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PALEOZOIC COAL-SWAMP FORESTS

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Vol. 12, No. 4, August, 1997  
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# Oribatid Mites and the Decomposition of Plant Tissues in Paleozoic Coal-Swamp Forests

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PALAIOS, 1997, V. 12, p. 319–353

*Although oribatid mites are essential to the decomposition of plant tissues in modern temperate forests by assisting conversion of primary productivity to soil organic matter, little is known of their paleoecologic history. Previously there has been scattered and anecdotal evidence documenting oribatid mite detritivory in Pennsylvanian plant tissues. This study evaluates the incidence of oribatid mite damage for seven major coal-ball deposits from the Illinois and Appalachian sedimentary basins, representing a 17 million year interval from the Euramerican tropics. Although this interval contains the best anatomically preserved plant tissues with oribatid mite borings in the fossil record, coeval oribatid mite body-fossils are absent. By contrast, the known body-fossil record of oribatid mites commences during the Middle Devonian, but does not reappear until the Early Jurassic, at which time mite taxa are modern in aspect.*

*All major plant taxa occurring in Pennsylvanian coal swamps, including lycopsids, sphenopsids, ferns, seed ferns and cordaites, were consumed by oribatid mites. Virtually every type of plant tissue was used by mites, notably indurated tissues such as bark, fibrovascular bundles and especially wood, as well as softer seed megagametophytic and parenchymatic tissues within stems, roots and leaves. Significant evidence also exists for secondary consumption by mites of tissues in macroarthropod coprolites. Our data indicate that oribatid mites consumed dead, aerially-derived plant tissues at ground level, as well as root-penetrated tissues substantially within the peat. Oribatid mites were important arthropod decomposers in Pennsylvanian coal swamps of Euramerica.*

*The wood boring functional-feeding-guild was expanded by insects into above-ground, live trees during the early Mesozoic. New food resources for insect borers resulted from penetration of live tissues such as cambium and phloem, and the invasion of heartwood and other hard tissues mediated by insect-fungus symbioses. Termites and holometabolous insects were prominent contributors to this second wave of wood-boring, exploiting gymnosperms and angiosperms as both detritivores and herbivores. An earlier em-*

*placement of oribatid mites as detritivores of dead plant tissues continued to the present, but without a documented trace-fossil record.*

## INTRODUCTION

Oribatid mites are the most successful group of soil arthropods in temperate forest ecosystems (Johnston, 1982; Norton, 1994), where they are key animals—along with millipedes, isopods and collembolan insects—responsible for the conversion of plant litter and wood to organic residues in terrestrial decomposer food chains (Spencer, 1951; Harding and Stuttard, 1974). Oribatid mites principally assist the decomposition of plant tissues by directly or indirectly interacting with the decomposer microbiota, especially saprophytic fungi (Clement and Haq, 1984; Norton, 1985; Affi et al., 1989), and thus assist in the comminution of plant and other biotal materials that eventually become integrated into the soil. The importance of oribatid mites is buttressed by their exceptional taxic diversity worldwide and recurring patterns of site-specific ecological dominance. Known oribatid mite diversity, excluding the Astigmata, consists of approximately 7000 nominal species within 1000 genera and 150 families, albeit the global tropical fauna remains largely uninvestigated (Norton, 1990, 1994).

Although Early Devonian microarthropod mycophagy has been strongly indicated by Kevan et al. (1975) and Sherwood-Pike and Gray (1985), there is sparse empirical evidence for microarthropods as major agents in decomposer food webs during the Late Paleozoic (Rolfe, 1980). Notable exceptions to this general paucity of data include Banks and Colthart (1993) and Edwards et al. (1995), who discuss evidence for microarthropod-fungi-plant interactions from the trace-fossil record. There has been no comprehensive community-wide synthesis of fossil evidence for the role of oribatid mites in the decomposition of plant material, with the exception of recent studies of Quaternary environments, summarized in Elias (1994). Currently, sufficient primary data exist that such a synthesis can be achieved for several, well-collected, coal-swamp floras that were deposited in the Illinois Basin and the Southern

and Central Appalachian Basins during the Pennsylvanian (Fig. 1). Whereas previous accounts of the presence of mite-bored woods and other tissues have suggested the occasional presence of oribatid mite decomposers (Baxendale, 1979; Cichan and Taylor, 1982; Stidd and Phillips, 1982; Scott and Taylor, 1983; Labandeira and Beall, 1990; Scott, 1977, 1992; Scott et al., 1992) extensive collections of permineralized coal-ball material now can supply a more comprehensive understanding of the extent and diversity of plant-tissue degradation during narrow time intervals within the Pennsylvanian.

There are four principal objectives of this report. First, we document new and extensive data indicating the pervasiveness of oribatid mites as important agents of decomposition in Pennsylvanian coal-swamp forests of Euramerica. These data document an abundant and detailed trace-fossil record of postmortem tunneling into diverse plant tissues and taxa. Second, we evaluate the known body-fossil record of oribatid mites, which we contrast with our new data on the fossil record of oribatid mite feeding traces. Third, we collate and summarize the existing literature on the insect trace-fossil record of plant borings, and compare it to the corresponding oribatid trace-fossil record. Finally, we place in spatiotemporal and paleoecological context the contrasting trace-fossil records of both oribatid mite and insect plant borers. From this comparison, we posit tentative conclusions regarding the taxic and ecologic evolution of arthropod-mediated decomposition of indurated plant tissues in terrestrial ecosystems.

#### ORIBATID MITES AND DECOMPOSITION

Oribatid mites possess impressive ecologic abundance, when gauged by the traditional measures of biomass and numbers of individuals. Most of the pioneering work and recent evaluations of the role that oribatid mites provide in the decomposition of various plant, fungal, and to a lesser degree animal tissues, originates from studies of temperate to boreal ecosystems in the Holarctic and Palearctic realms. For example, oribatid mites are the overwhelmingly dominant macroscopic organism in central European rendzina soils when evaluated as organismic biomass (Kubíková and Rusek, 1976) or in moder soils when calculated as fecal pellet biomass (Kubiena, 1955). In measures of individuals per unit of volume or area, oribatid mites are the most abundant arthropod component (Sai-chuae et al., 1972; Wallwork, 1983; Eisenbeis and Wigham, 1987; Vasiliu and Călugăr, 1987; Norton, 1990), at least for temperate forest communities. Wallwork (1957) determined from 2 to 15 mites/cm<sup>2</sup> occurred in a virgin hemlock/yellow birch forest in northern Michigan, whereas the same author later documented densities ranging from 5.6 mites/cm<sup>2</sup> in mixed deciduous hardwood forest from North Carolina, to 4.25 mites/cm<sup>2</sup> in a Scots pine forest from Sweden (Wallwork, 1983).

Although minimally studied, oribatid mites are also abundant in the tropics. Lasebikan (1977, 1981) documented three times more oribatid mite individuals than the next most abundant cohabiting arthropod group, gamasine mites, in the terminal stages of a decaying palm trunk. This numeric abundance is contrasted with depauperate to modest taxic diversities at the few tropical sites that have been studied (e.g., Beck, 1969, 1972)—consider-

ably less than the respectable 155 species in a plot of deciduous forest in the southern Appalachian Mountains (R. Hansen, pers. comm.). Within both tropical and temperate sites, the diversity of oribatid mites and other detritivorous arthropods is considerably less than that of superjacent herbivore communities. This disparity is partly attributable to minimal resource partitioning by oribatid mites, which results from the greater importance of decomposition state than the taxic affinity of the food substrate (Forsslund, 1939; Riha, 1951; Hayes, 1963; Anderson and Healy, 1972; Anderson, 1975, 1978). Nevertheless, evidence indicates that some species possess quantifiable taxic-based specificity for particular food substrates (Hartenstein, 1962a; Berthet, 1964; Mignolet, 1971; Luxton, 1972). While species-rich clades commonly show only modest morphological diversity, across all taxa there is a substantial range of body form and mouthpart structure (Schuster, 1956; Norton, 1994), and most of the latter has yet to be functionally analyzed.

Oribatid mites are small, chelicerate arthropods, and as adults range in size from 0.2 mm to 1.0 mm, rarely to 2.0 mm (Luxton, 1972; Wallwork, 1983), usually possessing a box-like exoskeleton superficially similar to that of a beetle. Individuals exhibit relatively long lives for microarthropods, lasting from one to four years for most species (Walker, 1964; Harding and Easton, 1984; Soma, 1990). Dietary correlates include poor nutritive value of ingested food, relatively low ingestion rates, and consequent minimal assimilation rates (Berthet, 1964; Luxton, 1972, 1979; Wallwork, 1983), which constrain their life-history parameters (Norton, 1994). These attributes are evidenced by their production of somewhat fewer than one to eight fecal pellets per day (Hartenstein, 1962b; Hayes, 1963; Berthet, 1964; Luxton, 1972). These pellets are inert objects that persist in the soil environment (Zachariae, 1965; Babel, 1975; Bal, 1982) and chemically differ minimally from their parent plant tissues (Edwards, 1974). Oribatid mites form communities principally in decomposing plant litter and wood (Snow, 1958; Woolley, 1960; Wallwork, 1976a) with some species acting as secondary consumers of dead but partially decayed plant material (Luxton, 1972; Kühnelt, 1976), others subsisting as coprophages on decomposer fecal pellets (Nicholson, et al., 1966; Wallwork, 1976b), and others, perhaps most, feeding principally or opportunistically on fungi (Forsslund, 1939; Hartenstein, 1962a, b, c; Luxton, 1966, 1972; Shereef, 1971; Anderson, 1975; André and Voegtlin, 1981; Wallwork, 1983; Clement and Haq, 1984; Norton, 1985; Afifi, et al., 1989). Most of this activity occurs in the L and upper F layers of temperate soils (the F<sub>2</sub> layer of Zachariae [1965] and Bal [1968, 1982]) where accessible plant organs, such as conifer needles and dicot leaves, are consumed by endophytic and exophytic decomposers (Mitchell and Parkinson, 1976), leaving intact more resistant tissues such as needle epidermal sheaths and broadleaf vascular bundles (Zachariae, 1965; Babel, 1975; Bal, 1982). These substrates become degraded through a spatiotemporal succession of ecologic guilds dominated by oribatid mites, with each guild specializing on plant tissue of a particular decomposition state (Harding and Stuttard, 1974; Wallwork, 1983).

Oribatid mites mediate four major aspects of the degradation of plant tissues. First, they increase the surface of

plant tissues through fragmentation, digestion, and defecation (Kevan, 1962; Macfadyen, 1964). The resulting pellets are preferentially colonized by microbial decomposers, such as yeasts and bacteria, when compared to adjacent, undigested plant tissues. Second, the incorporation of decomposer fungi in fecal pellets allows for germination of some fungi within the fecal pellet substrate (Forsland, 1939; Shereef, 1971; Luxton, 1972; Ponge, 1984), often at some distance from the site of initial ingestion if the pellets sift through soil vugs or are biologically transported (Woodring and Cook, 1962; Wallwork, 1967; Kühnelt, 1976; Kilbertus and Vannier, 1979; Behan-Pelletier and Hill, 1983). The ecological significance of this role has been debated (e.g., see Woodring, 1965); Pande and Berthet, 1973). Third, oribatid mites create a "humus form" (Müller, 1879; Bal, 1973) in which fecal pellets within the soil become cohesive and form a pelletal matrix of larger sub-units resistant to decomposition (Kubiena, 1955; Webb, 1977). This conglomeratic formation forms a distinctive stratal structure in many temperate soils and provides a biotope for further colonization by microarthropods (Kubiena, 1955). Last, oribatid mites and other microarthropods and macroarthropods are pivotal in the vertical translocation of organic matter downward into the soil column (Saichuae et al., 1972), partly as an effect of ecologic guild succession during the decomposition process. Vertical translocation within an "absorptively-saturated humus" (Kühnelt, 1976: 313) additionally enhances the effect of nutrient leaching by rainwater (Luxton, 1972).

Many oribatid mites are found within decomposing structural material of plants (Seastedt, 1984; Ramani and Haq, 1991), and inhabit both living and dead fungal fruiting bodies and lichens (Bellido, 1979, 1990). The specificity of the association, and the exact nature in which the mites exploit the material, covers a broad spectrum. In particular, pieces of decaying wood usually support an abundant and diverse oribatid mite fauna (Travé, 1963; Swift, 1977; Seastedt, 1984). Most oribatid mites found in decaying wood are probably fungivores (Norton, 1985; Seastedt et al., 1989), rather than strict xylophages, even though they may show moderate to high specificity for woody microhabitats (Wallwork, 1976a, 1976b). Along with other microarthropods, most extant oribatid mites living in wood or other indurated plant tissues inhabit interstices created by biotic factors (Kühnelt, 1976), such as space created by larger tunneling organisms or the wedging of penetrating plant roots. Of those mites that consume wood, many exploit these ambient spaces rather than tunnel (Travé and Duran, 1971).

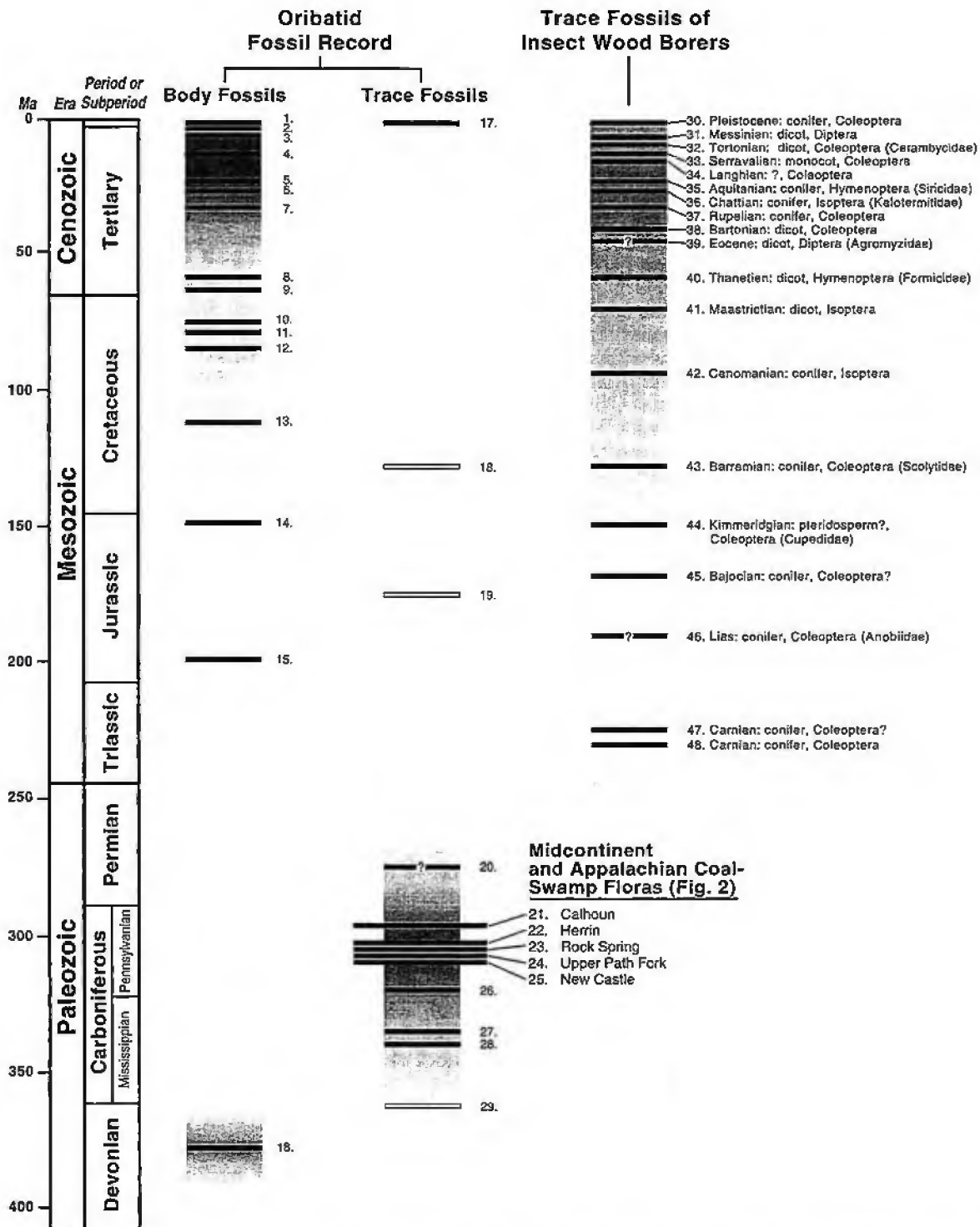
Oribatid mites that create living spaces by their feeding activity may do so in both adult and immature instars or, more commonly, only as immatures. They frequently create irregular feeding galleries that can become spacious relative to the size of the mite. Alternatively, true tunneling may occur, in which the living space is an elongated tube, gradually increasing in diameter as the mite grows (Wallwork, 1957), and packed with fecal pellets behind the active feeding region (Jacot, 1936; Gourbière et al., 1985; Lions and Gourbière, 1988, 1989). For some lineages, such as the Lohmanniidae (Haq and Konikkara, 1988), the type of endophagy is intermediate between these types, with tunnel-like areas produced by communal feeding. In general, oribatid mites tend to have broader microhabitat

ranges and possess more eclectic feeding habits as adults than as immatures.

The diverse feeding patterns of oribatid mites have been characterized in three major ways. Initially, Riha (1951) considered oribatid mites as generalists or specialists. Schuster (1956) later categorized the more specialized oribatid mites as microphytophages subsisting on microbial elements, and macrophytophages that consume higher plant tissues. Kühnelt (1976) characterized oribatid mites as endophages, subsisting in internal plant tissues or ectophages, as external feeders. Schuster's widely accepted categorization, was expanded by Luxton (1972) to include the more host-specific coprophages, zoophages, and necrophages, feeding respectively on fecal material, live animals, and dead animals. Zoophages and necrophages seem relatively inconsequential as oribatid mite dietary classes (Wallwork, 1983; Norton, 1990); coprophagy apparently occurs with greater frequency but is poorly documented (Schuster, 1956; Anderson and Healey, 1972; Luxton, 1972; but see Wallwork, 1967, 1976a). Macrophytophagy principally includes leaf and needle litter consumers, and wood consumers. Although cellulose is digested by various oribatid mite species with either intrinsically produced (Wallwork, 1983) or more likely microbially-borrowed cellulolytic enzymes (Zinkler, 1971; Stefaniak and Seniczak, 1976, 1981; Norton, 1985, 1994), lignin apparently is not digestible (Woolley, 1960; Harding and Stutard, 1974). Those macrophytophages feeding on wood initially probe moist and fungally prepared wood by entering clefts and fissures (Travé, 1963; Kühnelt, 1976) and commence boring at the termini of these cracks, avoiding resin canals during tunneling (Jacot, 1936), and in some cases entering heartwood (Pande and Berthet, 1973; Wallwork, 1976b). Recent experimental work (Scheu and Schulz, 1994; Schulz and Scheu, 1994) indicates that the term phytosaprophagy may be the most accurate description regarding the effect of mites on wood decomposition (see Woas et al., 1989). Macrophytophages feeding on foliar material preferentially devour parenchymatic tissues. Conifer needle fragments and petioles of dicot leaves are transformed into sacs of fecal pellets and undigested vascular tissue that are surrounded by epidermal sheaths (Gourbière et al., 1985, 1987; Lions and Gourbière, 1988, 1989), which eventually rupture as they are transported deeper into the soil horizon (Zachariae, 1965). Dicot leaf blades are skeletonized exophytically by attack through the leaf cuticle, resulting in the casting of fecal pellets on the substrate surface (Riha, 1951). Although our comments have emphasized that oribatid mites overwhelmingly consume fungi or dead plants, recent evidence indicates that many species are facultative herbivores (Wallwork, 1965, 1967; Ramani and Haq, 1984; Walter et al., 1994), mining the leaves (Coulson, 1971; Norton, 1983; Karg, 1984; Fernandez and Athias-Binche, 1986) or boring the twigs (Lan et al., 1986; Walter et al., 1994) or roots (Jacot, 1934; Goff and Bianchi, 1983) of live angiosperms.

#### FOSSIL HISTORY OF ORIBATID MITES

Several lines of evidence attest to the geological antiquity of oribatid mites, including Pangaeon biogeographical distributions of many extant genera (Hammer and Wallwork, 1979; Wallwork, 1979), a mosaic pattern of mor-



**FIGURE 1**—The documented fossil records of oribatid mites, and oribatid mite and insect wood-borings. Three panels of fossil occurrences display, from left to right, the oribatid mite body-fossil record, the trace-fossil record of oribatid mite borings, and the insect trace-fossil record of borings. Note the occurrence of Carboniferous and Early Permian oribatid mite borings to the exclusion of the fossil records of either oribatid mite body fossils or of insect borings. Solid bars represent secure identifications and stippled bars represent probable identifications; question marks indicate some geochronologic uncertainty in stage placement within an epoch. The geochronology is from Harland et al. (1990).

First panel (literature sources 1 to 16) represents the body-fossil record of oribatid mites (Krivolutsky and Druk, 1986; Krivolutsky et al., 1990). See Appendix 1 for details. Data sources are: 1-Quaternary; Hopkins et al., (1976), Scheivis (1987, 1990), and Erickson (1988); 2-Late Pliocene (Piacenzian); Gosolova et al., (1985); 3-Early Pliocene (Zanclian); Gosolova et al., 1985); 4-Middle Miocene (Serravallian); Pampaloni (1902); 5-Early Miocene (Aquitainian); Woolley (1971); 6-Late Oligocene (Chatian); Poinar (1992); Norton and Poinar, (1993); 7-approximately Early Oligocene (Rupelian); Sellnick (1919, 1931); 8-Late Paleocene (Thanetian); Baker and Wighton (1984); 9-Early Paleocene (Danian); Krivolutsky and Ryabinin (1976); 10-Late Cretaceous (Campanian); McAlpine and Martin (1969); 11-Late Cretaceous (Santonian); Bulanova-

phology characterizing primitive taxa (Krivolutsky et al., 1990; Woas, 1991), and notably their fossil record (Sellnick, 1927; Selden, 1988, 1993b; Dubinin 1991), particularly the presence of early derivative taxa from the Middle Devonian (Norton et al., 1988, 1989) and extant genera known from deposits as old as the Jurassic (Sivhed and Wallwork, 1978; Krivolutsky and Ryabinin, 1976; Niedbala, 1983; Krivolutsky and Druk, 1986). Although oribatid mites, as a clade, were present during the Early Devonian, one particular and important subclade, the Astigmata, originated within the oribatid lineage some time later, probably during the Late Paleozoic (O'Connor 1982, 1984). Astigmatic mites currently comprise about half of the species-level diversity of oribatid mites (Norton, 1994), and are consummate exploiters of plants, insects, and vertebrates. Of all arachnid groups, the fossil record of non-astigmatic oribatid mites is unique both in terms of the relatively good representation of adult instars with hardened exoskeletons (Bernini, 1986) and the occurrence of characteristic borings in indurated plant tissues, especially wood (Scott and Taylor, 1983). Ironically these two aspects of the oribatid mite fossil record—the body-fossil record of adult morphology and the trace-fossil record of behavior and life-habits—are geochronologically complementary (Fig. 1). Whereas the earliest known body fossils originate from a Middle Devonian deposit, the body-fossil record does not resume until after a hiatus of 170 million years, during the Early Jurassic, after which occurrences continue sporadically to the Recent. By contrast, the trace-fossil record is richest during much of that 170 million year gap, especially during the Carboniferous. Thus, the oribatid mite fossil record, although sparse and woefully understudied, offers a coarse chronology of both very early and essentially modern lineages (Krivolutsky, 1973), as well as a glimpse into the plant-feeding ecology and behavior of taxonomically unknown Paleozoic forms.

### The Body-Fossil Record

Fossils of oribatid mites occur in three preservational modes: as compact and unaltered cuticle, permineraliza-

tion in amber, and less commonly as compressions or impressions in mudstones. Both the oldest known oribatid mite fossils, described from Middle Devonian strata, and some of the youngest mite fossils, found as Quaternary subfossil material, are preserved as original cuticle. The oldest fossil material is highly flattened and exhibits somewhat disarticulated sclerites, retaining most appendages (Norton et al., 1988, 1989; see also Kethley et al., 1989), whereas subfossil material is three-dimensionally preserved but often with missing major appendages (Elias, 1994). These two differing results are attributable principally to microfossil processing techniques: Devonian rock is macerated in hydrofluoric acid and successively exposed layer by layer, whereas Quaternary sediment is typically sieved, resulting in a loss of appendages from abrasion. By contrast, preservation of oribatid mites in amber retains entire three-dimensional bodies, even of poorly sclerotized lineages and subadult instars (Krivolutsky and Druk, 1986). However, oribatid mites preserved in amber are known only from Late Cretaceous to Pleistocene material (Womersley, 1956; McAlpine and Martin, 1969; Aoki, 1974; Schlüter, 1978; Larsson, 1978; Poinar, 1992). Rare examples of oribatid mites are known from compressions and impressions in mudstones (Baker and Wighton, 1984; Pérez, 1988). In total, 104 pre-Pleistocene oribatid mite fossils have been described (Appendix 1), although many times this number have been recorded in Quaternary deposits (Elias, 1994). Quaternary oribatid mite paleoecology is a vast discipline that emphasizes use of fossils of modern species in establishing the recolonization dynamics of deglaciated Pleistocene landscapes (Karpinen and Koponen, 1973; Elias, 1994), seasonal variation in paleolimnological studies (Erickson, 1988), and evaluation of site-specific conditions at Holocene archaeological sites (Schelvis, 1987, 1990).

The earliest known oribatid mite fossils are *Protochthonius gilboa* Norton and *Devonacarus sellnicki* Norton from the Middle Devonian Gilboa mudstones in south-central New York state (Fig 1; Appendix 1; Norton et al., 1988, 1989). Each of these species comprises a monobasic family that is primitive in many respects, yet still exhibits

Zachvatina (1974); 12-Late Cretaceous (Turonian); Grimaldi, pers. comm.; 13-Early Cretaceous (Albian); Schlee (1972); Grimaldi, pers. comm.; 14-Late Jurassic (Tithonian); Krivolutsky and Ryabinin (1976); 15-Early Jurassic (Sinemurian); Sivhed and Wallwork (1978); and 16-Middle Devonian (Givetian); Norton et al. (1988, 1989).

Second panel (literature sources 17 to 29) represents the trace-fossil record of oribatid mite borings. Data sources are: 17-Quaternary; Haarløv (1967) and Koponen and Nuorteva (1973); 18-Early Cretaceous (probably Barremian); Seward (1923, 1924); 19-Middle Jurassic (Aalenian); Yao et al., (1991); 20-Early Permian (stage not designated); Goth and Wilde (1992); 21-Calhoun Coal-Ball Flora, early Late Pennsylvanian (Chamovnicheskian); this report; 22-Herrin Coal-Ball Flora, late Middle Pennsylvanian (Myachkovskian); this report; 23-Rock Spring Coal-Ball Flora, middle Middle Pennsylvanian (Podolskian); this report; 24-Upper Path Fork Coal-Ball Flora, early Middle Pennsylvanian (Kashirskian); this report; 25-New Castle Coal-Ball Flora, Early Pennsylvanian (Cheremshanskian); this report; 26-Early Pennsylvanian (Kinderhookian); Labandeira et al. (1994); 27-Middle Mississippian (Asbian); Chaloner, et al., (1991); 28-Middle Mississippian (Asbian); Rex (1986), Rex and Galtier (1986); 29-Late Devonian (Famennian); Arnold (1952), F.M. Hueber and Labandeira, (pers. observ.).

Third panel (literature sources 30 to 48) represents the trace-fossil record of insect borings. Family designations in parentheses designate the earliest, well-established record as trace fossils. Additional Cenozoic occurrences have been omitted for lack of space. Data sources are: 30-Quaternary; Scudder (1900); 31-Late Miocene (Messinian); Süss and Müller-Stoll (1975); 32-Late Miocene (Tortonian); Müller-Stoll (1989); 33-Middle Miocene (Serravallian); Call and Tidwell (1988); 34-Middle Miocene (Langhian); Guo (1991); 35-Early Miocene (Aquitian); Rosell and Feustel (1960); 36-Late Oligocene (Chattian); Rozefelds and De Baar (1991); 37-Early Oligocene (Rupelian); Bachofen-Echt (1949), Larsson (1978), and Krzemińska et al. (1992); 38-Middle Eocene (Bartonian); Gregory (1969); 39-Eocene (stage not designated); Süss and Müller-Stoll (1980); 40-Late Paleocene (Thanetian); Brues (1936); 41-Late Cretaceous (Maastrichtian); Rohr, et al. (1986); 42-Late Cretaceous (Cenomanian); Labandeira (pers. observ.); 43-Early Cretaceous (Barremian); Blair (1943) and Jarzembowski (1990); 44-Late Jurassic (Kimmeridgian); Tidwell and Ash (1990); 45-Middle Jurassic (Bajocian); Zhou and Zhang (1989); 46-Lower Jurassic (stage not designated); Jurasky (1932); 47-Late Triassic (Carnian); Walker (1938); 48-Late Triassic (Carnian); Linck (1949).

derived features. The known body-fossil record then pauses for 160 million years, and resumes during the Early Jurassic, in which two taxa referred to modern genera were described by Sihved and Wallwork (1978). The modern morphology of these Jurassic specimens (Norton, 1990) provide a stark contrast to Middle Devonian taxa that are assigned to extinct families. Body fossils of modern families also have been described from Late Jurassic, Late Cretaceous, and Cenozoic deposits (McAlpine and Martin, 1969; Woolley, 1971; Bulanova-Zachvatina, 1974; Krivolutsky and Ryabinin, 1976; Krivolutsky et al., 1990; Norton and Poinar, 1993). Additionally, of the 70 oribatid mite species described from Late Eocene Baltic amber (Sellnick, 1919, 1931; Keilbach, 1982), nearly all are assignable to modern genera (Krivolutsky et al., 1990). This pattern of taxic longevity again suggests that oribatid mites are an ancient group.

### The Trace-Fossil Record

The abundance of characteristic Mississippian to Early Permian borings in plants and coprolites indicates that oribatid mites exhibited significant levels of tunneling behavior in diverse vascular plants. These well-preserved permineralized trace-fossils provide unique insights into oribatid mite microhabitats, life-styles, and plant host preferences that are unavailable for any other part of the fossil record. The earliest known borings that are conceivably attributable to oribatid mites are undescribed tunnels occurring in *Prototaxites*, an enigmatic terrestrial organism, probably a basidiomycete (F. Hueber, pers. comm.), of Late Devonian age from New York state (Arnold, 1952). These *Prototaxites* "logs" contain simple, linear to undulating, occasionally joining tunnels in indurated mycelial tissue (F. Hueber and CCL, pers. observ.) that exhibit evidence of a reaction rim on the tunnel inner surface and contain coprolites of digested mycelia within the tunnels. However, tunnel diameters are several times wider than modern analogs, such as carabodid mites, which typically bore into living and freshly dead basidiocarps (Michael, 1882; Reeves, 1991, 1992) or into lichenized fungi (Bellido, 1979; Gjelstrup, 1979; Gjelstrup and Søchtig, 1979), producing dense networks of tunnels. From Carboniferous and Lower Permian deposits, suspected and well-confirmed oribatid mite tunnels and coprolites have been documented from every major plant group, including lycopsids (Scott, 1977; Chaloner et al., 1991), calamites (Taylor and Taylor, 1992), ferns (Lesnikowska, 1989; Scott et al., 1985, 1992; Rex and Galtier, 1986), seed ferns (Stidd and Phillips, 1982), cordaites (Cichan and Taylor, 1982; Scott and Taylor, 1983; Rolfe, 1985; Labandeira and Beall, 1990), and conifers (Goth and Wilde, 1992). Published accounts occur from at least 10 separate horizons spanning a 75-million-year interval, mostly from clastic- and peat-dominated swamp forests of Euramerica (Fig. 1). Although previous reports were largely anecdotal, in this report we expand documentation of both the intensity and diversity of tissues that were degraded by these early decomposers.

While exquisitely permineralized tissues of Pennsylvanian swamp forests provide an important, 17-million-year record of the early history of wood-borers, this taphonomic window apparently closed during the Early Permian (Fig.

1). Subsequently, evidence for wood-borers becomes available for the Late Triassic (Walker, 1938; Linck, 1949), and the frequency of relevant fossil deposits increases toward the present. However, the Late Triassic to Recent record of terrestrial wood borers is exclusively insect-driven, consisting overwhelmingly of Coleoptera and Isoptera, with subordinate occurrences of Hymenoptera and Diptera. These two, chronologically nonoverlapping records of taxonomically distinct arthropods undoubtedly represents the effects of differing taphonomic regimes in the fossil record, and in particular, large accumulations of degraded, often woody plant tissue during the Carboniferous, when compared to the post-Paleozoic (Robinson, 1990; Labandeira et al., 1994). Nevertheless, the emergence of new lineages of insect wood-borers during the Triassic may represent a profound shift from Late Paleozoic oribatid mites to Mesozoic and Cenozoic insects as the principal detritivores of lignified, above-ground plant tissues. Significantly, some of these insect lineages were dietarily herbivores, consuming live tissues adjacent to wood, such as phloem and various meristems.

Oribatid mites are the only arachnid group with both respectable body-fossil (Appendix 1) and trace-fossil records (Figs. 1–12). Yet these dual fossil records are separate and have not been linked, either by instances of tunnels harboring mite body fossils or by mite body fossils containing coprolites with identifiable plant tissues. It is possible that these independent fossil records eventually may be linked, although the relative preservation potential of coexisting plant and arthropod cuticle is poorly understood.

### MATERIALS AND METHODS

Bulk tissues from plants occurring in peat-dominated coal-swamp forests of equatorial Euramerica were frequently permineralized in sedimentary basins occurring at or slightly above sea level. These carbonate-permineralized tissues characteristically occur as coal ball zones in relatively planar coal deposits of Pennsylvanian age. The Pennsylvanian deposits examined in this study correspond to an absolute age from 315 to 298 million years (Fig. 2; Harland et al., 1990), representing a 17 Ma interval. Preservation of these plant tissues reveal anatomical detail at the whole organ, tissue, and individual cellular levels.

While coal balls can range in maximum dimension from several centimeters to more than 1 meter in the field, virtually all coal balls used in this study were at the small end of this range. Individual coal balls were rock sawed in the laboratory into slabs that were from 2 to 6 cm thick. Surfaces of these slabs were smoothed by grinding in moistened 500 grit carborundum powder, followed by acid etching in 5 percent hydrochloric acid for 12 to 17 seconds (for details, see Phillips et al., 1976). Acid etching exposed organic material on the coal-ball surface, such as cell walls, as it removed carbonate matrix. After the etched surface was air-dried, the surface was flooded with acetone, followed immediately by rolling a 2 or 3 mil sheet of transparent cellulose acetate onto the surface. Once the sheet was dry, it was lifted off, taking with it the embedded, thin layer of organic material exposed on the surface. This procedure was repeated until a biologically meaningful thickness of the coal-ball surface was captured as peels.

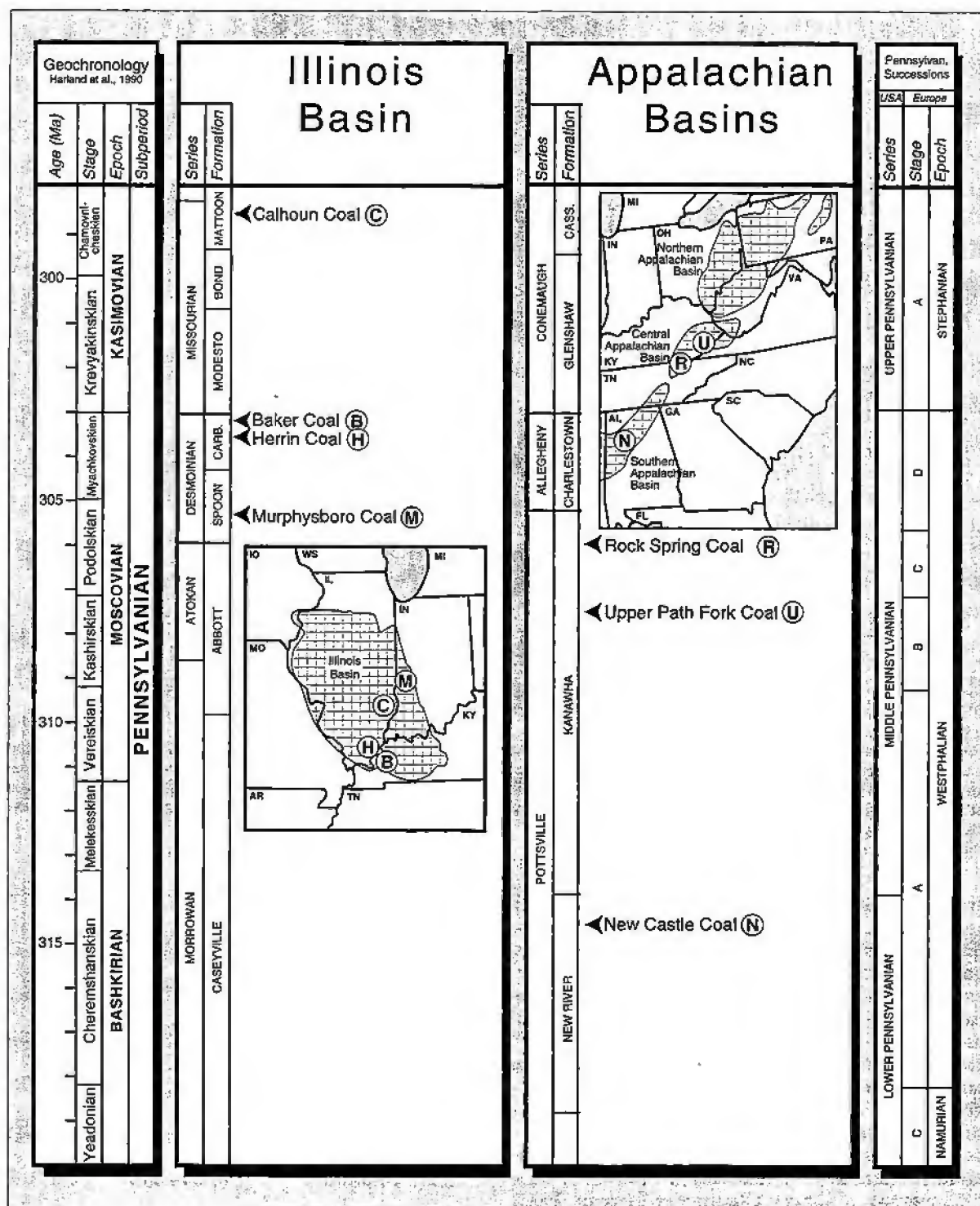


FIGURE 2—Stratigraphic, geochronologic, and paleogeographic context of coal-ball deposits referred to in text. Geochronologic calibration is from Harland et al. (1990); positions of Pennsylvanian basins are from Cross and Phillips (1990) and Winston and Phillips (1991). Abbreviations: Carb. = Carbondale Formation, Cass. = Casselman Formation.

For light microscope photography, regions of interest from the acetate peels were cut and mounted in embedding medium on microscope slides. An Olympus SZH microscope connected to an automatic photographic system was used to photograph slide-mounted peels.

Three dimensional reconstructions of mite borings in several types of plant tissues were based on camera lucida drawings of cellulose acetate peels. Initially, a slab with well-preserved plant tissues containing mite borings was selected, and then from 100 to 150 successive peels were



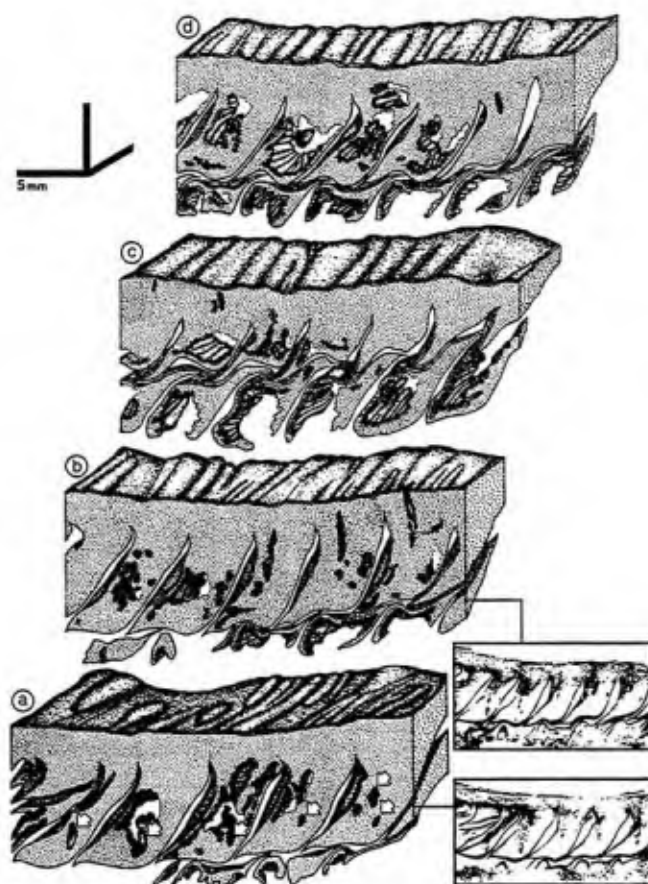


FIGURE 3—Three-dimensional reconstruction of mite galleries in leaf cushions of the lycopsid *Lepidophloios harcourtii* from the Central Appalachian Basin. Specimen 28969-Bbot. Stippled pattern represents leaf cushion parenchyma; elliptical objects in black represent parichnos. Mite excavated areas in leaf cushions were rendered without coprolites and tissue fragments for ease of viewing. Reconstructions were based on peel slices 1 to 24 (a), peel slices 25 to 49 (b), peel slices 50 to 74 (c), and peel slices 75 to 99 (d). Light photographs of peels No. 1 and 25 are attached to (a) and (b) respectively.

made. From each series of peels originating from a slab surface, every tenth peel was selected as a control. A camera lucida line-drawing of each control peel was made at 6× magnification on tracing paper, with plant tissues and mite-associated features labeled. Each successive camera lucida line drawing then was assembled, integrated, and three-dimensionally rendered by use of Spyglass Dicer<sup>®</sup> and Adobe Illustrator<sup>®</sup> software on a Macintosh Quadra computer. After the resulting printout was manually reproduced on mylar, it was photographically reduced for incorporation as elements in Figs. 3 and 4.

All coal ball specimens, acetate peels, and associated microscope slides reside at the Paleobotanical Research Center of the University of Illinois, Champaign-Urbana. Peels that were used for supplying microscope slides in this report are the following:

10765-Cbot	32274-15A-4top	38012-Dbot
28686-A	32277-Dtop	38022-Etop
28799-Btop	32330-Bbot	38030-Ktop
28892-Btop	32330-Btop	38035-Hbot

28938-Btop	32350-Cbot	38040-Gbot
28969-Bbot	32479-A	38043-Lbot
30679-Bbot	32479-Bbot	38066-Ctop
31024-Btop	32479-Ctop	38070-Etop
31272-Bbot	37112-Etop	38078-Ctop
31272-Ctop	37112-Itop	38374-Btop
32274-A3-Side 2	37326-Gbot	38600-Bbot

Microscope slides associated with the above peels that were used for photodocumentation in this report are the following:

22,329	22,438	22,577
22,354	22,441	22,608
22,363	22,446	22,612

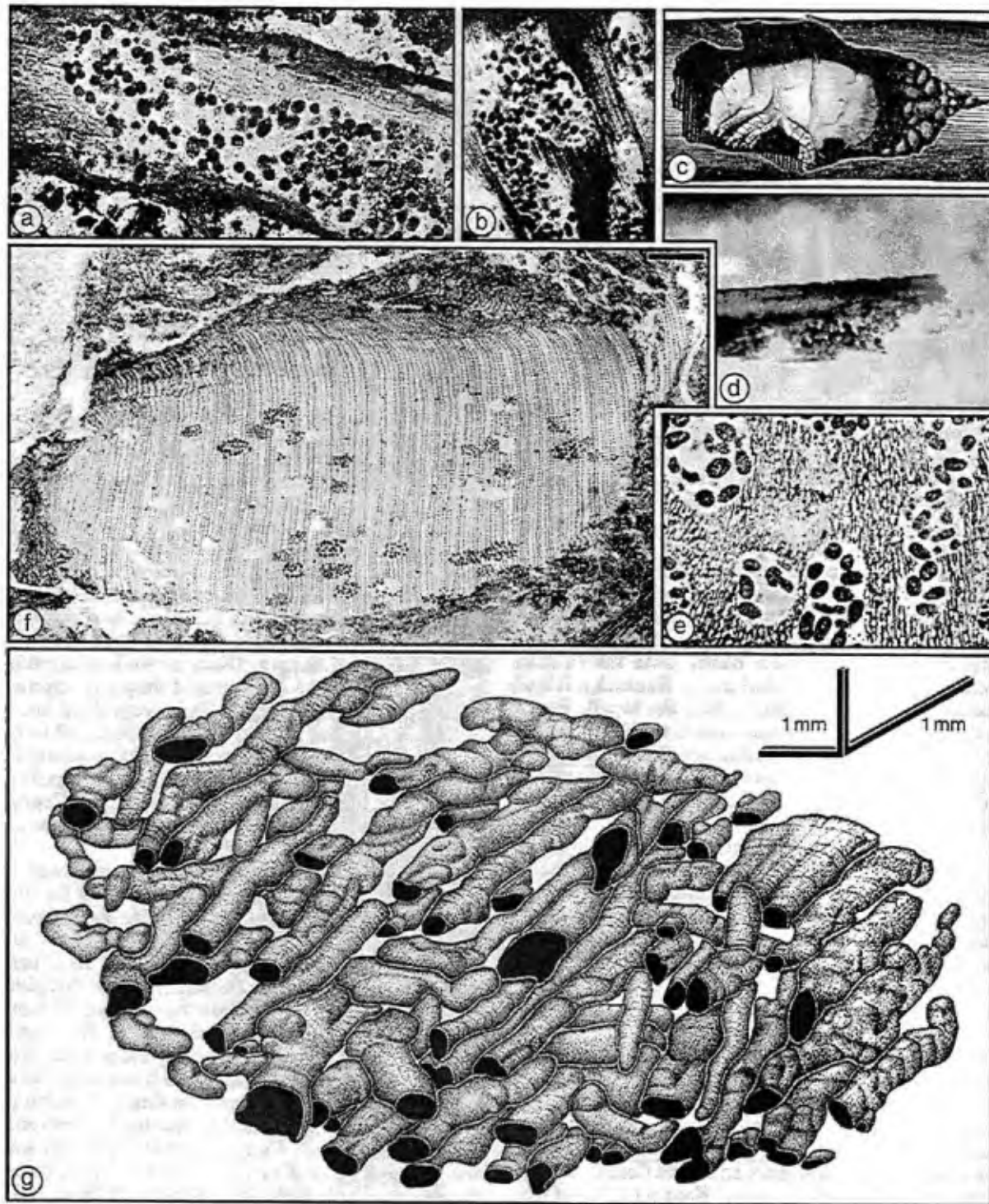


FIGURE 4—Mite tunnels in Recent plant tissues (a-e), republished with permission of the authors.

(a) A twig of *Quercus* (oak) from the A horizon of a moder rendzina soil, showing consumption of wood. From Kubíková and Rusek (1976, Plate 13, figure 1;  $\times 15$ ). (b) An unidentified fragment from a calcareous marl in a rendzina soil from Sierra Grossa, Spain. From Kubiena (1955, figure 13;  $\times 30$ ). (c) Deutonymph of *Hoplophorella thoreau* (Jacot) in a *Picea* (spruce) needle. From Jacot (1939, figure 1; length of mite about 0.5 mm). (d) A needle of *Pinus* (pine) containing a tunnel with fecal pellets. From Ponge (1988, figure 1; scale bar = 1 mm). (e) Fragment of *Pinus* wood from a litter/humus horizon, tunneled by *Rhysotritia duplicata*. From Drift (1964, figure 15;  $\times 18$ ). Middle Pennsylvanian wood (f-g) with mite galleries. (f) A fragment of calamitean wood, from the Rock Spring Coal-Ball Flora. Peel No. 9 of coal ball 3233-Btop (slide 22,407). Scale bar = 1 mm. (g) Three-dimensional rendering of tunnel network for peels 1-120 in f.

22,393	22,456	22,643
22,400	22,471	22,662
22,403	22,492	22,667
22,406	22,515	22,670
22,407	22,517	22,672
22,416	22,520	22,673
22,428	22,524	22,727
22,433	22,537	

## RESULTS

Plant tissues from seven important coal-ball floras from Pennsylvanian deposits of equatorial Euramerica were examined for damage by borers. From these seven deposits (Tables 1 and 2A; Figs. 3–12) the following were documented: (i) the size and shape of coprolites occurring in tunneled and galleried tissues, (ii) the incidence of tissue-boring, (iii) identities and percentage of the major plant taxa consumed by detritivorous borers, (iv) the spectrum of plant organs and tissue types preferred by tissue-borers for each coal-ball flora, and (v) the degradational condition of plant tissues at the time of consumption. These features are presented below as a temporal overview of the taxic, histologic, and edaphic patterns of borer-mediated plant damage among the earliest, well preserved, coal-swamp floras.

The coprolites documented in our study bear smooth surfaces and range from 47.3 to 106.6  $\mu\text{m}$  in diameter (Table 2A). Their diameters are within the size range reported from Middle Mississippian (Esnost and Roanne, France) to Lower Permian (Wetterau, Germany) permianized floras of several previous studies (Table 2B), some of which have attributed their coprolite producers to oribatid mites (Baxendale, 1979; Scott and Taylor, 1983; Goth and Wilde, 1992). Additionally, clusters of coprolites in many plant tissues often possess a stereotyped shape, with individual groupings having ovoidal, elliptical or rarely cylindrical shapes. Diameter-to-length ratios vary from approximately 1.6 for ovoidal shapes to approximately 2.8 for cylindrical shapes. These coprolites are always found in borings ranging in diameter from 100 to 450  $\mu\text{m}$ , and within dead plant tissues that include diverse types of parenchyma, phloem and xylem, and once-digested plant material of other detritivores and herbivores. Coprolites of the 40 to 110  $\mu\text{m}$  size class are almost always associated with endophytic detritivory (Table 2).

In Table 1, we determine the total percentage of peels with coprolite-bearing tunnels or galleries for all seven coal-ball floras. We list also the percentage of peels containing borings in tissue fragments from the five major plant taxa: lycopsids, sphenopsids, ferns, seed ferns, and cordaites. To determine the incidence of detritivory for each coal-ball flora we tabulate the number of identifiable tissue fragments from major plant taxa that contain demonstrable evidence of mite boring, and standardize these counts across all major taxa for each coal-ball flora. Thus each peel, which lacks or contains single or multiple mite-bored tissue fragments, contributes to the frequency data presented in Table 1. Comparison of previously gathered biomass abundance of major plant taxa for six of these floras (Phillips, et al., 1985; Winston and Phillips, 1991) with the corresponding incidence of borer damage for each plant group provides an assessment of whether borer detritivores are temporally tracking taxic trends in plant biomass.

The earliest well-documented coal-swamp deposit from North America is the New Castle Coal-Ball Flora, of Early Pennsylvanian age (316 Ma) from northwestern Alabama, in the Southern Appalachian Basin. Plant biomass from this deposit is overwhelmingly dominated by lycopsids (82.2 percent), and the subordinate volumes of sphenopsids, ferns, and seed ferns collectively represent 5.0 per-

Locality and stratigraphic information for the seven coal-ball floras investigated were based on superpositional relationships provided by Phillips (1980) and Phillips et al. (1985), and temporally calibrated by Harlan et al. (1990). The examined coal-ball floras are as follows, from oldest to youngest. The New Castle Coal-Ball Flora is located in the Southern Appalachian Basin, near Townley, Walker Co., Alabama. It is of Cheremshanskian age (about 315 Ma) within the Early Pennsylvanian Subperiod, and is assignable to the Westphalian A stage of classic European nomenclature. The Upper Path Fork Coal-Ball Flora is located in the Central Appalachian Basin, from the Cranks Creek locality, near Cawood, Harlan Co., Kentucky. It is of Kashirskian age (about 308 Ma) within the Middle Pennsylvanian Subperiod, and corresponds to the Westphalian B stage of classic European terminology. The Rock Spring Coal-Ball Flora is located in the Central Appalachian Basin, from the Cross Mountain locality, near Careyville, Campbell Co., Tennessee. It is of Podolskian age (about 306 Ma) within the Middle Pennsylvanian Subperiod, and corresponds to the Westphalian C stage of classic European terminology. The Murphysboro Coal-Ball Flora is located in the Illinois Basin, from the Maple Grove strip mine, near Cayuga, Vermillion Co., Indiana. It is of Podskolian age (about 305 Ma) within the Middle Pennsylvanian Subperiod, and corresponds to the early Westphalian D stage of classic European terminology. The Herrin Coal-Ball Flora is located in the Illinois Basin, from the Carrier Mills (Saline Co.) and Shawneetown (Gallatin Co.) localities, Illinois. It is of late Myachkovskian age (about 303 Ma) within the Middle Pennsylvanian Subperiod, corresponding to the late Westphalian D stage of classic European terminology. The Baker Coal-Ball Flora is located in the Illinois Basin, from the Hart and Hart Coal Company Mine, near Providence, Webster Co., Kentucky. It is of late Myachkovskian age (about 303 Ma) within the Middle Pennsylvanian Subperiod, and corresponds to the late Westphalian D stage of classic European terminology. The Calhoun Coal-Ball Flora is located in the Illinois Basin, from the Calhoun and Berryville localities, Richland Co., Illinois. It is of Chamovnicheskian age (about 298 Ma) within the Late Pennsylvanian Subperiod, and corresponds to the Stephanian A stage of classic European terminology. Additional details regarding localities and temporal occurrences of these floras are provided in Phillips (1980) and Fig. 2.

TABLE 1—Incidence of mite detritivory from North American coal-swamp floras of Pennsylvania Age.

Coal-ball flora	Coal-Ball collection <sup>1</sup>	Coal-Ball peels examined <sup>2</sup>	Number of peels examined	Number of tunnels & coprolites	Percentage of peels with tunnels & coprolites	Total number of feeding traces	Total biomass percentage contribution of major plant taxa <sup>3</sup> and extent of detritivory <sup>4</sup> for each major taxon (in parentheses)					Shoot to root ratio <sup>5</sup>
							Lycopods	Sphenopsids	Ferns	Seed ferns	Cordaites	
Calhoun	VS 1	all	370	106								
	VS 5	middle	518	116	25.0	292	1.9 (5.5)	9.3 (0.3)	<i>64.3</i> (76.7)	24.2 (15.1)	0.3 (2.4)	0.6
Baker	RS 2	middle	272	100	36.8	139	(52.5)	(8.6)	(7.2)	(15.1)	(16.5)	
Herrin	ES	middle	93	71								
	VS 4	middle	374	33	22.3	163	<i>68.9</i> (52.8)	4.1 (3.7)	10.1 (14.7)	16.3 (10.4)	0.5 (16.6)	1.89
Murphysboro	VS 9	middle	259	47	18.2	42	<i>75.0</i> (73.8)	3.0 (0)	6.5 (4.8)	1.0 (0)	14.5 (16.7)	1.69
Rock Spring	RS 1	all	1360	606	44.6	833	<i>50.9</i> (21.8)	9.4 (17.9)	4.0 (1.9)	2.7 (2.4)	<i>33.0</i> (55.9)	0.72
Upper Path Fork	RS 1	all	58	10								
	RS 2	middle	301	58	18.9	70	<i>54.5</i> (62.9)	3.6 (12.9)	3.1 (12.9)	2.1 (4.3)	36.7 (7.1)	0.47
New Castle	RS 1	all	408	74	18.1	72	<i>82.2</i> (95.8)	1.2 (2.8)	1.0 (1.4)	2.8 (0)	0 (0)	1.8

<sup>1</sup> Abbreviations: VS, Vertical Section; RS, Random Sample; ES, Ecology Studies.

<sup>2</sup> A middle peel represents a surface located approximately in the central region of a coal ball. For each coal ball, a middle peel was selected from a series of several peels from successively sawn coal-ball slices.

<sup>3</sup> Floristic data from Phillips, et al. (1985) and Winston & Phillips (1991). Italicized, entries represent floristically dominant taxa by biomass. Floristic data was not collected for the Baker Coal.

<sup>4</sup> Data from frequency counts of specimens with coprolites in borings, normalized to 100 percent. Detritivory in macrocoprolites and unknown tissues omitted.

<sup>5</sup> The shoot-to-root ratio is the proportion of biomass occurring as above-ground tissues versus below-ground tissues in the coal-ball floras examined.

cent of the deposit (Winston and Phillips, 1991). Cordaites are absent. Although the percentage of peels with evidence of mite detritivory across all taxa was 18.1 percent, lycopsids were overwhelmingly attacked by detritivores, accounting for 95.8 percent of all plant tissue fragments with mite tunnels. The principal plant hosts subjected to borer attack was the lycopsid *Lepidophloios* cf. *harcourti* (Fig. 5). Leaf cushions were the dominant tissue consumed, accomplished usually by a partial evacuation of inner parenchyma surrounding the vascular trace, resulting in expansive galleries interconnected by occasional tunnels (Fig. 5). Other lycopsid tissues that were consumed include the distal laminae of cones, roots and outer stem periderm. Two examples of borings in calamitean wood and one in a *Botryopteris* fern were noted.

Parenchyma in *Lepidophloios* leaf cushions was the favored tissue of wood-boring mites during the Early Pennsylvanian and early Middle Pennsylvanian in the Appalachian Basin (Figs. 3; 6a,b,d-h). This host preference also has been documented from the later Middle Pennsylvanian Mineral Coal-Ball Flora of Kansas (Baxendale, 1979). In both the New Castle and Upper Path Fork coal-ball floras, lycopsids are the dominant taxic constituent, although cordaites approach codominance in the Upper Path Fork (Table 1). Although representing 36.7 percent of the Upper Path Fork flora, only 7.1 percent of the documented feeding traces involved cordaites. Thus, despite rather similar contributions to biomass, lycopsid tissues were attacked about nine times more frequently than those of cordaites (Fig. 6). Upper Path Fork lycopsids, representing 54.5 percent of the flora, accounted for 62.9 percent of borer feeding traces. The underutilization of cor-

daites (though see Fig. 6i) is contrasted to greater frequency of detritivory in sphenopsids, ferns, and to a lesser degree seed ferns, each of which constitutes between 2 and 4 percent of the flora but between 4.3 and 12.9 percent of specimens with feeding traces made by mite borers. However, it is possible that this absence of cordaites detritivory may be more apparent rather than real, since in other coal ball floras cordaites wood is comminuted into unrecognizable detritus. One of the earliest examples of coprophagy in Euramerican coal-swamps, demonstrating the secondary consumption of tissues, is from the Upper Path Fork Coal-Ball Flora (Fig. 6c).

The Rock Spring Coal-Ball Flora, also from the central Appalachian Basin, contains a similar 1.5 ratio of dominant lycopsids (50.9 percent) to subdominant cordaites (33.0 percent). Both the Upper Path Fork and Rock Spring coal-ball floras possess low shoot-to-root ratios (Table 1), indicating a greater contribution from below-ground tissues than from aerially-deployed tissues, including trunks (Phillips et al., 1985). This absence of canopy-derived tissue suggests substantial degradational loss of litter, and is contrasted to the preponderance of below-ground structural tissues illustrated in Figs. 7 and 8, wherein tunneling detritivores attacked tissues ranging from apparently solid, undecomposed wood to punky tissues that were soft. (See Fig. 7a for end-members of this continuum.) Unlike the Upper Path Fork Coal-Ball Flora, Rock Spring cordaites are the principal taxic constituent consumed by detritivorous borers (but see Fig. 8e), comprising 33.0 percent of the plant biovolume but 55.9 percent of the attacks by borers, indicating for the first time that the approximate proportional consumption of lycopsid tissues differed. Al-

TABLE 2—Diameters of paleozoic coprolites attributed to oribatid mites.

Coal-ball flora	UIUC peel	UIUC slide	Plant tissue context of coprolites	Statistical characterization <sup>1</sup>				
				Maximum	Minimum	Mean	Variance	N
New Castle	38374-Btop	22,400	<i>Lepidophloios</i> leaf cushion parenchyma	61	135	95.5	18.117	58
Upper Path Fork	28729-Btop	22,726	<i>Lepidophloios</i> leaf cushion parenchyma	62	104	83.1	8.381	54
Rock Spring	32479-A	22,446	Cordaitean wood	43	58	49.8	3.782	42
Rock Spring	32479-Ctop	22,403	Cordaitean wood	41	64	50.2	5.390	54
Herrin	38070-Etop	22,612	<i>Myeloxylon</i> (medullosan) ground tissue	63	39	53.0	7.884	32
Herrin	38030-Ktop	22,515	tissue fragments in macrocoprolite	60	38	47.3	5.670	41
Herrin	38066-Ctop	22,354	tissue fragments in macrocoprolite	40	63	53.7	5.771	27
Herrin	38035-Hbot	22,512	<i>Alethopteris</i> palisade parenchyma	35	61	49.2	6.484	39
Baker	37326-Gbot	22,492	<i>Sphenophyllum</i> secondary phloem	44	81	59.6	7.866	49
Calhoun	10765-Cbot	22,670	<i>Psaronius</i> inner root mantle cortex	70	148	106.6	17.614	80
Calhoun	31024-Btop	22,329	<i>Psaronius</i> root parenchyma	55	100	71.2	12.925	46

Flora and age	Locality	Plant tissue context of coprolites	Diameter (μm)	Reference
Esnot (Middle Mississippian)	Esnot and Roanne, France	<i>Botryopteris</i> , fern stem	70–100	(Rex & Galtier, 1986; Rex, 1986)
Upper Path Fork (Kashirkian)	Cranks Creek, Kentucky	" <i>Premnoxylon</i> ", cordaitean wood	c. 40–55 <sup>2</sup>	(Cichan & Taylor, 1982)
Hamlin (Kashirkian)	Lewis Creek, Kentucky	" <i>Premnoxylon</i> ", cordaitean wood, other tissues	30–60, 50	(Taylor & Scott, 1983; Scott & Taylor, 1983)
Mineral (Podolskian)	West Mineral, & Lovilia, Kansas	<i>Cordaites</i> leaf mesophyll; <i>Lepidophloios</i> leaf cushion parenchyma	30–40	(Baxendale, 1979)
Rotliegende (Lower Permian)	Wetterau, Germany	<i>Dadoxylon</i> , probable cordaitean wood	20–30	(Goth & Wilde, 1992)

<sup>1</sup> Maximum, minimum and mean values given in micrometers (μm).

<sup>2</sup> Estimated from ovoidal and ellipsoidal shapes of coprolites in photographs and stated lengths of approximately 75 μm.

though lycopsids constitute about half of the biomass, they only represent 21.8 percent of borer feeding traces. Associated with these data is the observation that, since preserved cordaitean and calamitean tissues consist dominantly of secondary xylem (Costanza, 1983), the geometry of the borings changed to long, mostly unbranched tunnels that parallel the wood grain and only occasionally expand into galleries (Figs. 4f,g; 7; 8a–d,g). This style of tunneling contrasts with the expansive galleries in leaf cushions that are occasionally connected by narrow tunnels in the New Castle and Upper Path Fork coal-ball floras (Figs. 3; 5; 6a,b,d–h). The extensiveness of tunneling in Rock Spring cordaites reveals three types of borings: (i) tunnels with dense accumulations of coprolites that lack buildup of comminuted but undigested wood fragments (Figs. 7b–f; 8g), (ii) tunnels with well-formed coprolites amid significant accumulations of unprocessed and indistinctly layered wood fragments (Fig. 8a,b), and (iii) rare tunnels containing distinctly stratiform accumulations of comminuted frass with poorly-defined coprolites (Fig. 8c,d). Since xylophagous mites exhibit a variety of feeding styles in modern woods, these probably represent traces of different oribatid mite taxa.

The Murphysboro Coal-Ball Flora is of Middle Pennsylvanian age, and consists dominantly (75.0 percent) of lycopsid biomass (Phillips et al., 1985). Compared to previous coal-ball floras, the proportional contribution from cordaites was more than halved, to 14.5 percent. Other major taxa represent less than 11.0 percent of the flora. Al-

though lycopod abundance and frequency of consumption by mites are approximately 4.4 times greater than that of cordaites, both taxa seem equal in detritivore preference, since their proportional contributions to total incidence of detritivory is similar to their respective abundances (Table 1). The younger Herrin Coal-Ball Flora, from the Illinois Basin, similarly contains a high biomass value for lycopsids (68.9 percent), although the incidence of boring into lycopsid tissues (Figs. 9; 11e) tracks lycopsid dominance at a lower level of 52.8 percent. The proportional representation of ferns (Fig. 10h), seed ferns (Figs. 10a–g), and sphenopsids increases significantly, however, and is roughly congruent with the incidence of tissue boring. Cordaites represent only 0.5 percent of the total plant biomass but account for 16.6 percent of the incidence of detritivore consumption. Notably, there is evidence for borers attacking a broad spectrum of organs and tissues in host plant taxa, including for lycopsids not only leaf cushions (Figs. 9a–c; 11e), stem wood, and lateral laminae of cones (Figs. 9d–e), but also megasporangial wall (Figs. 9f,g) and cone axes. There is minimal evidence for mite consumption of peridermal tissues. Locally abundant foliar material also provides evidence for penetration by borers (Figs. 10 a–d); stem and petiolar tissue of medullosans and ferns demonstrate the selective penetration of sclerenchyma and parenchyma by small borers (Figs. 10f,h). Like lycopsid megaspores, large medullosan seeds with thick and indurated integuments occasionally exhibit invasion by arthropod detritivores (Fig. 10e). It is also significant that

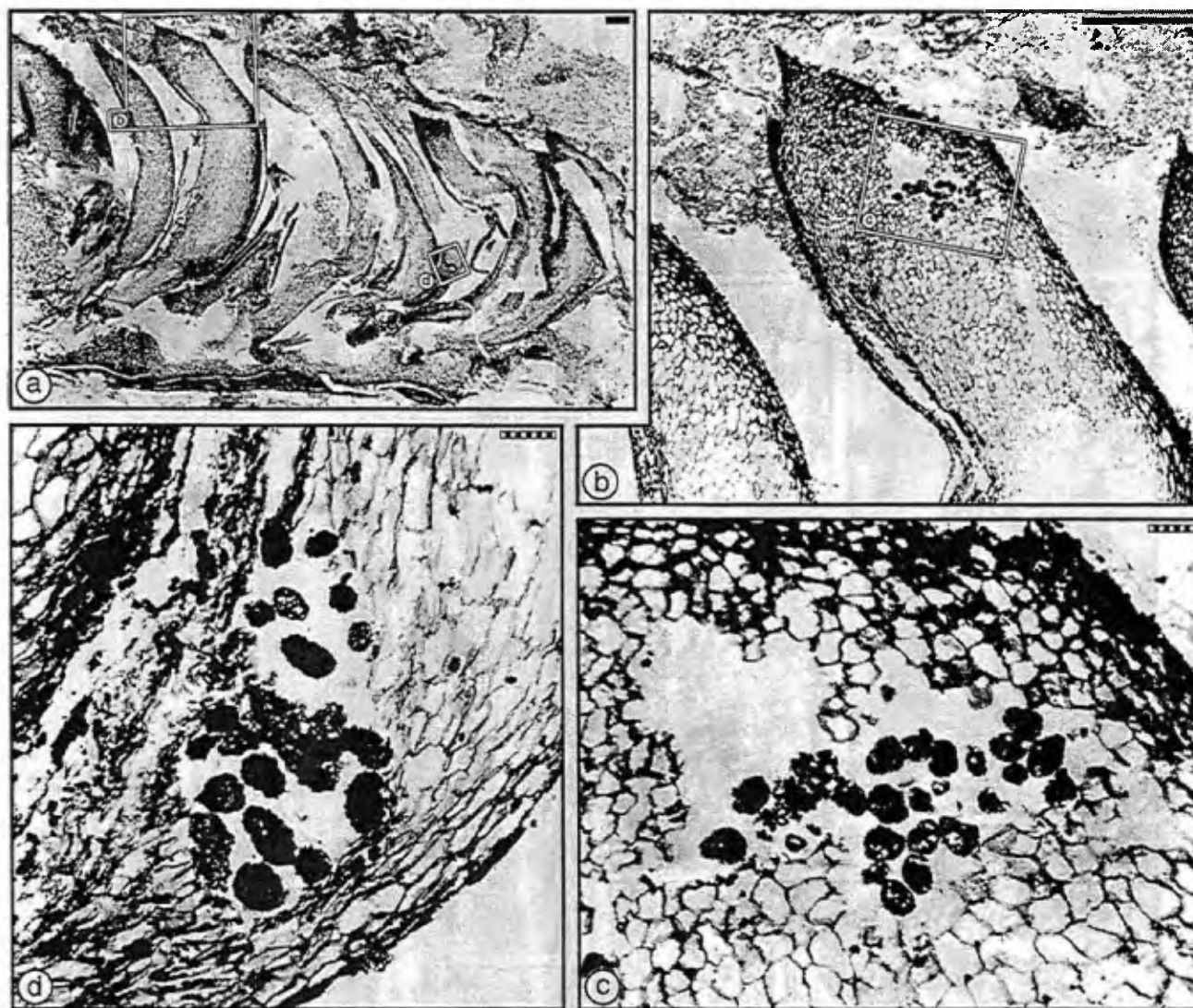
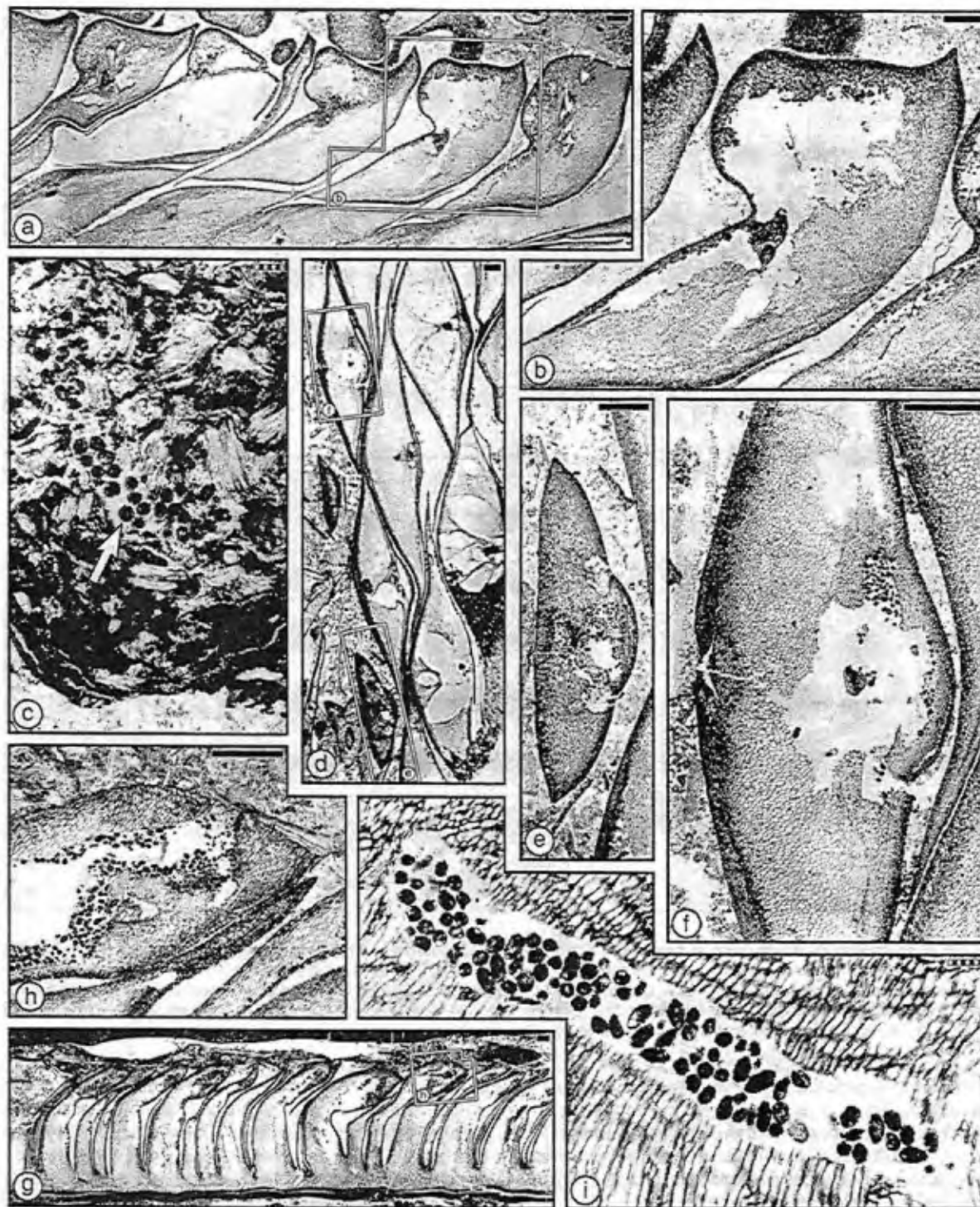


FIGURE 5—Mite consumption of leaf-cushion parenchyma in the lycopsid *Lepidophloios harcourtii*, from the New Castle Coal. (Winston and Phillips, 1991). All photographs are from slide 22,400 (peel specimen 38374-Btop). Solid scale bars = 1.0 mm; barred scale bars = 0.1 mm. (a) Oblique tangential section of leaf cushions from a segment of a *Lepidophloios* twig, some with galleries excavated by mites. (b) Enlargement of distal region of leaf cushion indicated at upper-left of (a), showing gallery and constituent coprolites in parenchyma. (c) Enlargement of gallery outlined in (b). (d) Enlargement of basal region of leaf cushion indicated at central-right in (a).

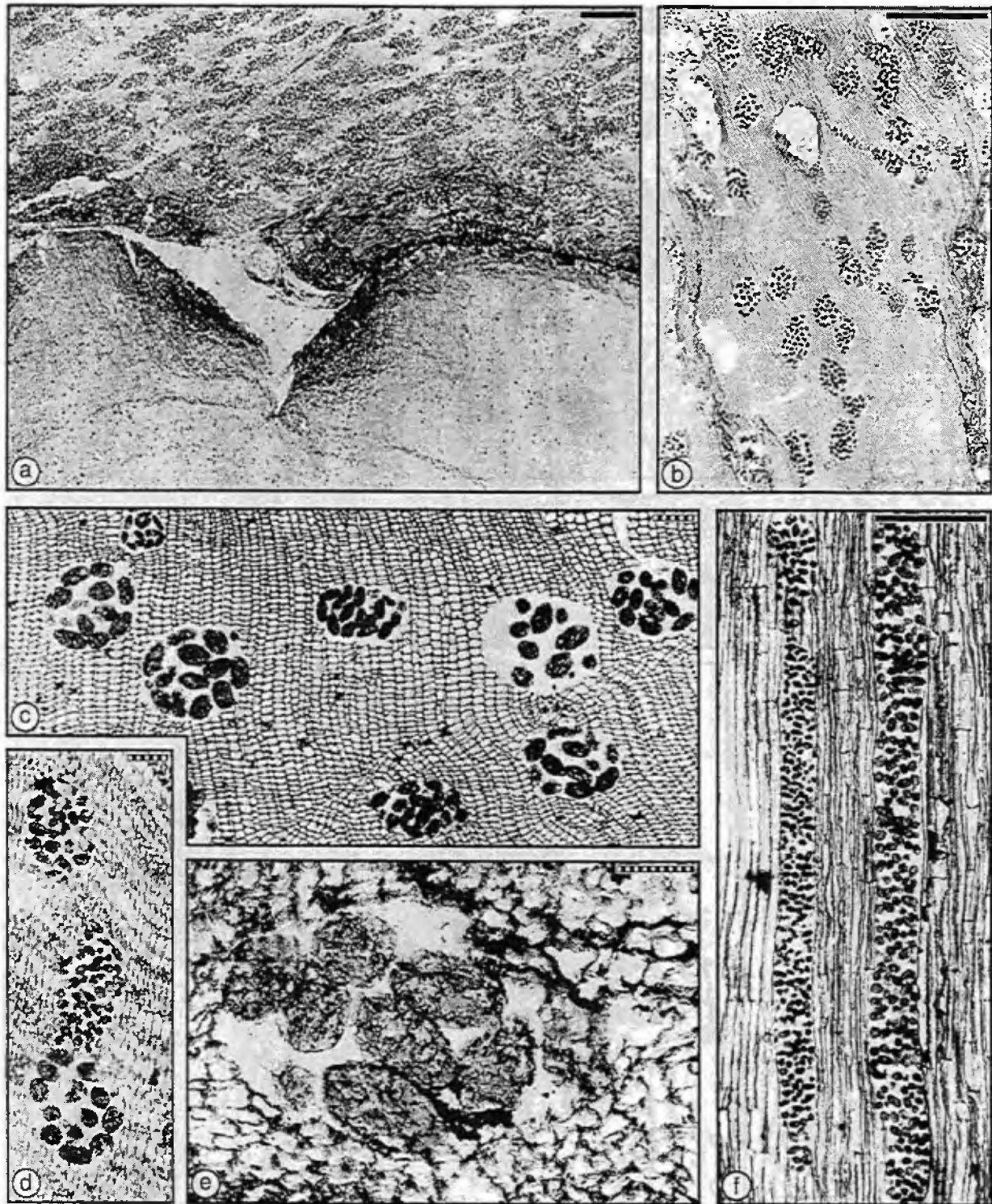
microdetritivore coprophagy has been documented in greater amounts (Figs. 11a–d) than in any previous coal-ball flora. This general pattern of major consumption of diverse lycopsid tissues and a substantial representation of detritivory in the other plant groups occurred in the younger Baker Coal-Ball Flora (Table 1; Figs. 11f,g).

After the demise of lycopsid-dominated forests at the end of the Middle Pennsylvanian, *Psaronius* tree-ferns became the dominant vegetation in the equatorial Euramerican wetlands until the Early Permian. In fact, *Psaronius* and other ferns account for 64.3 percent of the plant biomass, and 76.7 percent of feeding traces by borers. Lycopsids, dominant in both of these respects during the Early and Middle Pennsylvanian, shrink to 1.9 and 5.5 percent, respectively. Seed ferns are ranked second (24.2 percent) in overall biomass, and contribute 15.1 percent of the feeding traces by detritivores. Thus the character of early Late

Pennsylvanian coal swamps shifted to forests dominated by ferns and seed ferns, collectively accounting for approximately 90 percent of both biomass and consumption by detritivores. The peats resulting from these forests were penetrated extensively by roots, many of which contain tunnels with coprolites (Figs. 12a,c–e). Generally, in contrast to preserved Middle Pennsylvanian coal-ball floras, there was considerably more detritivore consumption of foliar and reproductive tissues (Figs. 12c,f,g), probably attributable to a relative paucity of structural tissues, especially wood. The aerial and subterranean root mantles of *Psaronius* trunks were a limited but conspicuous exception, showing evidence of tunneling within individual root elements (Fig. 12b). These observations undoubtedly reflect the decline of major woody cordaites during the late Middle to Late Pennsylvanian (Phillips et al., 1974; Phillips and Peppers, 1984; DiMichele and Hook, 1992). More-

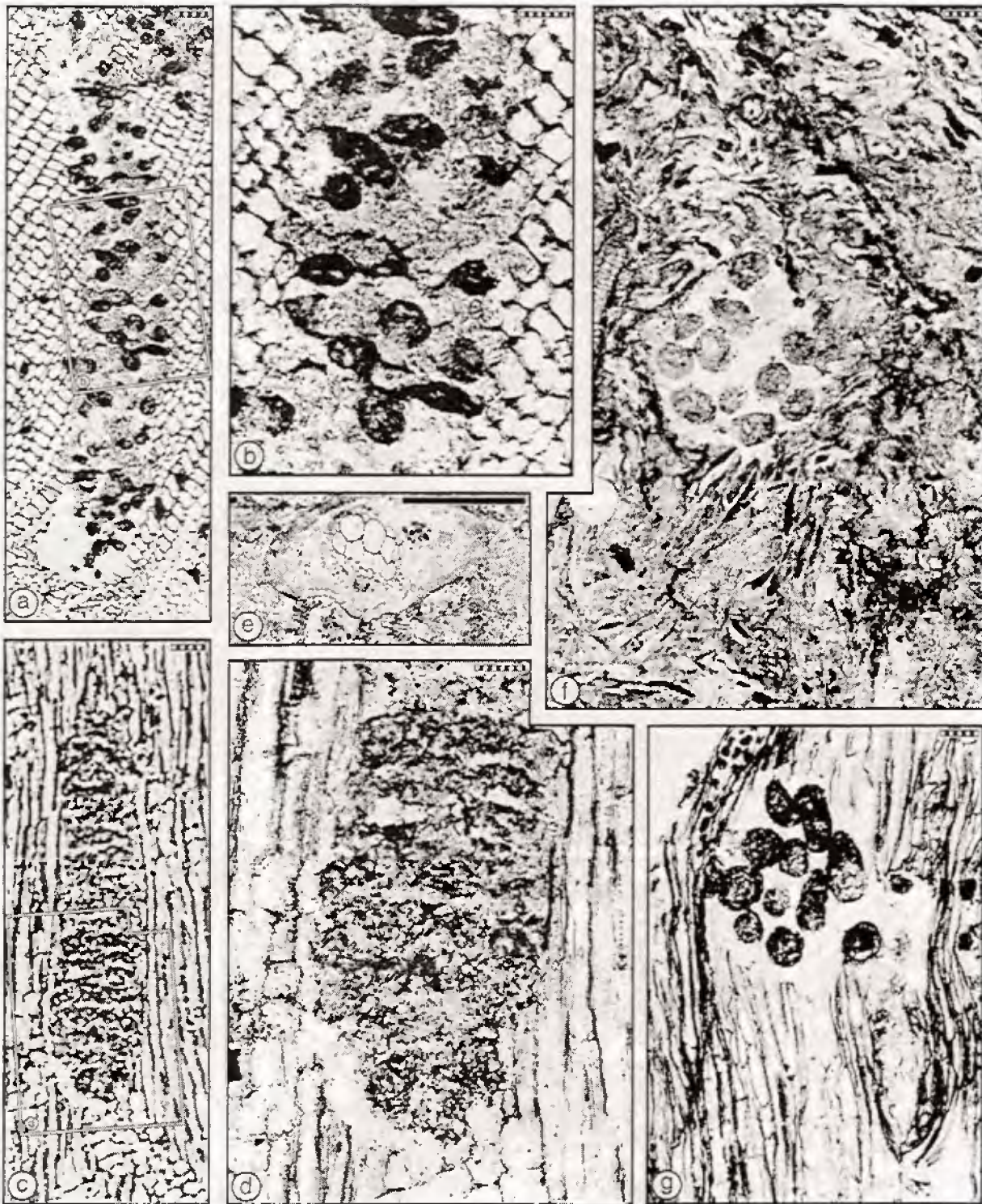


**FIGURE 6**—Tissue types, including foliar parenchyma, secondary xylem, and various macrocoprolitic fragments, of lycosids and cordaites consumed by mites in the Upper Path Fork Coal. Solid scale bars = 1.0 mm; barred scale bars = 0.1 mm. (a,b,d to h) : Radial and tangential sections of leaf cushions from the lycosid *Lepidophloios harcourtii*, shown with mite coprolites. (a) Radial section of an axis bearing five leaf cushions that exhibit excavation of leaf-cushion parenchyma. Slide No. 22,727 (peel 28686-A). (b) Enlargement of gallery region in one of the leaf cushions outlined in (a). (c) Tunnel, indicated by white arrow, containing mite microcoprolites within a macrocoprolite, evidence for coprophagy. Slide No. 22,438 (peel 28938-Btop). (d) Tangential section of axis bearing nine leaf cushions with coprolite-containing galleries. Slide No. 22,433 (peel 28892-Btop). (e) Enlargement of leaf cushion at lower-left in (d), exhibiting three major galleries. (f) Enlargement of leaf cushion at upper-left in (d), exhibiting two galleries connected by a tunnel. (g) Radial section of *Lepidophloios harcourtii* leaf cushions containing galleries of excavated parenchyma. Note empty regions in the distal part of several leaf cushions and replacement by clusters of small, isodiametric coprolites. (h) Enlargement of distal leaf cushion region in (g), showing the distribution of coprolite clusters at the margin of the central gallery. Slide No. 22,726 (peel 28729-Btop). (i) Tunnel containing microcoprolites in secondary xylem of the cordaites root, *Amyelon*. Slide No. 22,428 (peel 28799-Btop).

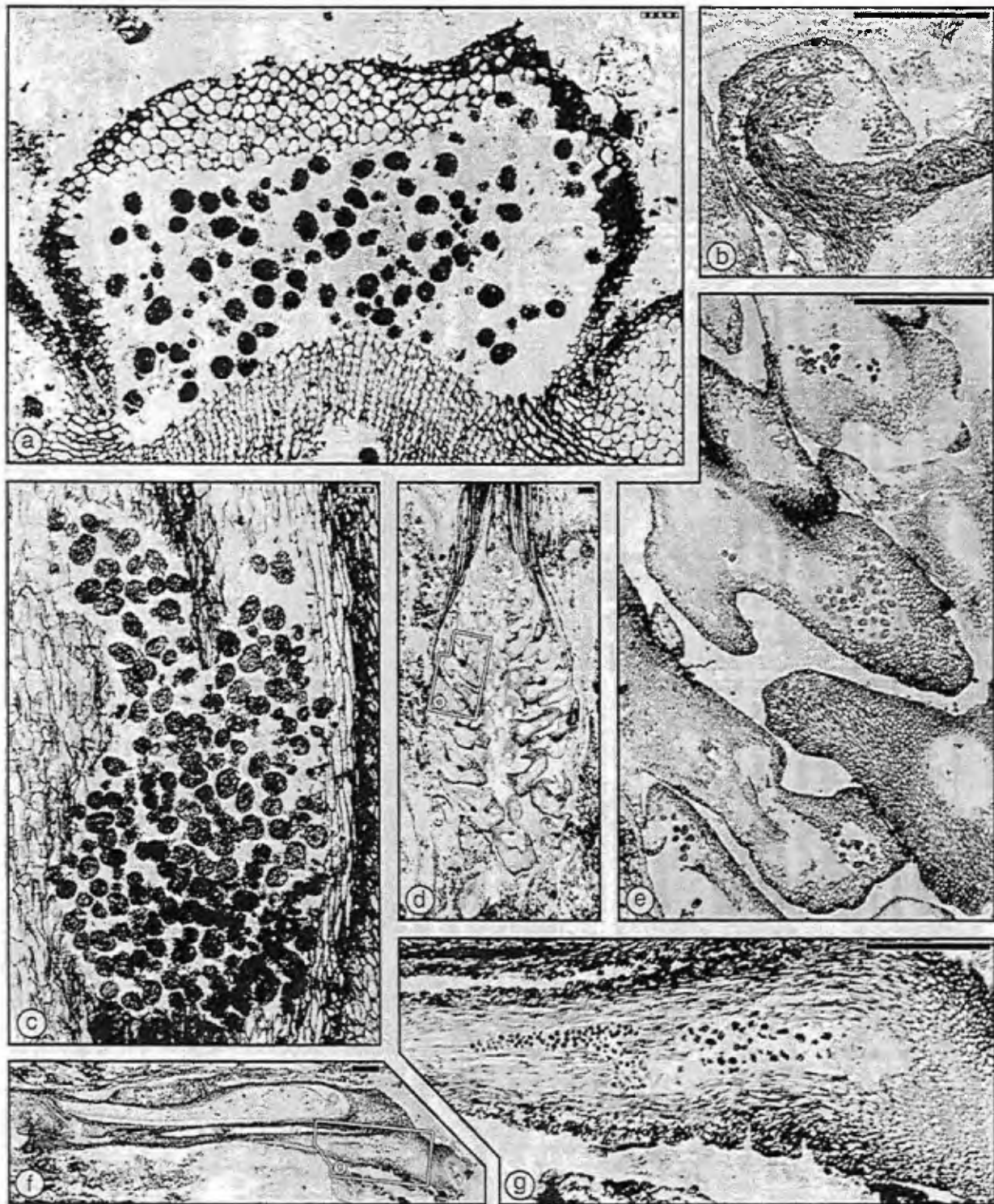


**FIGURE 7**—Mite consumption of wood from the Rock Spring Coal. Solid scale bars = 1.0 mm; barred scale bars = 0.1 mm. (a) Transverse section of two pieces of cordaitean wood, showing juxtaposition of undegraded cordaitean secondary xylem below, and mite-riddled, punky, wood above. Slide No. 22,446 (peel 32479-A). (b) Transverse section of cordaitean wood, showing circular to elliptical cross-sections of mite tunnels in secondary xylem. UIUC slide 22,403, from UIUC peel 32479-Ctop. (c) Cross-sections of mite tunnels from a transverse section of cordaitean wood. Slide No. 22,441 (peel UIUC 32479-Bbot). (d) Transverse to oblique section of three mite tunnels in cordaitean wood, showing variation in coprolite size that indicate instar stages. Slide 22,403 (peel 32479-Ctop). (e) Enlargement of circular tunnel showing the composition, shape, and texture of mite coprolites, probably in cordaitean wood. Slide No. 22,406 (peel 32330-Bbot). (f) Tangential section of probable calamitean secondary xylem, showing parallelism of wood grain and tunnel orientation. Slide No. 22,406 (peel 32330-Bbot).

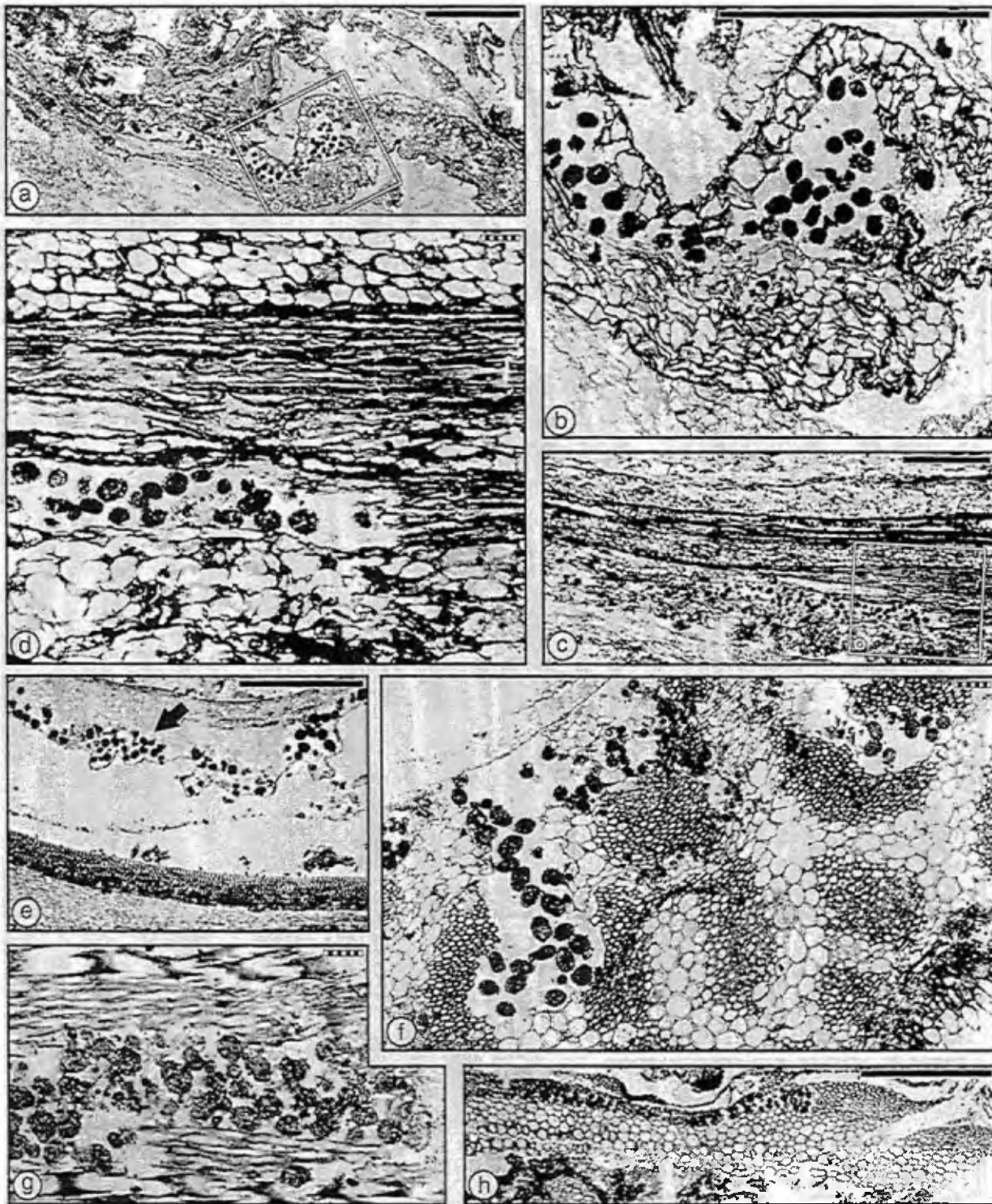




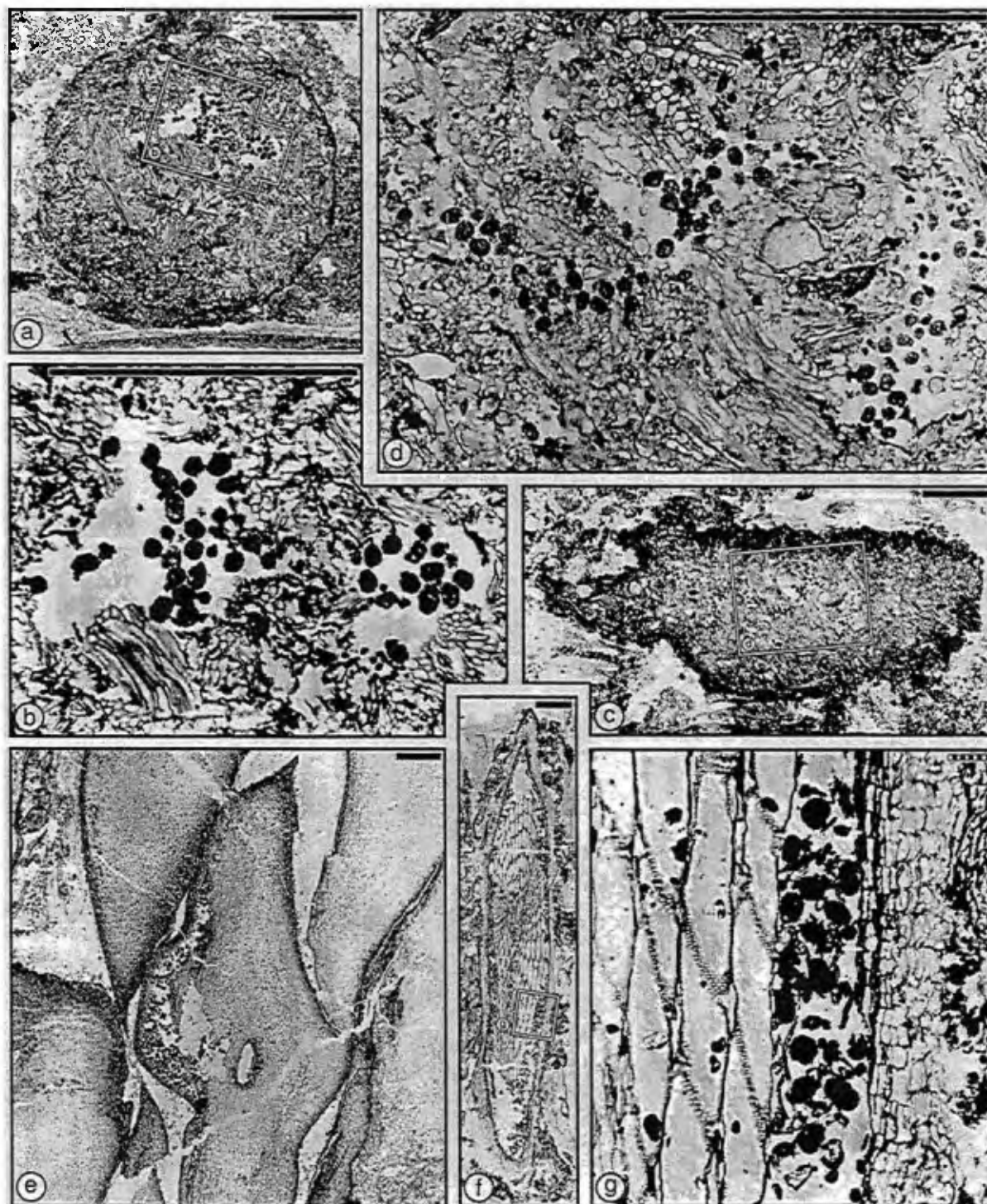
**FIGURE 8**—Mite consumption of tissues in cordaites, ferns, and macrocoprolites in the Rock Spring Coal. Solid scale bars = 1.0 mm; barred scale bars = 0.1 mm. (a) Transverse section of calamitean wood, containing a longitudinal section of a mite tunnel. Frass consists of ellipsoidal fecal pellets and comminuted wood within the tunnel. Slide No. 22,440 (peel 32350-Cbot). (b) Enlargement of region in outlined in (a). (c) Longitudinal section of a calamitean wood showing a longitudinal section of a mite tunnel with a characteristic layered pattern of frass and lack of well-formed coprolites. Slide No. 22,471 (peel 32277-Dtop). (d) Enlargement of region delineated in (c), showing the layered frass. (e) Cross-section of a foliar member of the filicalean fern, *Botryopteris*, displaying in outer ground tissue a tunnel containing a cluster of coprolites. Slide 22,673 (peel 32274-A3-side 2). (f) A cluster of coprolites in a tunnel occurring within a macrocoprolite. Note the heterogeneous tissue fragments with thickened cell walls in the macrocoprolite. Slide No. 22,456 (peel 32277-Dtop). (g) Longitudinal section of a degraded fragment of cordaites wood, containing a cross-section a mite tunnel and a penetrating root at lower right. Slide 22,672 (peel 32274-15A-4top).



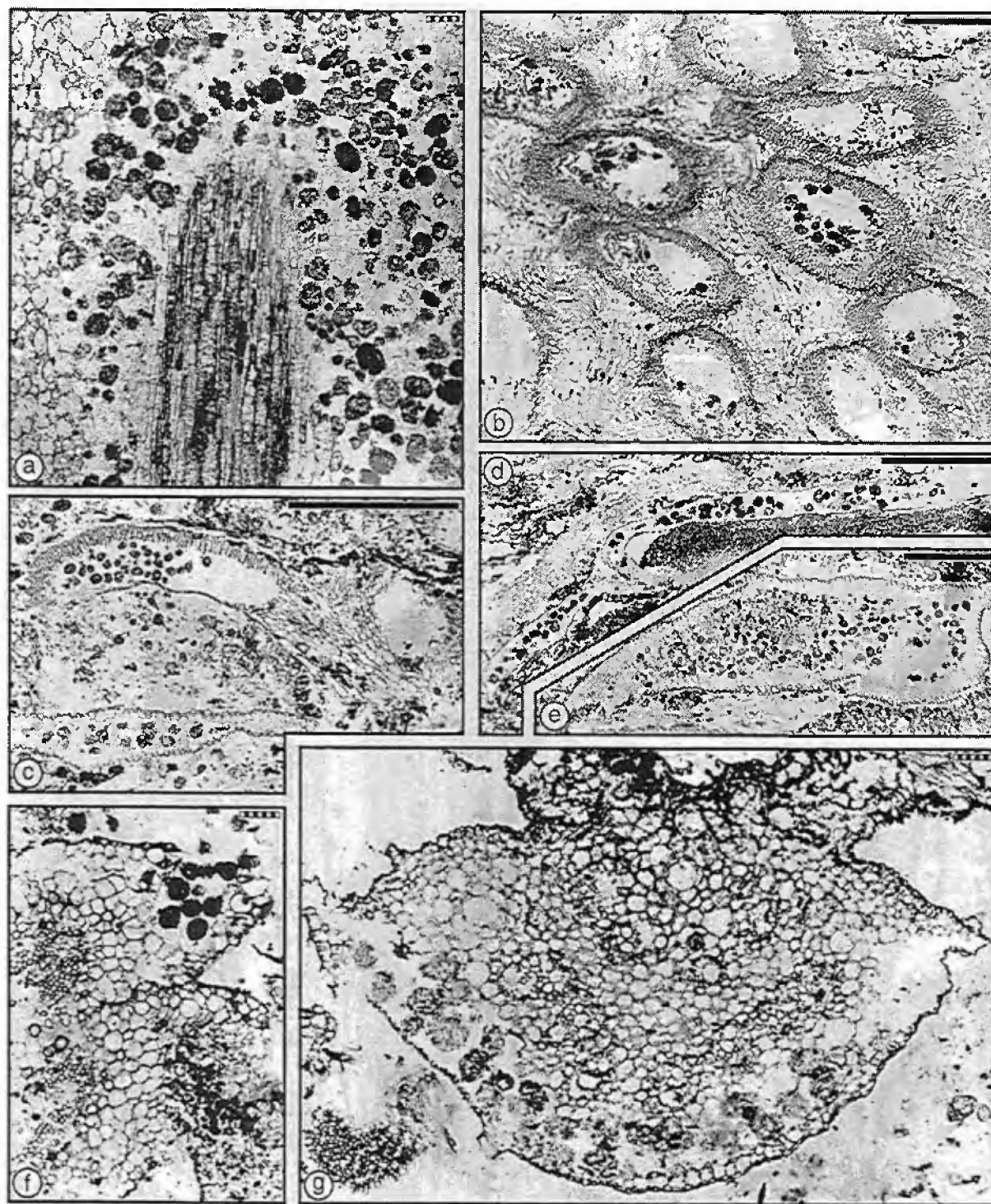
**FIGURE 9**—Mite consumption of various lycopsid taxa and tissue types in the Herrin Coal, from the Illinois Basin. Solid scale bars = 1.0 mm; barred scale bars = 0.1 mm. (a) Transverse section of *Diaphorodendron* stem, showing a leaf cushion with evacuated parenchyma and replacement by mite coprolites. Slide No. 22,537 (peel 38012-Dbot). (b) Part of a *Lepidocarpon* axis, with degraded tissue in the sporophyll. Parenchyma region in the sporophyll now occupied by mite coprolites. Slide No. 22,612 (peel 38070-Etop). (c) Mite excavation of parenchyma in *Lepidophloios hallii* leaf cushion. Slide No. 22,517 (peel 38040-Gbot). (d) Longitudinal section of the lycopsid cone tip, *Lepidocarpon*, showing sporophyll lateral laminae. Note that the basal indurated region of lateral laminae possess galleries filled with mite coprolites. Slide No. 22,524 (peel 38022-Itop). (e) Enlargement of basal regions of lateral laminae outlined in (d). (f) Longitudinal section of a *Lepidocarpon* megasporangial wall and lateral laminae. Note mite tunnels and chamber in the basal attachment region to the cone axis. Slide 22,363 (peel 37112-Itop). (g) Enlargement of region indicated in (f).



**FIGURE 10**—Mite consumption of tissues from seed ferns in the Herrin Coal. All specimens are from Shawneetown, except (h), from Carrier Mills. Solid scale bars = 1.0 mm; barred scale bars = 0.1 mm. (a) Transverse section of *Alethopteris* pinnule. Slide No. 22,520 (peel 38035-Hbot). (b) Enlargement of central pinnule region in (a), showing excavation of palisade and hypodermis layers, and vascular bundles. (c) Oblique longitudinal section of a *Myeloxylon* axis, exhibiting vascular strands, intervacular parenchyma, and resin canals. Note outlined vascular strand partly consumed by mites. Slide No. 22,577 (peel 38043-Lbot). (d) Enlargement of vascular strand in (c) with a coprolite-containing mite tunnel. (e) Sclerotesta of the medullosan seed, *Pachytesta* (at bottom), containing a row of mite coprolites (at top) within the nucellus tissue (arrow). Slide No. 22,416 (peel 37112-Etop). (f) The medullosan frond axis, *Myeloxylon*, showing mite galleries among ground parenchyma and fibrovascular bundles of the frond periphery. Slide No. 22,520 (peel 38035-Hbot). (g) Calamitean wood with a mite tunnel. Slide 22,612 (peel 38070-Etop). (h) Mite tunnel in outer sclerenchyma of a *Stipitopteris* tree-fern petiole. Slide No. 22,608 (peel 38078-Ctop).



**FIGURE 11**—Mite consumption of plant tissues from the Herrin (a-e) and Baker (f-g) Coals. All specimens are from Shawneetown, except a and b, which are from Carrier Mills. Solid scale bars = 1.0 mm. (a) Cross-section of a macrocoprolite consisting of digested tissue fragments and two galleries containing mite microcoprolites. UIUC slide 22,354, from UIUC peel 38066-Ctop. (b) Enlargement of galleries indicated in (a). (c) Longitudinal-section of macrocoprolite with pronounced exposure rind, composed of tissue fragments and microcoprolite-bearing tunnels. Slide No. 22,515 (UIUC peel 38030-Ktop). (d) Enlargement of tunneled region indicated in (c). (e) Obliquely transverse section of leaf cushions from the lycopsid *Lepidophloios*, showing an excavated gallery in a leaf cushion at center, and replacement by coprolites along inner region of epidermal tissue. Slide No. 22,730 (UIUC peel 38017-Ktop). (f) and (g): An obliquely transverse section of a stem of *Sphenophyllum*, indicating consumption of tissues between wood and periderm. Slide No. 22,492 (peel 37326-Gbot). (f) Entire stem, showing major tissues. (g) Enlargement of region at central-left, delineated in (f), exhibiting secondary xylem to left, microcoprolites in center, and phellem to right.



**FIGURE 12**—Mite consumption of various plant tissues in fern, sphenopsid, and lycopsid taxa from the Calhoun Coal. Solid scale bars = 1.0 mm; barred scale bars = 0.1 mm. (a) Oblique, longitudinal section of a *Psaronius* root, with the stele in the center surrounded by microcoprolites in the cortex. Slide No. 22,393 (peel UIUC 30679-Bbot). (b) Occurrence of mite coprolites in the inner root mantle lumina of *Psaronius*. Slide No. 22,670 (peel 10765-Cbot). (c) At top, a sphenopsid *Annularia* leaf in which the spongy mesophyll has been evacuated and replaced by a cluster of mite coprolites; note avoidance of palisade mesophyll with thickened cell walls. Fecal pellets occur in *Psaronius* root at bottom. Slide No. 22,667 (peel; 31272-Bbot). (d) Longitudinal section of a *Psaronius* root exhibiting a central tunnel of excavated tissue and replacement by mite coprolites. Slide No. 22,662 (peel 31272-Ctop). (e) Same as (d), but oblique transverse section. Slide No. 22,329 (peel 31024-Btop). (f) Oblique transverse section of *Alethopteris* foliage, exhibiting removal of mesophyll tissue between outer epidermis and inner vascular bundle. Slide No. 22,662 (peel 31272-Ctop). (g) Same as (f), but transverse section of midrib. Slide No. 22,643 (peel 38600-Bbot).

over, the ecologic radiation of new herbivore functional-feeding groups (Labandeira and Phillips, 1996a, 1996b) may have qualitatively altered those detritivore feeding strategies that survived into the Late Pennsylvanian.

## DISCUSSION

Recently, several studies have evaluated plant damage and coprolite contents preserved in peat litter from the earliest known forested ecosystems (summarized in Labandeira and Beall, 1990; DiMichele and Hook, 1992; and Scott et al., 1992). These, and our ongoing studies, have demonstrated that arthropods responsible for many feeding traces can not be identified with taxonomic precision. Only stereotyped or unique interactions can be assigned to the level of an insect taxonomic order or a more encompassing, specific clade of insects (Labandeira and Phillips, 1996a, 1996b). In our assessment of the tissue damage documented in this report, we recognize characters of life history and behavior that allow a more precise identification of the responsible arthropods than previously possible. This evidence supports oribatid mites, particularly the superfamilies Euphthiracaroidae, Phthiracaroidae, Hermannelloidea, Carabodoidea and Liacaroidae, as the arthropod clades responsible for the extensive borings into a diversity of Pennsylvanian plant hosts and plant tissues.

Autecological data such as borings, galls, foliage chew marks, and piercing-and-sucking tracks have now been documented from many Pennsylvanian plants (Labandeira and Beall, 1990; Scott et al., 1992; Labandeira and Phillips, 1996a, 1996b), indicating that previous statements, such as "the analysis of Scott and Taylor (1983) carries coprolite evidence as far as it can go" (Shear and Kukalová-Peck, 1990: 1829), were premature. The identities of plant-interacting arthropods probably will never be known at low taxic levels because most of the Paleozoic arthropod fauna was replaced by modern lineages after the Permo-Triassic extinction (Labandeira and Sepkoski, 1993; Selden, 1993a; Labandeira, 1994). Although Paleozoic trace fossils may suffer from poor taxonomic resolution, the taxic and ecologic data they represent are ontologically separate. The latter are in fact high-resolution data on the geochronological timing of functional-feeding-groups and dietary guilds in Paleozoic ecosystems.

### Oribatid Mites: Fabricators of the Borings

Organisms producing fecal pellets and occurring in stereotyped tunnels within decomposing plants can be determined with greater specificity and confidence than can those organisms excreting larger fecal pellets that occur in isolation within ambient soil litter, without an obvious plant-host association. Because of this greater potential for identification, we have specified five discrete lines of evidence for taxonomic assignment of these coprolites. They are (1) coprolite size, (2) coprolite shape, (3) coprolite surface texture, (4) coprolite contents, and (5) surrounding plant tissue context of the coprolite. When these five criteria are applied to the extensive literature on fecal pellets and tunneling behaviors produced by modern terrestrial annelids and arthropods, several groups are obvious candidates as producers of the coprolites and tunnels de-

scribed in this report. They are oligochaete annelids, insectan microarthropods, immatures of myriapodan and insectan macroarthropods, collembolans, and oribatid mites. Our evidence strongly indicates that oribatid mites were the producers of these distinctive coprolites within plant tissues.

Enchytraeid, lumbricid and other oligochaete annelids are common and numerically abundant constituents in organic rich soils and decomposing litter (Wallwork, 1976a, 1976b). Although oligochaetes consume organic soils rich in plant material, they rarely ingest solely plant detritus. Their fecal pellets occur in the lower F and especially H horizons, consist of a dark and nearly homogenous mixture with scattered mineralic matter, and have surfaces with considerable relief (Kubiena, 1955; Zachariae, 1965; Rusek, 1975; Ponge, 1988). The pellets also are rarely encountered intact, and have a tendency to disaggregate (Jongorius, 1963; Babel, 1968). Oligochaetes have fossil records extending to the Oligocene (Wills, 1993), but are not known to tunnel or otherwise subsist on wood diets (O'Connor, 1967). Similarly, fecal pellets from various externally-feeding insectan microarthropods, such as diplurans, archaeognathans and thysanurans, are not found within plant-host tissues, nor are they composed principally of ingested wood fragments. Additionally, archaeognathans and probably thysanurans have irregularly shaped fecal pellets with ragged edges characterized by projecting fragments (Hartnack, 1943; D.H. Headrick, pers. comm.). Some small adult insects are wood borers (Frost, 1959; Hickin, 1975; Eaton and Hale, 1993), but do not produce fecal pellets in the minuscule size ranges of the coprolites described herein. The smallest adult xylophagous insects—termites, bostrychid and scolytid beetles, and carpenter ants—produce fecal pellets of different shapes and significantly larger sizes than those described from Pennsylvanian plant tissues (Eckstein, 1939; Linsley, 1943; Weiss and Boyd, 1950; Simeone, 1965; Eaton and Hale, 1993).

Subadult instars of myriapods and insects produce fecal pellets that occur in litter and in association with live plant tissues. Some subadult instars of diplopods produce fecal pellets approaching the size range of oribatid mites, although their shape differs significantly by being elongate (often two or more times the diameter), possessing an irregular and bumpy surface, and containing well-defined and often identifiable fragments of plant tissues (Zachariae, 1965; Paulusse and Jeanson, 1977). Although myriapods were present during the Late Paleozoic (Almond, 1985), and although certain species are frequently found in decaying wood (Wallwork, 1976), millipedes are unlikely to have caused any of the traces seen in our study. When feeding as endophages in woody materials, they create relatively large chambers, rather than narrow tunnels. By contrast, many insect subadults—particularly endopterygote larvae of the Coleoptera, Diptera, Lepidoptera, and Hymenoptera—are wood borers and produce copious quantities of fecal pellets containing fragments of wood and other indurated plant tissues (Hickin, 1975; Mamaev, 1977; Crowson, 1981; Eaton and Hale, 1993). However, fecal pellet shapes of endopterygote larvae are fundamentally different than all other wood-boring arthropods: they consist of cylindrical segments of an extruded bolus mass whose ends indicate brittle fracture or other types of

TABLE 3—Published descriptions of modern oribatid mite and Collembolan hexapod fecal pellets.

Taxon	Stage	Pellet size (diameter × length)	Pellet shape	Data source
<b>Oribatid mites</b>				
Ameronothridae	all	45 × 68 μm to 100 × 150 μm 50 × 60 μm	elliptical, spheroidal	Schulte, 1976
Nothridae				
<i>Nothrus biciliatus</i> (Koch)	larva protonymph deutonymph tritonymph adult	27.3 × 40.6 μm 37.1 × 61.6 μm 52.5 × 87.5 μm 70.7 × 113.4 μm 93.8 × 176.4 μm	not mentioned	Saichuae, et al., 1972
Phthiracaridae				
<i>Phthiracarus ferrugineus</i> (Koch)	nymph adult	57 × 85 μm 100 × 160 μm	spheroidal and ovoidal	Riha, 1951 <sup>1</sup>
Phthiracaridae				
<i>Rhysotritia duplicata</i> Grandjean	unknown	140 × 220 μm	spheroidal and	Bal, 1968
<i>Microtritia minima</i> (Berlese)	unknown	7 × 12 μm	ovoidal	Bal, 1968 <sup>2</sup>
<i>Atropacarus striculus</i> (Koch)	unknown	34 × 57 μm to 75 × 100 μm		Bal, 1968 <sup>3</sup>
Oribatida	all	40 × 100 μm in length	?ovoidal	Drift, 1964
Oribatida	all	50 × 90 μm to 120 × 260 μm	not mentioned	Bal, 1970
Oribatida	all	30 to 150 μm	not mentioned	Babel, 1975
Oribatida	all	30 to 50 μm in diameter	ovoidal, spheroidal	Rusek, 1975
Oribatida	??	140 × 200 μm	ovoidal, spheroidal	Rusek, 1984
<b>Collembolan hexapods</b>				
Collembola	all	less than 50 μm	not mentioned	Jongerius, 1963
Collembola	all	50 to 200 μm in diameter	?ovoidal	Drift, 1964
Collembola	all	30 to 90 (>100) μm	spheroidal	Rusek, 1975, 1985
Collembola (probably)	all	30 × 50 μm to 90 × 125 μm	not mentioned	Rusek, 1975
Collembola	all	50 to 180 μm	not mentioned	Babel, 1975; Pawluk, 1985

<sup>1</sup> As *Phthiracarus ligneus* Willmann.<sup>2</sup> As *Rhysotritia minima* (Berlese).<sup>3</sup> As *Steganacarus striculus* (Koch).

breakage. These pellets often have six longitudinal furrows that are a consequence of six longitudinal muscles that contour the passing food bolus in the rectum (Grimstone et al., 1968). Thus the cylindrical fecal pellet shapes of endopterygote larvae are a consequence of continuous or periodic extrusion, and differ from the spheroidal to elliptical shapes in other terrestrial wood borers that result from individual and periodic packaging (Weiss and Boyd, 1950). For these reasons, oligochaete annelids, insectan microarthropods, and the subadult instars of myriapods and insects are excluded as candidates responsible for producing the endophytic coprolites documented in this report.

With regard to collembolans and oribatid mites, there is documentation of microarthropod fecal pellet size and shape in ground litter and peat-rich soils of modern north-temperate forests. Available records, compiled in Table 3, indicate that ovoidal fecal pellets, approximately from 30

× 40 μm to 140 × 200 μm, and spheroidal pellets from 30 to 200 μm in diameter, are common to very abundant in litter and upper soil horizons, and invariably originate from oribatid mites and collembolans. While their fecal pellets almost completely overlap in size, their shape and surface structure differ. Oribatid mite fecal pellets bear relatively smooth surfaces (Tarman, 1968; Červek, 1976) whereas collembolan fecal pellets are variously textured and irregular, with tissue fragments projecting beyond the general surface relief (Zachariae, 1963, 1965; Rusek, 1975). These distinctions of fecal pellet surface relief are related to the peritrophic membrane, present in mites (Woodring and Cook, 1962; Dinsdale, 1975; Evans, 1992), but apparently absent in collembolans, resulting in smoother surfaces of mite pellets. Additionally, differing mechanisms of processing food and perhaps diet in the two microarthropod clades contribute to differences in surface texture. Although there are some taxa in both groups that

exhibit dietary convergence, particularly on microfungi, most detritivorous oribatid mites prefer plant tissues with high cellulose content, including sclerenchyma and wood (Pande and Berthet, 1973). Collembolans consume softer tissues, preferring more digestible substrates such as bacteria, algae, fungi, partly degraded parenchyma, pollen and spores, fecal pellets, and dead animals (MacNamara, 1924; Poole, 1959; Christianson, 1964; Adams and Salmon, 1972; Schulte, 1976; Haq, 1982; Aitchison, 1983; Takeda and Ichimura, 1983). Selectivity is poorly developed in most collembolans (Christianson, 1964; Singh, 1969; Vegter, 1983; but see Shaw, 1988), and there is no indication that any species regularly subsists on wood or a similar cellulosic or lignified tissue.

As major microarthropod decomposers that have been documented in north-temperate ecosystems, oribatid mites physically reduce litter into particulate debris by consumption of a diverse spectrum of plant tissues. This detritivory is accomplished by unique mouthparts and chelicerae that are modified for finely comminuting plant material (Schuster, 1956; Wallwork, 1958; Dinsdale, 1974; Schulte, 1976; Haq, 1982). Adults and subadults in some groups bore through hard plant tissues such as wood, bark, and fibrovascular bundles, whereas those of other groups choose softer parenchymatous tissues in conifer needles (Fig. 4c-e), angiosperm broadleaves (Fig. 4a), roots, and other plant organs (Woodring and Cook, 1962). Thus tissue-boring oribatid mites are subdivided into three dietary types: (i) varied surface litter, mostly leaves that contain spongy parenchyma; (ii) wood (xylophagy), including taxa that commonly bore into leaf petioles, cone scales, or other indurated tissues; and (iii) pre-existing digested plant material found as arthropod fecal pellets (coprophagy). Collembolans, by contrast, lack appropriate mouthpart structure for boring into plant tissue (Goto, 1972). Although a few collembolan species bear mandibular incisors that can be used to tease apart woody tissues (MacNamara, 1924; Wolter, 1963), none are known to create tunnels or galleries by their feeding actions.

The process and consequences of oribatid mite consumption of plant tissues has been elucidated by studies of the immediate biologic fate of newly-fallen litter and the integration of degraded litter into the upper layers of organic soils (Butcher et al., 1971; Webb 1977; Swift, 1977; Seastedt, 1984). Historically, the best documented examples of litter degradation are (i) tunneling into conifer needles and, to a lesser degree, petioles of angiospermous leaves, (ii) surface skeletonization of angiosperm leaf blades, (iii) tunneling into conifer and dicot wood, and (iv) feeding on macroarthropod fecal pellets containing plant tissues. Two methodological approaches have been used to address the degradation of above-ground plant tissues—autecological studies emphasizing the role that species or individuals have in consuming particular plant tissues, and synecological examinations that evaluate multitrophic feeding strategies of microarthropod communities in litter breakdown.

Oribatid mites gain entrance into conifer needles by producing surface depressions (Harding and Stuttard, 1974) that range from 400  $\mu\text{m}$  in diameter (documented by Hartenstein, 1962c) to holes that are substantially smaller (Figs. 4c-e). These mites subsequently endophagously consume mesophyll parenchyma and softer tissues, leav-

ing vascular bundles and epidermal cuticle intact (Jacot, 1939; Dinsdale, 1974; Babel, 1975; Gourbière et al., 1985, 1987; Lions and Gourbière, 1988, 1989). Once conifer needles have been processed by oribatid mites in the L and upper F layers (Fig. 4b), they essentially consist of elongate sacs containing fecal pellets and occasional fragments of nondigestible tissue (Kubierna, 1955; Jongerius, 1963; Zachariae, 1965; Bal, 1973; Rusek, 1975). These sacs are eventually ruptured by macroarthropod and other invertebrate bioturbators, and become incorporated into deeper, organic-rich soil horizons. By contrast, planar angiosperm leaves are frequently skeletonized by detritivorous insects and particularly ectophagous and endophagous oribatid mites, resulting in intact primary and secondary veins and often a tertiary vein meshwork in more unpalatable species (Zachariae, 1965; Bal, 1968, 1982; Harding and Stuttard, 1974; Rusek, 1975; Kühnelt, 1976).

Tissue consumption of Pennsylvanian foliar parenchyma ranges from lycopsid leaf cushions (Figs. 5; 6a-e; 9a,b), to seed fern pinnules (Figs. 10a-d, 12f,g). These tissues are structurally identical to those documented in mite-consumed parenchyma of modern plants (e.g., Kubierna, 1955; Jongerius, 1963; Kubíková and Rusek, 1976; Babel, 1975; Cohen and Spackman, 1977; Cohen et al., 1989). Presently, there is a broad spectrum of oribatid mite taxa associated generally with consumption of parenchymatous tissues, including constituent subtaxa that commonly ingest leaf litter but are typically associated with wood, such as phthiracaroid, euphthiracaroid, and cepheoid mites (Pande and Berthet, 1973; Niedbala, 1992). Based on differences in fossil tunnel contents and geometry mentioned previously, it is highly likely that a diversity of oribatid mite taxa also were associated with the consumption of diverse foliar material during the Pennsylvanian.

The wood-boring life habit has originated several times within oribatid mites, occurring not only in the omnipresent box mites of the Phthiracaroida and Euphthiracaroida (Michael, 1882; Niedbala, 1992), but also in some members of the Epilohmanniidae (Norton, unpublished), Lohmanniidae (Haq, 1984; Haq and Konikkara, 1988), Hermaniellidae (Michael, 1882; Riha, 1951; Schuster, 1956; Wallwork, 1967), Carabodidae (Michael, 1882; Riha, 1951; Wallwork, 1967), Xenillidae (Michael, 1882; Norton, unpublished), Liacaridae (Gourbière et al., 1985, 1987; Lions and Gourbière, 1988, 1989) and Oribatulidae (Woodring and Cook, 1962; Wallwork, 1967). Virtually all of the textual and photographic documentation of wood boring in modern oribatid mites historically is of phthiracaroids and euphthiracaroids, particularly the prominent genera *Phthiracarus* and *Steganacarus* of the Phthiracaridae and *Oribotritia* of the Oribotritiidae (Jacot, 1936, 1939; Riha, 1951; Schuster, 1956; Wallwork, 1957; Haq, 1982; Ponge, 1988; Soma, 1990). Typically phthiracarid mites construct tunnels that parallel the grain of punky to recently fresh wood (Figs. 4a-e), and are circular in cross-section (Fig. 4e), usually of somewhat larger diameter than body width. Originating from the main tunnel in some species are side branches that are constructed by nymphs and enlarge distally (Wallwork, 1957). Ovoidal fecal pellets are packed within these tunnels, either as occasional clusters occupying the entire tunnel diameter (Riha, 1951; Wallwork, 1957; Drift, 1964), or as a rim of pellets plastered to the tunnel wall (Riha, 1951), or singly on the floor of the tun-



nel. As in fecal pellet size, diameters of tunnels vary with taxic affiliation and instar of the mite burrower; sometimes an entire ontogenetic sequence is preserved in the length of a tunnel of increasing diameter (Figs. 7d; 9g), reflecting a larva→protonymph→deutonymph→tritonymph→adult sequence (Wallwork, 1957). In modern, north-temperate, forested ecosystems, virtually every type of wood or similar indurated tissue is attacked by oribatid mites, including conifer wood (Drift, 1964; André and Voegtlin, 1981; Ponge, 1988), dicotyledonous angiosperm wood (Kubiena, 1955; Bal, 1968; Kubíková and Rusek, 1976), bark (Schuster, 1956; Wallwork, 1957; Harding and Stuttard, 1974), seed testas (Harding and Stuttard, 1974; Harding and Easton, 1984), ovuliferous scales of pine cones (Webb, 1978, 1989), roots (Jacot, 1936; Drift, 1964; Bal, 1968), and even shoreface wrack (Haq, 1984; Haq and Konikkara, 1988). This modern spectrum of tissue and organ types parallels the breadth of mite detritivory in Pennsylvanian coal-swamp forests.

In one of the few studies of a site-specific oribatid mite community occurring within wood, Wallwork (1957) documented the presence of tritrophic interactions. In decaying and moist birch (*Betula*) branches and twigs in surface litter, four species of xylophages that dwelled in the secondary xylem and lenticels were accompanied by six additional species coprophagous on the xylophage fecal pellets, with both groups occasionally consumed by three coexisting, predatory species. The presence of analogous taxa in Baltic amber (Sellnick, 1919, 1931; Appendix 1) indicates that the antiquity of similar communities based on wood-consuming mites extends minimally to the Early Cenozoic.

Increasingly, acarologists and soil biologists have documented the importance of secondary consumption of degraded plant tissue in the form of coprophagy. Although oribatid mite coprophagy occurs among nymphs subsisting on the fecal pellets of older, conspecific instars (Wallwork, 1958, 1967; Haq, 1984), it is most common in species consuming macroarthropod fecal pellets, including those of millipedes and insects (Schuster, 1956; Nicholson, et al., 1966; Bal, 1973). In fact, coprophagy may be a strategy for detritivorous mites that are more likely to encounter degraded, higher plant material and a surface microbial biota on ripened fecal pellets than in surrounding, undigested plant tissues. As a dietary strategy, coprophagy of macroarthropod fecal pellets was well-established during the Pennsylvanian (Figs. 6c; 8f; 11a-d), indicating that secondary detritivory and consumption of microbes may have been a significant source of nutrition.

With the exception of two apparently mycophagous species of Middle Devonian mites (Norton et al., 1988, 1989), the body-fossil record of oribatid mites is unilluminating prior to the Jurassic (Appendix 1). We know that some oribatid mite lineages extend to the Devonian (Norton et al., 1988), but certainly by Jurassic times the known oribatid mite fauna essentially was modern in taxic aspect (Krivolutsky and Druk, 1986). While the body-fossil record of oribatid mites is lacking during the Carboniferous to Triassic, the trace-fossil record of oribatid mites conversely is present during this interval. This window of well-preserved, ecological data provides complementary data on the life habits and behavior that contrasts to our lack of knowledge of oribatid mite morphology or systematics.

From this window of fossil borings in plants, modern patterns of tissue consumption are indistinguishable from that of the Pennsylvanian fossil record of coal-swamp plants. Wood-boring behavior and xylophagous diets already were well developed in woody and other indurated tissues (Figs. 7; 8; 9f,g; 10g), resembling in detail modern oribatid mite borings in gymnospermous and angiospermous wood (Wallwork, 1957; Drift, 1964; figure 15; Kubíková and Rusek, 1976, Rusek, 1985). Pennsylvanian-age plant tissues tunneled by oribatid mites include prominently cordaites (Figs. 6i; 7; 8a-d,f,g), but also consumed was the trunk-surrounding root mantle of psaroniaceus tree ferns (Fig. 12b), leaf cushions, megasporangial wall or lateral laminae of lycopsids (Figs. 5; 6a,b,d-h; 9f,g), and fibrovascular bundles within the trunks of medullosan seed ferns (Figs. 11c,d,f,g). This pulse of trace-fossil data indicates that a diverse spectrum of Pennsylvanian-age plant hosts and tissue types were consumed by oribatid mite detritivores, suggesting that at least modest taxic diversity was already associated with widespread ecologic diversity.

#### Contrasts in Wood Degradation from the Late Paleozoic to the Recent

The pattern that emerges from our study of Pennsylvanian plant borers and an examination of documented tissue-boring activity in the fossil record is provided in Fig. 1. The two obvious temporal concentrations of wood-boring are the Pennsylvanian for oribatid mites, and the later Mesozoic and Cenozoic for insects. These two dense occurrences result from differing geologic and taphonomic settings of oribatid mite and insect trace fossils, as well as the relative recency and, hence, greater likelihood for stratigraphic completeness of the insect trace-fossil record. The pulse of oribatid mite borings found in Carboniferous coal-swamp deposits is associated with large, regional accumulations of coal and permineralized peat; by contrast, later Mesozoic and Cenozoic fossil insect borings occur in plants from varied, mesic habitats, such as flood-plain forest and warm-temperate forest of lake margins. Consequently, in addition to the pull-of-the-recent mentioned above, the later Mesozoic and Cenozoic records of insect borings represent a considerably broader ecological spectrum of plant communities not associated with burial of large volumes of peat in unique habitats, such as those represented in Pennsylvanian deposits. Strengthening the environmental explanation of this pattern is that Paleozoic and post-Paleozoic compression floras are preserved in a similar way (Timell, 1962; Collinson et al., 1994). These and other qualitative distinctions in the oribatid mite and insect records of borers are provided in Table 4.

Dramatic ecologic, taxic, and geologic contrasts are evident between the trace-fossil records of oribatid mite and insect borers. The ecologic breadth of oribatid mite detritivores has survived admirably to the present, consuming virtually all types of dead plant tissue. For the Early and Middle Pennsylvanian, up to the demise of the lycopsid-dominated coal-swamps at the end of the Middle Pennsylvanian (Phillips et al. 1974, Phillips and Peppers, 1984), current evidence supports detritivory as the basis for consumption of not only hard plant tissues such as wood, bark, and sclerenchyma, but also most softer tissues. Dur-

TABLE 4—Comparison of the documented trace-fossil records of oribatid mite and insect borers.

Feature	Trace-fossil record	
	Oribatid mite borers	Insect borers
Plant host taxonomic group:	Lycopsids, calamites, ferns, cordaitan conifers, pteridosperms	Pteridosperms, cycadophytan and coniferan gymnosperms, angiosperms
Tissues attacked:	Dead tissues ranging from fresh (but fungally attacked) to punky; <i>detritivory</i>	Dead tissues; but more importantly live tissues, especially bast (phloem and cambium); <i>detritivory</i> + <i>herbivory</i>
Location of attacked tissues:	At or below ground level	At, below, and especially above ground level
Fossil occurrence:	Coal swamps	Subtropical to temperate mesic forests
Regional taphonomic correlates	Associated with large, regional accumulations of reduced plant material	Not associated with large, regional accumulations of reduced plant material
Geochronology:	Carboniferous	Late Triassic to Recent

ing the Late Pennsylvanian, this widespread mite detritivory was supplemented in the same environments by new types of insect herbivores occurring within the forest canopy not associated with consumption of hard tissues (Labandeira and Phillips, 1996a, 1996b). This transition occurred when psaroniaceae tree ferns achieved ecological dominance in lowland wetlands across much of the Euramerican equatorial belt. These new insect herbivores occupied several functional feeding groups during the Late Pennsylvanian, including external foliage feeding, piercing-and-sucking, galling, and sporangivory (Labandeira and Beall, 1990; Lesnikowska, 1990; Labandeira and Phillips, 1992, 1996a, 1996b; Labandeira et al., 1994), although the intensity of live plant-tissue consumption remains unknown. It is highly likely that tissue-nonspecific oribatid mites that inhabited structural tissues, peat, and litter simply persisted into the Late Pennsylvanian, during which an essentially new, canopy-based, trophic level of primary consumers became established. While taxonomic membership of both trophic groups has changed through time, their basic ecologic roles continue to the present day.

Lineages of insect wood-borers occurring in modern gymnospermous and angiospermous trees are frequently documented as originating during the Triassic. However, this early Mesozoic origin for insects boring into above-ground live and dead tissues in trees may be more apparent than real. The absence of any earlier damage by potential Permian insect-borers may reflect taphonomic bias and absence of searching, particularly since penetrating hard tissues is a life habit that is plesiomorphic in blattoid, isopteran, and many holometabolous insect lineages (Hamilton, 1978; Crowson, 1981; Gepp, 1984; Nalepa, 1994), most which appear as body fossils during the Permian and Triassic. While insect borer damage has not been described from Permian plants, by Late Triassic times evidently there was consumption of live tissue in standing woody plants. The incorporation of above-ground tissues—especially unaltered heartwood and live cambium and phloem—during the Early Mesozoic contributed new standing-crop tissue to animal food webs. For nutritionally unrewarding heartwood, the expansion of wood-boring insects was undoubtedly associated with mycophagy of fungi saprophytic on wood (Hickin, 1975; Crowson, 1981). This addition of new tissues previously exempt to borer consumption further integrated and solidified links between primary producers and arthropod consumers.

## CONCLUSIONS

In this paper we have established major ecological patterns defining the fossil record of oribatid mites and the vascular plants they consumed. We have determined from available fossil occurrences and modern ecological studies some of the ecologic roles that oribatid mites served in the degradation of plant tissues in Paleozoic coal swamps. From both our primary study of Euramerican coal-ball floras and our review of the available literature on fossil arthropod plant-borers, we conclude the following four points.

- (1) There was widespread consumption of diverse vascular plant tissues in Late Carboniferous (Pennsylvanian) Euramerican coal swamps by oribatid mites, producing spheroidal and ovoidal to cylindrical coprolites in the 45  $\mu\text{m}$  to 110  $\mu\text{m}$  size range, and tunnels within plant tissues that independently ranged from 100  $\mu\text{m}$  to 450  $\mu\text{m}$  in diameter.
- (2) The known fossil history of oribatid mites is characterized by both body-fossil and trace-fossil records. The body-fossil record commences during the Middle Devonian but does not resume until the Jurassic, during which essentially modern taxa are encountered. By contrast, the trace-fossil record is largely confined to the Carboniferous, and provides unique insights into feeding ecology of oribatid mites from Euramerican coal-swamp environments. These two fossil records are not only geochronologically complementary, but additionally reveal very different aspects of fossil oribatid mite biology. Notably, the trace-fossil record opens a unique 75-million-year window into oribatid mite life-history and behavior that closed during the Early Permian and did not reopen until the Quaternary.
- (3) In seven major Euramerican coal-ball floras of Pennsylvanian age, virtually all permineralized tissue types from the five dominant plant groups—lycopsids, calamites, ferns, seed ferns, and cordaites—exhibit tunneling by oribatid mites. Hard and often minimally altered postmortem tissues such as bark, fibrovascular bundles, and especially wood were bored, as were softer tissues, including various stem and foliar parenchyma and the gametophytic tissue of large seeds. Evidence for coprophagy of macroarthropod coprolites also is present. While mite-mediated detritivory is the most obvious form of arthropod consump-

tion of plant tissues during the Early and Middle Pennsylvanian, insect herbivory assumes greater documented importance during the Late Pennsylvanian, immediately after a major floral turnover from lycopsid-dominated to tree fern-dominated coal-swamp communities.

- (4) Whereas a qualitatively diverse assemblage of above-ground, canopy-focused herbivores coexisted with mite detritivores during the Late Pennsylvanian, true herbivory of wood and other hard tissues in arborescent plants is not convincingly demonstrated until the Late Triassic. These and subsequent herbivore culprits were insect lineages feeding on cambium and phloem, and increasingly included mycophagy in the heartwood of gymnospermous trees and later of woody angiosperms. Meanwhile, the trace-fossil record of oribatid mite detritivory is absent for this time interval. Modern studies of litter decomposition in north-temperate forests indicate that their ground-level and below-ground trophic web of Pennsylvanian detritivory has persisted to the present.

#### ACKNOWLEDGMENTS

This work would not have been possible without the efforts of many colleagues who have retrieved, processed and curated the coal ball collection at the University of Illinois for the past 35 years. Finnegan Marsh deftly drafted Fig. 1 and produced the layout for Figs. 2 to 12. We appreciate the commentary of W.A. DiMichele who reviewed an earlier draft of this manuscript. We acknowledge David Grimaldi of the Entomology Department at the American Museum of Natural History, Randi Hansen of the Institute of Ecology at the University of Georgia, David Headrick of the Department of Entomology at the University of California, and Francis Hueber of the Paleobiology Department at the National Museum of Natural History for providing comments from unpublished data. Some of this work was done while CCL was at the University of Illinois at Urbana-Champaign as a postdoctoral fellow. Financial support was provided by Scholarly Studies fund 1233S40F of the Smithsonian Institution. This is contribution no. 41 from the Evolution of Terrestrial Ecosystems consortium at the National Museum of Natural History.

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ACCEPTED SEPTEMBER 23, 1996



## APPENDIX 1

## Register of oribatid mite body-fossils.

Taxon	Family	Deposit	Endopha- gous taxon?	References
DEVONIAN				
Givetian				
<i>Devonacarus sellnicki</i> Norton 1988	Devonacaridae	Panther Mtn. Fm., Gil- boa	no	Norton et al., 1988, 1989
<i>Protochthonus gilboa</i> Norton 1988	Protochthoniidae	Panther Mtn. Fm., Gil- boa	no	Norton et al., 1988, 1989
JURASSIC				
Sinemurian				
<i>Hydrozetes</i> sp.	Hydrozetidae	Pankarp Fm.	possibly	Sivbed & Walwork, 1978; Krivolutsky & Druk, 1986
Tithonian				
<i>Achipteria</i> (?) <i>obscura</i> Krivolutsky 1976	Achipteridae	Burea Basin	no	Krivolutsky & Krassilov, 1977; Krivolutsky et al., 1990
<i>Cultoribula jurassica</i> Krivolutsky 1976	Astegistidae	Burea Basin	no	Krivolutsky & Krassilov, 1977; Krivolutsky et al., 1990
<i>Juracarus serratus</i> Krivolutsky 1976	Trhypochthoniidae	Burea Basin	no	Krivolutsky & Krassilov, 1977; Krivolutsky et al., 1990
<i>Jureremus foveolatus</i> Krivolutsky 1976	Cymbaeremaeidae	Burea Basin	no	Krivolutsky & Krassilov, 1977; Krivolutsky et al., 1990
<i>Palaeochthonius brasilovi</i> Krivolutsky 1976	Trhypochthoniidae	Burea Basin	no	Krivolutsky & Krassilov, 1977; Krivolutsky et al., 1990
CRETACEOUS				
Santonian				
<i>Eocamisia sukatshevae</i> Bulanava-Zachvatina 1974	Camisiidae	Taimyr amber	no	Zherikin & Sukacheva, 1973; Bulanava-Zachvatina, 1974; Keil- bach, 1982
<i>Rasnitsynella punctulata</i> Krivolutsky 1976	Plateremaeidae	Taimyr amber	no	Zherikin & Sukacheva, 1973; Bulanava-Zachvatina, 1974; Kri- volutsky & Ryabinin, 1976
Campanian				
Genus and species unidentified	Gymnodamaeidae	Manitoban amber	no	Ewing, 1937; McAlpine & Martin, 1969; Krivolutsky & Druk, 1986
Genus and species unidentified	Oribatulidae	Manitoban amber	possibly	Ewing, 1937; McAlpine & Martin, 1969; Krivolutsky & Druk, 1986
TERTIARY				
Danian				
<i>Sachalinella zherichini</i> Ryabinin 1976	Oribatulidae	Sakalin amber	possibly	Krivolutsky & Ryabinin, 1976; Krivolutsky & Druk, 1986
Thanetian				
<i>Hydrozetes</i> sp.	Hydrozetidae	Paskapoo Fm.	possibly	Baker & Wighton, 1984
Priabonian				
<i>Atropacarus multipunctatum</i> (Sellnick 1919)	Phtthacaridae	Baltic amber	yes	Sellnick, 1919; Keilbach, 1982; Krivolutsky et al., 1990; Niedba- la, 1992
<i>Autogneta longilamellatum</i> (Michael 1885)	Autognetidae	Baltic amber	no	Michael, 1885; Krivolutsky et al., 1990
<i>Brachychthonius</i> sp.	Brachychthoniidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Caleremaeus gleso</i> Sellnick 1931	Caleremaeidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Camisia segnis</i> (Hermann 1804)	Camisiidae	Baltic amber	no	Karsch, 1884; Sellnick, 1919, 1931 sub <i>Nothrus horridus</i> fr. <i>Camisia horridus</i> fr. <i>fossilis</i> ; Colloff 1993
<i>Carabodes coriaceus</i> Koch 1836	Carabodidae	Baltic amber	yes	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Carabodes dissonus</i> Sellnick 1931	Carabodidae	Baltic amber	yes	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Carabodes gerberi</i> Sellnick 1931	Carabodidae	Baltic amber	yes	Michael & George, 1879; Keilbach, 1982; Sellnick, 1931; Krivo- lutsky et al., 1990
<i>Carabodes labyrinthicus</i> (Michael 1879)	Carabodidae	Baltic amber	yes	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Cepheus implicatus</i> (Sellnick 1919)	Cepheidae	Baltic amber	possibly	Sellnick, 1919, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Ceratoppia bipilis</i> (Hermann 1804)	Peloppiidae	Baltic amber	no	Sellnick, 1919; Keilbach, 1982; Krivolutsky & Druk, 1986
<i>Chamobates difficilis</i> Sellnick 1931	Chamobatidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Cultoribula lauta</i> Sellnick 1931	Astegistidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982
<i>Cultoribula superba</i> Sellnick 1931	Astegistidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982
" <i>Cymbaeremaeus</i> " <i>acuminatus</i> Sellnick 1931	Cymbaeremaeidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Damaeus</i> (?) <i>genadensis</i> Sellnick 1931	Damaeidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Selden, 1993a
<i>Embolacarus pergatus</i> Sellnick 1919	unassigned	Baltic amber	no	Sellnick, 1919; Krivolutsky et al., 1990
<i>Eporibatula pellucida</i> Sellnick 1931	Oribatulidae	Baltic amber	yes	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Eremaeus oblongus</i> Koch 1836	Eremaeidae	Baltic amber	no	Sellnick, 1919; Keilbach, 1982; Krivolutsky et al., 1990
<i>Eupelops punctulatus</i> (Sellnick 1931)	Phenopelopidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990; Selden, 1993a

## APPENDIX 1. Continued.

Taxon	Family	Deposit	Endopha- gous taxon?	References
<i>Galumna clavata</i> Sellnick 1931	Galumnatidae	Baltic amber	possibly	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Galumna diversa</i> Sellnick 1931	Galumnatidae	Baltic amber	possibly	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Gradydorsum asper</i> Sellnick 1919	Eremaeidae	Baltic amber	no	Sellnick, 1919; Keilbach, 1982; Krivolutsky et al., 1990
<i>Gymnodamaeus sepotisus</i> Sellnick 1919	Gymnodamaeidae	Baltic amber	no	Sellnick, 1919; Keilbach, 1982; Krivolutsky et al., 1990
<i>Hermannella concamerata</i> Sellnick 1919	Hermannelliidae	Baltic amber	yes	Sellnick, 1919; Keilbach, 1982; Krivolutsky et al., 1990
<i>Hermannella tuberculata</i> Sellnick 1919	Hermannelliidae	Baltic amber	yes	Sellnick, 1919; Keilbach, 1982; Krivolutsky et al., 1990
<i>Licneremaeus fritschii</i> Sellnick 1931	Licneremaeidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Liebetadia similiformis</i> Sellnick 1931	Oribatulidae	Baltic amber	possibly	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Liodes quadriscutatus</i> (Sellnick 1919)	Liodesidae	Baltic amber	no	Sellnick, 1919; Keilbach, 1982; Krivolutsky et al., 1990
<i>Lucoppia</i> (?) <i>simplex</i> Sellnick 1931	Oribatulidae	Baltic amber	possibly	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Melanozetes federatus</i> Sellnick 1931	Ceratozetidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Melanozetes mollicornis</i> (Koch 1840)	Ceratozetidae	Baltic amber	na	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Micreremus reticulatus</i> Sellnick 1931	Micreremidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982
<i>Micreremus strobiculatus</i> Sellnick 1931	Micreremidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Neoribates orussicus</i> Sellnick 1931	Parakalumnatidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
" <i>Notaspis</i> " sp.	Achipteriidae	Baltic amber	no	Sellnick, 1919; Keilbach, 1982
<i>Nothrus illautus</i> Sellnick 1919	Nothridae	Baltic amber	no	Sellnick, 1919; Keilbach, 1982; Krivolutsky et al., 1990; Selden, 1993a
" <i>Nothrus</i> " <i>kuhli</i> Karsch 1884	Nothridae	Baltic amber	no	Karsch, 1884; Keilbach, 1982
" <i>Nothrus</i> " <i>punctulum</i> Karsch 1884	Nothridae	Baltic amber	no	Karsch, 1884; Keilbach, 1982
<i>Odontocephus</i> (?) sp.	Carabodidae	Baltic amber	yes	Sellnick, 1931; Keilbach, 1982; Selden, 1993a
<i>Oppia angustum</i> (Sellnick 1931)	Oppiidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Oppia curvicornis</i> (Sellnick 1919)	Oppiidae	Baltic amber	no	Sellnick, 1919, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Oppia medium</i> (Sellnick 1931)	Oppiidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Oppia sucinum</i> (Sellnick 1931)	Oppiidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Oribatella mirabilis</i> Sellnick 1931	Oribatellidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Oribotritia pyropus</i> (Sellnick 1919)	Oribotritiidae	Baltic amber	yes	Sellnick, 1919, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Oribotritia translucida</i> (Sellnick 1931)	Oribotritiidae	Baltic amber	yes	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Oripoda baltica</i> Sellnick 1931	Oripodidae	Baltic amber	possibly	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Otocephalus niger</i> Sellnick 1931	Otocephidae	Baltic amber	probably	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Otocephalus praesignis</i> Sellnick 1931	Otocephidae	Baltic amber	probably	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Plategeocranus sulcatus</i> (Karsch 1884)	unassigned	Baltic amber	no	Karsch, 1884; Sellnick, 1919; Keilbach, 1982; Krivolutsky & Druk, 1986
<i>Platylodes ensigerus</i> (Sellnick 1919)	Liodesidae	Baltic amber	no	Sellnick, 1919, 1931; Keilbach, 1982; Krivolutsky & Druk, 1986; Krivolutsky et al., 1990
<i>Protoribates langipilis</i> Sellnick 1931	Haplozetidae	Baltic amber	possibly	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Punctoribates</i> sp.	Mycobatidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Scapheremaeus undosus</i> (Sellnick 1919)	Cymbaeremaeidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Scheloribates apertus</i> Sellnick 1931	Schelorbatiidae	Baltic amber	possibly	Sellnick 1919, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Scheloribates arcatus</i> Sellnick 1931	Schelorbatiidae	Baltic amber	possibly	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Scheloribates setatus</i> Sellnick 1931	Schelorbatiidae	Baltic amber	possibly	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Scutoribates perornatus</i> Sellnick 1919	unassigned	Baltic amber	no	Sellnick, 1919; Keilbach, 1982; Krivolutsky & Druk, 1986;
<i>Sphaerozetes convexulus</i> (Koch & Berendt 1854)	Ceratozetidae	Baltic amber	no	Sellnick, 1919; Keilbach, 1982; Krivolutsky & Druk, 1986; Krivolutsky et al., 1990
<i>Sphaerozetes primus</i> Sellnick 1931	Ceratozetidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Strieremaeus cordiformatus</i> Sellnick 1919	Eremaeidae	Baltic amber	no	Sellnick, 1919; Keilbach, 1982
<i>Strieremaeus illibatus</i> Sellnick 1919	Eremaeidae	Baltic amber	no	Sellnick, 1919; Keilbach, 1982; Krivolutsky & Druk, 1986; Krivolutsky et al., 1990
<i>Suctobelbella subtrigona</i> (Oudemans 1900)	Suctobelbidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Oudemans, 1900; Selden, 1993a
<i>Tectocephus similis</i> Sellnick 1931	Tectocephidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Tectocymba rara</i> Sellnick 1919	Cymbaeremaeidae	Baltic amber	no	Sellnick, 1919, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Trhypochthonius corniculatus</i> Sellnick 1931	Trhypochthoniidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Trhypochthonius badiiformis</i> Sellnick 1931	Trhypochthoniidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Unduloribates parvus</i> (Sellnick 1931)	Unduloribatidae	Baltic amber	no	Sellnick, 1931; Keilbach, 1982; Krivolutsky et al., 1990
<i>Xenillus tegocraniformis</i> (Sellnick 1919)	Xenillidae	Baltic amber	yes	Sellnick, 1919; Keilbach, 1982; Krivolutsky et al., 1990
Eocene Unspecified				
<i>Marcovipeda magallanes</i> Pérez	unassigned	Zona Glauconítica Chatian	no	Pérez, 1988
<i>Allonothrus</i> sp.	Trhypochthoniidae	El Mamey Fm., Domini- can amber	no	Norton & Poinar, 1993
<i>Arthrovertex</i> sp.	Scutoverticidae	El Mamey Fm., Domini- can amber	no	Norton & Poinar, 1993

## APPENDIX 1. Continued.

Taxon	Family	Deposit	Endopha- gous taxon?	References
<i>Klapperiches</i> sp.	Carabodidae	El Mamey Fm., Domini- can amber	yes	Norton & Poinar, 1993, sub <i>Carabodes</i> ; R. M. Reeves, pers. comm.
<i>Dolicheremaeus</i> sp.	Otocephidae	El Mamey Fm., Domini- can amber	probably	Norton & Poinar, 1993
<i>Eremaezetes</i> sp.	Eremaezetidae	El Mamey Fm., Domini- can amber	no	Norton & Poinar, 1993
<i>Liodes</i> sp.	Liodidae	El Mamey Fm., Domini- can amber	no	Norton & Poinar, 1993
<i>Mochlozetes</i> sp.	Mochlozetidae	El Mamey Fm., Domini- can amber	no	Norton & Poinar, 1993
? <i>Oppia</i> sp.	Oppiidae	El Mamey Fm., Domini- can amber	no	Norton & Poinar, 1993
<i>Oribotritia</i> sp.	Oribotritidae	El Mamey Fm., Domini- can amber	yes	Norton & Poinar, 1993
<i>Oripoda</i> sp.	Oripodidae	El Mamey Fm., Domini- can amber	possibly	Norton & Poinar, 1993
<i>Sacculobates</i> sp.	Hermanniellidae	El Mamey Fm., Domini- can amber	yes	Norton & Poinar, 1993
<i>Teleliodides</i> sp.	Liodidae	El Mamey Fm., Domini- can amber	no	Norton & Poinar, 1993
genus and species unidentified	Galumnatidae	El Mamey Fm., Domini- can amber	possibly	Norton & Poinar, 1993
Aquitanian				
<i>Arthrovertex hurdi</i> (Woolley 1971)	Scutoverticidae	Simojovel Fm., Chiapas amber	no	Woolley, 1971; Keilbach, 1982; Norton & Poinar, 1993
<i>Benoibates chiapasensis</i> (Woolley 1971)	Oripodidae	Simojovel Fm., Chiapas amber	possibly	Woolley, 1971; Keilbach, 1982; Norton & Poinar, 1993
<i>Liodes brevitarsus</i> (Woolley 1971)	Liodidae	Simojovel Fm., Chiapas amber	no	Woolley, 1971; Keilbach, 1982; Norton & Poinar, 1993
<i>Mochloribatula smithi</i> (Woolley 1971)	Mochlozetidae	Simojovel Fm., Chiapas amber	no	Woolley, 1971; Keilbach, 1982; Norton & Poinar, 1993
<i>Oppia setifer</i> (Woolley 1971)	Oppiidae	Simojovel Fm., Chiapas amber	no	Woolley, 1971; Keilbach, 1982; Norton & Poinar, 1993
<i>Oppia mexicana</i> (Woolley 1971)	Oppiidae	Simojovel Fm., Chiapas amber	no	Woolley, 1971; Keilbach, 1982; Norton & Poinar, 1993
<i>Parapirnodus denaisi</i> (Woolley 1971)	Oripodidae	Simojovel Fm., Chiapas amber	possibly	Woolley, 1971; Keilbach, 1982; Norton & Poinar, 1993
<i>Schelorbates durhami</i> (Woolley 1971)	Schelorbatiidae	Simojovel Fm., Chiapas amber	possibly	Woolley, 1971; Keilbach, 1982; Norton & Poinar, 1993
Serravallian				
<i>Belbites disodolia</i> Pampaloni 1902	Damaeidae	Sicilian amber	no	Pampaloni, 1902; Krivolutsky et al., 1990
<i>Carabodites paesit</i> Pampaloni 1902	Carabodidae	Sicilian amber	yes	Pampaloni, 1902; Krivolutsky et al., 1990
<i>Oppites melitii</i> Pampaloni 1902	Oppiidae	Sicilian amber	no	Pampaloni, 1902; Krivolutsky et al., 1990
Zanclian				
<i>Crotonia ramus</i> (Womersley, 1956)	Crotoniidae	Australian amber; Al- lendale, Victoria	no	Womersley, 1956; Keilbach, 1982
<i>Diapterobates oblongus</i> (L. Koch)	Ceratozetidae		no	Gosolova et al., 1985; Krivolutsky & Druk, 1986
Piacenzian				
<i>Ceratoppia bipilis</i> (Hermann, 1804)	Peloppiidae		no	Gosolova et al., 1985; Krivolutsky & Druk, 1986
<i>Diapterobates notatus</i> (Thorell)	Ceratozetidae		no	Gosolova et al., 1985; Krivolutsky & Druk, 1986
<i>Diapterobates rostralis</i> Shaldybina	Ceratozetidae		no	Gosolova et al., 1985; Krivolutsky & Druk, 1986
<i>Epidamaeus</i> sp.	Damaeidae		no	Gosolova et al., 1985; Krivolutsky & Druk, 1986
<i>Galumna</i> sp.	Galumnatidae		possibly	Gosolova et al., 1985; Krivolutsky & Druk, 1986
<i>Hydrozetes</i> sp.	Hydrozetidae		possibly	Gosolova et al., 1985; Krivolutsky & Druk, 1986
<i>Proteremaeus macleani</i> Behan-Pelletier 1982	Eremaeidae	Beaufort Fm.; Prince Patrick Island, North West Territories	no	Matthews & Ovenden, 1990; Behan-Pelletier & Ryabinin, 1991
<i>Soalbardia rostralis</i> Druk 1982	Ceratozetidae		no	Druk, 1982; Krivolutsky et al., 1990
QUATERNARY				
Numerous occurrences; see Elias (1994)				