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PLANT-INSECT INTERACTIONS FROM EARLY PERMIAN (KUNGURIAN) COLWELL CREEK POND, NORTH-CENTRAL TEXAS: THE EARLY SPREAD OF HERBIVORY IN RIPARIAN ENVIRONMENTS

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Premise of research. Two previous studies examined the extent of insect herbivory in Early Permian habitats of north-central Texas, with varying results indicating minimal to modest levels of interaction diversity. In a comparison to two previous floras, we tested whether herbivory patterns in a third, slightly younger, assemblage, the Colwell Creek Pond (CCP) flora, most closely reflect plant host taxonomic affiliation, plant conspicuousness, habitat, geologic time, or other variable.

Methodology. We assessed the diversity and frequency of insect herbivory on 2140 specimens at CCP. We examined the percent of leaf area removed by herbivory as a third, independent, measure of the effect of insect herbivore removal of host plant photosynthetic tissue.

Pivotal results. In a moderately diverse flora of 12 taxa, we found evidence for hole feeding, margin feeding, surface feeding, piercing and sucking, oviposition, galling, seed predation, and wood boring. Some damage was fungally modified. Three herbivory measures consistently indicate that the two overwhelmingly herbivorized taxa were *Auritifolia waggoneri*, a peltasperm, and *Taeniopteris* spp., a form genus of unknown affinity. An approximate order of magnitude less herbivory was present for *Evolsonia texana*, a gigantopterid; indeterminate broad-leaved seed plants, possibly including a mixoneuroid odontopteroid and *Rhachiphyllum*; and *Walchia piniformis*, a conifer. A notable association occurred between *W. piniformis* and an aldegid hemipteran scale insect or precursor lineage. The remaining eight taxa displayed little or no herbivory. About 5% of seeds showed evidence for predation.

Conclusions. Herbivory dominance on *A. waggoneri* and *Taeniopteris* spp. at CCP supports a hypothesis that the early expansion of herbivory in clastic depositional settings tracked broad-leaved seed plants, a pattern likely modified by other factors, such as conspicuousness. Insects targeted particular host plants and were specialists on certain foliar tissue types, such as galling on *A. waggoneri* and oviposition on *Taeniopteris* spp.

Keywords: Adelgidae, component community, conifer, diet, galling, Late Paleozoic, paleoecology, peltasperm, plant-insect interactions, redbeds.

Introduction

A major event in the mid-Paleozoic colonization of land was the origin and early expansion of arthropod herbivory in two phases (Labandeira 2006*b*). Arthropod herbivory was launched during an initial event that transpired from the late Silurian (Prídolí age) to approximately the Middle Devonian (Givetian age) along the seacoasts of Euramerica and gradually expanded inland (Labandeira 2007). This first phase constituted limited emergence of a few feeding modes that opportunistically targeted live sporangial and stem tissues of primitive land plants by small, chewing, piercing and sucking, and borer arthropods, contributing to the earliest-known, though trophically simple, terrestrial ecosystems (Kevan et al. 1975; Shear and Selden 2001; Habgood et al. 2004; Labandeira et al. 2014). The development of more complex terrestrial food webs evidently commenced during the mid–Early Carboniferous (Visean age) and included a broader spectrum of plant hosts and herbivores (Labandeira 2006*a*, 2006*b*) that set the stage for the second phase of herbivory (Labandeira 2006*a*; Ward et al. 2006; Iannuzzi and Labandeira 2008). Compared to the first herbivory phase, the second pulse is associated with

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expanded diversity of plant-host taxa and significantly increased intensity levels of live tissue consumption. This second phase of herbivory penetrated lowland continental interiors through the colonization of new habitats.

Much of the second pulse of herbivory is known from interactions documented in coal-swamp forests of the Middle and especially Late Pennsylvanian of the Illinois Basin. Studies from other Euramerican regions have expanded the range of ecological settings that supported plant hosts and their insect herbivores (Castro 1997; Rößler 2000). In one of these biotas, the Kasimovian-age Calhoun Coal of central Illinois, insect herbivores consumed a broad spectrum of tissues principally from marattialean tree ferns and medullosan seed ferns and less intensively filicalean ferns, sphenopsids, and cordaites (Rößler 2000; Labandeira 2006*b*). The variety of insect and mite herbivory documented from the Calhoun Biota and other temporally close Euramerican habitats included margin feeding of pinnules (Scott and Taylor 1983; Labandeira 2006*b*); piercing and sucking in stem parenchymatic and vascular tissues (Labandeira and Phillips 1996*b*); galls in frond petioles (Lesnikowska 1990; Labandeira and Phillips 1996*a*) and sphenopsid cones (van Amerom 1973); pith borings in trunk ground tissues (Labandeira et al. 1997); seed predation (Scott and Taylor 1983; Labandeira 2002); and consumption of spores, sporangial tissues, and prepollen from reproductive organs (Labandeira 2006*b*). It was during this second phase, from the mid–Early Carboniferous to the end of the Late Permian, that modern herbivory-related trophic cascades were established, including fungal detritivore and saprobic associations and, importantly, almost all of the herbivore functional feeding groups (FFGs) that currently exist (Labandeira 2001, 2006*a*, 2013). This modernization of herbivory occurred in the equatorial wetlands, on peat substrates, and was superseded later in separate environmental settings. In these new habitats, herbivory extended deeper into the continental interior of western Euramerica and in particular on mineral soils occurring in fluvially dominated landscapes (Labandeira and Currano 2013). The Early Permian of north-central Texas provides a glimpse into a local ecosystem occurring in such a different habitat, consisting of distinctive plant hosts, insects, and their herbivore associations (Beck and Labandeira 1998; Labandeira and Allen 2007; Labandeira 2012).

Previous work on the plant-insect associations from the Early Permian of north-central Texas has consisted of two studies. Labandeira and Allen (2007) explored herbivory on the peltasperm-dominated Sakmarian-age Coprolite Bone Bed (CBB) assemblage, and Beck and Labandeira (1998) reported on the younger gigantopterid-dominated Artinskian-age Taint assemblage. These two studies examined the qualitative spectrum of herbivory and provided quantitative estimates of insect-mediated damage, based on the frequency and diversity of damage types (DTs) together with surface area of removed herbivorized tissue expressed as a percentage of total foliar surface area on taxonomically resolvable plant hosts. The current biota, the Colwell Creek Pond (CCP) assemblage, extends in time the previous studies by using the same methodologies of herbivory assessment on a younger early Kungurian-age site but on a compositionally very different flora that occupied a habitat different from the two older floras (Chaney et al. 2009). The published record of younger plant-insect associations closes sometime during the late Early Permian or early Middle Permian in western Euramerica (Beck and Labandeira 1998; Labandeira and Allen 2007; this study) but resumes at about the same time in eastern Euramerica (Geyer and Kelber 1987; Labandeira 1998; Krassilov and Karasev 2009; Labandeira et al. 2012), in Gondwana (Plumstead 1963; McLoughlin 1994*a*, 1994*b*, 2011; Adami-Rodrigues and Iannuzzi 2001; Adami-Rodrigues et al. 2004*a*, 2004*b*; Beatty 2007; Prevec et al. 2009; Cariglino 2011; Srivastava and Agnihotri 2011; Slater et al. 2012, 2014; Gallego et al. 2014), and in Cathaysia (Glasspool et al. 2003; Feng et al. 2010; Rozario et al. 2011). However, the occurrence of herbivory, particularly in later Permian Gondwana assemblages, is considerably richer in ovipositional damage (Prevec et al. 2009), whereas earlier Permian Euramerican herbivory is more dominated by external foliage feeding and, to a lesser extent, galling.

Geologic and Biologic Setting

Geologic Context

The source of the plant assemblage discussed in this report is the CCP deposit, consisting of USNM locality numbers 41005, 41006, 41007, 42292, 42305, and 42306, in Foard County, north-central Texas (fig. 1). Each locality number represents a replicate collection from the same shale bed. The CCP collections are here treated as a single collection. The CCP deposit is located toward the northern end of the N 5°E-trending Clear Fork Group outcrop belt across north-central Texas (Hentz and Brown 1987; Chaney et al. 2009; Mamay et al. 2009). Within the Clear Fork Group, the fossiliferous bed occurs in the informal middle unit (Nelson et al. 2001, 2013). These strata are of Leonardian age, equivalent to the earliest interval of the Kungurian age (Wardlaw 2005), based on the general correlation and revised timescale of Gradstein et al. (2012; fig. 1). The fossiliferous bed at the CCP site consists of finely laminated reddish claystones infilling what was probably an abandoned oxbow channel (Chaney et al. 2009). Deposition took place on the eastern coastal plain of the Midland Basin (Hentz 1988).

The CCP Flora and Comparisons to Relevant Early Permian Floras

The four most abundant taxa in the CCP flora, in decreasing rank order (table 1), are the unaffiliated platysperm species seed (e.g., Sharov 1973), the conifer *Walchia piniformis* (Looy and Duijnstee 2013), the possible cycadophyte *Taeniopteris* spp. (e.g., Gillespie and Pfefferkorn 1986), and the peltasperm *Auritifolia waggoneri* (Chaney et al. 2009). Although we are considering *Taeniopteris* spp. as a single species, it likely represents multiple species at CCP, based on variable features such as the secondary vein branching angle from the midrib and degree of bifurcation of the secondary veins. Five numerically uncommon elements are, in decreasing rank order, an indeterminate broadleaf category that probably includes multiple species such as *Rhachiphyllum* and a mixoneuroid odontopteroid, the gigantopterid *Evolsonia texana* (Mamay 1989), the peltasperms *Sandrewia texana* (Mamay 1975) and *Supaia thinnfeldioides* (White 1929), and the probable cycadophyte *Taeniopteris* sp. nov. The two rare taxa are *Callipteris* sp. 1

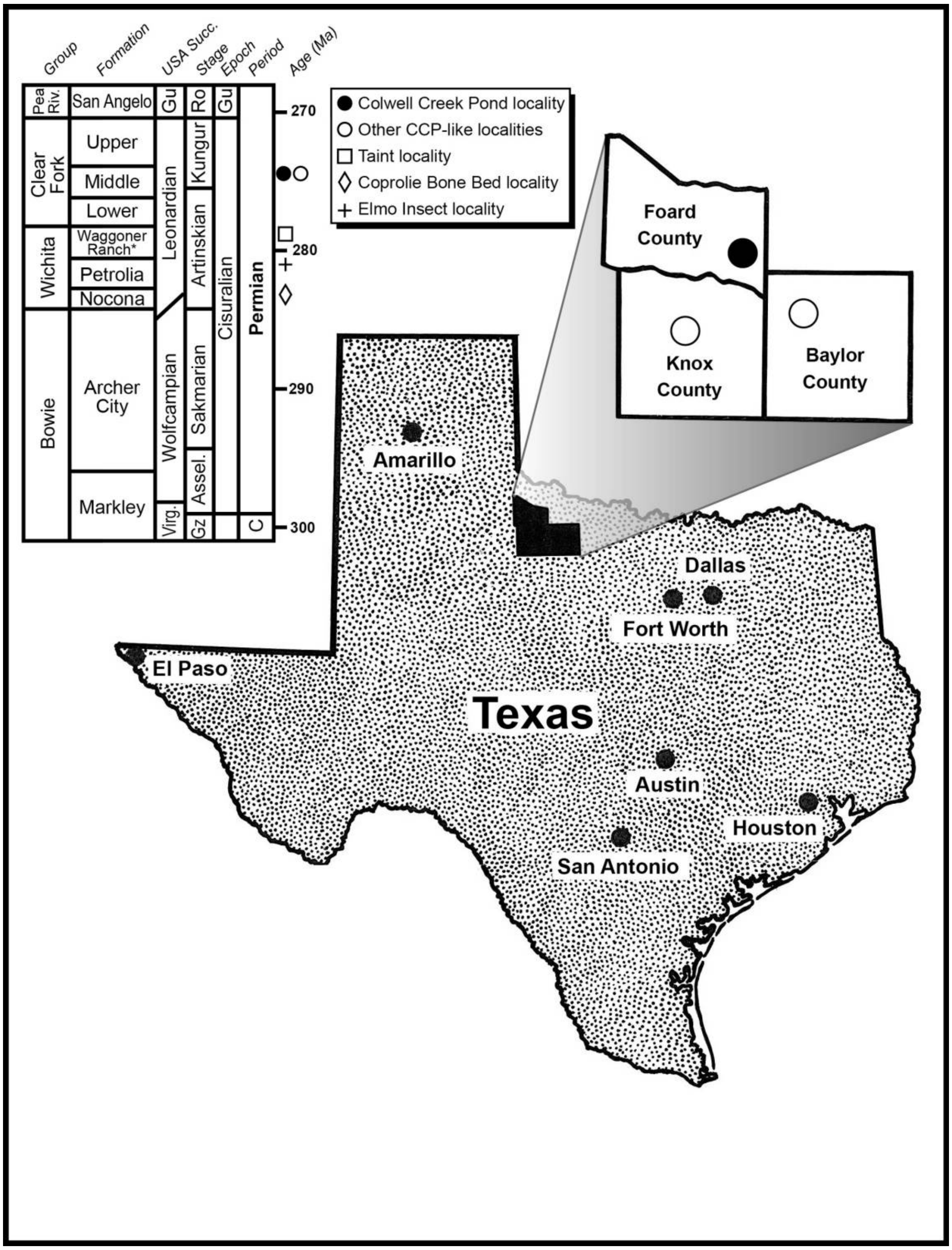

Fig. 1 Geographic and stratigraphic setting of the Colwell Creek Pond (CCP) flora, showing regional lithostratigraphy and stage-level assignments and global stage, epoch, and period equivalents. The stratigraphic and geographic positions of the CCP flora and other previously examined floras are indicated by symbols. Formational designations are largely from Hentz (1988), and global successions are based on Gradstein et al. (2012). For additional details on the CCP flora, see Chaney et al. (2009). Assel., Asselian; C, Carboniferous; Gu, Guadalupian; Gz, Gzhelian; Kungur, Kungurian; Pea Riv., Pease River Group; Ro, Roadian; succ., succession; and Virg., Virgilian. In the Waggoner Ranch Formation, indicated by an asterisk, the uppermost unit constitutes the Lueders Formation (not indicated).

Table 1

Total and Herbivorized Surface Area and Percentage Removal Expressed as Species and Bulk Values for the Colwell Creek Pond Site from the Early Permian (Kungurian) of Texas

				Herbivory per species from surface area				Herbivory frequency/species	
Foliar taxon (abundance ranked)	No. specimens in flora	Specimens examined as % flora	SA examined/ taxon as % flora	SA (cm^2) per taxon in flora	Herbivorized SA (cm^2)/ taxon in flora	% herbivorized area/taxon in flora	Herbivory index	No. herbivorized specimens in flora	Proportion of herbivorized specimens in flora
Walchia piniformis	448	20.93	31.44	12,376.60	.31	.05	.00	8	1.23
Taeniopteris spp.	430	20.09	18.61	7327.93	99.35	15.97	1.36	243	37.44
Auritifolia waggoneri	421	19.67	41.15	16,199.97	498.85	80.17	3.08	311	47.92
Indeterminate broadleaf	74	3.46	.77	303.37	1.51	.24	.50	19	2.93
Evolsonia texana	32	1.50	5.68	2234.72	21.28	3.42	.95	21	3.24
Sandrewia texana	25	1.17	.39	153.60	.14	.02	.09	5	.77
Supaia thinnfeldioides	9	.42	.31	122.90	.05	.01	.04	3	.46
Taeniopteris sp. nov.	7	.33	.09	36.28	.30	.05	.82	3	.46
Callipterid sp. 1	3	.14	.33	128.93	.08	.01	.06	1	.15
Sphenophyllum thonii	3	.14	.01	3.14	.00	.00	.00	0	.00
Indeterminate axis	59	2.76	.77	304.66	.09	.01	.03	2	.31
Platysperm seed[a]	629	29.39	.45	175.22	.33	.05	.19	33	5.08
Totals and averages	2140	100.00	100.00	39,367.32	622.26	100.00	1.58	649	100.00

Note. SA = surface area.

[a] Includes three probably distinct seed morphotypes.

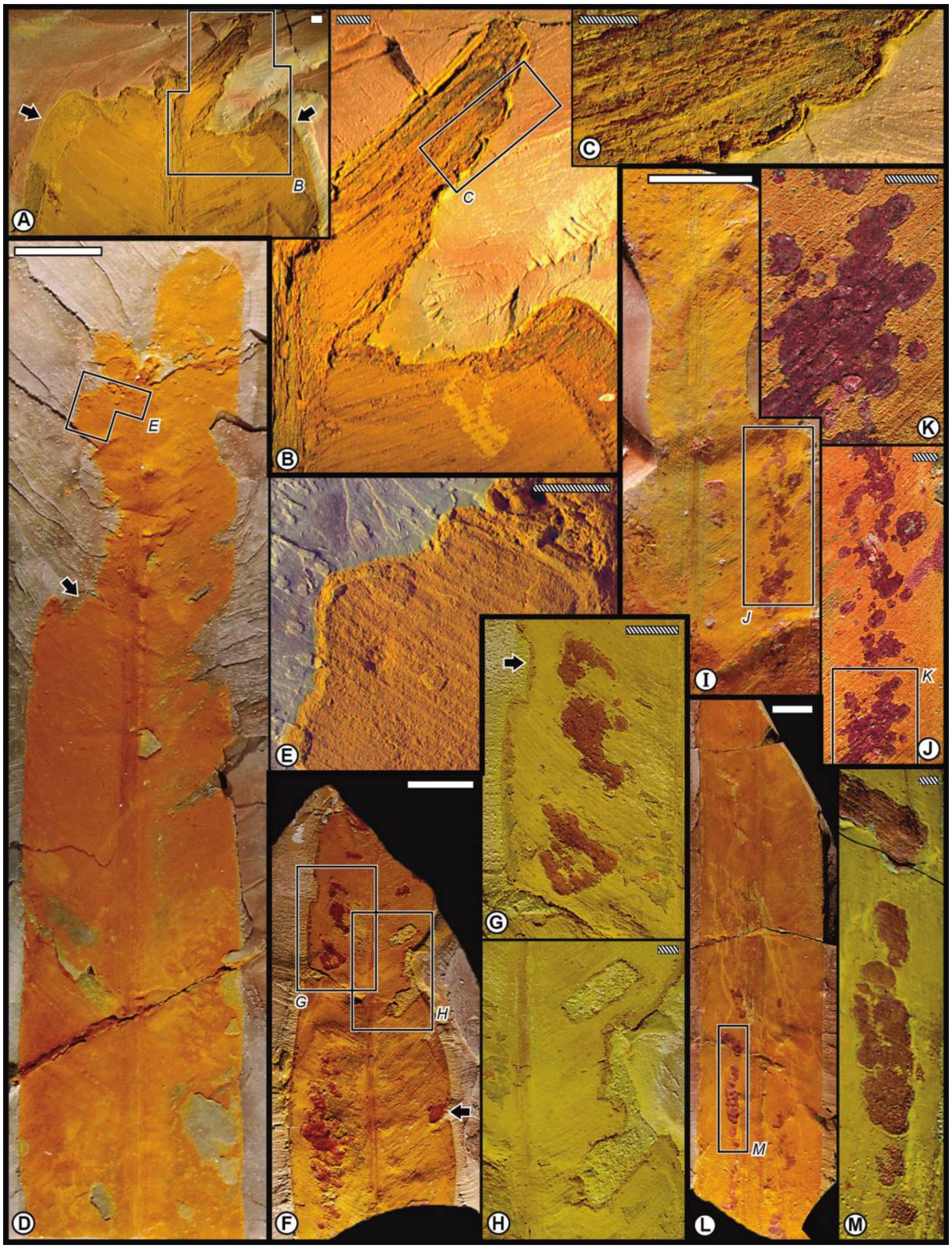

Fig. 2 Insect interactions on unaffiliated *Taeniopteris* spp. at Colwell Creek Pond from the Early Permian of Texas: margin feeding (*A–H*), hole feeding (*F, H*), and surface feeding (*F, G, I–M*). *A–C*, Margin feeding (DT12, DT13) on USNM-559816, with detail of the cut edge at *B* and cuspules at *C*, revealed by higher magnification. Other damage on *A* consists of DT27 (arrows), DT46, and DT103 (USNM loc. 42305). *D*, *E*, Margin feeding (DT12) present at the margin of USNM-559817, with reaction rims indicated by an arrow and in *E* at right. Other damage on *D* consists of DT7, DT14, and DT15 (USNM loc. 41007). *F–H*, Specimen USNM-559818 exhibiting slot hole feeding (DT8); margin feeding (DT12, DT15), enlarged in *G* (arrow) and *H*; and distinctive linear surface feeding that parallels the leaf margin (DT263). Other damage on *F* is the gall DT120 (USNM loc. 42306). *I–K*, A stereotyped linear pattern of surface-tissue consumption (DT263) on USNM-559819, showing consumption of surface tissues that parallel the leaf edge in *J* and *K* typified by rounded patches of surface tissue consumed preferentially along the venational trend (USNM loc. 42306). *L*, *M*, A third example of surface feeding (DT263), occurring along the leaf margin on USNM-559820, delimited by a distinctively rounded feeding border in *M* (USNM loc. 42306). Scale bars: solid, 10 mm; back-slashed, 1 mm.

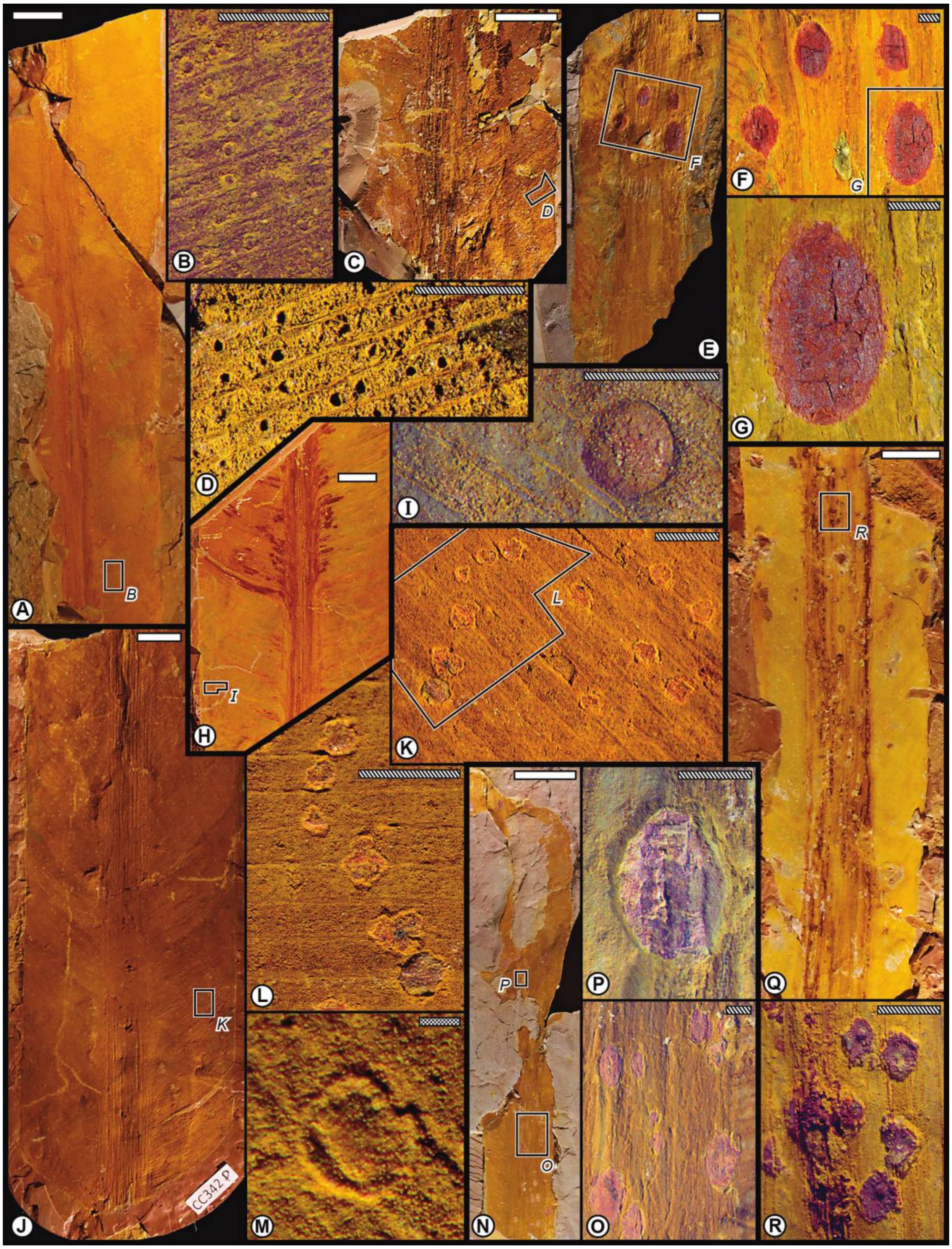

Fig. 3 Insect interactions on unaffiliated *Taeniopteris* spp. at Colwell Creek Pond from the Early Permian of Texas: piercing and sucking (*A–G*), oviposition (*J–R*), and galling (*H*, *I*). *A*, *B*, Piercing and sucking damage consisting of puncture marks on specimen USNM-559821, deployed as curvilinear files (DT138) at *B*, and nearby individual puncture marks (DT46). Other damage on this plant host is DT2, DT12, DT14, DT15, DT25, and DT120 (USNM loc. 43206). *C*, *D*, Possible intercostal, piercing-and-sucking punctures of DT46 also explained as tracheid pits, present on USNM-539324 (USNM loc. 42305). *E–G*, Ovoidal scale marks (DT183) defined by magenta to purple hues, positioned on buff-colored, thickened midvein tissues near the leaf base on USNM-559822 (USNM loc. 43206). *H*, *I*, A small spheroidal gall (DT80), detailed at *I*, on the leaf blade of USNM-559823, which also displays DT15 and DT101 (USNM loc. 42306). *J–M*, Oviposition deployed as

and the sphenopsid *Sphenophyllum thonii*. Indeterminate axes are common and unassignable to laminar foliage. Overall, the CCP flora is dominated by peltasperms, represented by the four genera *Auritifolia, Supaia, Callipteris*, and *Sandrewia* and possibly the gigantopterid *Evolsonia*.

The diverse spectrum of early Kungurian peltasperm taxa, prominent in the CCP flora of the lower Clear Form Group, contrasts significantly with the older (Artinskian) Taint flora of the Waggoner Ranch Formation, dominated by *Taeniopteris* sp., an indeterminate broad-leaved seed plant, and a diverse spectrum of other plants including the peltasperm *Comia* and the gigantopterids *Zeilleropteris* and the *Gigantopteridium-Cathaysiopteris* species complex (Beck and Labandeira 1998; fig. 1). The CCP flora also contrasts with the even older (Sakmarian) CBB of the Nocona Formation, dominated by the peltasperm *Autunia* sp. cf. *Autunia conferta* and, subordinately, the cordaite *Cordaites* sp., the conifer *W. piniformis*, and the probable noeggerathialean *Russellites taeniata* (Labandeira and Allen 2007).

Euramerican Terrestrial Arthropods of the Mid-Early Permian

Very few insect or mite fossils have been recovered from any of the numerous Early Permian redbed deposits, and CCP is no exception. Nevertheless, the Elmo insect fauna from the Wellington Formation, of early Artinskian age, in central Kansas provides a well-preserved and diverse assemblage of insects consisting of 152 described species (Lubkin and Engel 2005; Beckemeyer and Hall 2007). The relevance of this fauna to the insect damage at the Taint locality has been established (Beck and Labandeira 1998). Approximately 60 herbivorous species are represented in the Elmo insect fauna, and it is likely that their successor taxa were culprits for particular types of insect damage at the somewhat younger CCP locality.

Material and Methods

The study comprises two approaches, similar to those taken by Beck and Labandeira (1998), Adami-Rodrigues and colleagues (2001, 2004*a*), and Labandeira and Allen (2007). The first is the qualitative examination of foliar and associated plant material for evidence of herbivory. The second is a quantitative analysis of herbivory based on the frequency of attack and the percentage of removed surface area. These quantitative measures were compiled for each species and for the entire flora.

A foliar element is defined as any planate, photosynthetic structure with a measurable surface area including bracts, needle and scale leaves, pinnules, true leaves, and sphenopsid stems. Identifiable foliar specimens 0.5 cm^2 or larger seeds of all sizes ($N = 2140$) were examined for insect damage and are housed in the USNM Paleobotany Collections at the National Museum of Natural History, in Washington, DC.

Qualitative Analyses

The initial recognition of herbivory at CCP in the laboratory is based on several explicit criteria (Labandeira 1998; Scott and Titchener 1999; Labandeira et al. 2002). Due to the Paleozoic age of the CCP flora, lower-level taxonomic attribution to extant herbivorous taxa was rarely possible, such as is possible for floras from the late Mesozoic to Recent (Opler 1973; Waggoner and Poteet 1996; Wilf et al. 2000). This rarity of taxonomic uniformitarianism (Dodd and Stanton 1990) typically necessitated use of intrinsic attributes of the flora related to general structural, behavioral, and ecological knowledge of insect feeding patterns on modern vegetation (Labandeira 2002). Most important are insect modification of plant tissues during feeding, such as those of mandibulate external feeders (Boys 1989; Chapman and Joern 1990) and the various responses of host plants to insect-induced damage (Johnson and Lyon 1991; Tovar et al. 1995).

In addition to the rare cases of taxonomic uniformitarianism in Paleozoic floras, relevant features that indicate consumption of live tissue can be grouped into four criteria. First is the presence of thick, raised rims of reaction tissue, such as parenchymatous callus, that are produced by the host plant as a response to consumption or other modification by insect herbivores (Meyer 1987). Second is the presence of atypical and specific histological features associated with the external chewing or internal consumption of foliage. Examples of such features on foliage include veinal stringers or necrotized tissue flaps left by the inability of insect mouthparts to ingest completely physically resistant vascular tissue (Keen 1952; Weintraub et al. 1994; Araya et al. 2000). For example, the presence of contiguous cuspules formed along a cut leaf margin within larger cuspate excisions can reveal the trajectory of insect head movement and mouthpart action during feeding on live tissues (Gangwere 1966; Kazakova 1985). A third line of evidence is the recurring stereotypy of tissue removal patterns, based on shape, size, and juxtaposition of those areas with consumed tissue, as well as vein avoidance and the repeated occurrence of herbivory at particular leaf regions (Bodnaryk 1992; Heron 2003). Fourth is the preferential presence of plant damage on particular host plant tissues, organs, and species, indicating herbivore targeting rather than the more random patterns that would be expected from physical breakage (MacKerron 1976; Wilson 1980; Vincent 1990) or detritivory (Brues 1924; Mitter et al. 1988).

curvilinear to arcuate sets on veinal and intercostal tissues (DT54) on USNM-539333, progressively enlarged in *K–M*. Note overall circular shape of the oviposition marks that have angulate margins parallel to the vein trend and indiscriminate targeting of veinal and nonveinal tissues. The individual DT54 mark in *M* is too small to be adequately shown in *J*. Other damage inflicted on this leaf is DT14, DT46, DT76, and DT120 (USNM loc. 42305). *N–P*, Ovipositional damage of midvein tissues (DT76) on USNM-559824, showing a distribution in *O* and structural detail of an individual scar in *P*. In addition, DT101 is present on this leaf (USNM loc. 41006). *Q*, *R*, A cluster of six oviposition scars of DT76 in a deep purple hue contrasts with the buff colors on a massive midvein of USNM-559825, probably representing a single egg insertion event. Also found on this plant host are DT3, DT15, DT122, and DT246 (USNM loc. 42306). Scale bars: solid, 10 mm; back-slashed, 1 mm; stippled, 0.1 mm.

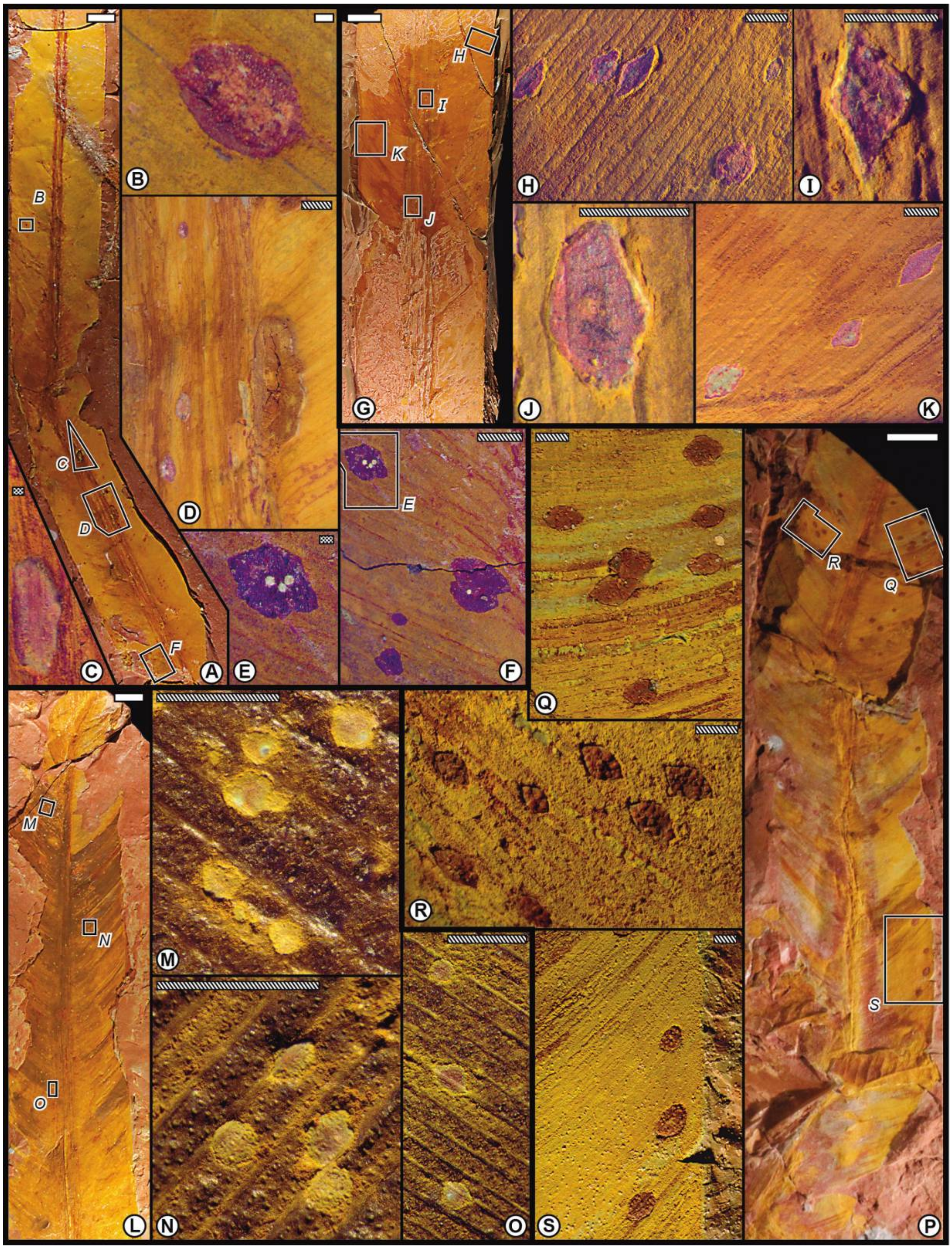

Fig. 4 Insect interactions on unaffiliated *Taeniopteris* spp. at Colwell Creek Pond from the Early Permian of Texas: oviposition (*A–S*). *A–F*, An extensively attacked USNM-559826 consisting of DT32, DT46, DT101, and DT103 and showing extensive oviposition on the stem and midvein (DT76) at *C* and *D* and on the lamina (DT246) at *B, E*, and *F*. The lenticular to ellipsoidal oviposition scars are differentially preserved as hues of deep purple, magenta, or reddish brown on a mostly orange to buff-colored background. Note overlapping oviposition scars at *B* and *F*, lighter-hued scar centers magnified in *B* and *E*, and the targeting of both primary and secondary vein tissues throughout (USNM loc.

After the distinction of herbivory from detritivory or physical battering was established, the spectrum of insect-mediated damage was qualitatively categorized into eight major types of insect folivory (Labandeira and Allen 2007). This was followed by a categorization of the insect damage into a system of explicitly defined DTs (Wilf and Labandeira 1999; Labandeira et al. 2002, 2007; Labandeira 2006*a*; Blois et al. 2013). Additionally, evidence of fungal modification of herbivorized tissues was noted.

Quantitative Analyses

First, we calculated the proportion of foliar elements that displayed herbivory, expressed as a percentage of the total number of examined foliar elements (Schmidt and Zotz 2000). Second, we calculated the herbivory index, expressed as the percentage of surface area of foliar elements removed by herbivores as a fraction of the total surface area (Landsberg 1989; Williams and Abbott 1991; O'Neal et al. 2002; Bradshaw et al. 2007). Both indices were expressed as values for each measured host plant species as well as for the bulk flora (for a modern example, see Mazia et al. 2004).

For image capture of foliar surface areas, each specimen was initially digitized under incandescent light with a Canon PowerShot G7 camera with a 1 : 2.8 to 1 : 4.8 7.4–44.4-mm-wide zoom lens or a Canon EOS 50D camera with a Canon EF-S 60 mm f/2.8 macrolens, using when necessary a MT-24EX twin strobe flash. After image capture, each foliar element and its insect-damaged zones, if any, were digitized using Adobe Photoshop Elements 10. A conservative approach was taken, as in previous studies (Adami-Rodrigues et al. 2004*a*), whereby foliar element silhouettes had to be justified anatomically or estimated based on previous knowledge of leaf shape outline and morphological variability (Adami-Rodrigues et al. 2004*a*, their fig. 3-3). Areas encompassed by total foliar and insect-herbivorized outlines were calculated in Media Cybernetics Image Pro Plus. For detailed resolution of insect herbivory damage to foliar surfaces, specimens were photographed under higher magnification using an Olympus SZX12 microscope with an Olympus DP25 camera. Images were white balanced, focused, and captured using Olympus DP2-BSW imaging software.

Results

General Patterns of Herbivory

There are 52 distinctive DTs in the CCP deposit, organized into the following FFGs: external foliage feeding, with three subgroups of (1) margin feeding, (2) hole feeding, and (3) surface feeding, and (4) piercing and sucking, (5) oviposition, (6) galling, (7) seed predation, and (8) wood boring. Four of these FFGs—the three of external foliage feeding and piercing and sucking—exophytically target plants, as they are made by insect culprits positioned outside of the targeted plant organ while the insect's mouthparts are engaged in consuming tissues (Labandeira 1997). The remaining four—oviposition, galling, seed predation, and wood boring—are endophytic, wherein the insect body, in most cases a nymph or a larva, occurs within the tissue being consumed (Coulson and Witter 1984). Fungal damage (Sinclair et al. 1987), frequently difficult to characterize, can occur on leaf surfaces, as epiphyllous fungi, or within leaf tissues (Labandeira and Prevec 2014), typically associated with infection of preexisting insect damage such as galls (Constantino et al. 2009).

Major examples of insect and perhaps mite herbivore damage encountered at CCP are documented in figures 2–15. This damage is presented as three themes. First, damage is displayed on the various plant hosts. Figures 2–5 illustrate herbivory on *Taeniopteris* sp.; figure 6 documents herbivory on *Evolsonia texana*; figure 7 includes herbivory on the four seed plants, a mixoneuroid odontopteroid, a possible *Rhachiphyllum* sp., *Sandrewia texana*, and *Walchia piniformis*; figures 8–12 consist of herbivory on *Auritifolia waggoneri*; figure 13 illustrates a variety of seed predation; figure 14 documents the herbivore community structure on the two most herbivorized plants, *A. waggoneri* (*top*) and *Taeniopteris* sp. (*bottom*); and figure 15 shows scanning electron micrographs of submicroscopic damage. Within each plant-host sequence, there is a second theme that focuses on a particular class of damage, ranging from external foliage feeding at the beginning of the series of figures, such as margin and surface feeding, to the internal foliage consumption in piecing and sucking, and ending in galling. A third theme illustrates three to seven particular specimens with insect damage for each figure, which are separated from other such figures by bold black borders. Within each leaf specimen ensemble are magnified areas that display enlargements of selected damage within the leaf, separated from each other by thin black lines.

External Foliage Feeding: Margin Feeding

Definition. Margin feeding is the consumption of laminate foliage along edges, such that there is histological evidence for the removal of all tissues of the leaf blade. The consumption of foliar tissues can be divided into single excisions of leaf regions such as the leaf margins some distance from (DT12 if shallow or DT15 if trenched) or adjacent to (DT14) a primary vein or the removal of the distal apical tip (DT13).

DTs represented. DT12, DT13, DT14, and DT15.

USNM figured specimens. CCP (USNM loc. 41006,

42306). *G–K*, Oviposition (DT76) on the midvein and lamina (DT101) of USNM-559827, showing darker-hued, lenticular oviposition scars bearing pinched to rounded ends enlarged at *I* and *J*, respectively. Note parallel orientation of oviposition scars along all secondary venation and targeting of veinal vascular tissue, enlarged in *I* and *J*. Other damage on this leaf is DT46, DT54, DT77, DT100, and DT246 (USNM loc. 41006). *L–O*, Extensive oviposition scars (DT245) on the blade of USNM-559829. In *M–P* the targeted foliar tissue is the epidermis and parenchyma of the secondary veins. Other damage on the host plant is DT32, DT33, and DT76 (USNM loc. 42292). *P–S*, Pervasive oviposition (DT245) on USNM-559828, showing parallel orientation along venational trend of oviposition scars and a general preference for intercostal tissues, magnified in *R–T*. Other evidence of insect damage on this leaf is DT32, DT33, and DT76 (USNM loc. 42305). Scale bars: solid, 10 mm; back-slashed, 1 mm; stippled, 0.1 mm.

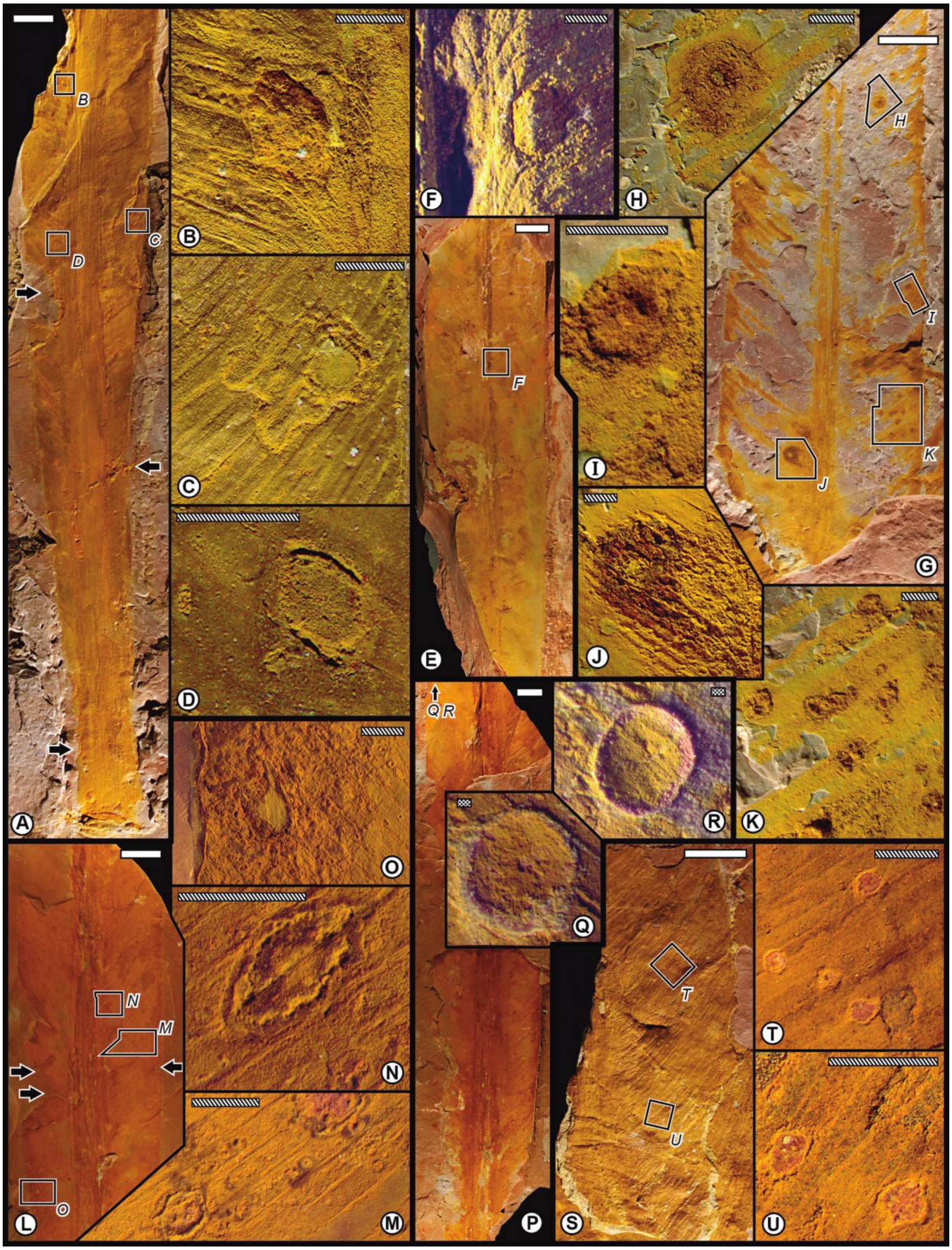

Fig. 5 Insect interactions on unaffiliated *Taeniopteris* spp. at Colwell Creek Pond from the Early Permian of Texas: hole feeding (*E, F, L, O*), oviposition (*L–N*), piercing and sucking (*S–U*), galling (*A–K, P–R*), and secondary fungal infection (*C*). *A–D*, Spheroidal galls of DT120 on USNM-539375, which also has margin feeding (DT13, DT15), indicated by arrows, and ovipositional damage (DT76, DT101). Note the prominent outer cell walls in *B–D* and the polylobate region of tissue necrosis caused by fungi (DT58) enveloping the gall and developed to the left in *C*, creating a secondary reaction front (USNM loc. 42306). *E, F*, Hole feeding (DT4) on the thickened midvein axis of USNM-559830, also bearing

41007, 42292, 42305, 42306). For DT12: figure 2*A*–2*C* (USNM-559816); figure 2*D*, 2*E* (USNM-559817); figure 2*F*–2*H* (USNM-559818); figure 3*A* (USNM-559821); figure 5*A* (USNM-539375); figure 5*L* (USNM-559832); figure 5*S* (USNM-559834); figure 14*K* (USNM-559852), figure 14*M* (USNM-539375), figure 14*N* (USNM-559837), and figure 15*D* (USNM-530923). For DT13: figure 2*A*, 2*B* (USNM-559816), and figure 5*A* (USNM-539375). For DT14: figure 2*D* (USNM-559817), figure 3*A* (USNM-559821), and figure 5*L* (USNM-559832). For DT15: figure 2*D*, 2*E* (USNM-559817); figure 2*F*, 2*H* (USNM-559818); figure 3*A* (USNM-559821); figure 5*A* (USNM-539375); figure 5*L* (USNM-559832); and figure 8*A* (USNM-559840).

Plant hosts. Cycadales: *Taeniopteris* spp. (DT12, DT13, DT14, DT15); indeterminate: indeterminate broadleaf (DT12); ?peltaspermales: *A. waggoneri* (DT12, DT14, DT15); and Gigantopteridales: *E. texana* (DT12, DT15).

Remarks. The spectrum of margin feeding at CCP is unexceptional. The DT spectrum is typical of a generalized feeding syndrome and lacks stereotyped patterns of damage that would indicate more specialized feeding modes. All margin-feeding damage at CCP is consistent with Mesozoic to modern external foliage feeding by mandibulate insects (Coulson and Witter 1984; Johnson and Lyon 1991; Tovar et al. 1995; Labandeira et al. 2007).

Distribution in Paleozoic habitats. Margin feeding is one of the earliest compression-based FFGs in the fossil record and becomes common during the Paleozoic compared to almost all other feeding modes. The earliest-known occurrence of margin feeding is DT13, where it co-occurs with limited hole feeding on the liverwort *Metzgeriothallus sharonae*, from the latest Middle Devonian of New York State (Labandeira et al. 2014). The next earliest-known occurrence of margin feeding is DT12 on *Triphyllopteris austrina*, an early seed plant referable to the Lyginopteridaceae, from the Serpukhovian of Australia (Iannuzzi and Labandeira 2008). Although initially rare, margin feeding, especially DT12, commonly occurs on a range of seed plant taxa throughout the later Moscovian to the latest Permian. In the Late Carboniferous of Euramerica, DT12 occurs sporadically on *Macroneuropteris scheuchzeri* and other medullosan foliage (Müller 1982; Scott and Taylor 1983; Castro 1997; Jarzembowski 2012). Later and throughout the Permian, a range of margin-feeding DTs occurs predominantly on ?peltasperm, taeniopteroid, and gigantopterid foliage (Geyer and Kelber 1987; Beck and Labandeira 1998; Labandeira 1998, 2006*b*). During the later Permian, margin feeding, particularly DT12 but also DT13, DT14, and DT15, is found in Gondwana almost exclusively on *Glossopteris* and other common glossopterid foliage morphotypes (McLoughlin 1994*a*, 1994*b*; Prevec et al. 2009; Cariglino 2011; Srivastava and Agnihotri 2011; Slater et al. 2012). In Cathaysia, where there is a dearth of studies, margin feeding has been documented sparingly on gigantopterid specimens (Glasspool et al. 2003).

External Foliage Feeding: Hole Feeding

Definition. Hole feeding is the consumption of the entire thickness of a leaf blade that is circumferentially enveloped by unaltered leaf tissue. Hole-feeding DTs are defined by a combination of hole size and shape, whereas damage from more complex modes of hole feeding is defined by shape.

DTs represented. DT1, DT2, DT3, DT4, DT5, and DT8.

USNM figured specimens. CCP (USNM loc. 41005, 41007, 42292, 42305, 42306). For DT1: figure 6*B* (USNM-559836). For DT2: figure 3*A* (USNM-559821) and figure 5*L*, 5*O* (USNM-559832). For DT3: figure 3*Q* (USNM-559825), figure 6*A* (USNM-559835), and figure 6*B* (USNM-559836). For DT4: figure 5*E*, 5*F* (USNM-559830); figure 7*A*, 7*C* (USNM-530921); and figure 14*K* (USNM-559852). For DT8: figure 2*D* (USNM-559817) and figure 2*F*, 2*H* (USNM-559818).

Plant hosts. Cycadophyta: *Taeniopteris* spp. (DT1, DT2, DT3, DT4, DT7); ?peltaspermales: *A. waggoneri* (DT2, DT3, DT4, DT5, DT7); Gigantopteridales: *E. texana* (DT1, DT2, DT3, DT4); and indeterminate: unaffiliated broadleaf (DT4).

Remarks. Like margin feeding, the range of hole feeding at CCP presents a standard repertoire of complete tissue excision away from leaf margins. This pattern of damage usually indicates a generalized feeding mode typically inconsistent with herbivore specialization on particular plant-host taxa (Currano et al. 2010). All hole-feeding damage at CCP likely occurred, as in modern plant-insect associations, by external foliage-feeding mandibulate insects (Coulson and Witter 1984; Johnson and Lyon 1991; Tovar et al. 1995).

Distribution in Paleozoic habitats. Hole feeding appears on the same hosts as margin feeding in the early compression fossil record of plants, in particular, DT2 on the liverwort *M. sharonae* from the latest Middle Devonian of New York State (Labandeira et al. 2014). However, throughout the Paleozoic, hole feeding is significantly less common than margin feeding. Hole feeding increases suddenly during the Late Carboniferous, principally on medullosan foliage different from those exhibiting margin feeding, suggesting colonization by a different assemblage of insect herbivores from those responsible for margin feeding. The greatest occurrence of hole feeding is on the mid–Early Permian gigantopterid taxa of *Gigantopteridium, Cathaysiopteris*, and *Zeilleropteris* at the Taint locality, in north-central Texas (Beck and Labandeira 1998), where it occurs with extensive margin feeding and surface feeding on

DT101 and DT103 (USNM loc. 41005). *G–K*, On USNM-559831 and at *H–K* are galls (DT120) with small circular central chambers and a thickened outer region attributable to a zone of nutritive tissue. Also on this leaf are DT46 and DT120 (USNM loc. 42292). *L–O*, USNM-559832 has a range of damage (DT14, DT15, DT29, DT30, DT76, DT97, DT247), including margin feeding (arrows), but prominently features lenticular and broad oviposition marks (DT120), detailed in *N* and *M*, and hole feeding (DT2) at *O*, the latter of which may be a breached oviposition mark (USNM loc. 42305). *P–R*, A hemispheroidal gall (DT80) on the blade tissue of USNM-559833, also containing DT76 (USNM loc. 42306). Images *Q* and *R* are the same gall, with lighting from opposite directions. *S–U*, Specimen USNM-559834 harboring DT12 and DT76 and ovipositional damage (DT245), characterized by small, broadly ellipsoidal slits with tapered or otherwise angulate ends, imaged in *T* and *U* (USNM loc. 42306). Scale bars: solid, 10 mm; back-slashed, 1 mm; stippled, 0.1 mm.

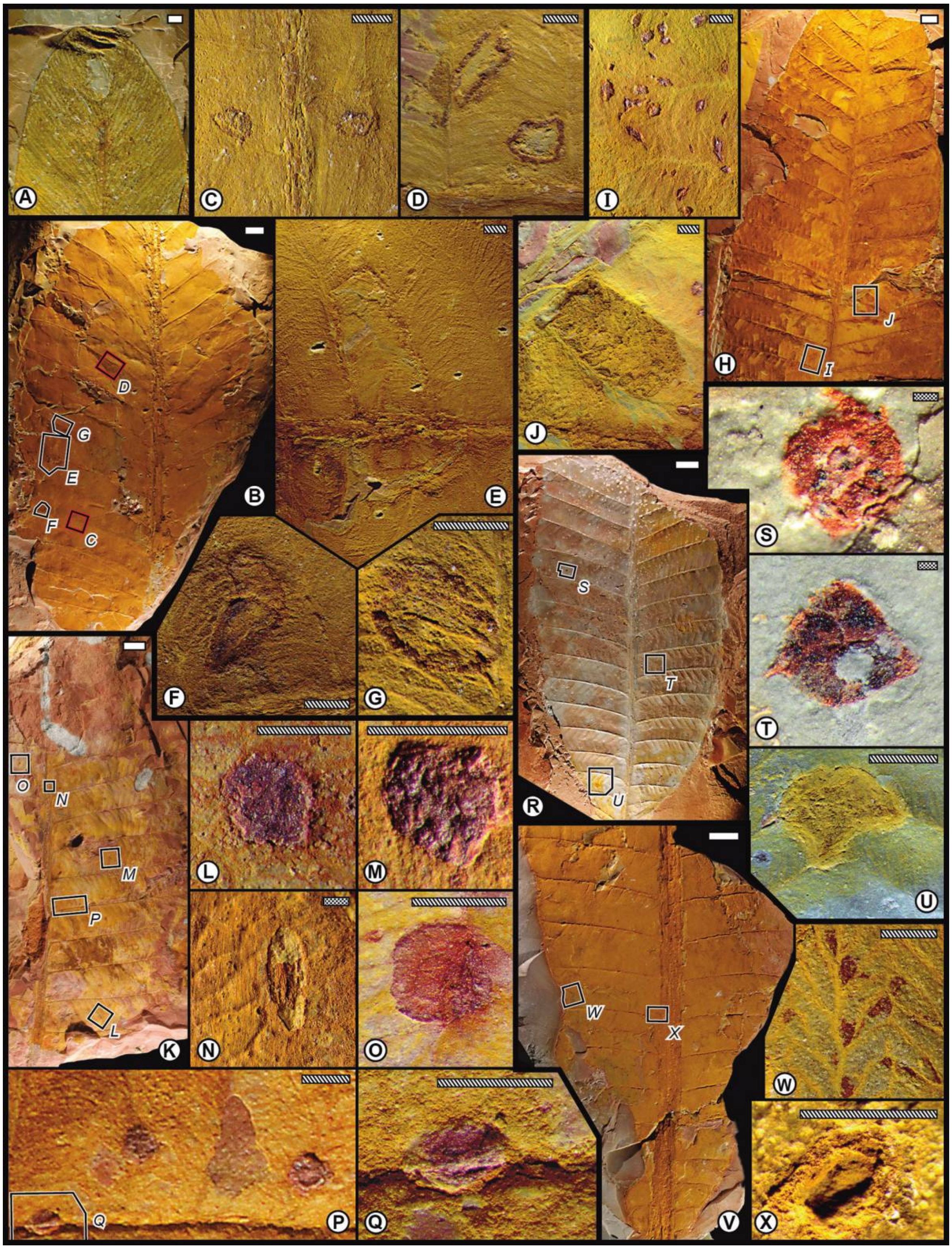

Fig. 6 Insect interactions on the gigantopterid *Evolsonia texana* at Colwell Creek Pond from the Early Permian of Texas: hole feeding (*A*), surface feeding (*B–H, J, R, U*), piercing and sucking (*H, I, V, W*), oviposition (*K, N, P, Q, V, X*), and galling (*K–M, O, P, R–T*). *A*, Hole feeding (DT3) on the distal pinnule margin of a larger leaf, USNM-559835, which also has DT12 (USNM loc. 42305). *B–G*, Extensive surface feeding on several areas of USNM-559836, displaying intercostal removal of surface tissues (DT103) at *E*, polylobate shapes at *D* and *F* (DT30), and circular to ovoidal shapes at *C* and *G* (DT31). The other damage on this leaf is DT1, DT3, DT29, DT32, DT34, DT77, DT80, and DT245 (USNM loc. 42306). *H*, *I*, Intercostal surface feeding (DT103) at *J* and a cluster of elliptical piercing-and-sucking scars (DT48) at *I* are present

the same leaves. Hole feeding on Permian foliage is skewed toward smaller-size holes, indicating that exophytic orthopteroid herbivores of the hole-feeding guild were more diminutive than their Pennsylvanian forbearers. Studies of modern insects based on head-capsule widths (Calvo and Molina 2008) and mandible size (Hochuli 2001) on a range of modern ectophytic herbivores indicate a positive relationship between insect body size and feeding hole size, although there are other factors that also affect hole size (Dalin and Björkman 2003).

External Foliage Feeding: Surface Feeding

Definition. Surface feeding consists of abrasion of surface tissues and the stripping of one or more tissue layers, such as epidermis or hypodermis, from the leaf surface without removal of the entire leaf blade.

DTs represented. DT25, DT27, DT29, DT30, DT31, DT97, DT103, DT130, and DT263.

USNM figured specimens. CCP (USNM loc. 41005, 41006, 42292, 42305, 42306). For DT25: figure 3*A* (USNM-559821). For DT27: figure 2*A*, 2*B* (USNM-559816). For DT29: figure 5*L* (USNM-559832); figure 6*H*, 6*J* (USNM-559837); figure 6*K*, 6*P* (USNM-538922); and figures 11*K*, 11*M*, 14*E* (USNM-559853). For DT30: figure 5*L* (USNM-559832); figure 6*B*, 6*D*–6*F* (USNM-559836); and figure 7*A*, 7*B* (USNM-530921). For DT31: figure 6*B*, 6*C*, 6*G* (USNM-559836), and figure 7*A*, 7*C* (USNM-530921). For DT97: figure 5*L* (USNM-559832). For DT103: figure 14*K* (USNM-559852). For DT130: figures 8*A*, 8*B*, 14*F* (USNM-559840). For DT263: figure 2*F*, 2*G* (USNM-559817); figure 2*I*–2*K* (USNM-559819); and figures 2*L*, 2*M*, and 14*H* (USNM-559820).

Plant hosts. Cycadophyta: *Taeniopteris* spp. (DT25, DT27, DT29, DT30, DT31, DT97, DT103, DT263); indeterminate: unaffiliated broadleaf (DT29, DT97); peltaspermales: *A. waggoneri* (DT29, DT30, DT31, DT130); and Gigantopteridales: *E. texana* (DT27, DT29, DT30, DT31, DT103).

Remarks. The pattern of surface feeding combines elements that would be expected for generalized herbivory (DT25, DT27, DT29–DT31) and more specialized patterns of herbivory (DT97, DT103, DT130). Modern examples of damage associated with DT103 and DT130 frequently are made by host-specific surface feeders that abrade the upper layers of tissues, particularly certain polyphagan beetle clades (Lin et al. 1990; Heron 2003), which originated during the later Mesozoic.

An intriguing interaction is new DT263, which represents a distinctively elongate, interrupted patch of surface abrasion on a *Taeniopteris* sp. leaf surface located medially between the leaf margin and the midrib (fig. 2*F*, 2*G*, 2*I*–2*M*). The leaf damage of this interaction is identical to that of a leaf folder or leaf roller in which an herbivorous nymph, larva, or adult insect rolls or folds a leaf around its body to secure protection from predators or parasitoids while accessing a reliable source of nutrition from the epidermal and subjacent layers of the enclosed leaf (Frost 1959). Leaf folding and leaf rolling typically require specialized features such as labial silk glands for tying leaves and a distinctive mouthpart structure for abrading surface plant tissue (Frost 1959; Fritz and Nobel 2008), and foliar enclosure enhances survivability in leaf-rolling compared to non-leaf-rolling insects (Fukui et al. 2002). Evidence for leaf folding or leaf rolling has not been demonstrated for any Paleozoic or preangiospermous Mesozoic flora. If confirmed, this interaction would be the earliest occurrence for leaf rolling or folding, a pattern that has been documented in some cases in Cenozoic surface feeding and skeletonization associations associated with DT19, DT22, DT27, and possibly DT130 (Labandeira et al. 2007).

New damage type DT263. Surface feeding consisting of linear arrays of polylobately abraded tissue parallel to primary vein and leaf margin, commonly occurring in linear clusters, 2–6 mm long and up to 2 cm wide, texturally distinct from surrounding foliage tissue (fig. 2*F*, 2*G*, USNM-559817; fig. 2*I*–2*J*, USNM-559819; and fig. 2*L*, 2*M*, USNM-559820).

Distribution in Paleozoic habitats. Surface feeding, typically consisting of DT29, DT30, and DT31, is the least common of external foliage feeding during the Paleozoic. The earliest occurrence is on the liverwort *M. sharonae* in New York State (Labandeira et al. 2014), where it is associated with small-scale margin and hole feeding made by microarthropods. There are no well-documented examples of surface feeding during the Late Devonian to Late Carboniferous, and the next occurrence is on the gigantopterid taxa of *Gigantopteridium, Cathaysiopteris*, and *Zeilleropteris* at the Early Permian Taint locality of north-central Texas, where it prominently co-occurs with extensive margin and hole feeding on the same plant hosts. Surface feeding is present very sporadically on glossopterid hosts from the Karoo Basin of South Africa, where it is documented at the Late Permian Kwa Yaya assemblage of Kwa Zulu-Natal, one of which is the surface-abrasion mode of DT103 (C. Labandeira and R. Prevec, unpublished observation, 2012). Surface abrasion frequently is mistaken for necrotic tissue resulting from fungal secondary invasion of lesions induced by arthropod herbivores. Paleozoic examples include fungal damage associated with DT97 on Late Carboniferous *M. scheuchzeri* (Stull et al. 2013) and secondary fungal colonization of hole feeding (DT2), margin feeding (DT13), and oviposition (DT101) on the K2 glossopterid morphotype series from the Late Permian Kwa Yaya assemblage of Kwa Zulu-Natal (Labandeira and Prevec 2014).

A particularly interesting case is DT97 (fig. 5*L*), which con-

on USNM-559837. Note that the lenticular piercing marks at *I* are positioned parallel to the tertiary meshwork venation (USNM loc. 41005). *K*−*Q*, Hemispheroidal galls (DT32) at *L, M, O*, and *P* and oviposition (DT76) at *N, P*, and *Q* on USNM-538922. Note the rather uniform size of the galls but variable lenticular shapes of the oviposition marks (USNM loc. 41005). (The large polylobate feature at right center in *P* is an exfoliated portion of the leaf surface.) *R*–*U*, Thickened galls (DT32) at *S* and *T* and flattened polylobate (DT120) at *U*, on specimen USNM-559838 (USNM loc. 42305). *V*–*X*, Probable piercing and sucking (DT48) detailed at *W*, located at angles subtended by the leaf veinules, and ovipositional damage (DT232), oriented perpendicular to the venation at *X* in USNM-539430. The other damage on this plant host is DT29 and DT76 (USNM loc. 42306). Scale bars: solid, 10 mm; back-slashed, 1 mm; stippled, 0.1 mm.

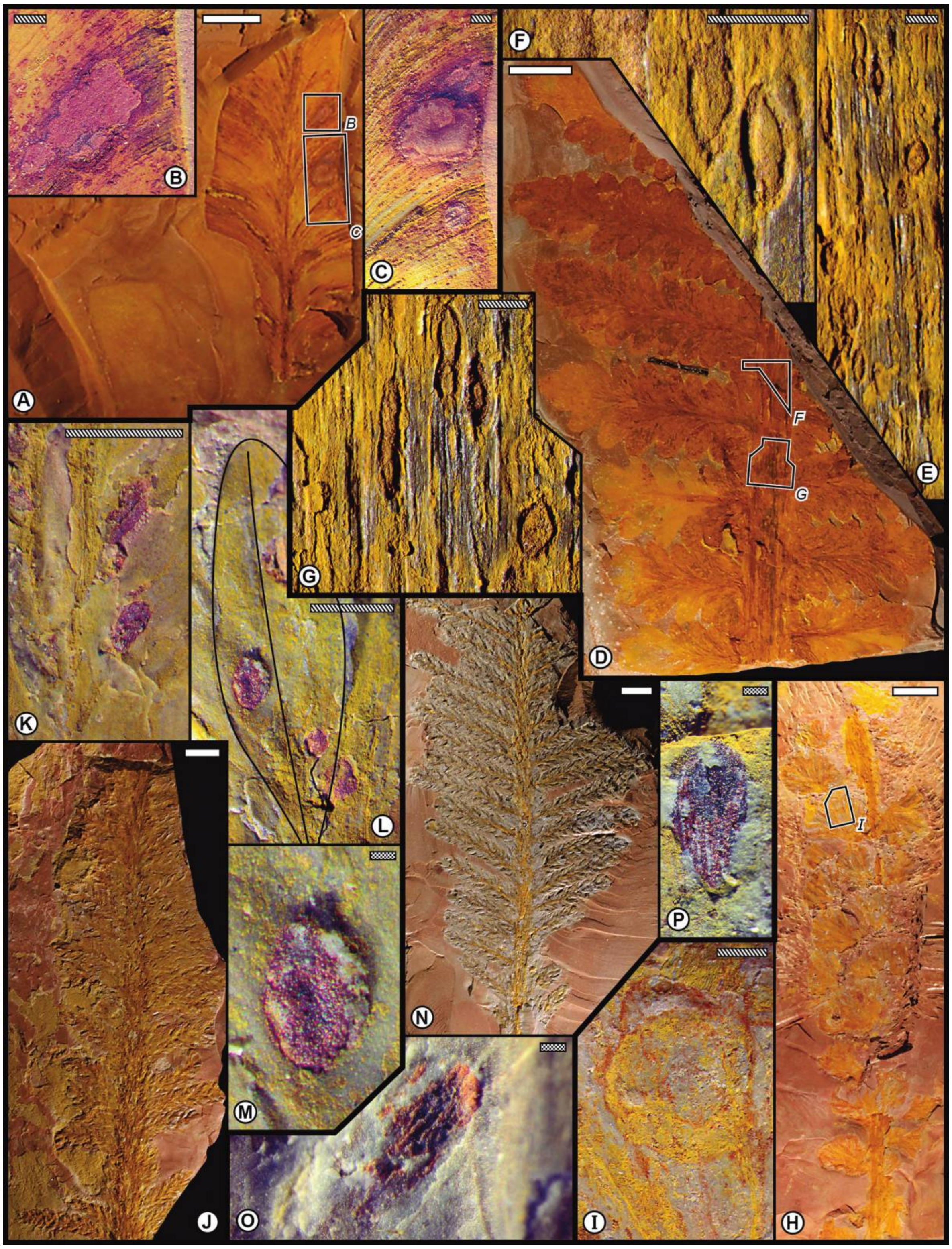

Fig. 7 Insect interactions at Colwell Creek Pond from the Early Permian of Texas on an indeterminate broadleaf specimen, the peltasperm *Sandrewia texana*, and the walchian conifer *Walchia piniformis*: hole feeding (*A, C*), surface feeding (*A–C*), oviposition (*D–G*), piercing and sucking (*J–P*), and galling (*H, I*). *A–C*, Polylobate (DT30) and circular (DT31) surface feeding and hole feeding (DT2) on USNM-530921, a probable mixoneuroid odontopteroid. Note the possible invasion of fungal tissue indicated by a magenta-colored zone bordering the surface abrasion at *B* and reaction rim surrounding the hole at *C* (USNM loc. 42292). *D–G*, Lenticular oviposition (DT76) on the midvein of USNM-

sists of thickened tissue in a U-shape pattern that generally parallels the secondary venation of medullosan neuropteroid foliage (Müller 1982). This DT likely represents a precursor interaction that gave rise to a gall that occurred on the medullosan host *Odontopteris readi* at Padgett, an Asselian-age locality in north-central Texas (Stull et al. 2013). Notably, the precursor of these galls is DT97, a widespread interaction that occurred throughout the late Middle and Late Pennsylvanian of Euramerica (Müller 1982; Labandeira 2006*b*) on medullosan seed ferns, particularly *M. scheuchzeri*. The presence of DT97 at CCP likely represents an antecedent of the earlier Permian Padgett gall that survived in a later Permian flora.

Piercing and Sucking

Definition. Piercing and sucking is the puncturing into plant tissue through the use of stylet-like mouthpart elements to access fluid tissues such as phloem, xylem, mesophyll, or pollen protoplasts. Two major categories of piercing-and-sucking damage are recognized in the compression-impression fossil record: individual puncture marks into plant tissues and ovoidal to ellipsoidal marks caused by the adpression and modification of plant surfaces from sessile scale insect bodies while piercing and sucking.

DTs represented. DT46, DT47, DT48, DT77, DT138, DT157, DT183, and DT244.

USNM figured specimens. CCP (USNM loc. 41005, 41006, 42292, 42305, 42306). For DT46: figure 3*A*, 3*B* (USNM-559821); figure 14*G* (USNM-559853); figure 14*I* (USNM-539333); figure 14*M* (USNM-539375); and figure 15*B* (USNM-539324). For DT47: figure 3*C*, 3*D* (USNM-539324). For DT48: figure 6*H*, 6*I* (USNM-559837); figure 14*E* (USNM-539333); and figure 6*V*, 6*W* (USNM-539430). DT77 is not illustrated. For DT138: figures 3*J*–3*M*, 14*I* (USNM-539333), and figure 14*H* (USNM-559820); DT157 is not illustrated. For DT183: figures 3*E*–3*G*, 14*L* (USNM-559822), and figure 8*I*–8*M* (USNM-559842). For DT244: figure 7*J*–7*M* (USNM-559839) and figure 7*N*–7*P* (USNM-530911).

Plant hosts. Cycadophyta: *Taeniopteris* spp. (DT46, DT47, DT48, DT77, DT138, DT157, DT183); indeterminate: unaffiliated broadleaf (DT46, DT47, DT77); ?peltaspermales: *A. waggoneri* (DT46, DT47, DT48, DT77, DT157, DT183); peltaspermales: *Supaia thinnfelioides* (DT46, DT47); Gigantopteridales: *E. texana* (DT48, DT77); and coniferales: *W. piniformis* (DT244).

Remarks. The damage categorized as DT46, DT47, DT48, and DT138 tends to be rather nondistinctive, although DT138 does indicate the tracking of particular tissues, such as veinal vascular phloem or intercostal mesophyll (fig. 3*J*–3*M*). However, the most evolutionarily and ecologically interesting of the piercing-and-sucking interactions are the distinctive scale marks indicated by DT77, DT157, DT183, and DT244, some of which indicate a general preference for particular seed plant hosts. One of these associations is new DT244, a distinctive ovoidal to ellipsoidal scale mark up to ca. 2 mm long by 1.2 mm wide that occurs only on the abaxial surfaces of the lanceolate needles of the early conifer *W. piniformis* (fig. 7*J*–7*P*). This interaction likely represents the attachment scar of a sessile wooly conifer aphid of the Adelgidae, a basal clade of phloem-feeding, sternorrhynchan Hemiptera that currently infest pinaceous conifers in the Northern Hemisphere, such as eastern hemlock *Tsuga canadensis* (McClure 1991; Young et al. 1995). The association between adelgids or their precursor lineage and conifers is considered ancient (Von Dohlen and Moran 2000), and evidence indicates that modern associations extend deep into the Mesozoic (Heie 1967; Shaposhnikov 1989). This host-specific association suggests promise for identification of a CCP association with an extant insect herbivore clade or more likely its Permian precursor lineage. Consistent with this assignment is an adelgid-like gall that occurs on the same plant host, *W. piniformis*, from the earlier Sakmarian-age CBB locality (Labandeira and Allen 2007, their figs. 6-*8*, 6-*9*). Although many modern adelgids are piercing-and-sucking hemipterans that leave ovoidal attachment marks on needles of the Pinaceae, others form bud galls that mimic vegetative buds but occur on anomalous sites on conifer branchlet systems, as in CBB damage.

New damage type DT244. Ovoidal to ellipsoidal structures with longitudinally striate to pustulose surfaces parallel to anterior-posterior scale insect axis; margins irregular and sometimes without a discernible biological border; 1.0–0.5 mm long by 0.5–0.10 mm broad; located at needle fascicle bases.

Distribution in Paleozoic habitats. The Paleozoic fossil record of piercing and sucking encompasses earlier occurrences that are three-dimensionally preserved in silica and carbonate as well as mostly later presence in compression-impression floras. The earliest occurrence of piercing and sucking is in the Rhynie Chert, Early Devonian Dryden Flags Formation, Scotland, where small stylet trajectories with accompanying disrupted tissue occur in silica-permineralized stems of early vascular plants (Kevan et al. 1975). The same type of preservation, with cone-shaped patterns of damage originating as multiple probes from a surface entry point, also occurs on silicified stems of early vascular plants but in younger Early Devonian deposits from Gaspé Peninsula, Québec, Canada (Banks and Colthart 1993). In the latest Middle Devonian Plattekill For-

536472, an unidentified peltasperm, possibly *Rhachiphyllum*, exhibiting scar reaction rims at *E*–*G*, with occasional vertically overlapping scars shown in *E* and *G* (USNM loc. 42305). The upper part of *E* largely corresponds to *G*. *H*, *I*, The peltasperm *S. texana* (USNM-530930), showing an inconspicuous hemispheroidal gall (DT120) at *I* (USNM loc. 42292). *J*–*P*, Piercing-and-sucking scale attachment scars on specimens *J* (USNM-559839, USNM loc. 41006) and *N* (USNM-530911, USNM loc. 41006) of *W. piniformis*, exhibiting ovoidal to ellipsoidal scars (DT244) in darker purplish hues, perhaps representing mineralized scale exocuticle. Close-ups of *K*–*M* are derived from *J*; close-ups of *O* and *P* are derived from *N*. At *L*, the indistinct needle margin and medial vein are drawn in. Note the orientation of all five scales subparallel to the axis of the small lanceolate leaves on this conifer. Scales *M* and *P* are preserved with a raised rim. Specimens *J* and *N* are *W. piniformis* conifer foliage that contain the enlarged herbivory of DT244 in *K*–*M* and *O, P*, respectively, although the damage is not evident at the lower magnification of the entire branchlet. Scale bars: solid, 10 mm; back-slashed, 1 mm; stippled, 0.1 mm.

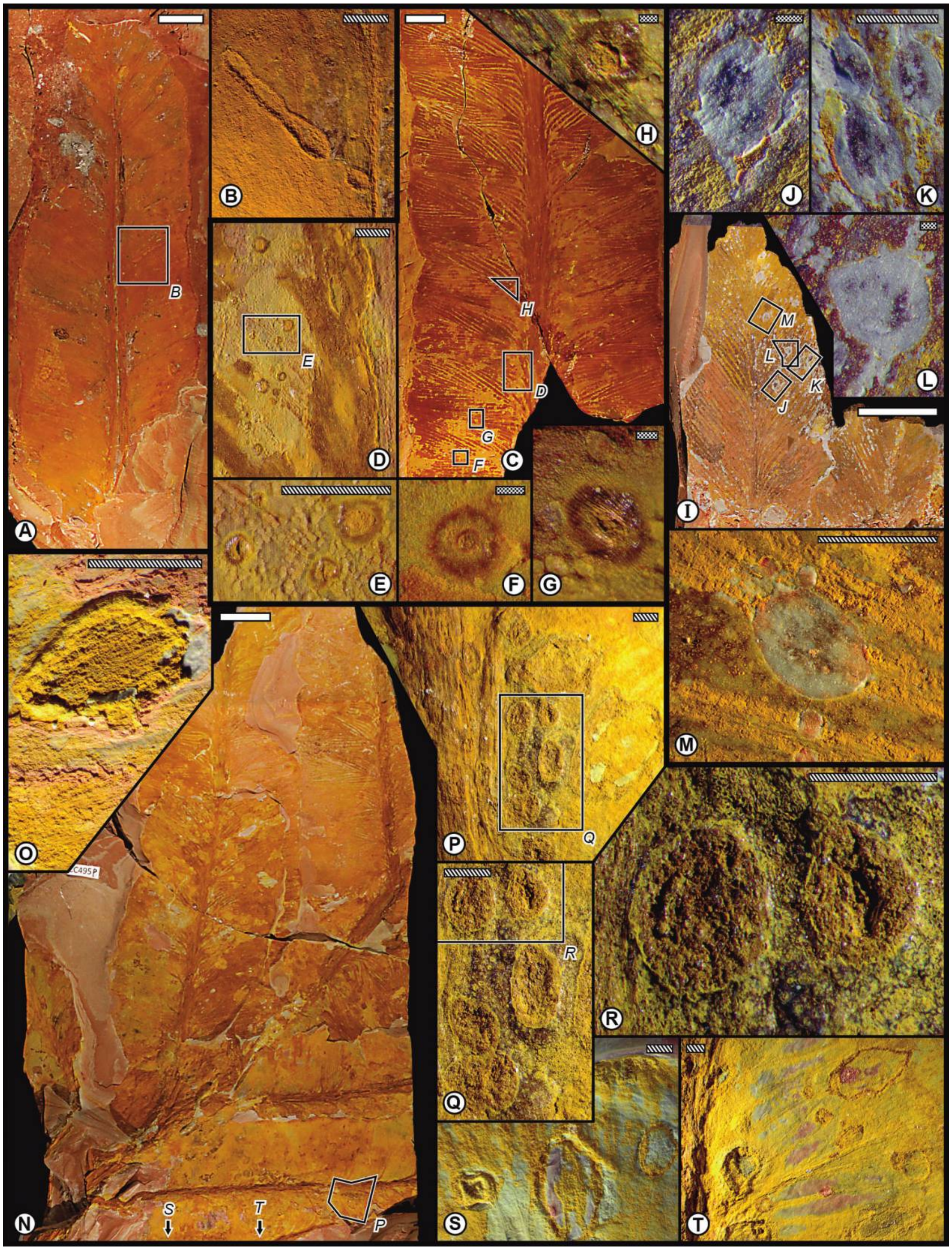

Fig. 8 Insect interactions on the ?peltasperm *Auritifolia waggoneri*: surface feeding (*A*, *B*), piercing and sucking (*C–H*, *I–M*), oviposition (*N*, *O*, *S*, *T*), and galling (*N*, *P–R*) at Colwell Creek Pond from the Early Permian of Texas. *A*, *B*, The distinctive scarring of surface tissues (DT130) that parallel the secondary pinnate venation in USNM-559840 is one of several damage types on this host. The image at *B* is from the counterpart of *A*. The other damage on this plant is DT15, DT29, DT31, DT80, DT101, DT120, DT246, and DT260 (USNM loc.

mation, near Albany in New York State, distinctive clusters of ovoidal stylet punctures with cratered centers (DT273) are found on the liverwort *M. sharonae* (Labandeira et al. 2014). Three-dimensionally preserved carbonate permineralizations of stylet tracks penetrating the stem and rachis cortical tissues of ferns (*Etapteris, Psaronius*) are known from Late Carboniferous Euramerican coal-ball deposits (Scott and Taylor 1983; Labandeira and Phillips 1996*b*). The remaining record of Paleozoic piercing and sucking essentially consists of Permian compression-impression plants preserving single occurrences of cratered or uncratered ellipsoidal or circular puncture marks (DT46, DT47, DT48) on a range of seed plant foliage or, rarely, sphenopsid stems. During the Late Permian, linear rows of puncture marks are present on glossopterid foliage, which indicates specificity for mesophyll or vascular tissue (Prevec et al. 2009) and the targeting of pollen protoplasts by punch-and-sucking microarthropods (Wang et al. 2009). Plant-feeding arthropods that could have created this damage include the paleodictyopteroids, hemipterans, thysanopterans, and possibly some terrestrial mite lineages.

Oviposition

Definition. Ovipositional scars consist of a prominent lenticular or ovoidal rim of callus tissue surrounding a central flattened region in which there is disruption of epidermal tissue at one end, marked in certain cases by the presence of a slit or, rarely, evidence of an insect egg. Although oviposition is not a feeding mode, it does represent the effects of slicing plant tissue with a swordlike, egg-laying abdominal device, the ovipositor.

DTs represented. DT54, DT72, DT76, DT100, DT101, DT108, DT175, DT245, and DT246.

USNM figured specimens. CCP (USNM loc. 41005, 41006, 42292, 42305, 42306). For DT54: figure 4*G*, 4*H*, 4*K* (USNM-559827). DT72 is not illustrated. For DT76: figure 3*J* (USNM-539333); figure 3*N*, 3*O* (USNM-559824); figure 3*Q*, 3*R* (USNM-559825); figure 4*A*, 4*C*, 4*D* (USNM-559826); figure 4*G*, 4*J* (USNM-559827); figure 5*A* (USNM-539375); figure 6*K*, 6*N*, 6*P*, 6*Q* (USNM-538922); figure 7*D*–7*G* (USNM-536472); figure 9*A*–9*D* (USNM-559844); figure 9*E*–9*G* (USNM-559845); figure 11*I*, 11*J* (USNM-528610); figure 12*O*, 12*P* (USNM-559855); figure 14*A* (USNM-596951); figure 14*B* (USNM-559843); figure 14*D* (USNM-596952); figure 14*E* (USNM-559853); figure 14*J* (USNM-559820); and figure 14*M* (USNM-539375). DT100 is not illustrated. For DT101: figure 4*I* (USNM-559827); figure 6*V*, 6*X* (USNM-539430); and figure 8*N*, 8*O* (USNM-559843). DT108 is not illustrated. For DT245: figure 6*B* (USNM-559836) and figure 4*L*–4*O* (USNM-559828). DT175 is not illustrated. For DT246: figure 4*A*, 4*B*, 4*E*, 4*F* (USNM-559826); figures 4*P*–4*S*, 8*S* (USNM-559828); figures 8*P*, 8*T*, 14*J* (USNM-559829); figure 14*A* (USNM-596951); figure 14*C* (USNM-559854); figure 14*D* (USNM-596952); and figure 14*N* (USNM-559857).

Plant hosts. Cycadophyta: *Taeniopteris* spp. (DT54, DT76, DT100, DT101, DT245, DT246); ?Cycadophyta: *Taeniopteris* sp. (DT76, DT246); indeterminate: unaffiliated broadleaf (DT76); peltaspermales: *S. texana* (DT72, DT101, DT246); ?peltaspermales: *A. waggoneri* (DT54, DT76, DT100, DT101, DT108, DT175, DT245, DT246): peltaspermales: *Callipteris* sp. (DT76); and Gigantopteridales: *E. texana* (DT76, DT101, DT175, DT245, DT246).

Remarks. Of the broad spectrum of oviposition at CCP, three interactions stand out in importance. The distinctive ovipositional pattern of DT54 is typical of a highly stereotyped pattern that consists of arcs of eggs that occasionally crisscross. The arcs of egg sets are inserted in leaf tissue from the tip of a swinging abdomen that is repositioned to a new thoracic pivot point during the same ovipositional event (fig. 3*G*–3*K*). This pattern of associated arcuate sets of oviposited egg sets is typical for the Cenozoic (Sarzetti et al. 2009) but occurs rarely in the later Mesozoic and has not been previously encountered in the Paleozoic. It is possible that a paleodictyopteroid lineage bore an external, laterally compressed, sawtooth ovipositor and associated egg-laying behaviors (Labandeira 2006*b*) that evolved convergently with other piercing ovipositors, such as those of odonatans, paleodictyopteroids, and orthopterans and, after the Paleozoic, sawfly hymenopterans.

A second interesting association is DT175 (not illustrated), in which elongate egg insertions and associated scar tissue are deployed end to end in a series of three or more ovipositional events. This DT previously had an earliest occurrence in the late Middle Jurassic of China (C. C. Labandeira and J.-H. Ding, unpublished observation, 2012). An odonatopteran, or post-Paleozoic, dragonfly lineage is suggested as the culprit for the mid-Mesozoic occurrences, but it is unknown as to what Early Permian dragonfly, paleodictyopteroid, or other group of insects bearing a robust, external ovipositor was responsible for this damage.

The third type of ovipositional damage, DT245, is a new DT and occurs on *A. waggoneri* and *Taeniopteris* spp., the two dominant host plants. Each ovipositional mark is a strongly rounded, teardrop-shaped lesion, with sharply curved angulate ends on both sides of the mark, indicating the effectiveness of the ovipositor saw. DT245 is miniscule compared to other ovipositional damage and must have been made by an exceptionally small ovipositor-bearing insect capable of delivering relatively rectilinear insertions of eggs on foliar surfaces (fig. 4*P*–4*S*). There is indication that the linear files of egg insertions had the same pattern of subparallel to somewhat overlapping sets as demonstrated in DT54 above. Oviposition

41006). *C–H*, Oviposition and galling on USNM-559841, consisting of lenticular oviposition of DT76 on the midvein at *D* and small circular to broadly ellipsoidal galls (DT80), commonly with central chambers at *D–H*. Other damage on this specimen consists of DT46, DT77, DT101, DT120, DT246, and DT260 (USNM loc. 41006). *I–M*, Distinctive scale marks characterized by bluish scar tissues with inner dark purplish areas (DT183) occur on USNM-559842. These scale marks are broadly lenticular at *K* and *M* to occasionally broadly polylobate at *L* (USNM loc. 42306). *N–T*, Oviposition and galling occur on USNM-559843, including DT76 on major veins at *P* and on foliage at *O, S*, and *T* and circular to broadly ellipsoidal galls (DT120) on stem tissues at *P–R*. This specimen also hosts DT101 at *O* and DT246 at *S*. Note the thickened gall tissues and thin outer wall at *R* (USNM loc. 42306). Scale bars: solid, 10 mm; back-slashed, 1 mm; stippled, 0.1 mm.

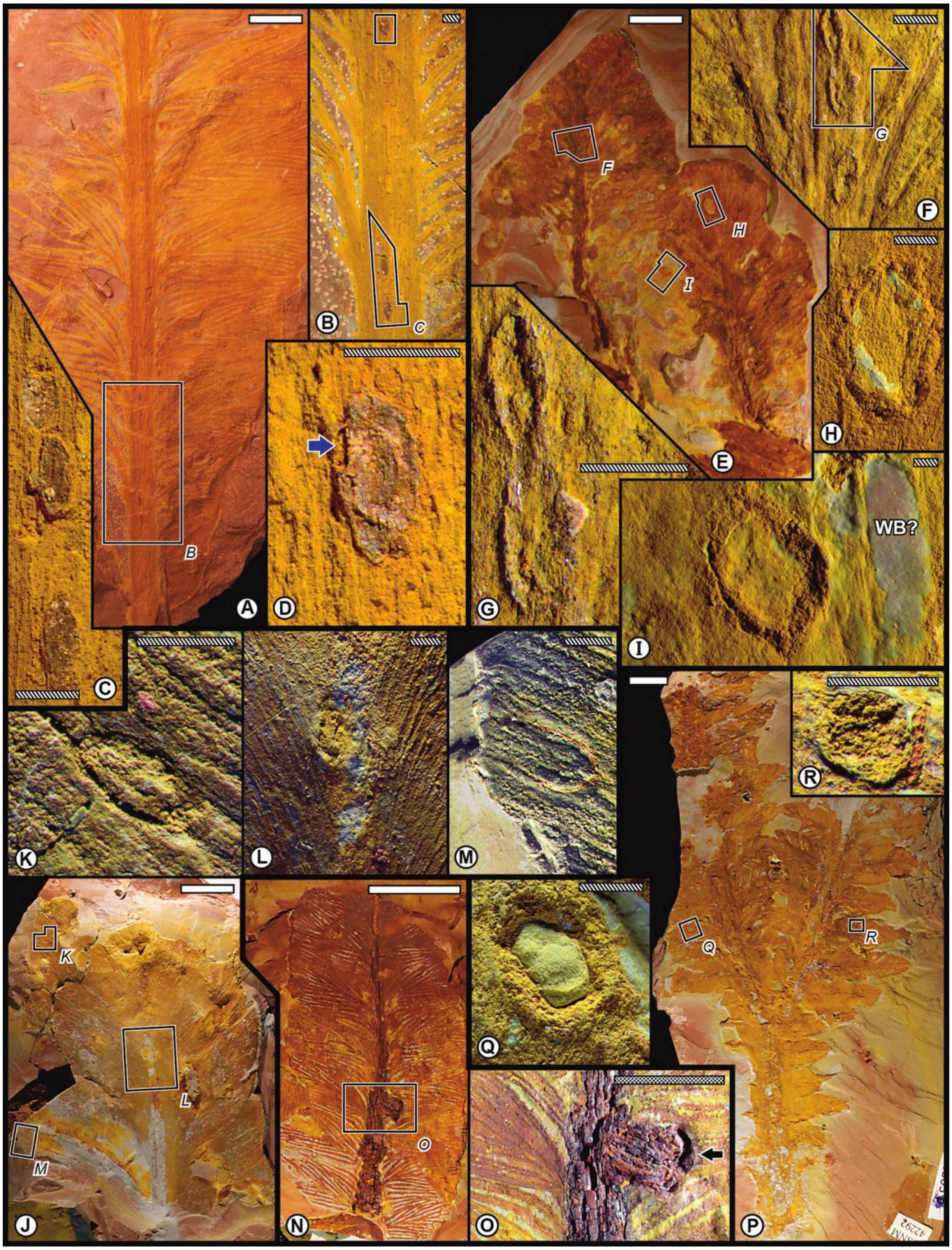

Fig. 9 Insect interactions on the ?peltasperm *Auritifolia waggoneri*: oviposition (*A–I*) and galling (*J–R*) at Colwell Creek Pond from the Early Permian of Texas. *A–D*, Oviposition (DT76) on the midvein of USNM-559844, shown in detail at *B* and enlarged at *C* and *D*. The oviposition mark at *D*, from a more distant portion of the frond at *A*, displays an inner second wall. This plant also hosts DT12, DT29, DT101, DT120, and DT260 (USNM loc. 42292). *E–I*, Oviposition (DT76) on the midvein of USNM-559845, shown at *F*, *G*, and *I*; a gall (DT120)

represented by DT245 may be represented in an SEM (fig. 15*C*) of USNM-539324, which shows the molds and casts of two small egglike structures.

New damage type DT245. Minute oviposition scars, between 0.3 and 1.0 mm in length, occurring in large numbers, parallel to venation across the entire leaf surface, including the midvein and lamina. Shape ranges from circular to teardrop shaped to lenticular; may have an outer rim.

New damage type DT246. Wide teardrop-shaped oviposition scars oriented parallel to leaf venation, with a length-to-width ratio between 2 : 1 and 1 : 1. In many cases the scars vary greatly in size on a single specimen and can occur singly or in clusters. Scars are at least 1.0 mm in length and range in shape from lenticular to short ellipsoidal to almost circular, with a round to gently undulatory outer margin.

Distribution in Paleozoic habitats. Oviposition DTs frequently are associated with particular organs and tissues of host plants, indicating moderate to high levels of plant targeting by insects bearing slicing ovipositors. Likely insect lineages bearing plant-piercing ovipositors during the Late Paleozoic include paleodictyopteroids, odonatopterans, hemipteroids, and orthopterans (Labandeira 2006*a*), responsible for the rich fossil record of oviposition during the Paleozoic. Among the oldest examples of oviposition are distinctive scars on the surfaces of calamitalean stems from the Late Pennsylvanian (Gzehlian) of France (Béthoux et al. 2004). However, Paleozoic oviposition does not become common until the Late Permian of Gondwana, particularly on glossopterid leaves in which both midribs and blades sporadically display extensive lenticular-shaped lesions (Prevec et al. 2009; McLoughlin 2011). The earlier but limited Late Carboniferous occurrences of oviposition mostly on sphenopsid axes can be contrasted with Late Permian expansion of oviposition on seed plant foliage. The ovipositional pattern of the Late Carboniferous also can be compared with analogous damage at CCP, reflecting targeting of the midribs and blades of peltasperm and taeniopteroid foliage, for example, by the insect that caused the considerable ovipositional scarring of DT245.

Galling

Definition. Galls are compact, differentiated, anomalous tissues occurring in organs of plant hosts that are developmentally induced by the hormonal control of a gall inducer such as an insect or mite. Insect gallers develop in a typically spheroidal chamber within the gall that is enveloped by nutritive or similar consumable tissue, in turn surrounded by a protective commonly hardened or woody tissue. Galls are a distinctive plant-insect association in which the host plant not only responds to an endophytic intruder by creating reaction tissue but also is developmentally directed by the endophytic galler to produce anomalous protective and nutritionally rich tissue.

DTs represented. DT32, DT33, DT34, DT80, DT120, DT122, DT247, DT259, DT260, and DT262.

USNM figured specimens. CCP (USNM loc. 41005, 41006, 42292, 42305, 42306). For DT32: figure 6*K*–6*M*, 6*O*, 6*P* (USNM-538922); figure 6*R*–6*U* (USNM-559838); and figure 14*E* (USNM-559853). For DT33: figure 4*L* (USNM-559828). For DT34: figure 6*B* (USNM-559836). For DT80: figure 5*P*–5*R* (USNM-559833); figure 10*L*, 10*M* (USNM-559850); and figure 15*A* (USNM-539324). For DT120: figure 5*A*–5*D* (USNM-539375); figure 5*G*–5*K* (USNM-559831); figure 5*L*–5*N* (USNM-559832); figure 7*H*, 7*I* (USNM-530930); figure 8*C*–8*H* (USNM-559841); figure 8*N*, 8*P*–8*T* (USNM-559843); figure 9*E*, 9*H*, 9*I* (USNM-559845); figure 9*J*–9*M* (USNM-559846); figure 9*P*–9*R* (USNM-530932); figure 10*G*–10*K* (USNM-559849); figure 11*E*–11*H* (USNM-528672); figure 14*A* (USNM-596951); figure 14*C* (USNM-559854); and figure 14*D* (USNM-596952). DT122 is not illustrated. For DT247: figure 10*L*, 10*N* (USNM-559850). For DT259: figure 11*A*–11*D* (USNM-559851) and figure 11*E*–11*H* (USNM-528672). For DT260: figure 10*A*–10*F* (USNM-559848); figure 12*A*–12*H* (USNM-559854); figure 12*I*–12*N* (USNM-528206); and figure 12*O*–12*R* (USNM-559855). For DT262: figure 9*N*, 9*O* (USNM-559847).

Plant hosts. Cycadophyta: *Taeniopteris* spp. (DT32, DT33, DT34, DT80, DT120, DT122, DT120, DT247, DT262); ?Cycadophyta: *Taeniopteris* sp. (DT120); indeterminate: unaffiliated broadleaf (DT32, DT33, DT120, DT247, DT260); peltaspermales: *S. texana* (DT120); ?peltaspermales: *A. waggoneri* (DT32, DT33, DT34, DT80, DT120, DT247, DT259, DT260, DT262); ?peltaspermales: *S. thinnfeloiodes* (DT32, DT120); and Gigantopteridales: *E. texana* (DT32, DT33, DT34, DT80, DT120, and DT247).

Remarks. Although the two dominant foliar taxa at CCP are heavily galled, they share most gall DTs. Shared gall types DT32, DT33, DT34, DT80, DT120, and DT122 occur from the Permian to the Holocene (Labandeira et al. 2007) and form on the foliage of a wide range of host plant taxa. The gall DT120 is the most abundant gall at CCP, occurring on multiple hosts and in many cases at high densities on the foliar surface. The more distinctive galls, DT247, DT259, DT260, and DT262, have unique features that include shape and size, chamber number, inner gall tissue development, ornamentation of the wall surface, wall thickness, and response of the host foliar tissue to gall presence. These distinctive galls also tend to occur on only one host plant, usually *A. waggoneri*. The identified gall types indicate that CCP has a more diverse gall than any other known flora from the Permian of north-central Texas.

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occurs at *H* (USNM loc. 42306). *J–M*, Foliar galls on USNM-559846 shown toward the leaf tip at *L* (DT120), medially placed on the blade at *K* (DT120), and along the leaf edge at *M* (DT120); WB? indicates a possible wood boring. This host also has DT31 and DT245 (USNM loc. 42305). *N*, *O*, A spheroidal woody gall (DT262) on USNM-559847, detailed at *O*, formed from modified midrib tissues, displaying ribbing and thick outer wall (arrow) that may represent teratological files of indurated tissues. This plant host also has DT32 and DT260 (USNM loc. 41005). *P–R*, Thick hemispheroidal galls (DT120) at *Q* and *R* of USNM-530932, a probable *A. waggoneri*. Note the central chamber at *Q*, with three-dimensionally preserved contents. This plant also hosts the damage of DT2 and DT76 (USNM loc. 42306). Scale bars: solid, 10 mm; back-slashed, 1 mm; stippled, 0.1 mm.

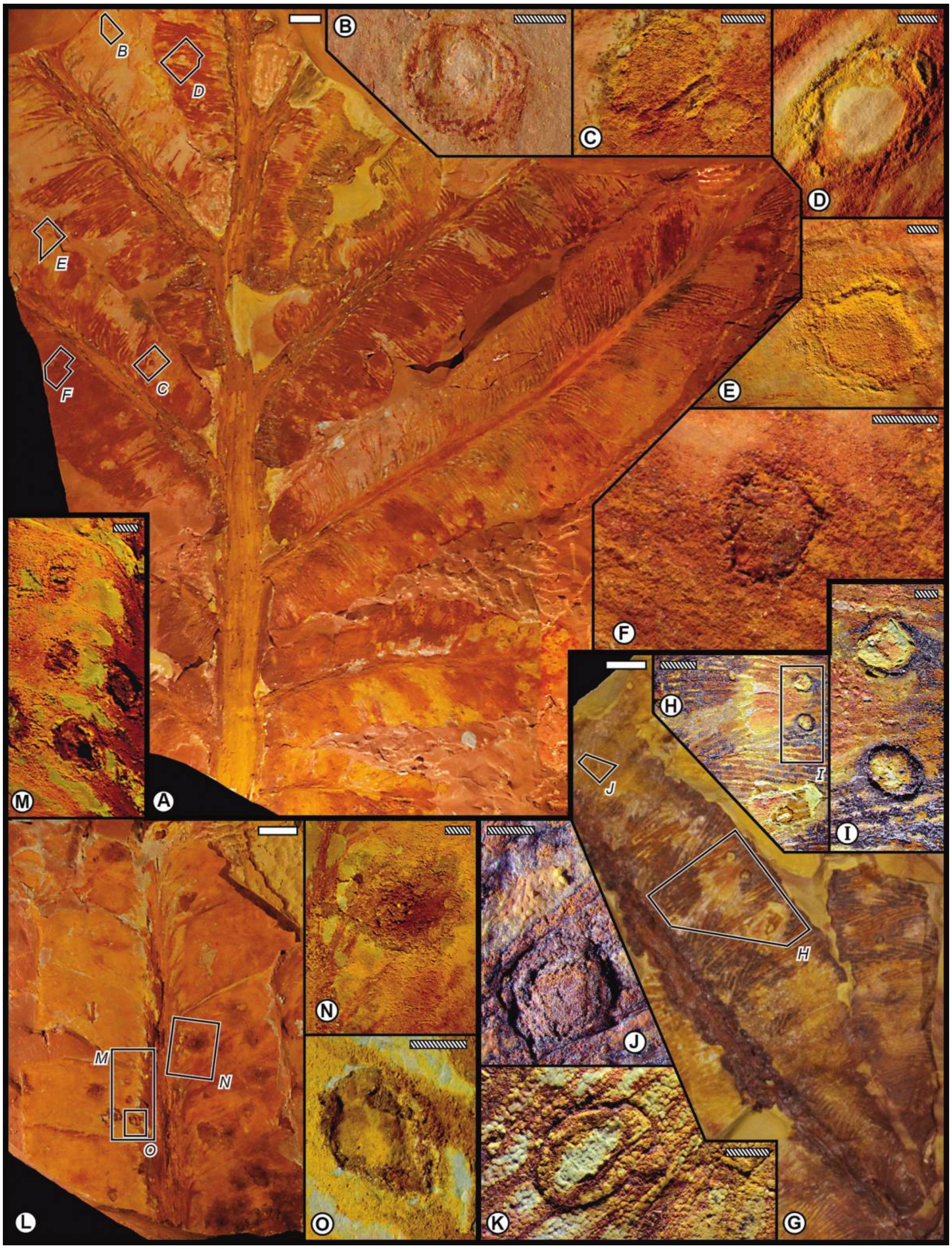

Fig. 10 Insect interactions on the ?peltasperm *Auritifolia waggoneri*: galling (*A–O*) at Colwell Creek Pond from the Early Permian of Texas. *A–F*, The prominent gall on USNM-559848 is the circular, domed DT260, shown at *B–F* and consisting of a thick outer wall and a featureless central chamber. This host also has a smaller gall, DT80, and ovipositional damage of DT76 and DT101 (USNM loc. 41005). *G–K*, The three types of galls that characterize USNM-559849 are DT80 and DT262 (not shown) and DT120 at *H–K* with a thick outer wall. Note placement of galls in G and *H* along the leaf margin. The origin of *K* is from an adjacent part of the leaf not shown in G (USNM loc. 41005). *L–O*, A heavily galled USNM-559850 consists of three gall types: DT80 (not illustrated), DT246 at O, and DT247 at *N*. This leaf also has DT29 and DT101 (USNM loc. 41005). Scale bars: solid, 10 mm; back-slashed, 1 mm.

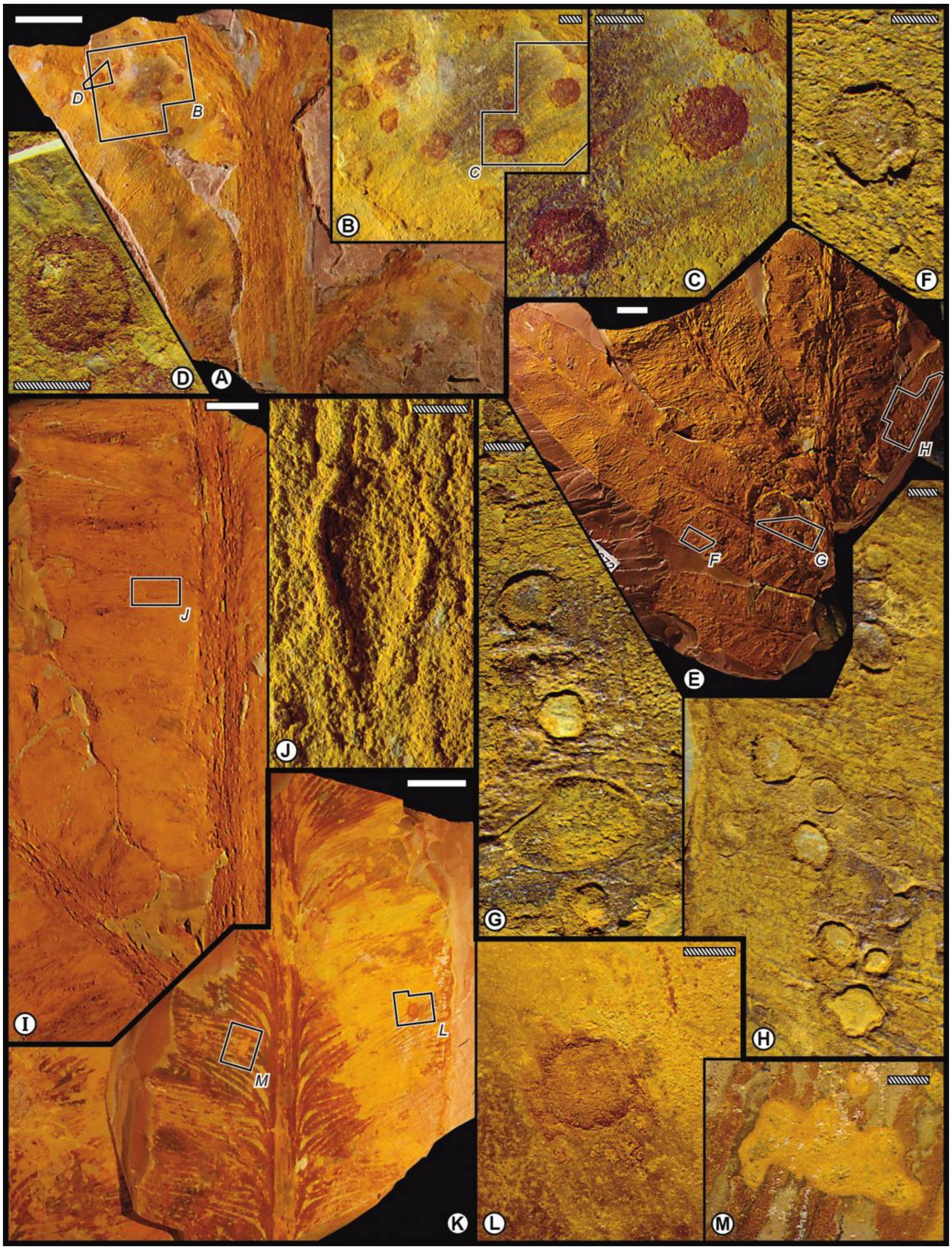

Fig. 11 Insect herbivore interactions on the ?peltasperm *Auritifolia waggoneri*: galling (*A–M*) and surface feeding (*L, N*) at Colwell Creek Pond from the Early Permian of Texas. *A–D*, USNM-559851 has clusters of circular hemispheroidal galls at *B* with moderately furrowed surfaces (DT259), detailed at *C* and *D*. This specimen also has ovipositional damage of DT76 and DT101 (USNM loc. 42306). *E–H*, USNM-528672 at *E* exhibits galls (DT260) with spheroidal, ovoidal, and almost polylobate shapes that bear distinctively smooth outer walls (*F–H*). Some galls are distributed in linear files, seen at *G* and *H*. Other damage on this specimen is DT2, DT7, and DT101 (USNM loc. 41005). *I–K*, USNM-559852 exhibits a typical gall of DT260 at *J* and DT80 at *K*. *L–N*, USNM-559853 shows a spheroidal gall with a thick outer wall (DT120) at *M* and an example of polylobate surface feeding (DT29) at *N* but lacking a defined reaction rim. This latter damage likely represents detritivory rather than herbivory. Other recorded damage on this host includes DT76 and DT260 (USNM loc. 41006). Scale bars: solid, 10 mm; backslashed, 1 m.

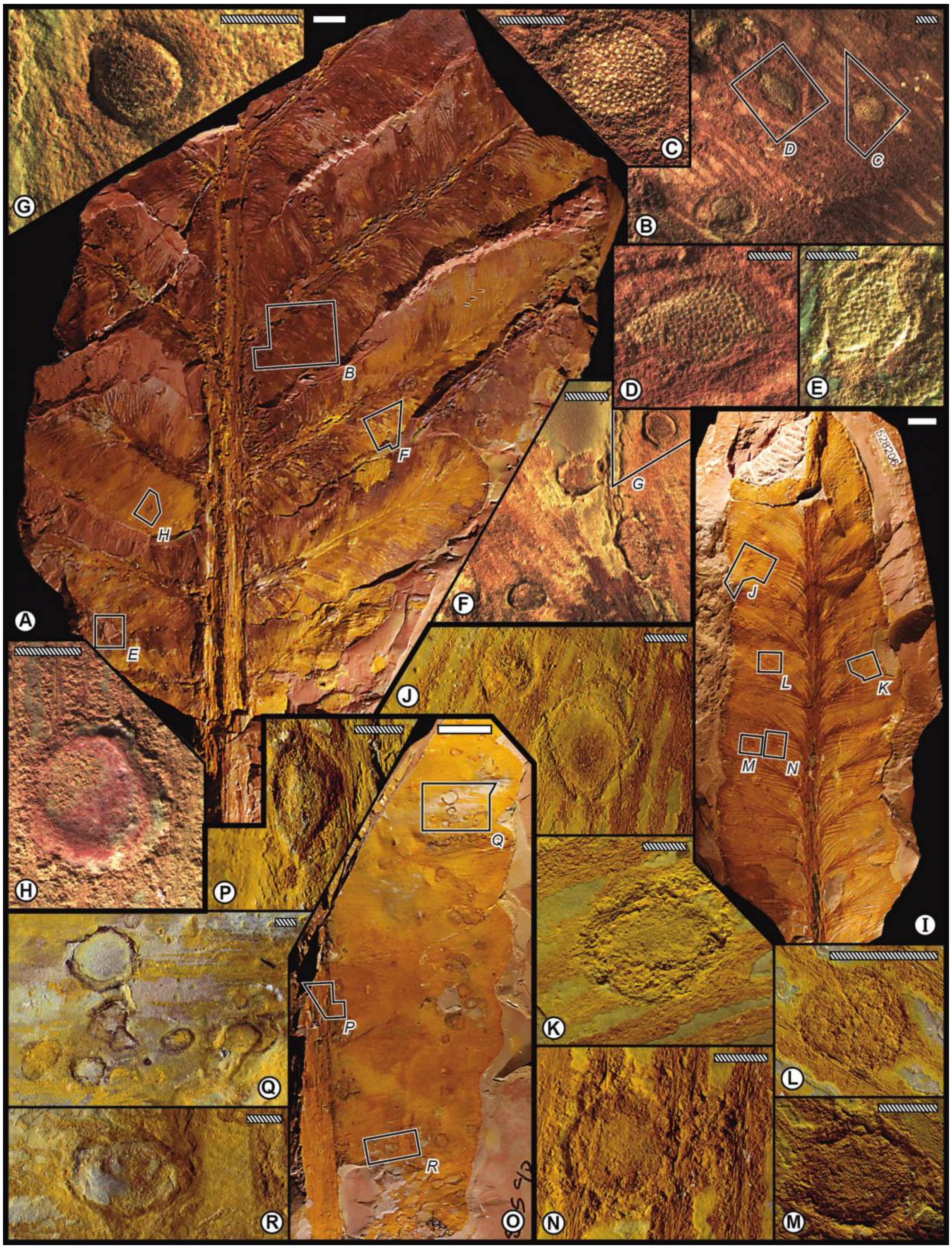

Fig. 12 Insect herbivore interactions on the ?peltasperm *Auritifolia waggoneri*: galling (*A–O, Q, R*) and oviposition (*O, P*) at Colwell Creek Pond from the Early Permian of Texas. *A–H*, A frond at *A* (USNM-559854), showing several examples of the distinctive, circular, hemispheroidal gall DT260, characterized by a medial gall tissue layer with a pustulose surface figured at *B–E* and a thick outer wall at *G* and *H*. A cluster of these galls is shown at *B* and *F*; individual galls are illustrated in *C–E, G*, and *H*. Gall DT262 also is present on this specimen (USNM loc. 41005). *I–N*, Circular hemispheroidal galls with thick outer walls (DT260) on specimen USNM-528206, four examples of which are illustrated in *K–M* (USNM loc. 41005). *O–R*, On USNM-559855 and at *Q* is a cluster of irregularly shaped galls of varying sizes (DT260) with pustulate wall surfaces seen at *R*. Associated with DT260 is unspecified fungal damage of DT58 narrowly enveloping the gall at *R*. Also occurring on this leaf is the ovipositional damage of DT101 (USNM loc. 41006). Scale bars: solid, 10 mm; back-slashed, 1 mm.

New damage type DT247. Formless, circular to polylobate flattened surface galls with multiple chambers and a prominent reaction rim; highly variable in size and shape. Surfaces are distinguished from surrounding foliar material by minute desiccation cracks and locally by spongy tissue. See figure 10*L*–10*O* (USNM-559850).

New damage type DT259. Dark, spheroidal, single-chambered galls; inner structure homogenous, surrounded by a broadly botryoidal but muted surface sculpting the outer wall surface; eccentric markings at edge; thin, dark, smooth reaction rim; gall 0.5–1.5 mm in diameter. Outer margin spheroidal in shape, occurring singly or in loose clusters. See figure 11*A*–11*D*.

New damage type DT260. Circular to ellipsoidal galls occurring on midrib and blade, one wall layer distinctively pustulose, enveloped by a thick outer sclerenchymatous wall. Outer margin spheroidal but frequently irregular and polylobate. Very variable in size, from 0.6 to 11 mm in maximum dimension. Typically single chambered, possibly compound in mature specimens, occurring singly or in loose clusters. See figure 12*A*–12*H* (USNM-559854) for best material; see also figure 12*I*–12*N* (USNM-528206); figure 12*O*, 12*Q*, 12*R* (USNM-559855); figure 11*E*–11*H* (USNM-528672); figure 10*A*–10*F* (USNM-559848).

New damage type DT262. Massive, woody, single-chambered midrib gall consisting of a thick to hemispherical cylindrical to spheroidal structure ranging from 1 to more commonly 5 mm across, with distinctive, thick ridges originating from the base and extending to the distal gall region; in some cases, galls are linked together but invading blade tissue. See figure 9*N*, 9*O* (USNM-559847); figure 9*P*, 9*Q* (USNM-530932).

Distribution in Paleozoic habitats. The fossil record of galls commences in the Early Pennsylvanian (Labandeira 1998), where the apical strobilus of the calamite *Paracalamostachys* was galled in a developmental mode similar to that of bud galls in higher plants (van Amerom 1973). Well-documented Late Pennsylvanian galls occur within the inner parenchyma of *Stipitopteris* petiolar fronds borne by the tree fern *Psaronius chasei* Morgan (Labandeira and Phillips 1996*a*; Redfern 2011). These petiolar galls were occupied by an early holometabolous larval insect that was surrounded by tufts of proliferating tissue, coprolites, and other types of frass. During the Early Permian, the best-documented galls are anomalous strobilus-like proliferations appearing as anomalous buds on walchian conifers (Florin 1945; Labandeira and Allen 2007).

Late Carboniferous galls were involved in developmental control of particular meristematic tissues within axial organs and differ from the overwhelmingly greater number and broader spectrum of Permian galls that occurred on foliar tissues from a variety of floras worldwide. From a temporal perspective, the shift from axial to foliar galls continues at a meager pace throughout the remaining Permian (Stull et al. 2013). Galls are absent from the Taint flora and rare at CBB. Galls exhibit a broader spectrum of shapes and morphologies at CCP, providing a contrast to the simple and highly stereotyped morphologies found in earlier floras. During the Late Permian, galls are particularly noticeable on Gondwanan glossopterid foliage (Prevec et al. 2009).

Seed Predation

Definition. Seed predation is the consumption of live megagametophytic and in some cases embryonic tissues in dispersed or plant-attached seeds and invariably results in the death of an entire plant disseminule.

DTs represented. DT73, DT74, and DT257.

USNM figured specimens. CCP (USNM loc. 41006, 42306). For DT73: figure 13*A*, 13*B* (USNM-539326), and figure 13*L*, 13*M* (USNM-559859). For DT74: figure 13*A*–13*D* (USNM-539326) and figure 13*J*, 13*K* (USNM-559858). For DT257: figure 13*E*–13*G* (USNM-559856) and figure 13*H*, 13*I* (USNM-559857).

Plant hosts. Unknown Spermatophyta seeds: platysperm sp. 1 (DT73, DT74); platysperm sp. 2 (DT74, DT257); platysperm sp. 3 (DT73), collectively designated herein as platysperm sp. seed.

Remarks. In the absence of ovulate fructifications with organic connection to vegetative material at CCP, it is impossible to assign platysperm sp. 1–3 to particular respective seed plant lineages. These three platysperm seed morphotypes may represent multiple species, including a walchian conifer with a diminutive micropylar region and other seed plant taxa with more prominent micropyles. For this reason, we are considering all three platysperm seed morphotypes as one categorical unit in this analysis until further study can define the limits of each morphospecies or establish whole-plant taxon affiliations.

Generic winged platysperm seeds occur in many floras throughout the Permian and Triassic and have been assigned to a variety of major lineages, including gigantopterids, cordaites, corystosperms, and ginkgophytes (Anderson and Anderson 2003; Taylor et al. 2009). A notable feature of the seed predation at CCP is the elevated incidence of DT73 and DT74 when compared to other Permian floras. Also present is a different form of piercing and sucking in DT257, which represents a scale insect that is specific to platysperm sp. seed and likely fed on the seed's megagametophytic and wing tissues. The scale attachment scars appear frequently lodged between the sulcus formed by the seed wing and main body. The closest modern analogue of this association is scale insect predation on the winged seeds of pinaceous conifers (Turgeon et al. 1994).

Although three of the occurrences of DT257 (fig. 13*F*–13*H*) are on the main body of platysperm type 2 seeds, the other seven occurrences of seed predation, consisting of DT73, DT74, and DT257, occur on the wings of platysperm type 1, 2, and 3 seeds. One explanation for this pattern is that a host plant cue was missed for targeting the megagametophytic tissues of the seed main body. An alternative and more likely possibility is that the scale insect seed predator had a more eclectic spectrum of tissue specificities and consumed wing as well as megagametophytic tissues. Seed predator consumption of photosynthetic wing tissue currently occurs in a variety of plant hosts by a variety of seed predators. These associations include several species of *Abies* (fir) consumed by the fir seed gall midge *Dasyneura abiesemia* (Diptera: Cecidomyiidae; Keen 1958, fig. 13), *Tsuga* (hemlock) attacked by the elongate hemlock scale *Fiorinia externa* (Hemiptera: Diaspididae; McClure 1979; Johnson and Lyon 1991, fig. 45C), and the maple samara leaf miner *Etainia sericopeza* (Lepidoptera: Nepticu-

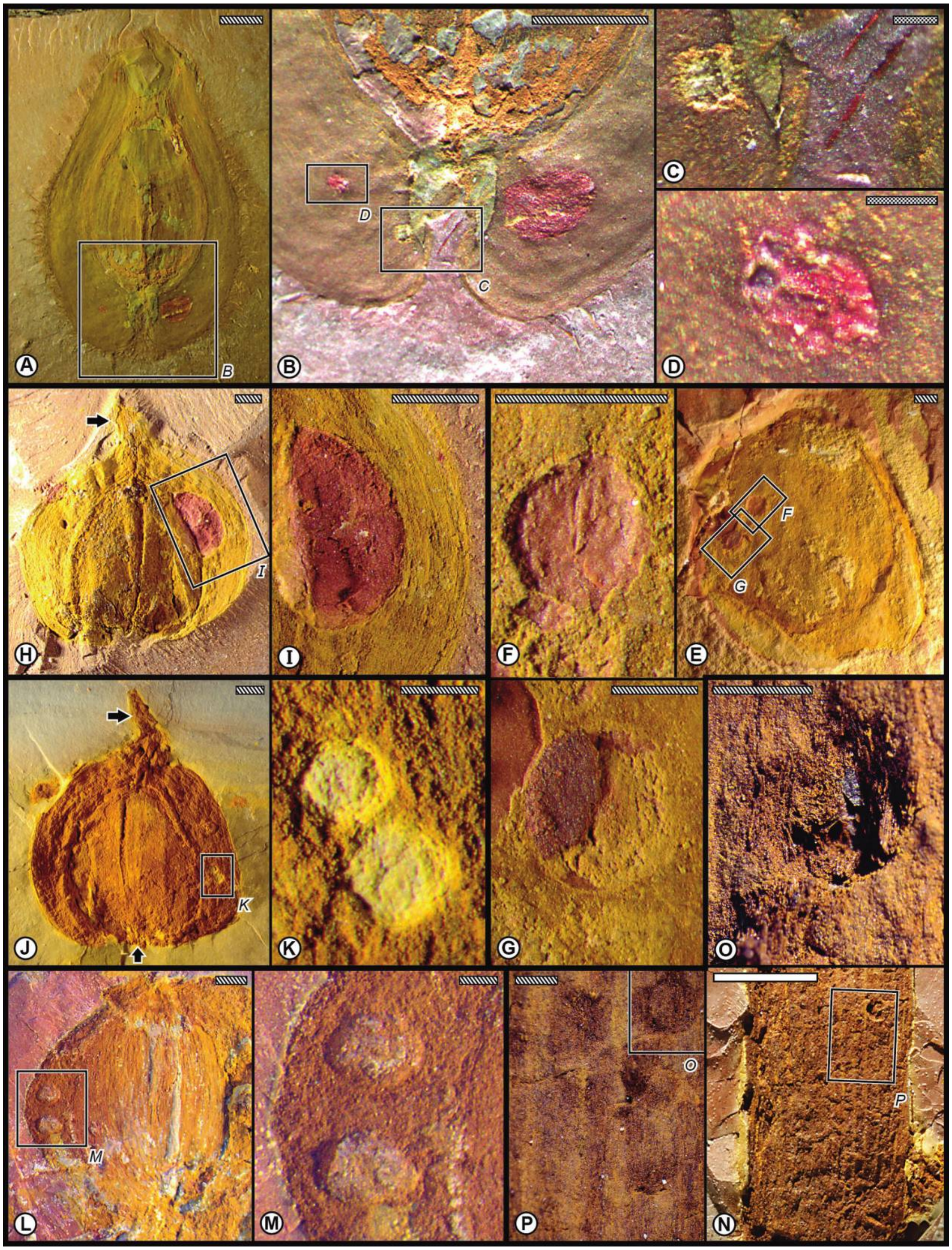

Fig. 13 Insect seed predation on platysperm sp. seed morphospecies (*A–M*) and a wood boring on an unidentified axis (*N–P*) at Colwell Creek Pond from the Early Permian of Texas. The platysperm seeds likely represent multiple taxa originating from walchian conifers and other seed plant lineages. *A–D*, Three instances of seed predation on the wings of a platysperm type 1 showing the disruption of surface tissues. At *A* are two examples of DT74, enlarged to the left in *B* and further magnified in *C* and *D*; an example of DT73 occurs in *A* and is enlarged to the right in *B* (USNM-539326, USNM loc. 42306). *E–G*, A different type of seed predation (DT257) is represented by five circular to broadly

lidae; Puplesis 1994, fig. 809). Based on these patterns of herbivory in modern counterparts, it is highly likely that platysperm types 1–3 bore photosynthetic tissues in their wings.

New damage type DT257. Circular to broadly ovoidal scale scars, 0.8–1.5 mm maximum dimension; surface texture smoother or spongier than surrounding seed test. Occurring on seeds, on the central body and wings.

Distribution in Paleozoic habitats. While seed predation is a recognizable FFG based on a very distinctive trophic interaction, the means of predation are similar to other such groups, such as piercing and sucking in the case of paleodictyopteroid and hemipteran insects (Shcherbakov et al. 2009) or the creation of larval galleries by seed weevils (Janzen 1971) during the Mesozoic. In many cases, seed predation requires mouthpart structures to puncture or chew through hard or thick integumental structures that enclose seeds, such as an outer sclerotesta or inner fibrous pericarp.

The earliest documented seed predation originates during the Early Pennsylvanian, consisting of small round perforations into the Euramerican medullosan seed *Trigonobalanus* (Labandeira 2007). The same style of seed predation occurs in Late Pennsylvanian platysperm cordaitalean seeds from the Chunya locality of the Tunguska Basin, Russia (Sharov 1973). Identical damage on winged cordaitalean seeds also has been described from the Russky Island site of the Prospelovo Formation of the Pechora Basin, Russia, on *Samaropsis danilovii* Suchov (Shcherbakov 2008). This locality, about the same age as CCP, bears a similar type of small circular perforation that targeted megagametophytic tissues of the central body. This type of damage has been attributed to the stout, probing beaks of some Palaeodictyopteroidea (Sharov 1973), in which piercing-and-sucking action flushed out the contents of megagametophytic tissues in a manner similar to seed bugs (Lygaeidae) of modern Hemiptera (Ralph 1976).

Borings

Definition. Borings are tunnels and galleries produced by arthropods in indurated tissues such as wood and sclerenchyma or engravings in softer tissues such as cambia or pith parenchyma wherein a discrete network is present that may contain frass, fungi, or infilled sediment.

DT represented. DT243.

USNM figured specimens. CCP (USNM loc. 42305). For DT243: figure 13*N*–13*P* (USNM-559860).

Plant hosts. Incertae sedis: an indeterminate axis, petiole, or isolated midrib of a seed plant leaf.

Remarks. Eight simple borings of relatively small diameter compared to other Paleozoic occurrences (Weaver et al. 1997; Noll et al. 2004; Naugolnykh and Ponomarenko 2010) were found on a single specimen of a CCP woody element. Although the woody axis lacked any attached branches or foliage, its overall robustness and heavily vascularized structure are suggestive of a rachis of *A. waggoneri*. Wood borings on such small branches are especially rare in the fossil record, attributable to hydrodynamic qualities of small axes that disallow their incorporation into fossil leaf layers or, alternatively, are too small to enter the permineralized record.

New damage type DT243. Small (ca. 1–1.4 mm diameter) borings perpendicular to wood surface infilled with fine-grained matrix.

Distribution in Paleozoic habitats. Borings are rare in plant compressions and impressions but are commonly encountered in permineralized woods, where three-dimensional preservation allows for observation of tunnel detail. Several features are important in the determination of tunnel culprits, including the elucidation of three-dimensional tunnel and gallery network geometry, frass infilling contents, and behavioral targeting of nutritious tissues such as cambia (Tovar et al. 1995; Labandeira 2002). Generally, Permian-age borings are uninformative regarding the identities of both the targeted host plant and the wood-boring arthropod.

Borings have a sporadic fossil record during the Pennsylvanian, occurring principally in the central tissues of medullosan trunks (Labandeira 1998), *Psaronius* tree fern rachises (Rößler 2000; Labandeira and Phillips 2002), and calamite stems (Rößler 2006). Much of this damage, however, involves nonwoody pith or other medullary tissues that are amenable to tunneling by insects. These tunnels lack structures typical of those boring into harder substrates such as wood. Nevertheless, there is a detectable shift beginning during the Early Permian toward rare borings present in the more indurated tissues of calamites (Rößler 2006) and especially seed plant taxa, particularly the wood of coniferophytes and glossopterids (Zavada and Mentis 1992; Weaver et al. 1997; Noll et al. 2004; Rößler 2006). Throughout the Permian, borings in mostly arborescent gymnosperms are present, where the larvae of archostematan beetles have been cited as offending culprits (Naugolnykh and Ponomarenko 2010).

Fungal Damage

Definition. Fungal damage consists of the pathogenic invasion of live plant tissue through a breach in a plant's integument, commonly introduced through lesions produced by insect herbivory. Pathogenic features resembling fungi also may be caused by physical conditions such as absence of essential nutrients or abnormal temperature conditions.

DT represented. DT58.

USNM figured specimens. CCP (USNM loc. 41006,

ellipsoidal scale scars at or near the junction of the main body with the wing of platysperm type 2 (USNM-559856, USNM loc. 41006). *H*, *I*, Also found on platysperm type 2 (USNM-559857) is another example of a broadly ellipsoidal scale scar of DT257 at the main body wing interface (USNM loc. 42306). *J*, *K*, A platysperm type 2 specimen (USNM-559858), bearing piercing-and-sucking damage (DT74) on wing tissues (USNM loc. 42306). *L*, *M*, Another example of piercing and sucking (DT73) on the main body of wingless platysperm type 3 (USNM-559859, USNM loc. 41006). *N*–*P*, The only example of wood boring (DT243) at Colwell Creek Pond occurs as small borings on an isolated thick twig or midvein, possibly of *Auritifolia waggoneri* (USNM-559860, USNM loc. 42305). Scale bars: solid, 10 mm; back-slashed, 1 mm; stippled, 0.1 mm.

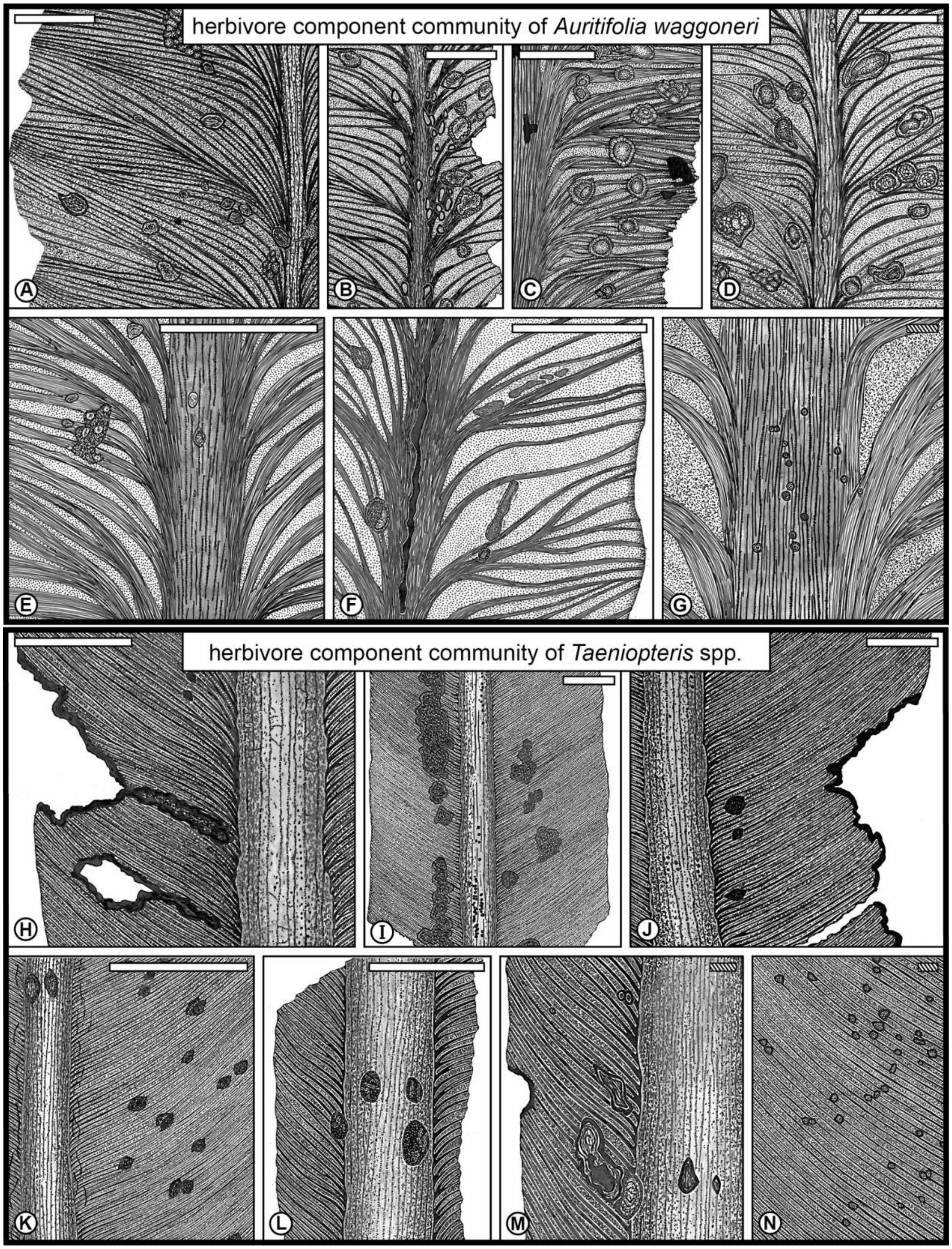

Fig. 14 Camera lucida illustrations of the component herbivore community (Root 1973) of *Auritifolia waggoneri* (*A–G*) and *Taeniopteris* spp. (*H–N*) at Colwell Creek Pond from the Early Permian of Texas. A representative spectrum of the more obvious insect-mediated damage is provided; not all functional feeding groups or damage types (DTs) are represented. Of the eight DTs shown for *A. waggoneri* and 11 DTs for *Taeniopteris* spp., four occur on both hosts (DT46, DT76, DT101, and DT246). *Top*, in *A–G* are the more commonly occurring interactions

42292, 42306). For DT58: figure 5*C* (USNM-539375), figure 7*B* (USNM-530921), figure 12*R* (USNM-559855), and figure 14*M* (USNM-539375).

Plant hosts. ?Cycadales: *Taeniopteris* spp.; indeterminate: unaffiliated broad-leaved seed plant; and ?peltaspermales: *A. waggoneri*.

Remarks. As currently conceived, DT58 consists of generic unassigned fungal damage. A recent examination of the compression-impression fossil record indicates that many instances of pathogen-mediated plant disease, including fungal damage, are significantly underrecognized (Labandeira and Prevec 2014). Nevertheless, several examples of fungal necroses exist at CCP, principally through fungal invasion from open foliar wounds (figs. 5*C*, 7*B*, 12*R*). Examples include entry at the ruptured tissue at the base of a DT120 gall (fig. 5*C*) or after surface abrasion caused by the maker of DT31 (fig. 7*B*) and the apparent colonization of foliar tissue without any evident connection to a wound entry caused by an herbivore (fig. 12*Q*). The pattern of pathogenic fungal infection at CCP reflects a general pattern that also occurs on other well-documented Permian floras (Prevec et al. 2009; McLoughlin 2011; Labandeira and Prevec 2014).

Distribution in Paleozoic habitats. Much of the fossil record of plant-insect associations is linked with secondary pathogenic infection, particularly fungi (Labandeira and Prevec 2014). For the late Paleozoic, fungal damage is present as zones of texturally distinctive necrotic tissue that surround inner tissues exposed by external foliage feeding (Labandeira 2006*b*; Stull et al. 2013) and oviposition marks (Prevec et al. 2009). Fungal associations also have been documented for Permian woods (Dieguez and López 2005) whose necroses resemble the rots and other pathogenic signs of extant woods (Sinclair et al. 1987). The overall lack of documentation presumably is attributable to an absence of appreciation of fungal damage or to difficulties in assignment to a particular pathogen sign to a causative organism, such as a virus, bacterium, fungus, or nematode (Labandeira and Prevec 2014).

Patterns of Herbivory Revealed by DT Occurrences

Of the 2140 plant specimens examined at CCP, 649, or 30.33%, displayed one or more instances of herbivory (table 1). A total of 1390 instances of herbivory were observed throughout the CCP flora: 1346 on broadleaf taxa, 8 on conifers, 2 on axes, and 34 on seeds (table 2). Multiple DTs and FFGs were frequently found on individual specimens. Of the instances of herbivory recorded for the CCP flora, those allocated to the galling FFG constituted one-third of all DT occurrences; those of the oviposition FFG had one-third of all DT occurrences; and those of the external foliage feeding FFG, represented by the hole-feeding, margin-feeding, and surface-feeding subgroups, provided one-fifth of all DT occurrences. Minor levels of herbivory were present for the piercing-and-sucking FFG, responsible for one-tenth of all DT occurrences, and the remainder FFGs constituted 3.0% of all DT occurrences. Clearly, oviposition, galling, and external foliage feeding were the dominant FFGs at CCP. External foliage feeders targeted *Taeniopteris* spp., galling preferentially occurred on *A. waggoneri*, and oviposition was distributed evenly between these two most herbivorized taxa.

Of the 12 taxa represented in the CCP flora, four—*W. piniformis, Taeniopteris* spp., *A. waggoneri*, and platysperm sp. seed—constituted 90.09% of the flora (table 1), based on the numbers of specimens, and 91.67% of the herbivory. Of these, the two dominant herbivorized taxa were *Taeniopteris* spp. and *A. waggoneri*, which disproportionately constituted an elevated 37.44% and 47.92%, respectively, of the herbivorized specimens in the flora, clearly the two most herbivorized taxa (table 1). Perhaps unsurprisingly, *A. waggoneri*, the fourth most abundant host but the most abundant monophyletic broadleaf taxon, represented almost half of all herbivore-inflicted damage. By contrast, the conifer *W. piniformis*, the second most abundant taxon in the CCP flora, expressed a very low incidence value of 1.23%, likely a consequence of minimal exposure of surface area and structurally defended tissues that would be unavailable to herbivores. Similarly, the platysperm sp. seed, the most abundant taxon at CCP, bore a higher but still modest incidence of herbivory of 5.08%. Although a respectable value for seed predation of the Paleozoic and Mesozoic, this value likely was due to the poor development of the seed predation feeding guild before and during the Early Permian, particularly as megagametophytic tissues would be accessible and nutritious sources for consumption, unlike the more refractory and digestively more difficult foliar tissues of *W. piniformis*.

The remaining eight taxa, mostly broad-leaved medullosan, callipterid, gigantopterid, and probable cycadophyte seed

of *A. waggoneri* and its insect herbivores. The predominant interactions on *A. waggoneri* are botryoidal DT120 galls in *A*, *C*, and *D* and DT246 pustulate-walled galls (*A*, *C*, *D*), which frequently co-occur and target veinal and intercostal tissues of leaf blades. A rare occurrence of generic DT32 galls is at *E*. Two types of oviposition are present, DT76 on leaf midrib tissues (*A*, *B*, *D*, *E*) and DT101 on leaf blade tissues (*A*, *B*, *F*). Piercing and sucking is documented as DT46 on midrib vascular tissue at *G*. Surface feeding occurs as surface abrasions of DT29 at *A* and *E* and DT130 at *F*. *A*, USNM-596951 (USNM loc. 44292). *B*, USNM-559843 (USNM loc. 42306). *C*, USNM-559854 (USNM loc. 41005). *D*, USNM-596952 (USNM loc. 42306). *E*, USNM-559853 (USNM loc. 41006). *F*, USNM-559840 (USNM loc. 41006). *G*, USNM-559853 (USNM loc. 41006). Bottom, at *H–N* are the more commonly occurring interactions on *Taeniopteris* spp., highlighting the predominance of oviposition. Oviposition consists of DT76 (*J*, *M*), penetrating midrib tissues, and DT101 (*M*), DT245 (*K*), and DT246 (*J*, *N*), affecting leaf-blade tissues. Common external foliage feeding is displayed as margin feeding (DT12) at *K*, *M*, and *N*; as hole feeding (DT4) at *K*; and as surface feeding (DT103) at *K* and DT263 at *H*, the latter suggestive of leaf rolling or folding damage. Piercing and sucking targeted vascular tissue at *H* and *I* (DT138), mesophyll tissue at *I* (DT46), and midrib phloem tissue at *L* (DT183). The relatively common foliar gall (DT120) is present at *G*. Secondary fungal infection (DT58) of an oviposition mark (DT101) occurs at *M*. *H*, USNM-559820 (USNM loc. 42306). *I*, USNM-539333 (USNM loc. 42305). *J*, USNM-559829 (USNM loc. 42292). *K*, USNM-559852 (USNM loc. 42292). *L*, USNM-559822 (USNM loc. 42306). *M*, USNM-539375 (USNM loc. 42306). *N*, USNM-559837 (USNM loc. 42306).

plants, constituted 9.01% of the flora and a collective herbivory of 8.33%, commensurate with their collective abundance. However, there was significant variability of herbivory within this group, with taxon-specific values ranging from a high of 3.24% for the gigantopterid *E. texana*, with 32 specimens, to the absence of herbivory on the sphenopsid *S. thonii*, with three specimens. The taxon-specific herbivory values for these considerably less abundant eight taxa may indicate that arthropod herbivores were tracking overall taxa abundance, though only among broad-leaved foliage, as this pattern breaks down when the comparatively low values of herbivory are considered for the two most abundant taxa, the non-broad-leaved *W. piniformis* and platysperm sp. seed.

Patterns of Herbivory Revealed by Surface Area Removal by Herbivores

An assessment of the CCP flora also was made based on the amount of leaf surface area removed by herbivores. The total surface area examined was 39,367.32 cm^2, and the amount of herbivorized surface area was 622.26 cm^2, a removal of 1.58% for the total CCP flora (table 1). Although oviposition is not a type of feeding and rather represents the response of egg insertion into plant tissue, it is treated as herbivory in all analyses presented here because of its conspicuous fossil record and its feeding-like use of plant tissue as a resource. Individual leaves measured up to 481.99 cm^2, the largest specimen, and the smallest specimens were seeds and seed fragments that ranged in size from 0.03 to 1.50 cm^2. We note that the taxon with the most surface area removed by herbivory was *A. waggoneri*, with a value of 3.08%; this single taxon represented an astounding 80.17% of all surface area removed at CCP. The second most herbivorized taxon was *Taeniopteris* spp., with 1.36% of its surface area removed, but only representing 15.97% of all surface area removed at CCP. The rank order of *A. waggoneri* (first) and *Taeniopteris* spp. (second) matches the same rank order of taxa for the proportion of herbivorized specimens (table 1; fig. 14); however, *A. waggoneri* has a much greater representation of herbivorized surface area than *Taeniopteris* spp. These two dominantly herbivorized taxa account for 96.14% of the removed surface area, a value greater than the 85.36% of herbivorized specimens in the flora that these two taxa contribute.

The remaining CCP taxa constituted only 3.86% of the herbivorized surface area removed. Of these, the gigantopterid *E. texana* was the most common, with 3.42% (table 1), representing 88.6% of the remaining herbivorized surface area. The remaining taxa either lacked or had only trace amounts of foliar tissue removed.

Discussion

Two aspects of the results deserve special mention. The first discussion involves documentation of the major patterns of herbivory within the CCP flora, including the extent of generalized associations versus specialized associations and the presence of antiherbivore defenses. The second discussion is an evaluation of the trajectory of herbivory among the three assemblages from the Early Permian of north-central Texas that have been studied to date: CBB, Taint, and CCP.

Patterns of Arthropod Herbivory at CCP

Much of the herbivory at the CCP flora was generalized, particularly for *Taeniopteris* spp., *Auritifolia waggoneri*, and *Evolsonia texana*, the three most herbivorized taxa. *Taeniopteris* spp. and *A. waggoneri* exhibit approximately equal amounts of generalized and specialized DTs (table 2). *Evolsonia texana*, third in rank order, is instructive regarding specialized herbivory. Of the 44 occurrences of *Evolsonia* damage, approximately half (21 DTs) represent generalized herbivory, principally, various forms of external foliage feeding, whereas the other half (23 DTs) represent more specialized DTs such as piercing and sucking but especially oviposition and other modes of galling. Similar values were present for *Sandrewia texana*, fourth ranked in herbivore attack, consisting of 10 DTs assigned to generalized consumption and 11 DTs assigned to more specialized feeding modes. The other taxa provided a paucity of data—too few specimens, too few DTs, or both—for interpretation.

Taeniopteris spp. and *A. waggoneri* are the most herbivor-

Table 2

Damage Type (DT) Occurrences on the Plant Hosts at Colwell Creek Pond from the Early Permian (Kungurian) of North-Central Texas, Organized by Functional Feeding Group (FFG) and Subgroup and DT

Plant host	Hole feeding	Margin feeding	Surface feeding	Piercing and sucking	Oviposition	Galling	Seed predation	Wood boring	Fungal	Total
Auritifolia waggoneri	15	37	26	34	224	364	...	...	5	705
Callipteris sp.	...	...	...	...	1	...	...	...	...	1
Evolsonia texana	8	2	8	3	14	15	...	...	...	50
Indeterminate broadleaf	1	2	4	4	5	10	...	...	...	26
Sandrewia sp.	...	...	...	...	3	2	...	...	...	5
Supaia thinnfeldioides	...	...	...	2	...	3	...	...	...	5
Taeniopteris sp. nov.	...	...	...	...	3	1	...	...	...	4
Taeniopteris spp.	24	113	44	87	219	63	...	...	...	550
Walchia piniformis	...	...	...	8	...	...	...	...	...	8
Indeterminate axis	...	...	...	...	...	1	...	1	...	2
Samaropsis sp.	...	...	...	...	...	...	34	...	...	34
Total	48	154	82	138	469	459	34	1	5	1390
FFG %	3.45	11.08	5.90	9.93	33.74	33.02	2.45	.07	.36	100

Table 3

A Comparison of Herbivory on *Taeniopteris* spp. and *Auritifolia waggoneri*

Herbivory feature	*Taeniopteris* spp.	*A. waggoneri*
Percentage of herbivorized specimens (%)	37.44	47.92
Foliar surface removed by herbivory (%)	1.36	3.08
Total DT occurrences	552	705
Dominant functional feeding groups	Oviposition (8 DTs, 220 occurrences); external foliage feeding (15 DTs, 178 occurrences)	Galling (8 DTs, 364 occurrences); oviposition (10 DTs, 224 occurrences)
Most common DT occurrence	DT76 (oviposition, 85 occurrences)	DT120 (galling, 173 occurrences)
Second most common DT occurrence	DT246 (oviposition, 57 occurrences)	DT101 (oviposition, 100 occurrences)
DT spectra	35 DTs, 25 in common with *Auritifolia waggoneri*:	32 DTs, 25 in common with *Taeniopteris* spp.:
External foliage feeding	16 DTs	10 DTs
Hole feeding	DT01, DT02, DT03, DT07	DT02, DT04, DT07
Margin feeding	DT12, DT13, DT14, DT15	DT12, DT14, DT15
Surface feeding	DT25, DT27, DT29, DT30, DT31, DT97, DT103, DT263	DT29, DT30, DT31, DT130
Piercing and sucking	(7 DTs) DT46, DT47, DT48, DT77, DT138, DT157, DT183	(6 DTs) DT46, DT47, DT48, DT77, DT157, DT183
Oviposition	(6 DTs) DT54, DT76, DT100, DT101, DT245, DT246	(8 DTs) DT54, DT76, DT100, DT101, DT108, DT175, DT245, DT246
Galling	(6 DTs) DT32, DT33, DT34, DT80, DT120, DT247	(8 DTs) DT32, DT34, DT80, DT120, DT247, DT259, DT260, DT262

ized plant hosts (table 1). This conclusion is supported by (1) the percentage of herbivorized plant host specimens, (2) the percentage of removed foliar surface area, and (3) the elevated number of DTs on each host plant (table 3). Oviposition and subordinately external foliage feeding dominated herbivory on *Taeniopteris*, whereas galling and subordinate oviposition were the most important sources for *A. waggoneri*. These and other host-specialized DTs are confined to one or the other of the two hosts. Surface feeding of DT103 and DT263 and galling of DT122 and DT120 are restricted to *Taeniopteris* spp., whereas piercing and sucking of DT138, oviposition of DT175, and galling of DT259 occur solely on *A. waggoneri* (table 3). Each of these plants supports a component community that consists of the source plant and all directly or indirectly trophically dependent organisms that derive energy from a resource provided by the plant (Root 1973). These interactions appear to be examples of host specialization that are overshadowed by more extensive co-occurrence of other DTs on both *Taeniopteris* spp. and *A. waggoneri*. The component arthropod herbivore community of *Taeniopteris* spp. prominently consists of external foliage feeding (DT4, DT12, DT103, DT263) and oviposition (DT76, DT245, DT246) but also piercing and sucking (DT46 and DT183) and galling (DT263; fig. 14*H*–*N*; table 3). By contrast, the component community of *A. waggoneri* records the predominance of galling (DT80, DT120, DT246, DT260) and oviposition (DT76, DT101) but also external foliage feeding (DT29, DT130) and various types of piercing and sucking (fig. 14*A*–*G*; table 3).

These general trends for greater palatability of certain seed plants are relevant for the greater levels of herbivory for certain hosts seen at CCP. Several lines of evidence from CCP plants suggest a constitutive antiherbivore defense syndrome. (Constitutive defenses are structural or chemical antiherbivore defenses that are intrinsic to basic plant architecture; by contrast, induced defenses are acquired by the plant host as a direct response to previous insect herbivory; Karban and Baldwin 1997.) The constitutive defenses for the two most herbivorized taxa of *Taeniopteris* sp. and *A. waggoneri* were (1) thickened, rigid cuticles; (2) thick foliage; (3) the perfusion of the lamina with robust, closely spaced, and hardened primary to tertiary veins that are expressed at the surface; and (4) prominent secondary reaction rims along necrotic zones (e.g., figs. 2*B*, 3*D*, 9*A*, 14, 15). There was no evidence for spines, stiffened trichomes, or glandular structures such as those found by Pott et al. (2012) on bennettitalean fronds. All of the physical constitutive defenses at CCP would have minimized herbivory. However, these metabolically costly structural features are most prominent in the two most heavily herbivorized plant hosts, indicating that a host plant–herbivore arms race was present at CCP. This suggests an escalated relationship (Vermeij 1987) between key plant hosts and their arthropod herbivores.

The absence of skeletonization at the CCP site is noteworthy. Skeletonization, like hole feeding, is the consumption of the entire thickness of intercostal leaf tissue but with one or more orders of veins remaining, forming a fine to coarse lacelike network (Coulson and Witter 1984). Skeletonization commonly occurs along a primary or secondary vein that serves as a structural barrier confining feeding damage to a portion of the leaf, such as angularly constrained tissue formed at junctures of robust primary and secondary veins (Heron 2003). The robustness of the remaining veins forming the skeletonized lattice can provide evidence for the mouthpart morphology and efficacy of chewing by the suspect herbivore. These relationships have been based on the modern relationship between the mode of plant damage and mandible type (Gangwere 1966; Bernays and Janzen 1988; Labandeira 1997). This type of feeding damage becomes gradually more abundant during the

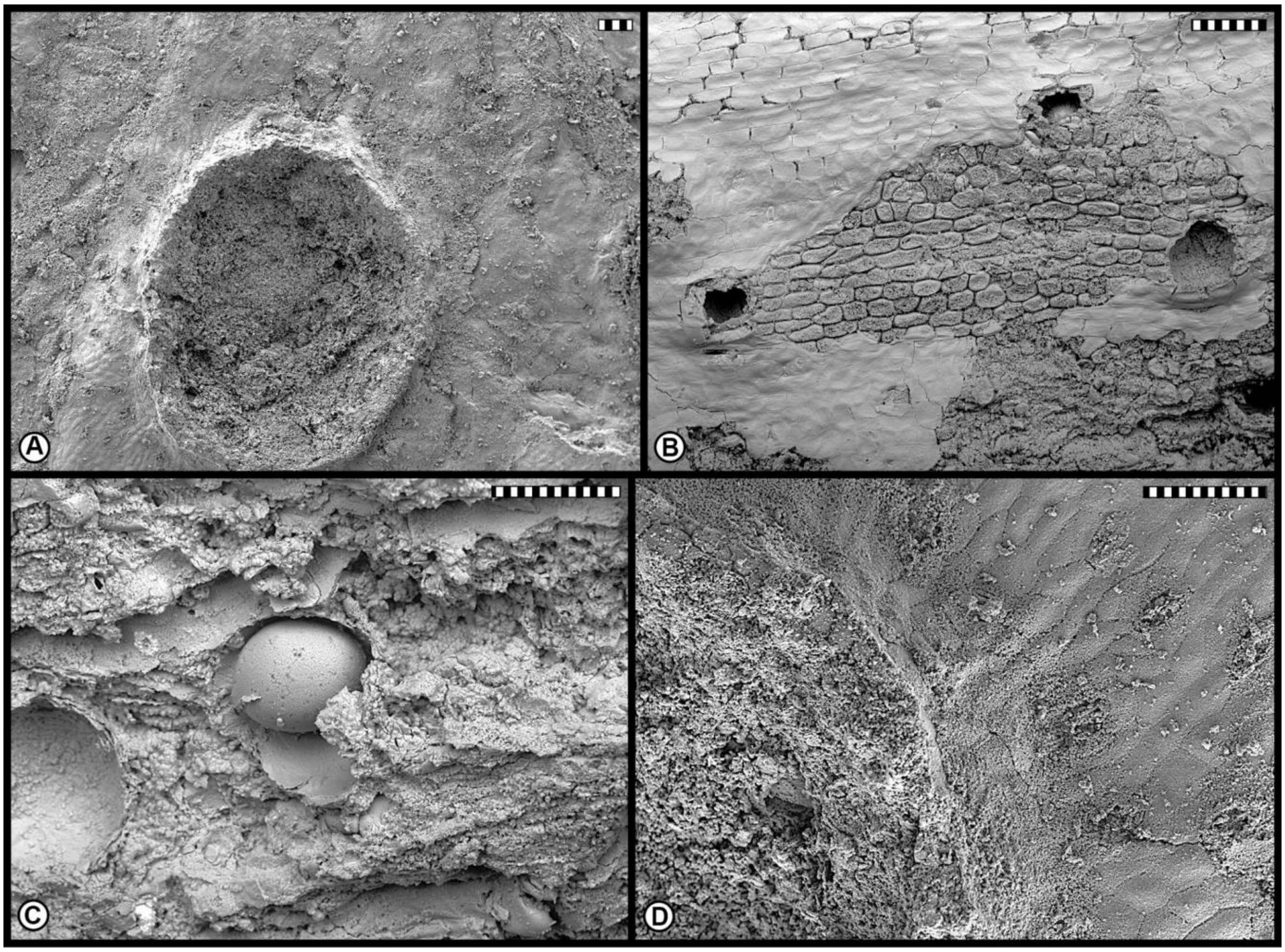

Fig. 15 Scanning electron microphotographs of the surface and internal structure of *Taeniopteris* sp. (*A–C*; USNM-539324, USNM loc. 42305) and *Auritifolia waggoneri* (*D*; USNM-530923, USNM loc. 42292), from Colwell Creek Pond of the Early Permian of Texas. This damage shows at a submicroscopic level margin feeding, piercing and sucking, and galling of these herbivorized plant hosts. *A*, Small gall (DT80) displaying an outer indurated wall tissue and either a collapsed or evacuated central area (USNM-539324). *B*, Puncture marks (DT46) made by a piercing-and-sucking insect on epidermal tissue and positioned over veins. *C*, A possible cast of insect eggs, representing an unknown damage type, inserted into foliar tissue. *D*, Margin feeding along a leaf edge (DT12), showing tissue distortion along the cut edge. All scale bars indicate microns.

preangiospermous Mesozoic plant record. One notable exception and an early example of more intense skeletonization is the Late Triassic fern *Dictyophyllum nathorstii* Zeiller, which has extensive skeletonization (Feng et al. 2014). Skeletonization becomes a significant type of damage for angiosperm-dominated floras of the Late Cretaceous to Neogene (Labandeira 1998, 2006*b*).

One possible explanation for the overall paucity of Permian skeletonization is the absence of derived lepidopteran and coleopteran lineages that originated during the Early Cretaceous to Paleogene and whose larvae are dominant skeletonizers today (Powell et al. 1998; Hunt et al. 2007). Another factor explaining the dearth of skeletonization at CCP is that the site harbors a high proportion of host plant taxa that displayed robustly thickened laminae with considerable interstitial tissue development, as well as massive petioles and primary veins, supporting fibers, abundant bundle sheaths, and sclerenchymatous, cuticular, and other structural tissues (fig. 15; Gillespie and Pfefferkorn 1986; Chaney et al. 2009; Looy 2013). These structural features would have impeded access of herbivores to leaf tissues, particularly for *Taeniopteris* and *Auritifolia*. However, some modern insect taxa select for consumption those leaves with robust leaf structural traits that otherwise would be interpreted as herbivore deterrents (Peeters 2002). Robust frond construction, including massive bundle sheaths, thickened pinnules, and possible semisucculence, have been described for the Artinskian peltasperm *Glenopteris splendens* Sellards from the Wellington Formation of Kansas (Krings et al. 2005), also indicating the possibility of strong mechanical herbivore deterrence. Although these histological foliar features provide several features of leaves consistent with host plant repelling of insect herbivory, it remains unknown whether or how chemical defense was used in CCP plants.

Table 4

A Comparison of Arthropod Herbivory on Broadleaf Foliage from the Three Lower Permian Localities Studied to Date

Flora	Lower Permian age	No. specimens examined	SA removed by herbivores	Proportion of herbivorized leaves (%)	Most herbivorized plant taxon	Inferred habitat	References
Colwell Creek Pond	Early Kungurian	2140	2.36	61.58	*Auritifolia waggoneri* (unassigned peltasperm)	A coastal environment with marine influences	This study
Taint	Late Artinskian	1289	2.58	33.20	*Zeilleropteris watti* (gigantopterid)	A small basin likely adjacent to a stream	Beck and Labandeira 1998
Coprolite Bone Bed	Late Sakmarian	520	.27	18.27	*Autunia* cf. *conferta* (callipterid peltasperm)	A perennial pond deposit on a flood plain	Labandeira and Allen 2007; Labandeira 2012

Note. SA = surface area.

Evolution of Insect Herbivore Component Communities during the Early Permian

Although additional assemblages are needed during the approximate 11-million-year interval of the Early Permian redbed sequence of north-central Texas, certain patterns already can be detected based on the current study of CCP (Kungurian) and on earlier studies of the Taint (Artinskian; Beck and Labandeira 1998; Labandeira 2012) and CBB (Sakmarian) floras (Labandeira and Allen 2007). A conspicuous pattern is that there is a broader range of FFGs and DTs at CCP than those of Taint or CBB. A second noticeable pattern is the approximate 10-fold increase in foliar surface area removed by herbivores and twofold increase in the proportion of herbivorized leaves between the CBB and Taint assemblages (table 4). This dramatic increase is followed by stabilization of both measures of herbivory between Taint and CCP.

Another trend is the consistent and elevated levels of herbivory on seed plant taxa at all localities, favoring highly herbivorized peltasperm or gigantopterid hosts. One explanation for this preference is the greater conspicuousness, or apparency (Feeny 1976), of seed plant foliage in the local environment. This increased herbivory matches the marked diversification of these plant groups in the southwestern United States during this time (Mamay 1989; DiMichele et al. 2005; Mamay et al. 2009). Alternatively, and more likely, is the greater palatability or availability of seed plants to a broad spectrum of local phytophagous insects (Labandeira and Currano 2013). The trend toward the preferential herbivory of broad-leaved seed plant leaves over other plant organs and vascular plants is indicated by the virtual absence of herbivory on non–seed plants at CBB, Taint, and CCP. In addition, this pattern already was present in Middle Pennsylvanian floras, during which medullosan foliage such as *Macroneuropteris* was preferentially consumed over non–seed plant taxa, especially the more abundant marattialean tree fern foliage of *Pecopteris* (Trout et al. 2000).

These data from the redbed sequence of north-central Texas (Chaney and DiMichele 2003) and an earlier study (Trout et al. 2000) strongly support the hypothesis that seed plant taxa were especially selected for consumption by local arthropod herbivores during the Early Permian (Beck and Labandeira 1998; Labandeira 2002, 2006*a*, 2006*b*, 2012; Labandeira and Allen 2007; Stull et al. 2013). This selectivity for seed plants also occurs in Permian floras of western Europe (Geyer and Kelber 1987), Cathaysia (Glasspool et al. 2003), and extensive glossopterid-dominated floras across Gondwana in South Africa (Prevec et al. 2009), India (Srivastava and Agnihotri 2011), Australia (McLoughlin 1994*a*, 1994*b*; Beattie 2007), Antarctica (Slater et al. 2012), and South America (Adami-Rodrigues and Iannuzzi 2001; Adami-Rodrigues et al. 2004*a*, 2004*b*; Cariglino 2011). A common observation from these studies is that the preferential targeting of seed plants was made by multiple FFGs, particularly external foliage feeders (Labandeira 2006*a*, 2006*b*; Labandeira and Currano 2013), piercers and suckers (Wang et al. 2009), ovipositing insects (Prevec et al. 2009; McLoughlin 2011), and gallers (McLoughlin 2011; Stull et al. 2013). The dominance of seed plant herbivory during the Permian is an extension of a pattern that began during the Late Mississippian (Labandeira 2007; Iannuzzi and Labandeira 2008), is sporadically documented throughout the Pennsylvanian (Scott and Taylor 1983; Castro 1997; Scott and Titchener 1999; Jarzembowski 2012), and achieves dominance during the Early Permian.

Conclusions

Data from this study support five major conclusions. These conclusions warrant further verification from investigations of additional new sites to clarify patterns of arthropod herbivory from the Sakmarian to the Kungurian interval of the Texas redbed sequence.

1. *Diversity of insect damage and plant hosts at CCP.* From the CCP Early Permian (Kungurian) flora of north-central Texas, we document 52 arthropod DTs representing the eight FFGs of external foliage feeding (hole, margin, and surface feeding), piercing and sucking, oviposition, galling, seed predation, and wood boring on 12 plant hosts. We also identified sporadic fungal damage.

2. *Broad herbivory patterns of the two most extensively targeted plant hosts at CCP.* The two overwhelmingly herbivorized taxa, in rank order, were *Auritifolia waggoneri*, a peltasperm, and *Taeniopteris* spp., a possible cycadophyte. The latter is a form genus that may or may not include closely related taxa. *Auritifolia waggoneri* represented 19.7% of the specimens but accounted for 47.92% of all instances of herbivory in the flora and constituted 41.15% of the total surface area examined in the flora while accounting for 80.17% of the surface area removed by insect herbivores. Analogous values for *Taeniopteris* spp. are 20.09% of specimens, 37.44% of all instances of herbivory, 18.61% of total surface area examined, and a surface area removal of 15.97%.

3. *Detailed herbivory patterns of the two most extensively targeted plant hosts at CCP.* In terms of DTs represented, the principal form of herbivory on *A. waggoneri* was galling and, secondarily, oviposition; *Taeniopteris* spp. exhibited a preponderance of oviposition and, secondarily, external foliage feeding. Although each of these taxa had similar numbers of DT occurrences—705 for 32 DTs recorded on *A. waggoneri* and 522 for 35 DTs on *Taeniopteris* spp.—25 of these DTs were shared between these two taxa and to a lesser extent among many of the less herbivorized taxa, suggesting that a generalized mode of herbivory was dominant at CCP. Specialized interactions included the galls DT260 and DT262 for *A. waggoneri* and surface feeding DT103 and DT263 for *Taeniopteris* spp.

4. *Herbivory patterns of other CCP plant hosts.* All other plant hosts exhibited approximately an order of magnitude less herbivory or the absence of herbivory when compared to *A. waggoneri* and *Taeniopteris* spp. The proportion of these herbivorized specimens ranged from 5.08% for unaffiliated platysperm sp. seed to 1.23% for the conifer *Walchia piniformis* and included the gigantopterid *Evolsonia texana* (3.24%) and an unaffiliated broad-leaved seed plant (2.93%) that may represent multiple species. Taxa that had trace amounts of herbivory, or <1%, in decreasing rank order, were the peltasperms *Sandrewia texana* and *Supaia thinnfeldioides*, the possible cycadophyte *Taeniopteris* sp., an indeterminate axis probably attributable to a taeniopterid host, and an un-

identified callipterid species. The sole non–seed plant, a horsetail (sphenophyte), lacks herbivory.

5. *Herbivory comparisons to other examined floras from the Early Permian redbed sequence.* When CCP is compared to two previously investigated older Early Permian deposits from north-central Texas, two markedly different amounts of herbivory are observed. There is an approximately 10-fold increase in the percent of surface area removed, from oldest (Sakmarian) CBB (0.27%) to (Artinskian) Taint (2.55%), while Taint and the youngest (Kungurian) CCP (2.36%) have approximately the same amount. A similar relationship, although not as dramatic, is also is evident with respect to the proportion of herbivorized leaves among these three sites. However, a far wider range of FFGs was found at CCP (8) than at CBB (4) or Taint (4), and many of these FFGs are represented by a wide range of DTs. The increase in the diversity of FFGs, DTs, and associated herbivore behaviors observed at CCP may be due to several factors, including insect herbivore evolution and site-specific habitat differences.

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