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Minimal insect herbivory for the Lower Permian Coprolite Bone Bed site of north-central Texas, USA, and comparison to other Late Paleozoic floras

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Abstract

An examination of 598 leaves from the Lower Permian (late Sakmarian) Coprolite Bone Bed (CBB) site in north-central Texas, USA, reveals low herbivory levels based on analyses of foliar surface-area removed (0.25%) and frequency of herbivorized leaves (15.6%). These values contrast with a similar study from a somewhat younger (mid-Artinskian) nearby site where analogous values are 2.55% and 31.8%, respectively. As at the younger site, when compared to all other co-occurring plant taxa, CBB pteridosperms were overwhelmingly herbivorized, particularly the peltasperm *Autunia* cf. *conferta* and the medullosan *Odontopteris* cf. *lingulata*, the latter preserving an exceptionally high herbivory level of 3.31%. These two host-plant taxa accounted for 96.8% of all herbivorized leaves and 96.4% of all leaf surface area removed by insects. For the bulk flora, four subgroups of feeding were documented: margin feeding (70.1% of all occurrences), hole feeding (24.1%), and minor skeletonization (earliest occurrence), and galling. Distinctive gall types, one on the midveinal region of *A.* cf. *conferta* and the other on a branchlet of *Walchia piniformis* (also occurring in the European Early Permian) add to an existing but depauperate insect gall record for the Pennsylvanian and Permian.

Emerging evidence indicates that herbivory intensity was spatiotemporally heterogeneous across fluvially-associated landscapes during the Early Permian in both western Euramerica (Texas, USA) and western Gondwana (Paraná Basin, Brazil), differing by an order of magnitude within each of these areas. Localities with the highest percentages of bulk leaf surface-area removed by herbivores in both realms ranged from 2.39 to 2.97%. This range approximates about a third of modern surface-area removal values by insect herbivores in both subtropical to tropical floras.

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1. Introduction

During the Early Devonian to Middle Pennsylvanian, new modes of feeding on live plant tissues emerged. These included external foliage feeding (van Amerom, 1966; van Amerom and Boersma, 1971; Scott and Taylor, 1983), piercing-and-sucking (Labandeira and Phillips, 1996a), stem borings with reaction tissue

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(Dunn et al., 2003), galling (van Amerom, 1973; Labandeira and Phillips, 1996b), and seed predation (Jennings, 1974; Scott and Taylor, 1983). By the end of the Early Permian, all but one of the several principal functional-feeding groups in modern ecosystems was present (Labandeira, 2006a); namely leaf mining, whose earliest occurrence is from the early Late Triassic (Rozefelds and Sobbe, 1987; Zherikhin, 2002a; Scott et al., 2004). Late Mississippian to Late Permian herbivory was associated with a diversity increase in the number of host plant taxa, as vegetational dominance shifted from pteridophytes to seed-plants (DiMichele and Hook, 1992). During this interval there was a significant terrestrial extinction of plant and probably arthropod taxa at the end of the Middle Pennsylvanian, at least for Euramerica (Phillips et al., 1974; Pfefferkorn and Thomson, 1982; Labandeira, 2005). Late Pennsylvanian-aspect wetland floras, depending on time and place, were replaced by more mesic and fluvially associated floras, particularly in southwestern Euramerica during the Pennsylvanian–Permian transition—a trend that continued throughout the Early Permian (DiMichele et al., 2005). Also at this time major glacial and interglacial cycles affected vegetation worldwide

(Gastaldo et al., 1996). In southwestern Euramerica, northern Texas provides ideal stratigraphic and paleoecological control for this transition, reflecting the subsequent dominance of seed-plant dominated floras in clastic-substrate landscapes amid watercourses and their interfluves.

Within this regional setting, the only source of quantitative data on plant–insect interactions from a diverse, abundant and well-preserved leaf assemblage has, until now, been from the mid-Artinskian (~281 Ma) Waggoner Ranch Formation at Taint in Baylor County (Beck and Labandeira, 1998). The flora from the Coprolite Bone Bed locality (CBB), analyzed in this report (Fig. 1), extends this range to the late Sakmarian (~288 Ma), and represents a significantly different host plant assemblage than preserved at Taint. These data are further compared with similar late Artinskian to early Kungurian studies from the Paraná Basin of Brazil (Adami-Rodrigues et al., 2004a), and to ongoing work from the Middle to Late Permian of the Karoo Basin in South Africa (Gastaldo et al., 2005).

CBB and other spatiotemporally proximal floras from Texas occurred in an approximately 20 Ma interval spanning the mid-Sakmarian to the earliest Kungurian

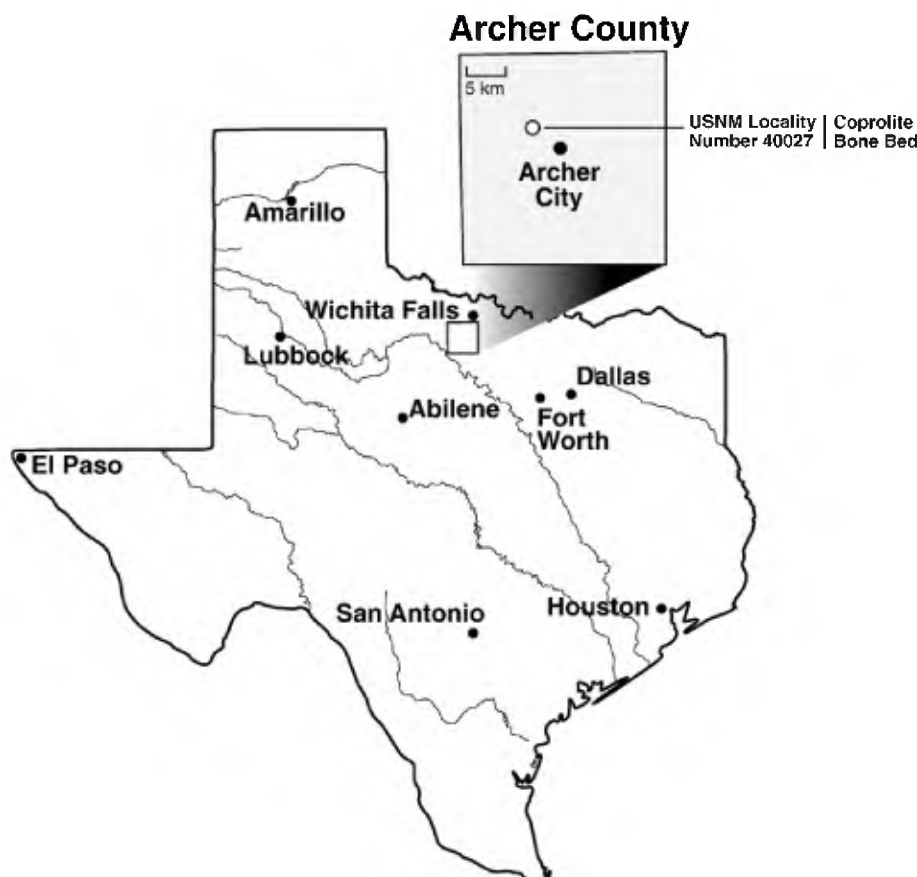


Fig. 1. Index map showing geographic setting of the Coprolite Bone Bed (CBB) flora in north-central Texas, USA.

and occupied a variety of changing fluvial and other subenvironments. Within the context of this biome-wide, late Paleozoic ecological transformation we are pursuing the following questions: What are the patterns in time and space that involve the spectrum and intensity of host plant use by insects? Do these patterns parallel taxonomic turnover, physiognomic differences, or other changes in the host plants and their herbivores? And finally, how do these patterns relate to broader environmental perturbations such as greenhouse–ice-house cycles? By ferreting out patterns of host-plant use by insects at local and more regional scales, the issue of how herbivory was launched during the late Paleozoic can be addressed.

2. Geologic and biologic setting

The CBB locality, in Archer County, Texas (USNM 40027; Fig. 1), was examined in the fall of 1992 by W. A. DiMichele, R. Hook, D. Chaney and C. Labandeira. This site is interpreted as a perennial pond deposit, possibly infilling an abandoned channel, and forms part of a floodplain drainage system at the base of the Nocona Formation that is considered to be of late Sakmarian (~288 Ma) age, and overlies the Archer City Formation and is overlain by the Petrolia Formation (Fig. 2; Sander, 1989). The fossil plants occur in a ~1 m thick, ~35 m wide, silty, red-mottled claystone that dips ~20° WSW and contains ironstone concretions, limonitic clayey nodules, coprolites, bone fragments and many plant organs preserved as limonite or silica in uncompressed, three-dimensional relief. These plant organs contain small thicknesses of both siliceous and limonitic material, some of which formed adjacent to or possibly within decaying plant matter early in diagenesis. Consequently, much of the foliar material is preserved in a relatively uncompressed, three dimensional state (Sander, 1989). The specimens studied in this paper were collected from the eastern exposure of this deposit about 3 to 5 m below a sandstone unit capping a channel meander belt. Extending laterally for 20 m this channel-fill deposit is overprinted by a pedogenic fabric that grades above and below into reddish, flood-plain siltstones. Within a local to regional context, this fluvial deposit is a tributary of a larger sinuous channel that apparently is part of a drainage system within a flood plain (Sander, 1989).

The first formal description of the CBB locality was by A. Romer (1935) as “Locality 2”. This site contains chondrichthyans, several taxa of paleonisciform, crossopterygian, and dipnoan fishes, the amphibians *Eryops megacephalus*, *Acheria crassidisca*, and *Diadectes*

sideropelicus, and the reptiles *Dimetrodon limbatus* and *Edaphosaurus boanerges* (Sander, 1989). The CBB fauna is indicative of a moderately diverse, multitrophic ecosystem.

The collection contained seven fossil plant taxa and represented an unbiased random sample. Foliar material was most common and a few large fronds were present but were impossible to retrieve because of weathering. Like other floras from the Lower Permian of Texas, the CBB flora is taxonomically dominated by phylogenetically disparate groups of seed plants. Typical of floras occurring throughout the mid- to Early Permian succession of north-central Texas (Sander, 1989), the CBB flora is dominated by pteridospermalean, cordaitalean, coniferalean and cycadophyte seed plants; by contrast, pteridophytes constitute an insignificant fraction of total abundance as measured by foliage surface area. The most abundant taxa are the callipterid peltaspermalean *Autunia* cf. *conferta* (Sternberg) Kerp, a species of the cordaitalean *Cordaites* Unger, the walchiacean conifer *Walchia piniformis* (Sternberg)

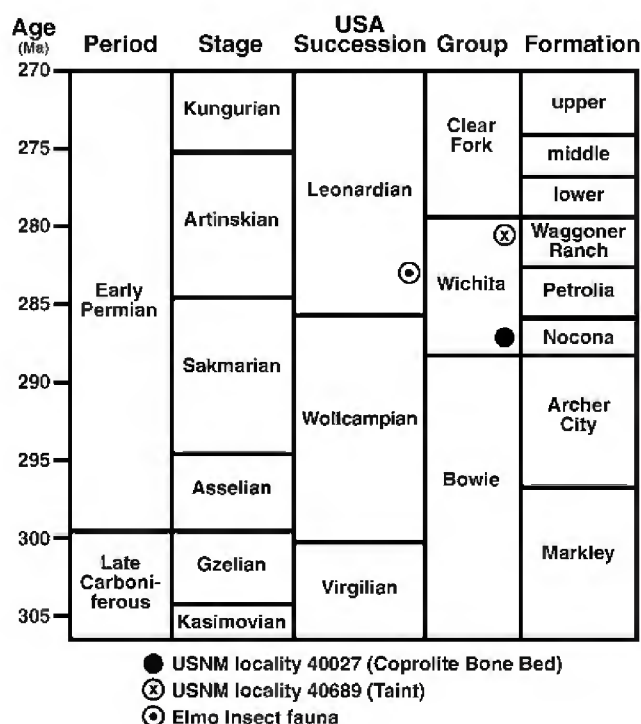


Fig. 2. Stratigraphic setting of the Coprolite Bone Bed flora, showing global stage-level assignments, local stratigraphic units, and equivalent geochronological assignments. Formational designations are from Hentz (1988) and the geochronology is based on Gradstein et al. (2004). For additional details on the CBB locality see Sander (1989), and for a general perspective of relevant Lower Permian floras see Read and Mamay (1964). Beck and Labandeira (1998) discuss insect herbivory from the nearby, somewhat younger Taint locality; Beckmeyer (2000) provides an overview of the Elmo insect locality in central Kansas.

Clement-Westerhof, and the cycadophyte *Russellites taeniata* Mamay. Collectively these species comprise 94.2% of the total diversity (Table 1).

3. Materials and methods

The study comprises two phases (Greenfest and Labandeira, 1997): (1) the qualitative examination of foliar and associated material for evidence of herbivory, and (2) the quantitative analyses of herbivory based on frequency of attack and the percentage of leaf surface-area removed by herbivores. These quantitative measures were compiled for each species and for the entire flora. These data parallel studies by Beck and Labandeira (1998) and Adami-Rodrigues and colleagues (2004a). All analyzed specimens are housed in the Paleobotany Collections of the National Museum of Natural History, in Washington, D.C.

3.1. Qualitative analysis

The initial recognition of herbivory at CBB in the laboratory was based on several explicit criteria (Labandeira, 1998a; Scott and Titchener, 1999; Labandeira et al., 2002). Due to the age of the CBB flora, no

attribution to extant herbivorous taxa was possible, such as is possible for floras from the mid-Mesozoic to Recent (Opler, 1973; Waggoner and Poteet, 1996; Wilf et al., 2000). This lack of taxonomic uniformitarianism necessitated the use of intrinsic attributes of the flora related to biomechanical, ecological and behavioral knowledge of insect feeding patterns (Labandeira, 2002a). 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). These features can be grouped into four criteria. First is the presence of thick upraised rims of reaction tissue, such as parenchymatous callus, that are produced by the host plant and occur on tissues that have been consumed or otherwise modified 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 on foliage include veinal stringers left by the inability of insect mouthparts to incompletely ingest physically resistant vascular tissue (Keen, 1952; Weintraub et al., 1994), contiguous cuspsules formed along the cut margin within larger cuspsate excisions

Table 1

Total and herbivorized surface area and percentage removal expressed as species and bulk values for the Coprolite Bone Bed, from the Early Permian of Texas

Foliar taxon (abundance ranked)	Number of specimens	Specimens examined of total number (%)	Herbivory per species from surface area ^a					Herbivory frequency/ species ^a	
			Surface area examined of total number (%)	Total surface area (cm ²)	Herbivorized surface area (cm ²)	Proportion of total herbivorized leaves (%) ^b	Herbivory index (%) ^c	Number of herbivorized leaves	Proportion of herbivorized leaves (%) ^d
<i>Autunia</i> cf. <i>conferta</i>	335	56.02	49.02	2420.34	10.32	83.16	0.426	85	91.40
<i>Cordaites</i> sp.	82	13.71	28.14	1389.66	0.43	3.46	0.031	2	2.15
<i>Walchia</i> <i>piniformis</i>	77	12.88	7.72	381.30	0.00	0.00	0	0	0
<i>Russellites</i> <i>taeniata</i>	69	11.54	13.47	665.12	0.02	0.16	0.003 ^e	1	1.08
<i>Odontopteris</i> cf. <i>lingulata</i> ^f	21	3.51	0.98	49.52	1.64	13.22	3.312	5	5.38
<i>Pecopteris</i> <i>hemitelioides</i>	13	2.17	0.62	30.38	0.00	0.00	0	0	0
<i>Annularia</i> sp.	1	0.17	0.05	1.53	0.00	0.00	0	0	0
Totals/ percent sums:	598	100.00	100.00	4937.84	12.41	100.00	0.251	93	100.01

^a External foliage feeding only; galling (4 occurrences) were excluded.

^b From surface-area data in column to immediate left; see Fig. 3-1 for graphical display.

^c Herbivory index = average herbivorized area per leaf species ÷ average total area per leaf species × 100; see Fig. 3-3 for graphical display.

^d From frequency data in column to immediate left; see Fig. 3-2 for graphical display.

^e Indicative of a miniscule amount of herbivory.

^f Another seed fern may be included in this total, possibly *Neuropteris ovata*.

attributable to the trajectory of insect head movement and mouthpart action during feeding (Gangwere, 1966; Kazakova, 1985), and necrotic tissue flaps (Araya et al., 2000). 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). Last 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).

After the distinction of herbivory from detritivory or physically-induced battering, the spectrum of insect-mediated damage was categorized into four major types of insect folivory (Greenfest and Labandeira, 1997) before being further subdivided into a system of explicitly-defined, discrete damage types (Wilf and Labandeira, 1999; Labandeira et al., 2002; Labandeira, 2006b). The major types of leaf damage are (1) margin feeding, (2) hole feeding, and (3) skeletonization, all types of external foliage feeding, and (4) galling. Leaf mining was initially thought to occur, although subsequent evidence has made this assignment highly unlikely.

Of the specimens collected at CBB, about 70% of the total (598) were examined as part of this study. These specimens were the most determinable material based on adequate or better preservation and did not exceed visually a minimum size of about 0.25 cm². Seven distinct foliar morphotypes were recognized among the examined specimens, and all specimens were assigned to a known species or plant morphotype.

3.2. Quantitative analyses

Two types of calculation, used in studies of Modern herbivory were applied to the CBB flora: First was the percentage of the surface area of foliar elements that were removed by herbivores as a fraction of the total (unherbivorized+herbivorized) surface area (Landsberg, 1989; Williams and Abbott, 1991), whereby a foliar element is defined as any planated, broad, photosynthetic structure with measurable surface area, including bracts, scales, pinnules, leaves, coniferous needles, or sphenopsid stems. Second was the determination of the proportion of foliar elements that displayed any indication of herbivory, expressed as a percentage of the total number of foliar elements (Schmidt and Zotz,

2000). Both indices were expressed as values for each measured host plant species as well as for the bulk flora (see Mazia et al., 2004, for a modern example).

For image capture of foliar surface areas, each specimen was initially digitized using a Panasonic WV-GP410 camera attached to a 1:3.5 to 1:3.8 24–28 mm wide zoom lens. After image capture, the outlines of each foliar element and their insect-damaged zones, if any, were traced using Adobe *Photoshop*. A conservative approach was taken, as in a previous study (Beck and Labandeira, 1998), whereby foliar element silhouettes had to be justified anatomically or estimated based on previous knowledge of leaf shape outline and morphological variability (e.g., Adami-Rodrigues et al., 2004a, Fig. 3-3). Areas encompassed by total foliar and insect-herbivorized outlines were calculated by *Image*, a public domain soft package provided by the National Institutes of Health. These data subsequently were entered into an *Excel* spreadsheet for statistical analyses. In similar fashion to the field collection strategy, every foliar element with a minimum level of preservation and greater in size than approximately 0.25 cm² was used in this study. These procedures were designed to eliminate as much investigator bias as possible.

4. Results

4.1. Patterns of herbivory

An assessment of the CBB flora was made based on total leaf-surface area. The total foliar surface area examined was 4937.84 cm². Specimens ranged in size from 0.20 cm² to 134.83 cm². When partitioned by taxon (Table 1), the pteridophytes *Annularia* Sternberg sp. and *Pecopteris hemitelioides* (Brongniart), constituted less than 1% of the examined material. Peltaspermalean foliage, *Autunia* cf. *conferta*, amounted to almost half (49.02%), the cordaitalean foliage, *Cordaites* sp., somewhat more than a quarter (28.14%), and the remaining seed plants, a conifer, a cycad, and one (or possibly two) pteridosperms, comprised somewhat less than a quarter (22.17%) of the total foliar surface area (Table 1). Four of the seven taxa showed evidence of external foliage feeding in the form of margin feeding, hole feeding or skeletonization. Of the total herbivorized surface area of 12.41 cm², 10.32 cm² (83.16%) was attributed to *A. cf. conferta*; the medullosan *Odontopteris* cf. *lingulata* had 1.64 cm² (13.22%); the cordaitalean *Cordaites* sp. 0.43 cm² (3.46%); and the cycadophyte *Russellites taeniata* Mamay (1968) 0.02 cm² (0.16%) (Fig. 3-1). Four galls were recorded for *A. cf. conferta* and the conifer *Walchia piniformis* (Sternberg) Clement-Westerhof.

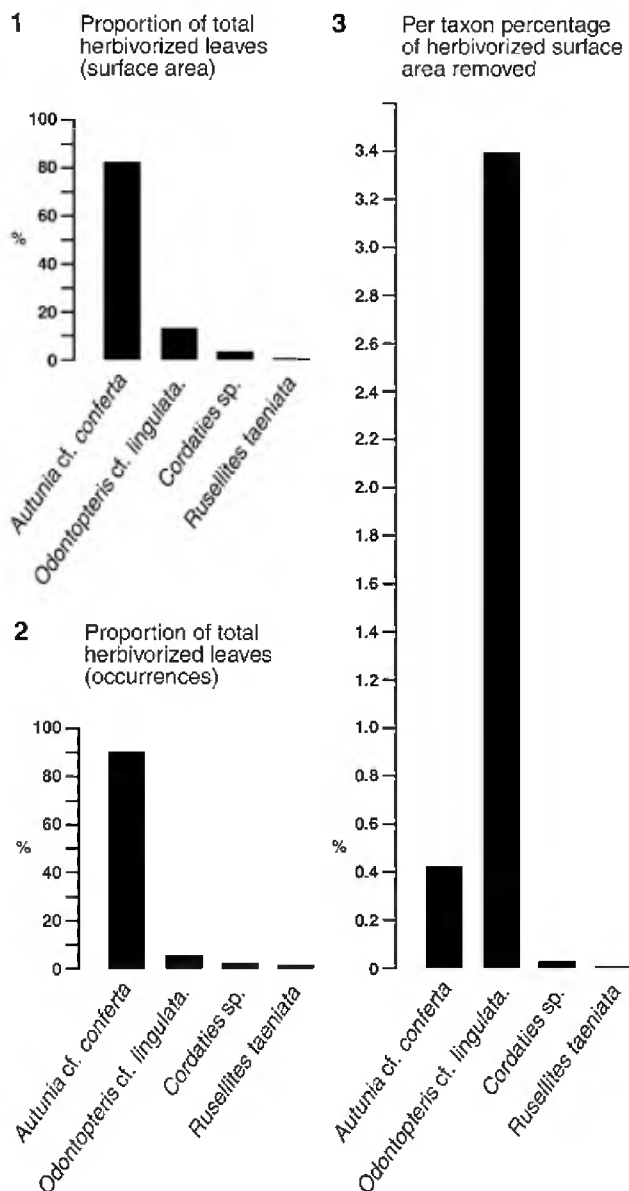


Fig. 3. Intensity of herbivory at the Coprolite Bone Bed site for the only four host plant taxa exhibiting insect-mediated damage. The measures are: (1), percentage frequency distribution for surface-area removal of all herbivorized leaves; (2), percentage frequency distribution of incidence of attack for all herbivorized leaves; and (3), Herbivory index. Note that 3.1 and 3.2 are frequency data whereas 3.3 are per taxon values.

Of the specimens that were examined, 93 (15.55%) exhibited signs of insect-mediated herbivory (Table 1). There were 137 distinct instances of herbivory observed; some specimens showed the presence of two functional feeding groups, typically margin and hole feeding, and one specimen exhibited margin feeding, skeletonization, and a gall. These presence–absence data indicated a frequency of herbivore attack of 91.40% (85/93) for *A. cf. conferta*, 5.38% (2/93) for *O. cf. lingulata*, 2.15% (2/93) for *Cordaites sp.*, and 1.08% (1/93) for *R. taeniata*

(Fig. 3-2). These trends were reversed for the two most herbivorized taxa, when the amount of foliar material removed from each of the four herbivorized taxa was considered on a percentage basis, expressed as the average herbivorized area per leaf species divided by the average total area for the same leaf species, multiplied by 100 (Beck and Labandeira, 1998). This measure, the herbivory index, resulted in a value for 0.426% for *A. cf. conferta*, but an almost eightfold increase to 3.312% for *O. cf. lingulata*, a considerably more herbivorized but less abundant species (Fig. 3-3). The remaining two plant hosts, 0.031% for *Cordaites sp.* and 0.003% for *R. taeniata*, possessed insignificant quantities of insect damage (Fig. 3-3).

For the entire CBB flora, the four distinct functional feeding groups had the following occurrences, sometimes as multiple presences per leaf (Table 2): margin feeding (96 occurrences, 70.07%), hole feeding (33 occurrences, 24.09%), and relatively rare skeletonization (4 occurrences, 2.92%) and galling (4 occurrences, 2.92%). The four instances of galling were deemed highly probable, based on observed structure and the occurrence of galls in other Pennsylvanian and Permian floras (Florin, 1945; van Amerom, 1973; Labandeira and Phillips, 1996b; Zherikhin, 2002a). No examples of leaf mining were detected based on any diagnostic features (see Hering, 1951).

Likely insect culprits for the observed herbivory are best preserved in the somewhat younger, early Artinskian (~284 Ma), Wellington Formation at Elmo, in Dickinson County, Kansas (Beckmeyer, 2000). This deposit has yielded about 195 species of insects from 53 families. Body fossils from this site include phytophagous and palynivorous taxa assigned to the Palaeodictyopteroidea, Orthoptera, Grylloblattida, “Protorthoptera” and “Hypoperlida” (both paraphyletic groups), Hemiptera, Miomoptera and Glosselytrodea (Zherikhin, 2002b). These clades and groups of insects have mandibulate (chewing) and piercing-and-sucking mouthparts consistent with the spectrum of herbivory at CBB. However, greater

Table 2

Occurrence of herbivory by functional feeding group from the Coprolite Bone Bed flora, of the Early Permian of Texas

Functional feeding subgroup	Number of occurrences	Proportion of total herbivory (%)
Margin feeding	96	70.07
Hole feeding	33	24.09
Skeletonization	4	2.92
Galling	4	2.92
	137	100.00

taxonomic specification of insect culprits will require more detailed microscopic analyses of mouthpart structure and affected plant tissues.

4.2. Types of damage

Ten types of insect-mediated herbivory are documented on foliage from the CBB site, based on previously published categorization of damage types (DTs) from Permian to Eocene deposits (Beck and Labandeira, 1998; Wilf and Labandeira, 1999; Labandeira, 2002b; Labandeira et al., 2002). By reference to this DT system, only two functional feeding groups are present at CBB, extensive external foliage feeding and rare galling. Representing these two functional feeding groups are four types of margin feeding (DTs 12, 13, 14 and 15), three types of hole feeding (DTs 2, 3 and 4), one type of skeletonization (DT17), and two types of galls (DTs 85 and 121). The greatest diversity of herbivory occurs on the highly targeted *A. cf. conferta*, a common peltaspermalean taxon from the Lower Permian of Euramerica (Kerp, 1988, 1996). This taxon hosts 6 of the 8 types of external foliage feeding (Figs. 4-6 and 8) and one type of galling (Figs. 6-6, 7 and 8-8). No evidence for fungal colonization of leaf surfaces (Rankin, 1923; Pirone, 1978) was evident. The damage types at CBB, described below, have been informally mentioned in the entomological literature (Coulson and Witter, 1984; de la Cruz and Dirzo, 1987), with precise definitions provided below. Additional documentation of these damage types (DTs) will be formally upgraded within a systematic ichnotaxonomic context (see Goldring et al., 1997) in a forthcoming contribution.

4.2.1. Margin feeding (DT12, DT13, DT14, DT15)

Margin feeding consists of cusped excisions of foliar tissue along pinnule margins ranging from 0.2 to 0.8 cm with indication of a highly developed rim of callus or other reaction tissue. In some instances a delicate, zigzag margin indicates the presence of veins resistant to insect chewing (Fig. 5-3 and -8), which are sometimes prolonged into longer veinal stringers (Fig. 4-9). Margin feeding at the CBB site is subdivided into four damage types. DT12 is the most common mode and consists of excisions that are uniformly cusped, amounting to 180° or less of semicircular arc. There is no indication of subordinate cusps within the larger cusps that would indicate feeding patterns similar to some modern orthopterans (Gangwere, 1966; Kazakova, 1985). The less common DT13 is a margin-feeding damage type whereby the pinnule apex to as much as half of the distal pinnule is removed, typically by an approximately

transverse excision. This pattern can occur on a single (Fig. 4-3) or on multiple pinnules of one pinna (Figs. 4-1, 2 and 5-4). The rarely occurring DT14 is characterized by lateral margin feeding that extends to a midvein, midrib or other major vascular structure defining a pinnule axis. This type of margin feeding frequently occurs on the terminal medial pinnule of a pinna (Fig. 5-6 and 7). Also rare is DT15, or trenched margin feeding, in which the feeding trace is deeply notched into the leaf margin. Examples of this damage type occur on *Odonopteris cf. lingulata* (Fig. 5-11 and 12) and *Autunia cf. conferta* (Fig. 7-7).

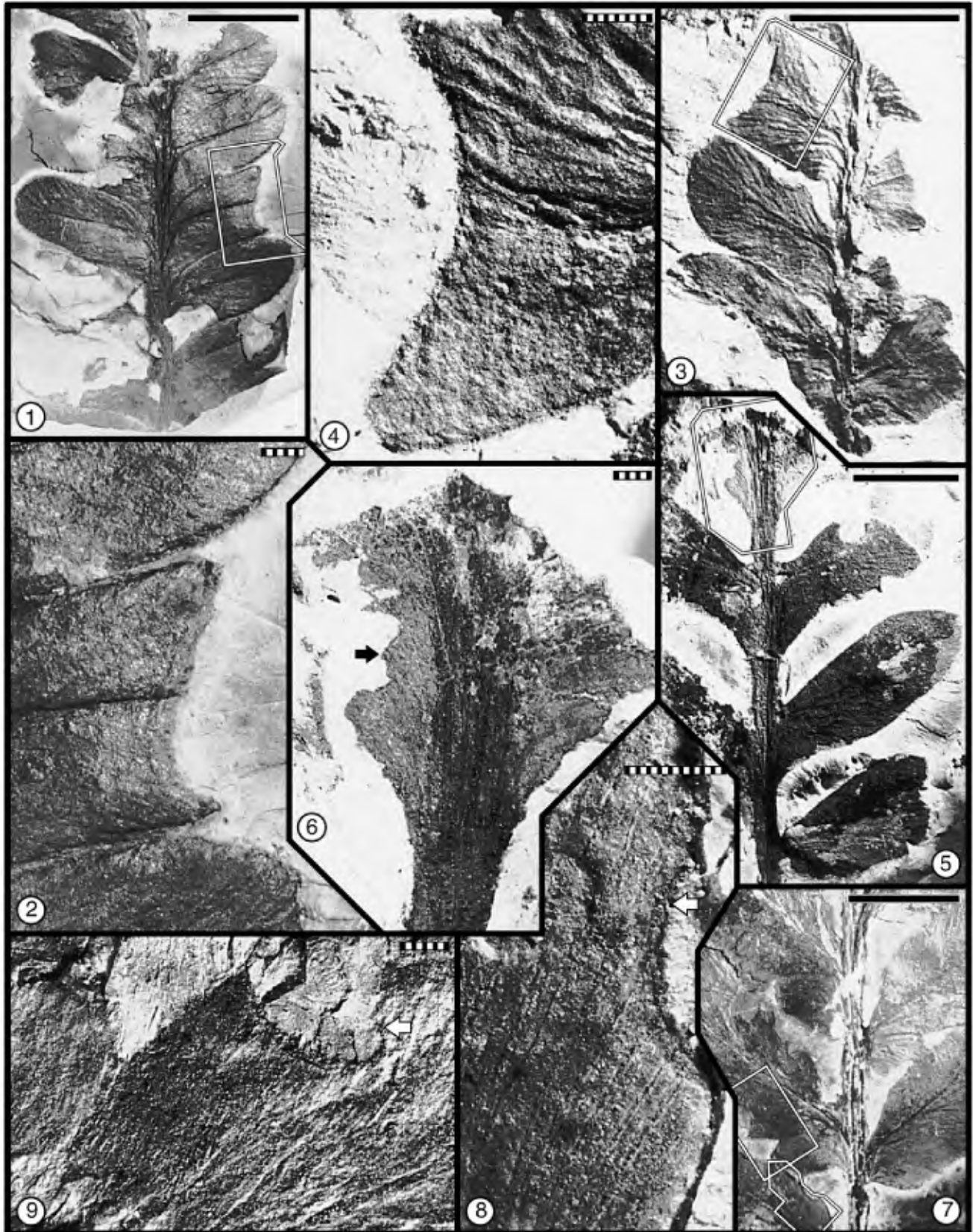
USNM figured specimens: Coprolite Bone Bed (USNM40026). For DT12: Figs. 4-7, 8, 9; 5-1, 3, 6, 7, 8, 9, 10; 6-5; 8-1 and 3. For DT13: Figs. 4-1, 4-1, 2, 3, 4; 5-4, 5; 8-2 and 4. For DT14: Fig. 4-5 and 6. For DT15: Figs. 5-11, 12 and 8-7.

Plant hosts: Peltaspermales: *Autunia cf. conferta*; Medullosales: *Odonopteris cf. lingulata*.

Remarks and Paleozoic distribution: Margin feeding is the most extensively documented plant-arthropod feeding trace in terrestrial Paleozoic compression deposits (Labandeira, 2006b) and is overwhelmingly dominant at CBB. The only extensive margin feeding in Permian Euramerica is on megaphyllous “gigantopterid” taxa of pteridosperm affinities from the Taint (Artinskian) and the South Ash Pasture (Roadian) localities (Beck and Labandeira, 1998; DiMichele et al., 2004). Extant-margin-feeding damage on filicalean ferns, including cusped excisions along the margin and truncation of pinnule termini (Beer, 1955; Welke, 1959; Balick et al., 1978; Floyd, 1993), resembles very closely that of the CBB pteridosperms. Outside of these three Texan localities, Permian occurrences of margin feeding are mostly confined to the Gondwanan Realm (Labandeira, 2006a,b). Margin feeding has been documented on glossopterid dominated floras, almost all of it on species of *Glossopteris* and *Gangamopteris*, from the Paraná Basin of southern Brazil (Adami-Rodrigues and Iannuzzi, 2001; Adami-Rodrigues et al., 2004a), the Karoo Basin of South Africa (Plumstead, 1963; van Amerom, 1966), the Rajmahal and Kashmir Basins of northern India (Chaudhan et al., 1985; Srivastava, 1987) and the Bowen and Sydney Basins of Australia (McLoughlin, 1994; Holmes, 1995). By contrast, there are very few studies of margin feeding in the Cathaysian Realm, although extensive margin feeding was documented on megaphylls of a true gigantopterid from the Kungurian–Roadian age Shihhotse Formation, of Shanxi Province, China (Glasspool et al., 2003). The Cathaysian damage patterns are reminiscent of those on

morphologically similar “gigantopterid” foliage from the Taint locality (Beck and Labandeira, 1998). Cusped margin feeding on *Supaia shanxiensis* Wang,

a probable peltasperm (DiMichele et al., 2005), has been illustrated from the same region but higher in the stratigraphic section by Wang (1997).



4.2.2. Hole feeding (DT1, DT2, DT3, DT4)

Hole feeding is the complete consumption of all foliar tissues within a circumscribed region of a leaf, resulting in circular to polylobate surface patterns that range from about 1 mm to 5 mm (or more) in longest dimension, surrounded by apparent to pronounced reaction rims. Damage types at CBB within this general category are DT1, DT2, DT3 and DT4, which are defined by size and shape. DT1 consists of round, elliptical or polylobate holes up to 1 mm in maximum dimension (Fig. 6-1 and 2). DT2 consists of round to elliptical holes from 1 mm to 5 mm in maximum dimension (Fig. 8-5). DT3 consists of polylobate holes from 1 mm to 5 mm (Fig. 5-1 and 2). DT4 consists of round to elliptical holes greater than 5 mm in maximum dimension (Figs. 6-3, 4 and 8-9). The most common hole size and shape are DT2 and DT3, which occur almost exclusively on *A. cf. conferta*.

USNM figured specimens: Coprolite Bone Bed (USNM40026). For DT1: Fig. 6-1 and 2. For DT2: Fig. 8-5. For DT3: Fig. 5-1 and 2. For DT4: Figs. 6-3, 4 and 8-9.

Plant hosts: Peltaspermales: *Autunia cf. conferta*; Cordaitaceae: *Cordaites* sp.

Remarks and Paleozoic distribution: When compared to margin feeding, hole feeding has an intermittent and occasional record throughout the later Pennsylvanian and Permian. The earliest occurrence is rare hole feeding present on *Macroneuropteris scheuchzeri* from the late Moscovian of the Illinois Basin, USA (Trout et al., 2000; Labandeira, pers. observ.). An early example of hole feeding (DT3) occurs on the ginkgoalean *Ginkgoites eximia* (Feruglio) Cúneo from the Lower Permian Río Genoa Formation of Chubut Province, Argentina (Cúneo, 1987). Beck and Labandeira (1998) documented extensive hole feeding on three species of megaphyllous “gigantopterid” from Taint: *Zeilleropteris wattii* Mamay, *Gigantopteridium americanum* White, and *Cathaysiopteris yochelsoni* Mamay. This extensive hole-feeding damage consisted of large, intercostal, circular to polylobate excisions that often parallel or otherwise avoid the secondary (but not intercalary) venation and is assignable to DT78. In addition, circular to polylobate holes ranging from DT1 to DT5, in more random foliar contexts, were present. From somewhat

younger Lower to Middle Permian boundary deposits of China, hole feeding (DT1, DT2) was documented on *Gigantoclea lagrelii* (Halle) Koidzumi and *G. hallei* (Asama) of Shanxi Province (Glasspool et al., 2003). Hole-feeding damage on *Autunia cf. conferta* at CBB closely resembles that of the aspleniaceous fern *Asplenium monanthes* L. (Balick et al., 1978).

4.2.3. Skeletonization (DT17)

Skeletonization comprises small to medium sized external feeding that is uncommonly more than 0.8 cm in longest dimension, whereby interveinal tissue is completely removed with retention of the primary or secondary venation, and the resulting circular to polylobate feeding damage is encompassed by a distinctive reaction rim. Only one type of rare skeletonization is represented at CBB, which is DT17, or generalized skeletonization organized into removed ovoidal to polylobate areas with a distinctive bordering reaction rim. This indicates that the leaf bore live tissue that responded histologically to herbivory. At CBB this type of skeletonization typically occurs at the base of the pinnule adjacent to its attachment to the pinna rachis (Figs. 7-1 and 8-6), revealing a fasciculate and dichotomous venation. Skeletonization at CBB is assigned to DT17 because of distinctive reaction rims that are indicative of true herbivory and is distinguished from DT16, which lacks significant response tissue and may be detritivorous in origin.

USNM figured specimens: Coprolite Bone Bed (USNM40026). For DT17: Figs. 6-1 and 8-6.

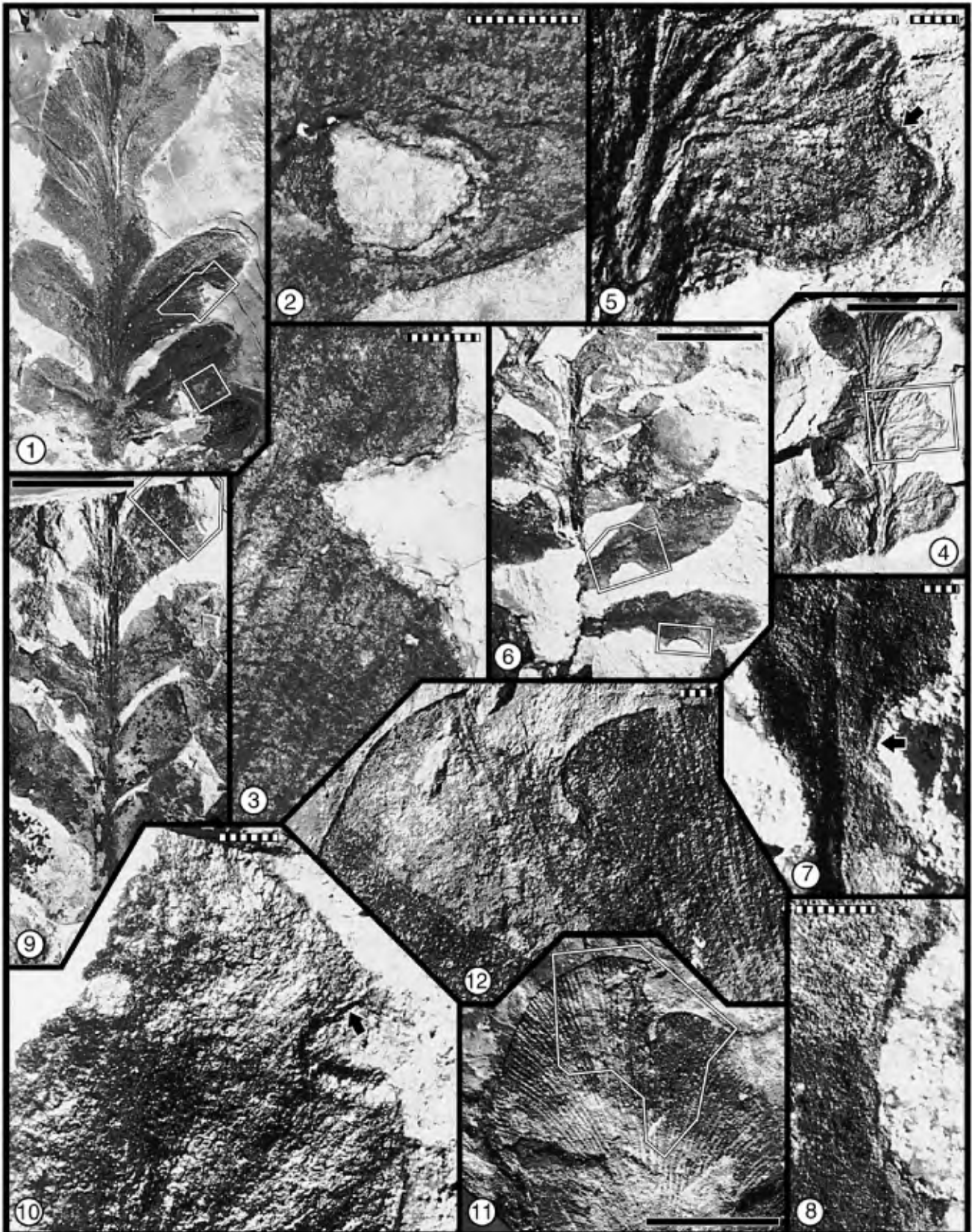
Plant hosts: Peltaspermales: *Autunia cf. conferta*; Noeggerathiaceae: *Russellites taeniata*.

Remarks and Paleozoic distribution: Evidence for Paleozoic skeletonization of leaves is very sparse. Examples of skeletonization have not been published for Pennsylvanian or earlier floras, and currently documentation is present for only three Permian localities: the CBB (the earliest known occurrence), the Sakmarian or Artinskian Morro do Papaléo Mine site in Rio Grande do Sul, Brazil, and the Taint site (Beck and Labandeira, 1998; Adami-Rodrigues et al., 2004b). The Brazilian site consists of skeletonized mesophyll and megaphyll leaves of the glossopterid taxa *Glossopteris communis* and *G. occidentalis* White,

Fig. 4. Margin feeding insect damage (DT12) on the peltaspermalean *Autunia cf. conferta* (Sternberg) Kerp (1–9), the dominant type of feeding at Coprolite Bone Bed. At 1 is a specimen of *A. cf. conferta* (USNM501037) showing tissue from a pinnule apex removed by herbivory, enlarged at 2. Similarly at 3 (USNM501033) is a pinnule apex with a herbivorized apex, magnified at 4; another example is provided at 5 (USNM501032), enlarged at 6 where a reaction rim (arrow) is present and foliar tissue is removed almost to the pseudomidveins. At 7 (USNM501031) are several examples of cusped margin feeding, enlargements of which are provided in 8 and 9 that show a ragged reaction rim edges (arrows) indicative of short veinal stringers. Scale bars at upper-right: solid, 1.0 cm; dashed, 0.1 cm.

whereas the Taint site exhibits skeletonization on somewhat larger leaves, mostly *Gigantopteridium americanum* but including *Z. wattii* and *C. yochelsoni*.

Interestingly, [Glasspool and colleagues \(2003\)](#) examined gigantopterid leaves of similar foliar architecture and large size to those of Taint, from a younger



Artinskian to Kungurian site in China, but presented no evidence of skeletonization.

4.2.4. Gallling (DT85, DT121)

Galls are atypical spheroidal to ellipsoidal teratological structures with one or more internal chambers, ranging in longest dimension from 1 to 100 mm that contain internal nutritive and outer protective (often sclerenchymatous) tissues; they occur on any plant organ and are produced by mites or insects (Scott et al., 1994). Two quite different types of galls are present at CBB. One is a gall that occurs on and parallel to the midveinal region of *Autunia* cf. *conferta* (Figs. 6-6, 7 and 8-8), about 1.5×4.5 mm in dimension (DT85). A second distinctive gall occurs on the conifer *Walchia piniformis* (Figs. 6-8, 9 and 8-10), basifixed on a leaf-bearing secondary branchlet, and consisting of a large conical structure approximately 4×9 mm in dimension, apparently bearing an apical, beak-like structure (DT121).

USNM figured specimens: Coprolite Bone Bed (USNM40026). For DT85: Figs. 6-6, 7 and 8-8. For DT121: Figs. 6-8, 9 and 8-10.

Plant hosts: Peltaspermales: *Autunia* cf. *conferta* (DT85); Walchiaceae: *Walchia piniformis* (DT121).

Remarks and Paleozoic distribution: The ichnofossil record of galling is sporadic throughout the Pennsylvanian and Permian of Euramerica (Labandeira, 1998a, 2002a). The most surprising feature of this gall record is the diversity of taxa, organs, and tissues that are galled, as well as evidence of galler monospecificity for particular host-plant species and tissues. Most occurrences of Pennsylvanian and Permian galls consist of morphologically distinct specimens. Inferred culprits include mites, hemipteroid groups and basal holometabolans, although taxonomic specification is difficult. The earliest known gall is probably *Acrobullillites* Amerom, of which several ichnospecies have been described on the stems and fructifications on calamitalean and equisetalean taxa (van Amerom, 1973). One type of these unusually swollen expansions was originally described as the fructification *Paracalamostachys spadiciformis* (Thomas, 1969) and is similar to certain modern galls on horsetails (Mimeur, 1949). By contrast, Late Pennsylvanian permineralized holometabolans

galls from the Illinois Basin, assigned to the ichnogenus *Pteriditorichnos* (Labandeira and Phillips, 1996b, 2002), are three-dimensionally and anatomically preserved features within the rhachises of *Psaronius chasei* tree ferns. Permian occurrences are similarly spotty. The Lower Permian of Texas contains an additional deposit where galls are probably present, although like *Acrobullillites*, they were initially considered as unusual fructifications. These structures are relatively large (2.5 to 9.0 mm long by 2.0 to 5.0 mm wide), ellipsoidal to irregularly shaped, minimally thickened but well delineated, extend to the leaf margin, and parallel to the secondary venation of a pinnately veined, neuropteroid leaf (Mamay, 1960). They were assigned to *Padgettia readi* Mamay (1960) and occur on medullosan foliage indistinguishable from a few species of *Neuropteris*. These features are more parsimoniously considered a blister or pit gall, particularly since an alternative interpretation would be an irregularly spaced, variably shaped “seed” embedded in foliar tissue that is unknown for any Permian pteridosperm taxa. By contrast, the only other galls from this period are from Late Permian deposits of Mamal, Kashmir, India. These structures are pouch-like, sessile, ostiolate galls on *Glossopteris taeniopteroides* Feistmantel from 0.3 to 0.6 cm in diameter (Pant and Srivastava, 1995). Similar ostiolate galls from 0.2 to 0.4 mm in diameter also occur on *G. browniana* Brongniart at the Murulidih Colliery from the nearby Mohuda Basin in Bihar (Banerjee and Bera, 1998). This diversity of late Paleozoic gall morphologies and of their host plants and galled tissues provides additional evidence against an angiosperm-only, Cretaceous origin of the galler life-habit (Raman et al., 2005). Evidence now includes the presence of early Mesozoic galls (Ash, 1997), also supporting an origin of the galling habit occurring deep within the Late Paleozoic.

The gall assigned to DT85 plausibly could be considered an oviposition scar of a Paleozoic paleopterous insect, which are known from the Pennsylvanian and Early Permian of other Euramerican and Gondwanan floras (Adami-Rodrigues et al., 2004b; Béthoux et al., 2004) and throughout the post-Mississippian Phanerozoic (Hellmund and Hellmund, 2002). However

Fig. 5. Hole feeding and margin feeding on the peltaspermalean *Autunia* cf. *conferta* (Sternberg) Kerp (1–10) and a terminal pinnule of the medullosan *Odontopteris* cf. *lingulata* (Goeppert) Schimper (11). Hole- and margin feeding on *A.* cf. *conferta* is at 1 (USNM501041), of which a hole (DT2) is enlarged at 2 with a distinctive rim of reaction tissue, and margin feeding (DT12) enlarged at 3, also showing an edge with reaction tissue. Margin feeding occurs on a pinnule apex (DT13) at 4 (USNM501019), enlarged at 5 with an arrow designating a reaction rim. At 6 is margin feeding (DT12) with multiple cusplules (USNM501017), examples of which are enlarged at 7 (arrow indicating a reaction rim) and 8. Another example of margin feeding (DT12) is provided at 9 (USNM501020), consisting of small cusplules, some of which are enlarged at 10 with reaction rim indicated (arrow). Trenched margin feeding (DT15) occurs at 11 (USNM501016), enlarged at 12, showing an involuted feeding pattern. Scale bars at upper-right: solid, 1.0 cm; dashed, 0.1 cm.



Fig. 6. Hole feeding, margin feeding and galling on three taxa of seed plants from the Coprolite Bone Bed flora. Hole feeding (DT1) is present on the peltaspermalean *Autunia* cf. *conferta* (Sternberg) Kerp at 1 (USNM501026), enlarged in 2. An example of hole feeding (DT4) is on *Russellites taeniata* at 3 (NMNH501002), magnified in 4, with a reaction rim indicated (arrow). At 5 is an example of margin feeding (DT12) on a leaf of *A.* cf. *conferta* (USNM501025). At 6 is a midveinal (“midrib”) gall (DT85) on *A.* cf. *conferta*, enlarged in 7 (NMNH501018). A second type of gall (DT121) occurs at 8 (NMNH501014), on a twig of *Walchia piniformis*, enlarged in 9. Scale bars at upper-right: solid, 1.0 cm; dashed, 0.1 cm.

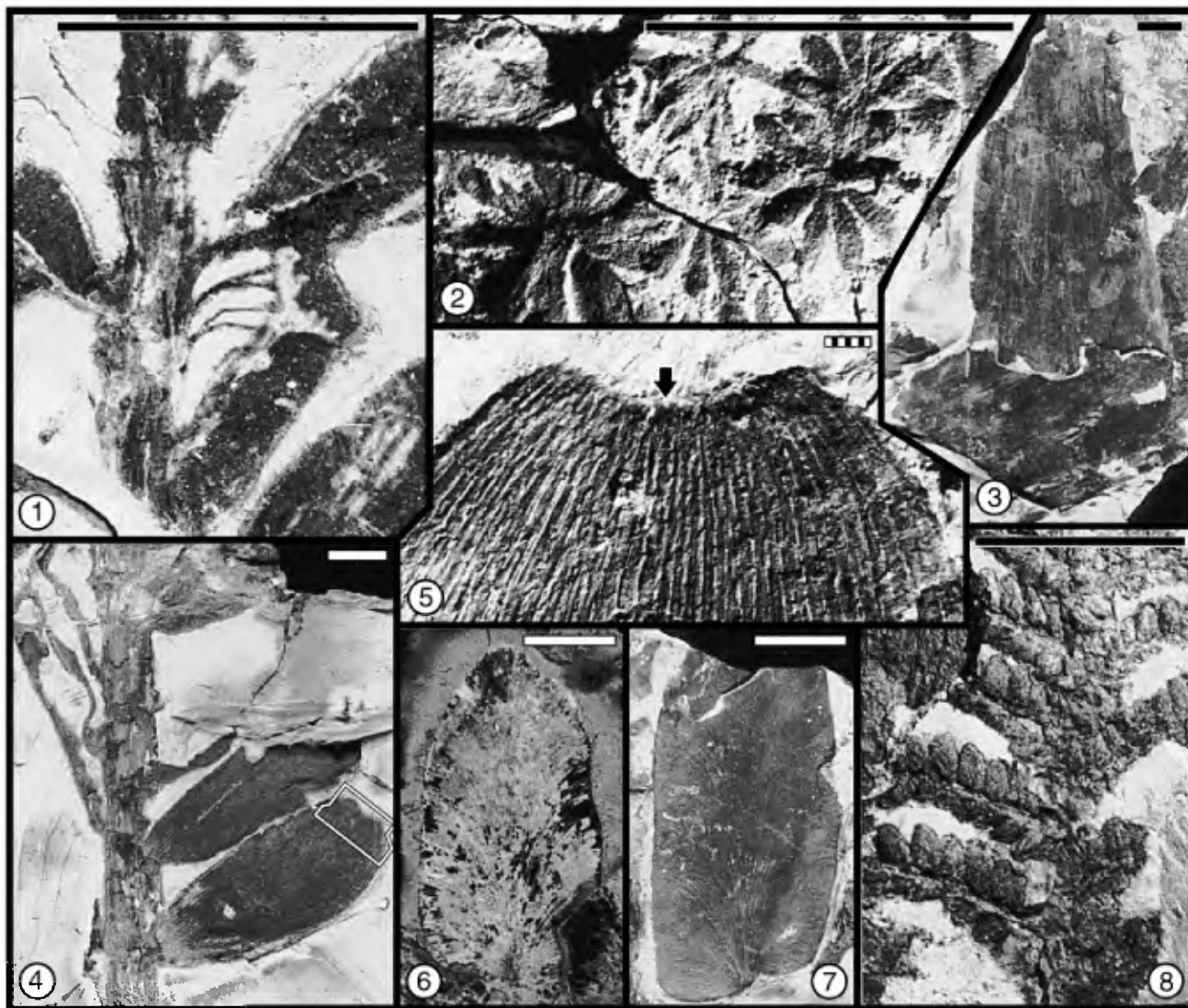


Fig. 7. The skeletonization (DT17) of the cycadophyte *Russellites taeniata* is provided at 1 (USNM501023), whereas the other specimens represent unherbivorized foliar elements from the Coprolite Bone Bed flora. Sphenopsid foliage of *Annularia* sp. is at 2 (USNM501024); two *Cordaites* sp. leaves are depicted at 3 (USNM501036). An example of foliar anatomical structure that may be mistaken for herbivory is *Russellites taeniata* at 4 (USNM501038), magnified (arrow) at 5. Two examples of the medullosan *Odontopteris* cf. *lingulata* (Sternberg) Clement-Westerhof are provided at 6 (USNM501042) and 7 (USNM501033). An example of marattialean fern foliage, *Pecopteris hemitelioides* (Brongniart), is displayed at 8 (USNM501015). Scale bars at upper-right: solid, 1.0 cm; dashed, 0.1 cm.

the structure on *A. cf. conferta* (Figs. 6-6, 7 and 8-8) lacks a bordering and confined reaction-tissue scar that typifies known fossil occurrences of insect oviposition. Instead, it presents a rounded, ellipsoidal profile that is consistent with a gall in which connections to nutrient-bearing vasculature are important (Shorthouse and Rohfritsch, 1992). This gall most closely resembles a petiole gall from an unknown galler on the extant marattialean fern *Archangiopteris henryi* from Yunnan, China (Christ and Giesenhagen, 1988). Other extant galls less structurally similar to the gall on *Autunia* include blister or pit galls often made by gall midges (Dreger-Jauffret and Shorthouse, 1992) (Diptera: Ceci-

domyiidae), a clade of insects not known to occur during the Paleozoic or early Mesozoic.

By contrast, the gall on *W. piniformis* (DT121) presents a very different morphology and host plant from that of above (Figs. 6-8, 9 and 8-10). It is characterized as having a bulbous base and a beaklike apex, possibly with narrow, needlelike structures emerging from the distal half of the gall. The gall evidently is attached basally to a branchlet, adjacent to typical needle-like leaves of *Walchia*. A gall of similar size and form was mentioned by Florin (1945; Plate 14, Figs. 19 and 21), also on *W. piniformis* from approximately contemporaneous strata of the Lower

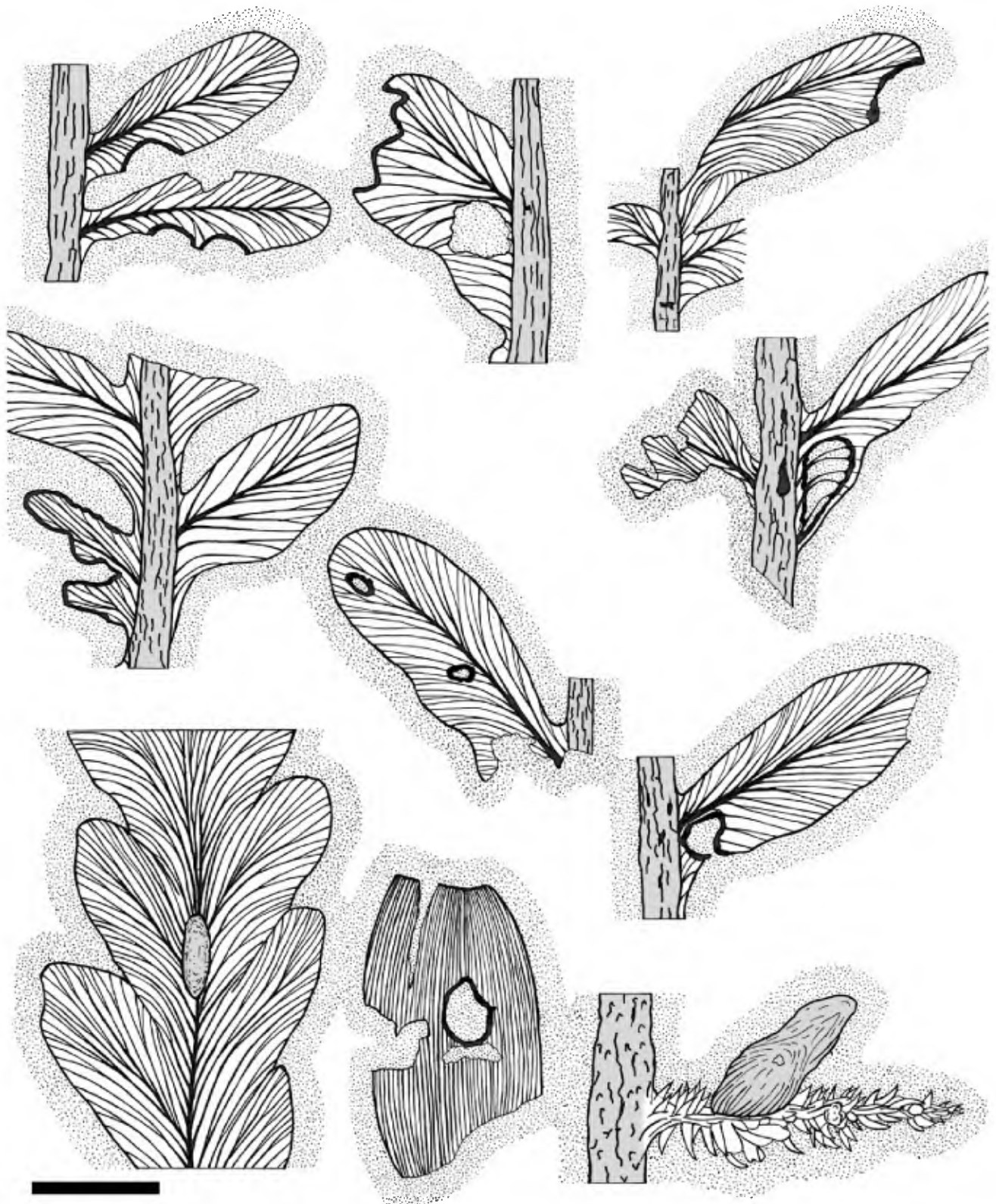


Fig. 8. Representative types of herbivory at the Coprolite Bone Bed locality. For host plant *Autunia* cf. *conferta*, margin feeding (DT12) occurs on the lateral aspect of pinnules at 1 (USNM501017) and 3 (USNM501035); margin feeding on the pinnule apex (DT13) is shown at 2 (USNM501039) and 4 (USNM501027); trenched margin feeding (DT15) is present at 7 (USNM501030); small hole feeding (DT1) is at 5 (USNM501021); skeletonization (DT17) is depicted at 6 (USNM501023); and a midrib gall (DT85) is present at 8 (USNM501018). Hole feeding (DT4) is present on *Russellites taeniata* at 9 (USNM501022), and one of the few galls (DT121) is shown at 10 on *Walchia piniformis* (Sternberg) Clement-Westerhof (USNM501014). All specimens are camera lucida drawings at the same scale. Scale bar at lower left: 1.0 cm.

Rotliegend in Saxony, Germany. This Rotliegend gall was noted by Zherikhin (2002a), who was uncertain as to its gall status. However, it does not resemble generic mite galls, which typically are lobate, irregularly shaped, internally numerous multichambered, and often pedicellate (Docters van Leeuwen, 1910; Rübsaamen, 1911; Occhioni, 1979). Both the CBB and Rotliegend galls occur on a conspecific host, have structures reminiscent of certain extant hemipteran galls on pinaceous and taxaceous conifers, such as the “pineapple gall” of *Adelges abietis* L. on *Picea excelsa* (Lamarck) (Plumb, 1953) or *Taxomyia taxi* (Inchbald) on *Taxus baccata* L. (Csóka, 1997), and include the frequent presence of exerted leaf-like structures from the distal part of the gall body (Plumb, 1953). Given the presence of hemipteroid and holometabolous insects during the Early Permian (Shcherbakov, 2000; Labandeira and Phillips, 2002), the most likely culprits are basal phytophagous clades of the basal Holometabola, or more likely the suborders Sternorrhyncha and Heteroptera of the basal Hemiptera. Sternorrhynchan or closely related hemipterans such as archescytinids, coeloscytids and pincombeids, as well as the auchenorrhynchan prosbolds, occur during the Lower Permian and were phytophagous (Shcherbakov, 2000), based on ovipositor adaptations consistent with inserting eggs into plant tissues (Becker-Migdisova, 1985) and on mouthpart structure. Most of these clades were associated with conifer floras (Shcherbakov, 2000). Additionally, the presumed ancestors of the Hemiptera, specifically certain lineages of the “Hypoperlida”, consumed gymnosperm pollen rather than pteridophyte spores, revealed by the gut contents of fossils, and thus were associated with seed plants (Krassilov and Rasnitsyn, 1997; Krassilov et al., 1999; Afonin, 2000). However, these clades are not known to have been gall producing, and such an inference is impossible to make from external body structure alone. Typical present-day galling Sternorrhyncha such as Aphidoidea, Psylloidea and Coccoidea originated during the earlier Mesozoic, based on their body-fossil records, as did the Tingidae, a gall-producing clade of the Heteroptera (Shcherbakov and Popov, 2002), and thus these extant clades are unlikely culprits.

5. Discussion

Global data on Late Pennsylvanian to Early Permian herbivory are becoming increasingly available (Labandeira, 1998a, 2002a; Zherikhin, 2002a,b; Glasspool et al., 2003; Adami-Rodrigues et al., 2004a; Labandeira, 2006b). These data, though still sparse, provide some

confidence for interpretations regarding the distribution of feeding patterns and preferences of host-plant taxa across Euramerican and Gondwanan landscapes and regions. In this context, tentative assessments can be made regarding Early Permian patterns of herbivory in the two most intensively investigated areas: Texas, USA, and southern Brazil.

5.1. Assessment of early Permian herbivory in north-central Texas

The level of insect folivory at CBB, as determined by the bulk Herbivory Index, is 0.25%. This is an exceptionally low level compared to most tropical and subtropical forests from the Recent, in which the bulk Herbivory Index ranges from 7.5 to 12.0% (Wint, 1983; Coley and Barone, 1996); although more temperate sites can approach lower values of around 2.5% (Carpenter and Cappuccino, 2005). The CBB level is also almost one-tenth that of the analogous 2.55% bulk Herbivory Index recorded for the somewhat younger Taint assemblage; a similar, taxonomically distinct, pteridosperm dominated flora in nearby Baylor County (Beck and Labandeira, 1998). In spite of the low intensity of insect herbivory at CBB, there are similarities with the results from the Taint locality, particularly the predominance of margin and hole feeding and the overwhelming targeting of pteridosperm taxa as evidenced by the high value (3.312%) for *O. cf. lingulata*. These two similarities, together with unpublished observations from other Lower Permian floras, indicate that insect herbivory from the Lower Permian of Texas was specific in both the dominant types of feeding present as well in preferences for certain host-plant taxa. As mentioned in Section 5.3, this tenfold difference of herbivory indices of localities within Texas parallels similar differences within Brazil (Adami-Rodrigues et al., 2004a). The same methodology was used in both groups of studies, suggesting considerable site-specific heterogeneity of herbivory in both regions.

The order of magnitude difference between the herbivore intensity of the Taint assemblage and that of CBB could be attributed to methodological or preservational biases. Supporting such a contention would be the presence of poorly preserved material that failed to exceed the threshold of acceptability for analysis. Thus, it is possible that a higher than average amount of insect damage was not included as data because of poor preservation, excluding an approximate visual cutoff value of 0.25 cm² that rarely included slightly smaller fragments. Also, the methodology used to quantify damaged material was conservative and could have

underestimated the amount of actual herbivory. This deficiency may have affected values for *Cordaites* sp., because of the combined features of large leaf size and fragmentary condition, possibly resulting in an underestimation of total leaf area. Nevertheless, a similar taphonomic context also existed for the Taint analysis (Beck and Labandeira, 1998), suggesting that such biases are insufficient to account for the extreme difference in total herbivory between the two floras. Additionally, an approximate order of magnitude difference also exists among four Lower Permian sites at Rio Grande do Sul, in Brazil (Table 3; Adami-Rodrigues et al., 2004a). Thus, this disparity in herbivore removal rate may represent the true nature of Lower Permian plant–insect associations in both western Euramerica (Texas) and western Gondwana (Brazil).

Studies of modern plant–insect associations have indicated that the extent and intensity of insect herbivory may vary seasonally and exhibit definite variation with respect to climate. Tropical floras typically exhibit significantly more diverse and frequent insect herbivory

than do temperate ones (MacLean and Jensen, 1985; Coley and Barone, 1996), though this probably is linked more to underlying host plant diversity in more tropical latitudes than to any finer partitioning of foliar food resources (Novotny et al., 2006). Accordingly, as the diversity of host plants (and damage types) is approximately similar for Taint and CBB, it appears that simple plant diversity does not explain the differing herbivory intensities. Species-specific differences, such as variability in the expansion period when immature leaves become vulnerable to herbivores (Aide, 1993; Moles and Westoby, 2000), provide a possible explanation for the variation in measured levels of herbivory. However, immature leaves are rare at CBB and Taint, indicating that leaf growth may have been rapid, or the production of new leaves was uncommon and seasonal, or both.

CBB is interpreted as a perennial pond deposit, while Taint is thought to represent an accumulation of time-pulsed strata in a (possibly abandoned) channel deposit marginal to a stream (Beck and Labandeira, 1998). This suggests that, given their stratal contexts, the deposits at

Table 3
A comparison of Early Permian Euramerican and Gondwanan insect herbivory

Locality	Stage ^a	Number of specimens analyzed	Total surface area (cm ²)	Herbivorized surface area (cm ²)	Surface area removed by herbivory (%)	Proportion of herbivorized leaves (%)	Most herbivorized taxon ^b
<i>Euramerica</i>							
(Texas, U.S.A.)							
Taint ^{c,d}	Arti	1346	11,526.24	293.8	2.55	31.8	<i>Zeilleropteris watti</i> (peltasperm)
Coprolite Bone Bed ^e	Sakm	598	4,937.85	12.41	0.25	14.72	<i>Autunia</i> cf. <i>conferta</i> (callipterid)
<i>Gondwana</i>							
(Rio Grande do Sul, Brazil) ^f							
Quitéria	Arti/ Kung	27	465.98	13.83	2.97	7.41	<i>Glossopteris</i> sp. (glossopterid)
Faxinal	Arti/ Kung	171	7,503.35	33.06	0.44	7.02	<i>Glossopteris</i> cf. <i>communis</i> (glossopterid) ^g
Morro do Papaléo (Stratum 4)	Sakm/ Arti	16	435.98	10.42	2.39	12.50	<i>Glossopteris</i> cf. <i>communis</i> (glossopterid)
Morro do Papaléo (Stratum 7/8)	Sakm/ Arti	138	7,885.99	19.13	0.24	9.42	<i>Cordaites hislopii</i> (cordaite)

^a Lower Permian stage abbreviations from older to younger: Sakm, Sakmarian; Arti, Artinskian; Kung, Kungurian.

^b Established by both the greatest area herbivorized and proportion of leaves with herbivory, unless otherwise specified.

^c From Beck and Labandeira (1998).

^d Some values were calculated to the nearest tenth decimal place.

^e This study.

^f From Adami-Rodrigues et al. (2004a).

^g Two other glossopterid taxa (*G. browniana*, and *G. brasiliensis*) also exhibited proportions of herbivorized leaves of 100%.

CBB are more seasonal (DiMichele et al., 2006b). However, both localities are approximately equivalent in duration and represent minimal time-averaging (see Wing and DiMichele, 1992; Behrensmeier et al., 2000). Thus, plant specimens from CBB and Taint may represent a similar temporal window of plant accumulation, emphasizing intrinsic differences in the spectrum of herbivory intensities and types at each site. Investigator-based analytic time averaging is a possibility, although the procedure for collecting specimens in the field and processing in the laboratory were virtually identical for both sites.

5.2. Comparisons to middle and late Pennsylvanian herbivory from Euramerica

During the Middle Pennsylvanian (Moscovian), there was continuation of significant earlier detritivory, typically oribatid damage within peat-forming environments, suggesting significant litter decomposition (Scott, 1977; Baxendale, 1979; Cichan and Taylor, 1982; Scott et al., 1992; Labandeira et al., 1997; Raymond et al., 2001). For herbivorous plant–arthropod associations, the Middle Pennsylvanian fossil record is characterized by isolated occurrences mostly from the British Coal Measures (Seward, 1906; Stopes, 1907; Holden, 1930), but other floras as well (Rothwell and Scott, 1983, 1988; Trout et al., 2000). Toward the end of the Middle Pennsylvanian (Moscovian) there are occasional descriptions of arthropod-mediated damage from entire floras (van Amerom, 1966; Müller, 1982; Scott and Taylor, 1983; Labandeira and Beall, 1990; Castro, 1997), conveying a sense of increased herbivory but within a dominantly detritivore ecosystem. During this time the only major plant host that bore relatively high levels of herbivory was the elongate, pinnate–fasciculate pteridosperm pinnule, *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute and Zодrow (1990), from western Euramerica (Scott and Taylor, 1983; Labandeira and Beall, 1990; Trout et al., 2000).

Following the extinctions and associated changes in vegetational patterns at the end of the Middle Pennsylvanian in Euramerica (Phillips et al., 1974; Pfefferkorn and Thomson, 1982), also indicated by the insect body-fossil record (Labandeira, 2005), a distinctive wetland ecosystem was established. The best documented flora within this Late Pennsylvanian ecosystem is from the Calhoun Coal, in which species of the marattialean tree fern *Psaronius* were the dominants, with subdominant arborescent medullosan pteridosperms. In addition, a variety of lycopsids, sphenopsids, ferns and cordaites comprised life forms ranging from pole-like swamp trees in standing water, to lianas, ground cover, and

shrubby vegetation occurring in drier sites (DiMichele and Phillips, 1996). Herbivory within this ecosystem of approximately 40 species was diverse (Labandeira, 1998b, 2001), centered on the tree fern *Psaronius* and on medullosan pteridosperms, and included external foliage feeders, piercer-and-suckers, palynivores, and galls in the crowns (Lesnikowska, 1990; Labandeira and Phillips, 1996a,b), detritivore pith and woody root-mantle borers in trunks, and root feeders within and on the ground (Labandeira and Phillips, 1996a; Labandeira et al., 1997; Labandeira, 2001; Labandeira and Phillips, 2002). Interestingly, whereas *Psaronius* had a greater richness of herbivore and detritivore functional feeding groups than *Medullosa*, evidence from an overwhelmingly greater abundance of dispersed coprolites in the matrix from the same deposit indicate that it was the *Alethopteris* foliage of *Medullosa* that was preferentially targeted and highly consumed by insect herbivores (Labandeira and Phillips, unpubl. data). By contrast palynivores overwhelmingly consumed *Florinites* Schopf cordaitalean pollen, to a lesser extent sporangia and spores of marattialean tree ferns, and very rarely pteridosperm prepollen. Focusing on the source (i.e., component) community of all dependent organisms on *Psaronius*, broadened to include the species *P. chasei* Morgan and *P. blicklei* Morgan (see Root, 1973 for a modern example), it is clear that a modern-aspect ecologic structure was established during the Late Pennsylvanian (Labandeira, 1998a), introducing a new regime of herbivory in at least some peat-wetland ecosystems within western Euramerica (see also Roßler, 2000). This was followed by the demise of the *Psaronius–Medullosa* wetland ecosystem around the Pennsylvanian–Permian boundary in Euramerica (DiMichele et al., 2005), which was replaced by environments similar to CBB, particularly in the western part of the paleocontinent. When contrasted to CBB, the Late Pennsylvanian wetland ecosystem had a greater number of functional feeding groups, more evident host-specificity, and probably greater levels of herbivory, though comparisons of permineralized and compression/impression data are difficult. It appears that the diversity, and probably the intensity, of CBB herbivory was depauperate compared to that of the Calhoun Coal.

5.3. Permian pteridosperm herbivory in biogeographical, phylogenetic and ecological context

A broad comparison of the host-plant taxa that are most intensively herbivorized in Euramerica, Gondwana and Cathaysia indicates that there was targeting of particular plant clades. In north-central Texas, “*Gigantopteris*,”

Autunia, and *Odontopteris* clearly were the most highly herbivorized taxa. By contrast, in Gondwana, a limited number of species of *Glossopteris* were preferred by insect herbivores throughout a broad geographic swath representing several depositional basins, regardless of whether the occurrences were in South America (Adami-Rodrigues et al., 2004b), South Africa (Plumstead, 1963; van Amerom, 1966), India (Srivastava, 1987), or Australia (McLoughlin, 1994; Holmes, 1995). This predilection for particular species of *Glossopteris* is best illustrated from quantitative studies in Rio Grande do Sul, Brazil, in which *G. communis* Feistmantel was the targeted taxon out of variously 4 to 6 species of glossopterid and cordaite taxa occurring in each of three sites (Adami-Rodrigues et al., 2004a; Table 3). Ongoing semiquantitative studies at the Clouston Farm locality in South Africa (Prevec and Labandeira, unpubl. data) support a similar pattern. For Cathaysia, the only significant study is by Glasspool and colleagues (2003), who demonstrated qualitatively that true gigantopterids, especially *Gigantonoclea*, had significant levels of herbivory. These data, both quantitative and qualitative, indicate that pteridosperms, in the broad taxonomic sense, were the preferred host-plant group of insect herbivores worldwide.

These disparate clades of peltasperms, “gigantopterids,” glossopterids and medullosans, each representing a distinctive lineage within the paraphyletic group of seed plants (Hilton and Bateman, 2006), apparently were prized by Pennsylvanian and Permian herbivores (Table 3); an observation earlier noticed by van Amerom and Boersma (1971) and independently observed by Labandeira (1998a). It is becoming clearer as to how these late Paleozoic pteridosperm lineages phylogenetically relate to one another, although the consensus is that no two of the four above clades are probably sister groups of each other and that they represent disparate evolutionary origins within the pteridosperm alliance (Doyle, 1998; Pryer et al., 2004; Hilton and Bateman, 2006). There may be only a broad taxonomic unity within these four clades that could represent a basis for common collective herbivory that is globally distributed. Elevated, indeed escalated, herbivory common to pteridosperms could be evidenced by the presence of a unique and collective phytochemistry (e.g., van Bergen et al., 1995) interpretable as an herbivore feeding deterrent to prized leaf tissues. Similarly, commonalities in leaf architecture and the presence of mechanical antiherbivore defenses (e.g., Schoonhoven et al., 2005) may have been present, notably the specialization of foliar trichomes (Krings and Kerp, 1999) or presence of refractory cuticles, both which have been demonstrated in a few taxa. Some Late Pennsylvanian to Early Permian

pteridosperm taxa bore foliage with long trichomes, multicellular glandular hairs, and other specialized hairs, including the peltaspermalean *Autunia conferta* (Kerp, 1996) and the medullosan *Blanziopteris praedentata* (Gothan) Krings and Kerp (1999), the latter possessing touch-sensitive specialized cells that secreted viscous exudates presumably for defense against herbivores (Krings et al., 2002). Such trichomes are important barriers to arthropod herbivory in extant plants (Levin, 1973). A different explanation for the spatiotemporally disparate prevalence of pteridosperm herbivory is the apparency hypothesis of Feeny (1976). Accordingly, the high incidence of herbivory is a consequence of earlier pteridosperm ecological dominance and elevated physical presence, or apparency, in Pennsylvanian and Permian environments sampled to date. This is consistent with the high abundance of shrubby or otherwise arborescent pteridosperms in drier habitats adjacent to watercourses during the Early Permian of western Euramerica. However, such elevated apparency could be masked by the taphonomic absence of heavily herbivorized understory vegetation such as true ferns in the fossil record (Scheihing and Pfefferkorn, 1984). Increased herbivory levels, however, necessarily need not be associated with elevated chemical or physical defenses (Schoonhoven et al., 2005).

5.4. Relevance of quantitative herbivore studies from modern ecosystems

The CBB, Taint, and Brazilian Lower Permian assemblages for which herbivory types have been examined are neither taxonomically analogous nor ecologically equivalent to any similar or identically studied modern plant community. However, particular plant growth-forms may have narrow, specific distributions in both Permian and Modern environments. The physiognomic spectrum of these growth forms includes herbaceous ground cover, evergreen pachycaul plants, lianas, tree ferns, and canopy-forming seed plants with single-stemmed, lignified trunks (Retallack and Dilcher, 1988; Dilcher et al., 2004; DiMichele et al., 2006a). Given the absence of taxonomic uniformitarianism between Lower Permian and modern plant communities and the current level of knowledge, studies of Paleozoic fossil-plant herbivory should best be considered as an exploratory examination of the distribution of herbivore damage types and levels at local and regional scales across particular landscapes. No implication or assertion of global herbivory levels should be inferred.

For some questions, such as the expansion of herbivory in compression floras during the Pennsylvanian

and Permian, an assumption (to be tested) can be made that initial levels during the beginning of this interval were close to zero in terms of the surface area removed and frequency of attack. Relatively few types of damage are present in these Paleozoic floras, typically 15 or less (11 for CBB), possibly compromising analyses based on presence–absence data. An alternative and perhaps more meaningful measure of herbivory is direct measurement of foliar area removed, buttressed with frequency measures of percentage of leaves exhibiting herbivore damage (Tables 1 and 3), provided herein, which can be compared cautiously to extant data. Currently, the alternate method of collecting presence–absence data for damage types (DTs) has only been implemented for angiosperm-dominated floras of the Late Cretaceous and Paleogene. In the context of CBB, presence–absence DT data are important for spatiotemporal comparisons to other, late Paleozoic floras (Labandeira, 2006b), allowing not only for functional-feeding-group assignments in bulk floras, but also attributions to more narrowly-defined feeding guilds, such as skeletonizers or midrib gallers, on particular host plants. Perhaps a more informative approach would be use of multiple methodologies of extending the leaf-area removal and frequency of attack measurements into the Mesozoic and Cenozoic, and reciprocally extend the damage-type system of analysis downward into the Paleozoic.

6. Conclusions

Five principle conclusions are drawn from our study of insect herbivory at the Coprolite Bone Bed (CBB) locality in conjunction with data from Taint (Beck and Labandeira, 1998), observations from the Early and Late Permian of north-central Texas and South Africa, and from recent studies from southeastern Brazil (Adami-Rodrigues et al., 2004a).

1. Early Permian levels of herbivory from fluvial environments have been assessed at two sites from north-central Texas. Herbivory levels (0.25%) at CBB (Sakmarian) are considerably less than those (2.55%) of the only other similarly quantified Euramerican site, at Taint (Artinskian). A similar heterogeneous pattern of herbivory levels also is present from younger Early Permian floras of southeastern Brazil.
2. As in the Taint flora, the most intensively herbivorized plants at CBB are pteridosperms, in this case a peltasperm and especially a medullosan. Other major clades, such as pteridophytes, cordaites or cycadophytes were minimally affected. This suggests insect herbivore targeting of a particular plant group.

3. The presence of two distinctive gall types from the CBB flora indicates a greater diversity of Permian gall morphologies than previously realized and thus provides additional evidence that is inconsistent with a Cretaceous origin of the galler life-habit.
4. These preliminary data suggest that the levels of herbivory within Early Permian fluvial environments were spatiotemporally heterogeneous across landscapes of stream courses and interfluves. Herbivory was more intensively expressed in some plant communities than in others.
5. Support or rejection of any of the above conclusions, or elucidation of other patterns, will require examination of similarly well-preserved and abundant floras across a variety of clastic fluvial and nonfluvial environments from the Lower Permian in tropical Euramerica as well as regions in Gondwana, Cathaysia, and Angara.

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