Insect herbivory, plant-host specialization and tissue partitioning on mid-Mesozoic broadleaved conifers of Northeastern China

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ABSTRACT

Insect-mediated damage was examined on 756 specimens of three broadleaved conifers *Podozamites*, *Lindleycladus* and *Liaoningocladus*, originating from five mid-Mesozoic localities in Northeastern China. These localities are the Late Triassic Yangcaogou Fm. (T3, ca. 205 Ma), the latest Middle Jurassic Jiulongshan Fm. (J2, 165 Ma), and the mid Early Cretaceous Yixian Fm. (K1, 125 Ma). Plant hosts from these three time intervals harbor five functional feeding groups (FFGs) of herbivores and 23 distinctive damage types (DTs), categorized using the widely applied DT system. The DTs were classified into the five FFGs of external foliage feeding (6 DTs), piercing and sucking (5 DTs), oviposition (3 DTs), galling (8 DTs) and leaf mining (1 DT). Damage-type richness and abundance was established for each FFG, encompassing from 10 to 16 DTs for each of the three time intervals examined. For this 80 million-year-long interval, foliar herbivory on broadleaved conifers was transformed from early predominance of external foliage feeding (T3), later replaced by an emphasis on piercing and sucking (J2), followed by bimodal expansion of endophytic interactions from oviposition and leaf mining (K1). This trajectory of herbivore succession indicates that, from T3 to K1, plant–insect associations were transformed from earlier reliance on a greater number of exophytic modes of herbivory to a later, increased variety in endophytic consumption. The transformation also was demonstrated by finer-grained partitioning of food resources and specialization on particular host-plant tissue types. This subdivision of tissue types likely promoted greater dietary saturation of tissue space by functional feeding groups. Possible explanations for these shifts in herbivory include ecological causes, long-term environmental changes, or both. Ecological factors, such as (i), evolution of a more differentiated plant-host spectrum available for consumption; (ii), long-term changes in plant physiognomy and deployment of antiherbivore defenses; (iii), change in herbivore partitioning of plant-host tissues; and (iv), emergence of the parasitoid guild for efficient regulation of insect herbivores. Long-term environmental variables may be linked to these shifts in insect herbivory style.

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1. Introduction

Investigations of insect herbivory during the Mesozoic Era have lagged considerably when compared to the more extensive exploration of Late Carboniferous and Permian floras of the late Paleozoic Era (e.g., Schachat et al., 2014). In addition, studies of Mesozoic herbivory have been even more overshadowed by extensive examination of the Cretaceous–Paleogene boundary and succeeding changes of the Paleogene that document the richness and intensity of insect damage during this interval of major, global climate change (Wilf et al., 2001; Wappler et al., 2009; Currano et al., 2010). However, it was during the Mesozoic that most modern, family-level insect lineages originated,

many of which herbivorized plant hosts (Labandeira, 2014a), resulting in new interactions and emergence of food webs that differed from those of the Paleozoic (Labandeira, 2002). The most significant development was expansion of angiosperms during the mid-Cretaceous, which irretrievably changed the structure of Mesozoic herbivore and pollinator relationships (Labandeira, 2014a), resulting in a major ecological break for the post mid-Cretaceous. The mid Mesozoic interval signals the replacement of a global, gymnosperm-dominated flora by a newly emerging angiosperm-dominated flora within a 34 m. yr. interval. Importantly for insect herbivore lineages, there was extinction, continuation and origination of taxa across this transformative floral shift (Labandeira, 2014a). Presumably, one important manifestation of this shift was evolution of the type and intensity of herbivory during this interval.

Considerable environmental and biotic change occurred during this formative time period, in which the global terrestrial flora and

arthropod fauna underwent a major evolutionary and ecological shift (Y.Q. Liu et al., 2009). These changes affected plant–insect associations (Labandeira, 2006), but also the broader food-web context involving the evolution of new, more diverse plant hosts and insect associates, such as the time series we describe below. Abiotic environmental factors may have played a role in this transformation of plant–insect relationships and could have been affected by geological events, such as major biogeographical realignments and environmental restructuring that included volcanism, tectonism, global warming and impact events. However, more important events likely were major biotic changes that included the Parasitoid Revolution (Labandeira, 2002), the Mesozoic Lacustrine Revolution (Cohen, 2003), and the Angiosperm Revolution (Friis et al., 2011). These singular but prolonged events assumed a major role in realignments of plant–insect relationships and of the transformation of land and linked freshwater food webs. Long after these events occurred, during the Paleogene Period, studies have assessed the extent of herbivory on dicot angiosperm species in floras that illuminate, for example, the herbivore response to geologically rapid changes in the global environment (Currano et al., 2010). Equally important are changes in plant–insect associations from bulk floral determinations at extinction events (Wilf et al., 2006; Labandeira, 2013b) or during more prolonged perturbations (Wilf et al, 2001; Dunne et al., 2014).

One alternative and novel approach of assessing the impact of biological and physical environmental transformations is an examination of changes in insect herbivory within a single evolving lineage or lineages with phenotypically very similar organs: in our case, broadleaved conifer leaves. This approach traces an insect community of herbivores on a single or on closely related source plants, the component community of Root (1973), to ascertain how herbivores evolve with their host lineage(s) in deep time. Such changes could be due to the transformation of biotic relationships or to long-term effects of the physical environment, or both. Herbivory of this distinctive isomorphic foliage will be tracked during the mid-Mesozoic of northeastern China, as insect herbivore lineages presumably responded to the vicissitudes of abiotic and biotic change.

In this study, insect herbivory is documented through time for one particular leaf morphotype. This morphotype is a series of broadleaved conifers that have entire-margined, lanceolate leaves, bear major and minor parallel veins which converge apically to an acute to acuminate apex, and possess a thickened, nearly clasping base (semiamplexicauly) attached to a branchlet. The three genera of examined broadleaved conifers are Podozamites C. F. W Braun, 1843, Lindleycladus Harris, 1979 and Liaoningocladus Sun et al., 2000. Podozamites is a Late Triassic to Early Cretaceous leaf form-genus from Northeastern China that may include several taxa (Sun et al., 2001). Based on cuticle structure, Harris (1979) divided Podozamites lanceolatus into those specimens with stomata transverse in orientation which are different from other P. lanceolatus specimens that have stomata longitudinal in orientation. As a result, Harris established a new genus, Lindleycladus, for those specimens possessing longitudinally oriented stomata. This new taxon retained the species name of lanceolatus, becoming Lindleycladus lanceolatus.

Liaoningocladus has had a different history of taxonomic recognition. Liaoningocladus formerly was known as Potamogeton (Yabe and Endo, 1935), Podozamites (Miki, 1964) and Orchidites (Wu, 1999), depending on the particular flora in which this leaf was recognized. From the affiliated cones and distinctive cuticle structure, Sun et al. (2000) established Liaoningocladus, in which the female reproductive organ was considered different from Cycadocarpidium, and foliage was linked to Podozamites (Nathorst, 1886). Liaoningocladus probably was affiliated with the extant conifer families Araucariaceae or Podocarpaceae (Wang Qi, pers. comm. 2015), although its' systematic relationships have not been formally assessed (Ding et al., 2014). Once these leaf taxa were taxonomically identified and established from the three examined time slices in northeastern China (T3, J2, K1), their insect damage and other linked data were qualitatively and quantitatively analyzed. Here,

the results of these analyses are reported with a focus on detailed patterns of insect herbivory. An interpretation of the patterns of insect damage follows, with a discussion of possible causes involved.

## 2. Materials and methods

2.1. Localities

All fossil leaf material was collected from northeastern China, in Liaoning Province and Inner Mongolia Autonomous Region (Fig. 1). The fossil leaf material collectively represents three slices of time from three well-known deposits. The deposits are the Yangcaogou Formation, of latest Late Triassic (Rhaetian) age at 205 Ma (Zhou, 1981; Liu, 1987; Yang et al., 2000), assigned the symbol T3; the Jiulongshan Formation (late Callovian), of latest Middle Jurassic age at 165 Ma (Wang et al., 2000; Shen et al., 2003; Chen et al., 2004), assigned the symbol J2; and the Yixian Formation (late Barremian), of mid Early Cretaceous age at 125 Ma (Swisher et al., 1999; Zhou et al., 2003), assigned the symbol K1. From the 756 total specimens that were examined, 220 specimens (29.1%) were collected from Yangcaogou Village of Liaoning Province (T3); 88 specimens (11.6%) were collected from Sites 1 and 2 at Daohugou Village, in Inner Mongolia Autonomous Region (J2); and 448 specimens (59.3%) were collected from the three sites of Dawangzhangzi Village, from Liaoning Province, and Liutiaogou and Duolun Villages from Inner Mongolia Autonomous Region (K1). All specimens are housed as vouchers at the Key Laboratory of Insect Evolution & Environmental Changes, College of Life Science, Capital Normal University, at Beijing, China (CNUB; D.R., curator).

2.2. Plant hosts

Examined broadleaved conifer material was preserved as adpression fossils (Shute and Cleal, 1986), and consisted of Podozamites lanceolatus, Lindleycladus lanceolatus, and Liaoningocladus boii. These three broadleaved conifers can be distinguished by their leaf cuticle and reproductive organs (Harris, 1979; Sun et al., 2001); however, their cuticle structure often was inadequately preserved and their reproductive organs were not attached. In addition, L. boii possessed flatter axes and their leaves were attached in a semiamplexicaulous fashion to their axis, differing in the condition found in Podozamites and Lindleycladus (Sun et al., 2001; Taylor et al., 2009). All relevant broadleaved specimens that we examined from the Yixian Formation were attributable to L. boii, and specimens from the Yangcaogou and Jiulongshan formations were assigned to a Podozamites–Lindleycladus species complex because foliar morphology was inadequate to provide a definitive assignment (Sun et al., 2001).

2.3. Functional feeding groups and damage types

All broadleaved foliage taxa and types of insect-caused damage were recorded. Only insect damage inferred to have occurred while the plant was alive was included as data, based on four types of direct and indirect evidence that is used to separate herbivory of live foliage from detritivory of plant litter (Labandeira, 1998). Insect damage was categorized based on the widely used damage type (DT) system (Labandeira et al., 2007). A damage type (DT) is the basic unit of an insect feeding pattern on a live plant that can be explicitly defined, diagnosed and compared to other such damage. A functional feeding group (FFG) is an assemblage of DTs caused by the same mode of feeding, such as all of the DTs formed by external foliage feeding, or similarly for leaf mining. Fossil foliage that constituted data included only specimens sufficiently well preserved for which a DT determination could be made, assuming its potential presence on a leaf. Consequently, leaf specimens smaller than 0.5 cm^2 in areal extent were excluded, as were other specimens for which accurate plant identifications could not be determined.
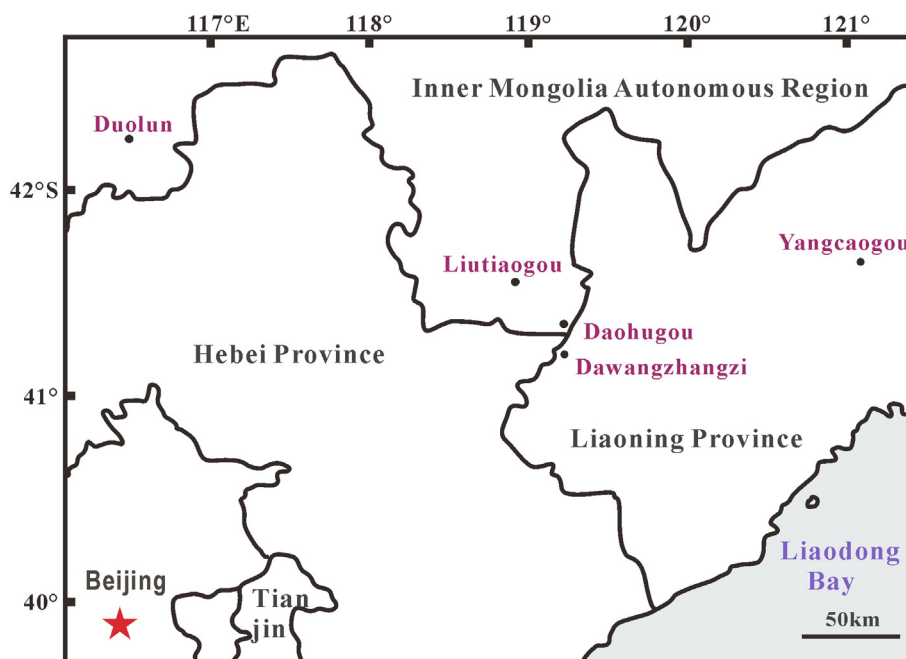
Fig. 1. The five fossil localities mentioned in this study. The Yangcaogou locality of the Yangcaogou Formation is of T3, or Late Triassic (Rhaetian) age. The Daohugou 1 and 2 localities of the Jiulongshan Formation are of J2, or latest Middle Jurassic (late Callovian) age. The Dawangzhangzi, Liutiaogou and Duolun localities are of K1, or mid Early Cretaceous (latest Barremian) age.

The raw presence–absence data is expressed as two variables, DT richness and DT frequency, both which figure prominently in the quantitative analyses of herbivory (e.g., Currano et al., 2010). For presence–absence data, those specimens that bore multiple examples of a particular DT, that particular DT was counted only once. We included within external foliage feeding the subgroups of margin feeding, hole feeding and surface feeding; skeletonization was absent. Although oviposition is a non-feeding functional feeding group, it was included in all summary DT abundance and richness data and analyses. Oviposition has a well-documented fossil record and historically has been treated as analogous to a feeding mode. Plant specimens recorded in the data-base were counted such that each specimen represented a single individual.

Table 1
Frequency of damage types (DTs) for each time interval (T3, J2, K1) and for each functional feeding group (FFG), including summary data at bottom.

| Functional feeding group	Damage type (DT)	Time interval						Frequency per FFG
		Late Triassic Yangcaogou Fm. (T3, 205 Ma)		Middle Jurassic Jiulongshan Fm. (J2, 165 Ma)		Early Cretaceous Yixian Fm. (K1, 125 Ma)		
External foliage feeding	DT1	10.5%	4.5%	0	6.8%	0	5.6%	16.9%
	DT8	0		0		0.2%		
	DT12	2.3%		2.2%		2.5%		
	DT13	0.5%		4.4%		0.9%		
	DT30	0.5%		0		0		
	DT103	0.9%		0		2.7%		
Piercing and sucking	DT46	0.9%	1.8%	16.7%	25.0%	0.9%	2.0%	28.8%
	DT48	0		12.2%		0.2%		
	DT77	0.5%		0		0.7%		
	DT128	0		2.2%		0		
	DT138	10.5%		6.7%		0.4%		
Oviposition	DT76	0	0.5%	2.2%	5.7%	0.2%	6.0%	12.2%
	DT101	0.5%		4.4%		3.6%		
	DT175	0		0		2.7%		
Galling	DT33	0	0.5%	1.1%	8.0%	0	3.3%	11.8%
	DT34	0		3.3%		0		
	DT80	0.5%		0		0.9%		
	DT116	0		2.2%		0		
	DT122	0		0		0.7%		
	DT127	0		0		0.9%		
	DT161	0		1.1%		0		
	DT240	0		0		0.9%		
Mining	DT280	0	0	0	0	3.3%	3.3%	3.3%
Frequency per time interval		7.3%		45.5%		20.2%		
Specimens examined		220		88		448		756
DT fraction of specimens per time interval		6.8%		33.0%		18.3%		
DT fraction of all DTs in data set		11.7%		56.8%		31.5%		100%

2.4. Imaging

Observations of DTs were made on a Leica M165C stereomicroscope. Macrophotographic images of insect-damaged foliage were taken on a Nikon D100 camera for specimens of entire leaves. Microphotographic images of insect damage taken at much higher magnification were on a Leica MZ12.5 stereomicroscope connected to a Nikon DXM1200C camera. The images subsequently were processed with Adobe Photoshop CS5 and CorelDRAW 12 software. Data providing fossil locality, specimen number, plant-host morphotype, damage type, photo log and specimen comments from each locality were recorded on Microsoft Office Excel spreadsheets.

2.5. Quantitative analyses

The data were plotted bivariately using four qualitative variables and five quantitative variables. The qualitative variables are: (i), geological time, as a proxy for deposit age, represented by age dates for the Late Triassic (T3) of the Yangcaogou Fm., latest Middle Jurassic (J2) of the Jiulongshan Fm. and mid Early Cretaceous (K1) of the Yixian Fm.; (ii), the five functional feeding groups (FFGs) of external foliage feeding (inclusive of the margin feeding, hole feeding and surface feeding subgroups), piercing and sucking, oviposition, galling and leaf mining; (iii), the 23 damage types (DTs) (Labandeira et al., 2007), that represent a finer-grained assessment of insect damage than the FFGs listed in Table 1 (raw data provided in Table S1); and (iv), the four major types of foliar tissues consumed by insect herbivores of epidermis, parenchyma, xylem and phloem (Labandeira, 2013a). These qualitative variables provide the entities which were used for various quantitative analyses.

Analyses of the five quantitative variables provide the data necessary for a quantitative assessment of herbivory on the broadleaved conifers. The variables are: (i), the number of specimens consisting of 220 specimens for T3, 88 specimens for J2, and 448 specimens for K1, for a total of 756 total specimens examined; (ii), DT and FFG abundances that provide the occurrences for each DT and FFG within each of the three deposits listed in Table S1; (iii), DT and FFG frequency of occurrence, expressing the proportional representation of each DT and FFG for each time period and for each of the three deposits, provided in Table 1; (iv), the frequency of food-resource targeting of epidermis, parenchyma, xylem and phloem; and (v), predicted DT richness, based on bootstrap–regression analyses that establishes the extent of capture of DTs that potentially were present for each of the three examined time intervals and on four of the five FFGs. These five quantitative variables would provide insight into abundance and frequency patterns of herbivory based on a more finely grained (DT) or coarser grained (FFG) approach to evaluating the damage inflicted by insect herbivores and on the type of foliar tissues consumed through time.
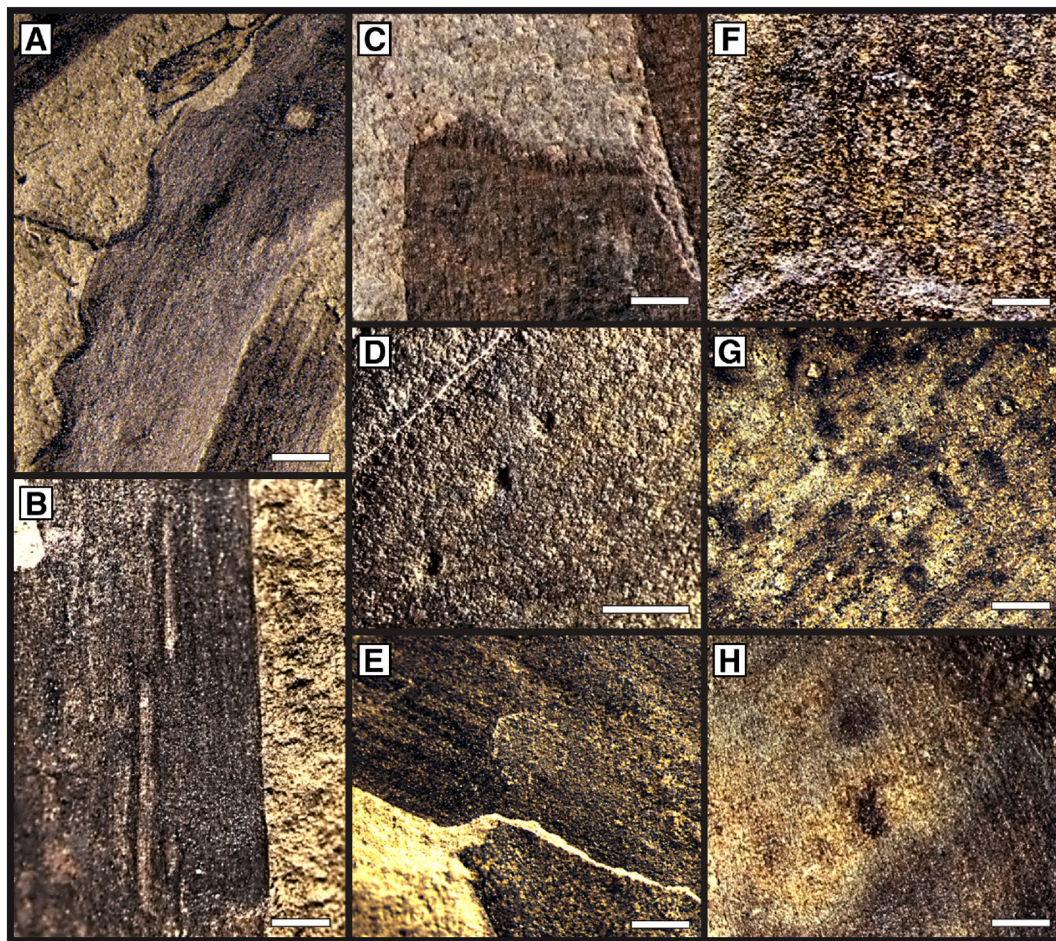
Fig. 2. Damage types on the broadleaved conifer *Podozamites lanceolatus–Lindleycladus lanceolatus* species complex from the Late Triassic (T3) Yangcaogou Formation. All specimens are from the Yangcaogou locality, Liaoning Province, in Northeastern China. A, External foliage feeding, consisting of hole feeding (DT01) and margin feeding (DT12) on CNU-CON-LB- 2010- 103-22. Note reaction rims on DT12. B, External foliage feeding of linear, slot-like, surface abrasion (DT103) on CNU-CON-LB-2010-042-6. C, External foliage feeding of margin feeding (DT13) on CNU-CON-LB-2010-106-1. Note veinal stringers at cut leaf margin. D, Piercing and sucking (DT138) targeting vein vascular tissue on CNU-CON-LB-2010-041-1. Note linear trajectory of punctures that parallel venation. E, Piercing and sucking indicated by a circular scale mark (DT77) covering the leaf surface of CNU-CON-LB-2010-043P-2. F, External foliage feeding of surface abrasion (DT30) on CNU-CON-LB-2010-057-1. G, Piercing and sucking of isolated, randomly positioned punctures (DT46) on surface of CNU-CON-LB-2010-065C-1. H, Galling of small, circular epidermal galls (DT80) on CNU-CON-LB-2010-104-2. Scale bars are 1 mm throughout.

Quantitative analyses of damage frequency and predicted damage richness was done in R, version 2.13.1 (R Development Core Team, 2011). For analyses of DT richness, the DT census data first were bootstrapped, consisting of 5000 random subsamples with replacement. The initially bootstrapped data expressed the number of DTs versus the number of specimens. Following the initial trends established by the bootstrapped datasets, the trendlines subsequently were regressed for the three time intervals (T3, J2, K1) and for the four FFGs of external foliage feeding, piercing and sucking, oviposition and galling in the J2 and K1 time intervals. (Leaf mining occurred only during the K1, and thus was excludEd.) The results of these bootstrap–regression analyses arrived at saturation values for each of the three time slices and the four analyzed FFGs. The most common interpretation of saturation values would be as an analog to rarefaction, wherein the expected but unsampled number of additional items (DTs) is calculated for assessing the completeness of the sampling process, and to provide an estimate of the total number of items (e.g., DTs) that would be present had sampling been complete. In our study, bootstrap–regression analyses were used as additional evidence for reconstructing the original DT abundance for each time interval and FFG (except leaf mining).

3. Results

Twenty-three DTs attributable to insect herbivory and oviposition were identified on the three broadleaved conifers from the three mid-Mesozoic deposits of northeastern China representing the T3, J2 and K1 time planes (Tables 1 and 2). These DTs were allocated to the five FFGs for each of the three time intervals (Figs. 2–5).

3.1. Insect damage

Examples of insect damage from each of the tree time slices—T3, J2 and K1—are provided in Figs. 2–5. Insect damage from T3 (Fig. 2) indicates the dominance of external foliage feeding, such as DT12 and DT13 (Fig. 2A, C), small hole feeding (DT01) (Fig. 2A), and the abrasion of surface tissue layers (DT103 and DT30) (Fig. 2B, F). Piercing and sucking occurred along vascular tissue in veins, such as DT138 (Fig. 2D), scale impression marks of DT77 that targeted deep-seated phloem (Fig. 2E), and individual DT46 punctures that probably probed for interveinal parenchyma (Fig. 2G). Rare galls occur, but are present as small, simple, hemispherical structures assigned to DT80 (Fig. 2H).

From J2 time, there was less external foliage feeding but a considerably greater amount of piercing-and-sucking damage (Fig. 3). External foliage feeding included DT12 and DT13 margin feeding (Fig. 3A, B). Oviposition occurred as DT76 on major veins and DT101 on the leaf lamina (Fig. 3C, D). Piercing and sucking was the predominant mode of insect damage, deployed as punctures linearly aligned along veins (DT138), more broadly as dispersed clusters (DT46), occasionally as isolated probes (DT48) into interveinal tissues (Fig. 3E, F), and distinctive DT128 hemipteran scale marks that accessed subsurface tissues (Fig. 3G). While galls were not abundant, they were diverse, and included simple, generalized galls on major (DT33) or minor (DT34) veins (Fig. 3H, I). More complex galls were the columnar DT116 structures deeply seated in leaf tissue that housed a central, longitudinal chamber (Fig. 3J–K), and circular blister galls of DT161 with pustulose surfaces (Fig. 3L).

The mid Early Cretaceous (K1) provided a greater variety of interactions and produced more specialized targeting of tissues (Figs. 4, 5). One
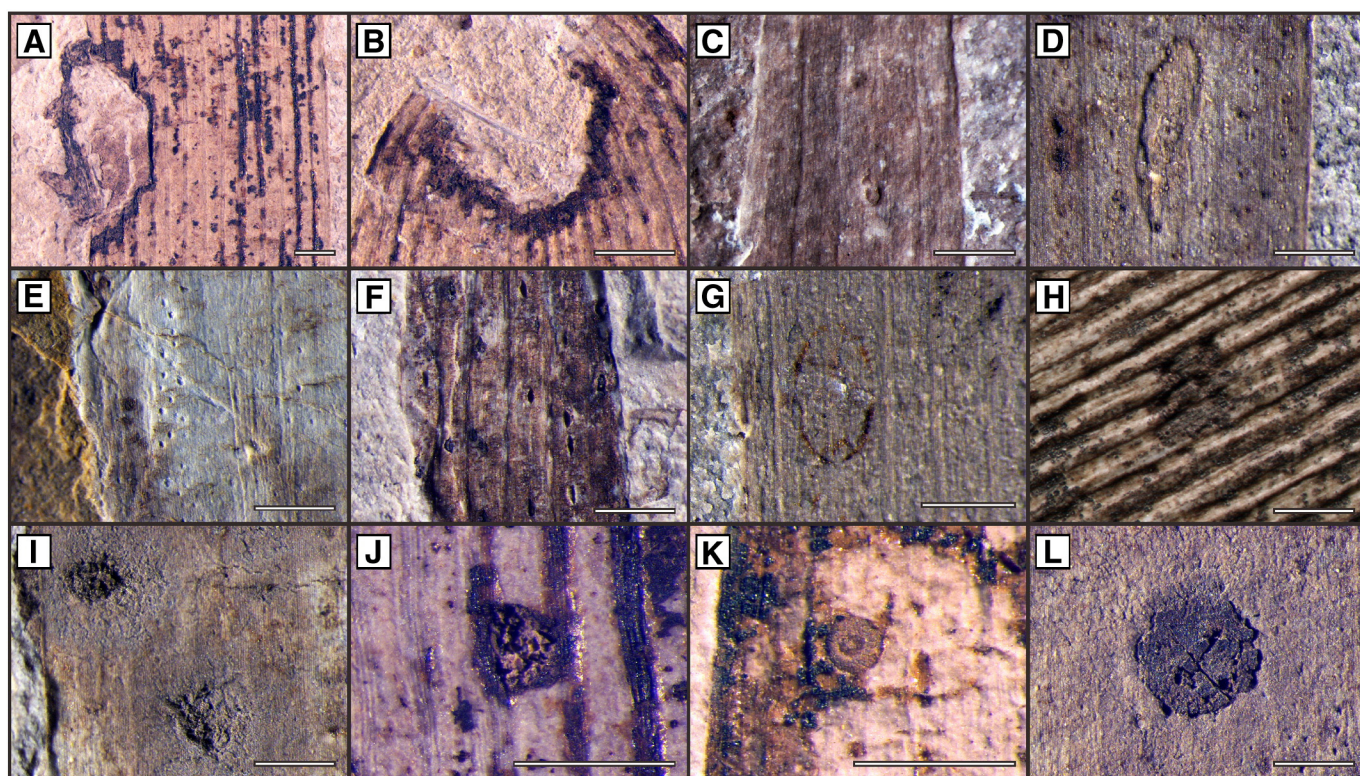
Fig. 3. Damage on the broadleaved conifer *Podozamites lanceolatus–Lindleycladus lanceolatus* species complex from the latest Middle Jurassic (J2) Jiulongshan Formation. All specimens are from the Daohugou 1 and 2 localities from the Inner Mongolia Autonomous Region, at its juncture with Hebei and Liaoning Provinces, in Northeastern China. A, External foliage feeding of DT12, a type of margin feeding, on CNU-CON-NN-2011-421P-1. B, External foliage feeding of DT13, another type of margin feeding, on CNU-CON-NN-2009-646P-1. Note well developed reaction callus. C, Oviposition (DT76) on a major vein of CNU-CON-NN-2011-634-1. D, Oviposition (DT101) exhibiting a pronounced outer reaction rim and disrupted inner tissues on CNU-CON-NN-2011-636-1. E, Piercing and sucking consisting of random punctures (DT46) and linear rows of probes (DT138) on CNU-CON-NN-2011-314P-1. F, Piercing and sucking (DT48) on CNU-CON-NN-2011-028-1. G, Piercing and sucking represented by a scale impression mark (DT128) on CNU-CON-NN-2011-633-1. Note the two concentric lineations on this structure. H, Galling indicated by a simple gall on major veins (DT33) of CNU-CON-NN-2010-662-2. I, Another example of galling, on the minor veins (DT34), on CNU-CON-NN-2009-604-1. J–K, The distinctive, columnar, deep-seated gall DT116 on CNU-CON-NN-2011-421P-1 at (J) and a better preserved specimen on CNU-CON-NN-2009-635-1 at (K). L, Epidermal cover gall (DT161) on CNU-CON-NN-2010-078-1. Scale bars are 1 mm throughout.
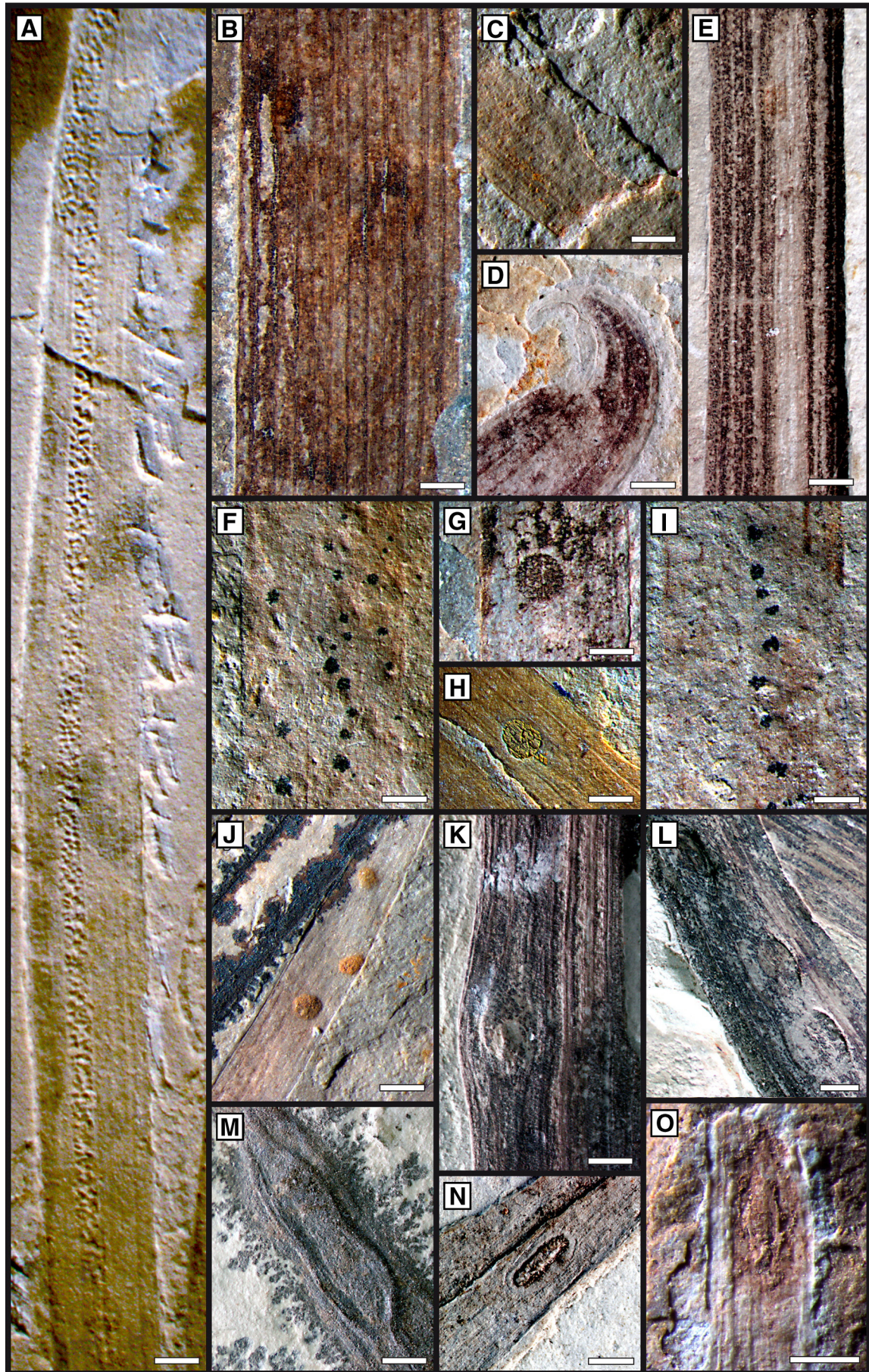
specialized interaction was a linear DT280 leaf mine consisting of a frass trail of particulate fecal pellets that resulted from consumption of mesophyll parenchyma and phloem (Fig. 4A). External foliage feeding was present as DT08 hole feeding (Fig. 4B), DT12 and DT13 margin feeding along leaf edges (Fig. 4C, D), and distinctive DT103 surface abrasion (Fig. 4E). Piercing and sucking occurred as isolated DT46 punctures (Fig. 4F), DT77 and DT122 scale marks indicating consumption of parenchymatic tissues (Fig. 4G, H), and linear DT138 targeting of vein vasculature (Fig. 4I). Oviposition lesions were present on tissues such as primary veins of DT76 (Fig. 4M), and interveinal tissue was penetrated by single incisions of DT101 (Fig. 4N, O). Galls retain their diversity in K1 as simple, small, hemispheroidal structures of DT80 (Fig. 4J), and the larger bulbous, hemispheroidal features of DT127 (Fig. 4K, L). The successive, end-to-end lesions of new damage type DT175 represents alteration of interveinal epidermal and parenchymatous tissue (Fig. 5A–D). DT240 (Fig. 5E–H) is a gall, attributable to a pemphigid (Hemiptera) or more likely a tenthredinoid (Hymenoptera) that affected leaves adjacent the axial region of branchlets. The new K1 damage types DT175 and DT240 are described in detail below.

3.2. Damage frequency

The overall pattern of insect damage frequency (all DTs) on broadleaved conifers from northeastern China (Figs. 6, 7; Tables 1, 2) was established by or during the Late Triassic (T3) with 15 DT occurrences, representing 6.8% of the 220 specimens examined (Figs. 2, 6; Table 1). The DT frequency increased and peaked during the latest Middle Jurassic (J2) with 29 occurrences, for 33.0% of the 88 specimens examined (Figs. 3, 6; Table 1). During the mid Early Cretaceous (K1), the presence of 82 DT occurrences representing 18.3% of 448 specimens examined resulted in a significantly decreased damage frequency (Figs. 4–6; Table 1). There are five discrete patterns of FFGs that characterize the DT frequency data (Fig. 6). First, the frequency of external foliage feeding ranged from a relatively even 4.5% to 6.8% for the three time planes. Second, from a low value of 1.8% in T3, there was a more than tenfold increase of piercing and sucking to 25.0% during J2, after which this FFG decreased to its previous level of ca. 2.0% in K1. Third, the frequency of oviposition had an initial low frequency of 0.5% in T3, rose tenfold to 5.7% during J2, and then stabilizing to 6.0% in K1. Fourth, the frequency of galling shows a significant increase from 0.5% in T3, to 8.0% during J2, and dropped to 3.3% for K1, approximating the pattern seen in oviposition. Fifth, leaf mining, absent in T3 and J2, had a comparatively modest frequency of 3.3% for the sole leaf-mine type of DT280 in K1. For each time interval, there is a characteristically dominant FFG and spectrum of prominent DTs and overall level of herbivory intensity (Figs. 6, 7). This pattern occurs for T3, where DT12 (external foliage feeding) was the most frequently encountered DT; for J2, where DT46 (piercing and sucking) was most abundant; and for K1, in which DT101 (oviposition) and DT280 (leaf mining) were bimodally most abundant (Fig. 6). The overall number of DT occurrences on specimens apparently did change significantly during the three time intervals, increasing by a factor of 6.1 from T3 to K1 (Table 1).

3.3. Damage richness

All of the four principal FFGs of external foliage feeding, piercing and sucking, oviposition and galling are represented in each of the three time intervals, and leaf mining additionally occurs in K1 (Figs. 6, 7). The richness (diversity) of total DTs seems not to have changed significantly (a long-term increase of 1.6%), ranging from 10 in T3, to 12 in J2, to 16 in K1. Nevertheless, there are disparities in the number of DTs for each FFG when compared by time interval, ranging between one (oviposition and galling for T3 and leaf mining for K1) and five (external foliage feeding for T3). For all data, the average number of DTs per FFG is 2.9. The most obvious divergences in the proportional representation of DTs for each FFG is the expansion of piercing and sucking during J2 and the addition of leaf mining during K1 (Figs. 6, 7).

3.4. Food resource partitioning

Four tissue types are consistently available to insect herbivores, based on modern patterns of insect and mite feeding patterns (Johnson and Lyon, 1991; Tovar et al., 1995). The most significant tissues are epidermis, parenchyma, xylem and phloem that were commonly accessed by insects belonging to various FFGs, each of which represented a distinctive feeding strategy for dietarily partitioning food resources (Labandeira, 2013a). During T3, all foliar tissues were accessed through their consumption by external foliage feeding; the targeting of single tissues was limited and confined to some piercing and sucking and galling (Fig. 6). For J2, there is an increase in the targeting of tissues, prominently by piercers and suckers that generally accessed parenchyma, and to a lesser extent, phloem (Fig. 6). Other FFGs of external foliage feeding, oviposition and galling reflect more eclectic tissue preferences, typically consuming three or four tissue types simultaneously. While external foliage feeders remained catholic in their tissue preferences, there was a simultaneous shift toward targeting epidermis and parenchyma by piercer and suckers and gallers. The single leaf miner of DT280 also targeted parenchyma, and was an effective consumer of phloem as well (Q.L. Ding et al., 2014).

3.5. Herbivory saturation levels

In one substudy, nonlinear regressions based on bootstrapped resampling curves (with replacement) for each of the three time slices indicate that DT richness approaches a saturation value of 16 DTs for J2 and 19 DTs for K1 (Fig. 8). However, the DT richness for T3 may be an overestimate at ca. 24 DTs, as the specimen number likely is insufficient for adequate extrapolation.

In a second substudy, reliable bootstrap analyses and non-linear regressions were done for each of the four relevant FFGs occurring for the J2 and K1 time slices (Fig. 9) (leaf-mining was not included, as it only occurs in K1). These non-linear regressions are consistent with results from census data for external foliage feeding and oviposition for both J2 and K1 (Fig. 9A, C), as well as for piercing and sucking for J2 and galling for K1 (Fig. 9B, D). However, the predicted richness of piercing-and-sucking for K1 and galling for J2 (Fig. 9B, D) is inordinately higher than the census data would indicate, characterized by the absence of a well-defined asymptote within the bootstrapped interval. These data and model tests indicate that in five of seven instances, the fossil record is reliably capturing the approximate number of DTs that provide realistic estimates for DT diversity. The exceptions, J2 galling and K1 piercing and sucking, probably represent undersampling and/or elevated DT diversities for these two FFGs during the two indicated time intervals.

Fig. 4. Damage on the broadleaved conifer *Liaoningocladus boii* from the mid Early Cretaceous (K1) Yixian Formation. Specimens are from the Dawangzhangzi locality (LL) of Liaoning Province, and the Duolun (ND) and Liutiaogou (NN) localities of Inner Mongolia Autonomous Region, in Northeastern China. A, A linear leaf mine with particulate frass (DT280), made by a buprestid beetle (Ding et al., 2014) on CNU-CON-LL-2010-062P-1. B, External foliage feeding is shown in (b) to (e), exemplified by slot feeding (DT08) on CNU-CON-ND-2010-015-1. C, Margin feeding of DT13 on CNU-CON-LL-2010-469-1. D, Margin feeding of DT12 on CNU-CON-LL-2010-223P-1. E, Surface feeding of DT103 on CNU-CON-ND-2010-230-1. F, Piercing and sucking, deployed as random punctures (DT46) on CNU-CON-NN-2009-893-1. G, Piercing and sucking showing a scale mark (DT77) embedded on the leaf surface of CNU-CON-NN-2010-021-1. H, Galling of distinctive DT122 on the leaf surface of CNU-CON-NN-2008-004-1. I, Piercing and sucking oriented along a vein (DT138) on CNU-CON-NN-2009-893-1. J, Galling, of the gall DT80 in CNU-CON-LL-2010-269P-1. K–L, Galling of DT127, a conspicuous, bulbous gall on CNU-CON-LL-2010-281-1 (K) and CNU-CON-LL-2010-281-1 (L). M, Oviposition of DT76 along a primary leaf axis of CNU-CON-LL-2010-270P-1. N–O, Oviposition of DT101 occurring on the leaf blade of CNU-CON-LL-2010-149P-1 (N) and on CNU-CON-LL-2010-362-1 (O). Scale bars are 1 mm throughout.

Fig. 5. The new damage types DT175 (A–D) and DT240 (E–H) on host *Liaoningocladus boii* from the Yixian Fm. (K1) of Northeastern China. DT 175 (A–D) is a mode of oviposition showing a row of successive ovipositional lesions in an end-to-end position. A, DT175, showing two series of oviposition scars on leaves at left and right (CNU-CON-LL-2010-322-1). B, Four DT175 oviposition scars at left arranged in a linear file, among other, isolated scars (CNU-CON-LL-2010-445-1). C, Three successive DT175 scars (CNU-CON-LL-2010-018-1). D, Seven DT175 scars arranged into a file (CNU-CON-LL-2010-018-1). DT240 (E–F) is a type of bulbous, gall emerging from central region of a branchlet. E, Entire branchlet with galled leaves, showing the position of DT240 (CNU-CON-LL-2010-064C-1). F, Enlargement of area outlined in (E). G, Lenticular, bulbous gall with a rugose surface occurring on axis of a branchlet (CNU-CON-LL-2010-066P-1). H, Enlargement of outlined area in (G). Scale bars: all specimens 1 mm, except (F), which is 5 mm.

3.6. New damage types

In the process of examining specimens of broadleaved conifers for insect damage, two new damage types, DT175 and DT240, were encountered (Fig. 5). The new DTs are informally described and documented herein and will be provided with formal ichnotaxonomic names at later date. These data will be included in the next version of the *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils* (Labandeira et al., 2007).

3.6.1. New damage type DT175

Short description.—Elongate-elliptical oviposition scars about 1.5 × 0.25 mm in dimensions, oriented in a single file end-to-end, typically at the margin or along a major vein in a parallel-veined leaf.

Long description.—Elliptical-elongate oviposition lesions (aspect ratio 1:3 to 1:5) about l.5 × 0.25 mm in dimensions with distinct outer reaction rim and inner disturbed tissue; scars arranged end-to-end, forming a file of up to seven (or more) scars oriented along to venation or margin in a parallel-veined leaf, occasionally with two files of scars alongside each other on the same leaf specimen or deployed along a major vein.

Functional feeding group.—Oviposition.

Illustrated material.—Fig. 5A–D.

Reference specimen.—CNU-CON-LL2010-018-1.

Occurrence.—Yixian Fm.; Dawangzhangzi, Liutiaogou, and Duolun villages, Liaoning Province and Inner Mongolia Autonomous Region, Northeastern China.

Age.—Late Barremian; 125 Ma (Swisher et al., 1999).

Host plant.—*Liaoningocladus boii* Sun et al., 2000 (Coniferales); also occurring on *Baiera manchurica* (Yabe and Oishi, 1933) (Ginkgoales) from the same formation.

Inferred insect culprit.—Zygopteran damselfly (Odonata).

Specialization index.—3.

Repository.—Capital Normal University, College of Life Sciences, Beijing, China.

Remarks.—This oviposition scar illustrates a distinctive ovipositional behavior that extends to the mid Mesozoic and perhaps earlier. The biology of this oviposition type has been linked to a variety of ovipositional behaviors currently found in zygopteran odonates (damselflies), several lineages of which are known from the mid Mesozoic (Ren et al., 2010). This ovipositional type also occurs in other floras not affiliated with a *L. boii* host plant, and may be attributable to other damselfly and dragonfly taxa.

3.6.2. New damage type DT240

Short description.—Lenticular, unichambered, elongate gall with roughened surface texture, ca. 16 × 2 mm in dimensions, occurring along elongate, parallel-veined leaves, typically nested along a branchlet axis.

Long description.—Elongate, rounded, lenticular gall with a single internal chamber, rugose outer surface texture; ca. 2 mm wide by 16 mm long, consisting of a puffed-out series of lenticular structures occupying multiple veins along a single leaf, and apparently originating near the leaf base, adjacent the insertion of leaf to the rachis and often extending through the leaves.

Functional feeding group.—Galling.

Illustrated material.—Fig. 5E–H.

Reference specimen.—Specimen CNU-PLA-LL-2010-064P/C.

Occurrence.—Yixian Fm.; Dawangzhangzi locality, Liaoning Province, northeastern China.

Age.—Late Barremian; 125 Ma (Swisher et al., 1999).

Host plant.—*Liaoningocladus boii* Sun et al., 2000 (Coniferales).

Inferred insect culprit.—For the K1 occurrence, a possible pemphigid aphid (Hemiptera) or more likely a tenthredinoid sawfly (Hymenoptera) caused the observed gall.

Specialization index.—1.

Repository.—Capital Normal University, College of Life Sciences, Beijing, China

Remarks.—This gall complements another probable tenthredinoid gall (DT289) that occurs on the same host and is bulbous, larger and more conspicuous (Wong et al., 2015). These galls likely were made by sawflies, especially tenthredinoids, some modern lineages which have angiosperms as hosts (e.g., willows and cottonwoods). Alternatively, it is possible that these are pemphigid galls whose hosts currently are pinaceous conifers.

4. Discussion

A broad spectrum of insect-herbivore feeding patterns is present in the distribution of FFGs and their DTs on broadleaved conifers in the three examined deposits. This distribution of feeding patterns provides a coarse-grained, long-term account of shifting patterns of herbivory in Northeastern China for three time slices. The interplay among plants, insects and their biological and physical environments probably was affected by a variety of factors, but likely by: (i) the availability of food resources; (ii) plant physiognomy and the effectiveness of antiherbivore defenses; (iii) inter-herbivore accommodation to plant resources such as new and differential targeting of tissues; and (iv) the effectiveness of predators, pathogens and especially parasitoids in controlling herbivore populations. Below, these four issues are addressed in the context of the varied feeding modes that plants and their interacting herbivores may have had in producing these patterns of herbivory. In addition, the role of climate may be a contributing factor to the observed patterns.

4.1. Availability of food resources

The regional Yangcaogou Flora consisted of intermontane, fluvial assemblages (Yang et al., 2000) that provided a diverse regional flora in Northeastern China (Zhou, 1981; Zhang and Zheng, 1987; Zan et al., 2008; Wang et al., 2009). This flora of T3 age was dominated by ginkgoaleans such as *Baiera* and *Sphenobaiera* and conifers that included *Podozamites* and *Pityophyllum*, and subdominant elements such as filicalean ferns (*Cladophlebis*, *Todites*) and sphenopsids (*Neocalamites*). Rare taxa were cycads (cf. *Lepidozamia*) occurring in dryer situations and bennettitaleans (*Pterophyllum*), corystosperms (*Umkomasia*) and other seed plants (*Taeniopteris*) at wetter sites. A major ecological element was *Podozamites–Baiera* riparian forest that occupied a prominent habitat during T3 time in northeastern China. When herbivory is assessed at the level of the Yangcaogou regional flora, the conifers *Podozamites* and *Lindleycladus* were the most attacked (18 DT occurrences), although bennettitaleans were disproportionately herbivorized (11 DTs) when compared to their rarity. Ferns exhibited the third highest level of consumption (6 DTs), commensurate with their abundance (Q.L. Ding, C. C. Labandeira and Q.M. Meng, unpublished data). At Yangcaogou conifers constituted the most important, herbivorized plant group and the level of herbivory was modest compared to that of J2 and K1.

The flora of the two Daohugou sites during J2 time was dominated by sphenopsids (*Equisetites*), which formed lakeside or streamside communities in wetter substrates. In drier situations, seed plants were dominant to subdominant, consisting of, in rank order, conifers (*Podozamites*, *Elatocladus*), bennettitaleans (*Anomozamites*), ginkgophytes (*Ginkgoites*) and czekanowskialeans (*Czekanowskia*). However, *Yanliaoa sinensis* Pan, a cupressaceous conifer related to modern *Sequoia* and present at Yangcaogou, also occurred at Daohugou where it was a member of the *Anomozamites–Yanliaoa* lakeside woodland (Pan, 1977; Zhang and Zheng, 1987). This community included other plant groups that were shared by other J2 habitats; for example, ferns (*Todites*, *Coniopteris*) and certain ginkgophytes were uncommon to rare members of streamside and lakeside communities (Yu et al., 1987; Zhang and Zheng, 1987; Q.L. Ding, C.C. Labandeira and Q.M. Meng, unpubl. data). General herbivory levels for these major plant groups have been determined for the most
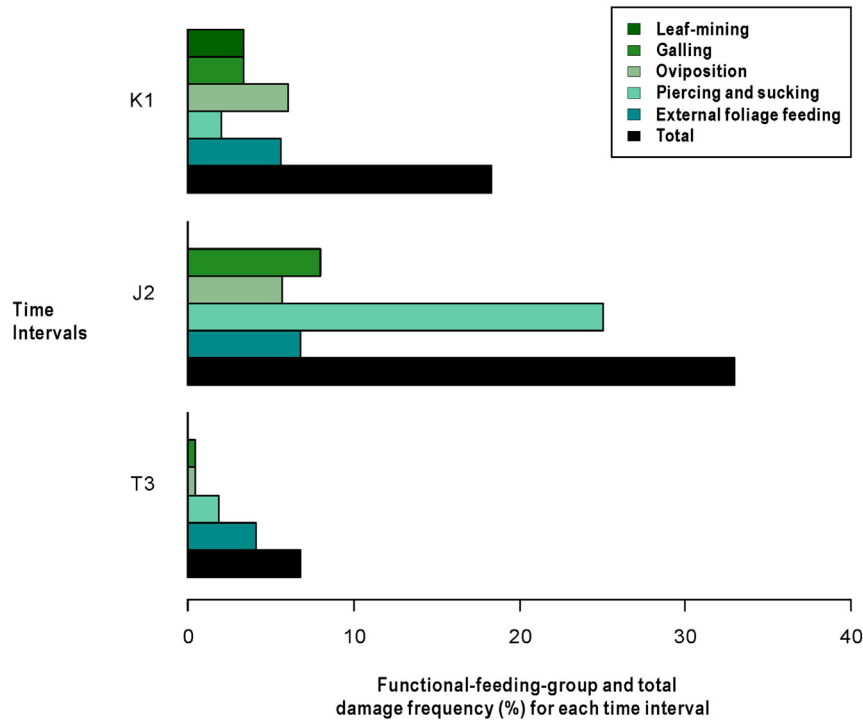
Fig. 6. Damage type frequency, expressed also as tissue types consumed for each of the five functional feeding groups of external foliage feeding, piercing and sucking, oviposition, galling and mining, expressed by time interval of T3 (Late Triassic), J2 (Middle Jurassic) and K1 (mid Early Cretaceous).

extensively documented locality, Daohugou 1 (Q.L. Ding, C.C. Labandeira and Q.M. Meng, unpubl. data). From a total of 1396 DT occurrences, the three most extensively herbivorized plant groups were bennettitaleans (62.1%), ginkgophytes (21.2%), and conifers (14.6%), with all other groups of sphenopsids, ferns, cycads, czekanoskialeans, caytonialeans and un-identified taxa accounting for the remaining 2.1% of all DT occurrences.

Conifers were the third least herbivorized, major plant group, and most herbivory on conifers was on the broadleaved taxa *Podozamites lanceolatus* and *Lindleycladus lanceolatus*. This general pattern indicates that the intensity of herbivory was disproportionately less than what the abundance of conifers would indicate. By contrast, bennettitaleans and ginkgophytes were preferently consumed by herbivores.
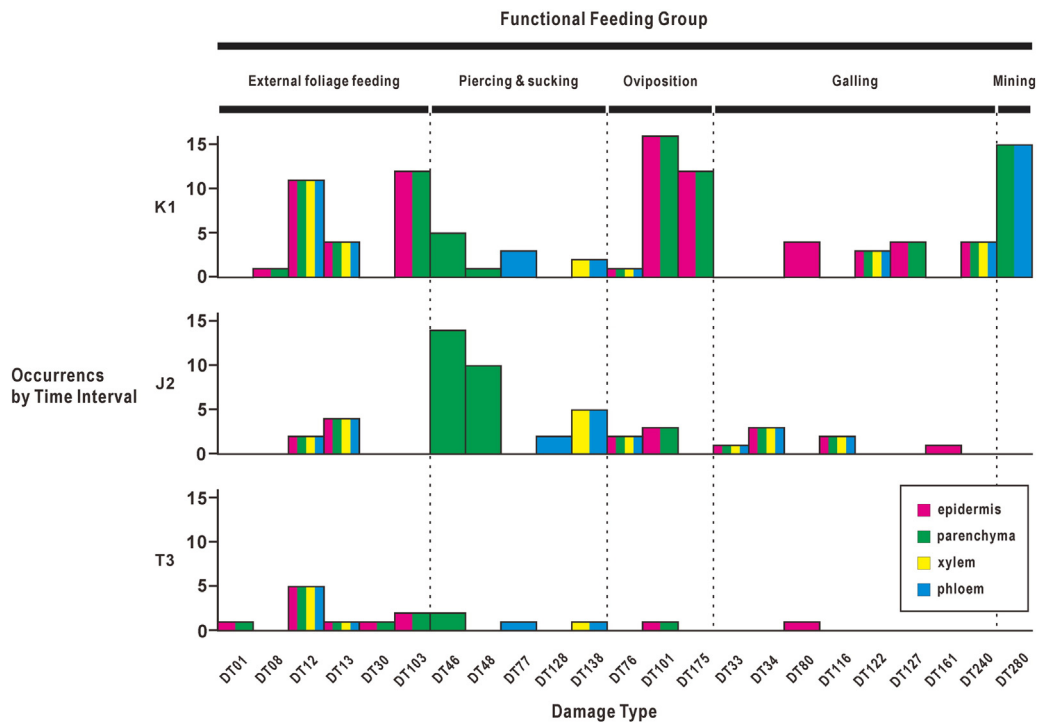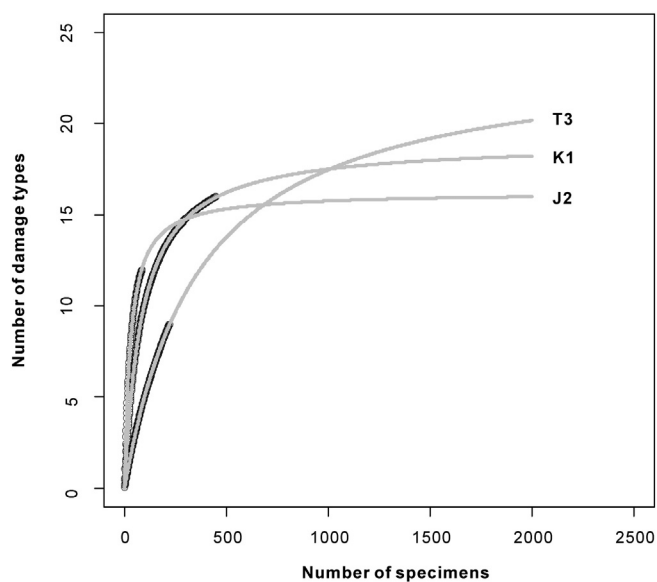

Fig. 7. The total number of DT occurrences in each of the three floras of T3 (Yangcaogou Fm., Late Triassic, J2 (Jiulongshan Fm., latest Middle Jurassic), and K1 (Yixian Fm., latest Barremian) from Northeastern China. The proportion of constituent functional feeding groups occurring for each time interval is indicated.

Fig. 8. Non-linear regressions (gray line) based on the bootstrap curves (black line) for three time slices (T3: latest Late Triassic; J2: latest Middle Jurassic; K1: mid Early Cretaceous) from Northeastern China. 5000 random subsamples with replacement were made for each bootstrapped run. The non-linear regression relationship is $y = x/(a*x + b)$.

Although conifers were a dominant group for the J2 Jiulongshan Flora, they became even more prominent in the K1 Yixian Biota (Wu, 1999), where they were the overwhelmingly dominant group (*Liaoningocladus*, *Pityophyllum*, *Schizolepis*). J2 conifers were associated with subdominant elements that typically occurred in wetter, mesic woodland and forested habitats consisting of ferns (*Todites*), cycads (*Ctenis*), czekanowskialeans (*Czekanowskia*), ginkgophytes (*Baiera*, *Sphenobaiera*) and rare bennettitaleans (*Williamsonia*) (Sun et al., 2001; Zheng et al., 2003; Ding et al., 2004; Q.L. Ding, C.C. Labandeira and Q.M. Meng, unpubl. data). These taxa were associated with *Liaoningocladus*–*Baiera* lakeside forest that constituted the dominant plant community in drier habitats. In more hydric K1 habitats there were sphenopsids (*Equisetites*), diverse filicalean ferns (*Xiajiajienia*), the earliest appearing angiosperms, particularly *Archaefructus liaoningensis*, which may have been a significant, though rare, emergent semiaquatic element along lake margins (Sun et al., 2001), although this plant may have inhabited substrates minimally associated with water (Friis et al., 2003).

The proportional representation of conifers increased from the J2 to K1 time interval, playing a gradually significant role during later K1 times, paralleled by increased DT richness in all FFGs on these plant hosts. However, when compared to the 1396 DT occurrences from J2 time, the plant assemblages of K1 time have considerably less herbivory for a comparable number of plant specimens examined, with only 182 DTs occurring among the three localities of Dawangzhangzi, Duolun and Liutiaogou. Also dissimilar from the J2 Biota was the proportional representation of total herbivory represented by the major plant groups: for the K1 conifers were the most herbivorized (52.7%), followed by sphenopsids (15.4%), ferns (9.3%), cycads (6.6%), czekanowskialeans (6.6%), unidentifiable taxa (6.0%), and ginkgophytes (2.7%). Bennettitaleans represented a barely detectible level of herbivory in K1, inverting its position as the most herbivorized group during J2.

These preliminary data suggest that, within the regional K1 flora, the distribution of herbivory was more evenly distributed among plant groups, although conifers generally and broadleaved conifers in particular had more elevated levels of consumption. The conifers apparently were targeted by a broad spectrum of insect FFGs, and included more specialized DTs than was present on J2 conifers 40 m.yr. earlier. The presence of conifers and other more xeromorphic plant taxa such as

cycads is consistent with an overall decrease in overall herbivory levels but an increase in galling, based partly on inferences from modern biotas (Hespenheide, 1991; Fernandes and Price, 1992). Also notable is the inconsequential status of angiosperm presence for herbivory, even though the K1 site is well within the initial angiosperm diversification interval (Labandeira, 2014a).

4.2. Plant physiognomy and host-plant defenses

Based on several proxy features that indicate a mesic foliar physiognomy, the broadleaved conifers that we examined apparently lacked the chemical defenses that are well documented in the foliage of many modern plants (Fürstenberg-Hägg et al., 2013). There also is no significant evidence indicating that the foliage of these broadleaved conifers possessed mechanical defenses, such as protective trichomes or exceptionally thick cuticles (Seone, 2001). The inferred physiognomy of these broadleaved conifers indicates deciduousness (Qi Wang, pers. comm.), also suggesting that *Liaoningocladus* leaves were mesic and foliose, as opposed to foliage that was sclerophyllous, thick and invested in substantial structural tissue (Sun et al., 2001; Ding et al., 2004). For J2 *Podozamites lanceolatus* and *Lindleycladus lanceolatus*, distinct epidermal hair or other defensive structures similarly were absent, in contrast to the stiff trichomes bordering the midribs of contemporaneous *Anomozamites villosus* (Pott et al., 2012), and thick cuticles on other bennettitalean foliage (Seone, 2001), that in extant plants are implicated in significant defense against insect herbivores (Müller, 2007). Consistent with minimal physical and chemical defenses were the elevated levels of herbivore attack, seen prominently in the Yixian Biota, but also documented significantly in the Jiulongshan and Yangcaogou Biotas. This prolonged interval of herbivory suggests a long-term accommodationist strategy rather than investment in strong antiherbivore defenses (Labandeira, 2007; Fürstenberg-Hägg et al., 2013). Such accommodationist strategies are similar to some dicotyledonous angiosperms that bear thin leaves with short lifespans, possess deciduousness and have greater palatability (Wilf et al., 2001), unlike thick leaves that have long lifespans, evergreen leaf persistence and elevated resistance to insect herbivores. By contrast *Liaoningocladus boii* leaves were ephemeral, and probably highly tuned to the life cycles of myriad generalist and specialist herbivores.

4.3. Interactions among herbivores for plant resources

Although the insect body fossils of Yangcaogou Formation remain unknown, the range of insect damage indicates that a trophically diverse insect herbivore fauna was regionally present during T3 time. The J2 and K1 Biotas are associated with known, diverse insect faunas and are well documented (P.J. Liu et al., 2009; Liu et al., 2010; Ren et al., 2010). Diverse J2 insects described from Jiulongshan Formation consist of 17 orders, 120 families, and ca. 490 species (Supplemental Material, Table S2). Similarly, diverse K1 insects described from the Yixian Formation have a similar distribution, consisting of 16 orders, 149 families, and ca. 440 species (Supplemental Material, Table S3). Included in these later totals are seven entirely to subdominantly herbivorous orders: Orthoptera, Phasmatodea, Hemiptera, Hymenoptera, Coleoptera, Diptera and Lepidoptera. Major herbivorous insect taxa from these clades likely produced the spectrum of DTs on broadleaved conifers during T3, J2 and K1 times (P.J. Liu et al., 2009; Liu et al., 2010; Ren et al., 2010; Zhang et al., 2013; Ding et al., 2014).

The species diversity of external foliage feeding, piercing and sucking, ovipositing and galling insects was compared between the J2 and K1 biotas (Fig. 9). In this substudy (not shown), for each of these four FFGs we identified candidate lineages, or those lineages consistent with a variety of evidence indicating that they were culprit herbivores responsible for the particular observed DTs. For these two time-based comparisons, obvious lineages were chosen for which modern data suggest a phytophagous diet (Johnson and Lyon, 1991; Tovar et al., 1995).

A) External foliage feeding

B) Piercing and sucking

C) Oviposition

D) Galling
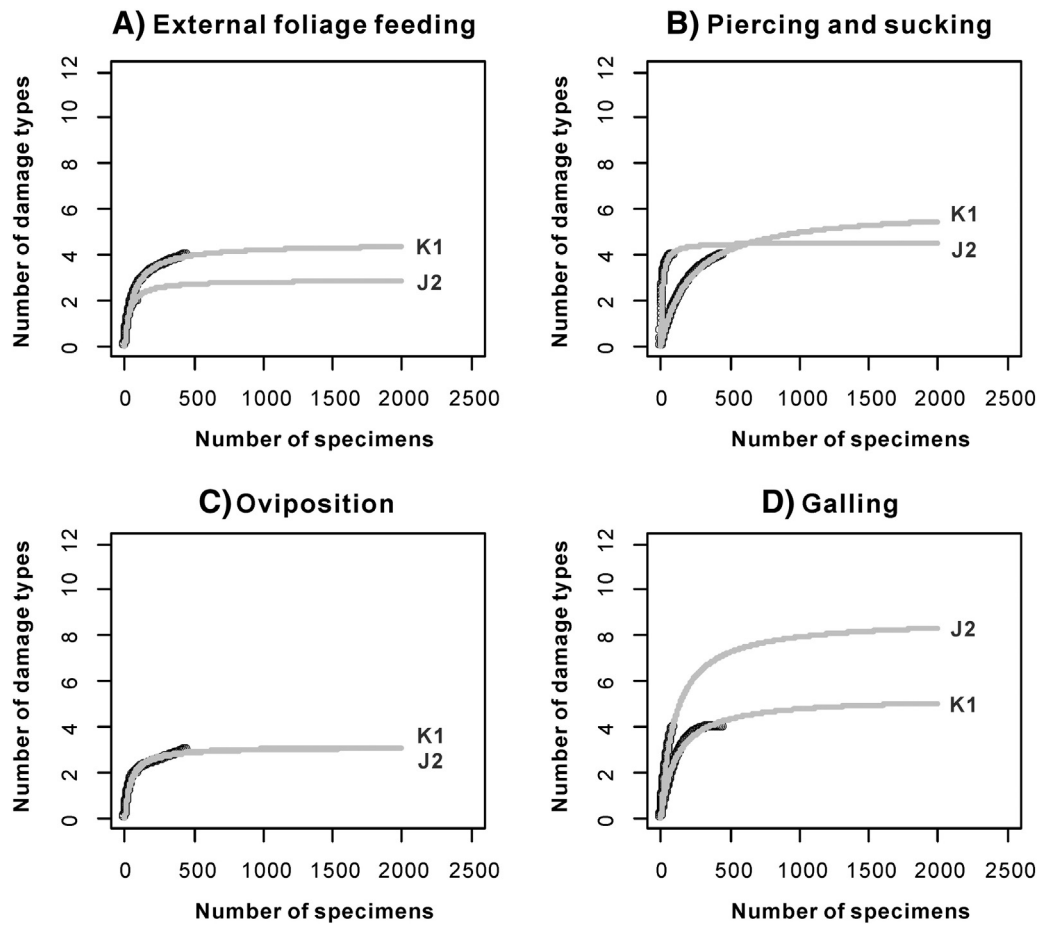
Fig. 9. Non-linear regressions (gray line) based on the bootstrap curves (black line) for each functional feeding group of the latest Middle Jurassic (J2) and mid Early Cretaceous (K1) from Northeastern China. 5000 random subsamples with replacement were made for each bootstrapped run. The non-linear regression relationship is y = x/(a ∗ x + b). A, Model for external foliage feeding; B, Model for piercing-and-sucking; C, Model for galling; D, Model for oviposition.

Inordinate application of an uniformitarian approach toward assigning diets from modern lineages to their mid-Mesozoic ancestral or otherwise related lineages initially was avoided, as it could introduce inaccuracies (Labandeira, 2002). However, separate evidence indicates that these lineages have remained relatively constant in their deep-time dietary preferences (Ding et al., 2014; Labandeira, 2014b). For herbivores of the five FFGs from J2, there are 26 species of Orthoptera, one species of Phasmatodea, 26 species of Hemiptera (overwhelmingly Sternorrhyncha), 16 species of Hymenoptera (Tenthredinoidea), 16 species of Lepidoptera and four species of Coleoptera (Polyphaga). This inferred spectrum compares with eight species of Orthoptera, four species of Phasmatodea, 15 species of Hemiptera (Sternorrhyncha and Heteroptera), 29 species of Hymenoptera (Symphyta) and 19 species of Coleoptera (Polyphaga) from K1 (Ren et al., 2010). These clades likely were the major herbivore groups responsible for external-foliage-feeding, piercing-and-sucking, ovipositing, galling and leaf mining.

This pattern suggests that the J2 biota bore more species-level feeding diversity of insect herbivores from all four FFGs than the K1 biota (Ren et al., 2010). The number of external foliage feeders during J2 is 65, versus 51 for K1, and it appears that the dominant external foliage feeders of J2 are the Orthoptera, whereas the principal external foliage feeders of K1 are Tenthredinoidea and Xyeloidea. The dominant piercing-and-sucking lineage, sternorrhynchan Hemiptera, is represented by a diversity of 26 species at the J2 sites but only 15 species in the K1 sites. For galling, 12 species were identified during J2 time as likely culprits whereas 21 species were selected as K1 candidate gallers. In an earlier, related study, the single DT280 leaf miner on *Liaoningocladus*

boii from the K1 time interval was identified as a coleopteran, a probable buprestid beetle (Q.L. Ding et al., 2014), based on a process of elimination. This process is being applied to other interactions from this deposit, such as a potential galler of the same plant host (Wong et al., 2015). One interpretation of these data is that the apparently elevated level of FFGs approached trophic saturation (May, 1974) for the J2 and K1 biotas (Fig. 9), requiring segregation of food resources and inducement of tissue partitioning that resembles the "niche separation" pattern of Lawton and Strong (1981).

4.4. The role of parasitoids

The three major trophic groups—predators, parasites and pathogens—are implicated in feeding on and regulation of insect herbivores during the mid Mesozoic. The contribution from predators toward controlling herbivores likely was relatively static throughout the mid-Mesozoic, and included spiders, odonatans, true bugs, large brachyceran flies such as asiloids, snakeflies, and coleopterans such as ground beetles (Labandeira, 2002; Grimaldi and Engel, 2005). By contrast, very little is known about the role of pathogens, particularly in their relationship toward vectoring diseases that would control insect herbivores (Labandeira and Prevec, 2014). However, it is the parasitoid guild that currently is most effective as top → down regulators of herbivores (Quicke, 1997). The parasitoid guild appeared prior to J2, during the Early Jurassic (Labandeira, 2002), thus rendering the T3 Yangcaogou deposits devoid of this crucial feeding guild. This absence suggests that the system of predation on herbivores must have been significantly different and less effective during T3 times.

Regulation of insect herbivory during T3 likely emphasized bottom → up, resource driven mechanisms, such as the availability of photosynthetic tissue provided to herbivores. Top → down controls would come from the superjacent trophic level of pathogens and predators, and would have been relatively inefficient (Labandeira, 2002). Later, the parasitoid guild became well established by J2 time, and was more pervasive during K1 time (Gao et al., 2010), implying higher mortality rates of herbivorous insect hosts and consequently more effective culling of the herbivore trophic level based on current understanding of parasitoid trophic interactions (Memmott et al., 2000) (Table S4). The principal parasitoid lineages that were present by K1 times were about 20 families of small wasps that were mostly members of the hymenopteran superfamilies Evanoidea, Ichneumonoidea, Proctotrupoidea and a few members of the aculeate superfamily Vespoidea (Table S4; Rasnitsyn, 1980; see Labandeira, 2002 for a global survey). Newly evolved parasitoid lineages of brachyceran Diptera contributed to the parasitoid guild, principally the families Nemestrinidae and Apioceridae (Zhang et al., 2010), but were less abundant. Small, parasitoid larvae target the internal organs of much larger herbivorous larval hosts, in which consumption of a particular succession of more important organs eventually leads to the host's death.

As the ectoparasitoid habit of larvae attacking their hosts externally preceded the endoparasitism of internal consumption of host tissues (Quicke, 1997), one likely consequence was an ecological shift of herbivorous host larvae from exposed ectophytic feeding of plants to hidden endophytic feeding. Both shifts in parasitoid and host-herbivore feeding modes probably resulted in more highly honed behaviors for both feeding guilds and greater intricacy of both types of life cycles. The trend from ectoparasitism to endoparasitism, coupled with a related trend from ectophytic to endophytic herbivory, is absent in T3, seen in the dominance of external foliage feeders and piercer and suckers. Both of these trends increase in J2 and become very important in K1 consistent with evidence indicating an increase of endophytically feeding insects such as leaf miners and gallers. It is likely that the shift from ectoparasitic to endoparasitic life habits in parasitoids was causally linked to the shift from ectophytic to endophytic modes of herbivory in their targeted prey hosts.

4.5. Mid-Mesozoic paleoclimate in northeastern China

The most important external environmental factor in determining plant physiognomy during the mid Mesozoic is climate (Zhu et al., 1984). Paleobiological and sedimentological evidence indicate that the general climate of northern China was humid and temperate during T3 to J2 times (Zhao, 1992; Wang et al., 1994). A major transition in climate began during the Bathonian to Callovian interval of the late Middle Jurassic in Northeastern China, in which sedimentological evidence demonstrates a gradual but pronounced change from a semi-humid to semi-arid regional climate (Vakhrameev, 1991; Zhao, 1992). Plant microfossils and megafossils are consistent with this pattern (Sun et al., 2001; Ding et al., 2003, 2004; Zheng et al., 2003). From J2 to K1 times, however, a portion of Northeastern China occupied a humid temperate belt while other adjacent regions in northern China shifted variously to a semi-arid moisture regime. This transformation provided a temperate to subtropical climate that affected the J2 and K1 biotas (Vakhrameev, 1991; Zhao, 1992). The biphasic, semi-humid or semi-arid climate from J2 to K1 is in accord with early occurrences of leaf mining in semi-humid habitats (Hespenheide, 1991) and simultaneous expansion of galling in semi-arid habitats (Fernandes and Price, 1992). This shift in paleoclimate mode likely appears to be associated with the shift from the dominance of feeding on bennettitalean hosts during J2 times to the expansion of herbivory on conifer hosts during K1 times.

5. Conclusion

There are four conclusions that can be made from this study of insect herbivory on three broadleaved conifer taxa from the Late Triassic (T3),

the Middle Jurassic (J2), and ending in the Early Cretaceous (K1) of northeastern China. This interval represents a coarse-grained, 80 m.yr. record of plant–insect interactions and host-plant use by insect herbivores during mid-Mesozoic time in northeastern China.

1. *Changing dominance of functional feeding groups (FFGs) and damage types (DTs).* Each of the three, major time slices represents the dominance of a particular insect herbivore FFG and DT on broadleaved conifer foliage. For T3 (Late Triassic), the dominant herbivores are external foliage feeders; for J2 (Middle Jurassic), it is piercer and suckers; and for K1 (Early Cretaceous), oviposition and leaf mining are jointly dominant. This pattern also is congruent with the damage type (DT) record for these taxa.

2. *Greater partitioning of foliar tissues by damage type (DT) through time.* With the general increase of the number of DTs per FFG from T3 to K1 time, there is an increased herbivore partitioning of epidermis, parenchyma, xylem and phloem tissues. This tissue partitioning is accomplished through subsequent targeting of one or two tissues rather than earlier modes of consumption favoring ingestion of portions of the entire leaf.

3. *Increased specialization of DT interactions on plant hosts through time.* There is a distinctive increase through time of more specialized interactions in which particular plant-host species become the sole targets for many insect herbivores. Evidence for specialization is provided by the greater number of generalized, external-foliage-feeding DTs over the overwhelmingly specialized DTs of oviposition, galling and leaf mining in T3, as opposed to the J2 and K1 intervals. This result is buttressed by regression results based on bootstrapped data. Most of this specialization is associated with the appearance of new DTs that leave highly stereotyped damage patterns on foliar surfaces.

4. *Four factors are proposed to explain temporal changes of insect feeding seen in the mid-Mesozoic record of Northeastern China.* The four factors are: (i), the changing phenotypic and physiognomic character of the plant hosts available for insect herbivory; (ii), the ability of herbivorized plants to use either accommodationist or antiherbivore defensive strategies in countering herbivore depredation; (iii), the nature of the resident herbivore fauna, including an increasing proficiency at partitioning host-plant tissues for selective feeding and use of strategies minimizing inter-herbivore competition; and (iv), the emergence of greater efficiency in parasitoid regulation of insect herbivores.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2015.09.007.

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