Insect Fluid-Feeding on Upper Pennsylvanian Tree Ferns(Palaeodictyoptera, Marattiales) and the Early History of the Piercing-and-Sucking Functional Feeding Group

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ABSTRACT We document the presence of the piercing-and-sucking functional feeding group and the dietary targeting of vascular tissue (phloem and xylem) in marattialean tree-fern rhachises from a Late Pennsylvanian (302 Ma) coal-swamp forest in the Illinois Basin. Our evidence originates from permineralized peat that exhibits cellular-level preservation of tissues from whole *Psaronius* tree-fern rhachises; it includes 3 stylet probes, each of which traverses epidermal tissues and parenchyma, and terminates in a distinctive feeding cavity within phloem and xylem of a vascular strand. The stylet probes are lined with an opaque, sheathlike material, and are principally intracellular, although large gum sac cells are avoided. One of their most diagnostic features is 1 or 2 ridges occurring on the inner surface of each stylet probe, paralleling most of the probe length. These ridges, documented by light and scanning electron microscopy, are interpreted as host tissue casts of interstyletal sulci. From these and other features of stylet-trace morphology, we conclude that the herbivore was an insect of the order Palaeodictyoptera rather than an hemipteroid insect. Well developed reaction tissue surrounding the stylet trace developed while the plant host was alive, demonstrating herbivory. Previous studies have documented piercing-and-sucking in several examples of plant damage from the Early Devonian to Late Pennsylvanian (395–290 Ma). The oldest credible examples are plant lesions indicating piercing-and-sucking arthropods from 2 Lower Devonian deposits. We hypothesize that in later Middle Pennsylvanian, equatorial, coal-swamp forests of Euramerica, the dominant arborescent plants possessed vascular tissues largely unavailable to insects, because they were either deeply embedded in thick cortical tissues or protected by outer indurated, peridermal tissues. Subsequent tree-fern forests of the Late Pennsylvanian provided accessible vascular and other tissues to surface-dwelling insects with stylate mouthparts–a condition which continued into the Permian and propelled the hemipteroid radiation.

KEY WORDS Palaeodictyoptera, Marattiales, piercing-and-sucking, plant–insect interaction, fossil insects

PIERCING-AND-SUCKING INSECTS ARE an important but underappreciated functional feeding group on terrestrial plants. Because the physical manifestation of damage by piercing-and-sucking insects is generally inconspicuous and difficult to quantify (Pollard 1973), they often are neglected in estimates of herbivore loads on modern plants. Although the few studies that have quantified plant tissue losses attributable to piercers-and-suckers have used only aphids and phylloxerans, collectively these data indicate major effects on plant-host fitness. Examples include Dixon (1970) who determined that, in the absence of aphids, the maple *Acer pseudoplatanus* (L.) could produce up to 280% more stem wood; Llewellyn (1972), who assessed that the effect of aphid herbivory per unit of vegetation on the basswood *Tilia* x *vulgaris*

Hayne was 24 times that of co-occurring caterpillars; Fedde (1973), who reported that 28% more seed was destroyed by chalcids from phylloxeran infested Fraser fir, *Abies fraseri* Poiret, than from noninfested populations; and I. C. Feller (personal communication) who concluded that the leaf area of black mangrove, *Avicennia germinans* (L.), was reduced 16.3% by the presence of aphid nymphs. These data indicate that piercing-and-sucking insects are a key herbivore group in many plant communities, and may be more significant than chewing insects (Pollard 1973; T. Whitham, personal communication). Additionally, piercing-and-sucking insects are important colonists of plants, a phenomenon that has been studied on model systems, such as bracken, *Pteridium aquilinum* Kuhn. Distinct piercing-and-sucking insect faunas have originated on bracken fronds repeatedly and independently in disparate biogeographic settings throughout the world (Lawton 1984, Lawton and MacGarvin 1985, Winterbourn 1987, Compton et al. 1989, Shuter

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1990, Lawton et al. 1993) during the late Cenozoic (Page 1979). These patterns suggest that a sizable pool of colonizing herbivores was available to exploit bracken dietarily. However, although piercers-and-suckers are consummate herbivores and adept at colonizing available food substrates in geologic time, the origin and early paleobiology of piercing-and-sucking is the poorest known of all herbivore functional feeding groups.

Diversity of Modern Piercing-and-Sucking Insects

Modern piercing-and-sucking insects consist principally of hemipteroids, Siphonaptera, and nematocerous Diptera, although the use of stylets for penetration of host tissues has originated at least 6 times within the Coleoptera (Labandeira 1990) when evaluated at the family level (Besuchet 1972, Sen Gupta and Crowson 1973, Dajoz 1976, Vit 1977, Crowson 1981, Pakaluk 1987, Slipinski 1988), and even within 2 subgroups of noctuid Lepidoptera (Darwin 1875, Bänziger 1980). Of fluid-feeding clades, herbivory occurs overwhelmingly among the condylognathan hemipteroids, particularly Thysanoptera, Sternorrhyncha, Auchenorrhyncha, and pentatomomorph and cimicomorph Heteroptera (Goodchild 1966, Backus 1988). The detritivorous Psocoptera, the most plesiomorphic extant hemipteroid clade (Goodchild 1966, Hennig 1981), retain the primitive condition of mandibulate mouthparts, although certain modifications, such as elongation of the maxillary laciniae into a "pick" and development of a prominent clypeal (or cibarial) pump (Burgess 1878, Weber 1938), foreshadowed structures in more advanced hemipteroids (Shear and Kukalová-Peck 1990, Kukalová-Peck 1991). Among the more derived hemipteroid clades of the Condylognatha (Hennig 1981, Boudreaux 1987), mandibles and laciniae are elongated into piercing stylets, although in the Thysanoptera this condition is modified by mouthpart and cephalic asymmetry (Borden 1915) and by a unique "punch-and-suck" mode of feeding for obtaining cellular contents from surface tissues, principally epidermis and parenchyma (Mound 1971, Mound et al. 1980, Hunter and Ullman 1989). By contrast, Hemiptera possess mandibular and maxillary stylets for penetration into deeper tissues, and extant Sternorrhyncha and Auchenorrhyncha occur almost exclusively on plants whereas only approximately half of Heteroptera feed on plants (Southwood 1973, Strong et al. 1984). Although there is pervasive evidence that ancestral hemipteroids possessed a ground-dwelling life style (Schaefer 1981, Wilson et al. 1994), considerable debate exists as to whether hemipterans were primitively fluid feeders on plants (Myers and China 1929, Miles 1972, Sweet 1979) or on insects (Cobben 1978, 1979). Nonhemipteroid clades of piercing-and-sucking insects are generally insectivores or blood-feeders on vertebrates, or less commonly fungivores or algivores. Stylate mouthparts

convergently arose among the 6 lineages of minute beetles principally by styliform elongation of mandibles and sometimes lacinae and commensurate conversion of adductor/ abductor muscles into protractor/retractor muscles by shifts in muscle attachment (for a review, see Labandeira 1990). All Siphonaptera and many adult nematocerous Diptera are blood feeders on vertebrates and other insects (Lehane 1991), although some nematocerans also use plant tissues as food (Knab 1910, Downes 1955).

Piercing-and-sucking insects bear various combinations of mandibular, maxillary, or hypopharyngeal stylets that are protracted and retracted from food tissue. The method of penetration into plant tissue by herbivorous species has been widely documented and consists of intercellular or intracellular stylet probes into particular targeted tissues such as phloem, xylem, mesophyll, and epidermis (Pollard 1969, 1973; Smith 1985; Miles 1987). Many hemipterans secrete a lipoproteinaceous salivary sheath when the stylet fascicle is in plant host tissue. Once within the tissue, stylets often exhibit considerable flexibility, and assume tortuous intercellular or intracellular trajectories toward the targeted tissue, sometimes terminating in a feeding cavity. These and other features of fluid feeding have been documented for some hemipterans with high economic effect, principally the sternorrhynchan aphids (Büsgen 1891, Horsfall 1923, Davidson 1923, Heriot 1934, Tate 1937, Nault and Gyrisco 1966, Sorin 1966, Evert et al. 1968), whiteflies (Pollard 1955, Walker 1985), and scales (Parr 1937, Schetters 1960); the auchenorrhynchan cicadas (Marlatt 1907, White and Strehl 1978), leafhoppers (Putman 1941, Houston et al. 1947, Carle and Moutous 1965, Pollard 1968), and planthoppers (Metcalfe 1968, Pollard 1969, Sonku and Sakuvai 1973, Cook and Denno 1994); and, to a lesser extent, phytophagous heteropterans such as tingids (Johnson 1937, Pollard 1959), mirids (Smith 1926, King and Cook 1932, Flemnion et al. 1954, Dale and Coaker 1958, Hori 1971), lygaeids (Painter 1928, Snelling et al. 1937, Miles 1959a), pyrrhocorids (Saxena 1963), pentatomids (Miles 1964, Hori 1968), and coreids (Krugman and Koerber 1969, Maschwitz et al 1987).

There has been extensive documentation of plant responses to piercing-and-sucking damage (summarized in Carter [1939, 1952], Miles [1964, 1969, 1972, 1978, 1987], Pollard [1973], Backus [1988, 1989], and Johnson and Lyon [1991]). Plant response prominently includes the production of response tissue surrounding the stylet trace and the secretion of lipoproteinaceous substances. An extensive, agriculturally based literature has documented these and other plant responses to stylet-induced trauma, particularly the process of stylet damage and the structure of response tissue.

Paleozoic History of the Piercing-and-Sucking Functional Feeding Group

Evidence for piercing-and-sucking insects in the fossil record occurs in 3 major forms: mouthpart-bearing insect body fossils, trace fossils of plant damage attributable to insect punctures, and gut contents. The widely documented presence of insect body fossils with well developed stylate mouthparts is known from the earliest insect-bearing Pennsylvanian deposits (Nelson and Tidwell 1987; Brauckmann 1988, 1991b; Kukalová-Peck and Brauckmann 1990). Some penecontemporaneous taxa, such as *Heterologopsis ruhrensis* Brauckmann & Koch 1982, had mouthparts that exhibited a tendency toward tissue penetration. *Heterologopsis* bore a clypeal dome and atypical mandibulate mouthparts with prominent, basally separated but elongated and forwardly projecting mandibles that occluded mesially (Brauckmann 1991b, figures 74 and 76).

The earliest insects with truely stylate mouthparts are members of the paleopterous assemblage Palaeodictyopteroidea, comprising the orders Palaeodictyoptera, Megasecoptera, Diaphanopterodea, and Permothemistida (Fig. 1). They possessed well developed, unsheathed, hypognathous beaks consisting of a pair of robust mandibular stylets with sharp, curved tips that were medially interlocked by a series of marginal denticles. A pair of adjacent maxillary stylets was modified lacinio-galeae that enclosed a needle-like hypopharyngeal stylet (Kukalová-Peck 1987, 1992). Ridges and corresponding troughs on all stylets resulted in an interlocked ensemble (Kukalová-Peck 1972). The labium of paleodictyopteroids consisted of a posteriorly placed, segmented, elongate ligula with distally, radially directed glossae and paraglossae that fanned outward on the plant host surface and presumably braced the beak in securing purchase of the substrate surface during feeding (Sharov 1973; Kukalová-Peck 1985, 1987, 1991). During styletal penetration of substrate tissue, the labium apparently was retracted progressively upward, assuming a folded Z-configuration while anchoring the stylets. Eight-segmented maxillary palps were as long or longer than the beak, and probably also assisted in positioning the beak on the host substrate. Morphological evidence indicates that a well developed clypeal pump with cibarial compressor muscles provided suction for imbibition of fluid food (Kukalová 1969a, b, 1970; Carpenter and Richardson 1968; Carpenter 1971; Wootton 1981); additionally, the gut contents of immature nymphs show that pteridophyte spores also were consumed (Kukalová-Peck 1991). Three of these features—the labium folding mechanism, arrangement of stylets within the fascicle, and cibarial pump—are convergently similar to modern hemipteroids, especially the Heteroptera. Unfortunately, whereas general mouthpart and associated cephalic structures are well documented for several paleodictyopteroid species; the microstructural detail revealed by stylets of modern taxa (compare Cobben 1978) so far have not been recognized in fossil forms. A plant- or animal-feeding habit can not be ascribed to any fossil specimen using microstructural criteria.

Although Dohrn (1866a, b) demonstrated the presence of stylets in a magnificently preserved specimen of the Lower Permian paleodictyopteran *Eugereon boeckingi* Dohrn, subsequent relegation of this specimen to the Hemipteroidea by Handlirsch (1906, 1937), Tillyard (1921), Guthörl (1934), Haupt (1949), and possibly to the Diptera by Crampton (1927) and Spooner (1938), obscured the true value of this fossil. The issue of whether paleodictyopterans had stylate beaks at all was not convincingly reestablished until Laurentiaux's (1952a, b) description of the beak of *Stenodictya* from the Late Pennsylvanian (Kasimovian Stage) of France. Until and sporadically after that time, this issue was contested, as evidenced by reconstructions of paleodictyopteroids, which conventionally were shown without mouthparts (Handlirsch 1906, 1925; Haupt 1949) or were assumed to be mandibulate (Baker and Hurd 1968, Smart and Hughes 1973). Recently, Kukalová-Peck and colleagues have documented a variety of stylate beak types in all paleodictyopteroid orders, providing crucial evidence for a diversity in robustness, shape, and size that spans more than an order of magnitude. Paleodictyopteroid beaks range from short, "mosquito-like", truncate forms ≈0.6 mm long to *Eugereon*, with a gracile beak 32 mm long (Haupt 1949; Müller 1977, 1978; Shear and Kukalová-Peck 1990; Kukalová-Peck and Brauckmann 1990; Kukalová-Peck 1991; Carpenter 1992). As a group of 4 related orders, paleodictyopteroids apparently achieved considerable ecological diversity as fluid-feeders and spore-imbibers, given their range in body size and possession of mouthparts of varied shape and size. Consequently, it has been inferred that, as the sole clade representing the piercing-and-sucking functional feeding group during the Pennsylvanian, and in lieu of any morphological evidence supporting fluid-feeding on animal tissues (but see Handlirsch 1937), paleodictyopteroids were targeting a variety of plant tissue types (Sharov 1973, Shear and Kukalová-Peck 1990, Carpenter 1992). The fossil record of Paleozoic plant damage caused by piercers-and-suckers has been meager: only a few brief illustrations of perforated seeds and stylet tracks in permineralized plant tissues are available (Schopf 1948, Sharov 1973, Scott and Taylor 1983, Lesnikowska 1989, Scott et al. 1992). Unfortunately, this documentation lacks structural details at the light- or scanning electron microscopic level.

The earliest evidence for the existence of the piercing-and-sucking functional feeding group in terrestrial ecosystems consists of reaction tissue and callus plugs occurring in rhyniophyte stems from the Lower Devonian (Pragian Stage) Rhynie
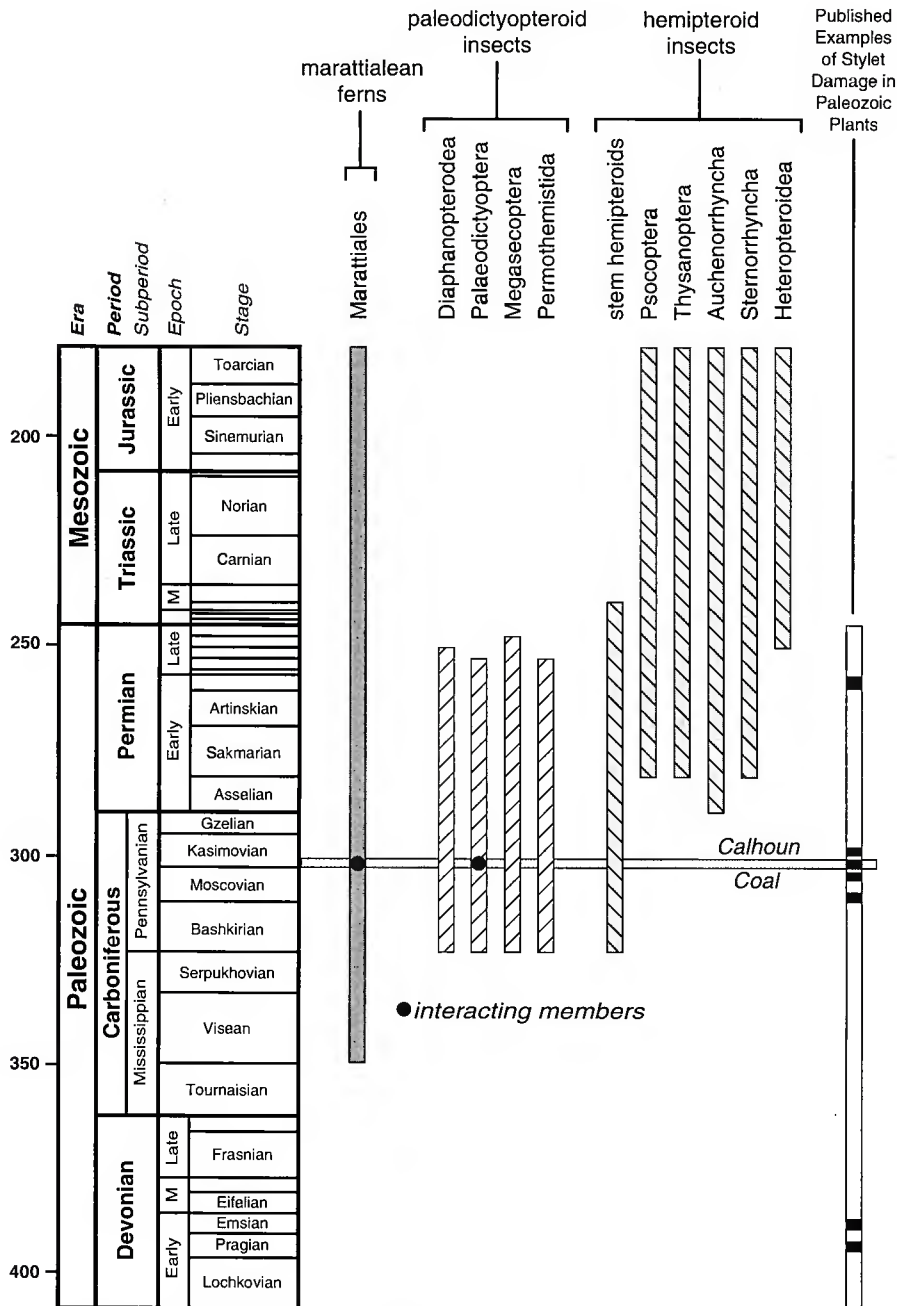
Fig. 1. Geochronologic distribution of late Paleozoic and early Mesozoic marattialean ferns, paleodictyopteroid and hemipteroid insects, and stylet damage in plant tissues. Stratigraphic horizon of the Calhoun Coal is indicated. Data for the temporal ranges of marattialean ferns is from Morgan (1959), Millay (1978), Hill (1987), Zhifeng and Thomas (1993), and Cleal (1993). The temporal ranges of paleodictyopteroid and hemipteroid insects are from Kukalová-Peck (1991), Carpenter (1992) and Labandeira (1994). These ranges include, for the Permothemistida, an Early Pennsylvanian occurrence of the Rectineuridae (Rohdendorf et al. 1991); for the Psocoptera, the Early Permian (Sakmarian) families Dichentomidae and Permopsocidae (Durden 1988, Carpenter 1992); and incorporation of the Lophioneuridae in the Thysanoptera (Vishniakova 1981, Durden 1988). Literature-based sources of stylet damage in plant tissues are found in Sharov (1973), Chaloner et al. (1975), Kukalová-Peck (1985), Lesnikowska (1989, 1990), Scott et al. (1992), and Banks and Colthart (1993). The geochronologic scale and its temporal calibration is from Harland et al. (1990).

Chert of Scotland (Fig. 1; Kidston and Lang 1921, Kevan et al. 1975, Chaloner and MacDonald 1980). These structures have been parsimoniously interpreted as plant response to punctures induced by land arthropods with stylate mouthparts, most likely mites or collembolans that occur in the same deposit (Hirst 1923; Greenslade 1988a, 1988b). Chaloner and MacDonald (1980) noted that long, open punctures or slits into the vascular strands of these stems exhibit a wound response of cell proliferation adjacent to the damaged area, and a dark exudation sealing off the lesion to the environment. Additional evidence for piercing-and-sucking comes from slightly younger, damaged trimerophyte stems from the Lower Devonian (Emsian Stage) of Gaspé, Québec (Banks and Colthart 1993), that display reaction tissue surrounding elongate, stylet insertion paths above subjacent wound periderm. This pattern of damage is qualitatively similar to tissue deformation caused by modern piercing-and-sucking arthropods, including eriophyid mites (Westphal 1977, Meyer and Maresquelle 1983), thysanopterans (Chisholm and Lewis 1984, Ananthakrishnan and Raman 1989, Childers and Achor 1991, Lewis 1991b), aphids (Tedders and Thompson 1981), and mirids (Smith 1926, King and Cook 1932, Hori 1971). It is possible that some of this damage is attributable to tissue-slicing by insect ovipositors.

The Lower Devonian material matches a syndrome of tissue damage documented in recent plants attacked by piercing-and-sucking insects. Histological features in common include a depression above each insertion site (Smith 1926; Westphal 1977, 1992; Tedders and Thompson 1981; Chisholm and Lewis 1984), a cone of hypertrophied epidermal and cortical cells (Chrystal 1925, King and Cook 1932, Meyer and Maresquelle 1983, Ananthakrishnan and Raman 1989, Childers and Achor 1991), disruption of cell walls within the cone (Smith 1926, Sorin 1966), and secretion of opaque, apparently resinous, bodies by the affected cells (Meyer 1987, Ananthakrishnan and Raman 1989). The stem damage at Rhynie and especially Gaspé is qualitatively similar in several ways to modern examples of tissue penetration and response induced by piercing-and-sucking mites and insects. Previous suggestions that these plant damage records solely represent abiotic-induced trauma (Kidston and Lange 1921, Rolfe 1985, Edwards and Selden 1991) lack compelling evidence, particularly because much of the Devonian plant damage possesses a highly stereotyped syndrome of tissue damage physiologically similar to the damage of a wide variety of modern piercing-and-sucking herbivores.

Later Devonian and Mississippian deposits lack trace-fossil evidence of piercing-and-sucking feeding, and body-fossil evidence for insects in general. The earliest known stylet-bearing insects are paleodictyopteroids of earliest Pennsylvanian age. They remain rather abundant throughout the Pennsylvanian, but lose dominance in more rich and diverse Early Permian insect faunas (Fig. 1). Sparse but important evidence for damaged plant tissues by insects that possessed stylate mouthparts occurs in permineralized coal-ball floras from Pennsylvanian deposits of Euramerica. These deposits are characterized by regional and local sedimentary deposits of in situ peats that were permineralized by a calcitic matrix, resulting in the anatomical preservation of plant tissues at the cellular and subcellular levels (Cross and Phillips 1990, Phillips and Cross 1991). Although there have been several described examples of wound reactions in permineralized coal-swamp plants such as ferns (Holden 1930, West 1962), lycopsids (Seward 1906, Wilkinson 1930), calamites (Stopes 1907), and seed ferns (Holden 1910), these fossils lack the stereotypical features of damage inflicted by arthropods with stylate mouthparts, and are interpreted as responses to abiotically induced trauma. By contrast, convincing evidence for piercing-and-sucking damage of plant tissues includes tissue response to punctures in the stems of the herbaceous zygopterid fern *Etapteris* (Scott and Taylor 1983, Taylor and Scott 1983) and in the frond rhachises of the marattialean tree-fern *Psaronius* (Lesnikowska 1989, this study). In Middle Pennsylvanian compression deposits from Siberia, Sharov (1973) described an external hole in a cordaitean *Samaropsis* seed, interpreted as a "boring" through the epidermis and sarcotesta and into embryonic tissue. Additionally, of late Middle Pennsylvanian age are the spore gut contents of a diaphanopterid nymph, figured by Kukalová-Peck (1987, 1991), which indicate consumption of fine, particulate matter. Of particular importance to the current study is an apparent insertion trace in the the seed fern microsynangiate organ, *Dolerotheca formosa* Schopf, occurring as a narrow, 1.2 cm long track terminating in a rounded feeding cavity that is surrounded by response tissue. The track was inserted from the sloping side of an ≈4 cm wide bell-shaped organ, targeting inner tissue containing prepollen or more likely sap from cell protoplasts. Although Schopf (1948) did not attribute the damage to an insect, Retallack and Dilcher (1988) discussed the extremely likely possibility that this track represents a palaeodictyopteroid stylet track. Lastly, small, Early Permian Diaphanopterodea from Kansas exhibit an amorphous, carbonized residue in the head, beak, and gut, indicating fluid-feeding (Kukalová-Peck, personal communication). Both plant damage from anatomically preserved, permineralized material, and insect gut contents from compression material, provide the best-documented evidence for identification of specific plant tissues targeted by piercing-and-sucking insects. Thus far, specific attributes of these punctures have not been identified, such as avoidance of certain cell types in the stylet probe, identification of targeted tissue, or presence of a terminal feeding cavity.

The trace-fossil record of Paleozoic piercing-and-sucking (Fig. 1) is almost exclusively confined to equatorial, lowland, swamp forests that were preserved 3 dimensionally as coal-ball permineralizations in coal basins. This contrasts with external foliage feeding by mandibulate insects, which generally has been found as 2-dimensional compression fossils in environments adjacent to peat-accumulating basins, especially on pinnules of medullosan seed ferns and marattialean tree ferns (Van Amerom 1966, Müller 1982, Srivastava 1987, Labandeira and Beall 1990, Stephenson and Scott 1992). Less commonly, bite marks have been documented from compression or impression floras that represent drier, more upland, and gymnosperm-dominated environments (Plumstead 1963).

Materials and Methods

Insect-damaged fossil plant material was collected from the Calhoun Coal of the Mattoon Formation, near Berryville, in east-central Illinois. This deposit is of Late Pennsylvanian age (Kasimovian Stage, Fig. 1), corresponding to a geochronologic age of 302 million years (Harland et al. 1990), and equivalent to the Stephanian B stage of classical European nomenclature (Phillips et al. 1985). The source peat of the Calhoun Coal accumulated in the Illinois Basin of western Euramerica, at a paleoposition of ≈10° N of the equator (Heckel 1977, Scotese and McKerrow 1990) and adjacent to an epicontinental, shallow sea to the west. The Calhoun peat-swamp forest was dominated by marattialean tree ferns, with medullosan seed ferns, sigillarian lycopsids, and calamitalean horsetails as arborescent subdominants, and rare cordaitalean gymnosperms. Understory plants consisted predominately of small ferns.

The insect-damaged material occurs in basal frond rhachises of the marattialean tree fern *Psaronius chasei* Morgan (1959). These rhachises are assigned to the form-genus *Stipitopteris*. *Stipitopteris* rhachises, together with *Pecopteris* pinnule foliage, *Scolecopteris* sporangia, and *Psaronius chasei* stems, comprise an assemblage of form-genera constituting an entire plant (Lesnikowska 1989). In this article the damaged fronds will be referred to as *Psaronius*, their conventional, whole-plant designation. All identifications were based on the criteria of Lesnikowska (1989).

Plant macrofossils are preserved in coal balls, which are usually early diagenetic mineral concretions of calcium carbonate that entombed the parent peat and preserved its fabric from subsequent compaction. The plant organs are thus 3-dimensionally preserved, resulting in anatomically accurate retention of detail at the tissue, cellular, and occasionally subcellular levels. Details of cell walls, tissue fabric, and insect damage are accurately preserved, with minimal syndepositional or postdepositional alteration. In addition to revealing rare relationships between insect herbivores and plant hosts, the surrounding peat litter provides valuable floristic data about the taxonomic composition of the larger plant community.

Because of exceptional histologic and cellular detail present in the Calhoun Coal, it is possible to reconstruct 3-dimensionally whole-plant organs and tissues using the peel technique (Phillips et al. 1976). In our study, cellulose acetate peels were made by rock-sawing slice B of the University of Illinois at Urbana-Champaign (UIUC) coal ball 8227 to the desired organ and tissue of interest, followed by smoothing the rough-sawed bottom surface in 500-grit carborundum powder. The smoothed surface subsequently was etched in 5% hydrochloric acid (HCl) for ≈12 s to expose organic material such as cell walls of tissues and spores. After air drying, the coal-ball surface was flooded with acetone, and a sheet of cellulose acetate was immediately rolled onto the flooded surface before evaporation occurred. The cell walls exposed on the coal-ball surface were embedded in the cellulose acetate peel, resulting in a facsimile reproduction of the coal-ball surface. These peels were pulled off the coal-ball surface and archived as numbered sheets in envelopes. This procedure was repeated until 175 peels were made. By measuring the slab thickness before and after the 175 peels, an average removal thickness was calculated for each peel. These peels revealed details of the subparallel stylet tracks and adjacent structures of interest. The gross anatomical context of the stylet traces was established by using every 5th peel of the series as successive templates for 3-dimensional rendering (Fig. 2b).

Cellulose acetate peels were used for both light- and scanning electron microscopy (SEM). Specimens were prepared for light microscopy (Figs. 2 c–f, 3, 4) by cutting out relevant, rectangular peel sections and mounting them on glass microscope slides (48 by 60 mm). Initial preparation involved clearing the peel of calcite matrix by immersion in 10% HCl for 5 min, followed by blotting and drying in an oven at 48°C. The cleared peel was then immersed in xylene, blotted, and mounted smooth-side-up on a glass microscope slide by using Canada balsam as an embedding medium. Mounted slides were heated on a slide warmer for several weeks and cleaned with ethyl alcohol before photography. Photography was done by use of transmitted light and an automatic exposure system on an Olympus SZH stereomicroscope. For SEM (Figs. 5 and 6 a–g), circular regions of interest from untreated cellulose acetate peels were cut and affixed rough-side-up on 2.55-cm-diameter SEM stubs. Slabs were then carbon coated and examined under the SEM.

Results

The 3 stylet probes in the rhachis specimen examined occurred in sclerenchyma and parenchyma below the epidermis, and terminated in vascular
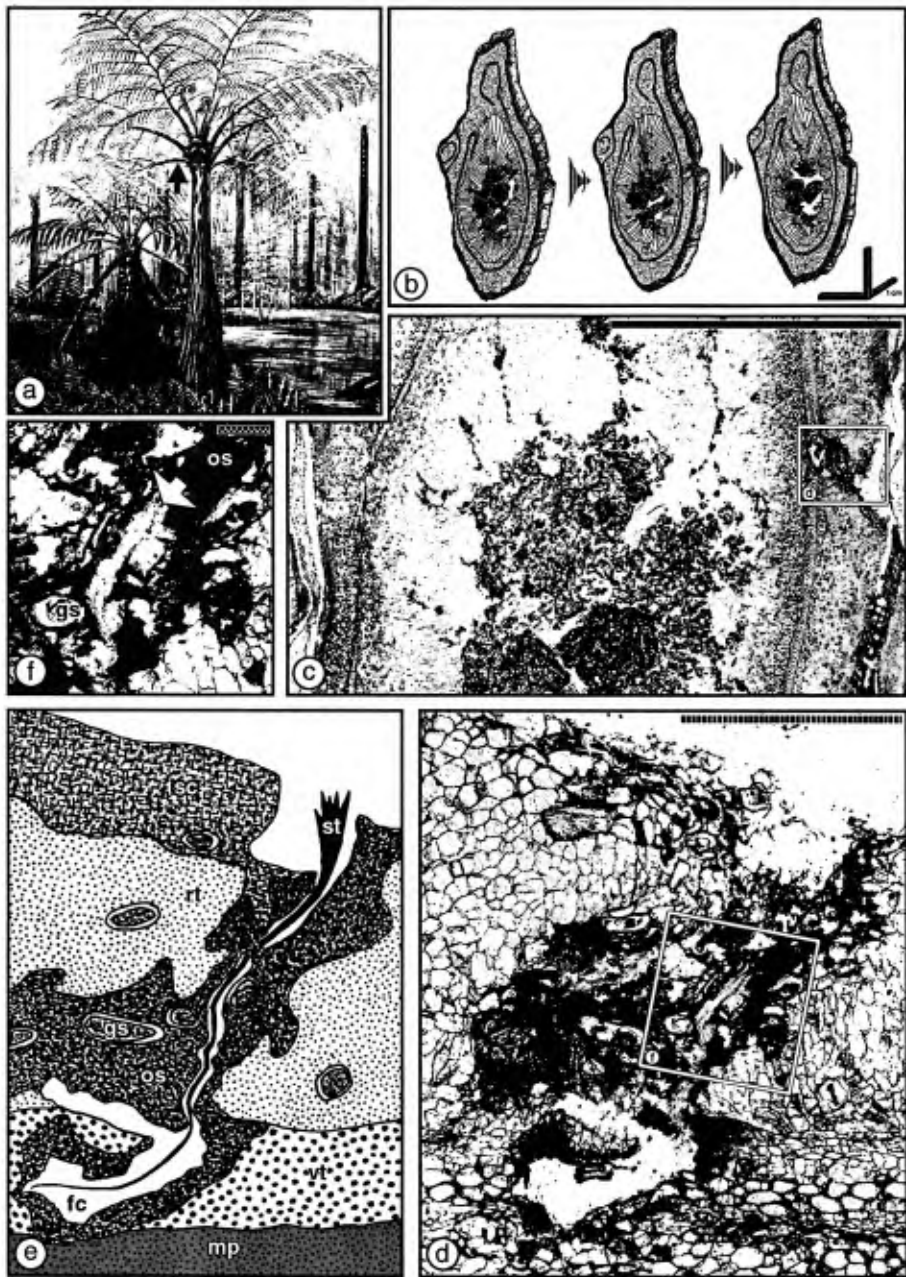
Fig. 2. Host plant and anatomical context of paleodictyopteran piercing-and-sucking damage on the marattialean tree fern, *Psaronius*. (a) Host plant of paleodictyopteran stylet damage, the Late Pennsylvanian marattialean tree fern, *Psaronius chasei* Morgan. (b) Three-dimensional reconstruction of a *Psaronius* frond rhachis, from UIUC coal ball 8227-Btop. (c–f) Light microscope photographs and a reconstruction of Stylet Probe No. 1 in UIUC specimen 8227-Btop. (c) Cross-section of a galled *Psaronius* rhachis at peel section No. 142, with a single stylet insertion of Stylet Probe No. 1 at right-center. (d) Photographic enlargement of (c), showing stylet path, adjacent black material, response parenchyma, and feeding cavities in cortical parenchyma and vascular tissue. Note orientation of stylet track to lower left. (e) Interpretive drawing of (d), with presumed position of stylets. (f) Photographic detail of region boxed in (d), showing median interstyletal ridge delimited by white arrow.

Scales: solid bars, 1 cm; striped bars, 1mm; stippled bars, 0.1 mm (100 μ). Abbreviations: an, antenna; ar, artifact; be, basal expansion of the stylet; ce, compound eye; cp, cortical parenchyma; cr, clypeal region; cw, cell wall; f, food canal; fc, feeding cavity; ga, gall; gs, gum sac cell; h, hypopharynx; ir, interstyletal ridge; md, mandibular stylet; mp, medullary parenchyma; mx, maxillary stylet; nt, nutritive tissue; os, opaque substance; ph, phloem; pl, prothoracic leg; pm, maxillary palp; rt, reaction tissue; s, salivary canal; sc, sclerenchyma; sp, stylet probe; st, inferred stylet; sw, stylet lumen wall; vt, vascular tissue; xy, xylem.
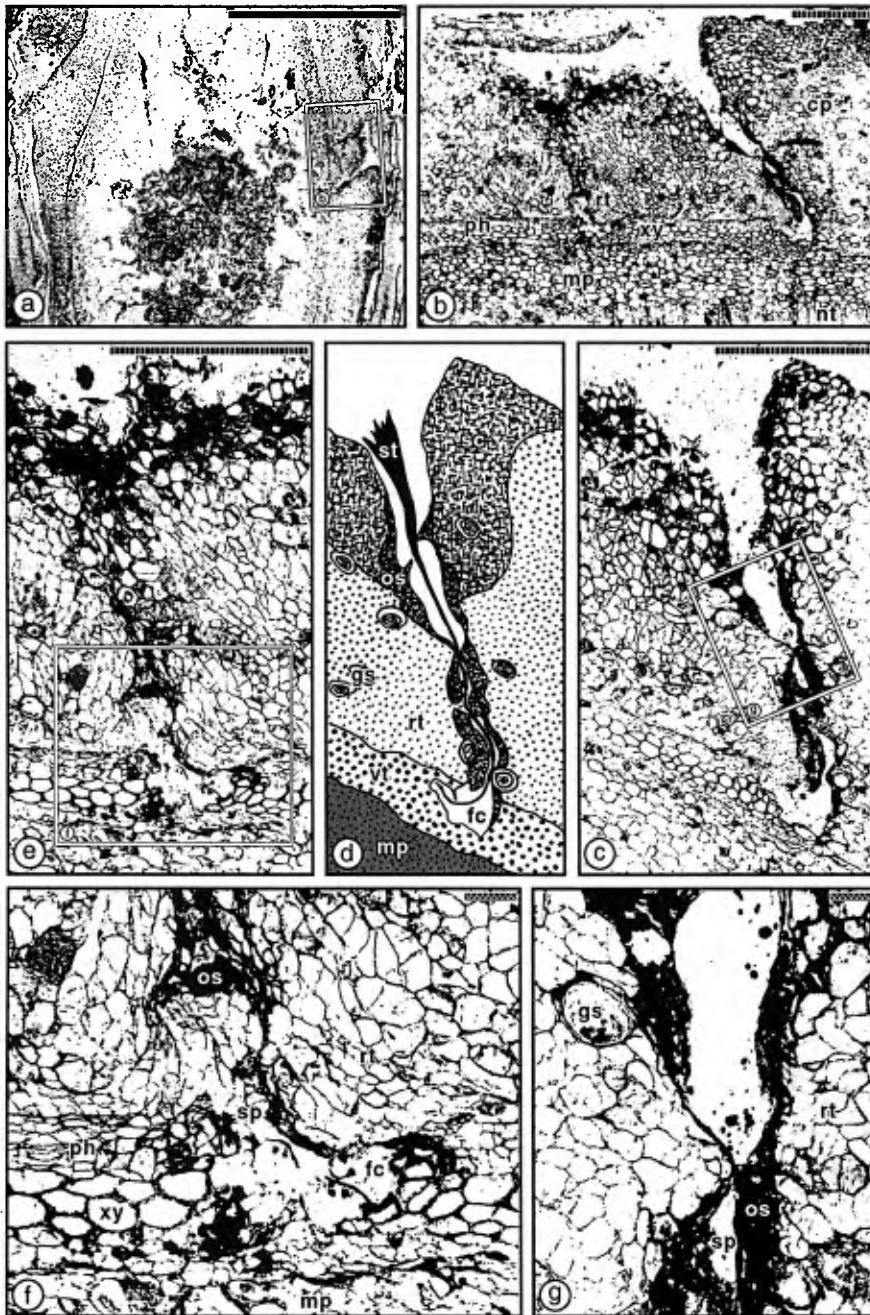
Fig. 3. Light microscope photographs and a reconstruction of Stylet Probe Nos. 2 and 3, equivalent to right and left traces respectively, and associated structures for UIUC specimen 8227-Bbot, at level represented by peel section No. 109, 33 peels removed downsection from Fig. 2. (a) Continuation of cross section of specimen in **Fig.** 1 (b) Enlargement of boxed right-center area in (a). Note the appearance of 2 new, subparallel stylet tracks, Stylet Probe Nos. 2 and 3, oriented toward the lower right. (c) Enlargement of right stylet track, Stylet Probe No. 3, in (b), showing tissue in upper region wedged apart, adherent opaque material along stylet path, avoidance of gum-sac cells, and terminal feeding cavity in xylem and phloem. Exmedian stylet diameter in upper cortical region is 0.30 mm. (d) Interpretive drawing of (c), with the position of inferred stylet complex. (e) Enlargement of left stylet track, Stylet Probe No. 2, in (b), showing response tissue, adjacent opaque material, and the feeding cavity within xylem and phloem. The lumen of the stylet track is not evident in this section. (f) Enlargement of feeding cavity boxed in (e), showing the evacuation principally of xylem. (g) Enlargement of midregion from the right stylet track, boxed in (c). Note the upper expansion of the stylet lumen, and downhole constriction of stylet path. See Fig. 2 for scales and abbreviations.
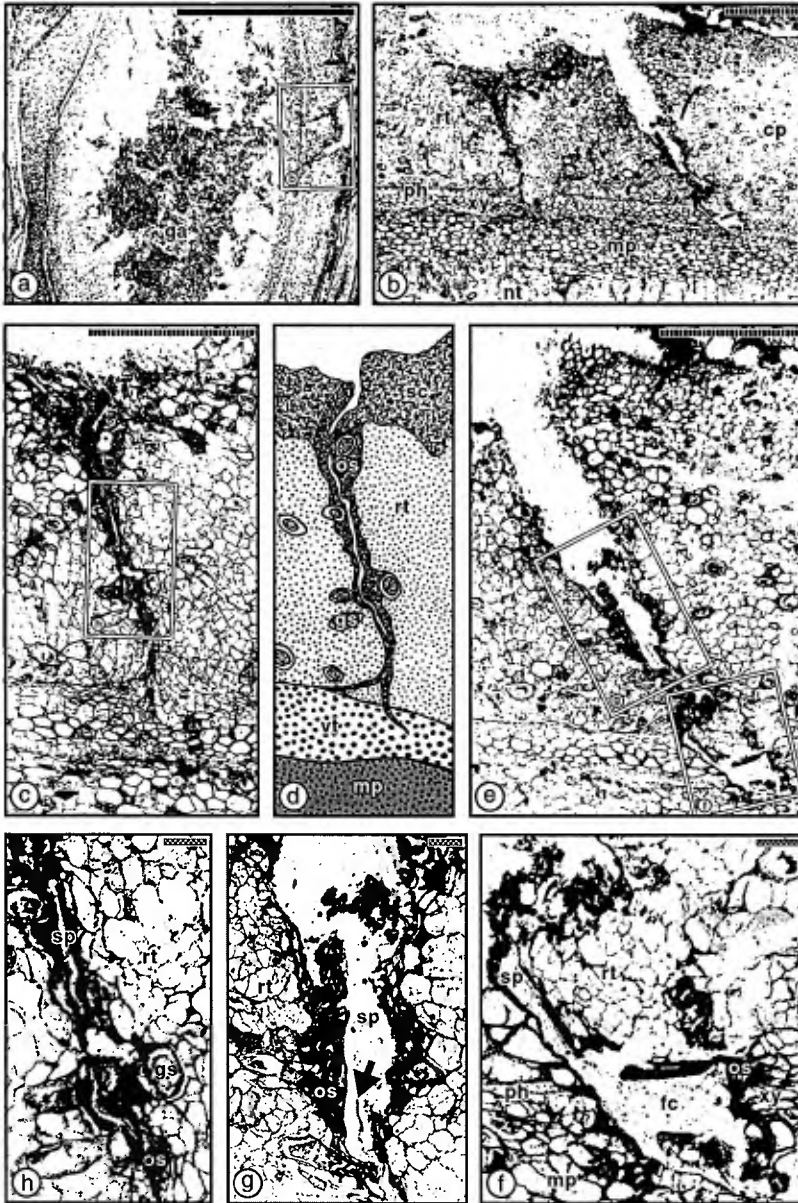
Fig. 4. Light microscope photographs and a reconstruction of Stylet Probe Nos. 2 and 3, equivalent to left and right traces, respectively, and associated structures for UIUC specimen 8227-Bbot, at level represented by peel section No. 93. (a) Continuation of cross-section of same *Psaronius* rhachis in Fig. 3, revealing the structure of Stylet Probe Nos. 2 and 3, 16 peels removed downsection from Fig. 3. As in Fig. 3, Stylet Probe Nos. 2 and 3 are at center-right: both are directed in subparallel fashion to targeted xylem and phloem in vascular cylinder. (b) Enlargement of center-right area of (a), with stylet traces expressed as Stylet Probe Nos. 2 and 3 in rest of figure. (c) Enlargement of Stylet Probe No. 2 in (b), at an exmedian section, showing stylet path in upper region. Note avoidance of gum sac cells, curved styletal pathway, files of cells forming response tissue at lower half of stylet probe, and termination of the probe in the vascular xylem and phloem. (d) Interpretive drawing of (c). (e) Enlargement of Stylet Probe No. 3 in (b), at an exmedian section along most of the stylet path, showing separated tissue in upper stylet region, avoidance of gum-sac cells, curved intracellular trajectory in lower stylet region, surrounding black material, response parenchyma, and feeding cavity in xylem and phloem tissue. Median stylet diameter in upper parenchyma region is 0.45 mm. (f) Enlargement of feeding cavity in (e), showing stylet path from cortical parenchyma into vascular tissue, and feeding occupying an evacuated or collapsed xylem region. Note avoidance of gum-sac cells and tortuous styletal path at upper-left. (g) Detail of the midregion of the right styletal probe in (e) showing opaque material adherent to styletal wall, and interstyletal ridge in lower-center part of the probe, delimited by black arrow. (h) Detail of midregion of the Stylet Probe No. 2 in (c) illustrating the role of gum-sac cells in directing the stylet pathway. The surrounding parenchyma is reaction tissue. This is the same region as Fig. 6a. See Fig. 2 for scales and abbreviations.
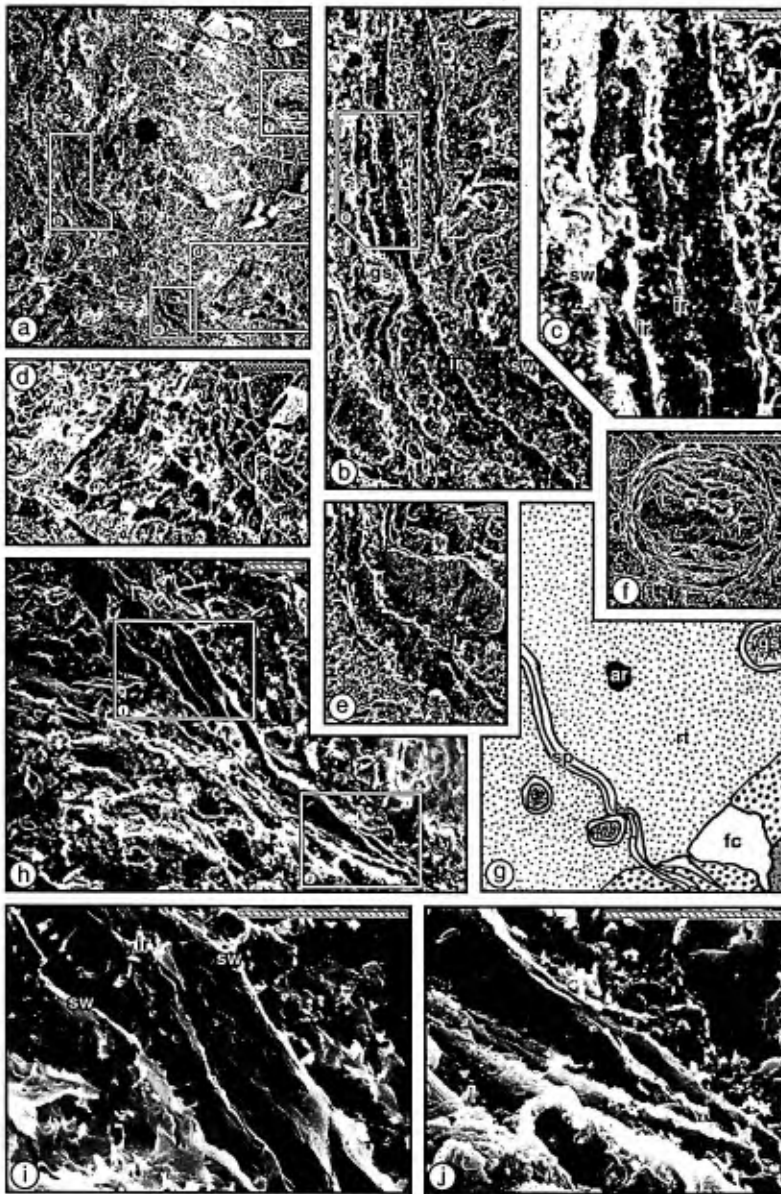
Fig. 5. (a–g) Scanning electron photographs of same Stylet Probe No. 1 illustrated in Fig. 2, at the adjacent level represented by the reverse surface of peel No. 143, mounted on SEM stub No. 5. In contrast to mounting the peel smooth side up in light microscopy, the peel was mounted rough-side up on the SEM stub, for carbon coating of ripped-up anatomical detail. (a) Anatomical context of stylet track. The stylet track, bracketed partly by 3 boxes, winds diagonally from the upper-left to the lower-right, terminating in a feeding cavity at the lower-right corner. Note conspicuous, ellipsoidal gum-sac cells with prominent, concentric outer membranes. (b) Detail of stylet track region boxed in (a), showing median, interstyletal ridge and marginal ridges formed by the lumen wall. The bulbous overhang at center-left is probably an avoided gum-sac cell. (c) Additional detail of stylet track in (b), showing 2 interstyletal ridges that probably delimit a central hypopharyngeal stylet, gum-sac cell, and stylet lumen wall. (d) Detail of feeding cavity region boxed in (a), showing excavated vascular tissue. (e) Stylet region immediately uphole from the feeding cavity, boxed in (a), showing stylet path and avoidance of object at left-center, perhaps representing a gum-sac cell wall. (f) Enlargement of gum-sac cell boxed in (a). (g) Reconstruction of stylet path, feeding cavity, and major tissue types in (a). Note 2 failed stylet probes left of the feeding cavity. (h–j) SEM photographs of left stylet trace, Stylet Probe No. 2, illustrated in Fig. 3, at the adjacent level represented by the reverse surface of peel No. 110, mounted on SEM stub No. 8. The mounting protocol is the same as Fig. 4 (a–g) above. (h) Detail of stylet pathway as it emerges out of cortical tissues in the center-bottom region of (a). (i) Detail of top-center boxed region in (h), showing interstyletal ridge and stylet lumen wall. (j) Detail of lower-right boxed region in (h) showing the exiting of the stylet trace from the peel section. See Fig. 2 for scales and abbreviations.

tissue (Fig. 2 a and b). The 3 stylet probes are straight to gently meandering, inclined ≈55° to the local plane of the vascular cylinder (Figs. 2c, 3b, 4b). Each probe ends in a characteristic feeding cavity within xylem and phloem of the vascular tissue (Figs. 2d, 3 c and e, 4 e and f, 5g). The average length of the stylet traces, when taking into account meander bends and some delamination of rhachis epidermis, is 4.0 mm. Each stylet probe consists of the following 3 regions: (1) an outer, wedge-shaped entry area in sclerenchyma and outer parenchyma, (2) a central linear to gently meandering region in inner parenchyma, and (3) a terminal feeding cavity in vascular tissue. The wedge-shaped region is enlarged toward the rhachis surface and is either open and filled with postmortem calcitic matrix, or is plugged with original opaque substance (Figs. 2d; 3c, e, g; 4 c, e, g). This 3-dimensional, cone-shaped region tapers to a diameter equivalent to the width of the stylet fascicle (0.45 mm) in the central region of the ground parenchyma. In the outer sclerenchyma and ground parenchyma the stylet trace is linear to meandering, with linear stretches intracellularly penetrating tissue (Figs. 5 c, h–j; 6 e and f). In contrast, occasional meandering regions are caused by avoidance of more resistant gum-sac cells (Figs. 2f, 3c, 4h, 6a) that are larger than typical parenchyma cells and contain resin-like substance in their protoplasts (Lesnikowska 1989). The avoidance of gum-sac cells by the stylet fascicle results in intercellular meandering that is distinct from the linear, intracellular perforation of normal parenchymatic cells. The stylet trace occasionally reveals 1 or 2 characteristic median ridges (Figs. 2f; 4g; 5 c, i, j; 6 e and f), which we infer to separate stylets of the penetrating fascicle. Lastly, the stylet trace terminates in the previously mentioned, distinctive feeding cavity within the deeper-seated vascular cylinder. The feeding cavity is formed by excavation of both larger-celled, centrally located xylem (Figs. 2d, 3f, 4f, 5d) and the more peripheral phloem. The shape of the feeding cavity is elongate, contains separate embayed excavations, and extends into the vascular layer (Figs. 2d; 3 c–f; 4 e and f).

The tissue surrounding the stylet lesion consists of 2 features that are atypical of normal *Psaronius* ground parenchyma and vascular tissue. The 1st is an opaque, dark substance immediately enveloping the stylet traces. The 2nd is extensive development of parenchyma-derived reaction tissue. The opaque substance apparently is generated at the stylet trace and consists of approximately a 0.1 mm thick cylinder surrounding the stylet puncture (Figs. 3 c and g; 4 c–f), although stylet probe 1 (Fig. 2d) has extensive development probably caused by repeated reinsertion at the distal probe region. The composition of the opaque substance is most likely sheath saliva of the insect; it also may contain mucilage secreted as a response by cells to stylet penetration. The same opaque substance surrounds the feeding cavity (Figs. 2d; 3 c and f;

4 b, e, f), and is probably an extension of the salivary sheath into vascular tissue.

The host reaction tissue occurs in parenchyma and consists of hypertrophied and sometimes hyperplasic, irregularly shaped cells arranged into files. These files of cells form compact masses whose discordant orientation contrasts with the bricklike, horizontally-layered structure of unaltered parenchyma. Reaction tissue is deployed as a zone around the stylet trace that expands in circumference toward the vascular cylinder (Figs. 2d, 3 c and e, 4 c and e). Whereas, individual cells of unaltered parenchyma have a polygonal shape, a regular pattern of buttressing, and are relatively constant in size, cells of reaction tissue possess a relatively large size range, are globose to highly angular and irregular in shape (Fig. 4f–h), and lack a regular network of intercellular buttressing. The reaction tissue surrounding the stylet probes is distinctive from adjacent parenchyma, and it is also different from nutritive tissue occurring in modern galls and from the interior parenchyma of the same specimen (Figs. 2 b and c, 3a, 4a). Gall-induced nutritive tissue is distinct histologically, and by contrast is characterized by regularly arranged files of cells organized into discrete, hemispherical tufts.

Discussion

Based on highly stereotypical damage inflicted on *Psaronius* rhachises, 2 major insect clades are the logical candidates—the Hemipteroidea and the Palaeodictyopteroidea. In this section, a brief review of modern hemipteroid feeding mechanisms and the type of documented host damage is provided for comparison to the stylet-inflicted damage on *Psaronius* rhachises. Additionally, data on paleodictyopteroid mouthpart morphology and inferred feeding mechanisms also are discussed in the context of assessing whether this extinct group of Paleozoic insects could have been responsible for the damage.

It is important to acknowledge that the cell and tissue types occurring in Late Pennsylvanian treefern rhachises are qualitatively identical to those occurring on modern ferns, and modern herbaceous angiosperms. Consequently, based on the pattern of cell and tissue damage and the concomitant plant response, valid comparisons can be made for cell types and tissues in common, even though interacting and taxonomically different herbivores have been widely separated in time and space.

Hemipteroid Feeding Strategies

Although plesiomorphic hemipteroids are documented throughout the Pennsylvanian (Kukalová-Peck 1991), a more derived clade that evolved tissue-piercing, stylate mouthparts enveloped by a labial sheath is not known until the Early Permian (Bekker-Migdisova 1985, Durden 1988, Carpenter
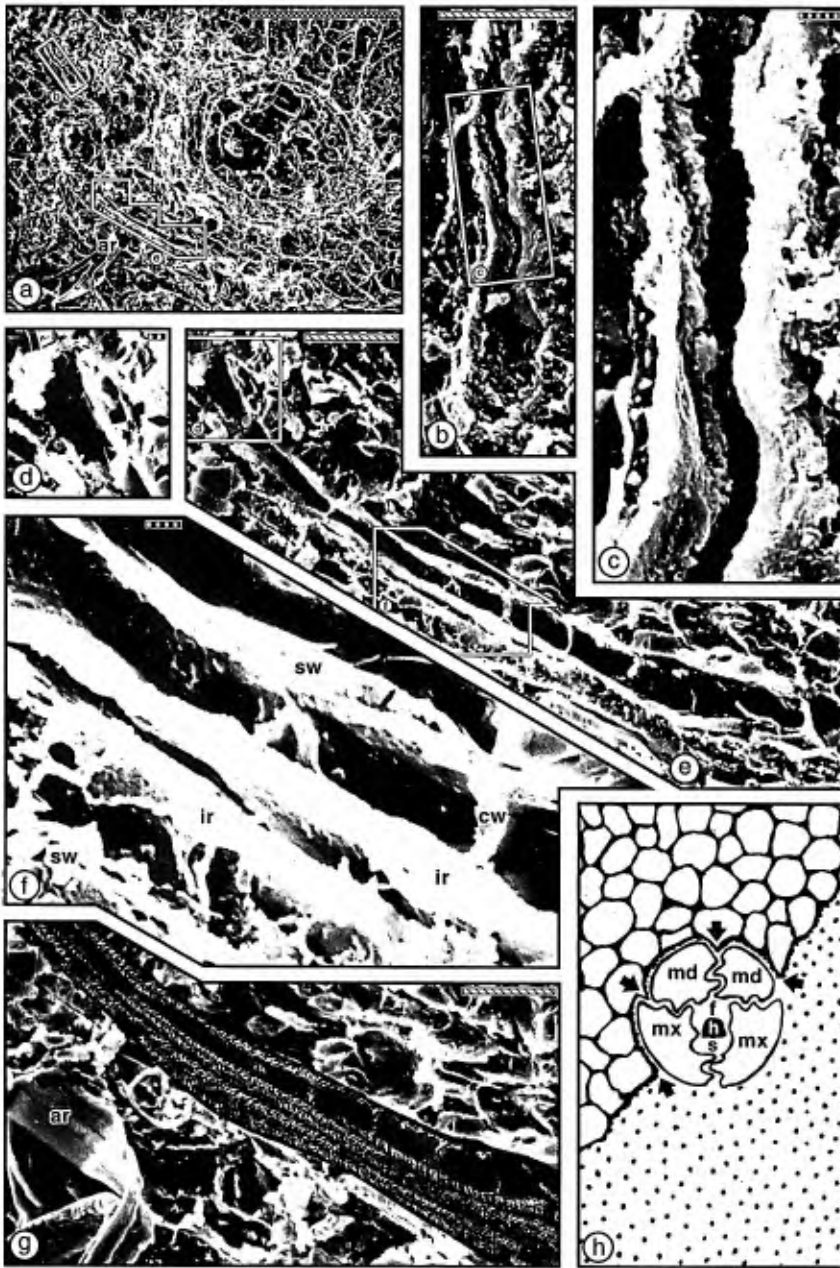
Fig. 6. Scanning electron photographs of left stylet trace, Stylet Probe No. 2, in Figs. 3 and 4, represented by peel surface No. 123, mounted on SEM stub No. 7. Same mounting protocol was used as in Fig. 5. (a) Anatomical context of stylet track. The stylet track, entirely bracketed by outlines (b) and (e), emerges as an ovoidal hole from the peel section immediately above smaller gum-sac cell at left center, and reenters the peel surface immediately below the same gum-sac cell. Note apparent large gum-sac cell at center right. This is the same region as Fig. 4h. (b) Enlargement of upper stylet track and exit hole from peel surface in top-left box in (a). Note ovoidal exit hole and exmedian section of stylet lumen. (c) Detail of exmedian stylet lumen boxed in (b). (d) Detail of stylet reentry hole below center-left gum sac cell in (a). (e) Enlargement of lower stylet track and reentry hole from peel surface in bottom-left box in (a). Note severed cell walls in stylet lumen. (f) Detail of stylet probe structures in (e), including severed cell walls within the stylet lumen, 2 median interstyletal ridges probably delimiting a hypopharyngeal stylet, and enclosing stylet lumen walls. (g) Same SEMs as (e), but with authors' interpretation of stylets in a track, showing 2 median, interstyletal ridges and stylet lumen walls. (h) Cross-section of paleodictyopteran stylet fascicle (adapted from Kukalová-Peck 1985, 1991) as it is penetrating cortical parenchyma (upper left), producing 2 interstyletal ridges and stylet lumen walls (arrows). Lower right area (stipple) represents cortical parenchyma removed by the coal ball peel process. See Fig. 2 for scales and abbreviations.

1992, Labandeira 1994). Pennsylvanian-age hemipteroids include taxa with generalized venation, protruding orthopteroid-like ovipositors, and nominally mandibulate mouthparts that bear some specializations such as a hypognathous mouthpart position, an inflated clypeus, and elongated although not styliform laciniae (Rohdendorf and Rasnitsyn 1980, Kukalová-Peck 1991). The earliest, well-preserved hemipteran body fossil for which there is good anatomical evidence for piercing-and-sucking mouthparts and clypeal modifications are 3 auchenorrhynchan species belonging to the Prosbolidae and Prosbolopseidae. These are *Permocicada integra* Bekker-Migdisova and *Prosbolopsis* sp., probable phloem ingesters that possessed an expanded clypeal region; and *Sojanoneura kazanensis* Zalessky, a probable xylem feeder with an unenlarged clypeus. All 3 taxa are from Late Permian (Wordian Stage) localities along the Soyana River near Arkangelsk, Russia (Bekker-Migdisova 1940, 1946, 1948, 1960). Although there are other well-preserved body fossils with mouthpart structures occurring in Paleozoic and Mesozoic deposits (for example, Richards 1966, Bekker-Migdisova 1985, Hamilton 1990), there is no indication that their mouthpart structure deviated from the 3 major strategies that hemipteroids currently use in the uptake of plant sap.

The 3 fundamental strategies of fluid-food extraction by phytophagous condylognath hemipteroids (Miles 1972, Backus 1988) are punch-and-suck feeding of surface tissues by Thysanoptera (Heming 1978, Kirk 1984, Lewis 1991b) and possibly the heteropteran Tingidae (Johnson 1937); salivary-sheath ingesting of deeper tissues by Sternorrhyncha, most Auchenorrhyncha, and pentatomomorph Heteroptera (McLean and Kinsey 1965, 1968; Miles 1968, 1987); and lacerate-and-flush feeding, also of deeper tissues, in some Auchenorrhyncha and some pentatomomorph and cimicomorph Heteroptera (Miles 1959a, Pollard 1959, Saxena 1963, Kabrick and Backus 1990). These 3 major strategies, as well as their subtler modifications, have been extensively described from microscopic sections of often highly stereotyped damage in modern plant tissues. Because this damage of economically important plant tissues has been intensely investigated by agricultural entomologists during the past 70 yr, there is a substantial literature documenting specifics such as stylet trajectory patterns into host tissue, modification of penetrated host cells and tissue by stylet penetration, and subsequent plant response to major types of trauma from stylet insertion.

Punch-and-Suck Feeders. For thysanopteran punch-and-suck feeding, the prelude to stylet insertion into host tissue consists initially of adpressing the mouthcone firmly to the host substrate, followed by tactile sensing of the adjacent surface by maxillary and labial palps, then retraction of mouthcone paraglossae to expose the labial pad, and finally thrusts of the single mandibular stylet from the labial pad into epidermal tissue (Heming 1978, 1993;

Hunter and Ullman 1989; Lewis 1991a). After an initial opening, the mandible is protracted deeper into the host tissue, followed by deployment of the maxillary stylet pair, which consists of a tube with a figure-8 cross-section (Wiesenborn and Morse 1988; Lewis 1991a, b; Heming 1993). Although the food canal of the maxillary stylet is from 1 μm to a few micrometers in diameter (Mound 1971, Chisholm and Lewis 1984), much larger in diameter chloroplasts can be sucked up by squeezing the organelles into the food canal (Chisholm and Lewis 1984). Generally, the maximal depth of penetration of the maxillary stylets into host tissue is from 0.03 to 0.1 mm (Hunter and Ullman 1989; Lewis 1991a, b; Heming 1993); however, *Adrothrips intermedius* (Bianchi) (Phlaeothripidae), feeding on woody twigs of Australian *Casuarina* trees, have stylets up to 0.8 mm in length (Mound 1970). Known thysanopteran plant damage is limited to epidermal or mesophyll tissue (Childers and Achor 1991), and is characterized by a figure-8 puncture on a surface depression caused by shrinkage of subsurface tissue due to the sucking out of cell protoplasts (Chisholm and Lewis 1984, Lewis 1991a). Surface plant tissues are the target of thysanopterans, and consequently the damage they inflict lacks the long, often tortuous, deep-seated stylet tracks and secreted salivary sheaths found in most phytophagous hemipterans.

Feeders Secreting a Salivary Sheath. Because of their profound effect on agriculture and forestry, aphidoid hemipterans (aphids, adelgids, and phylloxerans) have been studied the most intensively of any phytophagous piercing-and-sucking insect group. From this extensive examination, aphidoids will serve as the model hemipteran piercer-and-sucker in the ensuing discussion. Aphidoids are predominantly phloem ingesters that generally penetrate host tissues intercellularly, produce a salivary sheath from cephalic glands, and bear long and flexible stylets. Although most aphid species ingest primarily from phloem sieve elements (Evert et al. 1968, Dixon 1975, Bing et al. 1991), some aphidoids variously consume epidermis, mesophyll, phloem parenchyma, and companion cells (Nault and Gyrisco 1966, McLean and Kinsey 1967, Tjallingii 1990), and xylem, involving the penetration of wood (Heriot 1934, Balch 1952, Evert et al. 1968, Hain et al. 1991). The typical aphidoid path of host tissue penetration is intercellular (Büsgen 1891; Davidson 1923; Horsfall 1923; Kloft 1955; Evert et al. 1968, 1973; Pollard 1971), frequently tortuous (Tate 1937, Sorin 1966, Pollard 1973), and generally of considerable distance, ranging up to 5 times the body length in the case of some phylloxerans (Balch 1952, Forbes and Mullick 1970). Documented stylet lengths range from 0.12 mm in *Rhopalosiphum maidis* (Fitch) (Aphididae) attacking leaf mesophyll (Bing et al. 1991), to 1.9 mm in various species of *Adelges* (Adelgidae) consuming cortical parenchyma (Balch 1952, Kloft 1955, Forbes and Mullick 1970), and to a known maximum of 12.5 mm in *Longistigma*

caryae Harris (Aphididae) feeding on stem phloem (Dixon 1975). Typical aphidoid stylet fascicle diameters range from 0.0002 to 0.0005 mm (Miles 1959b, 1987; Nault and Gyrisco 1966; Pollard 1971). An aphidoid salivary sheath is formed by secretion of 2 basic types of stylet-associated saliva. An initial "watery" substance containing pectinase and other lytic enzymes dissolves the middle lamella and other substances between cells (McAllan and Adams 1961), to assist intercellular penetration and lateral wedging of cells by the stylets (Dreyer and Campbell 1984). As the stylet fascicle penetrates predominantly intercellularly, a thicker, lipoproteinaceous substance is secreted by the stylet tips that rapidly congeals when exposed to plant tissues, eventually hardening to form an impermeable salivary sheath (Miles 1987). This salivary sheath is beaded on its external surface when it is unconstrained by cell walls (McLean and Kinsey 1965, 1967) and may function in the following 3 ways: (1) supporting and stabilizing the stylet bundle in its path through host tissue, or (2) preventing escape of stylet-secreted substances or entry of unwanted plant substances before contact with the targeted tissue, or (3) serve as an inert plug of a plant wound to minimize physiological plant response (Miles 1959b, 1968, 1972, 1987).

Although aphidoid penetration of host tissue begins at surface epidermis cells and is dominantly intercellular, evidence also supports the occasional use of stomata as entry points into mesophyll, and the occurrence of intracellular damage in some species. During initial puncture of the surface, a disk-like flange is formed at the entry site, which is confluent with the subjacent salivary sheath (Nault and Gyrisco 1966). As the stylets physically alter surrounding cells during penetration of epidermal and cortical tissue, the host plant responds in several ways. Although generally laceration of host cells is minimal and cell-wall parting is the dominant mode of disruption (Pollard 1969, 1973), cells adjacent to the salivary sheath undergo important cytological changes. These changes include nuclear swelling and possible disintegration of cells, cell wall thickening, degeneration of plastids and protoplasm, and callose formation around the salivary sheath (Davidson 1923; Horsfall 1923; Carter 1939, 1952; Evert et al. 1968; Pollard 1973). Additionally, there is hypertrophy and hyperplasy of cortical cells surrounding the salivary sheath (Smith 1967; Evert et al. 1968; Miles 1968, 1969). In the case of penetration of *Picea* by the adelgids *Chermes* and *Dreyfusia,* nutritive tissue, a special type of reaction tissue, develops as a response to stylet insertion. This tissue is a special, local proliferation of hypertrophied parenchyma that is structurally differentiated from normal cortical parenchyma and rich in carbohydrates (Chrystal 1925, Kloft 1955, Miles 1969, Rohfritsch 1981, Hain et al. 1991, Rohfritsch and Anthony 1992). In some species a circular plug of suberized cells occurs as wound periderm (Hain et al. 1991).

Once the stylets approach the target tissue, the salivary sheath frequently exhibits a dendritic branching pattern caused by repeated retraction of the flexible stylets and reinsertion into a new interor intracellular path (Zweigelt 1915, Davidson 1923, Sorin 1966, Evert et al. 1968, Pollard 1969). In some cases, feeding cavities have been documented, wherein successive back-and-forth penetration of a phloem or xylem region has resulted in local enlargement into a chamber (Büsgen 1891, Horsfall 1923, Pollard 1971), caused by chemical lysis from salivary enzymes (Chatters and Schlehuber 1951). The partial lining of this feeding cavity with material similar to the salivary sheath was documented by Horsfall (1923).

In addition to the above patterns of feeding and induced plant damage in the Sternorrhyncha, there are parallel data from the other major infraorder of homopterous Hemiptera, the Auchenorrhyncha, but mostly for 2 groups: the Delphacidae (planthoppers) of the Fulgoroidea, and the Cicadellidae (leafhoppers) of the Cicadelloidea. Although these data are not so extensive as those for Aphidoidea, they document 3 major departures from the typical aphidoid pattern of feeding and plant damage. A general structural distinction separating many auchenorrhynchan stylets from other hemipteran taxa is that the maxillary stylets, rather than the mandibular stylets, are deployed in front of the mandibular stylets during penetration of host tissue (Pollard 1969, Backus 1988). This condition within the Hemiptera may be responsible for the 2nd major feature, namely, that auchenorrhynchan stylet penetration is mostly intracellular, rather than the intercellular condition for sternorrhynchans (Putman 1941; Pollard 1968; Sōgawa 1973, 1982; Cook and Denno 1994; but see Günthart and Günthart 1983). As a consequence, stylet progression into host tissue assumes approximately a linear trajectory rather than a curved or highly convoluted path (Figs. 7 d and f; Backus 1988), although it can be modified by a dendritic pattern caused by the successive protraction and retraction of stylet probes into adjacent tissue (Büsgen 1891, Vidano 1963, Backus 1989). Lastly, in contrast to the dominantly phloem-ingesting aphidoids and other sternorrhynchans, auchenorrhynchans prefer a greater variety of tissue types of food sources, including xylem for the Cicadoidea, Cercopoidea, and cicadelline Cicadellidae; mesophyll for typhlocybine Cicadellidae; as well as phloem for Fulgoroidea, Membracidae and deltocephaline Cicadellidae (Miles 1968, 1972; Pollard 1968, 1969; Backus 1988; Carver et al. 1991; Wilson et al. 1994).

Lacerate-and-Flush Feeders. The lacerate-and-flush style of feeding characterizes cimicomorph and certain pentatomomorph and cicadellid (typhlocybine) taxa. These taxa use a stereotyped mechanism of fluid food retrieval from seeds or various meristematic tissues without the benefit of a solidly secreted salivary sheath (Miles 1968,
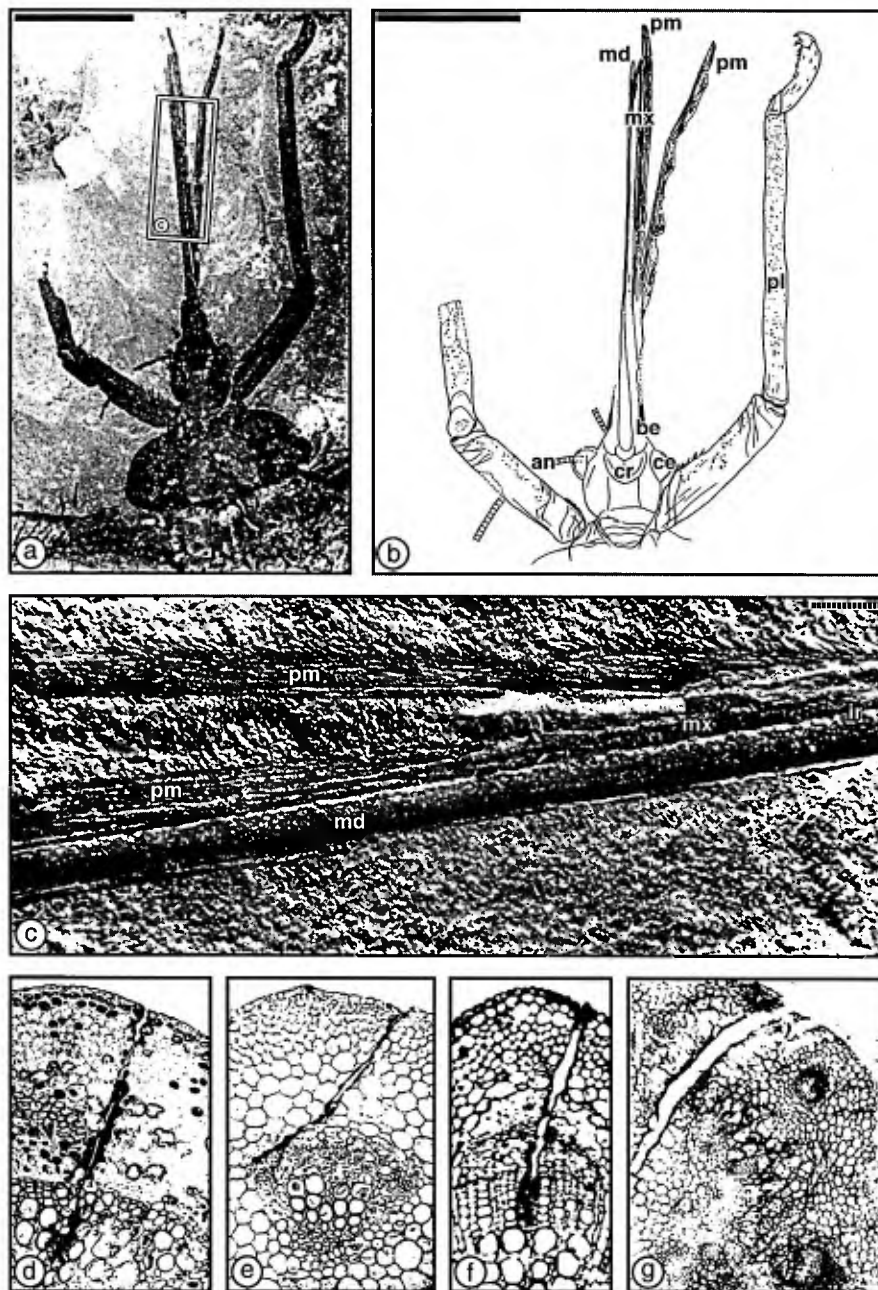
Fig. 7. (a–c) Mouthpart and head structure of the paleodictyopteran *Eugereon boeckingi* Dohrn (1866b) from Leback Beds, in the Lower Rotliegendes succession, of Early Permian (probably Sakmarian) age. Holotype, from Schwarzenbach, near Birkenfeld, Rheinland-Pfalz State, Germany. Figs. a–c are reproduced with permission from Müller (1977, 1978). (a) Complete specimen of *E. boeckingi.* (b) Camera lucida drawing of head and mouthpart region in a. (c) Enlargement of central mouthpart region in (a). See Fig. 2 for scales and abbreviations. (d–g) Hemipteran stylet damage to modern angiospermous crop plants. (d) Damage by the leafhopper, *Scaphoideus littoralis* Ball (Cicadellidae), to petiolar phloem and xylem of grape, *Vitis vinifera* L. (From Carle and Moutous, 1965, Annales des Épiphyties, 16, INRA, figure 2; ×45].) (e) Damage by the capsid bug, *Stictocephala festina* Say (Miridae), to petiolar phloem of cotton, *Gossypium barbadense* L. (Malvaceae). (From King and Cook [1932, plate 3, figure B; ×92].) (f) Damage by the leafhopper, *Draeculacephala minerva* Ball (Cicadellidae), to stem xylem of grape, *Vitis vinifera* L. (From Houston et al. [1947, figure 1b; ×145].) (g) Damage by the lygus bug, *Lygus hesperus* Knight (Miridae), on stem xylem of guayule, *Parthenium argentatum* A. Gray (Compositae). (From Addicott and Romney [1950, Botanical Gazette, 112, University of Chicago Press, figure 5; ×45].)

Table 1. Comparison of *Psaronius* damage to modern hemipteroid damage and paleodictyopteran mouthpart morphology

Stylet-track features and Geochronology	*Psaronius* Rhachis Damage	Modern Hemipteroidea	Paleozoic Palaeodictyopteroidea
1. Stylet length	4 mm	0.001 mm to 2 mm; rarely longer	1 mm to 32 mm
2. Midsection stylet width	0.45 mm	0.0001 mm to 0.002 mm	0.1 mm (?) to 3 mm
3. Surface entry area	Conical, tapering	Straight and not broadly tapering; rarely narrowly tapering	Conical and broadly tapering
4. Stylet trajectory	Straight, minor flexing	Straight to tortuous	Straight; minor flexing
5. Tissue penetration	Intracellular	Intercellular or intracellular	Probably intracellular
6. Stylet track ridging	1 or 2 ridges	None; never documented?	1 or 2 ridges consistent
7. Salivary sheath	Present	Present or absent	Unknown
8. Feeding cavity	Present	Present or absent	Unknown
9. Targeted tissue	Phloem + xylem	Virtually all tissues	Spores, others unknown?
10. Host response tissue	Reaction tissue, as files of hypertrophied cells	Reaction tissue or specialized nutritive tissue	Unknown
11. Geochronological timing	Earliest Late Pennsylvanian (Krevyakinskian)	Early Permian (Asselian) to Recent	Early Pennsylvanian (Kinderscoutian) to Late Permian (Longtanian)

1972; Backus 1988), although sheath material is used to form a rim encircling the feeding hole on the plant surface (Miles 1959a). Once a local feeding pocket is reached by intracellular or intercellular penetration (Fig. 7 e and g), the combination of slashing stylets (Livingstone 1969) and secretion of cellulytic enzymes results in the maceration of tissue and its conversion to a particulate slurry. This mixture of saliva and food fragments is imbibed, leaving an emptied food pocket surrounded by tissue (Fig. 7g) or, in the case of endosperm ingesting, an empty seed husk (Miles 1972). This emptied food pocket is a distinctive feature that is surrounded by plasmolyzed cells and is often lined with a brown layer (Smith 1926, Hori 1971), and has been termed variously an area of collapsed cells, a cavitation structure, or a feeding cavity or chamber (Smith 1926, Painter 1928, Addicott and Romney 1950, Flemnion et al. 1954, Pollard 1959, Hori 1971). According to Hori (1971, p. 88), the cavity is formed from the "...probing thrust of the stylets," and consists of both insect- and plant-derived substances. After feeding, the epidermal region of the wound sometimes contains a conical plug of sheathlike material or callose (Smith 1926). This feeding mechanism has been best documented for the homopteran typhlocybine Cicidellidae, and heteropteran Miridae (Fig. 7 e and g), Piesmatidae, Lygaeidae, and Pyrrhocoridae; Tingidae apparently also use lacerate-and-flush feeding for shallower epidermal tissues and mesophyll.

Hemipteroids and Paleodictyopteroids in the Evaluation of *Psaronius* Damage

Several features of *Psaronius* stylet tracks and associated histological context can be compared with modern hemipteroid insects and their associated plant damage, and also to descriptions of paleodictyopteroid mouthpart morphology (Tables 1 and 2). These features are the stylet trace dimensions, details of the region of puncture entry and the path of styletal penetration of tissue, medial ridges in the stylet trace, the salivary sheath, and reaction tissue. Also considered is the temporal relationship of the *Psaronius* damage to the geochronologic ranges of Paleodictyopteroidea and Hemipteroidea.

Stylet Trace Dimensions. A prominent feature of the *Psaronius* stylet trace is its rather long length of 4 mm by modern standards. This value exceeds almost all documented values for modern hemipterans, although limited data on cicadas indicate that their salivary sheath lengths can approach this value (e.g., White and Strehl 1978), and unlike paleodictyopteroids, stylet lengths can substantially exceed beak lengths in some hemipteran species (China 1931, Maschwitz et al. 1987). However, a beak length of 4 mm is consistent with a known range of 1.7–32 mm for paleodictyopteroid beak lengths (Table 2), and is attributable to a paleodictyopteroid species that was small in size, or was large in size but possessed an abbreviated beak length, or was a subadult instar of larger-sized species. Similarly, the estimated *Psaronius* stylet diameter of 0.45 mm. at midsection, taken as the widest distance across the stylet lumen in cortical tissue, is considerably wider than modern hemipteroid values, but acceptably narrower than the 0.5–2.1 mm range of midsection beak widths for well documented paleodictyopteroids (Table 2). All known paleodictyopteroid beaks whose lengths have been documented in the literature are from large individuals, probably imagines (Table 2); beaks from relatively small species or from smaller nymphs of large species are largely unknown, a feature probably attributable to the poorer preservational potential of smaller specimens.

Zone of Entry and Styletal Trajectory. Two additional features of the stylet trace are the shape of the entry area and its trajectory pattern through host tissue. A broadly flared entry area immediately below the *Psaronius* rhachis surface, in upper cortical tissue, is partially filled with a conical plug

Table 2. Beak lengths and widths for well-preserved Palaeodictyopteroidea

| Taxon | Beak | | References |
	Length, mm	Width, mm[a]	
Diaphanopteroidea			
Namurodiapha sippelorum Kukalová-Peck & Brauckmann	1.7	0.7	Kukalová-Peck and Brauckmann 1990
Prochoroptera calopteryx Handlirsch	2.7	0.5	Kukalová-Peck and Brauckmann 1990
"*Uralia*" *maculata* Sharov	2.4	?	Sharov 1973
Megasecoptera			
Lameerites curvipennis Handlirsch	7.0	0.6	Carpenter and Richardson 1968; C.C.L., unpublished data
Monsteropterum moravicum Kukalová-Peck	20.0	1.7	Kukalová-Peck 1972
Palaeodictyoptera			
Eugereon boeckingi Dohrn	32.0	0.95	Dohrn 1865a, Müller 1978, Shear and Kukalová-Peck 1990, Carpenter 1992
Homaloneura dabasinskasi Carpenter	?	1.7	Carpenter and Richardson 1971
Homioptera vorhallensis Brauckmann & Koch	23.5	2.1	Brauckmann, Lutz and Kemper 1985; Brauckmann, 1991a
Lithomantis carbonarius Woodward	11.0	0.8	Smart and Hughes, 1973
Mecynostoma dohrni Brongniart	20.0	0.6	Kukalová-Peck 1969a, Shear and Kukalová-Peck 1990
Paradunbaria pectinata Sharov & Sinitshenkova	2.8	?	Sharov and Sinitshenkova 1977
Stenodictya laurentiauxi Kukalová-Peck	8.6[b]	0.95	Laurentiaux 1952b, Kukalová 1970

[a] Width of beak at midsection.
[b] Preserved length; estimated length 15 mm.

of opaque substance, possibly suberized cortical parenchyma. This zone represents the initial styletal puncture of surface tissues. Although this flared surface region is rare in modern hemipteroids, subtler versions are found in a few lacerate-and-flush feeders such as tingids (Pollard 1959) and typhlocybine cicadellids (Vidano 1967; Backus, personal communication). However, the *Psaronius* expansion (Figs. 2 c and d, 3 b and c, 4 b and e) is more consistent with a basally expanded paleodictyopteroid beak that is broadly tapering in overall profile (compare Figs. 3c and 4b with 7a and b.), than it is with a parallel-sided fascicle that may be modestly flared only at the base.

The paleodictyopteroid stylet trajectories are dominantly intracellular, gently curvilinear while avoiding intervening gum sac cells, and terminate in vascular tissue. By comparison with extant hemipteroids, these tracks are unusually straight for a vascular tissue feeder. Modern hemipteroids that feed on vascular tissue generally pursue considerably more tortuous and intercellular paths (Pollard 1973). The relatively straight stylet probe resembles more a lacerate-and-flush feeder (Miles 1987; Fig. 7 e and g), but also is consistent with known paleodictyopteroid mouthpart apparati, particularly that of *Eugereon boeckingi* Dohrn (Fig. 7 a–c), wherein the beak is a fascicle of 5 long and thin stylets (Dohrn 1866a, b; Haupt 1949; Müller 1977, 1978; Shear and Kukalová-Peck 1990) that probably was capable of limited flexibility (Kukalová-Peck 1969a). Both the size and trajectory pattern of the *Psaronius* stylet tracks thus indicate a paleodictyopteroid maker.

Medial Ridges in Stylet Tracks. A recurring and conspicuous structure in both light and SEM is 1 or 2 median ridges on the inner surface of the stylet trace (Figs. 2f; 4g; 5 b, c, i; 6 h–j). Such ridges have never been documented by light or SEM in modern hemipteroids. We interpret a single ridge to represent the infilling of pierced plant tissue into a longitudinal sulcus traversing the distal to midsection region of the stylet fascicle. This single sulcus occurs either at the articulation of the mandibular and maxillary stylet pairs or at the articulation of the intermandibular or the intermaxillary stylet pairs (Figs. 6h, 7 b and c). (For structural details of the beak, see Carpenter and Richardson [1971], Müller [1977, 1978], and Kukalová-Peck [1972, 1985, 1991, 1992].) Accordingly, 2 median ridges resulted when the longitudinal plane of the stylet track was such that it revealed a sulcus created by the interlocking of the mandibular and maxillary stylet pairs, as well as another sulcus created either by the interlocking of the intermandibular stylet pair or the intermaxillary stylet pair (Figs. 6h and 7c). All *Psaronius* stylet traces additionally exhibit lateral ridges that delimit the margins of the stylet lumen wall (Figs. 5 b, c, h–j; 6 e–h) as it pierced through plant tissue (Figs. 5 b, c, i; 6f). The occurrence of median stylet ridges strongly suggests that a paleodictyopteroid was the piercing-and-sucking agent.

Salivary Sheath. A salivary sheath in *Psaronius* is suggested by the presence of an opaque substance lining the stylet track throughout the cortical parenchyma and vascular tissue, including the feeding cavity (Figs. 2 d and e; 3 b–f; 4 b, e, f; 5

a, d, g). Salivary sheaths are well documented in modern homopterous and pentatomomorph Hemiptera (Fig. 7 d–g; Miles 1959a, Hori 1968), although Hori (1971) indicates that in mirids a "brown-colored layer" (for example, Fig. 7 e and g) may be a combination of plant-derived and non-lipoprotein insect-derived substances. It is unknown whether paleodictyopteroids secreted salivary sheaths. Likewise, although feeding cavities similar to those in *Psaronius* have been documented in a few hemipteran groups—particularly mirids (Fig. 7 e and g; Smith 1926, Flemnion et al. 1954, Hori 1971), aphidids (Büsgen 1891, Horsfall 1923, Chatters and Schlehuber 1951), cicadellids (Fig. 7 d and f), and lygaeids (Painter 1928)—no data address whether paleodictyopteroids also fluid fed in host tissue by sucking inflowing sap from a feeding cavity. The targeted tissue of xylem and phloem in the feeding cavities of *Psaronius* is a combination rarely found in modern hemipteroids, which usually specialize either on xylem or phloem (Pollard 1969, Backus 1988, Carver et al. 1991; but see Carle and Moutous 1965, Khan and Saxena 1984). This modern specialization has been explained as a consequence of very different mechanisms for fluid uptake, particularly those involving the cibarial pump: xylem, which is negatively pressurized, requires active pumping, whereas positively pressurized phloem is imbibed largely by valvular regulation (Kennedy and Mittler 1953, Pollard 1969, Raven 1983, McLean and Kinsey 1984, Backus 1985, Tavella and Arzone 1993). Consequently, the presence of salivary sheaths lining the feeding cavities of evacuated xylem and phloem in *Psaronius* is not helpful in determining a potential culprit.

Reaction Tissue. Because modern plants respond to hemipteroid stylet penetration in 2 fundamentally different ways—production of relatively disorganized reaction tissue and of highly differentiated nutritive tissue—the type of tissue response by *Psaronius* to stylet laceration may be important. Cortical parenchyma cells adjacent to the stylet trace exhibit thickening and internal deposition of an opaque substance; those closest to the sheath apparently were plasmolyzed and have shrunken contents. The major histological change is the general enlargement and proliferation of cells surrounding the stylet trace. This reaction tissue forms masses of anisodiametric cells different from the regular arrangement of isodiametric cells paralleling the epidermis and vascular tissue in undisturbed cortical parenchyma. Examples of similar reaction tissue resulting from modern stylet laceration are known for aphidids (Chrystal 1925, Evert et al. 1968), phylloxerids (Balch 1952), cercopids (Ewan 1961), cicadellids (Poos and Wheeler 1943, Kabrick and Backus 1990, Ecale and Backus 1995), aleurodids (Walker 1985), asterolecanids (Parr 1937), and mirids (King and Cook 1932).

By contrast, there is no indication of nutritive tissue typical of true insect galls. Cells comprising recent hemipteroid-induced nutritive tissue are characteristically dense, rich in starch and lipids, and organized into globose tufts of bricklike cells oriented toward the gall stimulus (Rohfritsch 1981, Meyer 1987, Ananthakrishnan and Raman 1989). Notably, gall-induced nutritive tissue has been documented in several *Psaronius* specimens from the same deposit, including UIUC-8227 (unpublished data), but is located in axial, medullary parenchyma (Figs. 2 b and c, 3 a and b, 4 a and b), where it is structurally distinct from the stylet-induced reaction tissue. Our data indicating that stylet-induced *Psaronius* reaction tissue is very similar to recent, hemipteroid-induced plant damage is based on only the few examples presented herein: There is no other histological documentation of plant response to paleodictyopteroid-inflicted damage.

Geochronologic Timing. Lastly, the geochronologic occurrence of piercing-and-sucking damage occurring in early Late Pennsylvanian *Psaronius* vascular tissue is parsimoniously attributable to a paleodictyopteroid, rather than an hemipteroid. By comparison with wing structure of known Permian Hemiptera possessing piercing-and-sucking beaks, the earliest known hemipteroids capable of this damage occurred during the Asselian Stage of the Early Permian (Fig. 1; Evans 1956, 1963, 1964; Labandeira 1994). However, an earlier, structurally diverse, hemipteroid stem group, initially established by Rohdendorf and Rasnitsyn (1980) and later characterized by Shear and Kukalová-Peck (1990) and Kukalová-Peck and Brauckmann (1992), encompassed 25 families that were not closely related to paleodictyopteroids, but possessed tenuous (though controversial) phylogenetic links to Permian heimpteroids. Its members lacked specific piercing-and-sucking mouthparts capable of producing the *Psaronius* damage. By contrast, paleodictyopteroids had reached their peak diversity during the Late Pennsylvanian (Labandeira and Sepkoski 1993), and represented at least 35 families during the Kasimovian Stage (Labandeira 1994).

Elucidation of the Palaeodictyopteroid Culprit

The Palaeodictyopteroidea represents an extinct clade of 4 orders of piercing-and-sucking insects and are among the earliest winged insects known in the fossil record (Nelson and Tidwell 1987; Brauckmann 1991a, 1991b). Their collective geochronologic range is from earliest Pennsylvanian to Late Permian (Fig. 1; Labandeira 1994). Because head and mouthpart structure is well known for several species (Crampton 1927; Laurentiaux 1952b; Sharov 1973; Müller 1977, 1978; Shear and Kukalová-Peck 1990; Kukalová-Peck 1991, 1992), inferences regarding their interactions with plants have been based on mouthpart morphology and rarely on physical evidence of plant damage or gut contents. Fortunately, several features of the *Psa-*

ronius stylet traces warrant assignment of the culprit to a paleodictyopteroid insect.

The following 4 features implicate a paleodictyopteroid as the culprit: (1) a relatively large beak size; (2) a stylet track characterized by a conical surface entry area and an intracellular, highly linear trajectory into cortical and vascular tissue; (3) presence of 1 or 2 median, interstyletal ridges; and (4) occurrence during a geochronologic interval dominated by paleodictyopteroid, piercing-and-sucking insects and preceding the earliest documented hemipteran by ≈10 million years (Table 1). The other characteristics of *Psaronius* damage—a salivary sheath, feeding cavity, host response tissue, and a target tissue of xylem and phloem—are found in recent hemipteroids but also may have been present in paleodictyopteroids. Thus, these 4 latter features are agnostic with regard to our identification of a culprit.

Of those features implicating paleodictyopteroids, the size, shape, and linearity of the trajectory is highly consistent with known paleodictyopteroid beaks. A stylet length of 4 mm and a midsection stylet width of 0.45 mm is within the paleodictyopteroid range (Fig. 7 a–c), although it is possible that known modern cicadid and pentatomomorph hemipterans may have robust, tissue-penetrating stylets approximating this length. The avoidance of *Psaronius* gum sac cells, suggesting some flexibility of the beak, would be expected for forms with long, gracile beaks of the contemporaneous paleodictyopteran Eugereonidae and Mecynostomatidae (Müller 1977, 1978; Shear and Kukalová-Peck 1990; Carpenter 1992; Fig. 7 a–c), but not of the more massively built, often triangular and basally flaring beaks of Megasecoptera, Diaphanopterodea, and some robust Palaeodictyoptera. Notably, large modern hemipterans such as Cicadidae and Cercopidae that bear relatively long and gracile beaks, are capable of substantial flexibility during host tissue penetration (Murti 1929, Ewan 1961). Another feature is the expanded, flared opening of the puncture toward the surface tissues. This flared entry zone accommodates paleodictyopteroid beaks with broad, expanded bases, and is unlike the few modern hemipteroid beaks which possess stylet fascicles that are small and have only modestly flared bases adjacent the head. All known paleodictyopteroid beaks possessed flared bases (Fig. 7 a–c) that probably wedged apart surface plant tissues during ingesting of deeper tissues such as xylem or phloem.

The presence of 1 or 2 pronounced ridges in longitudinal sections of stylet tracks is an important attribute that also suggests a paleodictyopteroid maker. These characteristic ridges, evident in both light photographs and scanning electron photographs, are consistent with an unsheathed paleodictyopteroid beak that bore an interlocking mandibular pair of stylets that articulated with an interlocking and larger maxillary pair of stylets (Laurentiaux 1952a; Carpenter and Richardson 1971; Kukalová-Peck 1972, 1985, 1991). The interstyletal sulci of this stylet fascicle would appear as a ridge in the lumen of a puncture in plant tissue (Fig. 6 g and h), particularly if the host tissue was nonlignified and deformable parenchyma. Depending on the orientation of the stylet fascicle revealed in longitudinal section, 1 or 2 interstyletal ridges would be present (Figs. 6 g and h; 7 a–c). Unlike hemipteroids, the labium was free and consisted of long, Z-articulated ligula that guided and braced the beak during probing and piercing of food tissue. Additionally, long maxillary palps also guided and stabilized the beak during probing and piercing.

Recent examination of well-preserved paleodictyopteroid fossils has elucidated their head and beak morphology. General patterns of beak length, width, and robustness now are known for Diaphanopterodea, Megasecoptera, Palaeodictyoptera (Table 2), and marginally for Permothemistida (Shear and Kukalová-Peck 1990, Kukalová-Peck 1991). When contrasted with the *Psaronius* stylet trace length of 4 mm, the Diaphanopterodea are excluded because available evidence indicates that their beaks were compact, triangular, and short (Kukalová-Peck and Brauckmann 1990, Kukalová-Peck 1991). One mid-Permian lineage possessed a considerably longer and robust beak (Sharov 1973; Kukalová-Peck 1983, 1992), but it probably fed on the contents of pteridophyte cones, as it possessed a beak designed for cutting as well as piercing tissue (Kukalová-Peck, personal communication), and related nymphs bear gut contents with spores (Kukalová-Peck 1987, 1991). With the exception of 1 family, the Permothemistida occurred exclusively during the Permian, and had short mouthparts, some approaching 1 mm in length (Shear and Kukalová-Peck 1990, Kukalová-Peck 1991). During the Late Pennsylvanian, the Megasecoptera and Palaeodictyoptera were the only piercing-and-sucking insects capable of producing the observed damage on *Psaronius* (Table 2; Shear and Kukalová-Peck 1990, Kukalová-Peck 1991).

Several features of the beak separate the Megasecoptera from the Palaeodictyoptera. All known megasecopteran beaks were massive and consisted of stylets that were basally broad and rapidly tapered terminally, appearing more triangular than parallel-sided in profile. It is likely that such beaks were used for wedging apart tissues in imbibing particulate material, either as a fluid suspension or possibly as spores (Sharov 1973; Smart and Hughes 1973; Kukalová-Peck 1985, 1991; Retallack and Dilcher 1988; Shear and Kukalová-Peck 1990). Although most paleodictyopteran beaks were equally long and robust, at least those of the Eugereonidae (Fig. 7 a–c) and Mecynostomatidae were exceptionally slender and parallel-sided in profile (Laurentiaux 1952b), having a subdued taper from the beak tip to its base (Kukalová 1969a, Müller 1978, Shear and Kukalová-Peck 1990). Proof of beak flexibility is provided by a sharply bent, but not

broken, beak of an adult of the spilapterid paleodictyopteran, *Homaloneura lehmani* Kukalová-Peck (1969a, figure 8). Additionally, from the same deposit as the *Psaronius* damage, Schopf illustrated an apparent stylet trace in the seed fern prepollen organ *Dolerotheca*. This slender, approximately 1.2 cm long, disruption of microsynangiate tissue terminates in a feeding pool (Schopf 1948, plate 104, figure 3) that is consistent with fluid feeding. These data indicate that a biomechanically reasonable diet for paleodictyopterans with long, narrow beaks was sap from vascular tissue.

Late Pennsylvanian Tree-Fern Forests Promoting Hemipteroid Diversification

A diet of plant sap has been suggested for paleodictyopteroids by Laurentiaux (1952b), Kukalová (1970), Sharov (1971, 1973), Scott and Taylor (1983), and Carpenter (1992), although Shear and Kukalová-Peck (1990) indicated that paleodictyopteroid beaks were too rigid, too broad, and insufficiently long to penetrate bark and cortical tissues for imbibition of deep-seated vascular tissues. In terms of both clypeal pump development, and the length, width, and robustness of their mouthparts, the remarkable structural diversity of paleodictyopteroids (Carpenter 1971, DiMichele and Hook 1992) was too great for only 1 type of feeding style and diet. Notably, beak lengths exceeded an order of magnitude, and massive beaks with broad bases were undoubtedly more rigid than long, gracile beaks. Most likely, Middle Pennsylvanian paleodictyopteroids with long, robust beaks consumed nutrient-rich fructifications (Sharov 1973, Rohdendorf and Rasnitsyn 1980, Retallack and Dilcher 1988, Kukalová-Peck 1992); others with modest-sized beaks probably subsisted on foliage, although presently there is no direct fossil evidence for this.

Whereas most plants dominant during the Middle Pennsylvanian possessed deeply embedded vascular tissue protected by thick cortical or peridermal tissues (Smart and Hughes 1973, DiMichele and Hook 1992), the rhachises of subdominant tree ferns and smaller herbaceous ferns bore vascular tissue that was accessible to stylate insects with beaks as short as 4 mm (Scott and Taylor 1983). During the Middle to Late Pennsylvanian transition, major environmental disruption forced the extinction of the dominant lycopod genera, resulting in the appearance of dominantly *Psaronius* tree-fern forests with closed canopies. The *Psaronius* trees of the Late Pennsylvanian coal swamps were much larger than those found during the Middle Pennsylvanian coal swamps and, with minor exceptions, were comprised of different species (Lesnikowska 1989). Additionally, most coal-swamp species of *Psaronius* became extinct near the Middle to Upper Pennsylvanian boundary. Consequently, the Late Pennsylvanian coal swamps were colonized by *Psaronius* tree ferns from nearby habitats on mineral substrates. The phloem, xylem, and even medullary parenchyma, were situated on *Psaronius* rhachises less than a centimeter from the epidermal surface, and thus their fluids were available for extraction by palaeodictyopteroid insects with relatively short beaks.

We hypothesize that the dominance and widespread distribution of *Psaronius* tree ferns during the Late Pennsylvanian, after the major Euramerican extinctions (Phillips et al. 1974, 1985) offered a major, plentiful, and accessible food source to sap-sucking insects in equatorial ecosystems. Thus, although Megasecoptera and Palaeodictyoptera also suffered a major extinction at the end of the Middle Pennsylvanian (Laurentiaux 1952b, Labandeira and Sepkoski 1993), of the remaining families from these 2 orders that survived into the Late Pennsylvanian, 73% were Palaeodictyoptera (Labandeira 1994) that possessed various modifications of piercing-and-sucking mouthparts. Many of these paleodictyopterans existed in a restructured coal-swamp community where tree-fern dominants locally constituted as much as 80% of the biomass (Phillips et al. 1985, Lesnikowska 1989), offering previously unparalleled opportunities for herbivore extraction of fluid tissue, including vascular sap. It is likely that the emergence of these tree-fern forests in Upper Pennsylvanian swamp forests, followed by the spread of diverse gymnospermous taxa during the Pennsylvanian to Permian transitional interval, offered new food resource opportunities for hemipteroid ancestors. These restructured plant communities, at least in equatorial, wetland environments, propelled the hemipteroid radiation, eventually replacing their paleodictyopteroid ecologic analogs by the Late Permian. We suggest that it was accessibility of insects to a diversity of sap-rich tissue types that allowed for the evolution of the 3 distinctive feeding styles characterizing hemipteroids today.

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