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Early Permian insect folivory on a gigantopterid-dominated riparian flora from north-central Texas

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Abstract

Quantitative analysis of 11,562 cm² of foliar surface area from an Early Permian flora from north-central Texas reveals that 2.6% was removed by insect folivores. Of the 1346 foliar items analyzed, 31.8% were attacked by insect folivores. This Permian insect herbivory approximated one-third the level in modern tropical to temperate forests. Three taxa of Gigantopteridaceae exhibited disproportionately high insect consumption levels, ranging from 3.1 to 4.4% of leaf area, and attack frequencies of 39.6 to 82.8% — levels comparable to taxon-specific values for modern woody dicotyledonous angiosperms. Qualitative analysis of folivory type also indicates that five of the eight categories of herbivore damage occurring on this flora were confined to or overwhelmingly represented on Gigantopteridaceae, suggesting preferential host specificity for Gigantopteridaceae by insect folivores. By contrast, other pteridophylls, conifers, cycadophytes, and two taxa of uncertain affinity, showed low levels of leaf area removal and attack frequencies. The Gigantopteridaceae, an enigmatic group of Permian plants with large, megaphyllous foliage, foreshadowed physiognomic attributes occurring in later angiosperms. Both groups had similar consumption patterns and intensities by insect folivores. In this moderately diverse Early Permian flora, insect folivory was significant, at least in one riparian environment outside the Euramerican coal-swamp ecosystem, indicating that modern modes and magnitudes of insect consumption of vascular plant tissue were in place during the Late Paleozoic. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

Recent research into the evolutionary biology of phytophagous insects and their interactions with vascular plants predominantly have emphasized the presence of congruence between the phylogenies of

insect and their associated plant host clades. Although conceptually pioneered by the landmark paper of Ehrlich and Raven (1964) on the coevolution of butterflies and their host plants, recent exposition of this interest has been highlighted in seminal studies that take a synoptic perspective of insect/plant associations (Mitter et al., 1988; Farrell et al., 1991). More focused analyses have singled out particular insect clades, such as the leaf-beetles *Ophraella* (Futuyma and McCafferty, 1990) and *Tetraopes* (Farrell and Mitter, 1993) for closer scrutiny of whether par-

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allelism exists between the species-level phylogenies of the insect herbivores and their plant hosts. Collectively, these studies have focused overwhelmingly on angiosperm hosts and exclusively on the extant insect clades that dominate particularly the later Cenozoic, rarely extending to the Mesozoic (Farrell et al., 1991; Farrell and Mitter, 1993; Labandeira et al., 1994). In contrast, plant–insect associations of the taxonomically distinctive Late Paleozoic insect and vascular plant biota have not been evaluated in a significant macroevolutionary context. The Late Paleozoic insect fauna largely became extinguished during the end-Permian extinction (Wootton, 1990; Labandeira and Sepkoski, 1993), and contemporaneous Late Paleozoic vascular plant lineages also underwent extirpation or were largely replaced during the early Mesozoic (Niklas et al., 1985). Since both potentially interacting, Late Paleozoic groups are now absent, approaches that are typically used for modern lineages are unavailable, necessitating di-

rect examination of the plant and insect fossils (Scott and Paterson, 1984).

Few comprehensive studies have investigated the potential role between Paleozoic insects and the more ancient lineages of vascular plants, particularly ferns, conifers, seed ferns and cycadophytes. In this study we evaluate insect herbivory in a well-preserved, moderately diverse and abundant, Early Permian compression flora from north-central Texas (Fig. 1). Because insect body fossils rarely are present in this and other associated Early Permian deposits of north-central Texas, it is not possible to identify with certainty the lower-level insect taxa responsible for the plant damage. However, unlike previous paleoentomological and paleobotanical studies, this study will provide qualitative patterns of insect herbivory and their quantitative measurement for the first time in a fossil flora. We assess the relative extent of plant host specialization by insect herbivores, defined as the extent to which an insect is restricted

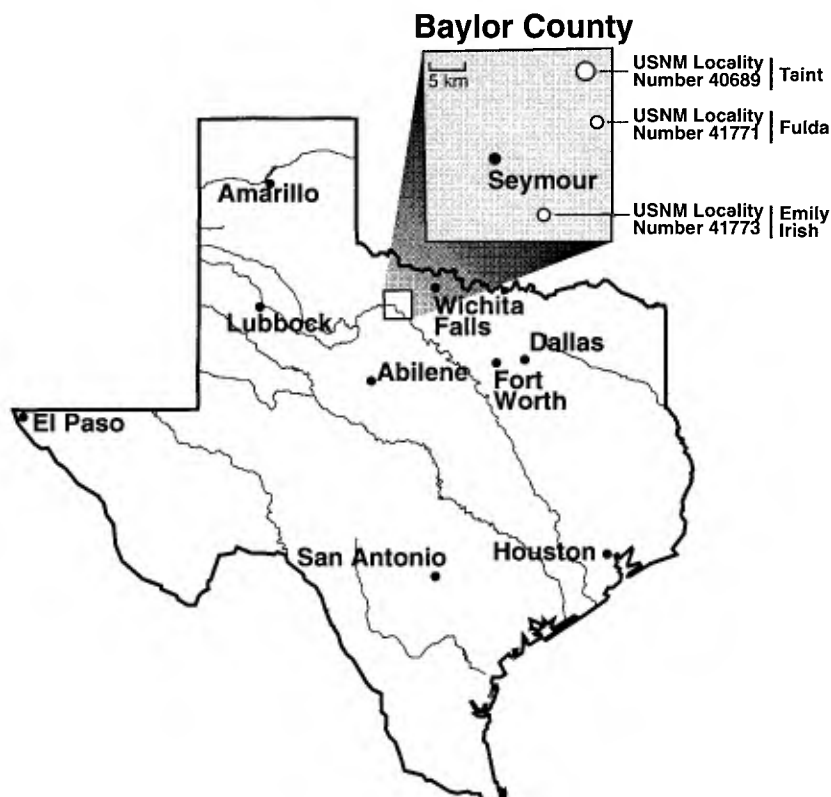


Fig. 1. Index map showing geographic setting of the Taint and other floras mentioned in this study.

in its feeding to one species of plant (Lincoln et al., 1985), and compare the overall percentage of insect herbivory to analogous measures in modern plant communities. These Late Paleozoic data are particularly relevant since a pervasive theme in the literature of Paleozoic plant–insect interactions is that there is minimal evidence for Paleozoic insect herbivory (Cox, 1974; Zwölfer, 1978; Strong et al., 1984; Shear, 1991; Hughes, 1994), with the possible exception of feeding on fructifications (Sharov, 1973; Rohdendorf and Rasnitsyn, 1980; Kukalová-Peck, 1990). However, recent examination of mite- and insect-mediated plant damage from three-dimensionally preserved, Euramerican coal-swamp floras, particularly the Calhoun Coal from the Illinois Basin has demonstrated the presence of several herbivore functional-feeding-groups (Lesnikowska, 1990; Labandeira, 1996, 1998, 1999). They include piercer-and-suckers (Lesnikowska, 1989; Labandeira and Phillips, 1996a), galls (Labandeira and Phillips, 1996b), stem borers (Labandeira and Beall, 1990; Labandeira, 1998), and folivores and sporangiovores (Labandeira and Phillips, 1992; Labandeira, 1996) and detritus borers (Labandeira et al., 1997). Although the flora investigated herein is about 35 million years younger, it is floristically different, probably representing mesic vegetation occurring on a periodically drained, elastic substrate in an alluvial plain.

There has not been any previous, comprehensive, site-specific documentation of the occurrence and intensity of insect herbivory occurring outside lowland, peat dominated, wetlands of the Late Paleozoic. Primary documentation of insect damage from these ‘upland’ floras is generally anecdotal, limited to a few often conspicuous examples of external-foilage-feeding on selected plant taxa, and lack quantitative determinations of foliar tissue removed or frequency of attack (Scott et al., 1996; Labandeira, 1998). Included in this literature is documentation of margin- and hole-consumption by insects on pteridophytes (Kelber and Geyer, 1989; Castro, 1997), glossopterid and medullosan seed ferns (Plumstead, 1963; Van Amerom, 1966; Van Amerom and Boersma, 1971; Scott and Taylor, 1983; Srivistava, 1987; Labandeira and Beall, 1990; Scott et al., 1992) and cycadophytes (Geyer and Kelber, 1987; Kelber and Geyer, 1989; Jarzembowski, 1989). By contrast, far less is known for galls, of which few examples

have been convincingly demonstrated (Larew, 1992; Scott et al., 1994; Labandeira and Phillips, 1996b). Leaf mining remains enigmatic, although Müller (1982) has described U-shaped structures on seed fern pinnules of *Macroneuropteris scheuchzeri* from Germany that were bounded by secondary veins enclosing a blotch of necrotic tissue. These curious structures also have been found on *Macroneuropteris* pinnules in slightly older deposits of Illinois (Labandeira and Beall, 1990) and in northern Texas Early Permian deposits approximately 30 million years younger (Labandeira, pers. observ.). In addition there is possible evidence for piercing-and-sucking on *Samaropsis* seeds in younger deposits from Russia (Sharov, 1973). Kukalová-Peck (1987) has documented undetermined pteridophyte spores in the gut of a diaphanopteroidean insect nymph. Similarly, gymnospermous and possibly seed-fern pollen have been described in the gut of a hypoperlid, grylloblattid and unknown insect species in the latest Early Permian of Russia (Rasnitsyn and Krassilov, 1996a,b; Krassilov and Rasnitsyn, 1997), providing direct support for sporivory and pollinivory (Labandeira, 1997a,b, 1998). In addition, pollination syndromes for Paleozoic insects have been suggested (Taylor and Millay, 1979; Crepet, 1983). Judging from this disparate documentation, there is evidence that insect herbivory was present on some plant taxa growing on mineralic substrates during the Pennsylvanian and Early Permian. However, there has been no quantitative evaluation of bulk-collected and well-sampled floras that can address unambiguously the currently received view that Paleozoic insect herbivory was negligible.

2. Materials and methods

The fossil plant material statistically analyzed in this study originates from a single locality that is segregated into separate subcollections from a continuous excavation, in north-central Texas (Fig. 1), and is informally designated as the ‘Taint’ site. The term ‘Taint’ is an informal designation referring to an unnamed creek adjacent the fossil site that occurs between two named creeks. Specimens from two other localities, not included in the quantitative analyses, were also examined and illustrated in this

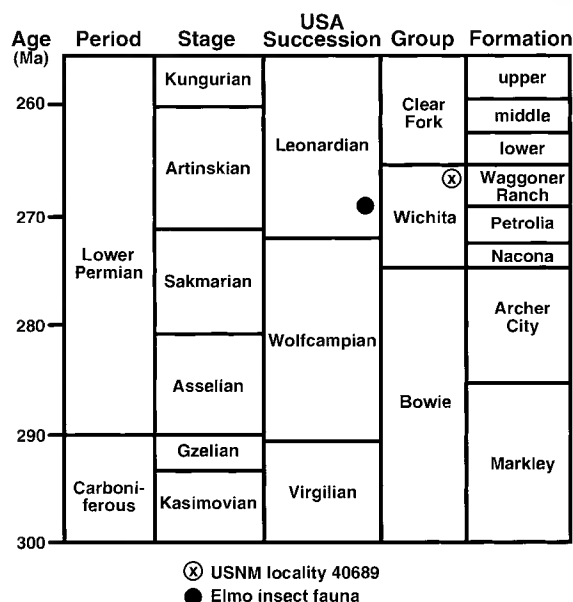


Fig. 2. Stratigraphic setting of the Taint flora. Stage-level terminology, local stratigraphic units, and equivalent geochronological assignments. Formational designations are from Hentz (1988). For additional details regarding the Fulda and Emily Irish sites, see Read and Mamay (1964); Mamay (1968). Carpenter (1930) provides information on the Elmo insect locality in central Kansas.

paper. Those collections, made by S.H. Mamay and A.D. Watt in the 1950s, were made at the Emily Irish locality (USGS locality 8959) and the Cowan

Ranch locality at Fulda (USGS locality 10063); both localities are in Baylor County, and the fossiliferous strata are of early Artinskian age (Fig. 2). The 'Taint' site is approximately 53 km SSW of Wichita Falls, Texas. USNM locality numbers assigned to this site are 40039, 40040, 40042, 40043 and 40689; each number corresponds to a separate trench within the excavated site. Approximately 78% of the foliar items and surface area from this flora were collected by W.A. DiMichele, D.S. Chaney and R.H. Hook in 1993 using a representative sample method; C. Labandeira collected 22% of the flora in 1993 and 1994, using a collection strategy in which all recognizably foliar material greater in area than approximately 1 cm² was obtained, regardless of preservational state or likelihood of taxonomic assignment. This site consists of five adjacent trenches deployed along approximately 15 m of outcrop exposure, each dug to a depth of from 0.4 to 1.0 m. The first phase of this study consisted of retrieval and wrapping of foliar specimens at the outcrop, transportation to the lab, and preparation to reveal additional foliar surface. This material was identified taxonomically to genus, although 5.5% of the foliar specimens remained taxonomically unresolved. All material of this analysis resides at the NMNH paleobotany collections.

The second phase of this study was taxonomic identification of specimens and qualitative assessment of the damage type, provided in Plates I–VII.

PLATE I

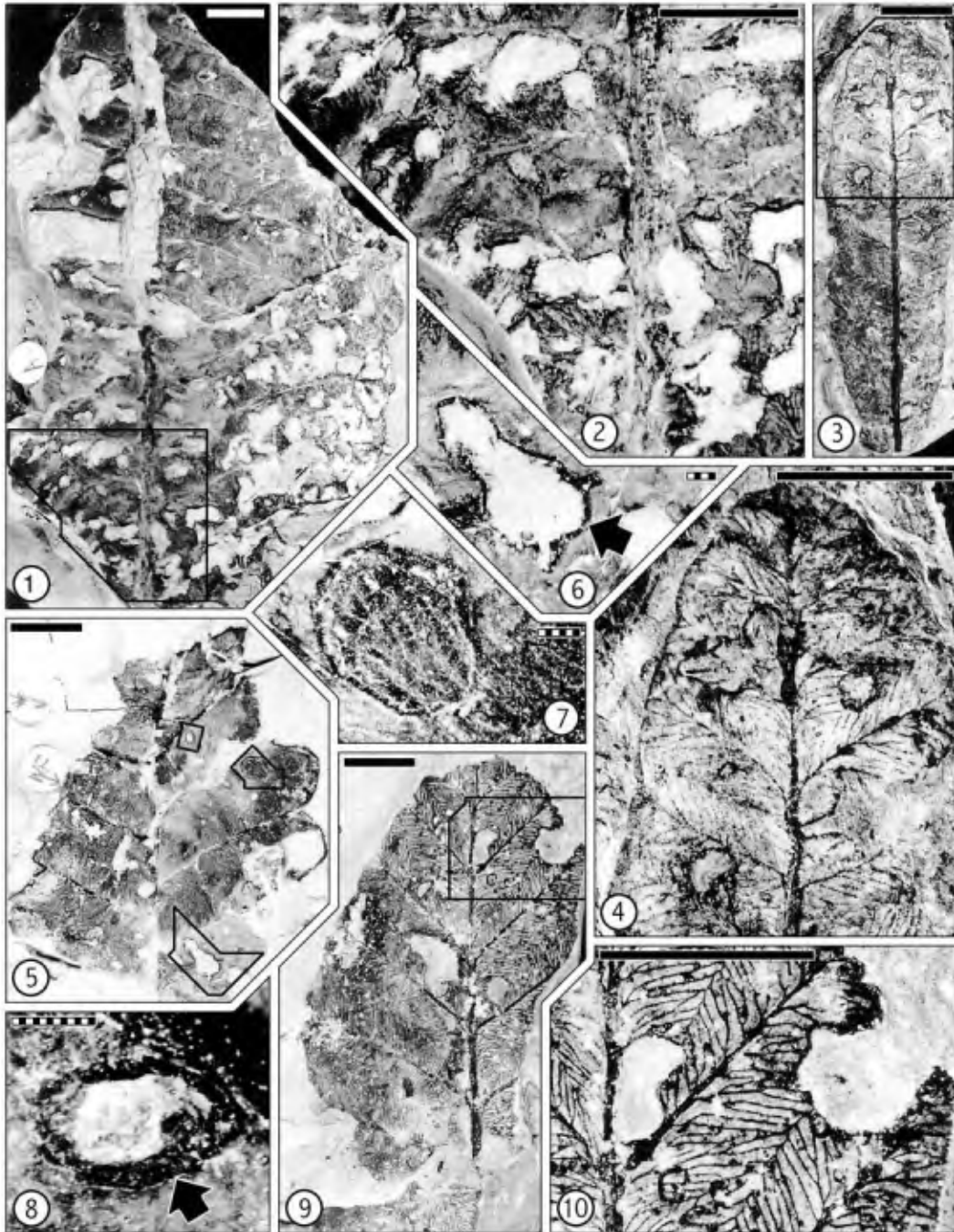
Intercostal hole-feeding on gigantopterid plants.

- Part of larger frond of *Gigantopteridium americanum* (USNM-483620) with prominent intercostal hole-feeding. Note nine successive feeding holes along the right side of the midrib.
- Enlargement of region in 1 showing lobate shape of feeding holes.
- Further enlargement of area in 2, showing trenched margin-feeding and reaction tissue at arrow.
- Part of larger frond of *Gigantopteridium americanum* (USNM-483621) showing size variation in intercostal hole-feeding.
- Enlargement of area in 4, showing location of many feeding holes in the adaxial region of the blade, surrounded by midrib and secondary veins.
- Part of larger frond of *Gigantopteridium americanum* (USNM-483622) exhibiting feeding holes ranging from narrow perforations to ovoidal, polylobate forms.
- Enlargement of central-left region of 6.
- Enlargement of lower-left region of 6 showing four, similarly-sized feeding holes in successive intercostal areas suggestive of bud-boring.
- Fragment of a larger frond of *Zeilleropteris wattii* (USNM-483623) showing considerable variation in intercostal hole size and orientation.
- Enlargement of two feeding holes at top-right of 9. Scale bars: solid pattern = 1 cm; striped pattern = 0.1 cm.

PLATE I



PLATE II



Damaged zones within the foliar surfaces were determined by a four step procedure. This procedure consisted of: (1) recognition of thick, upraised, or otherwise teratological reaction rims along holes or margins; (2) demonstration of stereotyped feeding patterns or some other indication of insect herbivore behavior reflected in the type and location of foliar damage, (3) detailed examination of damaged margins of foliar elements, revealing small mandible marks, secondary vein stringers, or other anatomical evidence indicating extraction of foliar tissue by a mandibulate insect, and (4) patterns of host specificity, particularly if stereotyped damage patterns were associated with particular plant host taxa or even particular foliar regions of the same plant host taxon. Some plant damage was not attributable to insect herbivory, and was considered fungal in origin (Masse, 1910; Sinclair et al., 1987) or the result of postmortem degradation or premortem physical breakage consistent with the architectural designs of the foliar elements (Vincent, 1990). In this study, the term 'foliar element', equivalent to a specimen, referred to any photosynthetic organ, occurring as a digitizable unit surrounded by rock matrix, regardless of anatomical origin. Foliar elements included leaves, pinnae, bracts, needles and similar structures. Extreme care was taken to not duplicate parts and counterparts of foliar elements in this analysis.

The third phase of this study involved quantitative determination of total foliar element area and the percentage of the total foliar element area attributable to insect herbivory, for each plant taxon. This process was accomplished by scanning foliar elements into version 1.58 of the National Institute of Health *Image* software for the Macintosh. *Image* capture

was performed by a Panasonic WV-GP410 camera attached to a Tamron 1:3.5–3.8, 24–48 mm, wide zoom lens. Once images were captured, the Digitizer Plus program was used to digitize relevant foliar outlines for determination of original and herbivorized areas. To eliminate potential lens distortions at variable focal lengths, measurements were calibrated by linear scales at the lowest magnifications that would accommodate the specimen field of view. Determination of foliar area absent due to insect herbivory was based on surface area measurement of perforations, various incisions at foliar margins, and other damaged foliar tissue. Estimation of missing herbivorized areas on the foliar element margin was based on knowledge of foliar element shape and outline from previously scanned specimens of the same taxon. For bilaterally symmetrical pinnae or leaves, this was done by doubling the external margin of the unaffected side onto the damaged side, and, with appropriate calibration, subtracting the herbivorized area. Herbivorized margin tips or regions of foliar elements for which the margin contour was inadequately known were assessed as the minimal area subtracted by a chord from the intersection points of the damaged area with the normal foliar margin. A conservative approach was taken in quantification of missing foliar element area due to insect herbivory, and only those missing foliar surfaces that could be substantiated by knowledge of foliar outlines were included as data.

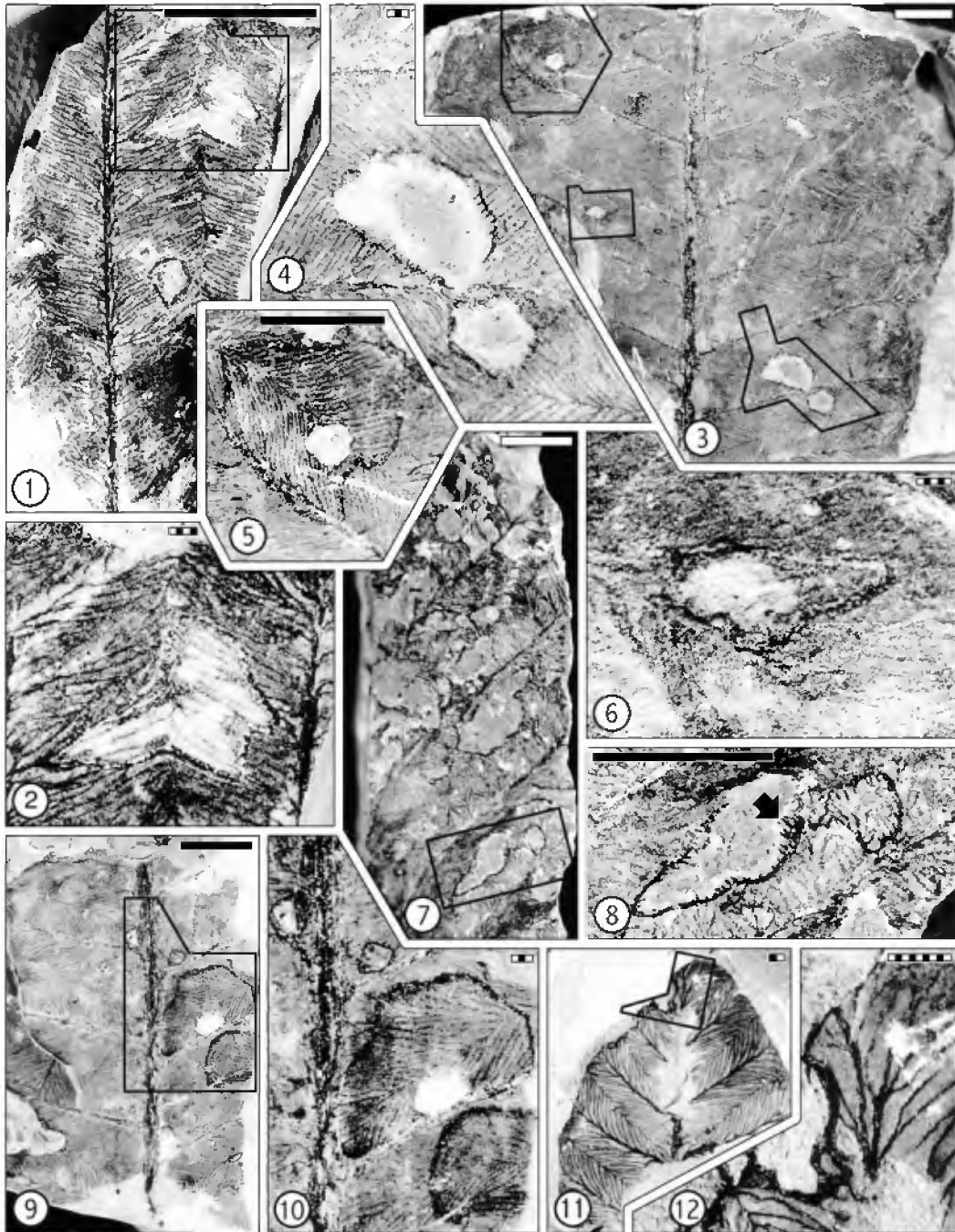
The total original surface area and total damaged area assigned to insect herbivory was determined for each plant genus in the flora, presented as cm² in Fig. 3. These raw data were converted to the average original area for each plant taxon

PLATE II

Intercostal hole-feeding, and small circular hole-feeding on gigantopterid plants.

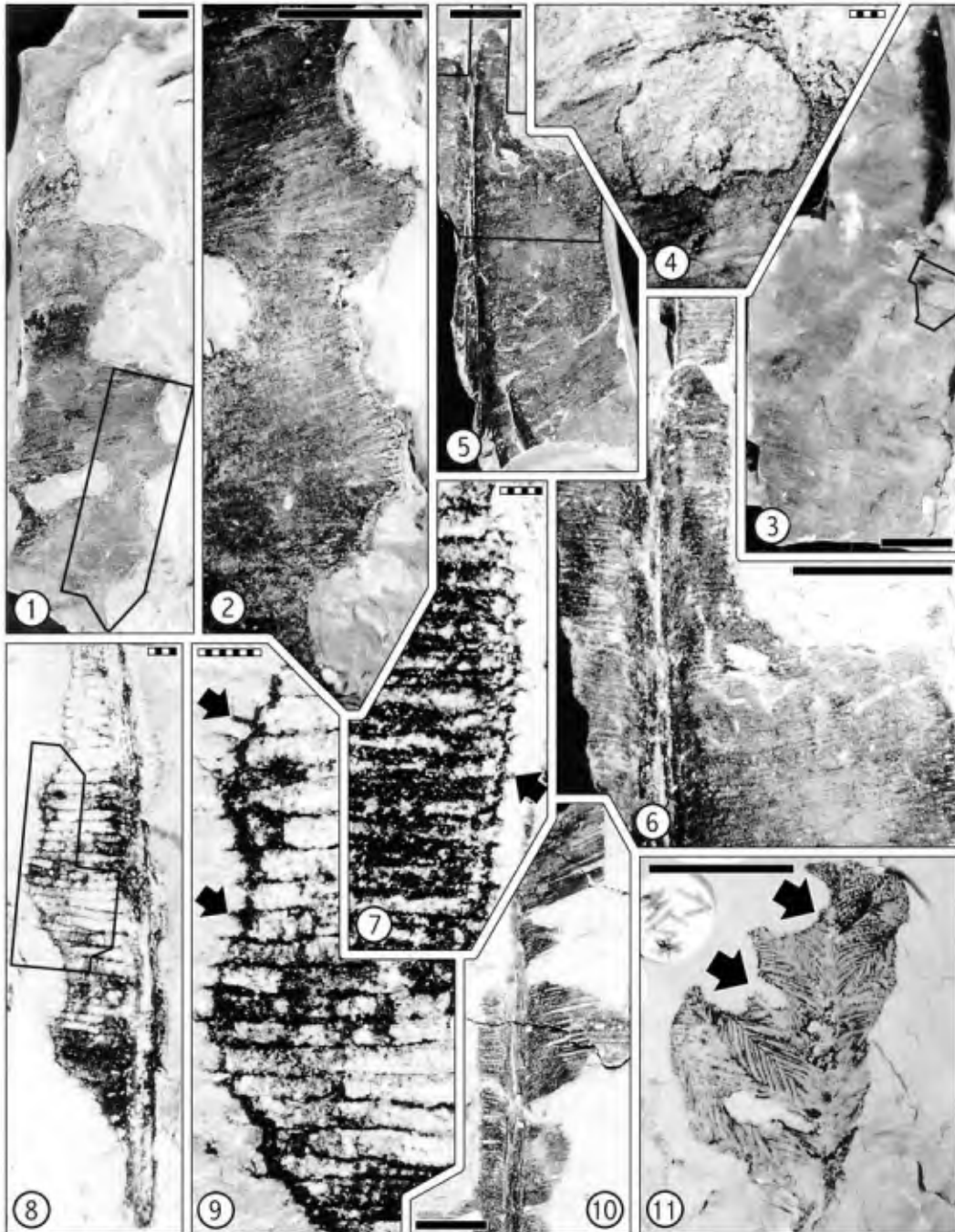
1. Extensive intercostal hole-feeding on *Zeilleropteris wattii* (USNM-483624) showing merged feeding holes at bottom-right.
2. Enlargement of bottom region of 1, showing interconnected and atypically branched feeding holes.
3. Elliptical frond of *Gigantopteridium americanum* (USNM-483625) exhibiting small, circular hole-feeding on apical half.
4. Enlargement of top third of 3.
5. Slightly distorted frond fragment of *Zeilleropteris wattii* (USNM-483626) bearing small, circular hole-feeding.
6. Enlargement of feeding hole in bottom-right region of 5; arrow points to well-developed reaction tissue rim.
7. Enlargement of structure at center-right of 5, showing ovoidal reaction rim enclosing necrotic zone with venational continuity.
8. Enlargement of ovoidal feeding hole in center-top of 5, showing prominent reaction tissue rim at arrow.
9. Frond of *Gigantopteridium americanum* (USNM-483627), showing a variety in hole- and margin-feeding shapes.
10. Enlargement of hole- and margin-feeding area at top-right of 9. Scale bars: solid pattern = 1 cm; striped pattern = 0.1 cm.

PLATE III



For description see p. 149.

PLATE IV



For description see p. 149.

PLATE V



(total foliar area divided by the number of foliar elements) and respective average herbivorized area (total herbivorized area divided by the number of foliar elements) in Fig. 4. Simple herbivory indices

— average herbivorized area per leaf \div average total area per leaf $\times 100$ — for each foliar element in the assemblage are provided in Fig. 5. An alternative method of estimating the intensity of herbivory,

PLATE III

Skeletonization, intercostal hole-feeding, blotch-feeding, and apical margin-feeding on gigantopterid plants.

1. Skeletonization (top-right) and hole-feeding (center) on a *Gigantopteridium americanum* (USNM-483628) frond.
2. Enlargement of skeletonized area in 1; note continuity of secondary and sutural veins.
3. Example of intercostal hole-feeding and blotch-feeding in a frond fragment of *Cathaysiopteris yochelsonii* (USNM-483629).
4. Enlargement of bottom-right area in 3; note avoidance of secondary vein.
5. Blotch-feeding with a pointed adaxial margin, central necrotic tissue, and an included eccentric hole. The necrotic tissue may represent subsequent fungal attack.
6. Enlargement of similar, smaller structure to 5, at center-left in 3.
7. Fragment probably of *Zeilleropteris wattii* (USNM-483630), displaying extensive intercostal hole-feeding.
8. Enlargement of bottom-right in 7, showing secondary vein stringers projecting into the lobate feeding hole.
9. Frond segment of *Gigantopteridium americanum* (USNM-483631) probably of the same frond as 3, showing blotch-feeding.
10. Enlargement of blotch region at center-right in 9; note ovoidal hole and surrounding necrotic tissue that may be fungal damage.
11. Apical margin-feeding on a small *Gigantopteridium americanum* frond (USNM-483632).
12. Enlargement of margin-feeding region at the top-center in 11. Scale bars: solid pattern = 1 cm; striped pattern = 0.1 cm.

PLATE IV

Examples of margin- and hole-feeding on *Taeniopteris* sp., and apical margin-feeding on a gigantopterid.

1. Hole-feeding and several cusped excavations on the margin of a *Taeniopteris* sp. leaf (USNM-483633).
2. Enlargement of bottom-right area in 1, showing arcuate nature of the feeding incision and the associated zone of reaction tissue.
3. Hole-feeding on a *Taeniopteris* sp. leaf (USNM-483634).
4. Enlargement of herbivorized hole at center-right in 3; note modestly developed reaction tissue rim.
5. Margin-feeding on a *Taeniopteris* sp. leaf (USNM-483635), with the adaxial portion of the bite mark paralleling the midrib.
6. Enlargement of the top half of 5, showing the initial cusped entry into the blade during feeding.
7. Detail of the linearly chewed margin in 6, showing persistence of vascular tissue strands at arrow.
8. Cusped margin-feeding on a *Taeniopteris* sp. leaf (USNM-483636).
9. Detail of central-left herbivorized margin in 8, with wisps of projecting vascular tissue indicated by arrows.
10. A *Taeniopteris* sp. leaf (USNM-483637) showing margin-feeding extending to the midrib.
11. Apical margin-feeding on a *Gigantopteridium americanum* frond fragment indicated by arrows (USNM-483638). Scale bars: solid pattern = 1 cm; striped pattern = 0.1 cm.

PLATE V

Surface grazing on *Comia* sp.; blotch- and hole-feeding on gigantopterids.

1. An approximately three-fourths complete pinna of *Comia* sp. (USNM-483639) bearing five similarly-sized, elliptical lesions apparently caused by surface feeding.
2. Enlargement of lesion at center-right in 1.
3. Enlargement of lesion at center-left in 1; note continuity of secondary venation.
4. Enlargement of lesion at top-center in 1.
5. Portion of a *Gigantopteridium americanum* frond consisting of two, overlapping elements of a frond (USNM-483640), each bearing ovoidal blotches in their apical portions.
6. Enlargement of top-right region in 5, showing several ovoidal blotches, each surrounded by a modestly developed reaction tissue border.
7. Ovate structure from the top-right of 5.
8. Small, circular hole-feeding mark in center of 5.
9. Blotch at extreme top-right of 5.
10. Prominent, intercostal hole-feeding on *Gigantopteridium americanum* (USNM-483641).
11. Enlargement of damaged area in 10; note similarity to Plate 3, 4. Scale bars: solid pattern = 1 cm; striped pattern = 0.1 cm.

PLATE VI



the percentage of foliar units subject to herbivore attack, is given in Fig. 6. Finally, a comparison of collection strategies is shown in Table 2 and Fig. 7, where the data are partitioned into a subset characterized by the representative sample method of DiMichele, Chaney and Hook in 1993 (Subset A), and the total specimens approach of Labandeira in 1993 and 1994 (Subset B). All raw data was entered into the software program, SYSTAT, which was used for statistical analysis.

3. Geologic and biologic setting

In this section an overview of the geologic context of the Taint locality is given, followed by a brief description of the flora, and ending in an assessment of what currently is known of the approximately contemporaneous Early Permian insect fauna from Elmo, in central Kansas.

3.1. Geologic context

The flora from the Taint locality occurs within a narrow lens, perhaps several tens of meters long, within coarser-grained clastic strata of the Waggoner Ranch Formation (Fig. 2), a nonmarine sequence that includes rocks mapped by Romer (1974) as the Clyde Formation. Its chronostratigraphic assignment is the lower Artinskian Stage, corresponding to an approximate geochronologic date of 265 Ma (Harland et al., 1990). The flora from Taint lies within the stratigraphic range of the “older *Gigantopteris* flora” (Zone 14) of Read and Mamay (Mamay, 1976).

From an assessment of the sedimentary struc-

tures and stratigraphic facies associated with this locality, we conclude that deposition occurred in a fine-grained, basinal environment of limited extent, probably marginal to a stream drainage. Presence of intact, typically nonabraded, foliar laminae up to 15 cm long indicates minimal transportation prior to burial. Plant fossils are preserved as several horizons of compressions, less frequently impressions, in a matrix ranging from medium-grained siltstone to claystone. Evidence of altered, original organic matter is present as carbonized foliar surfaces; notably detail of higher- and lower-order venation extends to quaternary vein meshwork in many of the giantopterid taxa. The presence of similarly preserved giantopterid and associated floral material at nearby sites in north-central Texas (Read and Mamay, 1964) indicate that the preservation at the Taint locality is not a local taphonomic anomaly. Because of the lack of evidence for significant transportation of foliar elements and the joint presence of robust and delicate vegetation at this site, we conclude that the floral assemblage at Taint is a fairly accurate representation of the local standing vegetation.

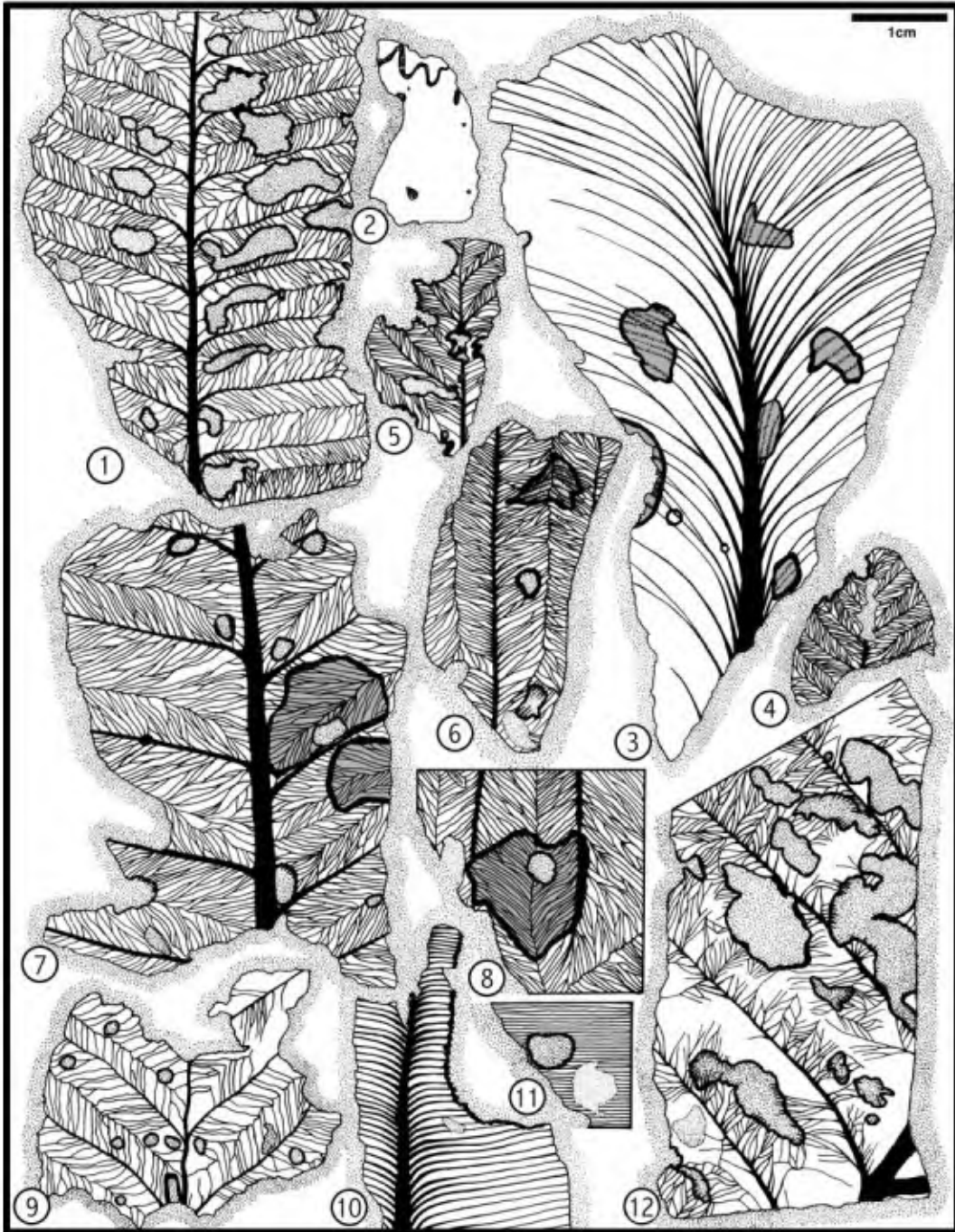
The Lower Permian “older *Gigantopteris* flora” was geographically circumscribed, floristically characterized, and delineated as a biostratigraphical unit (Zone 14) by Read and Mamay (1964). Mamay (1960, 1966, 1968, 1986, 1988, 1989) and Mamay et al. (1986, 1988) have described several plant taxa from several sites within this zone, principally from north-central Texas. Although floras from these localities have never been extensively monographed, the generic limits of most constituent taxa are known. However taxa such as *Wattia* remain enigmatic. The presence of giantopterid plants with large, proba-

PLATE VI

Small circular hole-feeding on a giantopterid, a possible leaf mine, and taxa lacking herbivore damage.

1. Region of small circular hole-feeding on the apical portion of a *Gigantopteridium americanum* frond (USNM-483642).
2. Enlargement of upper area of 1, showing nine feeding holes.
3. Enlargement of bottom-center region in 2.
4. Possible serpentine leaf mine on an unassigned giantopterid (USNM-483643).
5. Enlargement of top region of 4, displaying serpentine path of mine-like structure. Arrow designates a probable seed.
6. *Samaropsis* sp. seed (USNM-483644).
7. Cf. *Neuropteris* sp. foliage (USNM-483645).
8. *Samaropsis* sp. seed with bifid tip (USNM-483646).
9. Branchlet and cone of ?*Brachyphyllum* sp. USNM-483647.
10. Foliar element of *Wattia texana* (USNM-483648). Scale bars: solid pattern = 1 cm; striped pattern = 0.1 cm.

PLATE VII



bly fleshy laminae, the subdominance of taeniopterid cycadophytes and peridophylls, and the depauperate representation of conifers confers a distinctive taxonomic aspect to this flora.

3.2. *The flora from the Taint locality*

Foliar diversity at the Taint locality consists of 12 distinctive genera. This flora is dominated by a poorly understood, dominantly Permian, group of megaphyllous plants collectively known as gigantopterids. Gigantopterids were originally described in eastern Asia by Schenk (1883) and placed in systematic context by Koidzumi (1936) and Asama (1959). Several early authors thought that the Gigantopteridaceae taxonomically characterized the Cathaysian Biogeographic Province, but specimens congeneric with East Asian taxa were later discovered in the southwestern United States and especially in Texas (White, 1912; Mamay, 1986, 1988). Currently three Asian gigantopterid genera are known from Texas (Mamay, 1986, 1988), whereas other genera apparently are phytogeographically confined to the southwestern United States (Mamay et al., 1986, 1988; Mamay, 1989). A broader, global conspectus of Permian floras, including discussion of biogeography, is provided by Ziegler (1990).

In North America gigantopterid leaves are usually simple, either as forked or unforked leaves, with entire laminae, some approaching 1 m in length (Mamay, 1989). In China they are large, simple or pinnately compound fronds. All forms are charac-

terized by 3 to 4 orders of bifurcating venation, the terminal intersecondary veins often ending in an intercostal, sutural vein. They bear crenate margins and pronounced midrib and secondary veins that were vascularly robust and formed a truss architecture resistant to flattening upon sedimentary compression. The higher order veins frequently comprise a “herringbone pattern” (Mamay et al., 1986) with a quaternary reticulum that resembles leaves of the Gnetales and angiosperms (Mamay et al., 1988; Hickey and Taylor, 1996; Trivett and Pigg, 1996). An abscission zone is indicated by petioles that flare and are truncated basally, suggesting deciduousness (Mamay et al., 1988). At Taint, the gigantopterid taxa includes the distinctive *Zeilleropteris wattii* and *Gigantopteridium americanum*. However *Cathaysiopteris yochelsoni* may represent a morphological continuum with *G. americanum*, because rare intermediate morphotypes can not be assigned unambiguously. For this reason we have treated this combination of *G. americanum*, *C. yochelsoni*, and intermediate morphotypes as an artificial grouping for convenience of reference in this study.

The form-genus *Taeniopteris* is probably the leaf of a cycadophyte. Suites of specimens from single localities in north-central Texas are notoriously variable in shape, length, venation angle with respect to the midrib, secondary vein density, and the number of vascular strands forming the midrib. Thus it is possible that *Taeniopteris* at the Taint locality may represent more than one cycadophyte species (Remy and Remy, 1975). *Taeniopteris* sp. is typically a sim-

PLATE VII

A representative spectrum of herbivory types on major plant hosts at the Taint flora. All specimens are camera lucida drawings at the same scale.

1. Large intercostal hole-feeding on a *Gigantopteridium americanum* frond (USNM-483620).
2. Possible serpentine leaf mine on a gigantopterid foliar fragment (USNM-483643). Image is reversed.
3. Surface feeding lesions on a *Comia* sp. pinna (USNM-483639).
4. Apical margin-feeding on a small *Gigantopteridium americanum* frond (USNM-483632).
5. Cusped margin-feeding on a *Gigantopteridium americanum* frond fragment (USNM-483638).
6. Skeletonization and hole-feeding on a *Gigantopteridium americanum* frond fragment (USNM-483628).
7. Blotch- and hole-feeding on a *Gigantopteridium americanum* frond (USNM-483631).
8. Blotch-feeding from a section of a *Gigantopteridium americanum* frond (USNM-483629).
9. Small, circular hole-feeding on a *Gigantopteridium americanum* frond fragment (USNM-483642).
10. Margin-feeding on a *Taeniopteris* sp. leaf (USNM-483635).
11. Hole-feeding on a *Taeniopteris* sp. leaf (USNM-483634).
12. Large intercostal hole-feeding probably on a *Zeilleropteris wattii* frond (USNM-483630).

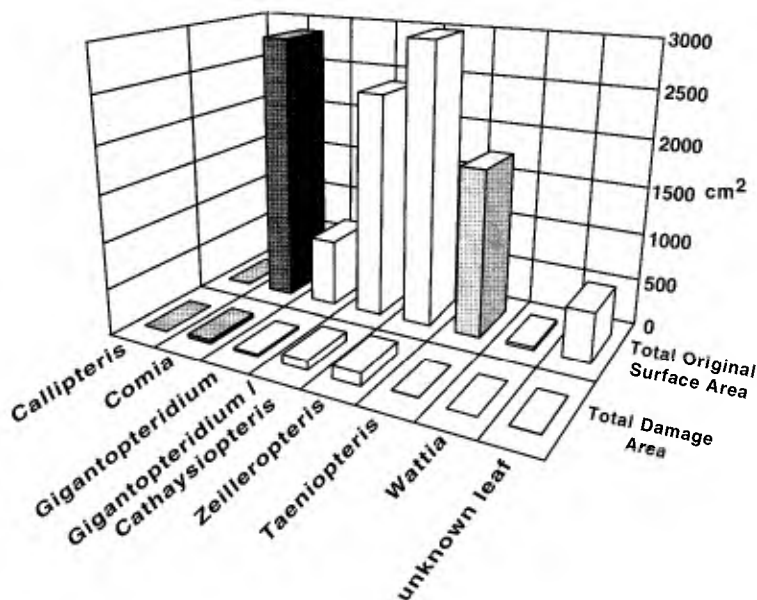


Fig. 3. Absolute values of total original surface area (background) and total damaged area (foreground) for plant taxa from the Taint flora. Nonherbivorized taxa minimally represented by specimens (see Table 1) are excluded.

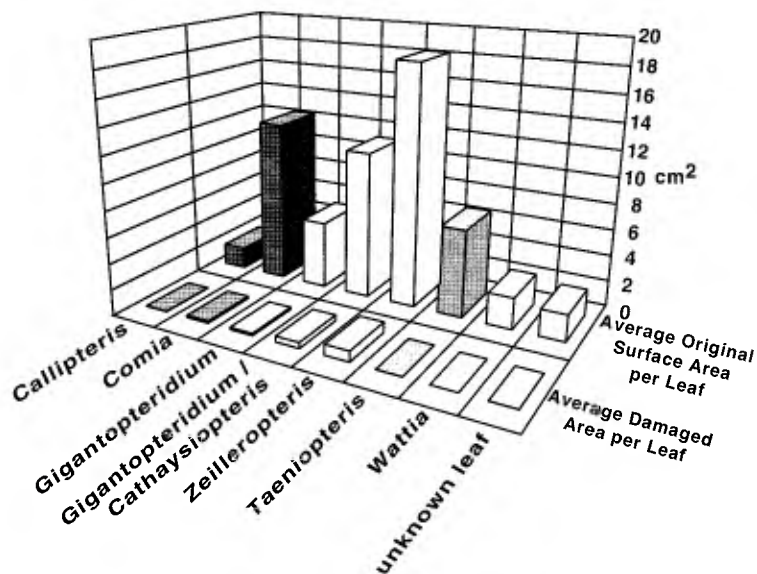


Fig. 4. Standardized values of the average leaf size for each plant host taxon, showing original surface area (background) and damaged area (foreground) at the Taint flora. The scale for damaged area is expanded for clarity. Nonherbivorized taxa minimally represented by specimens (see Table 1) are excluded.

ple, pinnately-veined leaf with a robust midrib and closely positioned, subparallel secondary veins that terminate at an entire leaf margin. Judging from their

preservational features, taeniopterid leaves were robust, and perhaps leathery. In general they exhibit low levels of herbivore damage.

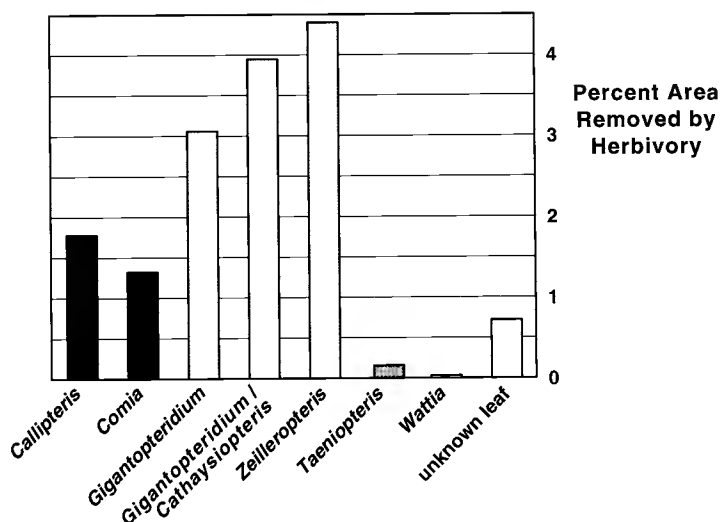


Fig. 5. Percentage of herbivorized foliar area removed for each plant host taxon from the Taint flora (the herbivory index). Nonherbivorized taxa minimally represented by specimens (see Table 1) are excluded.

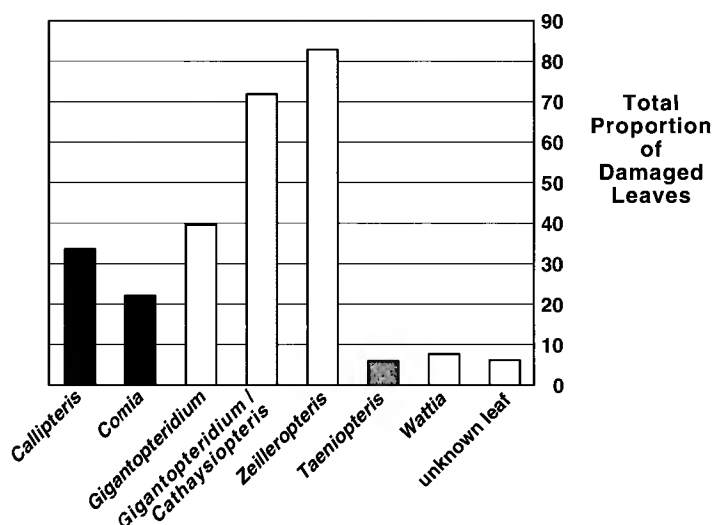


Fig. 6. The proportion of specimens displaying some form of herbivory from the Taint flora. Nonherbivorized taxa minimally represented by specimens (see Table 1) are excluded.

Leaves of *Comia*, a pteridophyllous form-genus, was originally described from the Upper Permian of the Pechora Basin of Russia. Although approximately 20 species have been identified from Angara and Cathaysia (Mamay et al., 1996), it occurs sporadically in some Lower Permian floras of north-central Texas. *Comia* is a pinnately-compound leaf with three-ranked and open venation, producing fascicu-

late vein clusters of widely-spaced secondary veins that arise from the midvein (Mamay et al., 1996). Although possibly representing a peltasperm based on foliage cuticle, the lack of attached fructifications has not allowed any taxonomic assignment.

Foliar elements that are rare at the Taint locality include the sphenopsid foliage *Sphenophyllum* and *Asterophyllites*, the pinnate pteridophyll *Callipteris*,

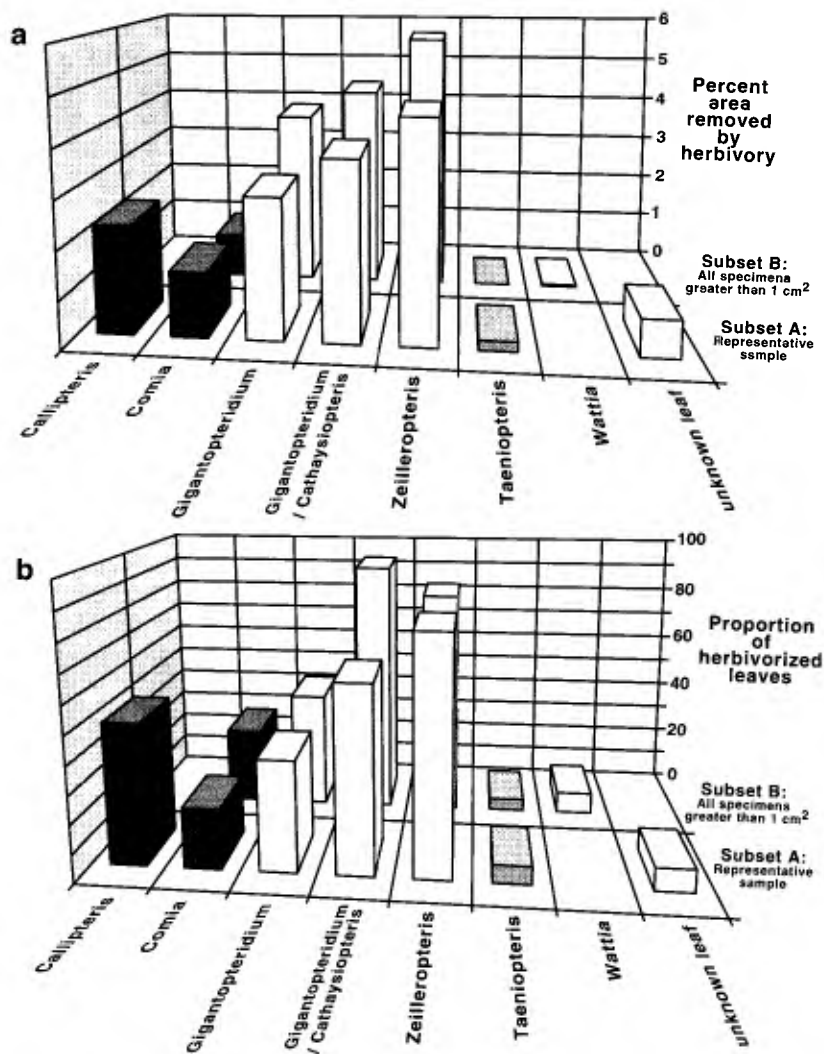


Fig. 7. Comparison of the effect of differing collection strategies on computed herbivory levels at the Taint site. (a) Herbivory indices for subsamples collected using a 'representative sample' method. (b) Subsamples in which all material greater than approximately 1 cm² was collected.

and the scale-like conifer foliage of *?Brachyphyl- lum*. The enigmatic *Wattia* is an acuminate, subparallel-veined, entire-margined appendicular organ of uncertain affinities (Mamay, 1967).

3.3. The coeval insect fauna at Elmo, Kansas

Insect body fossils were not found at the Taint locality. Thus, mention should be made of ecologically relevant and approximately coeval insects at Elmo, about 600 km to the north (Carpenter, 1930).

The deposit at Elmo has been interpreted as a repeating cycle consisting of brackish-water lagoonal, swamp, and fresh water lacustrine environments, facing a shallow, retreating epicontinental sea to the northeast (Dunbar, 1924; Tasch, 1964). Numerous excellently preserved insects co-occur with fragmentary plant material (Sellards, 1909) in planar and massive, fine-grained limestones known only from a geographically very restricted outcrop in central Kansas. The Elmo insect fauna comprises 19 orders and approximately 160 species of insects, including

diverse ‘protorthopterans’, orthopterans, and early representatives of modern holometabolous lineages such as Mecoptera and Neuroptera (Moore, 1964; Carpenter, 1992).

As a paraphyletic assemblage of generalized, mandibulate insects with a primitive, orthopteroid facies, ‘protorthopterans’ are likely candidates for consuming Early Permian foliage. Their mouthparts are consistent with either detritivorous or herbivorous feeding (Gangwere, 1967; Labandeira, 1990, 1997a; Shear and Kukulová-Peck, 1990), and they are well-represented in Pennsylvanian and Early Permian insect faunas (Labandeira and Sepkoski, 1993). At least 20 orthopteroid species are known from Elmo, and they are probably the most diverse component (Moore, 1964; Carpenter, 1966, 1976, 1992). True saltatorial Orthoptera are represented at Elmo by six species belonging to the Anelcanidae, Permelcanidae, Oedischiidae, and Permorrhophidiidae. Orthopterans probably were responsible for folivory (Rohdendorf and Rasnitsyn, 1980; Shear and Kukulová-Peck, 1990, but see Gangwere et al., 1989), particularly since greater than 99% of modern British orthopterans feed on live vascular plant tissue (Price, 1977), a figure that is applicable worldwide (Southwood, 1973). Caloneurodeans, including three species at Elmo, bore specialized psocopteran-like mouthparts with elongate maxillary laciniae that, in conjunction with triangular, orthopteroid mandibles (Kukulová-Peck, 1990), may have been used for slicing live foliar tissue. The assemblage of holometabolous insects at Elmo also comprises some of the earliest known lineages. They are the modern orders Neuroptera and Mecoptera, as well as members of the extinct orders Glosselytrodea and possibly Miomoptera. The larvae of extant basal neuropterans are feeders on live roots (Faulkner, 1990) whereas mecopteran larvae are only rarely herbivorous (Byers, 1987); virtually nothing is known of the feeding habits of glosselytrodean and miomopteran larvae (but see Rohdendorf and Rasnitsyn, 1980, who suggest they were endophytic). From this sketch of potential herbivores at Elmo, it is most likely that the dominant mandibulate herbivores were orthopteroids, either as Orthoptera or possibly the diverse ‘Protorthoptera’; conceivably the larvae of basal holometabolous lineages were consuming live plants as well.

4. Results

4.1. Qualitative analysis

The foliar damage data in this study were assigned to five categories of external-foliage-feeding, defined by Coulson and Witter (1984) for modern insect damage. Present at the Taint locality was hole-feeding, margin-feeding, free-feeding, window-feeding, and skeletonization. Most abundant was hole-feeding. In hole-feeding there is removal of all laminar tissue within a confined area, resulting in encirclement on all sides by a reaction tissue rim that contacts an undamaged lamina surface. Also abundant was margin-feeding, consisting of consumption of all tissue along the edge of a foliar element. Rare free-feeding, an extreme form of margin-feeding, is characterized by the near-total consumption of a foliar element, leaving only major veins and associated flaps of adjacent tissue. Window-feeding, common although often difficult to detect, is the extraction of one or more layers of foliar tissue, but without complete removal of the entire blade. Skeletonization, the consumption of all foliar tissue except for major and sometimes minor veins, was rarely encountered. All five external-foliage-feeding types are pooled in the quantitative analyses of this report.

Eight distinctive types of insect damage have been detected on foliar elements from the Taint locality, most of which occur on particular plant hosts. We have identified (1) prominent hole-feeding in intercostal areas of gigantopterid foliage; (2) much smaller and delicate, circular hole-feeding also on gigantopterid foliage; (3) rare skeletonization on gigantopterid foliage, characterized by mesophyll removal and intact secondary and sutural veins; (4) relatively large, pyriform structures on gigantopterid foliage characterized by a strong, thick, meandering reaction rim enclosing a darker necrotic zone, often containing an excentric circular or ovoidal perforation; (5) nibbled apical margins on small, gigantopterid frond elements; (6) extensive margin-feeding, mostly as cusped excavations or incisions paralleling the midrib in *Taeniopteris* sp. leaves; (7) relatively small, polylobate and necrotic blotches surrounded by well-developed reaction rim tissue, lacking enclosed perforations; and (8) a possible leaf mine on an unidentifiable foliar element. Notably, the first five of these eight

types of herbivory occur on gigantopterid foliage, indicating an overall herbivore preference. Because of the recurrence of most of these stereotyped damage types on numerous specimens of particular plant species, it is likely that they were produced by the same or taxonomically related herbivorous insects.

In the following section question marks attached to figured specimens or plate figures indicate possible or probable assignments. We also have italicized short descriptions that unambiguously define each of the eight types of plant damage. We have included specimens from the Fulda and Emily Irish sites — material that also is of Artinskian age and from Baylor County. These two latter localities were not included in the quantitative analysis.

4.1.1. Large intercostal perforations

Ovoidal to variously lobate excisions characterized by rounded margins surrounded by well-developed tissue reaction rims. These complete excisions of foliar mesophyll tissue are localized at intercostal regions between prominent, often upraised, secondary veins proximal to the midrib. The excisions range in maximum length from a few mm to 1.5 cm; larger excisions generally bear a major axis parallel to secondary venation. Although primary and secondary venation is consistently avoided, some examples exhibit extensions of tertiary venation projecting beyond the reaction rim, into the excavated area. Some excisions are narrow, long, and deployed into a straight to gently meandering course. Apparently no region of the frond or its subdivisions was preferentially targeted.

USNM figured specimens. Taint: 483620, 483621, 483622, 483623, 483624, 483626, 483627, 483629, 483630, 483634, 483641; Fulda: 483650, 483652. Taint: Plate I, 1–10; Plate II, 1, 2, 5, 6, 9, 10; Plate III, 1, 3, 4; Plate IV, 3, 4; Plate V, 10, 11; Plate VII, 1, 11, 12; Fulda: Plate IX, 1, 2, 5.

Plant hosts. Almost entirely on Gigantopteridaceae (*Cathaysiopteris yochelsonii*, *Gigantopteridium americanum*, *Zeilleropteris wattii*); minimally on the cycadophyte *Taeniopteris* sp.

Remarks. Modern perforations of similar shape and size are characteristic of a diverse spectrum of small- to medium sized caterpillars and adult insects that occur on the foliar surface and feed initially by surface abrasion and subsequently by

edge-feeding. The occurrence of elongate and narrow feeding traces may indicate juvenile instars, whereas larger, more equidimensional, polylobate perforations probably represent adult feeding. The avoidance of tougher vascular tissue is consistent with a culprit located on the leaf blade.

It is possible that this pattern of recurring ovoidal to circular feeding holes in adjacent intercostal spaces represents bud feeding. However, knowledge of gigantopterid venation would be needed to confirm such a possibility, and depending on the taxon, bud feeding may or many not avoid fibrous secondary venation (Johnson and Lyon, 1991). Currently, the earliest documented record of bud feeding is on an Upper Cretaceous coryphoid palm (Labandeira et al., 1995).

4.1.2. Small circular perforations

Small (1 to 2 mm in diameter), circular to ovoidal perforations surrounded by modestly-developed, black tissue reaction rims. Except for the avoidance of primary and secondary venation, these perforations occur throughout the blade and probably are clustered. Perforations of this size range are discretely separated from much larger feeding marks of the larger intercostal feeding holes mentioned above.

USNM figured specimens. Taint: 483625, 483626, 483640, 483642. Taint: Plate II, 3–5, 8; Plate V, 5, 8; Plate VI, 1–3, Plate VII, 9.

Plant hosts. Gigantopteridaceae: mostly on *Gigantopteridium americanum*; to a lesser extent on *Zeilleropteris wattii*.

Remarks. Balick et al. (1978, fig. 4) show similar damage, attributed to a presumed insect and with a conspicuous reaction tissue rim, on modern *Asplenium monanthes*. This pattern of feeding is reminiscent of modern phytophagous beetles, particularly Chrysomelidae and Curculionidae (Johnson and Lyon, 1991). However, the earliest relevant phytophagous beetles occur in Late Triassic and Jurassic deposits (Medvedev, 1968; Zherikin and Gratshev, 1993).

4.1.3. Skeletonization

Medium-sized, polygonal perforations surrounded by well-developed rims of reaction tissue that enclose an interior of continuous secondary and sutural venation. Nonvascular mesophyll tissue is absent

among the vein meshwork. The few well documented specimens are approximately 1 cm in length and width, and apparently occur randomly within the intercostal region.

USNM figured specimen. Taint: 483628, ?483630; Emily Irish: 483649; Fulda: 483653. Taint: Plate III, 1, 2, ?7, ?8; Plate VII, 6; Emily Irish: Plate VIII, 1–7; Fulda: Plate IX, 7, 8.

Plant host. Gigantopteridaceae; mostly *Gigantopteridium americanum*; other gigantopterids also attacked.

Remarks. This rare interaction type grades into hole-feeding. An intermediate condition is characterized by strands of vascular tissue that project into the excavated area to various degrees. However these vascular tissue remnants are discontinuous and do not join centrally. In some cases skeletonization is intense and occurs extensively on foliar surfaces (Plate VIII, 1). A similar type of feeding damage has been documented for modern orthopteran feeding on certain dicotyledonous leaves (Kazakova, 1985).

4.1.4. Large blotches with angulate reaction rims

Ovoidal to pyriform blotches of necrotic tissue, often characterized by one or two acute projections controlled by local venational patterns, and surrounded by a dark, well developed, and curvilinear rim of reaction tissue. The discolored zone inside the reaction tissue rim is darker than the surrounding foliar tissue, and contains accentuated venation. At least three of the larger specimens contain well-developed, ovoidal, eccentric perforations with modest reaction rims. Of four measured specimens, minimum dimensions are 0.8 cm and maximum dimensions are 1.7 cm. Boundaries of these structures are constrained by primary and secondary, but not tertiary venation.

USNM figured specimens. Taint: 483626 (immature example), 483628, 483631, 483640; Fulda: 483654. Taint: Plate II, 7, Plate III, 3, 5, 6, 9, 10, Plate VII, 7, 8; Fulda: Plate IX, 9, 10.

Plant host. Gigantopteridaceae: *Cathaysiopteris yochelsonii*, *Gigantopteridium americanum*, *Zeilleropteris watti*.

Remarks. This feeding trace superficially resembles that of blotch- or blister mines produced by some modern insects on pteridophytic foliage. Modern fern-mining taxa producing blotch mines include principally the Diptera, especially several species of

Chirosia (Anthomyiidae; Lawton, 1976; Brown and McGavin, 1982); and *Melanagromyza* sp., *Phytolirionomyza felti* (Malloch) and *Phytomyza dryoptericola* Sasakawa (Agromyzidae; Frost, 1924; de Meijere, 1940, Sasakawa, 1961; Spencer, 1990). Other documented groups are coleopterans, such as species of *Neotrachys* (Buprestidae; Hespeneide, 1982) and an undescribed lepidopteran cosmopterygid (Shuter, 1990). The insect damage on modern pteridophytic foliage is probably the best modern analog to anatomically similar Permian gigantopterid foliage. Alternatively this structure may represent the radial spread of epiphyllous fungi around a feeding perforation (Wang, 1997), or possibly preservationally indistinct surface grazing that is occasionally marked by an ovoidal perforation.

4.1.5. Apical margin feeding

Shallow and continuous extraction of foliar margin tissue, with occasional, moderately arcuate excisions occurring deeper into the apex of frond lamina. Reaction tissue rims are well developed; there is no indication of extension of veins beyond the herbivorized margin or of mandible marks. This damage occurs principally on frond apices, especially of smaller and possibly immature foliage.

USNM figured specimens. Taint: 483627, 483632. Taint: Plate II, 9, 10; Plate III, 11, 12; Plate VI, 1, 2; Plate VII, 4.

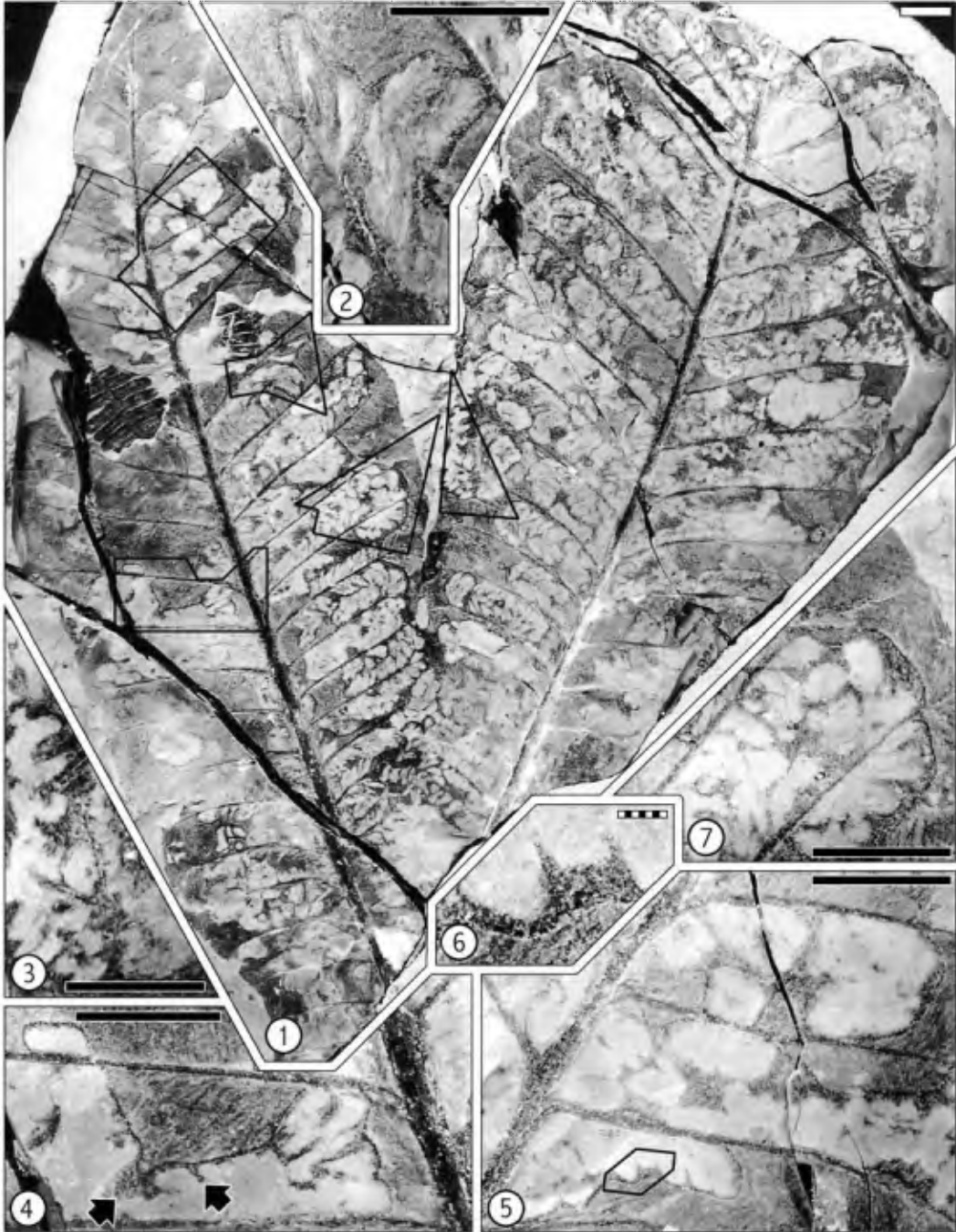
Plant hosts. Gigantopteridaceae: Mostly *Gigantopteridium americanum*.

Remarks. This type of feeding is consistent with a relatively small insect nibbling the immediate edge of a foliar margin. A shallow and continuous feeding pattern along the foliar margins of younger or smaller gigantopteridaceous leaves also indicates that the herbivore culprit was relatively diminutive and bore weaker mandibulate mouthparts than the taeniopterid margin-feeder described below.

4.1.6. Extensive cusped margin-feeding

Large cusped excisions of foliar tissue ranging in length along the leaf margin from 0.5 to approximately 2.0 cm, with robust, often upraised, reaction tissue rims. Occasional segments of characteristic strands or stubs of vascular tissue project beyond the reaction tissue, and often are highlighted by lighter-colored rock matrix. In some specimens small inden-

PLATE VIII



tations into the excavated margin suggests mandible chew marks of the foliar tissue.

USNM figured specimens. Taint: 483627, 483633, 483635, 483636, 483637; Fulda: 483651, 483652. Taint: Plate II, 9, 10; Plate IV, 1, 2, 5–11; Plate VII, 5, 10; Fulda: Plate IX, 3–6.

Plant hosts. Principally *Taeniopteris* sp.; to a lesser degree the gigantopterids *Gigantopteridium americanum* and *Zeilleropteris wattii*.

Remarks. The large size of the cusped excisions on the foliar margin suggests that the culprit was a large, possibly protorthopteran or other orthopteroïd insect, that gained purchase of the foliar element by possessing clasping prothoracic legs and well-developed, elongate mouthparts (Gangwere, 1966; Edwards and Wratten, 1980). Taphonomic evidence suggests that the foliar texture of *Taeniopteris* sp. was sufficiently leathery that a strongly mandibulate insect was required clasp the leaf edge for consumption of fibrous tissue. The presence of veinal strands along the incised margin is almost identical to modern orthopteran damage to parallel-veined monocot leaves (Kazakova, 1985). Similar damage is caused by insects on modern pteridophytes including modern *Marattia* and *Angiopteris* (Labandeira, pers. observ.), *Hypolepis* and *Polypodium* (Balick et al., 1978, fig. 2), and other fern taxa (Blackith, 1973; Rowell, 1978; Rowell et al., 1983; Floyd, 1993).

4.1.7. Small blotches with lobate reaction rims

Typically elliptical, mono- to polylobate, regions of internal foliar damage approximately 0.7 to 1.0 cm in maximum and 0.4 to 0.7 in minimum diameter. These well-developed, sinuate rims of reaction tissue enclose central blotches that bear disrupted

mesophyll but apparently have normal surface tissues. Well-preserved and carbonized veins traverse the blotches and are confluent with venation in the surrounding, unaffected lamina. The position of the damage is throughout the pinnae, but with a strong concentration adjacent the midrib.

USNM figured specimens. Taint: 483639. Taint: Plate V, 1–4; Plate VII, 3.

Plant host. The pteridophyll, *Comia* sp.

Remarks. These feeding traces are tentatively interpreted either as insect surface grazing of upper foliar tissues, or as a blotch leaf miner. The presence of an apparently necrotic region surrounded by a reaction tissue rim and the persistence of wisps of vascular tissue across the lesion indicate that feeding was tissue selective. Unlike the necrotic surface blotches discussed above, these lesions on *Comia* sp. lack an ovoidal perforation with surrounding reaction tissue. Balick et al. (1978, fig. 3) have figured a similar type of damage on modern *Adiantum tenerum* Swartz., replete with accentuation of venation and presence of surrounding reaction tissue rims.

4.1.8. Possible leaf mine

A sinusoidal, line of carbonized tissue surrounded by foliar tissue, similar in structure to a rim of reaction tissue, such as the serpentine reaction rims mentioned above. This feature consists of three successive crests of similar amplitude and wavelength, and increases in width from approximately 0.2 mm to 1.0 mm. The absence of interpretable surrounding venation does not allow a comparison of the relationship of this feature to adjacent foliar architecture.

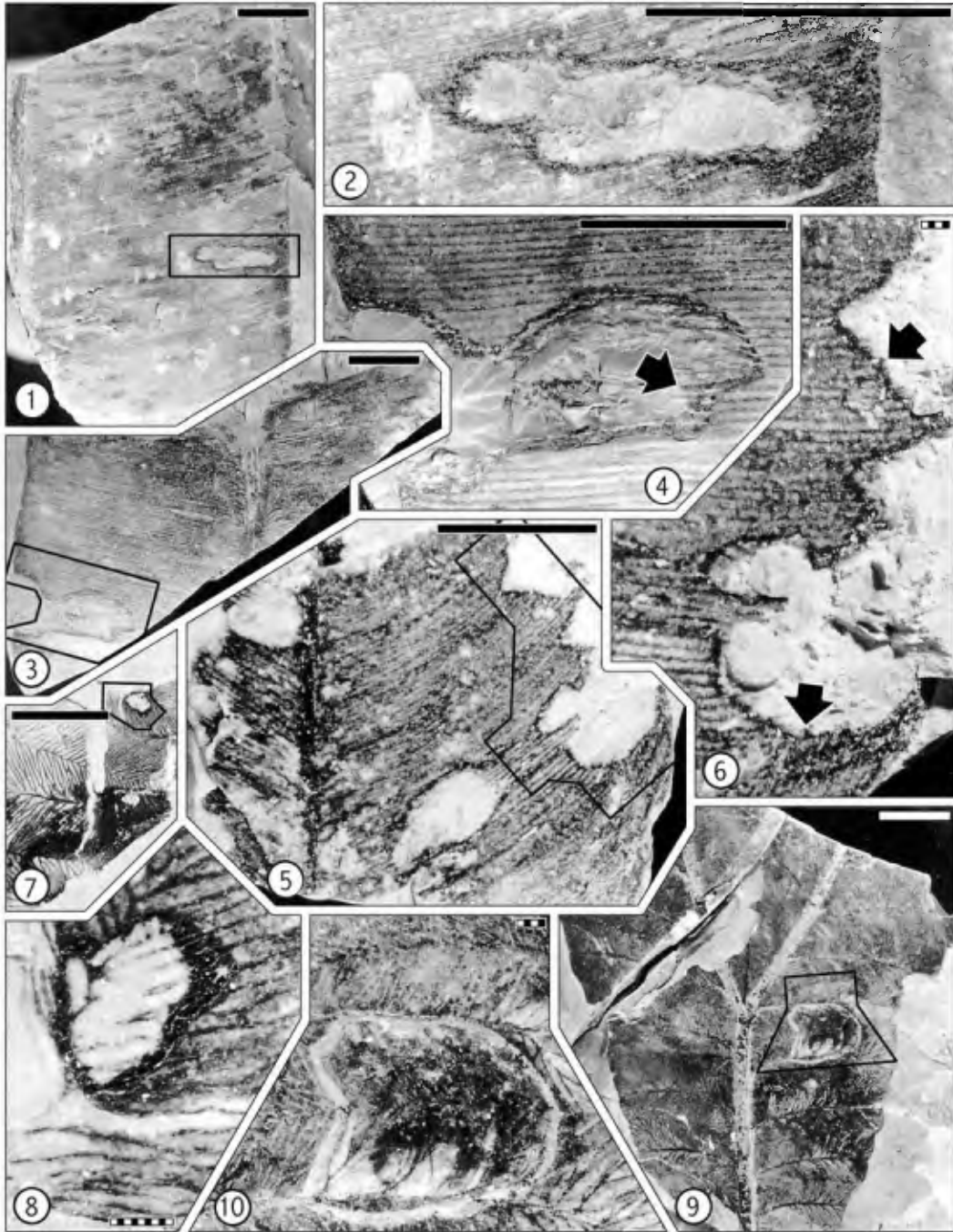
USNM figured specimens. Taint: 483640, 483643. Taint: ?Plate V, 5, 9; Plate VI, 4, 5; Plate VII, 2.

PLATE VIII

An example of a skeletonized specimen of *Gigantopteridium americanum* (USNM-483649) from the penecontemporaneous, nearby Emily Irish locality (USGS loc. 8959), approximately 25.5 to 26.5 km SW of Seymour, Baylor Co., TX (Mamay, 1968).

1. Entire skeletonized frond; maximum length of frond fragment is 26 cm (USNM-483649).
2. Detail of left half of frond at the upper-left of 1, showing skeletonized area, including thick rim of reaction tissue.
3. Detail of right half of frond at center-right in 1, showing skeletonized area along frond margin.
4. Detail of left half of frond at lower-left in 1, showing wisps of tissue containing tertiary venation, two which are highlighted by arrows.
5. Detail of left half of frond at upper-left in 1, displaying skeletonization and wisps of tissue containing tertiary venation at lower-left.
6. Enlargement of lower-left area in 5 showing tissue stringers left behind by selective feeding.
7. Enlargement of skeletonized area of the left-half of the frond at center-left in 1. Scale bars: solid pattern = 1 cm; striped pattern = 0.1 cm.

PLATE IX



Plant host. Unknown giantopterid, possibly *Gigantopteridium americanum*.

Remarks. The plant host (483643) is mostly an impression that lacks any indication of venation, except for a few faint, gray lines near the putative mine. Two small, dark seed-like structures occur impressed on the foliar surface. Close examination of this specimen reveals that the sinusoidal, mine-like trace does not form the edge of the leaf; rather it lies within the lamina. A similar structure, possibly belonging to this interaction type, occurs in a second richly-veined specimen of *Gigantopteridium americanum* (483640). This sinusoidal line, although faint and not documented photographically, occurs along the margin of the foliar surface, shallowly truncating tertiary venation, and following a path that is broadly controlled by the secondary venational pattern.

4.2. Quantitative analysis

Distinctive patterns of host plant use are documented in Table 1 and Figs. 3–6, indicating that giantopterids are the preferred host of insect herbivores. These data originate from an evaluation of 1,346 foliar items, representing a total foliar surface area of 11,526.24 cm². In terms of linear square dimensions these data represent somewhat more than one square meter (107.35 cm × 107.35 cm). The raw data (Fig. 3) provides total original surface area and total insect-damaged area recorded for each plant taxon. These raw values for total orig-

inal and damaged surface areas were recalculated to represent the average original and herbivorized foliar areas for each taxon (Fig. 4). This was done by dividing the total original surface area (cm²) by the number of foliar elements for each taxon. When converted to a herbivory index expressing the proportion of herbivorized area removed (Fig. 5), all three giantopterid taxa exhibited elevated levels of plant tissue removal, ranging from a low of 3.05% for *Gigantopteridium americanum*, to 3.96% for *G. americanum/Cathaysiopteris yochelsonii*, to a high of 4.4% for *Zeilleropteris wattii*. Remaining but relatively abundant taxa exhibited relatively low levels of herbivory, notably *Callipteris* sp. at 1.78%, *Comia* sp. at 1.32%, and *Taeniopteris* sp. at a very low 0.16%. The remaining plant taxa, including specimens of uncertain affinity, lacked demonstrable foliar damage or bore only a trace of herbivory. A summary of foliar tissue removed by insects at Taint resulted in a bulk value of 2.55%. This value, like the percentage of herbivorized leaves (31.8%), is approximately a third of modern levels.

The frequency of attack of foliar elements (Table 1, Fig. 6) parallels the pattern found in the area removal analysis above. All three giantopterid taxa reveal relatively high levels of attack frequency, ranging from 39.6% for *Gigantopteridium americanum*, to 71.8% for *G. americanum/Cathaysiopteris yochelsonii*, and 82.8% for *Zeilleropteris wattii*. By comparison, the frequency of foliar attack is relatively low for *Comia* sp. at

PLATE IX

Examples of insect folivory on *Taeniopteris* sp. and *Gigantopteridium americanum* from the slightly younger, nearby Fulda locality (USGS loc. 10063) (Read and Mamay, 1964).

1. Hole-feeding adjacent the margin of a *Taeniopteris* sp. leaf fragment (USNM-483650).
2. Enlargement of folivorized area in 1, showing well-developed and thick rim of reaction tissue.
3. Margin-feeding on a *Taeniopteris* sp. leaf fragment (USNM-483651).
4. Enlargement of folivorized area in 3, displaying reaction rim tissue and wisps of secondary venation and associated tissue at arrow.
5. Fragment of *Taeniopteris* sp. (USNM-483652) with hole- and margin-feeding.
6. Detail of folivorized margin in 5, illustrating the overall cusped pattern of the feeding damage, and a smaller mandible chew marks along the regions indicated by the arrows.
7. Skeletonization in a *Gigantopteridium americanum* frond fragment (USNM-483653).
8. Detail of skeletonization in area at the upper-right of 7, showing a pronounced reaction tissue rim and continuity of tertiary venation within the damaged area.
9. A *Gigantopteridium americanum* fragment (USNM-483654) with a large necrotic blotch containing an angulate reaction rim.
10. Detail of large necrotic blotch at center-right in 9, displaying well-developed reaction rim that is angulate adaxially and curvilinear abaxially. Scale bars: solid pattern = 1 cm; striped pattern = 0.1 cm.

Table 1

Bulk floral original and herbivorized surface area and percentage removal for the Taint Locality from the Early Permian of Texas

Foliar taxon	Number of specimens	Total original surface area (cm ²)	Total herbivorized area (cm ²)	Proportion of herbivorized area removed (%) ^a	Average original area per leaf (cm ²)	Average herbivorized area per leaf (cm ²)	Proportion of herbivorized leaves ^b (%)	Herbivory index ^a (%)
<i>Asterophyllites</i>	1	1.76	0	0	1.76	0	0	0
? <i>Brachyphyllum</i>	45	102.62	0	0	2.28	0	0	0
<i>Callipteris</i>	3	5.05	0.09	1.78	1.68	0.03	33.3	1.78
<i>Comia</i>	231	2887.68	38.16	1.32	12.50	0.17	22.1	1.32
<i>Gigantopteridium</i>	139	724.23	22.13	3.06	5.21	0.16	39.6	3.05
<i>Gigantopteridium</i> / <i>Cathaysiopteris</i>	213	2406.08	95.12	3.95	11.30	0.45	71.8	3.96
<i>Sphenophyllum</i>	6	28.07	0	0	4.68	0	0	0
<i>Taeniopteris</i>	269	1813.51	2.86	0.16	6.74	0.01	5.97	0.16
<i>Wattia</i>	13	31.45	0.01	0.03	2.42	0.001	7.7	0.41
<i>Zeilleropteris</i>	163	2987.55	131.57	4.4	18.33	0.81	82.8	4.40
Indeterminate broadleaf	258	528.91	3.8	0.72	2.05	0.02	6.2	0.73
Indeterminate conifer	4	2.21	0	0	0.55	0	0	0
Fructifications	1	7.12	0	0	7.12	0	0	0
Totals/averages	1346	11526.24	293.80	2.55	8.56	0.22	31.8	2.55

^a Proportion of herbivorized area removed (%) = (total herbivorized area ÷ total original surface area) × 100; herbivory index = (average herbivorized area per leaf ÷ average total area per leaf) × 100.

^b Proportion of herbivorized leaves = (number of damaged leaves ÷ total number of leaves) × 100.

22.1%, and *Taeniopteris* sp. at 6.0%. Other pteridophylls and unassigned taxa, some of which were rare and thus not adequately sampled, had attack frequency levels of 7.7% or lower, or lacked herbivory (Table 1, Fig. 5).

A comparison of the two outcrop collection strategies represented in the Taint floral data is provided in Table 2 and Fig. 7. The lower panel of Fig. 7 shows a strategy in which all foliar material greater than 1 cm² was retrieved; the upper panel exhibits a representative sample method in which selected foliar items were retained for inclusion in the collection. Although the first method only represents approximately 22% of the collection (21.5% of the foliar items and 22.1% of the surface area), it is a literal record of foliar material at the outcrop. The second method, representing a sample of outcrop foliar material, is probably an underestimate of herbivorized area. In this study, we have included both collection strategies as our data (Table 2, Fig. 7), realizing that our values probably underestimate somewhat the actual levels of insect herbivory at the outcrop. It is

suggested that future studies use a collection strategy in which all material greater than 1 cm² is retrieved for those sparsely-distributed bulk floras represented by low total foliar surface area. Under conditions of high outcrop abundance and high total foliar surface area, a representative sample method may be appropriate (see Burnham, 1993, for discussion).

5. Discussion and conclusions

This study is the first combined qualitative and quantitative investigation of insect herbivory from a bulk-collected, abundant, and well-preserved flora from the Paleozoic. Previous investigations of plant–insect associations from Paleozoic compression floras have been examinations of selected, albeit revealing, insect damage on one to several, illustrated leaves that originate from larger paleobotanical collections. Currently, there is no assessment of variation of herbivory intensity among varied floras within a regionally extensive, isochronous landscape for the

Table 2

Original and herbivorized surface area and percentage removal for the Taint Locality from the Early Permian of Texas, partitioned by collection strategy

Foliar taxon	Number of specimens	Total original surface (cm ²)	Total herbivorized area (cm ²)	Proportion of herbivorized area removed ^a (%)	Average original area per leaf (cm ²)	Average herbivorized area per leaf (cm ²)	Proportion of herbivorized leaves ^b (%)	Herbivory index ^a (%)
A. Representative sample subset								
<i>Asterophyllites</i>	1	1.76	0	0	1.76	0	0	0
? <i>Brachyphyllum</i>	2	21.77	0	0	10.89	0	0	0
<i>Callipteris</i>	2	3.95	0.09	2.28	1.98	0.05	50.0	2.28
<i>Comia</i>	207	2583.89	35.21	1.36	12.48	0.17	21.3	1.36
<i>Gigantopteridium</i>	125	635.42	18.71	2.94	5.08	0.15	39.2	2.95
<i>Gigantopteridium</i> / <i>Cathaysiopteris</i>	167	1695.90	63.41	3.74	10.16	0.38	65.9	3.74
<i>Sphenophyllum</i>	6	28.07	0	0	4.68	0	0	0
<i>Taeniopteris</i>	220	1379.751	2.84	0.21	6.27	0.01	6.4	0.21
<i>Wattia</i>	0	–	–	–	–	–	–	–
<i>Zeilleropteris</i>	107	1782.40	81.89	4.59	16.66	0.77	83.2	4.59
Indeterminate broadleaf	200	487.98	3.80	0.78	2.44	0.02	8.0	0.78
Indeterminate conifer	3	1.53	0	0	0.55	0	0	0
Fructifications	1	7.12	0	0	7.12	0	0	0
Totals/averages	1041	8629.54	205.95	2.39	8.29	0.20	31.00	2.39
B. Subset representing collection of all specimens greater than 1 cm²								
<i>Asterophyllites</i>	0	–	–	–	–	–	–	–
? <i>Brachyphyllum</i>	43	80.85	0	0	1.88	0	0	0
<i>Callipteris</i>	1	1.1	0	0	1.1	0	0	0
<i>Comia</i>	25	308.36	2.95	0.96	12.33	0.12	28.0	0.96
<i>Gigantopteridium</i>	14	88.81	3.42	3.85	6.34	0.24	42.9	3.85
<i>Gigantopteridium</i> / <i>Cathaysiopteris</i>	47	714.43	95.12	4.44	15.20	0.68	93.6	4.45
<i>Sphenophyllum</i>	0	–	–	–	–	–	–	–
<i>Taeniopteris</i>	269	429.19	2.86	0.01	9.13	trace	4.3	0
<i>Wattia</i>	13	31.45	trace	0.03	2.42	trace	7.7	0.04
<i>Zeilleropteris</i>	163	747.16	42.49	5.69	20.75	1.18	83.3	5.69
Indeterminate broadleaf	258	40.93	0	0	0.71	0	0	0
Indeterminate conifer	4	0.68	0	0	0.68	0	0	0
Fructifications	0	–	–	–	–	–	–	–
Totals/averages	285	2442.96	80.64	3.30	8.57	0.28	31.6	3.30

^a Proportion of herbivorized area removed (%) = (total herbivorized area ÷ total original surface area) × 100; herbivory index = (average herbivorized area per leaf ÷ average total area per leaf) × 100.

^b Proportion of herbivorized leaves = (number of damaged leaves ÷ total number of leaves) × 100.

Early Permian, or within a vegetational type across macroevolutionary time (Scott et al., 1996; Labandeira, 1997b). This analysis is the first installment of an ongoing examination of insect herbivory in the fossil record. Although the data obtained herein are tentatively compared with modern values, there are other related and conceptual themes germane to our results.

5.1. Spectrum and intensity of Early Permian herbivory

The material of this study, preserved as compression fossils with extensive foliar surfaces, documents several prominent subtypes of external foliage feeding. There has been previous recognition of the timing of appearance of major external fo-

liage feeding types in the fossil record (Stephenson and Scott, 1992; Scott et al., 1992), albeit our data indicates a much earlier occurrence for skeletonization, hole-feeding and probably surface feeding than previously assumed. The predominance of several types of external foliage feeding at the Taint site and associated compression floras is supplemented by somewhat older plant/insect interaction data derived from taphonomically different, three-dimensionally preserved, coal-swamp deposits about 1100 km to the northeast in Illinois. Examination of plant–insect interactions in these coal-ball floras indicates the presence of piercing-and-sucking, galling, stem boring, and sporivory-feeding types that are impossible or difficult to detect in compression floral material. Thus these two, different yet complementary, modes of foliar preservation currently present our best glimpse into Paleozoic insect herbivory on disparate vegetational types at a continental scale.

The spectrum of external foliage feeding at the Taint locality contains several types of margin- and hole-feeders, skeletonizers, and probable surface feeders. Additionally, with the exception of the conifer ?*Brachyphyllum*, all abundant foliage was attacked to some extent. Though herbivore intensities varied by taxon, broadleaved foliage collectively was used by external feeders in a variety of ways. It is difficult to establish whether particular insect taxa were specializing on all tissue types at the margins of foliar elements, on nonmarginal interveinal mesophyll, or on adaxially located surface tissues. However, three lines of evidence — stereotyped patterns of plant damage, evidence for host specificity (see following section), and the structural diversity of numerous insect species in a well-documented, nearby and coeval insect fauna — jointly provide strong support for inferring the presence of insect folivore specialization.

A comparison of the spectrum of Lower Permian herbivory to that of recently documented early Mesozoic floras is instructive. While margin-feeding, hole-feeding and skeletonization are dominant on gigantopterids at Taint, all three feeding modes are found during the early Mesozoic, but on a taxonomically different flora consisting of filicalean ferns, bennettitaleans, conifers and enigmatic gymnosperms known from the Middle and Late Triassic of Europe (Grauvogel-Stamm and Kelber, 1996) and Late Triassic of the southwestern United States (Ash, 1997). By the Late

Triassic some hole feeding had been transformed into elongate slot-feeding (Ash, 1997) resembling damage produced by modern chrysomelid beetles (Selman, 1988; Oyama and Dirzo, 1991). Additionally, twig- and shoot galls are evident on conifers and other gymnosperms (Grauvogel-Stamm and Kelber, 1996; Ash, 1997); borings of cambial and adjacent woody tissues are described from several coniferous taxa (Walker, 1938; Linck, 1949); and leaf-mines are recorded in seed-ferns (Rozefelds and Sobbe, 1987). Very little is known of Late Permian and Early Triassic floras that can potentially link these two suites of plant/insect associations.

5.2. *Insect host specificity and gigantopterid foliar structure*

Whereas the pteridophyll *Comia* and cycadophyte *Taeniopteris* were relatively abundant elements at the Taint locality, they exhibited significantly lower levels of herbivory than other co-occurring taxa. Interestingly, all three gigantopterid taxa, irrespective of their measured original surface area, exhibit approximately the same elevated proportion of foliar element area removal by insects: from 3.0 to 4.4%. Insect preference for gigantopterid hosts also is supported by parallel data indicating that the percentage of herbivorized gigantopterid foliar elements was significantly greater than herbivorized foliar elements of other taxa. Furthermore, of the eight types of herbivore damage recognized, five occur entirely or predominantly on gigantopterid taxa.

Several authors have mentioned the similarities between gigantopterids and anthophytes, based on features of the foliage (Mamay et al., 1988; Mamay, 1989), fructifications (Li and Yao, 1983), vernation (Mamay et al., 1988), and possibly vessel elements (Li and Tian, 1990; Li et al., 1996). Alternative interpretations for the affinities of gigantopterids cite the absence of well-documented reproductive structures and the occurrence of parallel foliar morphologies in gymnosperm lineages (Li et al., 1994, 1996; Trivett and Pigg, 1996). Although the phylogenetic relationship between gigantopterids and anthophytes currently remains unresolved, the large and undivided foliar surfaces, buttressing secondary veins, and other features of foliar physiognomy present in the Taint gigantopterids, are associated with elevated

levels of insect herbivory. Apparently gigantopterid foliage was sufficiently abundant and nutritionally rewarding that it was consumed preferentially by a varied insect fauna. Notably, several specimens at Taint and two nearby coeval localities (Plate I, 1–10; Plate II, 1, 2; Plate VII, 1, 12; Plate VIII, 1–6) exhibit extensive riddling of gigantopterid laminae, similar to Cenozoic and modern patterns of coleopteran or larval lepidopteran damage on dicotyledonous leaves (Stephenson and Scott, 1992; Johnson and Lyon, 1991). Although gigantopterid floras are poorly understood, examination of published illustrated material from several sources does reveal evidence for insect herbivory, including Read and Mamay (1964; pl. 17, fig. 1), Asama (1976, pl. 30, fig. 6) and Li et al. (1994, fig. 3).

The significantly decreased palatability of pteridophyll, cycadophyte, and other, unidentified, foliage is notable. Possible reasons for herbivore avoidance of these plants include deterrent secondary compounds, such as tannins, insect-mimicking hormones, and other secondary compounds that occur in modern ferns and cycads (Hikino et al., 1973; Jones and Firm, 1979; Moretti et al., 1981; Cooper-Driver, 1985; Vovides et al., 1993). Additionally, the leathery and resin-laden glandular physiognomy of Taint *Taeniopteris* sp. leaves (Mamay, 1976) may have deterred insect consumption. It is a common observation that pteridophyll and cycadophyte foliage exhibit minimal damage in all known Lower Permian floras from north-central Texas (Mamay and Labandeira, pers. observ.). Based on qualitative data, this pattern apparently does not extend to seed fern foliage in earlier, peat- and clastic-substrated swamp forests (Labandeira and Beall, 1990; Labandeira, 1997b, 1998).

5.3. Plants, insects, and escalation

Perhaps the most intriguing result of our evaluation of the Lower Permian flora at the Taint locality is that 2.55% of overall surface area was removed by herbivory. It is significant that this value is approximately a third of the level of herbivore-removal percentages in various bulk-sampled, extant tropical and subtropical forests (Wint, 1983; Robertson and Duke, 1987; Lowman, 1987, 1992; Wright and Giliomee, 1992; Aide, 1993). It also is approxi-

mately a third of the value that Hendrix and Marquis (1983) found, on average, for modern orthopteran herbivory on three Costa Rican fern species. In particular, the gigantopterid *Zeilleropteris wattii* exhibits a foliar area removal value of 4.4%, about half the modern value for bulk floras, and a frequency-of-attack percentage of 81%, approaching modern values of around 95 to 100%. In studies of leaf-area removal by modern insect herbivores, the value for *Zeilleropteris wattii* is comparable, for example, to the $4.3 \pm 3.3\%$ for the evergreen Mediterranean shrub *Daphne laureola* L. (Thymelaeaceae), the $3.2 \pm 1.5\%$ for the deciduous North American tree *Acer pensylvanicum* L. (Aceraceae) (Marquis, 1988; Alonso and Herrera, 1996), and the 3 to 8% for the Neotropical liana *Connarus turczaninowii* Tr. (Connaraceae) (Aide and Zimmerman, 1990). From these comparisons, we conclude that one taxonomic component of the flora at Taint — the gigantopterids in general and *Zeilleropteris wattii* in particular — were being consumed by insect herbivores in essentially modern styles and intensities. This test, however, needs to be broadened to determine escalation between plants and insects in macroevolutionary time (Van Valen, 1973; Vermeij, 1987): Additional data needs to be collected from other vegetational types in time and space.

A herbivore removal area of 2.55% is probably an underestimate since preservational and methodological biases tend to minimize original herbivorized surface area. These biases include a conservative approach to reconstructing original foliar size and shape, the inability to detect foliar elements almost entirely or totally consumed by insect folivores (Coley, 1982; Lowman, 1984), a collection strategy in which herbivory was underestimated in 78% of the flora (Table 2, Fig. 7), and the tendency of fragile and typically more insect-palatable, herbaceous vegetation (Scriber and Slansky, 1981) to be more poorly-preserved than more architecturally durable foliage of arborescent plants (Thomas and Spicer, 1987). A related issue are several recent studies that have expressed concerns about measurement of standing crop biomass that do not account for the annual variability in damage type and intensity (Lowman, 1985; Coley, 1988; Filip et al., 1995; Coley and Barone, 1996). These studies suggest that such measures must be conducted during the entire course of a growing sea-

son to provide a more accurate annual rate of herbivory (Newberry and De Foresta, 1985; Coley and Barone, 1996). Since the flora from the Taint locality undoubtedly is a time-averaged assemblage representing many years of leaf fall, temporal variability in herbivore removal rates was integrated as the deposit formed (cf. Behrensmeier and Hook, 1992).

Virtually all previous accounts discussing insect feeding strategies and levels during the Late Carboniferous and Early Permian have relegated mandibulate folivores to an insignificant or nonexistent role (Karny, 1926; Cox, 1974; Zwölfer, 1978; Strong et al., 1984; Shear and Kukulová-Peck, 1990; DiMichele and Hook, 1992; Hughes, 1994), focusing instead on the ubiquity of detritivory (Hamilton, 1978; Pearce, 1989; Labandeira, 1998) and occasional acknowledgments that piercing-and-sucking palaeodictyopteroids may have fed on live, spore-bearing fructifications (Carpenter, 1971; Sharov, 1973; Rohdendorf and Rasnitsyn, 1980; Kukulová-Peck, 1990). Nevertheless our documentation of elevated folivory by mandibulate insects, at least in one riparian-associated vegetational type, should not be surprising. The diversity of Early Permian mandibulate insect body forms and mouthpart types suggests that some taxa were herbivorous. Furthermore, foliar tissues deployed as conspicuous photosynthetic organs had been present for tens of millions of years, extending minimally to the widespread Euramerican, tree-fern dominated coal- and clastic-swamp forests of the Late Pennsylvanian (Labandeira, 1998, 1999). The appearance of gigantopterids during the Early Permian, bearing large and varied frond shapes, accentuated this trend. It is in this nonuniformitarian context of a physiognomically and taxonomically varied flora, with many taxa lacking comparisons to modern vegetational types, that understanding of Paleozoic insect herbivory should be made. Recent pteridophyte and gymnospermous taxa, many of which are relictual and represent a fraction of their preangiospermous range of morphotypes, are sub-optimal analogs for understanding Paleozoic plant–insect interactions.

Considerable additional data from various Late Carboniferous and Permian plant communities are needed to address the issue of whether the type and intensity of insect herbivory conforms to the ecological saturation hypothesis (ESH) or the ex-

panding resources hypothesis (ERH), both of which were placed in macroevolutionary context by Strong et al. (1984). ESH maintains that insects ecologically invaded plant tissues and established plant associations relatively early in macroevolutionary time (Raup, 1972; Gould, 1981; May, 1981; Foote, 1993), whereas ERH holds that such plant–insect interactions occurred gradually, accumulating incrementally during macroevolutionary time (Schoener, 1974; Whittaker, 1977; Zwölfer, 1978; Futuyma, 1986; Mitter and Farrell, 1991; Cornell and Lawton, 1992). The singular data of this Lower Permian flora, although representing only one sample in a varied, vegetated landscape, in addition to qualitative results from coal-swamp floras, suggest that early ecological saturation may be the more realistic hypothesis.

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