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Early Cretaceous mealybug herbivory on a laurel highlights the deep-time history of angiosperm–scale insect associations

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Summary

- Insect fluid-feeding on fossil vascular plants is an inconspicuous and underappreciated mode of herbivory that can provide novel data on the evolution of deep-time ecological associations and indicate the host-plant preferences of ancient insect herbivores. Previous fossil studies have documented piercing-and-sucking herbivory but often are unable to identify culprit insect taxa.
- One line of evidence are punctures and scale-insect impression marks made by piercing-and-sucking insects that occasionally provide clues to the systematic identities and relationships of particular insect herbivores.
- We report here the earliest occurrences of piercing and sucking on early angiosperms as evidenced by scale insect covers, impression marks, punctures and body fossils – notably a mealybug – from the Lower Cretaceous Rose Creek Flora of the Dakota Formation (*c.* 103 Ma), in southeastern Nebraska, USA. The mealybug, two other scale insect taxa, and several distinctive damage types on laurel leaves and seed-plant stems at Rose Creek document a diverse guild of piercing-and-sucking insects on early angiosperms.
- The discovery of an Early Cretaceous female mealybug indicates an early herbivorous association with a laurel host. These data provide direct evidence for co-associations and possible coevolution of scale insects and their plant hosts during early angiosperm diversification.

Introduction

Insect fluid-feeding is a diverse and important guild among herbivorous insects, and piercing-and-sucking insects presently are found in almost all terrestrial ecosystems on Earth (Dixon, 1970; Miller *et al.*, 1999; Kondo & Muñoz, 2016; Wan *et al.*, 2020; Xia *et al.*, 2021). Piercing-and-sucking herbivory originated in the Early Devonian (Kevan *et al.*, 1975; Labandeira *et al.*, 2014), and was considerably expanded by paleodictyopteroid insects during the Pennsylvanian Period (Labandeira & Phillips, 1996; Correia *et al.*, 2020). Hemipteroid insects soon thereafter colonized seed plants during the Permian (Wang *et al.*, 2009; Schachat & Labandeira, 2015; Schachat *et al.*, 2015; Labandeira *et al.*, 2016; Xu *et al.*, 2018; Maccracken & Labandeira, 2020). Piercing-and-sucking insects, especially scale insects (Hemiptera: Coccoidea), have been documented widely in Mesozoic (Wang *et al.*, 2015; Vea & Grimaldi, 2016; Poinar *et al.*, 2020), and especially Cenozoic (Johnson *et al.*, 2001; Harris *et al.*, 2007; Wappler & Ben-Dov, 2008) and modern (Miller & Kosztarab, 1979; Francis *et al.*, 2016) communities. Since the Early Devonian, piercing-and-sucking insects span a 410-Myr interval that colonized plants on multiple continents. Although evidence of piercing-and-sucking damage in the fossil record frequently is not associated with a particular insect herbivore, identification of a piercing-and-sucking insect herbivore occasionally is based on indirect evidence, principally the pattern of plant damage, but also mouthparts of co-occurring insects, biology of co-occurring plants and uniformitarian application of an appropriate modern analog (Labandeira & Phillips, 1996; Labandeira *et al.*, 2007; Wang *et al.*, 2009). The identity of ancient piercing-and-sucking insect herbivores, however, is important, as it can provide clues about the evolution of particular plant–insect associations and host plant preferences, and may be used in fossil-calibrated molecular phylogenies (Miller & Kosztarab, 1979; Labandeira & Phillips, 1996; Grimaldi & Engel, 2005; Hodgson & Hardy, 2013; Vea & Grimaldi, 2016; Maccracken *et al.*, 2021). (See Supporting Information Notes S1 and S2 for an extended account.)

Nevertheless, most piercing-and-sucking punctures on fossil plants cannot accurately be assigned to a particular insect herbivore culprit, a feature attributable to the convergence of insect feeding behaviors and mouthpart structure across several major groups of insects that bear stylate mouthparts (Labandeira & Phillips, 1996; Labandeira, 2019). Piercing-and-sucking insects puncture plant tissues, such as phloem, xylem, mesophyll, endosperm and pollen protoplasts to varying depths using their stylate mouthparts. Major phytophagous insect lineages possessing stylate mouthparts for piercing-and-sucking include the extinct Paleozoic orders Paleodictyoptera, Megasecoptera, Diaphanopterodea and Dicliptera, and the extant orders Hemiptera (cicadas, aphids, whiteflies, scale insects, hoppers, true bugs) and Thysanoptera (thrips), and to a much lesser extent isolated taxa of Coleoptera (beetles) (Labandeira, 2019). Owing to the small size and often times indistinct patterns of punctures made by piercing-and-sucking insects (Labandeira & Phillips, 1996; Labandeira *et al.*, 2007; Wang *et al.*, 2009), most piercing-and-sucking damage has resisted identification beyond the taxonomic level of order. Nevertheless, mid-Mesozoic scale insects are of interest to paleoecologists, as some scale insects likely switched hosts from gymnosperms to angiosperms contemporaneously with the radiation of angiosperms (Gullan, 1997; Labandeira, 2014; Wang *et al.*, 2015; Vea & Grimaldi, 2016). Interest in early scale insect–angiosperm associations is heightened because of the poor documentation from patterns of tissue consumption during the Early Cretaceous (Labandeira, 2006; Wang *et al.*, 2015) (Notes S1, S2).

In this report, we record a variety of piercing-and-sucking damage on the tissues of a lineage of Early Cretaceous Lauraceae (laurels). In particular, we document the earliest occurrence of herbivory of an adult female mealybug, also known as an unarmored scale insect. This specimen was preserved as a body fossil on an early angiosperm leaf. We also present two other scale insect taxa, referred to Coccidae, commonly known as soft scales or wax scales, that were hosted on seed-plant stems from the same Early Cretaceous flora. These three discoveries push back the record of scale insects directly feeding on angiosperms by *c.* 55 Myr and provide documentation for a spectrum of early scale insect–host plant associations. These insect herbivores likely were specialized on early angiosperms and played a role in the co-diversification of flowering plants and insect herbivores during their early ecological expansion.

Materials and Methods

Over 4000 fossil plant specimens from several localities of the Dakota Formation, housed at the Florida Museum of Natural History in Gainesville, FL, USA (Notes S3), were examined and photographed for a study of mid-Cretaceous insect damage (Xiao *et al.*, 2021; L. Xiao *et al.*, unpublished). The highly fossiliferous Rose Creek locality (UF15713) is a late Albian Age (*c.* 103 Myr old) deposit that crops out within the Janssen Clay Member of the Dakota Formation, located in Jefferson County, SE Nebraska (Township 1N, Range 2E of the Fairbury SW 7.5′ Quadrangle map), USA. The Rose Creek locality is well-known for its diverse early angiosperms, (Upchurch & Dilcher, 1990; Manchester *et al.*, 2018), which have provided data for two studies that have analyzed insect damage on flowers (Xiao *et al.*, 2021) and foliage (L. Xiao *et al.*, unpublished). Several uninformative fragments of insect wings also were found in association with the fossil plant material (Upchurch & Dilcher, 1990) (Notes S4).

Insect damage types (DTs) were classified and described using the *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils* (Labandeira *et al.*, 2007), and subsequent addenda as outlined in the functional feeding group (FFG)–DT system (Wilf & Labandeira, 1999; Xu *et al.*, 2018). Identification of insect damage, as opposed to physical damage, was based on several criteria, especially the presence of reaction rims as a response to herbivorized tissue, zones of necrotic or chlorotic tissue surrounding the damage (Labandeira *et al.*, 2007), and distinctive puncture trajectories and patterns on the leaf surface (Filer *et al.*, 1977), typical of modern damage (Ahmed *et al.*, 2013). Qualitative and quantitative analyses also were conducted to estimate the diversity of herbivory on three species of *Pandemophyllum*, the lauraceous host plant of the mealybug described from this flora.

The first example of a scale insect, a mealybug, was discovered on a fossil leaf from Rose Creek (Notes S5). The scale insect was found on an angiosperm leaf (UF15713–16188A) (Fig. 1a), identified as *Pandemophyllum kvacekii* (Upchurch & Dilcher, 1990), an early lauraceous host plant with festooned, brochidodromous, secondary venation (Upchurch & Dilcher, 1990) (Fig. 1b), that is similar to the extant *Eusideroxylon zwageri* Teijsm. & Binn. (Lauraceae). The *P. kvacekii* leaf is 75.34 mm in length and 26.04 mm at widest extent (Fig. 1a), with a surface area of 1353.53 mm^2. Two additional fragments of fossil leaves occur in association with this specimen but cannot be identified beyond a eudicotyledonous angiosperm.

Results

Systematic paleontology

Order Hemiptera Linnaeus, 1758
Superfamily Coccoidea Handlirsch, 1903
Family Pseudococcidae Heymons, 1915
Pseudococcidae genus et species incertae sedis, morphotype 1
Material: UF15713–16188B.

Description: A single, wingless, female mealybug, apparently sedentary, present directly on the primary vein of its host leaf (Fig. 1a). The specimen (Fig. 1h) is an impression of the body surface of an adult Pseudococcidae (Hemiptera: Coccoidea) based on approximately 15 distinctive wax filaments originating along the periphery from each side of the body (Fig. 1h). The distinctive body is ovate in overall shape, dorsoventrally flattened, displays a head region, three broad thoracic segments, and eight, narrower, evident abdominal segments, although segmentation is indistinct. Anterior area narrowly rounded, posterior area broadly rounded; specimen *c.* 2.2 mm long × 1.1 mm wide (Fig. 2a–d). Eyes, antennae, legs and the ventral aspect of the insect body are not visible. Micro-CT scans clearly show flexed wax filaments connected to the body along the lateral margin, some of which overlap or cross in dorsal view (Fig. 2b) (Notes S6).

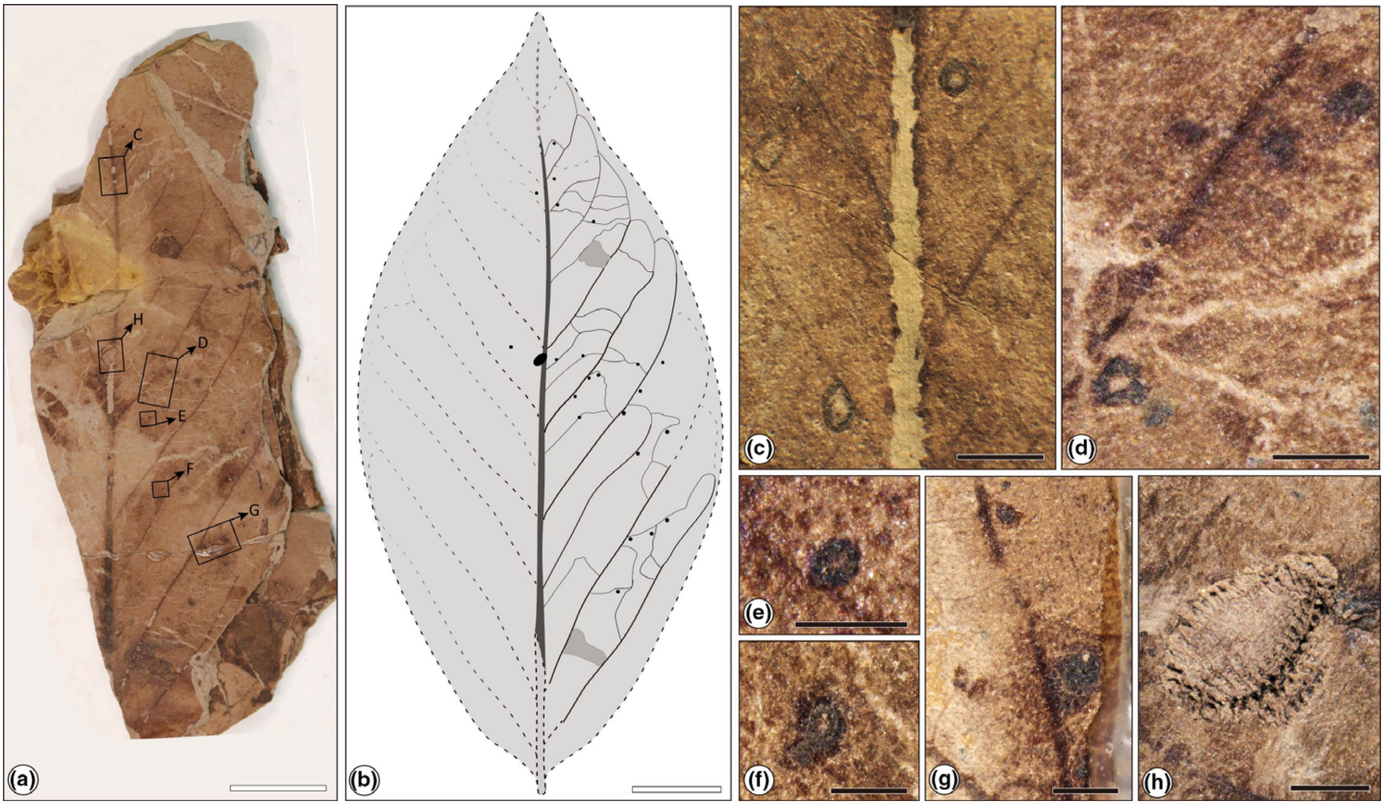

Fig. 1 A specimen of scale insect morphotype 1 (DT384), an adult mealybug preserved on an Early Cretaceous laurel leaf (Lauraceae) from the Rose Creek locality of Nebraska, USA, displays piercing-and-sucking herbivore damage. (a) Host *Pandemophyllum kvacekii* (Lauraceae) displays several punctures of DT46. (b) Line drawing of the fossil leaf; the solid line represents the leaf fragment on the slab, whereas the dashed lines indicate the rest of the leaf composited from multiple specimens at the same locality (see below for details). (c–g) Sections indicated by templates in (a), enlarged, showing encircling necrotic tissue. (h) Magnified mealybug body. (In (b), the two gray areas represent missing sections of the fossil leaf. The black oval on the major vein is the mealybug body. Dark gray, circular structures represent puncture sites along leaf veins. As a result of continuing expansion of the leaf during development, these punctures have shifted away from the leaf veins somewhat, the probable source of initial phloem feeding.) Bars: white, 1 cm; black, 1 mm.

Host plant: *Pandemophyllum kvacekii* Upchurch and Dilcher, 1998 (Lauraceae) (Fig. 1).

Associated damage type: DT384 (Notes S7). The specimen is associated with isolated occurrences of DT48, a cratered puncture of broadly elliptical to lenticular shape, present on adjacent primary or secondary veins, and with exceptionally thick reaction rims.

Comments: The DT384 specimen has few diagnostic characters that are visible, and formal assignment to a modern genus is not possible (Notes S8). Nevertheless, based on the shape, size and attachment of the wax filaments and overall habitus, this taxon has an affiliation to extant genera such as *Phenacoccus*, *Pseudococcus* and *Formicococcus* of the subfamily Phenacoccinae (Hemiptera: Pseudococcidae) (Notes S9).

Family Coccidae Stephens 1829

Coccidae genus et species incertae sedis, morphotype 2

Material: UF15713–12710B (Fig. 3a,b).

Locality: Rose Creek, Jefferson County, NB, USA.

Description: Seventeen specimens irregularly but compactly clustered along a twig, the specimens often abutting or marginally overlapping; each specimen displays a highly domed, hemispheroidal to slightly ovoidal or ellipsoidal, scale insect impression mark or scale insect cover, 4–7.5 mm in diameter or longest dimension, with an unornamented, smooth outer surface, some exhibiting an indistinct to distinct apparent growth ring. Size distribution appears continuous, not allowing for instar distinctions.

Host plant: Unidentifiable seed-plant twig, *c.* 1 cm in diameter, probably an angiosperm.

Associated damage type: DT394, possibly affiliated with DT46 on smaller twigs (Notes S7–S10).

Comments: DT394 is similar to wax scale covers of extant Coccidae such as *Toumeyella* and *Didesmococcus* (*Archangelskaya*) (Fig. 3c–e; Notes S10A–B) (Burns & Donley, 1968; Borden & Dale, 2016).

Coccidae genus et species incertae sedis, morphotype 3.

Material: UF15713–119525B (Fig. 3f–g).

Locality: Rose Creek, Jefferson County, NB, USA.

Description: Specimens represented by scale insect molds present as isolated or loosely clustered individuals on a large woody branch; each specimen moderately elliptical in shape, with an aspect ratio mostly of 2 : 1, with three apparent instars of 0.4 mm wide × 0.7 mm long, 0.7 mm wide × 1.0 mm long, and 1.0 mm wide × 1.6 mm long; anterior and posterior margins subrounded to subtly broadly angulate; bearing a prominent, dorsal, medial ridge with lineations occurring perpendicularly to a highly inclined angle along the median ridge and extending to the margin.

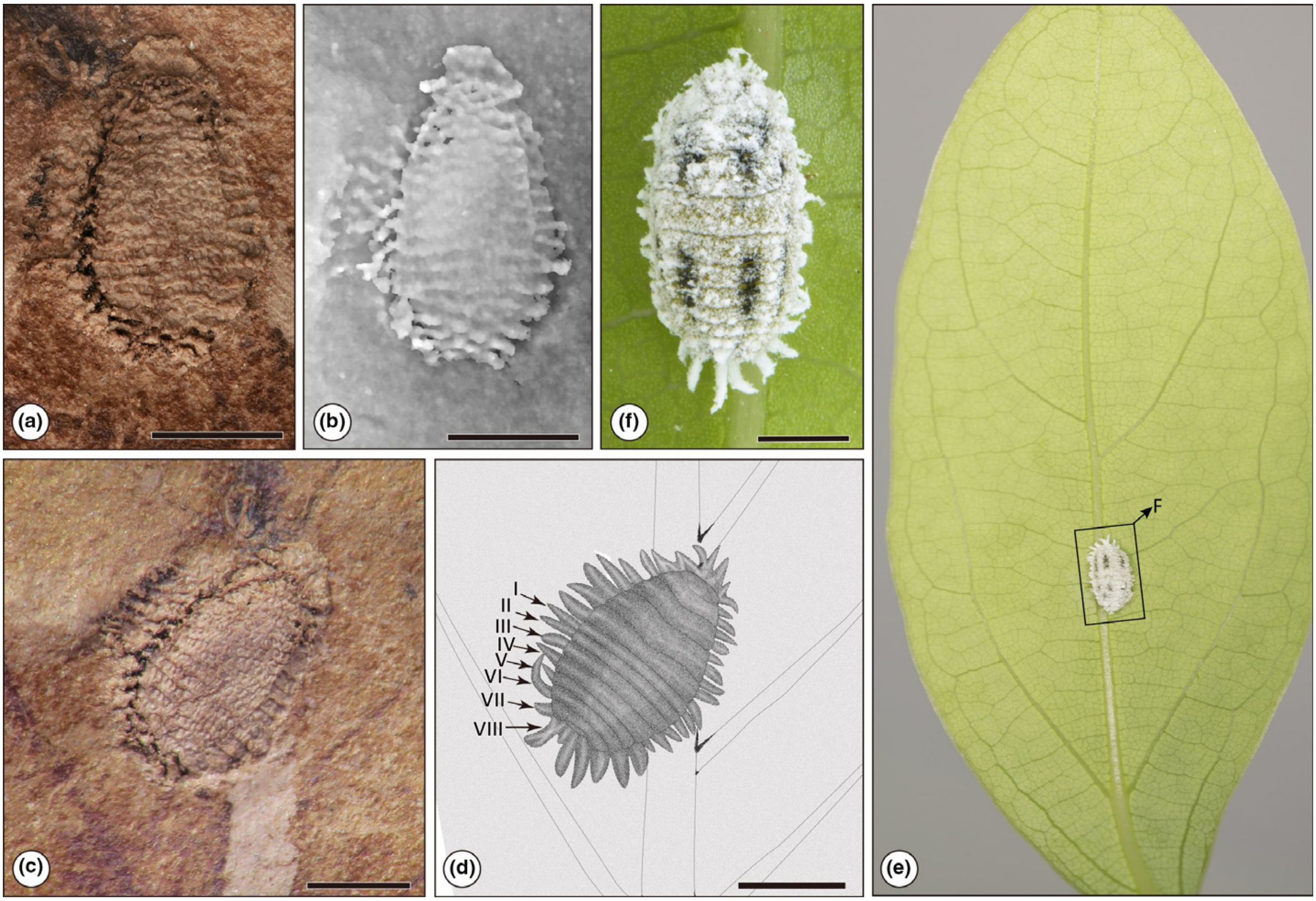

Fig. 2 Specimen of scale insect morphotype 1 (DT384), a mealybug on a fossil laurel leaf, from the Early Cretaceous Rose Creek locality of Nebraska, USA, and its modern analog *Phenacoccus solenopsis* Tinsley 1898. (a) 3D view of the fossil mealybug (UF15713-16188B). (b) Micro-CT scan of the fossil mealybug. (c) The same fossil mealybug at a broader context on the primary vein of a *Pandemophyllum kvacekii* leaf; possibly accessing phloem tissue. (d) Hypothesized reconstruction of the mealybug on its host plant. (e) Extant *Phenacoccus solenopsis* (Pseudococcidae: Phenacoccinae) on a *Cinnamomum camphora* (Lauraceae) leaf (the mealybug enlarged in (f)). Bars: black, 1 mm (images of extant scale insects on *C. camphora* lack bars). (e, f) was taken by Huayan Chen at Guangzhou City, Guangdong Province, China.

Host plant: Unidentifiable large, seed-plant branch, *c.* 6 cm in diameter, probably an angiosperm.

Associated damage type: DT406, possibly affiliated with DT46 punctures on larger twigs or stems.

Comments: Structurally, this scale insect is similar to several extant soft scales. The closest matches are the extant Cottony Camellia Scale *Pulvinaria floccifera*, the Brown Soft Scale *Coccus hesperidium* and the Citricola Scale *Coccus pseudomagnoliarum* (Fig. 3h–j) (Łagowska *et al.*, 2017; Ahmed & Stocks, 2020; Stathas & Karipidis, 2020).

Twelve piercing-and-sucking DTs were found as various configurations of punctures on the three species of *Pandemophyllum* – *P. kvacekii*, *P. attenuatum* Upchurch & Dilcher, 1990, and *Pandemophyllum* sp. 1 (L. Xiao *et al.*, unpublished) in addition to the three types of scale insect impression marks or covers detailed above that represent the impressions or covers of body fossils. The 12 kinds of puncture and scale insect DTs collectively represent an herbivorized surface area on *Pandemophyllum kvacekii* of 4.55 mm^2, constituting a herbivorization removal rate of 11.82% for the piercer-and-suckers. The DTs range includes: individual random punctures such as DT46, DT47, DT48 and DT392; linear rows or looping trajectories of DT138, DT338 and DT358; variously clustered punctures of DT281, DT330 and DT383; and a spectrum of scale insect impression marks in DT77 and DT183 (Fig. 4; Notes S11). For example, DT46 consists of small, circular and isolated punctures, with a central depression encircled by a reaction rim, distributed without a clear pattern on the foliage surface (Fig. 1c–g). DT392 represents a series of irregular punctures occurring on major leaf-vein tissue (Fig. 4b–d), whereas DT138 is a row of linear to somewhat curved punctures present along the sides of secondary veins (Notes S11). DT358 is a curvilinear, looping and occasionally spiraling trajectory of punctures present in areas between major veins. DT281 is a cluster of punctures associated with secondary veins and leaf margins, in which each puncture includes an encircling necrosis that increases in size toward major veins. The variety of feeding strategies in accessing virtually every tissue type on the three species of *Pandemophyllum* includes deeper seated phloem (and probably

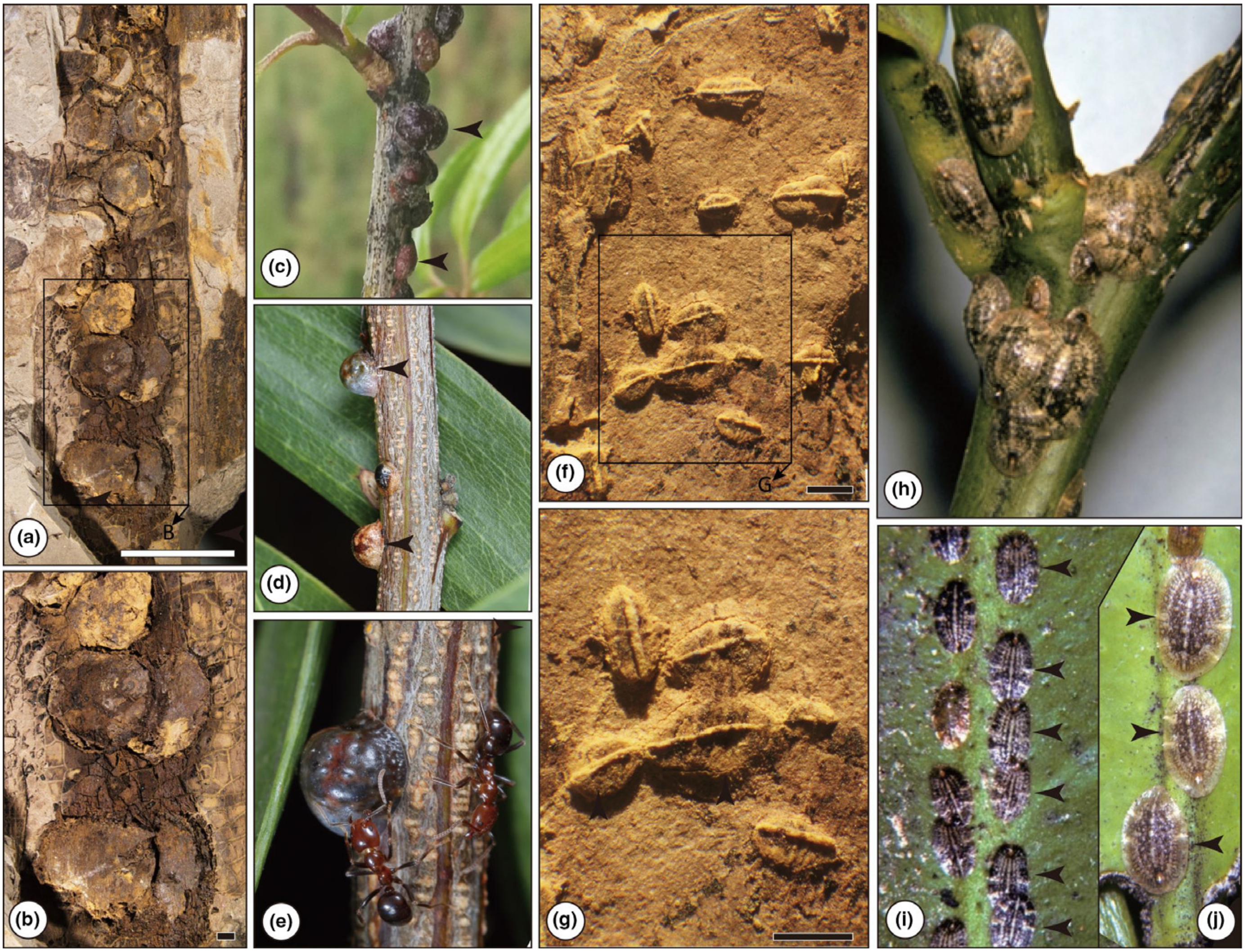

Fig. 3 Specimens of scale insect morphotype 2 (DT394) and morphotype 3 (DT406) from the Early Cretaceous of the Rose Creek locality, Nebraska, USA, and their modern analogs. (a) Seventeen occurrences of DT394 (Hemiptera: Coccidae) consisting of female scale insect impression marks or possibly covers, clustered on an unidentified seed-plant stem, probably an angiosperm. (b) Five individuals of the highly domed, hemispheroidal scale insect impression mark or cover of DT394, enlarged. (c) Cluster of immature stages of extant Coccidae (black arrows) attached to an oak branch (Fagaceae: *Quercus*); the adult female reaches *c.* 10 mm in diameter. (d) Randomly distributed Coccidae (black arrows) attached to an acacia twig (Fabaceae: *Acacia*), tended by ants and representing a tritrophic association. (e) One adult scale insect enlarged from (d). (f) Fifteen occurrences of DT406 (Hemiptera: Coccidae) scale insects feeding on an unidentified seed-plant stem, likely an angiosperm, from the Rose Creek flora. (g) Five examples of immature stages of scale insect impressions enlarged from (f); two are indicated by black arrows. (h–j) Modern Citricola Scale, *Coccus pseudomagnoliarum* (Coccidae: Aurantioideae), feeding on an orange branch (Rutaceae: *Citrus sinensis*); individual scales are indicated by black arrows in (i, j). Adult Citricola Scale female is *c.* 7 mm long. Bars: solid white, 1 cm; solid black, 1 mm (images of extant scale insects lack bars). Credits: (c) Lifang Xiao, Washington, DC; (e) Zhenhua Liu, Canberra, Australia; (h–j) United States Department of Agriculture at http://www.idtools.org/id/citrus/pests/factsheet.php?name=Citricola%20scale.

xylem) on twigs and leaf midveins, mesophyll in areas between midveins, and shallow epidermis. These data collectively indicate that the piercing-and-sucking functional feeding guild was a major herbivore component for *Pandemophyllum* early in angiosperm history.

Discussion

The body of a sedentary, wingless insect bearing lateral waxy filaments is identified as an adult female mealybug that was associated with the lauraceous plant-host genus *Pandemophyllum* from the Early Cretaceous. Currently, the family Pseudococcidae – mealybugs or unarmored scale insects – comprises *c.* 260 genera and > 2000 known species worldwide, and is the second largest family within the superfamily Coccoidea (Kaydan *et al.*, 2015; García-Morales *et al.*, 2016). The discovery of a fossil mealybug feeding on an early lauraceous host plant provides the earliest evidence to date for scale insect feeding on an angiosperm and likely is among the earliest such associations. Below, we discuss four aspects of these discoveries from piercing-and-sucking insects and their plant damage at the Rose Creek locality.

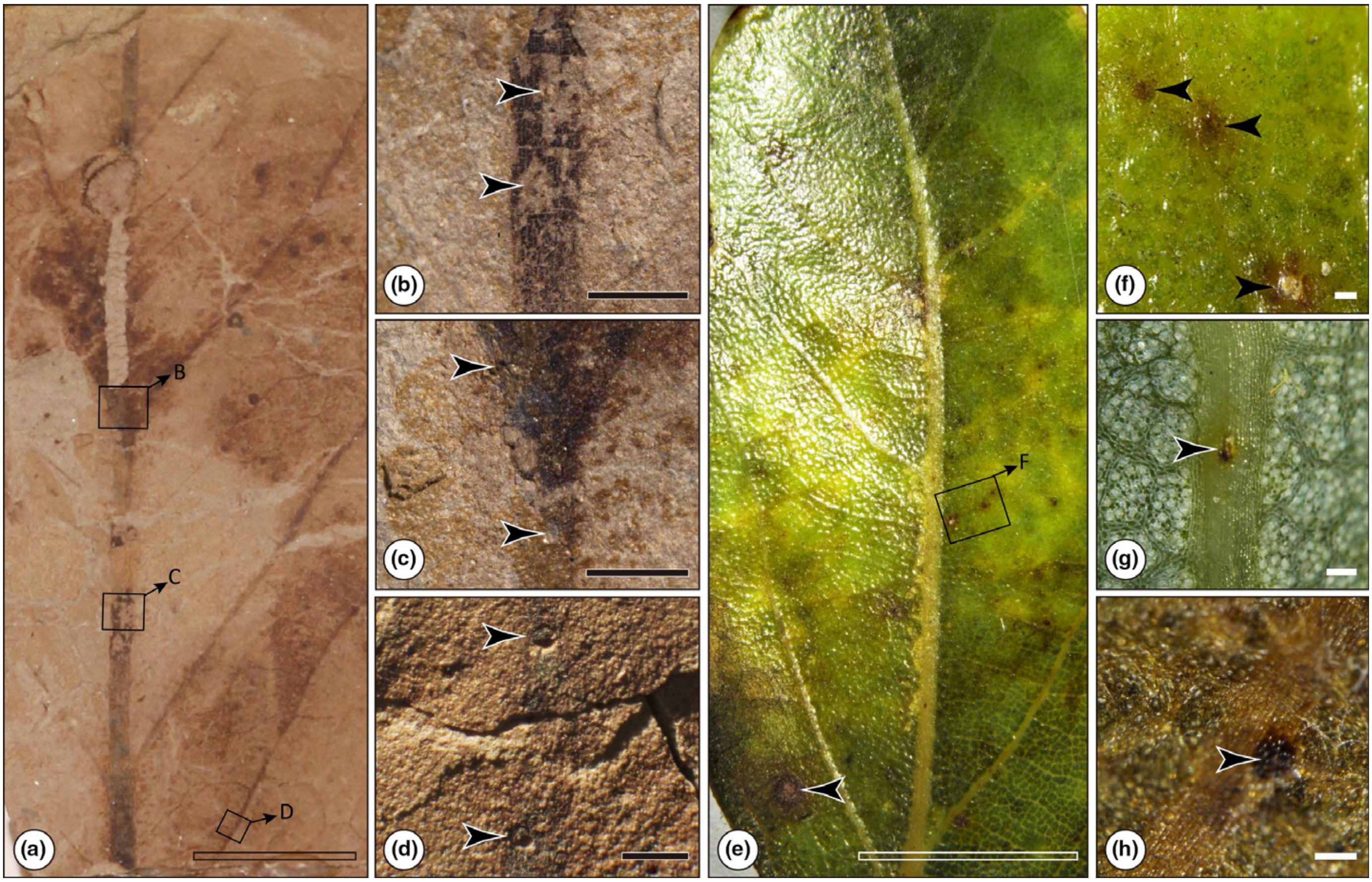

Fig. 4 Host plant of *Pandemophyllum kvacekii* from the Early Cretaceous Rose Creek locality of Nebraska, USA, associated with piercing-and-sucking damage present along major veins, and modern analog damage on an extant *Cinnamomum camphora* (Lauraceae) leaf. (a) Primary vein of *P. kvacekii* illustrating mealybug punctures along the leaf vein. (b–d) Two examples of DT392 punctures (black arrows), enlarged. (e) Primary vein of modern *C. camphora* leaf, with black arrows pointing to prominent, dark brown punctures. (f–h) Several other punctures, enlarged: (f) three DT138 punctures occurring along the secondary and tertiary veins (black arrows) on the leaf upper epidermis; (g) punctures (black arrow) on the leaf lower epidermis of extant *C. camphora*. (h) punctures (black arrows) on the leaf lower epidermis of fossil *P. kvacekii*. Bars: black outline, 10 mm; solid black, 1 mm; white outline, 5 mm; solid white, 0.1 mm.

Evidence of scale insect herbivory on early angiosperms

By the mid-Mesozoic, piercing-and-sucking DTs were moderately diverse, although the affected hosts were confined to cryptogams, ferns or gymnosperms (Labandeira & Phillips, 1996; Labandeira *et al.*, 2014; Labandeira *et al.*, 2014, 2017; Schachat *et al.*, 2014, 2015; Ding *et al.*, 2015; Labandeira *et al.*, 2016; Xu *et al.*, 2018; Correia *et al.*, 2020) (Notes S1, S2, S5; Table S1). During the Early to mid-Cretaceous, piercing-and-sucking punctures on emergent angiosperms are rare, principally due to the absence of studies and lack of recognition of this inconspicuous type of damage. Occasional instances of early piercing-and-sucking on angiosperms are documented from the Albian–Cenomanian lower Hatira Formation of Israel (Krassilov *et al.*, 2008). However, piercing-and-sucking punctures were abundant on angiosperms of the Rose Creek flora (L. Xiao *et al.*, unpublished), which is slightly older than that of the Hatira Formation. In particular, the three species of *Pandemophyllum* harbored 12 DTs and 1149 separate occurrences of piercing-and-sucking herbivory (Notes S1). Of the three *Pandemophyllum* species, *P. kvacekii* contributed more than half of all occurrences of these individual feeding events. Mealybug piercing-and-sucking damage are described here as DT384 (Notes S7) on a *P. kvacekii* leaf specimen, in addition to two other scale insects assigned as DT394 and DT406 on the twigs and stems of two unidentifiable seed-plants, probably angiosperms. With the possible exception of DT77 (L. Xiao *et al.*, unpublished), these impression marks are the first direct evidence of scale insect herbivory on this host for the Rose Creek flora. The scale insect evidence complements the other 12 DTs of piercing-and-sucking present on *Pandemophyllum* (Notes S12). Previously, the earliest evidence of a scale insect feeding on a fossil angiosperm was an armored scale insect (Diaspididae) on a middle Eocene palm and an undetermined dicot from the middle Eocene Messel and Eckfeld Maar localities of central Germany (Wappler & Ben-Dov, 2008). The Rose Creek occurrence pre-dates the Messel occurrences by *c.* 55 Myr.

The antiquity of associations between mealybugs and their Lauraceae hosts

Lauraceae is a magnoliid clade of flowering plants that consists of approximately 50 genera and 3500 known species presently occurring principally in warm temperate, subtropical and tropical regions (Rohwer, 1993; Chanderbali *et al.*, 2001; Song *et al.*, 2020). Extant Lauraceae are chemically and physically defended against a wide array of insect herbivores (Gottlieb, 1972), although defense strategies often are undetectable in fossil Lauraceae (Upchurch & Dilcher, 1990; but see McCoy *et al.*, 2021). Lauraceae harbor a diverse suite of modern insect herbivores (Shen, 1986), of which mealybugs are the richest component of the piercing-and-sucking feeding guild (Notes S9). At present, 47 species of mealybugs are widely documented on 20 species of extant Lauraceae plants, some of which are specialists on those host plants (Wang, 1985; Miller *et al.*, 1999; Kwon *et al.*, 2002; Kaydan & Gullan, 2012; Chong *et al.*, 2015; García-Morales *et al.*, 2016; Kondo & Muñoz, 2016; Wu *et al.*, 2016; Zhang *et al.*, 2016; Marcelo *et al.*, 2020; Suh, 2020). For example, the economically important avocado, *Persea americana* Mill., is herbivorized by approximately 25 species of mealybugs, and *Cinnamomum camphora* (L.) J. Presl, the source of cinnamon, hosts four species of mealybugs. In particular, extant *Phenacoccus solenopsis* Tinsley, 1898, the cotton mealybug, is known to feed on *C. camphora* (Figs 2e–f, 4e–h). These associations, which are analogous to mealybug feeding on *P. kvacekii*, suggest that the relationship between scale insects in general and mealybugs in particular is an ancient one, although it remains to be seen if host-plant specialization is a primitive trait as well.

Cretaceous scale insect partitioning of host-plant organs in deep time

Extant scale insects are mostly polyphagous herbivores and commonly are found on multiple types of plant organs, including leaves, stems, roots, fruits and flowers (Miller & Kosztarab, 1979; Downie & Gullan, 2004; Wappler & Ben-Dov, 2008; Moghaddam, 2013). Scale insects have limited dispersal capabilities (Miller & Kosztarab, 1979; Gullan, 1997; Choi *et al.*, 2018; Ahmed & Stocks, 2020), and individuals of the same species nevertheless tend to be distributed on one or more organs of the same plant (Dabbour, 1981; Hanks & Denno, 1993, 1994). In the case of the fossil scale insects described herein, it is most likely that individuals of the same species were distributed throughout each individual plant host. On *P. kvacekii* specifically, herbivory occurred as phloem feeding on the primary veins (Figs 2e, 5), although phloem feeding also occurred on the unidentified woody seed-plant branches (Fig. 3a,b) and stems (Fig. 3f,g). In contrast with this generalization of scale insect preferences for host-plant organs, the 22 other piercing-and-sucking DTs inflicted by hemipterans and thrips on Rose Creek angiosperms show more finely partitioned feeding niches (Xiao, *et al.*, 2021, L. Xiao *et al.*, unpublished) (Fig. 5).

The presence of scale insects on multiple plant organs of early angiosperms may be used to test proposed evolutionary trajectories of scale insects on the plant organs of their lauraceous and other hosts (Notes S13). For example, Ortheziidae (ensign scale insects) transitioned from ground-dwelling to roots of plants in early appearing lineages, to areal parts in late appearing lineages (Kaydan *et al.*, 2016), a pattern that also may occur for Margarodidae (giant scale insects) (Gullan, 1997; Hodgson, 2014). The various transitions of scale insects involving roots, stems, bark, leaves and flowers imply a partitioning of plant-host resources over deep time (Lawton & Strong, 1981; Gullan, 1997; Singer & Stireman, 2005), as indicated by the extensive modern record. Such patterns may be detectible in the fossil record of scale insects with sufficient sampling (Notes S14).

Fig. 5 Piercing-and-sucking insect community on a laurel and two probable angiosperm stems, from the Early Cretaceous Rose Creek flora, southwestern Nebraska, USA. This reconstruction of 103-Myr-old *Pandemophyllum*, a lauraceous angiosperm, displays six feeding patterns on its leaves based on distinctive types of damage punctures. In addition, two woody plant stems of different taxa show single and clustered individuals of a domed wax scale at center, and individuals of a soft scale at right on the bark of a larger plant. Thirteen distinctive feeding patterns, including the mealybug association, have been documented for this plant host, indicating that a diverse assemblage of piercing-and-sucking insects was present on this laurel genus early in angiosperm history. Illustrated by Xiaoran Zuo.

Indirect evidence for scale insect shifts from non-angiosperm to angiosperm plants during the Aptian–Albian Gap

The mealybug–*P. kvacekii* association reveals that this lineage of scale insects switched from non-angiosperm host plants to angiosperm host plants within the 25 Myr-long Aptian–Albian Gap (125–100 Myr ago (Ma)) (Labandeira, 2014). During this time interval, gymnosperm-dominated floras mostly were replaced by angiosperm-dominant floras globally, and for insect herbivores there was extinction or continuation of gymnosperm-feeding lineages, replacement of gymnosperm by angiosperm-feeding lineages, or origination of new angiosperm-feeding lineages (Labandeira, 2014). Accordingly, hypotheses based on molecular phylogenetic estimates and limited Cenozoic fossil records (Notes S15) postulate that mealybugs are an earlier Mesozoic group (Gullan & Cook, 2007), evolved by the late Jurassic (Vea & Grimaldi, 2016), and were present before the rise of angiosperms. Previously, associations between early mealybugs and early angiosperms were unknown, but with the presence of a mealybug herbivorizing Lauraceae during the latest Early Cretaceous, there is the likelihood of older, underlying mealybug–gymnosperm associations. How such a gymnosperm-to-angiosperm shift occurred would require discovery of pseudococcid fossils on earlier gymnosperm hosts.

Conclusions

In this report, we describe the earliest fossil mealybug feeding on a lauraceous angiosperm, *P. kvacekii*, from the Lower Cretaceous Dakota Formation (*c.* 103 Ma), of Nebraska, USA. The distinct wax filaments issuing from the lateral margin of the fossil provides strong evidence that this specimen is an adult female mealybug of Pseudococcidae. Five piercing-and-sucking damage types of DT46, DT138, DT281 and DT392, and the mealybug scale insect impression mark of DT384, also were identified on this lauraceous host, and two additional scale insects attributable to Coccidae on probable angiosperm stems are from the same deposit. Mealybugs and Lauraceae plants have maintained an association for > 103 Myr, surviving major plant extinctions at the Cretaceous–Paleocene boundary and profound climate changes during the Cenozoic. These three scale insects – as well as the presence of 22 other piercing-and-sucking DTs on angiosperms at the Rose Creek locality – demonstrate that partitioning of tissue resources on early angiosperms was a major feature during the Cretaceous Terrestrial Revolution.

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Author contributions

CCL, DR and SAM conceived and designed this study; LFX, CCL and YBD contributed methodology; DLD collected fossil specimens; and LFX, CCL, YBD, SAM, CKS, DLD and DR identified specimens, analyzed the data, wrote and revised the manuscript. All authors read and approved the final manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Notes S1 Scale insect DTs associated with the history of vascular plants.

Notes S2 Summary of Pennsylvanian piercing-and-sucking DTs attributed to scale insects and associated vascular plants.

Notes S3 Additional methods – photodocumentation.

Notes S4 General geology and paleobiology of the Rose Creek locality.

Notes S5 Rose Creek locality map for the Dakota Formation, KS and NB, USA.

Notes S6 Description of Pseudococcidae gen. et sp. incertae sedis.

Notes S7 Description of new piercing-and-sucking damage types DT384, DT394 and DT406.

Notes S8 Fossil history and differential diagnosis for Pseudococcidae gen. et sp. incertae sedis.

Notes S9 The record of modern mealybug (Pseudococcidae) feeding on laurels (Lauraceae).

Notes S10 Scale insect impression marks and casts preserved on plant stems.

Notes S11 Piercing-and-sucking punctures of DT138 and DT281 on *P. kvacekii* leaves.

Notes S12 Piercing-and-sucking damage by scale insects on *Pandemophyllum* leaves at Rose Creek.

Notes S13 Phylogeny of major lineages of Lauraceae and Coccoidea with their fossil records.

Notes S14 Fossil record of lauraceous plants during the Cretaceous–Pliocene interval.

Notes S15 Fossil record of scale insects during the Cretaceous–Miocene interval.