocene* **26**, 1676–1691. (doi:10.1177/0959683616646841)

112. Sun J-H, Liu Z-D, Britton KO, Cai P, Orr D, Hough-Goldstein J. 2006 Survey of phytophagous insects and foliar pathogens in China for a biocontrol perspective on kudzu, Pueraria montana var. lobata (Willd.) Maesen and S. Almeida (Fabaceae). *Biol. Control* **36**, 22–31. (doi:10.1016/j.biocontrol.2005.09.007)

113. Yanyu W. 2000 The species diversity of subfamily alticinae (Coleoptera: Chrysomelidae) communities in Wuyishan nature reserve. *Wuyi Sci. J.* **1**, 108–114.

114. Wu Y, Yuan D. 1997 Biodiversity and conservation in China: a view from entomologists. *Insect Sci.* **4**, 95–111. (doi:10.1111/j.1744-7917.1997.tb00078.x)

115. Adeli E. 2009 Beitrag zur Kenntnis der im Forst schädlichen Insekten des Iran: I. Coleoptera. *Z. Ang. Entomol.* **70**, 8–14. (doi:10.1111/j.1439-0418.1972.tb02144.x)

116. Wang SY. 1997 Coleoptera, Chrysomelidae: Chrysomelinae. In *Insects of the Three Gorge Reservoir area of Yangtze River* (ed. XK Wang), pp. 855–862. Chongqing, China: Chongqing Publishing House.

117. Wiley EO. 1988 Vicariance biogeography. *Annu. Rev. Ecol. Syst.* **19**, 513–542. (doi:10.1146/annurev.es.19.110188.002501)

118. Li J, Bogle AL, Klein AS. 1999 Phylogenetic relationships of the Hamamelidaceae inferred from sequences of internal transcribed spacers (ITS) of nuclear ribosomal DNA. *Am. J. Bot.* **86**, 1027–1037. (doi:10.2307/2656620)

119. Li J, Bogle AL, Klein AS. 1999 Phylogenetic relationships in the Hamamelidaceae: evidence from the nucleotide sequences of the plastid genematK. *Plant Syst. Evol.* **218**, 205–219. (doi:10.1007/BF01089228)

120. Li J, Bogle L, Donoghue MJ. 1999 Phylogenetic relationships in the Hamamelidoideae inferred from sequences of trn non-coding regions of chloroplast DNA. *Harv. Pap. Bot.* **4**, 343–356.

121. Xiang X, Xiang K, Ortiz RDC, Jabbour F, Wang W. 2019 Integrating palaeontological and molecular data uncovers multiple ancient and recent dispersals in the pantropical Hamamelidaceae. *J. Biogeogr.* **46**, 2622–2631. (doi:10.1111/jbi.13690)

122. Zhang Y-Y, Shi E, Yang Z-P, Geng Q-F, Qiu Y-X, Wang Z-S. 2018 Development and application of genomic resources in an endangered Palaeoendemic tree, *Parrotia subaequalis* (Hamamelidaceae) from Eastern China. *Front. Plant Sci.* **9**, 246. (doi:10.3389/fpls.2018.00246)

123. Mengoni A, Gonnelli C, Brocchini E, Galardi F, Pucci S, Gabbrielli R, Bazzicalupo M. 2003 Chloroplast genetic diversity and biogeography in the serpentine endemic Ni-hyperaccumulator *Alyssum bertolonii*. *New Phytol.* **157**, 349–356. (doi:10.1046/j.1469-8137.2003.00664.x)

124. Mummenhoff K, Brüggemann H, Bowman JL. 2001 Chloroplast DNA phylogeny and biogeography of *Lepidium* (Brassicaceae). *Am. J. Bot.* **88**, 2051–2063. (doi:10.2307/3558431)

125. Der JP, Thomson JA, Stratford JK, Wolf PG. 2009 Global chloroplast phylogeny and biogeography of bracken (Pteridium; Dennstaedtiaceae). *Am. J. Bot.* **96**, 1041–1049. (doi:10.3732/ajb.0800333)

126. Dong W, Liu J, Yu J, Wang L, Zhou S. 2012 Highly variable chloroplast markers for evaluating plant phylogeny at low taxonomic levels and for DNA barcoding. *PLoS ONE* **7**, e0035071. (doi:10.1371/journal.pone.0035071)

127. Yan M, Xiong Y, Liu R, Deng M, Song J. 2018 The application and limitation of universal chloroplast markers in discriminating east Asian evergreen oaks. *Front. Plant. Sci.* **9**, 569. (doi:10.3389/fpls.2018.00569)

128. Karban R, Agrawal AA. 2002 Herbivore offense. *Annu. Rev. Ecol. Syst.* **33**, 641–664. (doi:10.1146/annurev.ecolsys.33.010802.150443)

129. Thompson J. 1999 What we know and do not know about coevolution: insect herbivores and plants as a test case. In *Herbivores: between plants and predators* (eds H Olff, VK Brown, RH Drent), pp. 7–30. Oxford, UK: Blackwell Science.

130. Agrawal AA. 2000 Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. *Trends Plant Sci.* **5**, 309–313. (doi:10.1016/S1360-1385(00)01679-4)

131. Garcia LC, Eubanks MD. 2018 Overcompensation for insect herbivory: a review and meta-analysis of the evidence. *Ecology* **100**, ecy.2585. (doi:10.1002/ecy.2585)

132. Järemo J, Tuomi J, Nilsson P, Lennartsson T. 1999 Plant adaptations to herbivory: mutualistic versus antagonistic coevolution. *Oikos* **84**, 313. (doi:10.2307/3546728)

133. Adroit B, Wappler T, Terral J-F, Ali AA, Girard V. 2016 Bernasso, a paleoforest from the early Pleistocene: new input from plant–insect interactions (Hérault, France). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **446**, 78–84. (doi:10.1016/j.palaeo.2016.01.015)

134. Bouchal JM, Güner TH, Denk T. 2018 Middle Miocene climate of southwestern Anatolia from multiple botanical proxies. *Clim. Past* **14**, 1427–1440. (doi:10.5194/cp-2018-76)

135. Cohen KM, Finney SC, Gibbard PL, Fan J-X. 2013 The ICS International Chronostratigraphic Chart *Episodes* **36**, 199–204.

136. DeChaine EG, Martin AP. 2006 Using coalescent simulations to test the impact of quaternary climate cycles on divergence in an alpine plant-insect association. *Evolution* **60**, 1004. (doi:10.1554/05-672.1)

137. Milne RI. 2006 Northern hemisphere plant disjunctions: a window on tertiary land bridges and climate change? *Ann. Bot.* **98**, 465–472. (doi:10.1093/aob/mcl148)

138. Suc J, Popescu S. 2005 Pollen records and climatic cycles in the North Mediterranean region since 2.7 Ma. *Spec. Publ.Geol. Soc. Lond.* **247**, 147. (doi:10.1144/GSL.SP.2005.247.01.08)

139. Biltekin D, Popescu S-M, Suc J-P, Quézel P, Jiménez-Moreno G, Yavuz N, Namık MÇ. 2015 Anatolia: a long-time plant refuge area documented by pollen records over the last 23 million years. *Rev. Palaeobot. Palynol.* **215**, 1–22. (doi:10.1016/j.revpalbo.2014.12.004)

140. Bińka K, Nitychoruk J, Dzierzek J. 2003 *Parrotia persica* C.A.M. (Persian witch hazel, Persian ironwood) in the Mazovian (Holsteinian) Interglacial of Poland. *Grana* **42**, 227–233. (doi:10.1080/00173130310016220)

141. Jiménez-Moreno G, Fauquette S, Suc J-P. 2010 Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. *Rev. Palaeobot. Palynol.* **162**, 403–415. (doi:10.1016/j.revpalbo.2009.08.001)

142. Theissinger K, Bálint M, Feldheim KA, Haase P, Johannesen J, Laube I, Pauls SU. 2013 Glacial survival and post-glacial recolonization of an arctic–alpine freshwater insect (*Arcynopteryx dichroa*, Plecoptera, Perlodidae) in Europe. *J. Biogeogr.* **40**, 236–248. (doi:10.1111/j.1365-2699.2012.02793.x)

143. Li C, Wang W, Sun Q, Li F, Zhang J, Wang X, Li J, Chen P. 2000 Stratigraphical sequence of diato-maceous beds within Shanwang Formation, Linqu Country, Shandong Province, China. *Bull. Bot.* **17**, 247–251.

144. Meischner D. 2000 Europäische Fossillagerstätten. In *Der pliozäne Teich von Willershausen am Harz* (ed. D Meischner), pp. 223–261. New York, NY: Dieter Meischner.

145. Vinken R. 1967 Kurzer Überblick über die Geologie der Umgebung von Willershausen. *Ber. Naturhistorischen Ges. Hann.* **115**, 5–14.

146. Aide TM. 1992 Dry season leaf production: an escape from herbivory. *Biotropica* **24**, 532–537. (doi:10.2307/2389016)

147. Alarcón R, Waser NM, Ollerton J. 2008 Year-to-year variation in the topology of a plant–pollinator interaction network. *Oikos* **117**, 1796–1807. (doi:10.1111/j.0030-1299.2008.16987.x)

148. Bale JS et al. 2002 Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Change Biol.* **8**, 1–16. (doi:10.1046/j.1365-2486.2002.00451.x)

149. Thompson JN, Fernandez CC. 2006 Temporal dynamics of antagonism and mutualism in a eographically variable plant–insect interaction. *Ecology* **87**, 103–112. (doi:10.1890/05-0123)