

EARLY HISTORY OF ARTHROPOD AND VASCULAR PLANT ASSOCIATIONS¹

Conrad C. Labandeira

Department of Paleobiology, Smithsonian Institution, National Museum of Natural History, Washington, DC 20560; labandec@nmnh.si.edu

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ABSTRACT

Although research on modern plant-arthropod associations is one of the cornerstones of biodiversity studies, very little of that interest has percolated down to the fossil record. Much of this neglect is attributable to dismissal of Paleozoic plant-arthropod interactions as being dominated by detritivory, with substantive herbivory not emerging until the Mesozoic. Recent examination of associations from some of the earliest terrestrial communities indicates that herbivory probably extends to the Early Devonian, in the form of spore feeding and piercing-and-sucking. External feeding on pinnule margins and the intimate and intricate association of galling are documented from the Middle and Late Pennsylvanian, respectively. During the Early Permian, the range of external foliage feeding extended to hole feeding and skeletonization and was characterized by the preferential targeting of certain seed plants. At the close of the Paleozoic, surface fluid feeding was established, but there is inconclusive evidence for mutualistic relationships between insect pollinivores and seed plants. These data are gleaned from the largely separate trace-fossil records of gut contents, coprolites, and plant damage and the body-fossil records of plant reproductive and vegetative structures, insect mouthparts, and ovipositors. While these discoveries accentuate the potential for identifying particular associations, the greatest theoretical demand is to establish the spectrum and level of intensity for the emergence of insect herbivory in a range of environments during the Pennsylvanian and Permian.

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INTRODUCTION

During the past 100 years, a rich and extensive literature has formally described thousands of vascular plant and arthropod (overwhelmingly insect) taxa from numerous terrestrial deposits of the Late Paleozoic. Increasingly this alpha-level documentation has placed in systematic context early members of what have become the two most diverse and interactive groups of macroscopic organisms. Even though vascular plant and arthropod taxa from well-known Late Paleozoic terrestrial biotas have been characterized taxonomically—for example Mazon Creek in north-central Illinois (Janssen 1965, Shabica & Hay 1997), Elmo in central Kansas (Sellards 1909, Moore 1964), and Chekarda in the central Urals of Russia (Martynov 1940, Meyen 1982)—little is known of the associations that occurred between these two ecologically dominant groups of organisms (Wootton 1981, Meyen 1987). Comprehensive evaluations of plant-arthropod associations are not available for even well-documented Paleozoic biotas, and overwhelmingly the available data consist of selected interactions, often on a single plant organ and anecdotally documented by one to several specimens. Virtually all of the primary documentation has been uncovered during the past 25 years; several review articles (Scott & Taylor 1983, Labandeira & Beall 1990, Scott et al 1985, 1992, Chaloner et al 1991, Scott 1991, 1992, Stephenson & Scott 1992, Smith 1994) provide partial summaries of the known record.

By contrast, significant studies of modern plant-arthropod associations extend from the late 1800s (e.g. Packard 1890, Riley 1892a). An intellectual renaissance characterized the 1960s–1980s, when several influential articles, proposing novel mechanisms for observed patterns of interactions between vascular plants and insects (e.g. Ehrlich & Raven 1964, Feeny 1976, Berenbaum 1983), reinvigorated multidisciplinary interest in the field. Most recently, a widespread interest in the mechanisms that generate biodiversity has focused on the multiplicative and often intricate associations between plants and insects (Thompson 1994). A testament to this heightened interest has been publication of brief but accessible summaries of the field (Edwards & Wratten 1980, Hodkinson & Hughes 1982, New 1986) and several prominent volumes (Howe & Wesley 1988, Abrahamson 1989, Price et al 1991) during the past decade.

Perhaps the dearth of documentation for Paleozoic vascular plant-arthropod associations represents a consequence rooted in reality—namely that arthropods were overwhelmingly if not exclusively detritivorous and consequently were not directly involved with live plant tissue. This view has been the reigning paradigm during the past 30 years (Hughes & Smart 1967, Cox 1974, Zwölfer 1978, Rolfe 1985, Shear & Kukalová-Peck 1990, Hughes 1994, Edwards et al 1995), although its origins were considerably earlier (Riley 1892b, North 1931). However, some paleobiologists and entomologists have proposed that some

Paleozoic insect clades were actively herbivorous (Popov & Wootton 1977, Rohdendorf & Rasnitsyn 1980) and a few even endophytic and thus consuming internal plant tissues from within (Lameere 1917, Malyshev 1966, Sharov 1966, Labandeira & Phillips 1996b). A critical distinction for this issue is realization that the fossil insect record is divisible into two taxonomically distinctive and evolutionarily separable faunas: the Paleozoic Entomofauna and the post-Paleozoic Modern Entomofauna. The Paleozoic Entomofauna is separated from the Modern Entomofauna by both the terminal Permian extinction and by previous replacements of major taxa during the Permian (Wootton 1990, Labandeira & Sepkoski 1993, Ross & Jarzembowski 1993). Thus, these two major faunas are evolutionarily distinguishable at the highest taxonomic levels (Carpenter 1977, Carpenter & Burnham 1985). The Paleozoic Entomofauna is ecomorphologically analogous to the Modern Entomofauna (Labandeira & Sepkoski 1993) in terms of the spectrum of mouthpart types (Labandeira 1990, 1997a), functional feeding groups (Labandeira 1998), and dietary guilds (Labandeira 1998). In fact, following the Permian extinctions, levels of Late Paleozoic family-level and presumably lower-level diversity were not re-established until the Middle Jurassic (Labandeira & Sepkoski 1993), during which the variety of feeding strategies, based on other criteria, coarsely approximated the spectrum of today (Labandeira 1996, 1998). In addition, evidence from Paleozoic floras preserved as three-dimensional coal balls and two-dimensional compressions indicates a wealth of plant-arthropod interactions equivalent in variety (Scott & Taylor 1983, Scott et al 1992, Labandeira 1996) and comparable in intensity (Beck & Labandeira 1998) to that of the post-Paleozoic. As detailed later in this review, the spectrum of herbivores associated with the Paleozoic Entomofauna occupied almost all of the same ecological niches as ecologically analogous taxa for the Modern Entomofauna (Labandeira 1996).

Theoretical interest in documenting Paleozoic vascular plant and arthropod associations are relevant for addressing hypotheses that explain the role of arthropods in structuring the development of trophic webs on land. Specifically, to what extent did insects channel primary plant productivity to degraded carbon through the process of detritivory, and when was this process supplemented by the more direct route of herbivory (DiMichele & Hook 1992)? When herbivory was established, how were plant organs and tissues partitioned and when did plant-host specificity and elevated levels of plant consumption originate? Did the evolution of these herbivore trophic relationships proceed in a geochronologically rapid fashion during the Paleozoic or as a prolonged accumulation into the Mesozoic and Cenozoic (Strong et al 1984)? Because these questions are central to this review, there is a special emphasis placed on herbivory, unlike previous summaries that emphasized documentation of detritivory (Hughes & Smart 1967, Rolfe 1985, Shear & Kukulová-Peck 1990, Shear 1991).

TYPES OF EVIDENCE

Paleozoic plant-arthropod associations occur in deposits preserved either as three-dimensional permineralizations (e.g. Rothwell & Scott 1988) or as two-dimensional compressions and impressions (e.g. Beck & Labandeira 1998). Within these two widespread taphonomic modes, evidence for plant-arthropod associations can be accessed from damaged plants, structures on insect bodies such as mouthparts and ovipositors, and diagnostic anatomical features of plants. For plant damage, candidate material must be evaluated by several explicit criteria to differentiate insect feeding from alternative causes of tissue damage, such as wounding caused by fungi (Dilcher 1965, Sinclair et al 1987, Parbery 1996) or abiotic trauma (Lucas et al 1991, Wright & Vincent 1996). Plant wound structures produced by insects also are evaluated by understanding how insects use their mouthparts in feeding (Sharov 1973, Smith 1985), as manifested in microscopic patterns of damage attributable to mouthpart element structure or hardwired behavior (Gangwere 1966, Schmidt & Parameswaran 1977, Kazikova 1985). Well-preserved fossil foliar material can provide some clues for identifying the responsible herbivore culprits (Labandeira & Phillips 1996a,b, Beck & Labandeira 1998).

Qualitative Categories

The ichnofossil record of Paleozoic plant-arthropod associations can be condensed into five qualitative categories. The evidence for these categories ranges from the direct display of insect gut contents, where particular consumer and consumed species are identified, to the indirect example of reproductive and vegetative plant morphology, where possible pollination syndromes can be ascribed to a potential insect clade. Most of the evidence lies between these two extremes, especially stereotyped patterns of insect feeding attributable to culprits at intermediate taxonomic levels.

GUT CONTENTS Until 1996, only sporadic instances of gut contents in Paleozoic arthropods were known. In almost all of these examples, spores were documented from ironstone nodules containing late Middle Pennsylvanian insects. Notable instances are the ancestral hemipteroid *Eucaenus* with lycopsid microspores lodged in its intestinal tract (Scott & Taylor 1983, Scott et al 1985), an "indeterminate protorthopteran" containing calamite spores (Scott & Taylor 1983), a diaphanopterodean nymph with undetermined spores (Kukalová-Peck 1987), and other examples (Richardson 1980). A large arthropleurid myriapod with lycopsid tissues in its gut (Rolfe & Ingham 1967, Rolfe 1980) probably represents detritivory, although *Monoletes* prepollen from a medullosan seed fern on the leg of another *Arthropleura* specimen (Scott & Taylor 1983) may represent a dispersal mechanism (Richardson 1980) or pollinivory. Better-preserved

material recently has been recovered from fine-grained Lower Permian shales at Chekarda, Russia, where consumption of pollen from peltasperm and glossopterid seed ferns and a coniferalean gymnosperm is documented for ancestral hemipteroids, the Grylloblattida, and an unassigned species (Rasnitsyn & Krassilov 1996a,b, Krassilov & Rasnitsyn 1997). These examples, coupled with the well-preserved record of spore-bearing coprolites in earlier permineralized material, demonstrate that spores, prepollen, and pollen were important dietary components for late Middle Pennsylvanian to Early Permian insects. This feeding strategy probably was an important precursor to suggested Paleozoic pollination mutualisms (Labandeira 1997a,b) that occurred between insects and medullosan seed ferns (Halle 1929, Dilcher 1979, Taylor & Millay 1979, Taylor & Taylor 1993), cycadophytes (Mamay 1976), and conifers (Archangelsky & Cuneo 1987).

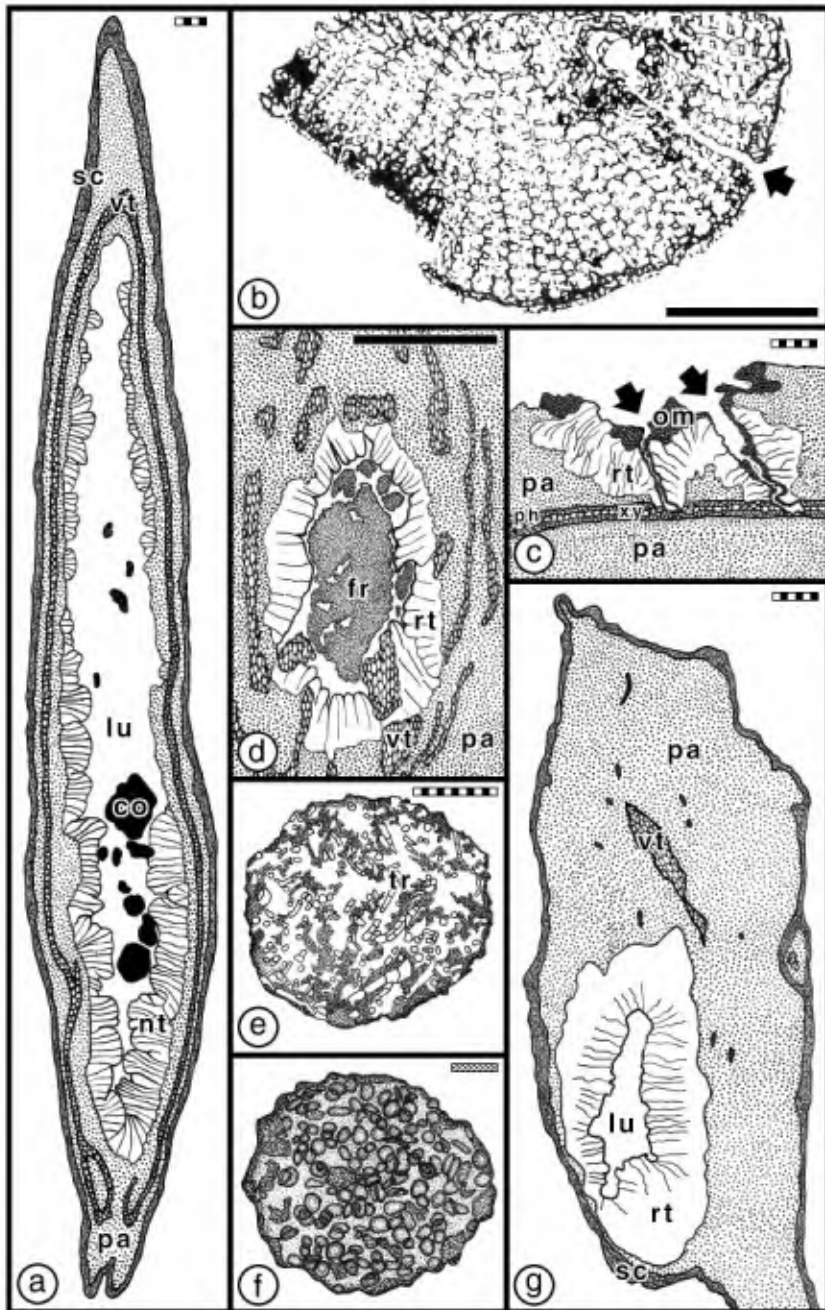
With the exception of indurated lycopsid tissues in the gut of *Arthropleura* (Rolfe & Ingham 1967), all documented gut contents of terrestrial Paleozoic arthropods consist of spores or pollen. By comparison, a vast array of modern insect lineages ingest spores and pollen, although documentation is best for springtails (Porsch 1958, Kevan & Kevan 1970, Lawton 1976), orthopterans (Grinfel'd 1957, Porsch 1958, Schuster 1974), thrips (Ananthakrishnan & James 1983, Heming 1993), numerous beetle groups (Gottsberger et al 1980, Irvine & Armstrong 1990, Picker & Midgley 1996), vespid wasps (Hunt et al 1991, Gess 1996), all bee lineages (Dietz 1969, Waddington 1987), flies such as bee flies (Grimaldi 1988) and hover flies (van der Goot & Grabandt 1970, Proctor et al 1996), and butterflies (DeVries 1979, Gilbert 1972). Some of these lineages may have had ancestral representatives during the Paleozoic (Grinfel'd 1973, 1975, Heming 1993); for example, plesiomorphic mouthpart modifications among some extant holometabolans suggest retention of an ancient spore/pollen feeding mechanism (Malyshev 1966, Kristensen 1995).

A few studies, mostly of pollenivorous bees and hover flies, document the physical modification of pollen as it moves through the digestive system (Dietz 1969, Holloway 1976, Klungness & Peng 1984). There often is minimal structural alteration of pollen during digestion, permitting identification of intact, crushed, or fragmented grains in the hindgut bolus or the excreted pellet (Waldorf 1981, Klungness & Peng 1983). Some insect clades that are putatively carnivorous or omnivorous in feeding habits have been shown to consume modest amounts of pollen upon examination of intestinal contents (Stelzl 1991). In particular, consumption of fern spores from sporangia has been documented recently in various bugs (Wieczorek 1973, Lawton 1976), beetles (Board & Burke 1971, Loyal & Kumar 1977, Leschen & Lawrence 1991), sawflies (Naito 1988), and especially moths (Swezey 1922, Needham 1947, Ottosson & Anderson 1983, Thien et al 1985; also see Owen 1993). Based on

occurrences of sporivory by insects from geologically young oceanic islands (Hendrix 1980, Paulay 1985, Leschen & Lawrence 1991), fern sporangia and foliage are diets acquired on macroevolutionarily short time scales.

COPROLITES Fossilized fecal pellets of arthropods, known as coprolites, are preserved in the compression fossil record in leaf mines (Opler 1973, Crane & Jarzembowski 1980, Labandeira et al 1994a), although the greatest histological detail occurs in carbonate permineralizations of peat from Pennsylvanian-age coals from Euramerica (Scott 1977, Baxendale 1979, Scott & Taylor 1983, Labandeira & Phillips 1996b). Plant tissues from these coprolites frequently are identified to the source plant taxon, even to specific organ and tissue types (Scott 1977, Rothwell & Scott 1988, Labandeira & Phillips 1996b). Distinctive tissue and cell types described in the paleobotanical literature often are conspicuous coprolite constituents, and they include diagnostic gum-sac cells from marattialean ferns (Stidd 1971, Lesnikowska 1989, 1990), monoserial trichomes and multicellular papillae (Barthel 1962, Reihman & Schabillion 1976, Cleal & Shute 1991; Figure 1e), epidermal cuticles of seed-fern pinnules (Barthel 1962, Reichel & Barthel 1964, Reihman & Schabillion 1978, Cleal & Zodrow 1989), and a variety of spore and pollen form-taxa (Peppers 1964, 1970, Courvoisier & Phillips 1975, Traverse 1988; Figure 1f). Several classes

Figure 1 Spectrum of associations between insect herbivores and vascular plants occurring in a Late Pennsylvanian (299 Ma) coal-swamp forest from the Illinois Basin, dominated by the tree fern *Psaronius chasei* (a, c, g) and medullosan seed ferns (b, d, e). This material was collected from the Calhoun Coal of the Desmoinesean Mattoon Fm. and originates from the Berryville locality of Lawrence County, Illinois. These are stereomicroscope camera lucida drawings of acetate peels mounted on microscope slides. Abbreviations: co = coprolite; fr = frass; lu = lumen, nt = nutritive tissue; om = opaque material; pa = parenchyma, ph = phloem, rt = reaction tissue, sc = sclerenchyma, st = stylet track; tr = trichome, vt = vascular tissue, xy = xylem. Scale bars: solid = 1 cm; striped = 0.1 cm; stippled = 0.01 cm. Repositories: UIUC = University of Illinois at Urbana-Champaign paleobotany collections; NMNH = National Museum of Natural History Department of Paleobiology collections. (a) Gall of holometabolous insect on an oblique section of the frond petiole of *Psaronius* (Labandeira & Phillips 1996b). Specimen UIUC slide 22655, from peel 31272-Bbot (section 84). (b) Boring-and-sucking of a paleodictyopterid insect on the pre-pollen organ of a medullosan seed fern. From Schopf (1948), plate 104, Figure 3; coal ball 129A. See also Retallack & Dilcher (1988). Arrow indicates stylet track. (c) Piercing-and-sucking of a paleodictyopterid insect on the vascular tissue of a *Psaronius* frond petiole (Labandeira & Phillips 1996a). Arrows indicate position of stylet tracks. Specimen UIUC slide 22736, from peel 8227-Bbot (section 94). (d) Boring in live stem tissue of a medullosan seed fern. Specimen NMNH slide 483989, from peel BV55-Dtop. (e) Insect coprolite containing conspicuous *Alethopteris* trichomes from foliage of a medullosan seed fern. Specimen NMNH slide 483987, from peel BV49-Gbot. (f) Insect coprolite containing indeterminate pteridophyte spores. Specimen NMNH slide 483988, Dtop. (g) Boring in live root tissue of *Psaronius*. Specimen NMNH 483986, from peel BV18-Itop.



of Euramerican coprolites can be characterized based on combinations of size (Baxendale 1979, Scott & Taylor 1983), internal composition and texture (Scott 1977, Meyen 1984, Rothwell & Scott 1988), and adjacent vegetational context (Williamson 1880, Cichan & Taylor 1982, Rothwell & Scott 1983, Goth & Wilde 1992, Labandeira et al 1997). The histological constituents of coprolites, in particular, provide data for inferring dietary strategies of arthropods in coal-swamp forests. Given the exquisite anatomic detail of most coprolitic contents and the presence of abundant yet diverse coprolite assemblages, particularly of canopy and trunk dwellers from Late Pennsylvanian deposits, the diets of coal-swamp arthropods can be reconstructed with greater precision than previous examples in Paleozoic food-web reconstructions (Scott 1980, Scott & Taylor 1983, Scott & Paterson 1984).

In this context, gross structural characterization of modern fecal pellets traditionally has been used for taxonomic identification of their producers (Nolte 1939, Morris 1942, Marcuzzi 1970, Solomon 1977). Recognizable tissue fragments within recent fecal pellets have been examined for interpreting arthropod diet and feeding mechanisms (Arriaga 1981, Pant et al 1981, Haq 1982, Stebayev & Pshenitsyna 1985), a procedure that rarely has been applied to permineralized Paleozoic material (Scott & Taylor 1983, Labandeira & Phillips 1996b). Whereas no monographic studies describe modern fecal pellets across major mite, myriapod, and insect taxa, sporadic data are available for economically important phytophagous taxa that are likely to have related lineages or ecological analogs in the Paleozoic. For example, during the Late Pennsylvanian, large, ovoidal coprolites that are subhexagonal in cross section are probably attributable to orthopteroid insects (C Labandeira, personal observation) because of the role their rectal papillae exert in shaping fecal pellets (Palm 1949, Wall & Oschman 1976). A modest literature exists for solid food feeders such as oribatid mites (Schulte 1976, Robaux et al 1977, Haq 1982), myriapods (Zachariae 1965, Paulusse & Jeanson 1977, Rusek 1985), springtails (Kilbertius & Vannier 1979, Rusek 1985), cockroaches (Hartnack 1943, Sweetman 1965), orthopterans (de Villalobos 1980, Stebayev & Pshenitsyna 1985, Gangwere 1993), and beetles (Eckstein 1939, Sweetman 1965, Hay 1968, Solomon 1977), as well as other holometabolous insects (Nolte 1939, Morris 1942, Zachariae 1965) with possible Paleozoic occurrences. Extensive studies of modern crop pests (Painter 1968, Bernays & Chapman 1994), and to a lesser extent the natural history of noneconomic species (Packard 1890, Johnson & Lyon 1991), demonstrate that insect herbivores consume foliage resulting in intestinal and fecal concentrations of digestion-resistant plant material. There is substantial documentation of such plant cuticle accumulation (Weiss & Boyd 1950, Gangwere 1962, Launois 1976), especially trichomes (Southwood 1986) in fecal pellets. Thus, trichome-laden Paleozoic coprolites (Figure 1e) almost certainly resulted from herbivory

because modern herbivores that feed on trichome-bearing foliage produce fecal pellets rich in undigested trichomes (Wellso 1973, Smith & Kreitner 1983, Stebayev & Pshenitsyna 1985, but see Cornaby 1977). By contrast, Paleozoic fluid-feeding insects, such as paleodictyopteroids and hemipteroids, undoubtedly excreted liquid or semiliquid feces similar to those of modern hemipteroids (Storey & Nichols 1937, Broadbent 1951) and lack a coprolite record. Small-particle feeders such as spore and pollen consumers have left a coprolite record (Mamay & Yochelson 1953, Scott 1977, Meyen 1984, Rothwell & Scott 1988, Labandeira & Beall 1990; Figure 1e) that is comparable in preservational quality to that of consumers of vegetative tissues (Scott 1977, Baxendale 1979, Scott & Taylor 1983, Rothwell & Scott 1983; Figure 1f).

PLANT DAMAGE The paleobotanical literature of plant damage in coal-ball permineralizations commences during the 1900s and consists of descriptions of anomalous tissue proliferation induced by trauma while the plant organ was alive. Examples are known from lycopsids (Seward 1906, Wilkinson 1930), sphenopsids (Stopes 1907), ferns (Holden 1930, West 1962), seed ferns (Holden 1910), and gymnosperms (Jeffrey 1906), although the causes—whether abiotic or biotic or, if biotic, whether insectan or noninsectan—generally are not convincingly demonstrated (Scott 1977). These earlier records lack a diagnostic suite of features indicating insect damage, including initial formation of frass-laden tunnels or chambers, subsequent reaction tissue, and further counter-responses such as bite marks and cross-cutting exit holes. An example of insect-mediated plant damage in permineralized tissues are Pennsylvanian marattialean ferns that bore frond petioles, whose internal tissues were consumed by piercer-and-suckers (Scott & Taylor 1983, Labandeira & Phillips 1996a; Figure 1c) and galls (Labandeira & Phillips 1996b; Figure 1a), and stems and roots damaged by borers (Rothwell & Scott 1983; Figure 1g). In addition, medullosan seed ferns, subdominant in the same Late Pennsylvanian deposits as marattialean ferns, bore bell-shaped prepollen organs with stylet-pierced tissues (Schopf 1948, Retallack & Dilcher 1988, Labandeira & Phillips 1996a; Figure 1b), foliage that was heavily targeted by mandibulate insects (Labandeira 1996; Figure 1e), and stem tissues in pithy trunks penetrated by oribatid mite and solitary insect borers (Williamson 1880, Cichan & Taylor 1982, Labandeira et al 1997; Figure 1d).

By far the most extensive examples of Paleozoic plant damage have been documented for external foliage feeding on seed ferns from compression floras. In particular, the ichnogenus *Phagophytichnus* and similar but taxonomically unassigned damage have been used to describe cuspsate excisions on the margins of Middle Pennsylvanian to Early Permian seed-fern leaves (Viyalov 1975) from Europe (Van Amerom 1966, Van Amerom & Boersma 1971, Müller 1982,

Jarzewowski 1989, Castro 1997) and North America (Scott & Taylor 1983, Labandeira & Beall 1990, Obordo et al 1994). Margin feeding also occurs on Early Permian gigantopterids from Texas (Beck & Labandeira 1998) and on Permian glossopterids from South Africa (Plumstead 1963, Van Dijk et al 1978), India (Srivastava 1987), and Australia (Chaloner et al 1991). Similar but less impressive insect-caused damage has been recorded for sphenopsid foliage from Spain (Castro 1997) and the United States (Obordo et al 1994) and for cycadophyte (Beck & Labandeira 1998) and cordaite (Obordo et al 1994) foliage from the United States. These observations single out seed ferns as the most targeted plant group for insect foliage feeding.

PLANT REPRODUCTIVE AND VEGETATIVE STRUCTURES The most indirect category of evidence for inferring Paleozoic plant-insect associations are vegetative and reproductive features of vascular plants that may have provided nutritional or other rewards in return for pollination or its ecological analog in spore-bearing vascular plants (Simpson & Neff 1983, Proctor et al 1996). Structures such as foliar glands, stem nectaries, secreted fluids, and even large-sized pollen have been cited as evidence for entomophily, although such structures, in lieu of direct evidence, can be explained often as features related to plant physiology or abiotic pollination. Evidently during the evolutionary history of many plant lineages, such structures became exaptations (Gould & Vrba 1982) that were co-opted for interactions with insects. It becomes progressively more difficult to assign insect-related functions to older, Paleozoic representatives without additional corroborative evidence (Labandeira 1997a). Current evidence indicates that plants were providing nutritional rewards and probably other attractants to insects during the mid-Mesozoic (Crepet 1974, Arnol'di 1977, Crowson 1991).

Several lines of circumstantial evidence implicate insect pollination of Late Paleozoic seed ferns and conifers. Of these Paleozoic seed plants, the evidence is best for seed ferns. Several types of prepollen organs (Taylor & Millay 1979, Taylor 1981; Figure 1b) bear *Monoletes* prepollen grains that are considered too large for wind transport, implying insect transfer (Taylor 1978, Dilcher 1979, though see Niklas 1992). In addition, fleshy tissue on ovules, external glandular hairs, and internal glands on conspecific prepollen organs may have offered nutritional rewards to visiting insects (Retallack & Dilcher 1988). The second example of a possible association is the presence of a ring of delicate, large-celled tissue surrounding the seed apex of the conifer *Fergliocladus* (Archangelsky & Cuneo 1987). Upon decomposition of these cells, fluid presumably filled the micropyle and the encircling micropylar depression, which suggests that it was an attractant for insects. This mechanism is a modification of the pollination drop mechanism, known to occur in seed ferns (Rothwell 1977), conifers (Haines et al 1984, Tomlinson et al 1991), ephedrales (Lloyd & Wells 1992, Kato & Inoue 1994), and cycads (Norstog 1987).

Glandular hairs restricted to pollen organs probably indicate an attractant to potentially pollinating insects, whereas more widespread coverage of a plant by glands suggests the opposite condition, herbivore deterrence (Retallack & Dilcher 1988). Examples cited as herbivore deterrents include the widespread occurrence of foliar glands on certain cycadophyte foliage (Beck & Labandeira 1998, but see Mamay 1976), the distribution of capitate glands on virtually all organs of the seed-fern *Lagenostoma* (Retallack & Dilcher 1988), and the presence on pinnules, rachises, and seeds of papillae "filled with black carbonaceous matter" on the Chinese seed fern *Emplectopteris* (Halle 1929, p. 22). Other possible deterrent features include substantial sterile tissue surrounding seeds (Crepet 1979, Taylor & Taylor 1993), leaves with thick and matted pubescence (Shear & Kukalová-Peck 1990), and secretion of mucilage and resins (Taylor & Millay 1979).

Late Pennsylvanian and Early Permian biotas purportedly demonstrate examples of leaf crypsis (Jarzembowski 1994). In several cases, cockroach species with leaf-like wings have been compared to co-occurring seed-fern pinnules that possess similar size, shape, and venation. This resemblance accordingly indicates that a predator would confuse potential cockroach prey for ambient foliage, allowing for cockroach survival. Pennsylvanian-age examples of these similarities have been mentioned by Scudder (1895) from Pennsylvania, Pruvost (1919) from northern France, North (1931) from southern Wales, and Fischer (1979) from Illinois. Rohdendorf & Rasnitsyn (1980) and Cuneo (1986) also cite examples from the Permian of Russia and Argentina, respectively. This phenomenon was formally acknowledged by Durden (1984), who provided the common name, pinnule insects, for Paleozoic cockroaches bearing external ovipositors and superficially resembling seed-fern pinnules. Leaf crypsis among Paleozoic cockroaches was extended to protorthopterans and horseshoe crabs (North 1931, Fischer 1979), although the phenomenon has been doubted by some (Jarzembowski 1994, Shear & Kukalová-Peck 1990) on several lines of evidence. A more parsimonious explanation is structural convergence that results when a planated, ovoidal organ is supplied and supported by an elongate and radiating network of veins (Jarzembowski 1994).

MOUTHPARTS AND OVIPOSITORS Mouthpart structure and function can complement the above approaches in ascertaining the associations between Paleozoic arthropods and vascular plants. Although the basic mouthpart types of modern insects (Matsuda 1965, Chaudonneret 1990) can be placed retrospectively in terms of their Paleozoic ancestry (Labandeira 1990, 1997a), there has not been a faunal inventory or ecological characterization of known mouthpart types from the Paleozoic. A modest literature has documented gross mouthpart and head structure occasionally from exceptional specimens (e.g. Carpenter & Richardson 1976, Müller 1978) and from species represented by abundant

material in well-preserved, diverse, and specimen-rich deposits (Labandeira 1997a), principally Mazon Creek (Shabica & Hay 1997) and Commeny (Brongniart 1893) from the later Pennsylvanian and the Kusnetsk Basin (Rohdendorf et al 1961), Elmo (Carpenter 1933), and Chekarda (Martynov 1940) from the earlier Permian. Structural characterization and associated functional interpretation of mouthpart elements, multielement mouthpart complexes, and associated head structures (Laurentiaux 1952, Brauckmann & Zessin 1989, Kukalová-Peck 1987, 1992) indicate in many instances a narrowed range of possibilities for determining diets of fossil insects. In other cases, where preservation of individual mouthpart elements is excellent, features such as the shape, articulation, and ornamentation of individual mouthpart elements provide detailed data for more specific conclusions. For example, examination of the head and mouthparts of certain mid-Permian ancestral hemipteroid taxa led to the conclusion that "these insects may have fed by gnawing the contents of gymnosperm megaspores" (Rasnitsyn 1977, p. 65), which also was a prediction (see also Rasnitsyn 1980) subsequently vindicated by the discovery of pollen in the guts of a closely related taxon (Rasnitsyn & Krassilov 1996a,b, Labandeira 1997b, but see Holden 1997). This approach can be used to infer aspects of feeding strategies such as the functional feeding group (piercer-and-sucker, external feeder, borer, pollen or spore feeder, etc), nature of the diet (herbivory, zoophagy, or omnivory), and form of the food (particulate, solid, or fluid) (Labandeira 1990, 1997a). Additionally, with the exception of the two extinct mouthpart types occurring among paleodictyopteroids (Carpenter 1971) and ancestral hemipteroids (Rasnitsyn 1977, 1980, Labandeira 1997a,b), all major Paleozoic mouthpart types are represented today (Labandeira 1990, 1997a), which allows for structural and functional comparisons.

Several Paleozoic insects had elongate, external ovipositors (Carpenter 1971) that were used for insertion of eggs into various substrates, including plant tissue (Becker-Migdisova 1985a, Shear & Kukalová-Peck 1990). Most of these ovipositors are laterally compressed, dagger-shaped (Becker-Migdisova 1985a), and ornamented variously by sawtooth ridges (Becker-Migdisova 1985a, Kukalová-Peck & Brauckmann 1992, Rasnitsyn & Novokshonov 1997), anteriorly directed stout hairs (Kukalová 1969), or denticles (Sharov 1966, 1968). Taxa that undoubtedly used ovipositors for inserting eggs in plant tissue include protodonatan dragonflies (Brauckmann & Zessin 1989) and paleodictyopteroids such as Palaeodictyoptera (Rohdendorf & Rasnitsyn 1980), Diaphanopteroidea (Carpenter 1971, Rasnitsyn & Novokshonov 1997), and Megasecoptera (Carpenter 1931). Other ovipositor-bearing lineages were protorthopterans (Martynov 1940), cockroaches (Laurentiaux 1951, Zalessky 1953, Sharov 1966), saltatorial orthopterans (Martynov 1940, Sharov 1968, Carpenter 1971), and among the hemipteroid assemblage, psocids (Becker-Migdisova 1962,

1985a), ancestral hemipteroids (Zalessky 1939), and several major groups of homopterous hemipterans (Carpenter 1939, Becker-Migdisova 1961, 1962, 1985b). Whereas the flattened, curved ovipositors of paleopterous taxa such as protodonates and paleodictyopteroids resembled those of modern plant-ovipositing orthopterans and sawfly hymenopterans (Carpenter 1971), others such as cockroaches possessed linear ovipositors that were approximately circular in cross section (Laurentiaux 1951, Vishniakova 1968). The most advanced ovipositors were those of the Archescytinidae, homopterous hemipterans possessing a very long thread-like ovipositor coiled within the abdominal cavity during retraction (Becker-Migdisova 1961), a feature reminiscent of a similar mechanism responsible for the retraction and deployment of mouthpart stylets in extant homopterous hemipterans (China 1931).

In a recent study analyzing ovoidal scars on the stems of Middle Triassic aquatic horsetails, Grauvogel-Stamm & Kelber (1996) suggested that Paleozoic protodonatan dragonflies oviposited in aquatic Paleozoic plants. These characteristically sized ovoidal scars, often occurring as a series of en echelon arcs (Kelber 1988), were previously described as enigmatic structures by paleobotanists (Roselt 1954, Krausel 1958). They now are interpreted as oviposition punctures attributed to a protodonatan dragonfly lineage that survived the Paleozoic extinction. Modern odonatan dragonflies also are known to oviposit in a variety of plant tissues, including stems of emergent aquatic plants such as horsetails, sedges, and reeds (Schiemenz 1957, Kumar & Prasad 1977) and fern leaves (Jurzitza 1974).

Differentiating Detritivory from Herbivory

Detritivory and herbivory are functionally and ecologically two very different modes of feeding. The biochemical, physiological, and structural mechanisms for sensing, consuming, and digesting live plant food are much more intricate and varied than for consumers of dead plant matter (Brues 1924, Anderson & Cargill 1987, Kukor & Martin 1987). For this reason the variety of major mouthpart types, spectrum of functional feeding groups, and dietary breadth is overwhelmingly greater for herbivores than for detritivores. Elaborate taxonomic patterns of plant host specificity and coevolution have occurred for insect herbivores that rarely are documented for detritivores (Mitter et al 1988, Farrell & Mitter 1990, Futuyama et al 1995, but see Swezey 1922). Thus, distinguishing detritivory from herbivory in the fossil record (Edwards & Selden 1991) becomes crucial for documenting the origin and macroevolutionary pattern of major insect feeding styles.

Four important and explicit criteria are used to recognize herbivory in the fossil record. Most important is detection of plant response tissue in the form of callus or other types of reaction tissue that feature abnormal cellular multiplication

and enlargement (Meyer & Maresquelle 1983). Second, the preferential targeting of particular plant host species, organs, or tissue types is important in demonstrating patterns of food specificity that would be unlikely among detritivores. This requires a modestly diverse floral assemblage, and in some instances detritivore monophagy cannot be excluded. Third, detritivory can be separated from herbivory by recognition of stereotypy in the pattern of damage (Coulson & Witter 1984, New 1986). Many modern herbivores have highly patterned modes of feeding on and especially in certain plant tissues. Last, there are specific features that often reveal herbivore presence, including larval and pupal chambers, exit holes, mined tissue, or other features indicating endophytic presence (Hering 1951, Meyer & Maresquelle 1983, Eaton & Hale 1993). In certain cases, these four criteria merge: The presence of an endophytic larval chamber is generally associated with reaction tissue and host monospecificity (Johnson & Lyon 1991, Labandeira & Phillips 1996b; Figure 1a–d). Application of these four criteria is ideally achieved in three-dimensionally permineralized material, although the gross patterns of herbivore damage are most evident and measurable in compression floras.

Quantitative Measurement of Herbivory Intensity

In addition to evaluating the qualitative spectrum of herbivore feeding strategies mentioned above, an assessment of the intensity of insect herbivory is important for comparing the extent of insect damage in fossil floras to widespread data from modern tropical and temperate forests (reviewed by Coley & Barone 1996). The impact of insect herbivory on particular floras can be determined by measuring the percentage of live foliar surface area removed by insects (Lowman 1984, Landsberg 1989, Williams & Abbott 1991), expressed as a defoliation index, or by the frequency of insect attack of foliar items (Robertson & Duke 1987). Typical modern defoliation values range from 7 to 15% for temperate and tropical forests (Wright & Giliomee 1992, Lowman 1992, Aide 1993), although variability exists for plant physiognomy attributable to rainfall and temperature regimes (Coley & Aide 1991, Coley & Barone 1996). Higher values can occur during pest outbreaks (Fox & Macauley 1977). With one exception (Beck & Labandeira 1998), no fossil flora has been measured for analogous foliar damage levels. While sampling problems exist for both modern (Filip et al 1995, Coley & Barone 1996) and fossil (Beck & Labandeira 1998) floras, representative fossil material can be retrieved by repeated sampling or multiple subcollections at the same general site (Burnham 1993). An advantage of examining fossil floras is that sites often represent accumulation of foliar material from multiple seasons (Behrensmeyer & Hook 1992), obviating concerns of significantly variable defoliation values in modern floras that are attributable to seasonality (Coley 1988, Lowman 1984, Filip et al 1995).

For the single study conducted to date (Beck & Labandeira 1998), an overall defoliation percentage of 2.55 was calculated for all plant taxa from a Lower Permian riparian flora dominated by pteridophyll foliage in a restricted site from north-central Texas. Although this value is approximately a third of the value of modern temperate forests (Coley & Aide 1991) and about two thirds of modern consumption levels for ferns (Hendrix & Marquis 1983), it is similar to modern taxon-specific values for certain angiospermous vines, shrubs, and trees (Marquis 1988, Aide & Zimmerman 1990, Alonso & Herrera 1996). Beck & Labandeira (1998) also documented the targeting of particular host-plant taxa and tissue types by insect herbivores, providing evidence for dietary specialization.

PATTERNS OF DETRITIVORE CONSUMPTION

Detritivory was the dominant mode of feeding on plants in terrestrial equatorial ecosystems for probably most of the Paleozoic. Commencing in the Late Pennsylvanian, consumption of live plants became qualitatively diverse (Labandeira 1996), although the intensity of this early insect herbivory remains largely unexplored. The modest literature on Paleozoic detritivory documents evidence for generalized detritivory occurring in coal-swamp forests (Scott & Taylor 1983, Chaloner et al 1991, Scott et al 1992), as well as a few examples of specific interactions between taxonomically better defined detritivores and particular plant hosts (Rothwell & Scott 1983, Labandeira et al 1997). A notable exception has been made for paleodictyopteroids, which have been characterized as consumers of spore-bearing strobili (Rohdendorf & Rasnitsyn 1980, Kukulová-Peck 1991) or even seeds (Sharov 1973).

Detritivory as the Working Hypothesis

Historically three major reasons have been cited for the ubiquity of Paleozoic detritivory. First is simple documentation from the fossil record. Second, and conceptually contributing to this view, is that detritivorous diets of modern phylogenetically basal insects are representative of earlier, Paleozoic ancestors (Labandeira 1998). Third, there is a recognition that living on plants requires surmounting impressive hurdles such as poor nutrition, susceptibility to desiccation, and difficulties inherent in the attachment of insects to plant surfaces (Southwood 1973, Strong et al 1984).

Two principal types of fossil documentation suggest that Paleozoic terrestrial arthropods were overwhelmingly, if not exclusively, detritivorous. They are the abundance of coprolites in permineralized floras typically assigned to detritivore culprits, and the paucity of documented examples of herbivory on compression material. Published coprolite studies originate from Lower and Middle

Pennsylvanian coal-ball floras (Williamson 1880, Scott 1977, Baxendale 1979, Cichan & Taylor 1982, Scott & Taylor 1983, Labandeira & Beall 1990) that are almost entirely dominated by root, trunk and other structural tissues from arborescent plants, with minimal input from canopy-derived tissues (Phillips et al 1985). The earliest coal-ball floras well sampled for insect damage and with significant input from canopy tissues are from the early Late Pennsylvanian (Rothwell & Scott 1983, Labandeira 1996, 1998, Labandeira & Phillips 1996a,b), in which considerable documentation for canopy-based herbivory is attributable to several functional feeding groups. The overwhelming dominance of detritivory during the Early to Middle Pennsylvanian may be real, but studies of coeval canopy-derived coal-ball floras are needed for confirmation.

The concept of widespread to exclusive Paleozoic detritivory has been based partly on analogy to recent forms. Accordingly, since extant lineages of plesiomorphic insects and related myriapods are dominantly detritivorous or less often mycophagous and carnivorous, so were their Paleozoic relatives (e.g. Rolfe 1985). Insect detritivory overwhelmingly occurs in phylogenetically basal clades of the Insecta such as Collembola (McNamara 1924, Christianson 1964), Archaeognatha (Wygodzinsky 1944, Delany 1954), Thysanura (Lindsay 1940, Modder 1969), Blattodea (Roth & Willis 1960, Nalepa 1994), and probably Plecoptera (Harper & Stewart 1984). Detritivorous feeding habits also are common among basal hemipteroid and holometabolan insects (Atkins 1963, Pilgrim 1972, Smithers 1979). For myriapod clades, historically considered as closely related to insects, herbivory similarly is rare (Rolfe 1985, Baily & de Mendonça 1990, Crawford 1992).

Insects overcame several major hurdles to achieve herbivory. Foremost is the low nutritional content of live plants when compared to other dietary sources (Bernays & Simpson 1990). The low nitrogen content of live plant matter, lacking the complement of microorganisms that occurs in detritus, is well known (Strong et al 1984). Also, there is evidence indicating that insect-deterrent chemical compounds (Feeny 1976, Clark & Clark 1991, Marquis 1992) are also important as a barrier to herbivory. Physical barriers to insect colonization include trichomes (Wellso 1973, Cano-Santana & Oyama 1992, Wilkens et al 1996), latex and resin canals (Farrell et al 1991), structural encapsulation of nutrient-rich cells (Hagen & Chabot 1986, Barbehenn 1989) and perhaps formation of wood (Fowler & Schlindwein 1991). These three categories of support—the Paleozoic fossil record, diets of modern plesiomorphic insects, and physiochemical barriers to living on plants—have supported the case for detritivory.

Coprolites in Permineralized Floras

Several studies have documented exceptionally preserved assemblages of coal-ball coprolites from the Pennsylvanian of equatorial Euramerica. These studies

provide a geologically unique glimpse into the cycling of dead but often histologically pristine plant tissues by terrestrial arthropods in the best documented and earliest known forest ecosystems of the Paleozoic. These coprolite assemblages have been characterized by composition, size, and shape, although rarely have assignments been made to their producers other than at the gross-est taxonomic levels. Preceding the advent of coal-swamp forests, the earliest well-documented terrestrial arthropod coprolite assemblages come from the Upper Silurian of Britain (Edwards et al 1995, Edwards 1996) and from the Lower Devonian of Britain and Quebec (Edwards et al 1995, Hotton et al 1996). These assemblages consist of flattened coprolites ranging in size from 0.2×0.5 mm to 1.3×3.3 mm and are composed mostly of undigested spores, vascular tissue and cuticles from rhyniophyte land plants attributable to either herbivores or detritivores.

Not until the Mississippian are there additional well-described coprolite assemblages. Scott (1977) examined compression coprolite assemblages from the Middle Mississippian of Scotland, describing large coprolites up to 7 mm wide by 20–26 mm long that bore 12 longitudinal ridges. These coprolites were tentatively assigned to a large millipede or a small arthropleurid (Scott et al 1992). In younger lower Middle Pennsylvanian black shales, Scott (1977) macerated 12 cylindrical to somewhat flattened coprolites up to 1×3 mm in size. These coprolites contained principally lycopsid megaspore fragments, some of which consisted of diverse tissues from the same plant. Also from Middle Mississippian deposits, Rex & Galtier (1986) reported on suites of coprolites from Esnost and Roannais in France. Four categories of coprolites were described, namely those 0.5×1 mm, containing sporangial annuli of the fern *Botryopteris*; other somewhat smaller coprolites consisting of lycopsid microspores; spheroidal to ovoidal forms from 70 to 100 μm in diameter; and very small and dense coprolites from 10 to 30 μm in diameter, whose contents are unidentifiable but are surrounded by a matrix of *Botryopteris* foliage. The presence of monospecific plant contents in these coprolites possibly provides early indications of host specificity by terrestrial arthropods that occurred in a modestly diverse community of lycopsids, ferns, and sphenopsids.

Baxendale (1979) described diverse and abundant assemblages of coprolites from the Middle Pennsylvanian of Kansas and Iowa and the Upper Pennsylvanian of Illinois. Most of these coprolites were an average size of 2.8×5.0 mm; they were partitioned by size and composition into four categories. The first category consisted of identifiable tissues restricted to a single plant taxon and included those with spore contents assignable to cordaites and calamites. The second category typically consisted of diverse tissue fragments derived from more than one plant taxon, with epidermal tissues, xylem tracheids, and probable sporangial annuli dominant in most specimens. Some contained lycopsid

and sphenopsid megaspores. The last category consisted of amorphous unidentifiable plant matter and bore a distinctive, often massive, rind. Distinct from these three types were clusters of spheroidal to subspheroidal coprolites, often occurring within plant tissue, and at least an order of magnitude smaller in size (see below). Baxendale attributed all of these coprolites to detritivore or herbivore source organisms, although he precluded assignment to any particular arthropod group, in part because of the absence of arthropod remains in the same coal-ball deposit. Scott & Taylor (1983) conducted a study similar to Baxendale's (1979), using Middle Pennsylvanian coal-ball material from Kentucky and a different classification of coprolites.

Well-Documented Associations

The coprolite types mentioned above were not assigned reasonably to any arthropod culprit, with the exception of the smallest coprolites occurring as distinctive clusters in tunnels and galleries within identifiable plant tissues. The producers of these coprolites have been referred to a well-recognized clade of arachnids, the oribatid mites (Baxendale 1979, Scott & Taylor 1983, Rolfe 1985, Rex & Galtier 1986, Labandeira et al 1997, but see Cichan & Taylor 1982 and Goth & Wilde 1992). Oribatid mite tunnels and galleries occur in virtually all major plant tissues, particularly parenchyma and structural tissues, ranging from the Middle Mississippian (Rex & Galtier 1986) to the Early Permian (Goth & Wilde 1992), but especially the Middle Pennsylvanian (Labandeira et al 1997). Clusters of oribatid fecal pellets occurring within tunnel and/or gallery networks have been found in lycopsids (Williamson 1880, Kubiena 1955, Scott 1977, Chaloner et al 1991), calamites (Taylor & Taylor 1993), ferns (Lesnikowska 1989, Scott et al 1985, 1992, Rex & Galtier 1986), seed ferns (Stidd & Phillips 1982), cordaites (Cichan & Taylor 1982, Scott & Taylor 1983, Rolfe 1985, Labandeira & Beall 1990), and conifers (Goth & Wilde 1992). In a study of a 17-million-year interval from the late Early to early Late Pennsylvanian, of coal-ball floras from the Southern and Central Appalachian and Illinois Basins, patterns of oribatid mite tissue consumption were found generally to track those of available biomass of the dominant plant group (Labandeira et al 1997). Thus consumption of these five major plant groups—lycopods, calamites, ferns, seed ferns, and cordaites—focused on rare canopy items at ground level, as well as roots and structural tissues such as bark, wood, and fibrovascular bundles within the peat.

A second interaction type, representing the opposite tendency among Pennsylvanian detritivores, is formation of a highly stereotyped tunnel and gallery system in the stems of two species of the marattialean tree fern *Psaronius*. Seven specimens of this interaction are known from late Middle to early Upper Pennsylvanian coal-ball deposits from the Illinois and Northern Appalachian

Basins (Rothwell & Scott 1983, Labandeira & Beall 1990). In this distinctive association, ground parenchyma has been evacuated from tree-fern stems, resulting in formation of tunnels often connected to expansive galleries. The adjacent indurated tissues of sclerenchyma, inner root mantle, and stem and root vasculature are consistently avoided, which indicates a predilection for consumption of softer tissues. The suspected culprit is a detritivorous insect, based on frass contents, especially fecal pellet morphology, tunnel and gallery geometry and size, and microenvironmental provenance (C Labandeira, personal observation). A modern ecological analog is cockroaches that inhabit and consume the softer tissues of dead monocot and tree fern trunks (Roth & Willis 1960).

PATTERNS OF HERBIVORE CONSUMPTION

Prelude: Late Silurian to Early Devonian

There is considerable recent debate on whether arthropods in the earliest terrestrial biotas were consuming plants as live tissue or as dead, degraded matter (Shear & Kukalová-Peck 1990, Edwards & Selden 1991, Shear 1991, Banks & Colthart 1993, Edwards et al 1995, Edwards 1996, Labandeira & Phillips 1996a, Hotton et al 1996, Shear et al 1996). The data are equivocal, since relevant arthropod body fossils are sparse, sample sizes from the several major deposits are small, and the modest plant-arthropod interaction record has been interpreted variously as dismissive, neutral, or supportive with regard to herbivory. Arthropod mouthparts and plant damage indicate the presence of three feeding strategies: external feeding, piercing-and-sucking, and boring (Labandeira et al 1988, Hotton et al 1996, Labandeira 1997a). Although studies of Devonian terrestrial arthropod paleoecology have been characterized as “a repeated hashing over of the same body of data [that has] reached a point of diminishing returns” (Shear 1991:288–89), recent discovery of additional coprolitic and plant damage material has suggested the presence of herbivores in Late Silurian and Early Devonian ecosystems (Edwards et al 1995, Edwards 1996, Hotton et al 1996, Shear et al 1996). These spore-rich coprolites provide evidence for consumption of monospecific spore taxa, which is interpreted either as specialization on plants or as limited availability of food type in a taxonomically impoverished habitat. More compelling evidence is the record of damage and response tissue in and on the axes of Early Devonian rhyniophyte and trimerophyte plants (Kidston & Lang 1921, Kevan et al 1975, Banks 1981, Trant & Gensel 1985, Banks & Colthart 1993, Labandeira & Phillips 1996a). Two types of induced trauma are found in these deposits: surface lesions with callus plugs and subepidermal penetrations surrounded by cones of reaction tissue radiating from the surface (Banks & Colthart 1993). This latter damage is

similar to that done by small piercing-and-sucking mites (Meyer & Maresquille 1983) and insects (Hori 1971, Tedders & Thompson 1981, Childers & Achor 1991).

Functional Feeding Groups

Although major recognizable types of herbivory have been categorized variously in the biological literature (Coulson & Witter 1984, Strong et al 1984, Lawton et al 1993; Table 1), the nine functional feeding groups of Figure 2 are ecologically meaningful, consistent with modern usage, and have been identified in the fossil record (Labandeira 1998). The external foliage-feeding and boring functional groups have been subdivided into constituent subgroups based on commonly recognized modes of feeding by modern insects on a wide variety of vascular plants (Coulson & Witter 1984, Johnson & Lyon 1991). External foliage feeding includes the category "generalized," which is equated with foliar detritivory and is included for comparison. The earliest occurrence of surface abrasion is latest Cretaceous (McAlpine 1970). Consumption of spores and pollen is differentiated from pollination mutualisms with plants.

EXTERNAL FOLIAGE FEEDING External feeding on foliage is an ancient association traceable to compression material from the late Middle Pennsylvanian. Although earlier occurrences on seed ferns should be expected, one of the earliest published examples is margin feeding on *Macroneuropteris* and other seed-fern foliage from the clastic-substrated Mazon Creek flora of the northern Illinois Basin (Scott & Taylor 1983, Labandeira & Beall 1990). During the early Late Pennsylvanian, additional occurrences of margin feeding on seed-fern foliage are known from several Euramerican localities, particularly northwestern Spain (Van Amerom 1966, Castro 1997), northern France (Van Amerom & Boersma 1971), England (Jarzembowski 1989), and Germany (Müller 1982). Early- to mid-Permian records are on *Glossopteris* foliage from Gondwanan floras in India (Srivastava 1987), Australia (Chaloner et al 1991), and South Africa (Plumstead 1963) and on other plants from floras in the southwestern

Figure 2 The geochronologic distribution of functional feeding groups involving associations between terrestrial arthropods and vascular plants. Each *horizontal line within a vertical column* indicates a datum occurrence; *solid lines* represent credible and *dashed lines* indicate less reliable reports. Data documentation is from Labandeira (1998); Paleozoic occurrences are abstracted in Table 1. *Vertical bars demarcated by lighter shading and a question mark* indicate possible to probable earlier occurrences. In this scheme, the external foliage feeding and boring functional feeding groups are subdivided into subgroups. Generalized external foliage feeding at left is indicated by *cross-hatching* and is equivalent to detritivory on plant litter; it has been included for comparison.

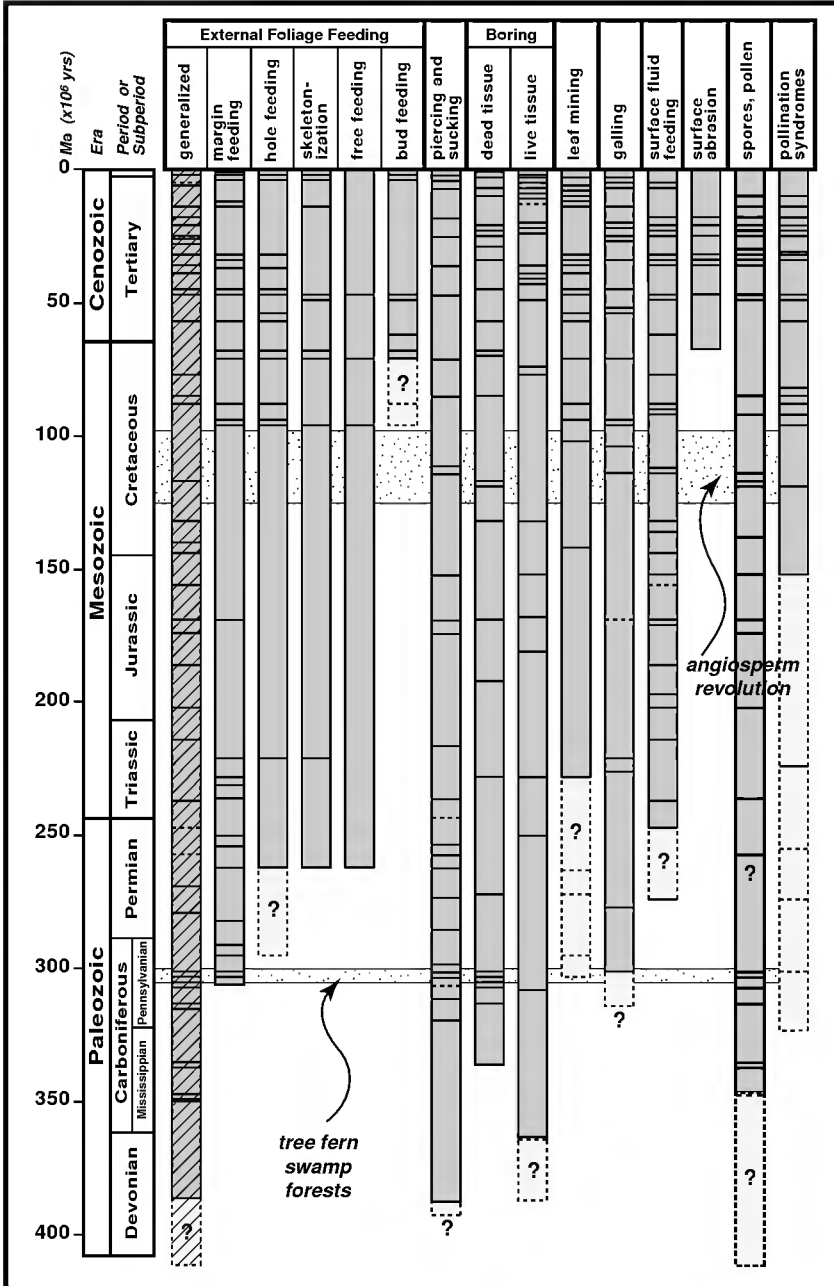


Table 1 Literature-documented examples of arthropod (mostly insect) herbivory on Paleozoic vascular plants

Host plant			Arthropod herbivore			Documentation	
Taxon/form-genus	Organ	Tissue	Inferred taxa ¹	Functional feeding group	Evidence type	Age	References
RHYNIOPHYTES							
<i>Streitspora</i>	Sporangia	Spores	Myriapoda	Sporivore/ pollinivore ²	Coprolite	Early Devonian	Edwards 1996
<i>Aneurospora</i>							
<i>Rhynia</i>	Stem	Epidermis, cortical parenchyma, vascular tissue	Acari, Collembola	Piercer-and-sucker	Plant damage	Early Devonian	Kidston & Lang 1921, Kevan et al 1975
TRIMEROPHYTES							
<i>Psilotophyton</i>	Stem	Epidermis, cortical parenchyma	Acari	External (foliage) feeder	Plant damage	Early Devonian	Banks 1981, Trant & Gensel 1985, Bank & Colthart 1993
<i>Psilotophyton</i>	Stem	Cortical parenchyma	Collembola	Piercer-and-sucker	Plant damage	Early Devonian	Banks & Colthart 1993, Labandeira & Phillips 1996a
SPHENOPHYTES							
Equisetales							
<i>Acrobolbitites</i>	Stem	Parenchyma	Holometabola	Galler ³	Plant damage	Middle Pennsylvanian	Weiss 1876, Thomas 1969, Van Amerom 1973
<i>Sphenopteris</i>	Leaves	Epidermis, mesophyll, vascular	Protrichoptera, Orthoptera	External foliage feeder	Plant damage	Middle Pennsylvanian	Castro 1997
<i>Calamospora</i>	Microsporangia	Microspore	Ancestral hemipteroid, Grylloblattida, Diaphanopteroidea	Sporivore/ pollinivore ²	Coprolite	Middle Pennsylvanian	Scott & Taylor 1983
LYCOPHYTES							
Lepidodendrales							
<i>Lycospora</i>	Microsporangia	Microspore	<i>Eucacenus</i> (ancestral hemipteroid; Eucaceniidae)	Sporivore/ pollinivore	Gut contents, coprolites	Middle Pennsylvanian	Scott & Paterson 1984
<i>Cappasporites</i>	Microsporangia	Microspore	Unidentified Protorthoptera or ancestral hemipteroid	Sporivore/ pollinivore	Gut contents	Middle Pennsylvanian	Scott & Taylor 1983

<i>Setosporites</i>	Megasporangia	Megaspore gametophyte	Palaeodictyopteroidea	Piercer-and-sucker	Plant damage	Middle Pennsylvanian	Scott & Taylor 1983
FERNS							
<i>Marattiales</i>							
<i>Stipitopteris</i>	Petiole	Vascular tissue	Palaeodictyoptera	Piercer-and-sucker	Plant damage, mouthpart structure	Late Pennsylvanian	Lesnikowska 1989, Labandeira & Phillips 1996a
<i>Stipitopteris</i>	Petiole	Parenchyma	Holometabola	Galler	Plant damage, coprolites	Late Pennsylvanian	Lesnikowska 1990, Labandeira & Phillips 1996b
<i>Pecopteris</i>	Leaves	Epidermis, mesophyll, vascular tissue	Protorthoptera, Orthoptera, Caloneurodea	External foliage feeder	Plant damage, coprolites	Late Pennsylvanian	personal observation
<i>Scolecopteris</i>	Sporangia	Spores	Diaphanopteroidea, ancestral hemipteroid	Sportivore/pollinivore	Coprolites	Late Pennsylvanian	Labandeira 1996, 1998
<i>Pxaronius</i>	Roots	Parenchyma		Borer	Plant damage	Late Pennsylvanian	See Figure 1g
Filicales							
<i>Etapteris</i>	Petiole	Epidermis, cortical parenchyma	Palaeodictyopteroidea	Piercer-and-sucker	Plant damage	Middle Pennsylvanian	Scott & Taylor 1983, Taylor & Taylor 1993
SEED FERNS							
Medullosales							
<i>Medullosa</i>	Stem	Parenchyma	Unknown	Borer	Plant damage	Late Pennsylvanian	See Figure 1d
<i>Linopteris</i>	Leaves	Epidermis, mesophyll, vascular	Protorthoptera	External foliage feeder	Plant damage	Middle Pennsylvanian	Castro 1997
<i>Macroneuropteris</i>	Leaves	Epidermis, mesophyll	Protorthoptera, Orthoptera, Caloneurodea	External foliage feeder	Plant damage, coprolites	Middle Pennsylvanian -Early Permian	Van Amerom 1966, Scott & Taylor 1983, Labandeira & Beall 1990, Obordo et al 1994
<i>Macroneuropteris</i>	Leaves	Mesophyll	Holometabola	?Leaf miner ³	Plant damage	Middle Pennsylvanian -Early Permian	Müller 1982, Labandeira & Beall 1990
<i>Odontopteris</i>	Leaves	Epidermis, mesophyll	Protorthoptera, Orthoptera, Caloneurodea	External foliage feeder	Plant damage	Early Permian	Müller 1982

(Continued)

Table 1 (Continued)

Taxon/form-genus	Host plant		Arthropod herbivore			Documentation	
	Organ	Tissue	Inferred taxa ¹	Functional feeding group	Evidence type	Age	References
<i>Paripiteris</i>	Leaves	Epidermis, mesophyll	Protorthoptera	External foliage feeder	Plant damage	Middle Pennsylvanian	Van Amerom & Boersma 1971
<i>Bernautila</i>	Microsporangia	Parenchyma, epidermis, prepollen	Palaeodictyopterodea	Piercer-and-sucker	Plant damage, mouthparts	Late Pennsylvanian	Schopf 1948, Retalack & Dilcher 1988, Labandeira & Phillips 1996a
<i>Feraxitheca</i>	Microsporangia	Parenchyma, epidermis, prepollen	Protorthoptera	External (foliage) feeder ²	Coprolite	Middle Pennsylvanian	Scott & Taylor 1983
<i>Trigonacarpus</i>	Seed	Endosperm	Palaeodictyopterodea	Piercer-and-sucker ³	Plant damage	Pennsylvanian	Scott & Taylor 1983
<i>Monoletes</i>	Microsporangia	Prepollen	<i>Artropileura</i> (Myriapoda: Arthropleurida)	Pollinivore ²	Size of pollen on leg surface	Middle Pennsylvanian	Taylor & Millay 1979, Taylor 1981, Taylor & Taylor 1993
Gigantopteridales <i>Zeiltropterus</i> , <i>Gigantopteridium</i> , and <i>Cathaysiaopterus</i>	Leaves	Epidermis, mesophyll, vascular	Protorthoptera, Orthoptera, Caloneurodea	External foliage feeder	Plant damage	Early Permian	Beck & Labandeira 1988
Glossopteridales <i>Australoxylon</i> <i>Dadoxylon</i> ⁴	Stem Stem	Wood Wood	Coleoptera Coleoptera, Acari (Orbatida)	Borer Borer	Plant damage Plant damage	Late Permian Late Permian	Weaver et al 1997 Zavada & Mentis 1992
<i>Glossopteris</i>	Leaves	Epidermis, mesophyll, vascular tissue	Protorthoptera, Orthoptera, Caloneurodea	External foliage feeder	Plant damage	Early Permian, Late Permian	Plumstead 1963, Srivastava 1987, Scott et al 1992, Van Dijk 1978
<i>Protiohaploxypinus</i>	Microsporangia	Pollen	<i>Idelopsocus</i> (Hypoperlida; Hypoperlidae); <i>Sojanidella</i> (Grylloblattida; Idelidae)	Sportivore/pollinivore	Gut contents, mouthparts	Early Permian	Rasnitsyn 1977, 1980, Rasnitsyn & Krasilov 1996a
Peltaspermales <i>Autunia</i>	Leaves	Mesophyll	Holometabola	Leaf miner ³	Plant damage	Early Permian	Potonié 1893, Potonié 1921, Müller 1982, Kerp 1988

<i>Supata</i>	Leaves	Epidermis, mesophyll, vascular tissue	External foliage feeder	Plant damage	Early Permian	Wang 1997
<i>Thuringia</i> ⁵	Leaves, pollen, microsporangia, etc	Epidermis, mesophyll, parenchyma, other tissues	External foliage feeder	Coprolite	Early Permian	Meyen 1984, Kerp 1988
<i>Vittatina</i> ⁶	Microsporangia	Pollen	Sporivore/pollinivore	Gut contents	Early Permian	Rasnitsyn & Krassilov 1996b, Krassilov & Rasnitsyn 1997
GYMNOSPERMS						
Cycadales						
<i>Taeniopteris</i>	Leaves	Epidermis, mesophyll	External foliage feeder	Plant damage	Early Permian	Beck & Labandeira 1998
Cordaitales						
<i>Samaropsis</i>	Seeds	Endosperm	Piercer-and-sucker	Plant damage, mouthparts	Early Permian	Sharov 1973
<i>Cordaites</i>	Leaves	Epidermis, mesophyll, vascular	External foliage feeder	Plant damage	Early Permian	Obordo et al 1994
<i>Florenites</i>	Microsporangia	Pollen	Sporivore/pollinivore	Coprolite	Late Pennsylvanian	C Labandeira, personal observation
Coniferales						
<i>Ulmannia</i>	Microsporangia	<i>Lunatisporites</i> pollen	Sporivore/pollinivore	Gut contents, mouthparts	Early Permian	Rasnitsyn 1977, 1980, Rasnitsyn & Krassilov 1996a,b

¹The designation of inferred taxon represents levels of confidence that range from pollen and spores in the guts of insects entombed in flagrant delicto, to the likely producers of coprolites occurring in litter and devoid of biological context. Plant damage and coprolites occurring within plant hosts represent intermediate levels of reliability.

²This interaction could be detritivory based on the lack of sufficiently diagnostic features to indicate herbivory.

³This interaction is based on indirect or otherwise circumstantial evidence, and may be assignable to a different functional feeding group.

⁴This *Dadoxylon* is tentatively assigned to the Glossopteridales.

⁵*Thuringia* is a coprolite.

⁶*Vittatina* pollen also could be of coniferous or gnetalean origin (Traverse 1988).

United States (Obordo et al 1994, Beck & Labandeira 1998). The earliest documented occurrences of hole feeding, skeletonization, and free feeding (Coulson & Witter 1984) occur in these latter floras associated with flood-plain environments (Beck & Labandeira 1998), principally on gigantopterid pteridophylls and seed ferns. These modes of external foliage feeding subsequently became prominent on angiosperms during the Cretaceous (Labandeira et al 1994a). Bud feeding is not known until the Late Cretaceous (Labandeira 1998).

Examination of how the mandibulate mouthparts of Paleozoic insects functioned may assist interpretation of foliage damage. Detailed study of well-preserved material such as Elmo or Chekarda is needed to generate insight as to which orthopteroid, ancestral hemipteroid, and early holometabolous lineages had detritivorous, herbivorous, or other diets. Unlike some large to gigantic protodonatan dragonflies that possessed comparatively large mouthpart elements, with detail such as dentition (Brauckmann & Zessin 1989, Kukulová-Peck 1991), reconstructions are more difficult for detritivorous and herbivorous species that are considerably smaller, with mouthpart microstructures approaching the grain size of the surrounding matrix. The sweeping taxonomic diversity and elevated structural variety of gross head and mouthpart structure for Paleozoic mandibulate insects mitigates against a singular dietary mode. Additionally, many modern insect taxa generally assumed to be overwhelmingly or exclusively consumers of angiosperms often are found as nonangiosperm feeders (Swezey 1922, Wieczorek 1973, Rowell et al 1983, Crowson 1991), and surveys of insect herbivory indicate fern feeding is more prevalent than once thought (Balick et al 1978, Hendrix 1980, Ottosson & Anderson 1983).

PIERCING-AND-SUCKING Piercing-and-sucking and spore consumption are probably the oldest modes of consuming live plant tissue, extending to the Devonian. As discussed previously, a parsimonious interpretation of rhyniophyte and trimerophyte tissue damage (Kidston & Lange 1921, Banks & Colthart 1993) indicates point-source injuries during life that are similar to lesions produced by modern piercing-and-sucking microarthropods (Labandeira & Phillips 1996a, but see Rolfe 1985). After an 85-million-year hiatus in the fossil record, plant damage from piercing-and-sucking insects appears approximately contemporaneous with expansion of insect lineages during the Early Pennsylvanian (Labandeira & Sepkoski 1993). Occurrences from Middle Pennsylvanian deposits include punctures with reaction tissue on zygopterid stems (Scott & Taylor 1983, Taylor & Scott 1983) and "borings" through the protective integument and into the embryonic tissue of cordaite seeds (Sharov 1973). A late Middle Pennsylvanian diaphanopteroidean nymph bore a mass of spores in its gut, which indicates either a piercing-and-sucking analog of particulate food similar to extant syrphid flies or modification of the typical paleodictyopteroid

stylet structure into a functionally mandibulate mode of ingesting spores (Labandeira 1997a). Late Pennsylvanian occurrences reveal a shift in dominance to tree ferns in lowland Euramerican forests (Phillips et al 1974), with rachises (Lesnikowska 1989, 1990, Labandeira & Phillips 1996a; Figure 1c) and prepollen organs (Schopf 1948, Retallack & Dilcher 1988, Labandeira 1998; Figure 1b) exhibiting 0.5- to 1.2-mm long punctures surrounded by a zone of reaction tissue and terminating into distinctive feeding chambers within the targeted tissue.

The Early Permian provides several lines of evidence for piercing-and-sucking. This evidence includes the presence of amorphous, carbonized residue in the beak and gut of a diaphanopterodean insect (J Kukulová-Peck, personal communication) and a suite of Early Permian homopterous Hemiptera bearing head- and mouthpart structures sufficiently well preserved to indicate beak structure and the presence of a suction pump located on the anterior head for imbibing internal plant fluids (Becker-Migdisova 1940, Shcherbakov 1996). Head- and mouthparts are also known for ancestral thrips (Vishniakova 1981), which probably pierced shallow foliar tissues. Analogously, paleodictyopteroid head, beak, and stylet structure, interpreted as fundamentally designed for sap- or spore-imbibition (Sharov 1971, 1973, Shear & Kukulová-Peck 1990, Carpenter 1992, but see Handlirsch 1937), has been documented from the earliest Pennsylvanian (Brauckmann 1991) to the mid-Permian (Kukulová-Peck 1992, Kukulová-Peck & Brauckmann 1992, Rasnitsyn & Novokshonov 1997).

BORING The two earliest terrestrial examples of boring into indurated host tissues by a putative arthropod are from the Lower Devonian of Québec and the Upper Devonian of Ontario (W Stein, personal communication; Hotton et al 1996). These borings occur on species of *Prototaxites*, an enigmatic, log-shaped, probable eumycotan fungus analogous to modern bracket fungi and restricted to the Devonian. Two very different borers are represented; the late Devonian example is characterized by a reaction rim of mycelial callus surrounding frass-containing, meandering tunnels, whose maximum diameters average 0.69 cm and occasionally enlarge into galleries two to three times the tunnel diameter (Arnold 1952, Hotton et al 1996). The unknown culprit penetrated living, wood-like tissue. Evidence for boring within plant tissues occurs in Middle Mississippian (Visean) deposits (Rex & Galtier 1986), assignable to oribatid mite detritivory (Labandeira et al 1997). The trace-fossil record of detritivorous oribatid mites resumes at the Mississippian/Pennsylvanian boundary (Labandeira et al 1994b) and becomes a conspicuous feature of the Euramerican Pennsylvanian in major coal-ball deposits until the early Late Pennsylvanian (Cichan & Taylor 1982, Labandeira et al 1997), although an isolated European occurrence is known from an Early Permian clastic deposit (Goth & Wilde

1992). During the late Middle to early Late Pennsylvanian, a unique association existed between a detritivorous insect and the relatively soft ground parenchyma of *Psaronius* tree-fern stems, which has been documented from three deposits in Illinois and Ohio (Rothwell & Scott 1983, Labandeira & Beall 1990).

Several authors have stated that association with wood, including wood boring, is a primitive life-habit for beetles and their immediate ancestors (Hamilton 1978, Crowson 1981, Lawrence & Newton 1982), which are known from Permian deposits (Ponomarenko 1969). Some Paleozoic borings have been attributed to this clade (Geinitz 1855, Zavada & Mentis 1992, Weaver et al 1997). Endophytic life habits in and on wood also are known for extant plesiomorphic flies (Krivosheina 1969), sawflies (Smith 1967), and moths (Connor & Taverner 1997), though with the possible exception of two early fly lineages (Wootton & Ennos 1989, Willmann 1989), these clades are absent from the Paleozoic. A likely candidate for an early holometabolous insect boring occurs in coalified compressions from cortical tissues of lycopsid roots (Geinitz 1855; see also Figures 1d,g). These borings from the Pennsylvanian/Permian transition of Germany are curvilinear, 1–3 mm wide, up to 20 cm long (Geinitz 1855), and apparently within the range of diameters of borings made by modern insects but outside the range of oribatid mites. These structures may have been made by teredinid mollusks, but the oldest teredinid fossil is Early Cretaceous (Skelton & Benton 1993).

GALLING Until recently a general consensus indicated that there was, at best, equivocal evidence for insect galling of vascular plant tissues during the Paleozoic. A few examples have been cited as likely candidates, most prominently the compression fossil ichnogenus *Acrobulbillites*, which was formally described as a possible or probable gall (Van Amerom 1973) for the anomalously swollen termini on fertile and sterile axes of certain Middle Pennsylvanian horsetails from Europe. Weiss (1876) and Jongmans (1911) previously had mentioned that these structures could be galls. Initially described as enlarged but normal shoots that gave rise to two or more whorls of calamitalean cones (Thomas 1969), these structures resemble modern but smaller hymenopteran galls in an extant Moroccan horsetail (Mimeur 1949). While *Acrobulbillites* is a likely gall, it lacks the necessary diagnostic histological detail. From younger Late Pennsylvanian material of the Illinois Basin, three-dimensional preservation of permineralized tissues in a marattialean tree-fern rachis has provided several lines of evidence supporting the earliest known gall (Labandeira & Phillips 1996b): (a) excavation of a larval chamber resulting from consumption of original parenchymatic tissue centrally located along the rachis axis, (b) production of callus or probably nutritive tissue by the plant as a response to induced

trauma, and (c) presence of exit holes. This structure, previously documented as a botanical abnormality (Stidd 1971) or as unattributed herbivory (Lesnikowska 1989, 1990), occurs on approximately 35 known specimens of *Psaronius chasei* Morgan, demonstrating not only tissue and organ monospecificity but also the targeting of a particular host-plant species (Labandeira & Phillips 1996b).

Other Paleozoic gall occurrences have been mentioned in the literature (Larew 1986, 1992). Weiss (1904) described the gall *Urophlyctites* from a Middle Pennsylvanian lepidodendrid lycopsid root in a permineralized coal ball. Although Weiss attributed the galler to a fungus, it may represent a simple boring rather than a gall. Potonié (1893) mentioned and figured the occurrence of "Runzelgallen" or wrinkle galls on *Odontopteris* seed-fern foliage from the Lower Permian of Germany. These spheroidal structures, preserved as compressions, in some instances overtake the entire sessile pinnule while adjacent and opposite pinnules remain unaffected. Although tantalizing, Potonié's material needs to be examined in greater detail.

LEAF MINING There is no compelling documentation supporting the presence of Paleozoic leaf mining. However, ferns, cordaites, and especially seed ferns are plant hosts for several published descriptions and illustrations of structures interpreted as leaf mines. Of these reports, the most likely are U-shaped structures on species of seed-fern foliage, *Macroneuropteris* spp., from the late Middle Pennsylvanian of the Illinois Basin (Labandeira & Beall 1990) and Germany (Müller 1982) and the Lower Permian of Texas (C Labandeira, personal observation). These U-shaped features parallel the major dichotomous, fan-like venation that extends from the pinnule margin but does not reach the medial axis. The two delimiting, subparallel veins of this feature bear a prominent reaction rim and define a central necrotic zone characterized by muted, often barely perceptible veins that are unlike the robust, ridged venation of the unaffected pinnule. These structures may be blotch mines, but confirmation will require examination of permineralized sections of *Macroneuropteris* foliage with histological detail. These U-shaped structures resemble features on a neuropterid seed-fern pinnule from the Lower Permian of Texas described by Mamay (1960) as *Padgettia readi*.

A second but less convincing example is a series of undulating crenulations occurring on foliage of the peltasperm seed fern, *Autunia conferta*, from the Upper Carboniferous or Lower Permian of Crock, Germany. Initially described by Potonié (1893) as a "Gangminen," or serpentine mines, additional material was figured by Potonié (1921) and Müller (1982) as the ichnotaxon *Asteronomus* (?) *meandriiformis*. Kerp (1988) also considered these crenulations as leaf mines. Albeit distinctive, this presumed leaf mine does not meet the standard criteria for leaf mining by a holometabolous insect, which include a frass

trail, indications of an oviposition site, a terminal expansion or chamber, or in the case of serpentine mines such as *Asteronomus* spp. (?), gradual or discrete stepwise increase in the mine width reflecting miner ontogeny. Because of the unusually small size of these sinusoidal lineations, it is possible that the culprit was a leaf-mining mite, a herbivorous life habit recently established for several extant species (Norton 1983, Karg 1984, Fernandez & Athias-Binche 1986). Similarly inconclusive examples are the anastomosing networks from the Late Pennsylvanian of Spain (Castro 1997) and sinusoidal traces from the Lower Permian of Texas (Beck & Labandeira 1998), both from pteridophyll foliage. Potonié (1893) also described and illustrated "Platzminen" from the *Odontopteris* seed-fern foliage, structures resembling pinnule blotch mines that may be seeds. Structures described by Paclt (1972) on cordaitalean foliage, described by Sternberg (1836) from southern Germany, are more likely attributable to taphonomic alteration.

SPORIVORY AND POLLENIVORY Sporivory and its subsequent functional equivalent, pollinivory, represent an unusual type of herbivory in which successful consumption is equated with death of an entire haploid plant. Sporivory extends to the Late Silurian based on evidence from spore-laden coprolites, and it undoubtedly was present during the Early Devonian (Edwards et al 1995, Edwards 1996). Later, in Pennsylvanian-age coal-ball floras of Euramerica, relatively intact microspores and macerated megaspores occur as constituents in a distinctive class of smaller, spheroidal, and often homogenous coprolites. This coprolite type occurs in virtually all assemblages studied to date (Scott 1977, Baxendale 1979, Scott & Taylor 1983, Labandeira & Beall 1990). Spores also occur as gut contents in late Middle Pennsylvanian (Richardson 1980, Scott & Taylor 1983, Kukulová-Peck 1987) and in mid-Permian (Krassilov & Rasnitsyn 1997) insects.

In addition to consumption of spores and pollen as discrete elements, another separate mode of feeding is ingestion of pollen and associated tissues in seed-fern prepollen organs by larger insects and perhaps other arthropods. This plant-specific diet is reflected in relatively large and distinctive coprolites such as those described by Scott & Taylor (1983), which contain disorganized seed-fern prepollen and sporangial tissue, including annuli and vascular elements, of a species of the prepollen organ *Feraxotheca*. Meyen (1984) described characteristic coprolites up to 2.5 cm long (Kerp 1988) from Late Pennsylvanian to Early Permian foliage from Germany. These coprolites, previously mistaken for a pollen organ under the name of *Thuringia*, contained *Vesicaspora* prepollen, *Pterispermotrobus* prepollen organ tissue, *Cyclocarpus* seeds, and *Autunia* foliage from the same plant species (Meyen 1984). Similarly Rothwell & Scott (1988) interpreted subspheroidal to ovoidal structures, approximately

1.0 mm wide by 3.7 mm long, as coprolites consisting of distinctive spores dispersed in the same associated plant tissue. These structures, from the Middle Mississippian of Scotland, were previously assigned to a lyginopterid prepollen organ known as *Bensoniotheca grievii*.

SURFACE FLUID FEEDING Unlike particulate or solid food, fluid food does not preserve as coprolites or identifiable gut contents in the fossil record. Thus the existence of Paleozoic surface fluid feeding is based on indirect evidence. Of the indirect evidence, most notable are specialized fluid-secreting plant structures (Fahn 1979), such as glandular hairs, capitate glands, hyadathodes, and probably nectaries, that occurred on vegetative and reproductive organs of various Paleozoic plants, including ferns (Lesnikowska & Galtier 1991), seed ferns (Oliver & Scott 1904, Halle 1929, Taylor & Millay 1979, Retallack & Dilcher 1988), and cycadophytes (Mamay 1976). These structures probably served an herbivore-deterrent function when occurring on all or most of the plant; alternatively, they may have attracted pollinators when confined to reproductive structures, such as glandular hairs on the pollen organs and resinous internal glands on the conspecific ovules of medullosan seed ferns producing *Pachyteta*-type ovules (Taylor & Millay 1979, Retallack & Dilcher 1988). Insects may have consumed watery fluids secreted by hyadathodes of Lower Permian marattialean tree ferns (Lesnikowska & Galtier 1991). Modern marattialean ferns bear nectaries on fronds (Bonnier 1879, Figdor 1891, Fahn 1979), although nectaries so far have not been detected in Paleozoic marattialean ferns.

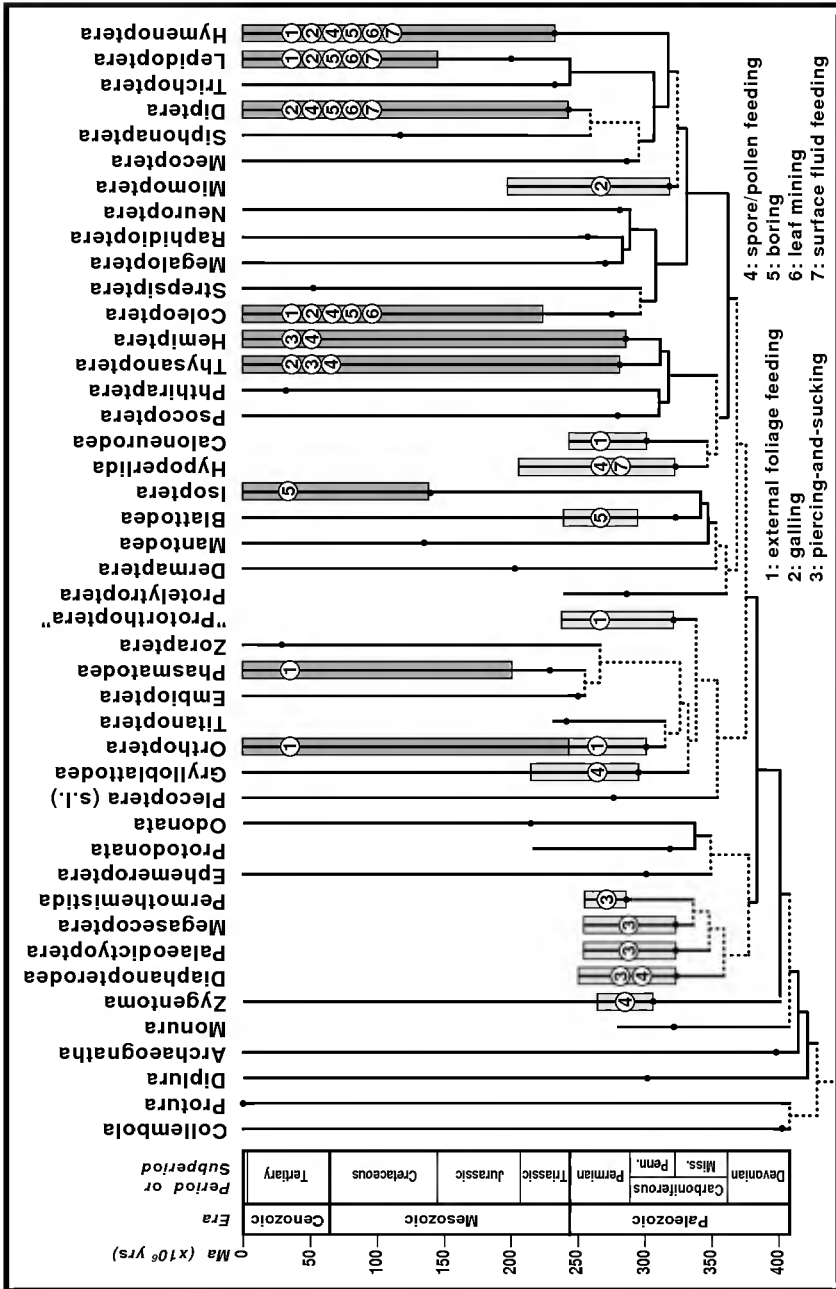
A second line of evidence is documentation of certain insect mouthpart types from the Paleozoic that were likely used for surface fluid feeding. Extinct lineages may have imbibed surface fluids, such as the Early Permian psocopteran *Dichentomum*, with rostrate mouthparts (Carpenter 1933, Kukulová-Peck 1991), and possibly some ancestral hemipteroids with mandibulate/sucking mouthparts. A more tangible example is the extant Nannochoristidae, a basal scorpionfly family traceable to the Late Permian (Riek 1953, Carpenter 1992, but see Willmann 1989), which possesses sponging mouthparts of fleshy, distally expanded labial palps similar to the labellum of certain nematocerous flies (Hoyt 1952, Hepburn 1969). Labellate nematocerous flies probably existed during the Late Permian as well (Riek 1953, Wootton & Ennos 1989) and subsisted on homopteran honeydew, a carbohydrate-rich source of food used by flies in lieu of flower nectar (Downes & Dahlem 1987). According to Downes & Dahlem (1987), the labellum is a unique and primitive mouthpart complex within the Diptera designed for sponging fluid or dried sugary films from plant surfaces (Knab 1910). Other forms of surface fluid feeding, such as the lapping-and-squeezing of Hymenoptera and the siphoning of Lepidoptera, originated during the mid-Mesozoic (Labandeira 1997a).

Postlude: The Triassic

In addition to detritivory, based on sketchy evidence from coprolites, damaged plants, and sections of *Prototaxites*, spore consumption, piercing-and-sucking, and boring (on fungal tissues) are the oldest documented feeding strategies of terrestrial arthropods, extending to the Lower Devonian (Hotton et al 1996, Labandeira & Phillips 1996a) or perhaps earlier (Edwards et al 1995). During the late Middle to early Late Pennsylvanian, there is good evidence for galling (Labandeira & Phillips 1996b) and external feeding on leaf margins (Scott & Taylor 1983). During the Early Permian, external foliage feeders diversified their repertoire, pursuing hole feeding, skeletonization, and free feeding (Beck & Labandeira 1998). This delay could be attributable to a poor Devonian and Mississippian land record of arthropods and plant-arthropod interactions. Current evidence indicates that surface fluid feeding originated during the Permian, whereas leaf mining is not convincingly demonstrated until the Late Triassic (Labandeira 1998). Suggestive evidence exists for insect pollination of Late Triassic gnetophytes and the enigmatic seed plant *Sanmiguelia* (Cornet 1989, 1996), but additional data are needed. In Figure 3, functional feeding groups tentatively have been assigned to taxa at the level of the conventional taxonomic order (see also Table 1). Note that these ecological assignments correspond to an earlier Paleozoic Entomofauna and a later Modern Entomofauna.

By the Late Triassic, the inventory of functional feeding groups consisted of modern taxa that replaced their analogs of the Paleozoic Entomofauna (Labandeira 1998). Evidence for this is based on isolated Triassic occurrences of insect associations on plants as well as two synthetic and recent studies of plant-arthropod interactions—one investigating a deltaic environment of Early Anisian to Late Ladinian age from France and adjacent Germany (Grauvogel-Stamm & Kelber 1996), and the other examining floodplain and lake environments of Late Carnian to Early Norian age from the southwestern United

Figure 3 Major clade-level herbivore participants in the Paleozoic Entomofauna (*light shading*) and the Modern Entomofauna (*dark shading*), based on a broad spectrum of available evidence. Evidence includes gut contents, mouthpart functional morphology, anatomical structure of damaged plant tissues, coprolites, and circumstantial evidence such as temporal occurrence (Labandeira & Sepkoski 1993, Labandeira 1997a, 1998). The list at *lower right* indicates those functional feeding groups described in the text that are documented for the Paleozoic. This is a composite phylogram after Rohdendorf & Rasnitsyn (1980), Hennig (1981), Wheeler (1989), Kristensen (1991, 1995), Kukulová-Peck (1991), Kukulová-Peck & Brauckmann (1992), and Byers (1996). The *dots on vertical branches* indicate documented earliest fossil occurrences; *dotted horizontal connectors* indicate tentative relationships, whereas *solid ones* are well corroborated. Abbreviations: Miss. = Mississippian (Lower Carboniferous); Penn. = Pennsylvanian (Upper Carboniferous).



States (Ash 1997). The record of external feeding on Middle and Late Triassic foliage consists of all commonly encountered major floral elements: sphenopsids, ferns, seed ferns, conifers, and cycadophytes. Middle Triassic material from France and Germany exhibits external foliage feeding on the margins of the sphenopsid *Schizoneura*, the fern *Neuropteridium*, and the cycadophyte *Taeniopteris* (Geyer & Kelber 1987, Grauvogel-Stamm & Kelber 1996). Somewhat younger material from the southwestern United States reveals cusped excavations on the tips of the filicalean fern *Cynepteris*, hole and window feeding on the cycadophyte leaf *Zamites*, and margin and hole feeding on the enigmatic gymnosperm *Marcouia* (Ash 1997). The margins of *Glossopteris* leaves from South Africa were damaged by folivores as well (Van Dijk et al 1978). There also is evidence for detritivory on dead plant tissue from other habitats (Retallack 1976, White & Taylor 1989).

There is more evidence for endophytic consumption of plant tissues during the Triassic than for the Late Paleozoic. Conifers evidently were the principal plant hosts for Triassic insects and possibly mite galls and leaf miners. The Triassic conifer record consists of foliar galls on the flattened leaves of the woody *Dechellyia* (Ash 1972, 1997), stem galls on woody *Voltzia* twigs (Grauvogel-Stamm & Kelber 1996), and the aborted cones of herbaceous *Aethophyllum* (Grauvogel-Stamm 1978, Larew 1992, Grauvogel-Stamm & Kelber 1996). Leaf mines of Carnian age occur on the voltziacean conifer leaf *Heidiphyllum* from southeastern Queensland in Australia (Rozefelds & Sobbe 1987) but are unassigned to a culprit. This interaction consists of overlapping, highly sinusoidal traces lacking frass and without increases in mine diameter that are similar to "coleopterous burrows," illustrated by Tillyard (1922) in a younger Triassic conifer or ginkgophyte leaf. The next oldest leaf mine is from a corytosperm seed fern from the Jurassic/Cretaceous boundary in northern Queensland (Rozefelds 1988); unlike the Triassic specimen, it possesses features typical of modern leaf miners and has been attributed to the Nepticuloidea, an extant but rather basal clade of Lepidoptera. Coniferous wood borings, attributed to beetles, are known in *Dadoxylon* wood from the Middle Triassic of Germany (Linck 1949) and in *Araucarioxylon* wood from the Late Triassic of Arizona (Walker 1938). Piercing-and-sucking hemipteroid insects, which feed endophytically on plant tissues but are located external to the plant, are evident from their body-fossil record (Labandeira 1998) and the presence of cicada-like burrows in Triassic paleosols (Retallack 1976). These diverse records indicate that conifers, especially those that bore planated leaves such as members of the Voltziaceae, were major host plants for a variety of insect herbivores.

Four types of associations between insect eggs and plants have been described from the Middle Triassic of France (Grauvogel-Stamm & Kelber 1996). Three of these associations are as follows: subaqueous occurrences of cylindrical

egg masses in a mucilaginous matrix, entwined on various aquatic plant debris; mucilage-embedded egg masses on the subaqueous surfaces of sphenopsid leaves; and arcs of ovoidal eggs inserted into the cortical tissues of subaqueous sphenopsid stems (see above). The fourth example consists of subaerial eggs laid end to end, parallel to the midrib of *Taeniopteris* leaves. An example similar to the subaqueous mass of eggs on foliar surfaces was described by Webb (1982) on *Dicroidium* leaves of similar age from Australia.

ONGOING AND FUTURE DIRECTIONS

From an inspection of the plant-arthropod interaction literature and an assessment of current studies investigating Paleozoic plant-arthropod associations, five immediate concerns have been identified for future examination. First is expansion of detailed reconstructions of insect diets from well-preserved and abundant coprolite assemblages in Euramerican coal-ball floras. Such assemblages represent the best opportunity known from the terrestrial fossil record for identifying diets of arthropod plant consumers at the level of tissues, organs, and specific host-plant taxa (Labandeira 1996). A primary goal of such studies is to establish patterns of nutrient flow from primary producers to varied consumers and saprophytes. A second direction is continued quantification of the intensity of herbivory in compression floras. Related to this is a third direction for future investigation: examination of the mouthparts of the consumers. Although the consumers and the consumed are rarely preserved in the same coal ball or bedding plane (Baxendale 1979, Labandeira 1997a), detailed examination of arthropod mouthpart structures, particularly those of mandibulate insects, has high potential for revealing mouthpart element detail or novel multielement structures that could assist in interpretation of Paleozoic feeding strategies. Advances in this area have been made mostly for piercing-and-sucking insects (Becker-Migdisova 1940, 1985b, Laurentiaux 1952, Kukulová-Peck 1991, Rasnitsyn & Novokshonov 1997) but also for a few mandibulate species (Sharov 1966, Carpenter & Richardson 1976). It is hoped that feeding strategy can be inferred from the combination of the trace-fossil record of varied plant-arthropod interactions and the body-fossil record of arthropod mouthparts (Labandeira 1990, 1997a).

A fourth direction is assessment of the role that the Late Pennsylvanian and Early Permian radiation of the Holometabola had for herbivory. It has been stated that the ancestral feeding modes of early holometabolous insects included endophytic consumption of plants (Lameere 1917, Labandeira & Phillips 1996b) and pollen consumption (Malyshev 1966, Kristensen 1995). Examination of plant consumption patterns during this interval may reveal features of early holometabolan dietary habits; it also may resolve enigmatic plant

structures that have been attributed to leaf mines, galls, or borings (Potonié 1893, Müller 1982, Kerp 1988, Labandeira & Beall 1990, Zavada & Mentis 1992). During this interval there was geographic retraction of swamp floras and expansion of new seed-plant taxa occupying better-drained, clastic substrates adjacent to water courses. It is among these seed-plant taxa, which include varied seed ferns, conifers, cordaites, and cycadophytes, that the fifth future challenge emerges. This goal is to ascertain in detail the earliest occurrences of pollination syndromes involving seed plants and insects. Evidence enlisted to document these syndromes include micropylar and other ovular modifications, pollen size and ornamentation, presence of attractant glands, insect mouthpart structure, and insect gut contents. Because of the historical reliance on circumstantial evidence for demonstrating pollination syndromes, such mutualisms are not convincingly documented until the mid-Mesozoic (Labandeira 1997a).

CONCLUSIONS

Arthropod detritivores in Paleozoic terrestrial ecosystems have been documented from several major studies of coprolite assemblages in deposits ranging from the Late Silurian to the Early Permian. Historically, these and other studies, such as examination of damaged plant tissues and more recently the elucidation of gut contents, have been the primary evidence for plant–arthropod associations. By contrast, direct functional examination of the insects themselves, such as inferring feeding strategies from mouthpart or ovipositor structure, has been significantly less important. The lack in understanding of the feeding strategies and diets of Paleozoic mandibulate insects is perhaps attributable to the lack of sufficient microscopic detail of feeding structures, but more likely it is a consequence of the lack of investigation. In this context, the current challenge is to integrate historically and topically disparate lines of evidence from different modes of preservation (compression, permineralization), types of fossils (trace, body), and organisms (vascular plants, arthropods) into coherent and interdependent research. This reformulation advocates linkage of these separate data types—for example, assemblages of coprolites devoid of culprits, soft-bodied arthropod fossils largely bereft of known feeding strategies, and a unique plant damage record often lacking reference to insect feeding mechanisms or life-habits. If there is one overarching principle resulting from these data, it is that the Late Paleozoic terrestrial world was very different taxonomically from the present, and arthropod ecologies, comparable to the *broad* spectrum of functional feeding groups occurring today, must be determined from disparate data.

The next phase in understanding Paleozoic vascular plant–arthropod associations is to chart the diversity of herbivore life-habits across a range of

environments during the Middle Pennsylvanian to Early Permian in Euramerica and Russia, where the floras have been intensely collected and are best known. To date, the only ongoing synecologic synthesis of herbivory is from one well-documented Late Pennsylvanian coal-swamp flora and from a restricted floodplain flora of the Lower Permian. Other studies are limited examinations of isolated plant or animal specimens from often well-known floras. By contrast, community-wide studies from unbiased and extensive collections could document the spread and importance of herbivore functional feeding groups in wetland and drier "upland" environments. An assessment of the spectrum of herbivores and measurement of their defoliation intensities (or lack thereof) for this crucial interval can narrow the time, place, and ecological context of when significant insect herbivory was launched. These data also are comparable to similarly obtained data from modern tropical to temperate plant communities.

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