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Silurian to Triassic Plant and Hexapod Clades and their Associations: New Data, a Review, and Interpretations

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> Abstract

A preliminary evaluation of hexapod herbivore damage from selected compression and permineralized biotas from the 220 million-year Late Silurian to Late Triassic interval has revealed many previously unknown patterns of hexapod herbivore use of vascular plants as well as detritivore and predator associations. Data was collected from 48 distinctive hexapod herbivore damage types (DTs) from 21 mostly compression biotas, but with special emphasis on the Rhynie Chert (Early Devonian, ~ 408 Ma), Calhoun Coal (Late Pennsylvanian, ~ 303 Ma) and Molteno Formation (Late Triassic, ~ 226 Ma). These data indicate a two-phase herbivore colonization of land; later expansion of hexapod functional feeding groups (FFGs) initially in the Late Pennsylvanian wetland environments of equatorial Euramerica, and subsequently in Early Permian fluvial systems in the rest of Euramerica, Gondwana, and Cathaysia; the devastating end-Permian extinction; and subsequent rebound of those same FFGs during the ensuing Triassic. Modern-aspect herbivore, detritivore, and predator FFGs are present in Late Pennsylvanian canopied forests, and the full spectrum of all terrestrial FFGs are in place during the Late Triassic. Freshwater FFGs are delayed when compared to the terrestrial record, originating during the Permian, experiencing expansion during the Triassic, and reaching modern levels of all major trophic types during the Late Jurassic. A major conclusion is the omnipresence of convergence in FFGs throughout this interval and the spatiotemporally changing and ephemeral nature of plant hosts and their hexapod herbivore taxa.

> Key words

Paleozoic, Triassic, plant-hexapod associations, Hexapoda, Insecta, vascular plants, herbivory, Calhoun Coal, Molteno Formation, coprolites, gut contents.

“What is most notable, however, is the degree of specialization, especially of adaptive structures, that insects had clearly attained by the end of the Paleozoic.”

F.M. Carpenter (1969: 1236)

“Though analyses of insect mouthparts hint that many [insects] fed on living plant material, there is relatively little direct evidence of damage to [Paleozoic] plants...”

W.L. Shear & J. Kukalová-Peck (1990: 1831)

1. Introduction

An important contribution toward understanding the morphological basis of the interrelationships among Paleozoic hexapods and other organisms was F.M. Carpenter’s (1969) article “Adaptations among Paleozoic insects.” In that article there was an ecologically-based evaluation and review of what was then known of the functional repertoire of well-preserved mouthparts, ovipositors, legs and wings from a wide variety of Paleozoic clades, a summary of which is provided in the first quote above. Like the statement provided over 35 years ago by Carpenter (1969), the present contribution concludes that Paleozoic hexapods were as broadly integrated ecologically to their terrestrial world as hexapods of today. This view recently has been reinforced by alternative approaches toward understanding the paleoecology of the hexapod fossil record that were unanticipated during Carpenter's time. An example are the data presented herein, based principally on analyses of Early Devonian, Late Pennsylvanian, Late Triassic and 18 other well preserved deposits that contain exceptional anatomical detail and reveal the intricacy of plant-hexapod and other associations. It now is clear that a Late Paleozoic terrestrial biota consisting overwhelmingly of extinct major clades of both hexapods and vascular plants had almost the full current spectrum of functional feeding groups (FFGs) and dietary guilds. Consistent with this thesis and provided for by considerable fossil evidence is that the ecological roles which were formed by these interacting taxa began about 420 million years ago (Ma), and have remained virtually the same during the past 325 million years (m.y.) in spite of near-complete turnover of the participating hexapod and plant clades (LABANDEIRA 2002a). Terrestrial trophic webs in these Late Paleozoic and Triassic ecosystems were analogous to those of modern ecosystems in terms of the wide variety of herbivory, although the spectrum of hexapod carnivore and detritivore types was more limited. The absence of evidence for parasites and parasitoids probably allowed for fewer and more generalized links among arthropod hosts and their predatory hexapod consumers, making the nonherbivore, consumer portions of trophic webs significantly less connected (LABANDEIRA 2002b).

This perspective has contrasted with an alternative view that emerged during the early 1990's (BEERBOWER et al. 1987; SHEAR 1991), in which Paleozoic terrestrial ecosystems were exclusively to overwhelmingly detritivore driven, with significant herbivory remaining on the trophic sidelines well into the Mesozoic. The second quote above, by SHEAR & KUKALOVÁ-PECK (1990), summarizes this view. Although exceptions, such as Paleozoic piercing-and-sucking, have been acknowledged, the general consensus under this view is that ecologically extensive associations among hexapods and vascular plants did not occur until the ascendancy of the angiosperms. This view of the early history of herbivory sees Paleozoic ecosystems more ecologically analogous to extant nondiverse communities, such as tundra, characterized by extensive detritivory over herbivory (COX 1974; MONTEITH 1986; BEERBOWER et al. 1987), rather than to modern but scaled-down communities, such as temperate forest, where there is a full repertoire of herbivore types. The evidence for this view stems from the apparent absence of arthropod body-fossils during the Late Silurian and Devonian that would reasonably provide functional analogues for herbivores. More important, there is the often cited and presumed absence of herbivory throughout the Paleozoic (also see DIMICHELE & HOOK 1992). However, rather than relying on the overused dictum, "absence of evidence is not evidence of absence", a more fruitful, empirical approach is to provide data from new approaches and better preserved deposits which can address this issue. Carpenter's evidence from external hexapod morphology (his "adaptations"), and more importantly recent extensive documentation of plant-arthropod associations from the Late Silurian to Late Triassic, indicate that the early origin and significant expansion of arthropod (overwhelmingly hexapod) herbivory during the Paleozoic more reliably accounts for the data than the detritivory hypothesis. For the rest of this contribution, I will present results from a few areas of recent research, as well as examination of the existing literature, but concentrate mostly on mechanisms of hexapod feeding and oviposition. The garnered data currently supports a trophically dynamic view of diverse herbivory rather than very limited herbivory in Paleozoic ecosystems (Figs. 1, 2). Thus the herbivory hypothesis is presented as an alternative to a hypothesis based on exclusive to overwhelmingly detritivory. Additionally, to provide a more complete account of trophic-web evolution during the Paleozoic, I will discuss also the presence of detritivory and predation throughout the Paleozoic, across the devastating end-Permian (P-T) extinction, and into a Triassic rebound phase. These patterns also will be put into an appropriate phylogenetic context of major participating vascular plant and hexapod clades.

2. A brief account of Late Silurian to Recent vascular plant-arthropod associations

Some of the earliest macroscopic, terrestrial floras exhibit evidence for live tissue consumption of sporangia and stems by unknown small- to medium sized arthropods. These floras consist of bryophytic to primitive vascular-plant grade taxa that occurred along the paleotropical shoreline of Euramerica from the Late Silurian (Prídolí, 418 Ma) to the Early Devonian (Pragian, 408 Ma) and exhibit evidence for palynivory of spores and sporangia as well as external feeding, piercing-and-sucking, and pith boring of stems (Fig. 2). The best known of these biotas is the Rhynie Chert and associated sites from Scotland. There also is evidence, with unpublished details, of arthropod borings in the massive, wood-like stipes of the columnar basidiomycete fungus, *Prototaxites*, during the Early and Late Devonian (HOTTON et al. 1996; HUEBER 2001). After this first colonization by herbivores representing four major FFGs, as well as extensive detritivory documented elsewhere, there is a prolonged hiatus from the Middle Devonian (late Givetian) to the late Middle Mississippian (late Visean) that encompasses "Romer's Gap", characterized by the virtual absence of terrestrial clade origination (Ward et al. 2006) and a dearth of evidence for herbivory. Occasional discoveries of arthropod body-fossils invariably indicate the presence of detritivores and carnivores during this interval.

Commencing during the end of the Middle Mississippian at around 335 Ma, and continuing into the Middle Pennsylvanian at 305 Ma, there was a second colonization of habitats by arthropod herbivores. This event was characterized by the consumption of live tissues such as leaves, roots, seeds and wood, organs and tissues that had evolved mostly during the Late Devonian (Labandeira 2006), and reached a culmination in the Early Mississippian to early Late Pennsylvanian, at which time all major herbivore FFGs were established, except for leaf mining and surface-fluid feeding (Fig. 1). The best example of this herbivore diversity is from an equatorial wetland community dominated by marattialean tree ferns and to a lesser extent medullosan pteridosperms (seed ferns), and comprising minor taxa of arborescent lycopsids, calamite sphenopsids, cordaites, and diverse, herbaceous ferns (Lesnikowska 1990; Labandeira & Phillips 1996a, 2002; Labandeira 2001). This community, the Calhoun Coal of the Illinois Basin, U.S.A., is a permineralized coal-ball deposit containing three-dimensionally and histologically detailed anatomical preservation of plant tissues as well as a varied spectrum of distinctive hexapod damage types (DTs). However, it is the compression floral record that contains the greatest spatiotemporal evidence for the global evolution of feeding patterns (Fig. 1). Superimposed upon this second, more ecologically extensive, wave of hexapod herbivore colonization (Plumstead 1963; Scott & Taylor 1983; Adami-Rodrigues & Iannuzzi 2001) is documented damage to dead tissues by oribatid mites and unknown pterygote insects as evidenced by the plant damage and dispersed coprolite records. Also present, based on mouthpart structure and hexapod body camouflage, was insectivory by large paleopterous protodonatans. Most of the data for these conclusions originate primarily from peat-dominated, Euramerican wetland communities that occurred astride the Paleotropics during the Middle and Late Pennsylvanian. These ecosystems were replaced by mesic to xeric vegetation recorded from fluvial environments and mineralic substrates, especially during the Pennsylvanian to Permian transition (DiMichele & Hook 1992).

At the Pennsylvanian to Permian boundary interval there emerged a different global cast of plant taxa that represented the dominance of stem- and early crown-group seed plants. For Euramerica, Angara and Cathaysia, these taxa included equisetalean and filicalean pteridophytes, and especially seed plants, such as peltasperms, cycads, lebachian conifers and cordaites. In Gondwana, glossopterids were dominant. Hexapod use of tissues from these plant-host clades was concentrated principally on external foliage feeding (particularly hole and especially margin feeding), piercing-and-sucking, and oviposition. (Although oviposition is not a type of feeding, it has a prominent role in hexapod use of plants throughout the Late Pennsylvanian to the Triassic.) More limited in distribution, both in individual bulk floras and globally, are examples of skeletonization, special external feeding types such as surface abrasion, galling, and seed predation (Fig. 1). The evidence indicates that glossopterid-dominated bulk floras from Gondwana – Paraná Basin of southeastern Brazil, Karoo Basin of South Africa, Ranigang Basin from India, and the Bowen and Sydney Basins of Australia – were modestly attacked by hexapod herbivores (Plumstead 1963; Srivastava 1987; McLoughlin 1994a,b; Holmes 1995; Adami-Rodrigues & Iannuzzi 2001), although the intensity and diversity of herbivory apparently increased proximal to the P-T boundary, at least in South Africa. Of these floras, three from Lower Permian sites in Brazil have been analyzed for the intensity of herbivory as measured by the ratio of hexapod-damaged to total surface area of documented and anthropogenically unbiased leaves (Adami-Rodrigues et al. 2004a,b). These Gondwanan, glossopterid floras are comparable to a Lower Permian flora dominated by gigantopterid peltasperms that has been similarly analyzed from north-central Texas, which exhibits a range of herbivore removal ranging from about 3.1 to 4.4 % of the foliar surface area, representing about a third of the value of herbivore removal in modern tropical forests (Beck & Labandeira 1998). These data collectively suggest that there were distinctive patterns of stereotyped hexapod damage, occasionally elevated levels of herbivory, and considerable targeting of specific tissues and particular plant taxa by a variety of hexapod FFGs during the Pennsylvanian and Permian.

The P-T extinction was devastating for terrestrial biotas (Erwin 2006), as evidenced by the richness of plant-hexapod associations occurring during the Late Permian that was lost in the Early Triassic. Although possibly attributable to a poor earlier Triassic fossil record, the Late Permian level of damage-type diversity was not recovered until the Late Triassic, as evidenced by the stunningly high level of associations preliminarily documented from the Molteno Formation in the Karoo Basin of South Africa, beginning approximately 25 m.y. after the P-T event. As well, the Late Permian level of plant-hexapod (and probably plant-mite) associations is significantly greater than that of the Middle Triassic based on the documented diversity of DTs from localities such as the Grès-á-Voltzia floras reported by Grauvogel-Stamm & Kelber (1996), occurring about 7 m.y. after the P-T event. The more diverse Molteno spectrum of associations is comparable to the range of associations in any Cretaceous or Cenozoic flora. There is a hint of the continuation of many of these associations into the subsequent Late Triassic, such as the Chinle flora from Arizona, U.S.A. However, the comparatively depauperate nature of the plant-hexapod associations of this flora, such as the absence of leaf mining and most galling DTs, may be attributable to anthropogenically biased collections or possibly insufficiently few numbers of specimens examined.

After the rebound and radiation of plant-hexapod and plant-mite associations during the Late Triassic, there is continuity throughout the Mesozoic. However, considerably fewer examples of associations are known for virtually all subsequent Mesozoic floras examined to date (Labandeira 2006). Jurassic and Early Cretaceous floras involve single occurrences rather than associations from bulk floral analyses, examples of which typically are wood borings attributed to a single culprit taxon, but also sparser occurrences of galls, leaf mines and seed predation, and surprisingly few instances of external foliage feeding. This depauperate interval of associations was supplemented by a more diverse array of DTs on emerging angiosperms during the late Early to mid Cretaceous, which eventually equaled, prior to the end-Cretaceous mass extinction, the numbers of DTs occurring in the Molteno (Labandeira et al. 2002a,b).

3. Types of evidence

There are five major categories of evidence from which conclusions have been drawn regarding the associations among fossil plants and hexapods (Labandeira 2002a). These categories result from the after-effects of hexapod consumption of plants as well as the interactive structural elements borne by both plants and hexapods that are involved in or related to feeding and oviposition.

First, and from the plant end of this continuum, are the reproductive and vegetative structures that include phenomena such as inducements for pollination (floral morphology) or deterrents to herbivory (trichomes, epicuticular waxes).

The second category is the most persistent and informative aspect of the plant-hexapod associational record – hexapod mediated plant damage – which is present in both permineralized and compression-impression floras. Plant damage is extremely varied, and includes bite marks, borings, galls, leaf mines, oviposition marks and other hexapod-induced deformations of plant tissue.

Third, and midway through the plant to hexapod spectrum, are dispersed coprolites, abundant particularly in permineralized deposits, that reveal in histological detail particular plant species and organs that were consumed by hexapods. While such coprolites frequently contain anatomically preserved contents that are identifiable to tissue type and source plant, their hexapod producers are much less identifiable taxonomically.

A fourth type of evidence consists of hexapod gut contents, typically deployed as food boluses with identifiable plant constituents, especially spores, prepollen and pollen, but also digestion-resistant vegetative material such as tracheids, cuticle sheets and trichomes. While gut contents preserve with high resolution the identification of especially palynomorphs, unlike dispersed coprolites, such evidence also preserves the identity of the hexapod culprit to the species level (Rasnitsyn & Krassilov 1996a; Krassilov et al. 1997; Afonin 2000).

Finally, external hexapod morphology, particularly mouthparts and ovipositors, often provide sufficient morphology for interpretations regarding the diet, mode of feeding or other host-plant use (Shear & Kukalová-Peck 1990; Labandeira 1990, 1997).

4. Evaluating the evolutionary ecology of fossil plant-hexapod associations

Traditionally, fossil plant-hexapod associations have been evaluated as one or a few interactions that occurred on a very limited number of plant hosts within a selected flora. Such evaluations have ranged in detail from casual mention to robust ichnologic analyses of associations. However, there frequently was little insight into how an ecological spectrum of hexapod-plant associations was representative of the larger plant community or how those ecological associations were placed within an evolutionary context from both plant and hexapod phylogenetic perspectives. For these reasons, an alternative approach recently has been attempted to understand the plant-hexapod associations of entire, well-preserved, diverse, and abundant biotas and their comparisons to other such biotas in time and space. In this context, preliminary evaluations will be made of existing data from the literature as well as several ongoing studies involving permineralized and compression floras in deposits as environmentally varied as Early Devonian hot spring deposits from Scotland (Kevan et al. 1975; Habgood et al. 2004), Late Pennsylvanian peat deposits from the Illinois Basin (Labandeira 2001; Labandeira & Phillips 1996a, 2002), Early Permian, fluvially-dominated redbeds of western Euramerica (Beck & Labandeira 1998; DiMichele et al. 2004; Labandeira & Allen 2007), late Early Permian fluvial and lacustrine strata from the Paraná Basin of southeastern Brazil (Adami-Rodrigues & Iannuzzi 2001; Adami-Rodrigues et al. 2004a,b), and the Late Triassic of the Karoo Basin of South Africa (Anderson & Anderson 1989; Scott et al. 2004; Labandeira & Anderson 2005). It is hoped that in the near future this approach will be augmented to understand more of late Paleozoic and Triassic herbivory.

Any understanding of the evolutionary ecology of plant-hexapod associations, such as those of the Late Silurian to Triassic, requires an approach that takes advantage of the best aspects of the fossil plant and hexapod records. Five necessary prerequisites should be present.

First, as ecologic rather than taxonomic data are being collected, there should be examination of material from the best preserved permineralized and compression deposits that have been collected in an anthropogenically unbiased way. Thus large numbers of museum-numbered specimens should be collected preferably by thousands rather than hundreds of fossil leaves. Particularly important are large slabs with multiple specimens and material sufficiently preserved to have recognizable hexapod damage patterns and identifiable host plants.

Second, deposits should be targeted that are appropriate for a given study design. Favored are deposits from successive, recurring paleoenvironments for vertical studies, or selection from multiple paleocontinents or other geographical regions for horizontal examinations of global scope.

Third, deposits should be investigated that contain as many types of evidence as possible (see Section 3 above). This criterion recognizes that compression deposits are typically restricted in the types of evidence available, depending on whether hexapods are present (with the potential for mouthpart structure and gut contents) and whether coprolite evidence is preserved together with plant damage occurring on the dominant floral elements. Plant damage is the most informative of the five types of evidence because it has the greatest spatiotemporal persistence during the past 420 m.y., especially in fluvial and lacustrine systems.

Fourth, the examined biotas should be well known paleobotanically, and if possible, plant hosts should be assigned to either morphotypes or Linnean binomials. Such assignments should refer to higher taxonomic categories whenever possible, if particular patterns of stereotyped host-plant use by hexapods are to be ascertained. Ideally, as much taxonomic resolution should be mustered for both the plant hosts and hexapod culprits, especially for studies that track associations between such clades for significant intervals of geologic time (Wilf et al. 2000).

Fifth, the gathering of presence-absence ecological data is essential. Semiquantitative presence-absence data can be tracked through time on host-plant lineages or on hexapod herbivore lineages. Alternatively, entire bulk floras can be compared for damage richness and frequency, which is amenable to various resampling techniques for standardizing data with unequal distributions, both for bulk floral and individual plant-taxon comparisons (Wilf et al. 2005). These procedures allow examination of phenomena such as periods of radiation, extinction, iterative evolution of associations during recovery events, and lineage-specific features such as the evolution of component herbivore communities (Labandeira 2002a). For temporal changes in the spectrum of herbivores inhabiting a component community on an evolving plant lineage, turnover, recruitment and extirpation of herbivore taxa can provide valuable data on colonization events at the plant-host species level. Such long-term data is difficult to extract by use of neobiological methods.

5. Plant damage types

As used in this contribution and in previous studies (Wilf & Labandeira 1999; Labandeira et al. 2002a; Wilf et al. 2001, 2005; Labandeira & Allen 2007), a damage type (DT) is a distinctive, well-defined, hexapod or other terrestrial arthropod induced alteration of normal land-plant tissue that is preserved in the fossil or present-day records. Each damage type has an explicit definition and diagnosis; is recorded from one or more plant hosts; has an assigned plant-host specificity that can be generalized, intermediate or specialized; is designated a type specimen associated with a type locality that can be periodically upgraded; and is provided a linked archival photo illustrating the best expression of a particular hexapod consumption pattern of plant tissues and concomitant plant response. Designated damage-type specimens are analogous to a similar system of leaf morphotypes that are used in palaeobotany (e.g., Johnson 2002). Currently there are 134 damage types throughout the compression/impression fossil record that are allocated to seven of the nine functional feeding groups: external foliage feeding, piercing-and-sucking, palynivory, boring, galling, seed predation, leaf mining, surface fluid feeding and nonfeeding oviposition. External foliage feeding is categorized into four functional feeding subgroups: hole feeding, margin feeding, skeletonization and special feeding types. The current spectrum of Paleozoic and Triassic DTs is based on previous documentation from the literature as well as ongoing work by the author and colleagues, and is provided in Fig. 1 from localities in Tab. 1. Much of this work is preliminary, and eventually all DTs will be upgraded to ichnotaxonomic Linnean binomials as each DT becomes systematically well understood in time and space.

An understanding of DTs in an ecological and evolutionary context can be done by tracking DTs through time on particular host plant taxa or lineages. The most persistent and ubiquitous DT for the Late Mississippian to Late Triassic interval is DT12, or cuspate margin feeding (Figs. 3–8), which represents the activities of external foliage feeders on various pinnule or leaf bearing pteridophytes and pteridosperms. Although a variety of major plant clades have been hosts for hexapods producing DT12, the earliest appearances and subsequent overwhelming number of occurrences have been on pteridosperms. This pattern indicates that this damage type (and undoubtedly external foliage feeding in general) was initially launched on pteridosperms rather than co-occurring pteridophytes, and that the comparatively high abundance of this damage type remained within core lyginopterid and especially medullosan pteridosperms (R. Iannuzzi & C. Labandeira unpubl. data; Figs. 5, 7, 8). Other seed-plant lineages were colonized iteratively during the Permian and Triassic (Figs. 3, 4, 6). Although this is a geochronologically coarse-grained example, more finely resolved examples of colonization patterns are possible, such as more host-specific DTs in detailed, intraregional stratigraphic sections (Adami-Rodrigues et al. 2004a,b).

What follows is documentation of the spatiotemporal distribution of major FFGs based on DTs and other data garnered mostly from 21 fossil biotas (Figs. 1, 2). These FFGs are illustrated from the three most informative biotas – the Early Devonian Rhynie Chert (Figs. 9–12), Late Pennsylvanian Calhoun Coal (Figs. 13–24) and Late Triassic Molteno Formation (Figs. 25–42) – and then summarized on host-plant and hexapod-herbivore clades in a phylogenetic context (Figs. 49, 50). The three best geochronologically positioned and most associationally diverse, keystone biotas are briefly introduced.

6. Keystone biotas

The following three deposits constitute a significant portion of the information for plant-hexapod associations during the Late Silurian to Late Triassic interval. The Rhynie Chert, Calhoun Coal and Molteno Formation represent taxonomically diverse floras when compared to other, penecontemporaneous deposits, and in particular have been known for their superb preservation, high abundances of specimens, high level of collection effort, and highly resolved identifications of constituent taxa. These features provide an important context for evaluating the unique richness of plant-arthropod associations in each flora.

6.1. Rhynie Chert

The Rhynie Chert, of the Early Devonian (Pragian, ~ 408 Ma), part of the Dryden Flags Formation of Scotland, has been interpreted as a hot-spring deposit (Trewin 1994) and, together with the nearby and coeval Windyfield Chert, constitutes one of a few earlier Devonian deposits along the littoral periphery of Euramerica. This deposit preserves early bryophytic and vascular plants, microarthropods and fungi within a local, early terrestrial ecosystem context (Trewin 1994; Taylor & Osborn 1996). Constituent land-plant taxa and lineages have been analyzed by Kenrick & Crane (1997) and an equally diverse terrestrial mycota by Taylor & Osborn (1996); arthropods have been discussed by Shear & Selden (2001), with a recent addition by Engel & Grimaldi (2004). Plant-arthropod associations, some of which undoubtedly involve hexapods, were initially broached by Kidston & Lang (1921) and considerably expanded by Kevan et al. (1975; Figs. 10–12) and recently by Habgood et al. (2004), who examined coprolites containing various mixtures of spores and vegetative tissues. Although some of the plant damage, particularly on the axes of the rhyniophyte *Rhynia* and the protracheophyte *Aglaophyton*, initially were considered as physically induced, more extensive and comparative evaluations parsimoniously conclude that a combination of arthropod herbivory and detritivory was present (Labandeira & Phillips 1996a; Labandeira 1998a, 2005b; Habgood et al. 2004). Similar types of associations – external feeding, piercing-and-sucking, boring, and sporivory – also occur in other Early Devonian deposits (Trant & Gensel 1985; Banks & Colthart 1993).

6.2. Calhoun Coal

A very different environment from that of the Rhynie Chert is represented by the Calhoun Coal, of the Late Pennsylvanian (Kasimovian, ~ 303 Ma) Mattoon Formation of the Illinois Basin, U.S.A. The preservation of this deposit consists of three-dimensional permineralization of plant organs embedded within a carbonate matrix that display histological detail at cellular to subcellular levels. This preservation allows recognition of particular tissues from galled and bored organs, as well as the specification of plant inclusions within a coprolite that can be traced to multiple source-plant species, species plant organs, and species plant tissues. The Calhoun Coal originated as a peat-substrated wetland community adjacent an interior epicontinental seaway, and is comprised of the dominant marattialean fern, *Psaronius*, the subdominant medullosan pteridosperm *Medullosa*, and less common calamite sphenopsids, sigillarian lycopods, cordaites, and herbaceous and lianine filicalean ferns (DiMichele & Phillips 1996). Approximately 40 whole-plant species are known (DiMichele & Phillips 1996; C. Labandeira unpubl. data) and consist of a wide variety of growth forms, including tree ferns, pole-like and multistemmed trees, lianas, epiphytes, and herbaceous ferns. There also is evidence for fungal decomposers and parasitism (Agashe & Tilak 1970; Stubblefield et al. 1984). Attributable to the acidic conditions of peat soils from the original wetland habitat, arthropods are not preserved in the Calhoun Coal (Labandeira & Phillips 2002); instead, there is significant, abundant, and well-preserved evidence for a diverse spectrum of plant-hexapod associations in the form of plant damage and coprolites, including external foliage feeding, piercing-and-sucking, pith borings, galling and palynivory (Figs. 13–24). The Calhoun Coal deposit represents the first significant occurrence of a plant community and associated herbivores and detritivores following the widespread turnover in equatorial Euramerica of wetland plant taxa (Fig. 1; Phillips et al. 1974). Equally important, the Calhoun Coal offers one of the few glimpses into the structure of herbivore component communities during the Paleozoic for which there is excellent anatomical detail, particularly for *Psaronius* and *Medullosa* (Lesnikowska 1990; Rössler 2000; Labandeira 2001; C. Labandeira & T.L. Phillips unpubl. data). A component community constitutes all of the trophically dependent organisms on a particular source organism, in this context a plant-host species (Root 1973).

6.3. Molteno Formation

A third keystone biota, representing a very different environment than either the Rhynie Chert or Calhoun Coal, is the Molteno Formation from the Karoo Basin in South Africa, of early Late Triassic age (Carnian, ~ 226 Ma), which represents about 100 sites that may span a 5 to 10 m.y. interval. Molteno preservation consists of compression and occasionally impression deposits, with rare iron-related permineralization, that include plant organs, typically leaves, seeds and stems, as well as hexapods (Riek 1974; Anderson & Anderson 1983, 1989, 2003). The diversity of plant and hexapod taxa is elevated compared to other Mesozoic biotas (Anderson et al. 1996, 1998), with some localities, such as Umkomas, producing as many as ~ 75 distinctive plant-organ taxa. Localities within the Molteno Formation sample several fluvially associated habitats representing 7 major vegetation types. These vegetation types include *Dicroidium* riparian forest, *Sphenobaiera* woodland, *Heidiphyllum* thicket, *Equisetum* marsh, and fern-*Kannaskoppifolia* meadow (Anderson & Anderson 2003). The plant-hexapod and plant-mite associational diversity currently is being investigated (C. Labandeira & J.M. Anderson unpubl. data), but a preliminary survey (Figs. 25–42) indicates that there was rapid expansion of endophytic modes of herbivory, particularly galling, leaf mining and seed predation compared to the Permian of the same basin. In addition, there was external puncturing of internal plant tissues by piercing-and-sucking and ovipositing insects, and a substantial richness of external foliage feeding on most of the available foliage within the various Molteno sites. The Molteno Formation represents a major radiation of leaf mining and other endophytic functional feeding groups approximately 100 m.y. prior to the first appearance of angiosperms in the fossil record (Labandeira & Anderson 2005).

7. Functional Feeding Groups

Throughout deep time, and across all major terrestrial and freshwater environments, hexapods have produced a diverse, but limited number of fundamental ways to access food. These modes or functional feeding groups (FFGs) are, for herbivores in the terrestrial realm, invariably (1) external foliage feeding, (2) piercing-and-sucking, (3) palynivory, (4) boring, (5) galling, (6) seed predation, (7) leaf mining, (8) surface fluid feeding, and (9) nonfeeding oviposition (Labandeira 2002a). For the aquatic realm, they are (10) predation, (11) shredding, (12) filtering, (13) scraping, and (14) gathering (Labandeira 1998a, 2005a). Most of these FFGs were present during the Paleozoic, and all of the basic ways on land that hexapods access microscopic, fungal, animal, and plant food were established by the end of the Triassic. Of this spectrum, the greatest diversity of FFGs are those that involve consumption of terrestrial plants, which has an origin extending from the latest Silurian to Early Devonian, and is based on the most complete evidence, namely the five categories of evidence mentioned above. Evidence for highly modified and distinctive aquatic modes of feeding such as filtering and shredding (Merritt & Cummins 1996) originated during the Triassic, and scraping and gathering during the Jurassic, prominently involving dipteran larvae (Labandeira 2005a). Typically, adult mandibulate types of feeding occurred earlier. Evidence for aquatic modes of feeding is dependent principally on the preservation of immature hexapod stages, and typically is scarce.

7.1. The terrestrial realm

The continental domain, as opposed to the marine domain, is divided into two realms: the terrestrial realm and freshwater aquatic realm. Most evidence for the terrestrial realm in the fossil record comes from the deposition of plant organs, hexapods and other organisms that either fall in situ from ground cover and tree or shrub canopies, or are transported from nearby distances by wind or water (Burnham 1989).

7.1.1. External foliage feeding

The most common and phylogenetically most basal type of feeding for hexapods is external feeding. External feeding probably originated during the Late Silurian by a mandibulate, detritivorous hexapod or stem-group insect that consumed live vegetative tissues from stems and rhizoids of phylogenetically basal land plants that lacked leaves. Only later, during the Late Devonian to Late Mississippian (R. Iannuzzi & C. Labandeira unpubl. data), did other hexapod clades consume the foliage of vascular plants, once leaves evolved. (The consumption of sporangia and spores is considered herein as the diet of a separate FFG, discussed as "Palynivory" below.) The most basal, extant hexapod clade with mandibulate mouthparts are the Archaeognatha, which have an Early to Middle Devonian fossil record and are characterized by monocondylic, "milling" mandibles that are adducted and abducted by relatively weak musculature when compared to the more strongly articulating dicondylic mandibles of the successively more apomorphic zygentoman and pterygote insects. Archaeognathan, and for that matter, zygentoman insects are typically detritivores of degraded material that do not require the energetic acquisition or intense comminution of tough tissues. However, the recent reinterpretation of *Rhyniognatha hirstii* – a pair of comparatively robust, dicondylic, toothed mandibles from the Early Devonian (Pragian) Rhynie Chert of Scotland – as belonging to a neopterous insect (Engel & Grimaldi 2004), may indicate that a more demanding mode of processing food was present considerably earlier than previously thought. Thus it is possible that a more powerful mode of food consumption existed as early as the Early Devonian, consistent with detritivorous, herbivorous, fungivorous or arthropodivorous diets. From what is known of the earliest hexapod body fossils, there were at least three major modes of procuring food from mandibulate mouthparts, as evidenced by the presence of dicondylic mandibles occurring contemporaneously with the earliest archaeognathan milling mandibles and with the more specialized, elongate-mandibulate (and also stylate?) mouthparts of entognathous hexapods. These three generalized and specialized types of hexapod mandibulate mouthparts belie a significant degree of mouthpart diversity for feeding on histologically rather monotonous organs that has been heretofore minimally appreciated. Evidence for the presence of generalized mandibulate feeding comes from the Lower Devonian of Gaspé, Canada, in which lesions occur on the surface tissues of permineralized trimerophyte stems that were quickly capped by thickened wound periderm (Trant & Gensel 1985; Banks & Colthart 1993).

Based on Late Mississippian to Late Pennsylvanian plant-damage patterns, in addition to hexapod mouthpart structure during much of this interval, several neopteran clades were involved in detritivory and herbivory. The earliest evidence for foliar herbivory is on a specimen of the early calamopityacean pteridosperm *Triphyllopteris austrina*, from the Late Mississippian of the Sydney Basin of Australia (R. Iannuzzi & C. Labandeira unpubl. data), in which several cuspate excisions, replete with smaller cuspules separated by veinal stringers, are nearly identical with modern orthopteran leaf damage (Gangwere 1966; Kazikova 1985). This occurrence indicates the presence of external feeding on foliage about 6 m.y. prior to the first appearance of likely folivore body fossils (R. Iannuzzi & C. Labandeira unpubl. data). Significantly, organs of early vascular plants consumed by mandibulate external feeders display a bimodal distribution: a first event during the Late

Silurian to Early Devonian of feeding on stems almost as soon as their initial appearance in the fossil record, and a second event during the Late Mississippian to Middle Pennsylvanian of feeding on foliage that is represented by a considerable lag between the origin of leaves in four vascular plant clades and their earliest consumption (Boyce & Knoll 2004; Ward et al. 2006; R. Iannuzzi & C. Labandeira unpubl. data). Evidence for this second event has been documented from Middle to Late Pennsylvanian compression (Figs. 7, 8) and permineralized (Figs. 17, 18) floras (Amerom 1966; Amerom & Boersma 1971; Labandeira & Beall 1990; Chaloner et al. 1991).

Pennsylvanian to Triassic history of external foliage feeding is characterized by two major trends. First, there was the initial origin and subsequent folivore targeting of pteridosperms, particularly medullosans such as *Macroneuropteris*, *Alethopteris* and *Odontopteris* (Figs. 5, 7, 8), and to a much lesser extent consumption of marattialean tree-fern foliage (*Pecopteris*), all during the Middle Pennsylvanian to Early Permian interval (Scott & Taylor 1983; Trout et al. 2000; Labandeira 2001; Labandeira & Allen 2007; Fig. 18). Second, there was the subsequent expansion of more intense folivory predominantly on a variety of other seed-plant host lineages throughout the Permian of Euramerica, Gondwana and Cathaysia. These additional plant hosts included cycadophytes (*Taeniopteris*; Fig. 3), gigantopterid peltasperms (*Zeilleropteris*, *Cathaysiopteris*, *Gigantopteridium*), callipterid peltasperms (*Autunia*, *Callipteris*), glossopterids (*Glossopteris*, *Gangamopteris*; Figs. 4, 6), unaffiliated taxa (*Comia*), and to a much lesser extent cordaites (*Cordaites*) and noeggeranthians (*Rusellites*) (Plumstead 1963; Srivastava 1987; Holmes 1995; Pant & Srivastava 1995; Beck & Labandeira 1998; Glasspool et al. 2003; Adami-Rodrigues et al. 2004a; Labandeira & Allen 2007). Herbivory on other vascular plants, such as lycopods and calamites (*Calamites*; Fig. 17), was minimally present. This damage was produced by several major groups of insect folivores, especially the Orthoptera, Grylloblattodea (sensu Storozhenko 1998) and "Protoblattodea", and perhaps most "Hypoperlida", Caloneurodea, Miomoptera, and larvae and adults of archostematan Coleoptera.

In contrast to the diversity of external foliage feeding from the Permian, the Early Triassic lacks evidence for external foliage feeding or any other FFG. The Permian spectrum of external foliage feeding is renewed during the Middle Triassic, evidence for which comes principally from the Grès á Voltzia and Lower Keuper deposits of Western Europe (Grauvogel-Stamm & Kelber 1996) on taxa such as the sphenopsid *Schizoneura*, the fern *Neuropteridium*, and the cycadophyte *Taeniopteris*. During the early Late Triassic there is more evidence for a greater spectrum of external foliage feeding from the Chinle Formation of Arizona, particularly on the filicalean fern *Cynepteris*, the pteridosperm *Sphenopteris*, the cycadophyte *Zamites*, and the unassigned gymnosperm *Marcouia* (Ash 1997, 1999). However, it is the Molteno Formation where the radiation of external foliage feeding is most extensively observed on minimally 20 host-plant species representing filicalean ferns and gymnospermous seed plants assigned to peltasperm (Figs. 27, 32), ginkgoalean (Fig. 26), czeskanowskialean, cycadophyte, voltzialean conifer (Fig. 30), bennettitalean, gnetopsid (Figs. 28, 29) and other clades (Fig. 31). Inferred Triassic taxa of folivores were holdovers from the Permian, such as the Orthoptera, Grylloblattodea and "Protoblattodea", and newly emerged clades such as early Phasmatodea, and variously larvae and adults of newly evolved lineages of symphytan Hymenoptera, nematocerous Diptera and archostematan and possibly polyphagan Coleoptera.

7.1.2. Piercing-and-sucking

Piercing-and-sucking, the second type of feeding, is almost as old as external feeding, and has an earliest appearance during the Early Devonian. There are three basic modifications of piercing-and-sucking mouthparts for the Late Silurian to Triassic interval: (1) the entognathous-stylate condition, (2) the ectognathous-stylate palaeodictyopteroid beak with interlocking stylets, and (3) the ectognathous-stylate hemipteroid beak with ensheathed stylets (Labandeira 1997). The earliest of these is the entognathous-stylate condition, in which one or more pairs of unensheathed stylets were housed in an oral chamber for piercing comparatively soft tissues such as plant cortical or even inner medullary tissues, and possibly fungal hyphae and algal filaments. Largely confined to small, litter dwelling hexapods such as Collembola, and by cladistic inference, the Protura, this Early Devonian mouthpart type was a unique construction that survives today in entognathous microarthropods and is convergent with some mouthpart ensembles of fungivorous beetle clades such as the Cerylonidae, Eucinetidae and Corylophidae (Besuchet 1972; Vit 1981; Pakaluk 1987). Evidence for this type of damage has been found in silicified *Psilophyton* and other, unnamed, trimerophyte branchlets from the Lower Devonian (Emsian) of Gaspé in Quebec, Canada (Banks & Colthart 1993). The Canadian specimens contain epidermal point sources from which originate cones of subdermal tissue defined by radiating stylet probes that were enveloped by wound periderm, indicating a piercing-and-sucking microarthropod. Different, less delicate, types of pierced structures occur in the somewhat earlier (Pragian) Rhynie Chert of Scotland (KEVAN et al. 1975; Fig. 12).

Appearing during the latest Mississippian (BRAUCKMANN et al. 1995) was the second type of piercing-and-sucking mouthparts, the paleopterous Palaeodictyopteroidea in which a tongue-and-groove system kept two pairs of styliform or stylate mandibles and maxillary galeae in articulation without any enveloping labial sheath, similar to the mechanism of many modern insect ovipositors (HEMING 2003). This interlocking ensemble enclosed a fifth, needle-like stylet, the hypopharynx and a separate tubular food canal (SHEAR & KUKALOVÁ-PECK 1990). Palaeodictyopteroid beaks had a wide range of aspect ratios, lengths and robustness. At one extreme, particularly in nymphs, were beaks a few millimeters long that had triangular shapes with wide bases adjacent the head capsule underside, and most likely were characterized by both adduction/abduction and protraction/retraction muscular movements. The structure of these beaks indicates that plant surface tissues were consumed to depths typically of a few millimeters by piercing-and-sucking, although more mandibulate modes of consumption, with limited mandibular and maxillary adduction and abduction, also was likely. Direct evidence indicates that certainly spores, and probably prepollen and pollen were consumed (see next section below). At the other end of the spectrum were long, thin and gracile beaks involved in fluid feeding, up to 3.2 cm long for adult *Eugereon bockingi* from the earliest Permian of Germany (MÜLLER 1978). Taxa bearing such prolonged beaks had significant styletal flexibility and capability to target subcortical plant tissues (LABANDEIRA & PHILLIPS 1996b). These more elongate beaks undoubtedly were responsible for Pennsylvanian-age vascular plant damage, such as those found in permineralized coal-ball peats from the Illinois and various Appalachian Basins of North America, that targeted xylem, phloem and subdermal parenchyma particularly in marattialean tree ferns (Fig. 23), "coenopterid" and other herbaceous filicalean ferns, and medullosan pteridosperms (SCOTT & TAYLOR 1983; LABANDEIRA & PHILLIPS 1996a; C. Labandeira unpubl. data). Intermediate-sized beaks, typical for most palaeodictyopteroid taxa (e.g., BRAUCKMANN 1991), were used for feeding on plant tissues, ranging from a few mm to about 1.5 cm in depth and consumed principally xylem and phloem, but also subcortical parenchyma (SCOTT & TAYLOR 1983; LABANDEIRA & PHILLIPS 1996a).

Of the three stylate beak types occurring in the Paleozoic, appearing last, during the Early Permian, was the ectognathous stylate beak of hemipteroid insects. Superficially resembling the palaeodictyopteroid condition, hemipteroid beaks are characterized by labial sheaths that encompass typically two pairs of stylets (BECKER-MIGDISOVA 1960), of which the outer mandibular pair is poorly coupled whereas the inner maxillary pair is frequently coupled or interlocking. These two pairs of stylets enclose two centrally located tubular canals, a smaller diameter salivary canal for extrusion of digestive fluids, and a larger diameter food canal for imbibation of fluidized food. A single, fifth structure, the hypopharynx, is present usually as a short, sclerified and elongate extension of the cibarial pump, occasionally styliform, and contributed to the delivery of fluids involved in liquefying a variety of indurated or otherwise inaccessible subsurface tissues (COBBEN 1978; CHAUDONNERET 1990). Although there were functional convergences between palaeodictyopteroid and hemipteroid beaks, the latter differ from the former by possession of more expansive and powerful suction pumps, more flexible beaks with lengths far exceeding even the gracile beak of *Eugereon* when compared to body length, and having internal head structures such as lever-based or watchspring stylet deployment-and-recoil mechanisms (PESSON 1944; COBBEN 1978; H. WEBER 1968). Both types of stylet deployment mechanisms can protract stylets for targeting of particular cell protoplasts deep within vascular plant tissues. Interestingly, an analogous watchspring stylet protraction device has been described for the ovipositors of Middle Permian sternorrhynchan hemipterans (BECKER-MIGDISOVA 1961), but is not known for any Paleozoic mouthpart type. Rather, archescytinids, pincombeids, coeloscytids and prosboleopseids had variously long but nonrecoilable beaks and modestly sized clypeal pumps (BECKER-MIGDISOVA 1940), indicating the absence of xylem feeding (ZHERIKIN 2002b). Hemipteroid beaks were involved in a wide repertoire of piercing-and-sucking feeding that included herbivory (MAMAY et al. 1988), carnivory, and by the Late Triassic, penetration into deeper plant tissues by scale insects (Fig. 39). In addition there was seed predation (see below; ANDERSON & ANDERSON 2003; Fig. 25) by most likely auchenorrhynchan or heteropteran hemipterans. Palaeodictyopteroid and hemipteroid beaks are one of the better cases of mouthpart structural convergence in the fossil record, although the greater functional capabilities of the hemipteroid condition was likely responsible for the displacement of palaeodictyopteroids in local fossil assemblages throughout the Permian long before they became extinct at the P-T event.

7.1.3. Palynivory

Consumption of spores, prepollen and pollen is the oldest documented type of herbivory among hexapods (Labandeira 2000). For hexapods, there are two basic types of mouthpart construction responsible for palynivory. They are piercing-and-sucking and standard mandibulate mouthparts, both of which have varied modifications for ingesting particulate matter.

Lineages with piercing-and-sucking mouthparts or some distinctive modification thereof can be classified into two major categories. The first, broached in the previous section, are palaeodictyopteroids with short, triangular beaks that had the ability to penetrate shallow tissues through protraction and retraction but retained the ability for limited transverse comminution of food such as pteridophyte spores. Direct evidence for spore-feeding and limited chewing originates from the gut contents of a late Middle Pennsylvanian terrestrial palaeodictyopteroid nymph (Kukalová-Peck 1987), and is indirectly supported by the dispersed coprolite record from an early Late Pennsylvanian coal-ball deposit in the same basin (Labandeira 2001). These occurrences indicate that smaller palaeodictyopteroid beaks were involved in the consumption of particulate plant material, especially entire spores, prepollen and pollen from microsporangiate organs of sphenopsids, marattialean ferns, pteridosperms and cordaites. While this mouthpart type has no modern analog, a second type of mouthpart construction is represented among modern spore- and pollen consuming Thysanoptera, and occurs among an early (likely) paraphyletic thysanopteran assemblage, the Lophioneurina. The Lophioneurina, judging from compression and especially Early Cretaceous amber material from Myanmar (Zherikin 2000), as well as extant Thysanoptera, have highly stereotyped, asymmetrical mouthparts housed in a downwardly directed structure, the mouthcone, and are characterized by two maxillary and a single, left-derived mandibular stylet that emerges terminally from a single orifice (Mickoleit 1963; Vishniakova 1981; Zherikin 2000). Modern palynivorous thrips use the punch-and-suck technique whereby spores or pollen are cracked or punctured first and the protoplasts are subsequently sucked out (Kirk 1984). This feeding type was likely present among Permian and Triassic lophioneurids based on mouthpart structure (Zherikin 2002b), although dietary evidence likely is absent because fluid food consumption disallows preservation as gut contents or in dispersed coprolites. From all that we know of Permian and Triassic hemipteran beaks (Becker-Migdisova 1940; Shcherbakov 1996), it is unlikely that particulate materials such as palynomorphs were consumed; apparently they were strict fluid feeders.

A diversity of mandibulate hexapod lineages occurred during the 220 m.y. latest Silurian to Triassic interval, and was involved in consumption initially of spores, then prepollen, and lastly pollen (Labandeira 2000). Evidence for palynivory comes principally from dispersed coprolites, mouthpart morphology and gut contents, although circumstantial evidence from plant damage also indicates the presence of palynivore feeding, but like dispersed coprolites, with minimal taxonomic specificity of the palynivore.

The most mysterious examples of palynivory are their earliest occurrences in the fossil record, found in latest Silurian and Early Devonian terrestrial deposits associated with the marine littoral of equatorial Euramerica (Edwards et al. 1995; Edwards 1996). Both compression and permineralized deposits from Euramerica contain small, variously shaped, coprolites that once were confused for degraded sporangia and other decomposed plant tissues (Figs. 9, 46). In the Welsh Borderland, the Rhynie Chert, and associated deposits in Aberdeenshire of the United Kingdom, there are nearly monospecific to highly diverse assemblages of distinctive coprolites. These coprolites consist almost exclusively of monospecific or mixed populations of spores from primitive vascular plants or less commonly fungi, as well as other populations enriched in various combinations of spores, vegetative tissues, arthropod chitin, mineral grains, fungal hyphae and amorphous organic matter (Edwards et al. 1995; Habgood et al. 2004). Although some have claimed that the consumption of latest Silurian and Early Devonian plant spores does not represent herbivory (Shear & Selden 2001), the overwhelming evidence based on taxonomic specificity of spores in many coprolites, condition of the spore constituents, the nutritive value of spore protoplasts versus that of the spore walls, as well as the known ecology of extant microarthropodan spore feeders (Ananthakrishnan & James 1983; Leschen & Lawrence 1991; Srivastava et al. 1997), strongly indicate that the consumption of live protoplasts is the most reasonable interpretation. Palynivorous culprits responsible for these coprolites obviously were microarthropods, but further taxonomic circumscription is speculative; possibilities include collembolans, certain mite clades, and the owner of the *Rhyniognatha hirstii* jaws (Kevan et al. 1975; Kethley et al. 1989; Engel & Grimaldi 2004). Virtually nothing is known about this FFG during the rest of the Devonian to Early Mississippian, albeit a very limited record of dispersed coprolites with spores and small sporangia commences during the Middle Mississippian (Rothwell & Scott 1988), and more occurrences are found throughout the Middle and Late Pennsylvanian (Meyen 1984; Kerp 1988; Labandeira 2001).

Better documented examples of palynivory, are gut contents that indicate consumed plant clades and their hexapod culprits, occurring in late Middle Pennsylvanian to late Early Permian deposits. Three principal insect lineages from the late Middle Pennsylvanian come from Mazon Creek compression fossils of the Illinois Basin, and contain gut contents of lycopsid (*Lycospora*) spores in an adult of the orthopteroid Eucaenidae (Scott & Taylor 1983), unidentified pteridophyte spores from a diaphanopterodean nymph probably representing the Prochoropteridae (Kukalová-Peck 1987; Fig. 47), and lycopsid (*Cappasporites*) spores from an unidentified early orthopteroid insect. It is notable that the limited evidence from the Middle Pennsylvanian indicates the consumption of pteridophyte spores rather than seed-plant prepollen or pollen. By contrast, dispersed, permineralized coprolites from the Late Pennsylvanian Calhoun Coal, occurring after a major extinction event in Euramerican coal-swamp forests of the Illinois Basin (Phillips et al. 1974), indicate extensive targeting by unknown hexapod clades of marattialean tree-fern spores (*Convolutispora* and *Apiculatosporis*; Fig. 19), a medullosan pteridosperm (probably *Monoletes*), and especially cordaite (*Florinites*) prepollen (Labandeira 2001; Fig. 20). However, it is not until the late Early Permian (Kungurian), after a 65 m.y. lapse, that additional instances are encountered of hexapods with gut palynomorphs, of which both palynivores and palynomorphs lack taxonomic similarity to those of the Middle Pennsylvanian, attributable to the intervening extinction event.

Early Permian examples originate from the Koshelevka Formation of Chekarda, Russia, and have been extensively documented by A.P. Rasnitsyn, V.A. Krassilov and colleagues in Moscow. Palynivory at Chekarda is known from three major clades – "Hypoperlida", Grylloblattodea and Psocoptera – based on gut contents and mouthpart structure. The early, probably paraphyletic, hemipteroid group Hypoperlida is represented by *Idelopsocus diradiatus* (Hypoperlidae), which consumed striate-protosaccate pollen (*Lunatisporites*) attributed to the conifer *Ulmannia* (Clement-Westerhof 1974), taeniate pollen (*Protohaploxypinus*) attributed to peltasperms but also found in extraregional glossopterids, and other prepollen and pollen (Krassilov & Rasnitsyn 1997). These dietary preferences are also supported by mouthpart structure with characteristic rod-like laciniae in related taxa (Rasnitsyn 1980), such as the Permarrhaphiidae in which *Mycteroptilia armipotens* bore distinctive mandibular and maxillary specializations housed in a prognathous, rostrate head (Novokshonov 1998). Another member of the Hypoperlida is *Synomaloptilia longipennis* (Synomaloptilidae), which consumed principally peltasperm (*Protohaploxypinus*) and other pollen types (Rasnitsyn 1977; Rohdendorf & Rasnitsyn 1980). Of the Grylloblattida, members of three families have revealed pollen lodged in their intestines, representing diets that are consistent with a recognizable mouthpart structure (Rasnitsyn 1977, 1980). The grylloblattidans are *Sojanidelia florea* (Ideliidae), which consumed *Vittatina* (peltasperm), *Protohaploxypinus*, and *Lunatisporites* pollen (Rasnitsyn & Krassilov 1996b); *Tillyardembia antennaeplana* (Tillyardembiidae) ingested principally *Cladaitina* (cordaite) pollen (Afonin 2000); and *Tschekardaenigma pollinivorum* (Tschekardaenigmatidae) consumed pollen resembling *Lunatisporites*, *Protohaploxypinus* and those gnetopsid taxa, although preservation is poor (Rasnitsyn & Krassilov 1996a). The Psocoptera is represented by *Parapsocidium uralicum* (Psociidae), which ate principally *Lunatisporites* and *Protohaploxypinus* pollen, although traces of cordaite *Florinites* and *Potonieisporites* pollen also were present (Krassilov et al. 1999). Novokshonov & Rasnitsyn (2000) have described the mouthparts and discussed the mandibular specializations of another psocopteran species from the same deposit, *Tshekarcephalus bigladipotens* assigned to the Tshekarcephalidae, which evidently had mouthpart and head specializations for palynivory.

Although hexapod fossils with gut contents laden with palynomorphs are not known for the Triassic, other evidence indicates the establishment of palynivore associations between new clades of hexapods and plants following the wake of the P-T mass extinction. Two such associations stand out. The first is a significant hexapod interaction that has been documented for a Late Triassic cycad fructification from Antarctica (Klavins et al. 2005), indicating that palynivory was present for a clade of host plants that significantly resemble the modern family Cycadaceae. Spheroidal coprolites consisting of pollen derived from an enclosing and damaged microsporangium were noted by the authors to resemble those of certain extant polyphagan beetles (Pant & Singh 1990; Chadwick 1993), indicating that modern-aspect cycad-hexapod associations are much older than some have previously suspected (Oberprieler 2004). The second example is the presence of adult xyelid sawflies from the Middle to Late Triassic of South Africa, Australia and Central Asia (Rasnitsyn 1964; Schlüter 2000; Engel 2006; Fig. 48). Jurassic xyelids have been found with cheirolepidiaceous and other gymnosperm pollen in their guts (Krassilov et al. 1997). Notably, extant Xyelidae are obligate consumers of pinaceous pollen (Burdick 1961).

7.1.4. Boring

Hexapod or other arthropod boring into indurated tissues has a unique history. Virtually all occurrences of borings within wood, bark, sclerenchyma, fibrovascular bundles and other hard tissues of plants and fungi require the preservation of three-dimensional axial material of significant diameters, typically by silica or carbonate permineralization. Even pith borings, typically occurring in softer tissues are found almost always as permineralizations. Borings commence with damage to silicified axes of the rhyniophyte *Aglaophyton major* from the Lower Devonian (Pragian) Rhynie Chert of Scotland (Figs. 10, 11). Analogous types of borings occur in the Paleozoic and Triassic record and are characterized by rare occurrences of larger petiole, stem, trunk or root organs where borings would be exposed either on cambial surfaces or in deeper xylary tissues revealed by fracture or mechanical sectioning (Rössler & Fiedler 1996). Given these taphonomic conditions, there are three major types of tissue borings that hexapods and mites produced during the Early Devonian to Late Triassic. They are (1) the exceptional fungivore borings in Devonian *Prototaxites*, (2) the extensive record of detritivore oribatid mite borings from the Early Mississippian through the Triassic and into the Recent; and (3) herbivore-fungivore-detritivore holometabolous insect borings commencing during the Middle Pennsylvanian, and largely re-evolving during the Triassic to Recent.

The first and most enigmatic and earliest of these types of boring are two different kinds (Hotton et al. 1996; C. Labandeira unpubl. data) occurring in lignified tissues of the massive, columnar, polypore-like basidiomycete fungus, *Prototaxites*. Some *Prototaxites* specimens were up to 6 m tall and about 1.3 m in diameter at the base (Hueber 2001). *Prototaxites* had a worldwide distribution, occurred only from the Early Devonian to the end of the period, and occupied coastal fluvial habitats. Borings are only known on Canadian *P. logani* from the Early Devonian (Emsian) of Gaspé, Quebec, and *P. southworthi* from the terminal Devonian (Fammenian) of Kettle Point, Ontario (Arnold 1952; Hotton et al. 1996, 2001). The earlier, Emsian occurrences consist of sheet-like networks of anastamosing borings on outer surfaces underlain by cortical tissues; by contrast, the later Famennian occurrences are tunnels and occasional galleries that histologically penetrate the central medulla. Both types of borings have average tunnel diameters of 0.7 mm, are filled with fungivore coprolites, and display hyphal reaction tissue indicating that the host fungus was alive during attack (Hotton et al. 1996). The culprits remain elusive, although microarthropod fungivory has been documented as dispersed coprolites in Late Silurian to Early Devonian land floras (Sherwood-Pike & Gray 1985; Habgood et al. 2004). Although an order of magnitude too large for oribatid mites, the diameters of these borings are consistent with most holometabolous larval wood-boring clades, but are ~ 55 m.y. too early for such attribution. A myriapod cause for these borings is plausible (Hotton et al. 1996), but would require a major life-habit shift based on current knowledge of Carboniferous to Recent arthropleurids and millipedes.

The second type of boring consists of much smaller, submillimeter sized, oribatid mite tunnels packed with distinctive ellipsoidal to spheroidal microcoprolites. The fossil record of this type of boring consists of silica-, carbonate- and rarely pyrite permineralizations that commence during the Mississippian (Scott 1977; Rex 1986; Tomescu et al. 2001; Hueber & Galtier 2002). Notably, some of these borings exhibit wound response (Dunn et al. 2003), indicating occasional consumption of live tissue. Oribatid mites became the dominant degraders of structural tissues throughout Pennsylvanian equatorial coal swamp habitats, at least in Euramerica (Labandeira et al. 1997). During the Permian and Triassic oribatid mites and perhaps collembolans bored into various structural tissues of a wide variety of plants that are typically preserved in silica-permineralized deposits (Goth & Wilde 1992; Ash 2000; Kellogg & Taylor 2004). The time interval and region with the greatest documentation for oribatid mite borings is the Pennsylvanian of Euramerica, during which there was major degradation of plant structural tissues. Bored tissues included calamite and cordaite wood, marattialean tree-fern root mantle, fern vascular tissue, medullosan fibrovascular bundles and seed sclerotesta, as well as softer tissues such as lycopod leaf cushions, marattialean tree-fern root aerenchyma (Fig. 14), medullosan foliar vascular tissue and trunk ground parenchyma, and even coprophagy of larger hexapod herbivore coprolites (Fig. 15) (Brzyski 1969; Baxendale 1979; Cichan & Taylor 1982; Scott & Taylor 1983; Labandeira et al. 1997). The extensive degradation of plant tissues provided by Paleozoic oribatid mites and possibly collembolans was supplemented by termites during the Mesozoic (Labandeira et al. 1997).

A third and almost as long record as that of the oribatid mites are pterygotan insect borings that occur in a variety of environments. This type of boring began during the Middle Pennsylvanian and continued throughout the Triassic and into the present. The earliest and best preserved borings are highly stereotyped, relatively large pith borings within the root-mantle-bound central stems of marattialean tree-fern trunks (Figs. 13, 22) and the aerenchyma tissues of peat-penetrating ground roots (Fig. 21). The trunk borings occur in at least three carbonate-permineralized coal-ball deposits of late Middle and early Late Pennsylvanian age from the Illinois and Northern Appalachian Basins; all reveal the targeted removal of stem parenchyma and replacement by tunnels and galleries that are filled with distinctive, relatively large, ellipsoidal coprolites (Rothwell & Scott 1983; Labandeira & Phillips 2002; also see Rössler 2000). The size and shape of these ellipsoidal coprolites as well as the pith boring and gallery geometry resemble that of some extant cockroach lineages, such as the Cryptocercidae, that inhabit fresh to decomposing xylic substrates (Nalepa et al. 2001; Labandeira & Phillips 2002). After these occurrences, there is minimal evidence for additional activity of hexapod boring into trunks, stems, or other hardened tissues until the Early Permian (Rössler & Fiedler 1996). In Gondwana, borings have been found in glossopterid or probable glossopterid axes from the Late Permian of the Paraná Basin of Brazil (Bolzon et al. 2004), *Australoxylon* trunks from Beaver Lake of East Antarctica (Weaver et al. 1997), *Dadoxylon* trunks from the Karoo Basin of South Africa (Zavada & Mentis 1992), and *Catenoxylon* wood from India (Pant & Singh 1987) – all of which are characterized by small but hexapod-sized tunnels with or without reaction tissue or fungal alteration. Collectively, these tunnels appear to have been bored through softer late-wood growth and are adjacent to ring boundaries (Zherikin 2002b), indicating climatic seasonality. The most likely culprits are small-sized beetle xylophages, such as the Permocupedidae and Tschekardocoleidae, which are basal coleopteran clades outside the monophyletic group formed by all extant beetles (Beutel 2005). By contrast, in Laurasia and particularly Western Europe and Texas, hexapod borings occur earlier during the Permian, are fewer, and are found typically on unidentified, silicified woody axes (C. Labandeira pers. observ.). No Middle or Late Permian hexapod borings are documented in Euramerica.

After the P-T extinction, it is not until the Middle Triassic that there is renewed and significant evidence for hexapod wood borings (e.g., Minello 1994). Most of the evidence comes from the silicified woods of the Chinle Formation of Arizona, U.S.A., which preserve hexapod cambium and heartwood borings in hosts such as *Araucarioxylon* and two other unaffiliated gymnospermous trees (Walker 1938; Ash & Savidge 2004; Creber & Ash 2004). The Chinle occurrences are reliably attributed to beetles, although more specific assignments by Walker (1938) to buprestid and scolytine curculionid beetles are tenuous, given the known fossil record of their encompassing clades. The Elateriformia, which includes the Buprestidae, has an earliest occurrence during the mid Early Jurassic, and the Cucujiformia, which encompasses the Curculionidae, appeared later at the Early to Middle Jurassic boundary (Ponomarenko 2002; Grimaldi & Engel 2005). The more apomorphic cucujiform clade Phytophaga, which includes the Curculionidae, has a more recent, late Middle Jurassic occurrence (Zhang 2005). Notably, one of the most plesiomorphic extant clades of Cucujiformia is the Lymexylidae, whose larvae are wood borers (Crowson 1981). Other major polyphagan clades that may help to constrain the earliest appearance of the Chinle wood borers are the Staphylinioidea, early representatives of which occur during the early Late Triassic (Fraser et al. 1996), and the Scarabaeoidea, whose first appearance range variously from the Middle Triassic (Ponomarenko 2002) to Late Jurassic (Grimaldi & Engel 2005). In addition, nonpolyphagan beetles of the Ademosynidae (systematic placement unresolved; Beutel 2005) were present during the Late Permian (Ponomarenko 2002). Ademosynid and early polyphagan larvae may have been wood borers, a condition that occurs today sporadically across Polyphaga. In addition to these larger-diameter borings, the presence of narrower-diameter heartwood borings in Middle Triassic *Dadoxylon* wood from the Keuper of Germany (Linck 1949) and from Chinle *Araucarioxylon* (Ash & Savidge 2004) have been said to resemble activities of Anobiidae, and if correctly attributed taxonomically, may be an example of an early polyphagan group of wood borers. However, more likely fabricators for these and some of the other borings are two subgroups of the Archostemata, namely the Cupedidae, present during the Middle Triassic and currently associated with subcortical bark habitats, and the presumably plant-associated Obrieniidae, previously considered erroneously as curculionoid polyphagans (Gratschev & Zherikin 2003). As well, the presence of diverse, stereotyped and beetle-like leaf mining of gymnospermous plants in the Late Triassic (Scott et al. 2004; Labandeira & Anderson 2005; see below) provides circumstantial evidence for the presence of additional endophytic Polyphaga. Although likely life-habits documented for the Polyphaga are based on a documented but confusing record of hexapod feeding damage, the early body-fossil record also remains murky.

7.1.5. Galling

Although curiously ignored in edited volumes discussing the evolutionary biology of galls (Shorthouse & Rohfritsch 1992; Williams 1994; Raman et al. 2005), there is a significant fossil record of hexapod and mite-induced galls that begins in the Early Pennsylvanian (Amerom 1973; Labandeira 2002a). The record of Paleozoic and Triassic galls is characterized by moderately diverse gall morphologies; some of which are described in histological detail. Four major morphologies are known based on three major criteria. These criteria are (1) most importantly, external and often internal structure; (2) specificity for particular plant organs; and (3) occurrence on particular plant-host taxa. Spatiotemporal distributions, given the current level of knowledge, are much less important, but may provide an additional criterion in the future.

The first of the four gall types occurs on a sphenopsid and was initially figured by Weiss (1876). This gall was described as a calamite cone, *Paracalamostachys spadiciformis*, by Thomas (1969), who commented on its unusual enlargement and anomalous structure of apical strobili. This structure was later interpreted by Amerom (1973) as a compound bud gall under the ichnogenus *Acrobulbillites*. There are three *Acrobulbillites* ichnospecies based on various length/width ratios and structural details. These galls occur from mid Early to mid Middle Pennsylvanian strata and probably were induced by a plesiomorphic hemipteroid lineage whose nymphs inhabited inner cone tissues. The ovoidal gall shape and presence of parallel-oriented, imbricate sporophylls or other scale-like structures parallel the morphology of similarly structured Early Permian galls on walchian conifer vegetation such as *Lebachia piniformis* described by Florin (1945) from the lower Rotliegende and similarly aged galls on "*Brachyphyllum*" from north-central Texas from the Waggoner Ranch Formation (Labandeira & Allen 2007). It is likely that these latter, bud galls were induced by a more apomorphic hemipteroid clade, most likely early sternorrhynchan Hemiptera such as the Archescytinidae, Paraknightiidae or Pincombeidae (Becker-Migdisova 1961; Shcherbakov 2000). Zherikin (2002b) mentioned the possibility that early miomopteran nymphs were associated with gymnospermous megasporangiate or microsporangiate organs (see also Rasnitsyn 1980), although evidence is circumstantial. Similar, less compact galls have been described from the early Middle Triassic Upper Buntsandstein Formation of eastern France (Grauvogel-Stamm & Kelber 1996). Collectively, these bud galls resemble the pineapple galls on various pinaceous hosts made by extant host-specific Adelgidae, which are sternorrhynchan hemipterans (Connold 1901).

The second gall type are petiole galls found in *Stipitopteris chasei*, a form genus applied to the rhachises of the whole-plant marattialean tree fern, *Psaronius chasei*, known to occur principally in the Calhoun Coal of the Late Pennsylvanian Mattoon Formation, from the Illinois Basin, U.S.A. (Labandeira & Phillips 1996b). This gall type, unwittingly figured by Stidd (1971) and considered as generalized herbivory by Lesnikowska (1990), occurs only on the inner parenchymatic tissues within the vascular cylinder of 35 carbonate-permineralized specimens of *P. chasei* (Labandeira & Phillips 2002). The distinctive structure of these galls involves the evacuation of inner parenchyma, followed by the production of surrounding nutritive tissue, an anomalous type of secondary parenchyma characterized by inwardly directed tufts of hyperplasic and hypertrophic files of cells (Fig. 24). This nutritive tissue, in turn, displays evidence of consumption from hemispherical bite marks and incorporation of large, indigestible gum-sac cells within the barrel-shaped coprolites lodged within the central cavity. Exit holes with plugs of nutritive tissue are present. However, there is an abundance of angular fragments of galled and ungalled parenchymatic tissue occurring within the central chamber and representing the purchase and mastication of ambient tissue but not its digestion or incorporation into fecal pellets. These tissue-, organ- and taxon specific galls have diameters that range from 0.5 to 1.0 cm and lengths from 2 to 24 cm, and resemble smaller, extant stem galls of certain symphytan hymenopterans such as the Blasticotomidae (Shaw & Bailey 1991). The most reasonable interpretation for a culprit responsible for this gall type is a mandibulate, endophytic, solid-feeding larval insect of the Holometabola. This is based on (1) the presence of solid, barrel-shaped coprolites with ends that are ragged rather than pinched off; (2) the occurrence of entire, distinctive, large gum-sac cells that are packaged within coprolites occurring in the central chamber; (3) presence of angular pieces of parenchymatic tissue that fill the inner cavity and remain undigested; (4) bite marks on tissue lining the chamber that were made by a mandibulate culprit; and (5) the elongate aspect of the petiole gall indicating the targeted consumption of inner parenchyma (Labandeira & Phillips 1996b, 2002).

These five features, documented in histological detail, clearly point to a holometabolous larva and that galling for this lineage probably originated from stem- or pith boring (O. Rohfritsch pers. comm.). Galls produced by this vermiform larva evolutionarily acquired response tissue from the host plant, followed by transformation of response tissue into nutritive tissue that served as a diet for hexapod consumption. The suggestion that a mite caused this gall (Grimaldi & Engel 2005) is highly misinformed because acarine gallers are an order of magnitude smaller; are fluid feeders, and all known mite galls are highly inconsistent with *Stipitopteris* gall structure (e.g., Keifer et al. 1982). This is particularly evident since extant and Triassic mites produce compound galls that have known internal and external structures that consist of miniscule submillimeter chambers (Figs. 36–38), rather than the expansive and comparatively large chambers of *Stipitopteris* petiolar galls. Similarly, another suggestion that these galls were caused by myriapods (Zherikin 2002a), presumably diplopods or perhaps small arthropleurids, is not in accord with known life-history features and external morphology of Pennsylvanian taxa (Shear & Kukalová-Peck 1990). Acceptance of Zherikin's (2002a) attribution would require ad hoc a major life-habit shift from earlier taxa that had ground dwelling, litter inhabiting, detritivorous habits. It is difficult to envision the presence of Pennsylvanian myriapods on *P. chasei* fronds within the canopy and living endophytically with inner petiolar parenchyma. Both suggestions are perhaps based on a reluctance to acknowledge the presence of a plesiomorphic holometabolan lineage within the Late Pennsylvanian, about 5 m.y. prior to the Early Permian expansion of the Holometabola, based on body-fossil evidence.

Other stem galls of the second type have been described from the voltzialean conifers *Aethophyllum stipulare* and *Voltzia* sp. of the early Middle Triassic Upper Buntsandstein Formation of the Grès à Voltzia region in France (Grauvogel-Stamm & Kelber 1996). *Aethophyllum stipulare* is an herbaceous species (Rothwell et al. 2000), with some stems that bore aborted male cones exhibiting conspicuous ovate expansions. These swellings are reminiscent of extant stem and petiole galls induced by coleopteran and lepidopteran larvae on herbaceous angiosperms (Korotyaev et al. 2005; Miller 2005).

The third gall type consists of foliar mite galls which bear distinctive, external and internal morphologies that colonized the Late Triassic Molteno Formation of the Karoo Basin in South Africa (Scott et al. 2004; C. Labandeira unpubl. data). The Molteno mite galls occur principally on one or more laminate pinnules (Fig. 37) and occasionally invade the adjacent frond rhachis in the peltasperm genus *Dicroidium*. Recognizably different gall morphologies occur on three species of *Dicroidium* that are found in Molteno localities across the Karoo Basin. These mite galls comprise a developmental sequence of initial surface tissue deformation in a localized pinnule patch, followed by progressive engulfment of the pinnule by more intensely galled and thickened tissue (Fig. 37), and ending with a characteristically three-dimensionally deformed pinnule with a bulbous, pockmarked, and often lobed surface (Fig. 38). At high magnification more mature galls consist of hundreds of small chambers (Fig. 36), each presumably occupied by a nymphal mite. These galls are anatomically and morphologically similar to extant mite foliar galls by *Eriophyes* described from angiosperm taxa such as alder (*Alnus*; Connold 1901) or walnut (*Juglans*; Keifer et al. 1982). Other, morphologically different foliar galls, with smoother surfaces and a single exit hole but a similar internal structure of more diffuse and cancellous tissue has been described for the gnetopsid *Dechellyia gormani* from the Chinle Formation of Arizona, of similar age.

The fourth type of gall is an hexapod-induced simple gall and is present on a wide variety of leaves from Permian and Triassic compression deposits. An early example, from the Early Permian (Sakmarian) Coprolite Bone Bed locality of north-central Texas, is an ovate midrib expansion on the leaf of *Autunia conferta*, a wide-ranging Euramerican callipterid peltasperm (Labandeira & Allen 2007). Another occurrence is from the late Early Permian of the Raniganj Basin of West Bengal in India, in which the gall features circular prominences on the lamina of a *Glossopteris* species (Banerjee & Bera 1998). From the Late Triassic Molteno Formation, host-specific foliar galls are present on species of *Dicroidium* and the ginkgoopsid genera *Sphenobaiera* and *Dejerysea*, among other seed-plant taxa (C. Labandeira & J.M. Anderson unpubl. data). The occurrences of these and a few other specialist but taxonomically unassigned galls apparently have targeted the foliar tissues of a diverse suite of major seed-plant clades.

7.1.6. Seed predation

There are four major patterns of seed or related predation during the Early Pennsylvanian to Triassic interval. These major patterns and their geochronologic timing represent the independent origin of the seed predation FFG in four major hexapod clades. They are the Ellipura (or possibly mites), palaeodictyopteroids, hemipteroids and early holometabolans. Each of these clades probably is represented by additional and iterative innovations in consuming megagametophytic and embryonic tissues from a wide variety of seed- and other plants that result in the death of an individual.

The first type consists of bored, beveled holes on lycopsid megaspores from the Pennsylvanian, probably caused by microarthropodan predators such as collembolans, proturans or even mites (Labandeira 1998a; Zherikin 2002a). While not seeds, megaspores are large, up to ~ 1 mm in diameter, and represent the nutritional equivalent to a microarthropod what a seed would be to a significantly larger arthropod. Because of the relatively small size of the megaspores and limited volume to sustain a single immature individual until emergence, it is most likely these structures were consumed from the outside.

The second pattern consists of circular holes in large radiospermic medullosan seeds such as species of *Trigonocarpus* from the Early and Middle

Pennsylvanian (Jennings 1974; Scott & Taylor 1983) and platyspermic cordaite seeds of *Samaropsis* sp. Both were probably consumed by palaeodictyopteroid insects. The latter occurrence is better documented and has been attributed to the adult palaeodictyopteran *Uralia maculata*. The example of *Uralia* seed predation on *Samaropsis* was documented from the late Early Permian of Chunya, occurring in the Tunguska Basin of Russia (Sharov 1973; Kukalová-Peck 1992; Rasnitsyn & Novokshonov 1997). Sharov (1973) presented strong evidence for the consumption by *U. maculata* of co-occurring *Samaropsis* seeds, some of which display holes that match the maximum beak diameter and cross-sectional shape of the aforementioned culprit. Zherikin (2002b) indicated that seed predation by palaeodictyopteroids with intermediate sized, more typically constructed beaks may be a plesiomorphic diet for the clade. Occurrences of seed predation are rarely encountered in younger Permian deposits, although cordaite seeds from the Lower Permian of China are known to have small intrusive borings (Hilton et al. 2001, 2002).

A third type of seed predation occurs on Late Triassic seeds from the Molteno Formation of South Africa. Several form-genera of seeds from this deposit have predation scars on their tests. One of these consists of small, circular scars approximately 0.5 mm in diameter in the dispersed seed of *Feruglioa papilioformis*. The other consists of rarer, larger, ellipsoidal to eye-shaped punctures ~ 1.0–2.0 mm long, frequently overlapping, and occurring on the thickest, central region of *Avatia bifurcata* seeds (Anderson & Anderson 2003; Fig. 25). These latter, elongate punctures enclose a region of disrupted texture and are surrounded by the striate ornamentation of the seed integument. The seed punctures are similar to bug damage produced by extant Coreidae on pine seeds (Krugman & Koerber 1969), although earlier Mesozoic heteropterans also may have had similar feeding habits (Zherikin 2002b). Both the smaller circular and larger ellipsoidal punctures are attributed to heteropteran Hemiptera based on the external form of the damage that reflects the cross-sectional shape of the presumed stylate beak.

Lastly, a fourth type of damage consists of three-dimensionally preserved *Peltaspermum turbinatum* seeds that very rarely are evacuated and contain remaining barrel-shaped coprolites (C. Labandeira unpubl. data). This distinctive damage reveals likely mandibulate holometabolan consumption of megagametophytic tissues, analogous in damage type to extant larval Agathiphagidae, a plesiomorphic lepidopteran clade on *Agathis* (Araucariaceae) seeds, or to bruchine Chrysomelidae, an apomorphic coleopteran clade that presently consumes overwhelmingly palm and legume seeds (Morse & Farrell 2005). Seed predation has not been documented for any other major Triassic flora such as the Buntsandstein, Keuper, Grès à Voltzia or Chinle floras.

7.1.7. Leaf mining

There is no definitive evidence for leaf mining during the Paleozoic or Early Triassic. Previous accounts have figured and discussed certain U- or V-shaped structures on medullosan pinnules, particularly *Macroneuropteris scheuchzeri* (Müller 1982; Labandeira & Beall 1990; Trout et al. 2000), a DT that also occurs on Middle to Late Permian glossopterid and Late Triassic peltasperm foliage of South Africa (Fig. 35). This DT is bordered by a thick callus rim that has an angulate or U-shaped origin near the midrib region, and surrounds an inner region of necrotic surface tissues and disorganized but recognized vasculature. Although once attributed to leaf miners (Müller 1982), this damage is best attributed to fungal or bacterial infection of epidermal to mesophyll tissue that has elicited a significant reaction front of callus tissue.

Very different, considerably smaller structures are the serpentine "Gangminen" illustrated by H. and R. Potonié (1893, 1921; also see Müller 1982) on the callipterid peltasperm *Autunia conferta* from the Lower Permian of Germany. Based on their figures, these structures are more consistent with a taphonomic origin in which waterlogged epidermal tissues experienced contraction immediately after deposition and prior to entombment, causing the distinctive wrinkled appearance of the pinnular surface.

Other Late Pennsylvanian and Permian examples of more linear structures embedded within deeper tissues have been noted on a variety of leaves from Euramerica and Gondwana (Paclt 1972; Castro 1997; Beck & Labandeira 1998; Adami-Rodrigues et al. 2004a) However, these occurrences collectively share the absence of features that would constitute evidence for leaf mining. Specifically, leaf mining would require evidence for at least some of the following: an oviposition site; enlargement of the oviposition area either as a blotch or a curvilinear trace; an indication of the evacuation of one or more layers of leaf tissue; successive series of mine width increases; evidence for a particulate or fluidized frass trail; detectible response tissue along the mine margin; tendency for the mine to parallel major architectural impediments in the foliage tissue such as veins; and some indication of a distinctive terminus (Hering 1951). Such a terminus could be an unexpanded or slightly widened trace with a hemispherical end, or an expanded chamber with or without internal frass, or a slit in the epidermal tissue (Hering 1951).

The earliest leaf mines for which most of the above criteria are applicable occur worldwide and almost simultaneously during the late Middle to early Late Triassic in localities from Kyrgyzstan, Australia, and especially South Africa (Tillyard 1922; Rozefelds & Sobbe 1987; Zherikin 2002a; Scott et al. 2004; Labandeira & Anderson 2005). Demonstrable leaf mines from these three localities occur on ovate-elongate, parallel veined, entire margined leaves of the peltasperm *Glossophyllum* sp. (Zherikin 2002a,b) and particularly the voltzialean conifer *Heidiphyllum elongatum* (Rozefelds & Sobbe 1987; Anderson & Anderson 1989; Scott et al. 2004) (Figs. 40, 41). These linear mines developed mostly parallel to the monocot-like venation of lanceolate-linear leaves and featured the consumption of inner, probably mesophyll, tissues by a mandibulate hexapod producing discrete, particulate frass (Fig. 42). While the Kyrgystanian and Australian occurrences are single instances of a leaf miner taxon consuming a plant host, by contrast, plant hosts among numerous localities in South Africa include not only the *H. elongatum* miner (Figs. 40–42), but also seven other plant hosts and three additional leaf-mine DTs representing a major colonization event of fern and especially seed-plant taxa. The probable culprits for these mines probably are polyphagan, cucujiform beetles such as the Pandrexidae, or elateriform beetles related to or confamilial with Buprestidae, or possibly the archostematan Obrieniidae. Alternatively, but less likely, a plesiomorphic lepidopteran lineage could have been responsible for some mine DTs. These occurrences, and particularly the diversity of four mine morphotypes, eight host-plant taxa, and inferred hexapod culprits, indicate that leaf mining originated sometime during the Middle Triassic probably on parallel-veined leaves of gymnospermous seed plants anatomically similar to those of extant *Podocarpus* (Podocarpaceae) and *Agathis* (Araucariaceae). By the early Late Triassic, there was colonization of filicalean fern, cycadalean, ginkgoalean, peltaspermalean and other seed plant taxa possessing architecturally very different foliage types.

7.1.8. Surface fluid feeding

The result of digestion of fluids by fossil hexapods leaves no effects that can be found as evidence in the typical categories of plant damage, coprolites, or gut contents. Because of this lack of usual evidence, inferences for surface fluid feeding are derived principally from an evaluation of mouthpart structure and, to a lesser extent, vegetative and reproductive structures of plants, such as the presence of nectaries, glands and other secretory tissues (Fahn 1979; Chaudonneret 1990). For plants, the presence of secretory structures can have multiple functions, such as physiological regulation of internal water content through guttation, or the presence of secondary chemicals in foliar capitate glands for herbivore deterrence, both of which do not involve lures for hexapod imbibation of fluids. For hexapods, it appears that specialized mouthpart adaptations for surface fluid feeding is primarily confined to holometabolans, particularly adult Antliophora, for which there are varied modes of imbibing fluids as diverse as honeydew, pollination drops, nectar, oils, resins, oozing lymph and blood, sweat and water (Downes & Dahlem 1987; Proctor et al. 1996). Major examples of the primary modes of surface fluid feeding, each with unique mouthpart structures that have been convergently acquired among unrelated clades, are sponging in dipterans and some trichopterans (Graham-Smith 1930; Crichton 1957), siphoning for mecopterans such as Aneuretopsychidae and dipterans such as Nemestrinidae (Rasnitsyn & Kozlov 1991; Mostovski 1998; Labandeira 1998b, 2005a), lapping and squeezing for hymenopteran Apoidea (Winston 1979), as well as the concealed nectar extraction apparatus of most parasitoid wasps (Jervis 1998; Jervis & Vilhelmsen 2000). Based on these data it appears that surface fluid feeding for holometabolan adults, as well as leaf mining for holometabolan larvae, are post-Paleozoic developments.

There is limited mouthpart evidence for Permian occurrences of surface fluid feeding, even though adult fluid-feeding antliophoran lineages from the Triassic and Jurassic lack convincing, Permian occurrences (Grimaldi et al. 2005). Instead, examples include archaic hemipteroids such as Middle Pennsylvanian *Eucaenus* and younger Permian Caloneurodea, which combine biting mandibles, elongate, pick-like maxillary laciniae, and a prominently domed clypeal pump that collectively suggest fluid feeding (Shear & Kukalová-Peck 1990). Additionally, the Early Permian psocopteran *Dichentomum* possesses hypognathous mouthparts resembling a modern rostrate mecopteran, including terminally articulating mandibles (Carpenter 1933). Relevant circumstantial evidence from late Paleozoic plants consists of ferns and seed plants with structures such as capitate hairs on cupules, glandular bodies on vegetative tissues and extranuptial nectaries which variously occur on the Early Pennsylvanian medullosan *Lagenostoma* (Taylor & Millay 1979), the Late Pennsylvanian medullosan vine *Blanzyopteris praedentata* (Krings & Kerp 1999), the Early Permian cycad *Phasmatocycas* (Mamay 1976), as well as extant lineages such as the marattialean fern *Angiopteris* (Bonnier 1879). These secretions of plant taxa have been considered as nutritive lures for attracting hexapod surface fluid feeders, although antiherbivore protection also is a possible explanation (Mamay 1976; Labandeira 1998a; Zherikin 2002b).

During the Triassic several early clades of Mecoptera and Diptera evolved fluid feeding mouthparts, based on membership in lineages with Jurassic occurrences that reveal mouthpart structure. Three families of Mesozoic mecopterans – Aneuretopsychidae, Mesopsychidae and Pseudopolycentropodidae – have Middle Jurassic to mid Cretaceous representatives with siphonate mouthparts (Rasnitsyn & Kozlov 1991; Novokshonov 1997; Grimaldi et al. 2005) that evidently extend to the Triassic based on assignments of wings (Grimaldi & Engel 2005). Additionally, nematocerous Diptera, such as the Tipulidae, were present during the Late Triassic (Fraser et al. 1996), of which labellate mouthparts were an ancestral body-plan feature. More remotely, it is possible that early brachycerous Diptera taxa with long-proboscate mouthparts, such as a stem group to the Nemestrinidae and Apioceridae, may have existed as early as the Late Triassic (Krzeminski & Evenhuis 2000).

7.1.9. Oviposition

The ovipositor is a ground plan structure of the Insecta. Although undoubtedly occurring as modest, slender structures in modern Archaeognatha, it is not evident in the Devonian fossils. The earliest direct fossil evidence of ovipositors is found among several lineages of Insecta during the Mississippian to Pennsylvanian transition of the Carboniferous (Carpenter 1969; Zeh et al. 1989), where they acquired a more robust shape, partly by the transformation of the coxal lobes into sheath-like gonoplacs (Mickoleit 1973). During the Pennsylvanian to Triassic, subsequent modifications of ovipositors are documented in the body-fossil record, occurring in six major clades. The first clade is the Odonatoptera, the body-fossil record of which commences at the Mississippian-Pennsylvanian boundary (Brauckmann & Zessin 1989); one of its subclades, the Odonata, becomes prominent during the Triassic. There is limited anatomical evidence from Pennsylvanian to Triassic odonatopteran body fossils (Kukalová-Peck 1991) and damaged plant tissues for the presence of ovipositors that sliced endophytically into mostly sphenopsid plant stems and peltasperm leaves (Roselt 1954; Béthoux et al. 2004; Scott et al. 2004). The natural history of extant odonatan ovipositors piercing into plant tissues has been documented by behavioral studies of modern zygopteran taxa (Wesenberg-Lund 1913; Jurzitza 1974), and detailed morphological and functional descriptions of ovipositors (Naito & Huang 1988; Heming 2003). Ironically, the ovipositors of palaeodictyopteroids, the second major ovipositor-bearing clade, are much better known (Carpenter 1969) than those of contemporaneous odonatopterans. Palaeodictyopteroid ovipositors are elongate and somewhat curved, laterally flattened and elliptical in cross-section, often bear sawtooth margins or asymmetrically ridged ornamentation that were designed to slice into plant tissues (Carpenter 1969; Kukalová-Peck 1972). Their structure is convergent with ovipositors of zygopteran Odonata and tenthredinoid Hymenoptera, both of which slice into plant tissues (Wesenberg-Lund 1913; Naito & Huang 1988). Palaeodictyopteroid clades for which ovipositor structures are known include Diaphanopteridae, up to 3 cm long (Béthoux et al. 2004), Asthenohymenidae (Carpenter 1931; Novokshonov & Willmann 1999), and Parelmoidae (Kukalová-Peck 1992; Rasnitsyn & Novokshonov 1997) for the Diaphanopterodea; the Foririidae (Béthoux et al. 2004) of the Megasecoptera; and the Homoiopteridae (Kukalová-Peck & Brauckmann 1990; Brauckmann 1991) and a taxon of indeterminate familial status (Kukalová-Peck 1972) for the Palaeodictyoptera. It appears that the Palaeoptera made extensive use of accessible plant tissues for oviposition.

Among the Neoptera, several clades have significantly elongate ovipositors, which may be a plesiomorphic feature. The third major ovipositor-bearing clade, the Dictyoptera, contained many plesiomorphic lineages that bore elongate ovipositors, some of which persisted into the mid Mesozoic. These relatively straight ovipositors were circular in cross-section and had smooth surfaces, apparently lacking ornamentation such as ridges and denticles (Laurentiaux 1951; Zalessky 1953; Vishniakova 1968), consistent with oviposition in soil substrates. However, at least one group of dictyopterans had shorter triangular ovipositors that apparently were laterally compressed (Fig. 44; leftmost structure). The typical, linear dictyopteran ovipositor also occurred in the possibly related Permian Grylloblattida (Storozhenko 1998). The fourth major ovipositor-bearing clade are the Archaeorthoptera (sensu Béthoux & Nel 2002), which comprises the Paleozoic Orthoptera and Triassic Titanoptera (Sharov 1968), most of which bore long, laterally compressed, ridged and sometimes denticle-bearing, plant cutting ovipositors (Kukalová-Peck & Brauckmann 1992). These clades continued the plesiomorphic trend found in more basal Pterygota, as in the Palaeodictyopteroidea, Odonata, and basal neopteran clades such as tenthredinoid Hymenoptera. Based on structural design, other Paleozoic orthopterans evidently possessed ovipositors more designed for depositing eggs on top of plant surfaces rather than in their tissues (Béthoux et al. 2004).

The fifth major clade of insects possessing external ovipositors is the Hemipteroidea, particularly ancestral “hypoperlid” clades such as the Permarraphiidae (Novokshonov 1998) and the sternorrhynchan Hemiptera. This early condition is derived with considerable modification from the plant-penetrating ovipositors of paleopterous and orthopteran lineages. Specialized sternorrhynchan ovipositors were long to very long, flexible, almost needle-like structures (Becker-Migdisova 1961) for insertion deep into inner plant tissues. They were activated by a lever-based, or more spectacularly, watchspring coil mechanisms that were capable of retraction into the abdominal cavity (H. Weber 1968). Watchspring-coiled ovipositors of some Paleozoic hemipterans were functionally analogous to the resilin-bearing, long stylate beaks of some extant hemipterans, both of which are deployed and wound up deep within body sinuses (China 1931).

The likely sister-group to the Hemipteroidea, the Holometabola, is the sixth major clade of ovipositor-bearing Pterygota. Among extant holometabolans, the plesiomorphic condition of the ovipositor has been best retained in the Hymenoptera. In addition, there is limited evidence during the Permian for a rectilinear, projecting, tapering process on the posterior abdomen of the stem-group to the Coleoptera (Kukalová 1969), although such structures may (Beutel 2005) or may not (Mickoleit 1973) have been true ovipositors. These ovipositor-like structures had an unknown function, unlike the more laterally compressed, curved and sawtooth-bearing ovipositors of the early Mesozoic Xyelidae, which are tissue-cutting and egg laying organs, based on morphological homology with extant confamilial descendants.

The earliest plant-insect associational record of oviposition originates from the Graissenessac Basin in Hérault, northern France, during the Late Pennsylvanian (Béthoux et al. 2004). This distinctive damage consists of ellipsoidal scars that are oriented parallel to the internodal stem vasculature of *Calamites* sp. sphenopsid stems, some of which are packed with multiple ovoidal eggs (Béthoux et al. 2004). Other occurrences of oviposition scars are known from the Lower Permian of Euramerica, such as “*Equisetites foveolatus*” (Roselt 1954), a presumptive plant form-genus subsequently shown to represent internodal stem surfaces characterized by dense constellations of oviposition scars, occurring in the Lower Permian and Middle Triassic of Germany (Kelber 1988). Other oviposition occurrences, from the Lower Permian of Germany, are ellipsoidal scars on cordaitalean foliage and seed-plant stems (H. Potonié 1893). From the Permian and Triassic of Gondwana, similar but smaller, circular oviposition scars are found typically in the midveinal regions of glossopterid foliage from the Paraná Basin of Brazil, misdiagnosed as hole feeding (Adami-Rodrigues et al. 2004a), the Karoo Basin of South Africa, misdiagnosed as circular leaf mines (Scott et al. 2004), and the Raniganj Basin of India (Srivastava 1987). Younger occurrences of ovipositional damage are documented in Euramerican sphenopsid stems from the Middle Triassic Lower Keuper Formation of Germany (R. Weber 1968; Grauvogel-Stamm & Kelber 1996), and in particular on Gondwanan species of Equisetaceae from the South African Molteno Formation (C. Labandeira unpubl. data). This type of insect damage interestingly has not been recorded from the penecontemporaneous Late Triassic Chinle Formation of Arizona, U.S.A. (Ash 1997), although it occurs in Middle Triassic sphenopsid stems from the Lower Keuper Formation of Western Europe (Grauvogel-Stamm & Kelber 1996). Oviposition also occurs extensively on sphenopsid stems (Fig. 34) and diverse seed-plant foliage from the Molteno Formation of South Africa, especially the broadleaved voltzialean conifer *Heidiphyllum elongatum* (Fig. 33).

7.2. The aquatic realm

The aquatic realm consists of freshwater habitats that are structured in a more three-dimensional manner than the terrestrial realm. Aquatic habitats merge either imperceptibly or discretely with land-based habitats at the edges of lakes, streams, and other water bodies where they often share amphibious taxa. Virtually all evidence for the aquatic realm in the fossil record originates from lacustrine deposits and fluvial and associated habitats such as interfluve pond, floodplain, and abandoned channel deposits. For both types of aquatic deposits, lotic and lentic environments and their hexapod occupants have good fossil records (Miller & Labandeira 2002).

7.2.1. Predation

Presently there is no convincing evidence for aquatic hexapods in Pennsylvanian ecosystems (Labandeira 2002a). The most likely candidates, the immatures of adult predaceous Odonatoptera, lack candidate naiads from known Paleozoic freshwater deposits (Zherikin 2002b). The Ephemeroptera, however, are represented by Early Permian naiads that had abdominal gills and evidently were predaceous (Kukalová 1968; Kukalová-Peck 1983), although their insectivorous mouthpart and leg specializations have been questioned by Zherikin (2002b). The Palaeodictyopteroidea, by contrast, had terrestrial nymphs (Kukalová-Peck 1987; Fig. 47) and were predominantly if not entirely plant feeders. Permian plecopteran naiads possessed abdominal gills, dorsoventral flattening and functioning mouthparts (Tschernova 1965; Kukalová 1968), and together with their inclusion within larger extant clades with known diets (Wootton 1988; Sinitshenkova & Zherikin 1996), were probably predatory. Overall, the history of aquatic predation can be traced to the Permian, with certain caveats (Miller & Labandeira 2002). During the Late Triassic there is the earliest evidence for odonatopteran naiads with labial masks (Zherikin 2002b), as well as the presence of early holometabolous clades, particularly the Neuropteroidea, some of which had predaceous aquatic larvae.

7.2.2. Shredding

The rich variety of mouthpart structures and feeding styles borne by aquatic larvae of nematocerous Diptera allowed their penetration and partitioning of lotic and lentic freshwater habitats. This process began by the Middle Triassic, during which the first evidence for shredders is present, and continued into the Late Jurassic with the appearance of scrapers (Labandeira 2005a). Shredders are characterized by comminution of dead and live material, especially plant tissues, in ways similar to that of terrestrial external foliage feeders, ingesting epibenthic, coarse particulate organic matter and pulverizing the contents with modified mandibulate mouthparts. Extant shredders comprise the basal subclades of especially Diptera, but also adephagan Coleoptera and Trichoptera, and to a much less extent the Plecoptera and Ephemeroptera (Merritt & Cummins 1996). The earliest evidence for shredding originates from the Middle and Late Triassic lacustrine hexapod faunas from the eastern United States, Western Europe and Central Asia (Krzeminski 1992; Shcherbakov et al. 1995; Fraser et al. 1996). Several phylogenetically basal and geochronologically early clades, such as the Tipulidae and Cylindrotomidae of the nematocerous Diptera and possibly some of the earliest documented Trichoptera, were shredders in lacustrine habitats during the Late Triassic.

7.2.3. Filtering

Towards the end of the Late Triassic, and during the Early Jurassic filterers appear. Filtering is the passive entrapment of suspended particulate matter, especially phytoplankton, through mouthpart structures such as labral fans or mandibular brushes that act as sieves or screens for the accumulation of suspended organic matter (Merritt & Cummins 1996). Early filterers were represented by larval instars of the nematocerous dipteran lineages, Culicidae and Simuliidae (Labandeira 2005a), and perhaps related clades. Later, during the Jurassic, newly originating dipteran clades became filterers. Much of the evidence for early Mesozoic filtering originates from uniformitarian inference of known larval ecologies of extant nematocerous dipterans (Wichard et al. 2002) in addition to rare occurrences of fossil larval mouthparts with filtering structures (Kalugina & Kovalev 1985). Another major functional feeding group of aquatic insects, gathering, has its first appearance during the Early Jurassic, among nematocerous Diptera (Labandeira 2005a).

7.3. Detritivory

Detritivory is the consumption of dead microbial individuals or multicellular tissues, whether plant, fungal or animal, by scavenging animals. Much of the Late Silurian to Triassic record of hexapod detritivory is mentioned above, particularly the sections on "External Foliage Feeding" and "Boring," which represents the predominance of evidence. Thus evidence for detritivory principally has originated from dispersed, foliage-rich macrocoprolites of Mississippian and Pennsylvanian permineralized coal ball or similar deposits, as well as small borings that are laden with microcoprolites within originally dead and indurated plant tissues as varied as cordaitalean wood, tree-fern root mantle, fern aphlebiae and sclerenchymatous tests of pteridosperm seeds. Additional, but less abundant, evidence for detritivory has come from damaged in situ plant axes that contain much larger, hexapod-sized borings and galleries lacking response tissue (Labandeira & Phillips 2002).

Examples of detritivory are best illustrated for cordaites in Middle Pennsylvanian coal balls from various Appalachian basins (Cichan & Taylor 1982), and also the marattialean tree fern *Psaronius chasei* from the Late Pennsylvanian Calhoun Coal of the Illinois Basin (Labandeira 2001). For *P. chasei*, there was consumption of root aerenchyma by oribatid mites (Fig. 14), and ground parenchyma of stems by smaller (Fig. 13) and larger (Fig. 22) hexapod pith borers as well as external feeders (Fig. 16). Additionally, oribatid mite coprophagy of hexapod coprolites (Fig. 15) was another common mode of Paleozoic detritivory. The decomposition of dead plant tissues by detritivores was the overwhelming mode of recycling primary productivity in Late Silurian to Middle Pennsylvanian ecosystems (Shear & Kukalová-Peck 1990; Shear

1991) where there was limited herbivory (Labandeira 1998a; Figs. 9–12). Toward the end of the Middle Pennsylvanian and commencing in a major way during the Late Pennsylvanian, diverse modes of herbivory emerged, exemplified by the varied herbivore FFGs of the Calhoun Coal (Figs. 16–21, 23, 24). After this rapid expansion, there is continuation of external foliage feeding, piercing-and-sucking, galling, seed predation and oviposition documented from Permian compression floras, followed by a renewed and eventually more diverse radiation of varied forms of herbivory during the Middle to Late Triassic, also found in compression floras (Grauvogel-Stamm & Kelber 1996; Ash 1997; Scott et al. 2004; Figs. 25–42). Notably, evidence for detritivory ranges throughout the Middle Pennsylvanian to Triassic interval, and occurs mostly in permineralized floras that are taphonomically and depositionally distinct from compression floras (R. Weber 1968; Goth & Wilde 1992; Ash 2000; Kellogg & Taylor 2004).

7.4. Predation

During the Late Silurian to Devonian, chelicerate arachnids, such as scorpions and trigonotarbids, and centipeds were the dominant arthropod predators on land (Shear & Kukalová-Peck 1990; Shear & Selden 2001; Fig. 43). Contemporaneous hexapods that included collembolans and archaeognathans were detritivores or engaged in limited herbivory (Labandeira 2005b). A likely function of the *Rhyniognatha* mandibles, redescribed by Engel & Grimaldi (2004) as a pterygote insect, was predation, as they seem to have pronounced incisiform processes that may be used for puncturing cuticles. It should be noted that coprolites interpreted as containing arthropodan sclerites have been described from this interval (Habgood et al. 2004), providing additional evidence for predation.

The ensuing fossil record of the Middle Devonian to Late Mississippian consists of occasional occurrences of scorpion, arachnid and centiped body fossils (Ward et al. 2006), indicating the pre-eminence of a predatory arthropod fauna that was not dominated by hexapods.

During the Mississippian-Pennsylvanian boundary and soon thereafter, insectivorous hexapods, principally adult Odonatoptera and the Ephemeroptera such as the Tripsolobidae and Bojophlebiidae, prominently featured raptorial mandibulate mouthparts (Kukalová-Peck 1991). Adult odonatopterans bore massive, robust mandibles designed for crushing hexapod prey that were captured aerially (Kukalová-Peck & Shear 1990), and probably deposited relatively large fecal pellets rich in hexapod sclerites (Fig. 44). The immatures of Odonatoptera likely were large terrestrial nymphs rather than aquatic naiads (Pritykina 1980; Sinitshenkova 2002), and during the Paleozoic it is unclear if they possessed the protractible labial mask of the more apomorphic subclade Odonata. No current evidence exists for the presence of aquatic odonatopteran naiads prior to the Late Triassic. On land, possible antipredatory devices have been noted for hexapods that were potential prey, including disruptive coloration, spinose thoraxes (Kukalová-Peck & Brauckmann 1992), large eyespots on the wings (Carpenter 1969; Fig. 45), and possibly sheer size (Shear & Kukalová-Peck 1990). In addition to odonatopterans and ephemeropterans, a large species of dipluran evidently was predaceous, as judged by its prominent cercal forceps modified for prey capture (Kukalová-Peck 1987). It also is possible that certain taxa or lineages of the basal complex of orthopteroid insects were insectivorous during the Pennsylvanian and Permian (Gorochov 1995; Zherikin 2002b), but evidence is wanting and their mouthpart structure is typically equivocal with regard to feeding habits. Larval forms such as the Early Permian *Permosialis* (Sharov 1953) were likely predatory based on mouthpart and head structure and may represent an early feeding strategy of the Holometabola.

New lineages of the Odonatoptera, namely those of the Odonata, in addition to surviving Paleozoic lineages, characterize the dominant aerial predators during the Triassic (Bechly 1994). The Titanoptera, very large orthopteroid insects, are presumed to have been predaceous (Sharov 1968; Engel & Grimaldi 2005). The expansion of hemipteran insects both on land and in water included insectivorous clades that appeared during the Late Triassic but became prominent in the Jurassic (Sinitshenkova 2002; Popov 1971). The Triassic also represents the beginning of a few major lineages of holometabolous insects that were mostly ground-based insectivores, notably the Neuropteroidea (Planipennia, Megaloptera and Raphidioptera) and the Coleoptera with the appearance of adephagan clades such as the Carabidae (Fraser et al. 1996). Triassic insectivory was present in both terrestrial and aquatic realms and many of the adaptations for insectivory involved major modifications in the larval mouthparts of the Holometabola (Labandeira 1997). There is no direct evidence for Triassic parasitism or parasitoidism, two profoundly important insectivore guilds that originated during the late Early Jurassic and permanently changed food-web structure of terrestrial ecosystems (Labandeira 2002b; Zherikin 2002b).

8. Discussion

The most challenging aspect of ascertaining the evolutionary biology of hexapod feeding in the fossil record is attributing hexapod clades to particular types of plant damage. The best cases can be made for highly stereotyped types of damage with known extant feeding biologies, such as that of WILF et al. (2000) for hispine chrysomelid damage on latest Mesozoic and Early Cenozoic gingers (Zingiberaceae). For the deeper past, most of the assignments of hexapod clades (Fig. 50) are based on a combination of characterizable types of plant damage (Figs. 1, 2, 49) and the availability of matching mouthpart types (CHAUDONNERET 1990; LABANDEIRA 1990, 1997) that were available to cause the damage in question within the same deposit. This is buttressed by ancillary data, such as fossil gut contents of known penecontemporaneous hexapod taxa and other varied types of evidence (LABANDEIRA 2002a). In contrast, there are simple types of generalized feeding damage that almost always lack taxonomic specification, but provide for valuable ecological data. Regardless of the degree to which identification of responsible hexapod culprits is possible, it is the ecological data that forms the essential basis for an understanding of how hexapods have interacted with other organisms, albeit at the more general clade ranks, during the past 420 m.y. What I have presented in this contribution is a coarse approach to the Late Silurian to Late Triassic record, spanning 220 m.y. of geologic time when hexapods first emerged in very simple trophic webs amid the earliest terrestrial ecosystems, through the expansion of herbivory in Pennsylvanian coal swamps and Permian fluvial environments, the massive P-T extinction, and ending in a diverse range of feeding styles that typify Triassic (and ultimately) extant terrestrial and aquatic ecosystems. A finer-grained spatiotemporal approach is needed to tease out the strands of more specific feeding types in selected stratal sequences with good preservation.

If there is one take-home point in this exercise, it is that FFGs and their DTs overwhelmingly have been virtually eternal for much of the deep past – unchanging and repetitively occurring in time and space. Moreover, plant-hosts and their hexapod herbivore clades invariably undergo periodic turnover, punctuated by periodic bouts of stasis. Evidence for this phenomenon comes not only from the recurrence of the same DT on different plant-organ taxa during intervals populated by different culprit hexapod clades (Figs. 3–8), but also in the amazing convergence in modern hexapod mouthpart types by unrelated taxa (LABANDEIRA 1997). Structural convergence also extends to plant-host foliar architecture, such as the reticulate venation of Early Permian gigantopterid peltasperms and Late Cretaceous angiosperms (BECK & LABANDEIRA 1998; WANG 2000), or the nutritional equivalence of megagametophytic tissues of Middle Pennsylvanian medullosan seeds and the endosperm of Neogene angiosperm seeds (JENNINGS 1974; MIKULÁŠ et al. 1998). It is this pervasiveness of convergent evolution – in how hexapods feed on other organisms, in how other organisms respond to that feeding, and in the characterization of the fundamental units of the associations between the two – that results in the conclusion that there are a limited, fixed number of ways that hexapods now and have always fed. For terrestrial herbivores, they are external foliage feeding, piercing-and-sucking, palynivory (with or without pollination), boring, galling, seed predation, leaf mining, surface fluid feeding, as well as oviposition. For aquatic herbivores, they are shredding, filtering, and gathering. In both instances, detritivores have entered some of these FFGs. For the terrestrial realm, these FFGs have meager beginnings during the Late Silurian to Early Devonian, but by the Late Pennsylvanian all but two were present, and by the late Middle Triassic, the entire modern spectrum was in place. For aquatic FFGs there was a significant delay into the Jurassic. These data collectively indicate that, from a trophic perspective, the global terrestrial hexapod fauna became modern during the Late Triassic and the aquatic hexapod fauna achieved similar modernity during the Late Jurassic. In both instances the current complement of FFGs preceded the earliest fossil appearance of angiosperms by tens of millions of years.

9. Summary and conclusions

In this contribution, new data as well as a review of the recent literature was presented for the Late Silurian to Late Triassic interval. The earliest documented associations between terrestrial arthropods and vascular plants are from the Late Silurian to Early Devonian interval from Euramerica. In these associations, phylogenetically basal hexapodan clades, such as collembolans, proturans and archaeognathans, probably played a role in the consumption of spores, piercing-and-sucking of and boring into softer stem tissues, and boring into harder tissues of large columnar fungi. Following this initial but modest trophic expansion there was a lull in associations during the Middle Devonian to Middle Mississippian, with detritivory playing a prominent role.

During the Late Mississippian and continuing into the Middle Pennsylvanian there was a second, more trophically extensive phase of herbivory by basal orthopteroid and blattoid mandibulate hexapods that targeted mostly pteridosperm leaves. In addition, palaeodictyopteroid piercing-and-sucking insects consumed seeds, deeper stem and petiolar tissues, and whole spores. This expansion of herbivory occurred in the context of land ecosystems that were characterized by extensive detritivory.

At the beginning of the Late Pennsylvanian there was establishment of many modern-aspect styles of herbivory in which component herbivore communities of external foliage feeders, piercer-and-suckers, gallers, borers, palynivores, as well as detritivores, were partitioning live and dead plant tissues on arborescent plant hosts such as marattialean tree ferns and pteridosperms. During the Early Permian, and after the demise of the coal-swamp forests, the record for Euramerican plant-hexapod associations shifts to fluvial environments, in which other clades of vascular plants – filicalean ferns, new medullosan lineages, peltasperms, cycadophytes, conifers – were consumed, some with host targeting by particular hexapod taxa. The taxonomic affinities of hexapod clades for this expansion are significantly different from those of the Pennsylvanian, and included, for external foliage feeders, mostly orthopterans, but also caloneurodeans and possibly psocopterans and miomopterans. For palynivores, some taxa of grylloblattodeans, "hypoperlids", and psocopterans consumed prepollen and pollen. In Gondwana, such as the Karoo Basin of South Africa, a similar expansion of herbivory occurred, but on a glossopterid dominated flora.

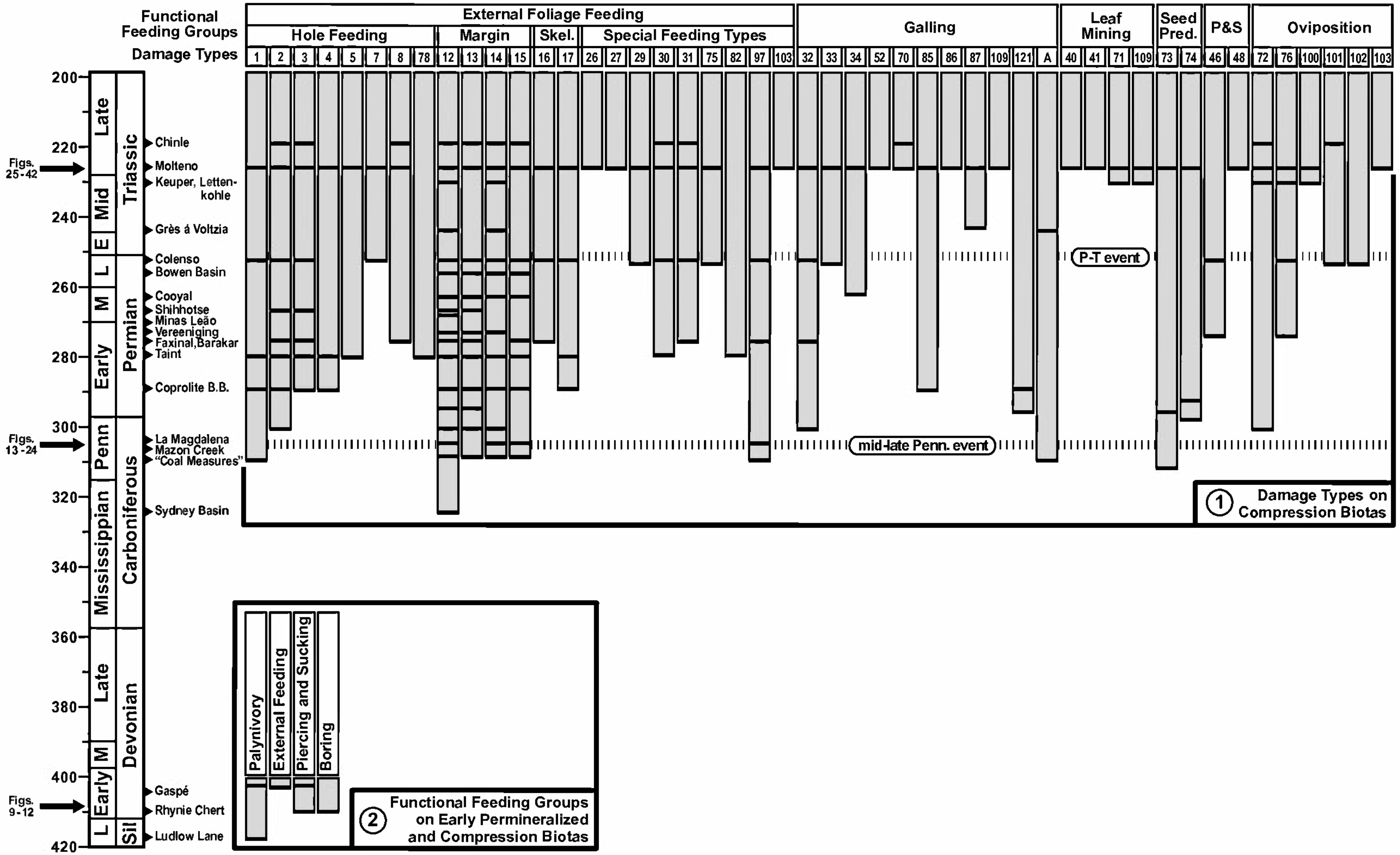
These associations typically came to an end at the P-T event, with minimal evidence during the Early Triassic for herbivore activity. There was a modest expansion of various types of herbivore damage in Western Europe during the Middle Triassic. However, for the early Late Triassic, there is a major expansion of herbivory in Gondwana, particularly from the Karoo Basin that is just as impressive as the radiation of herbivores associated with the angiosperm radiation during the earlier Cretaceous. Preliminary results indicate that this Late Triassic colonization event targeted a broad sweep of major pteridophyte and seed-plant clades, including filicalean ferns, cycads, peltasperms, ginkgoaleans, voltzialean conifers, bennettitaleans, gnetopsids and others, and was instrumental in the trophic modernization of terrestrial plant-hexapod associations. By the Late Triassic, surviving Paleozoic lineages of orthopteroid insects, the newly evolved Titanoptera and Phasmatodea, and the significant expansion of hemipteroid and holometabolous insect clades such as sternorrhynchan, auchenorrhynchan and heteropteran hemipterans, polyphagan beetles, symphytan hymenopterans and possibly basal lepidopterans provided for considerable activity in external foliage feeding, piercing-and-sucking, galling, leaf mining, and seed predation of the Karoo flora. Like leaf mining, surface fluid feeders first appear during the later Triassic, represented by basal mecopteroids and possibly the earliest brachyceran dipterans.

Aquatic plant-hexapod associations have a later lag than those on land. Aquatic associations commence during the Permian, principally involving predators (and probably detritivores) such as the naiads of Plecoptera and Ephemeroptera. Evidence for aquatic and predaceous odonatopteran naiads do not occur until the later Triassic, at which time there was expansion of nematocerous dipterans, adephagan coleopterans and probably early trichopterans – initially as shredders and subsequently as filterers. With the addition of collectors and scrapers during the Jurassic, aquatic associations became trophically modern by the end of the period.

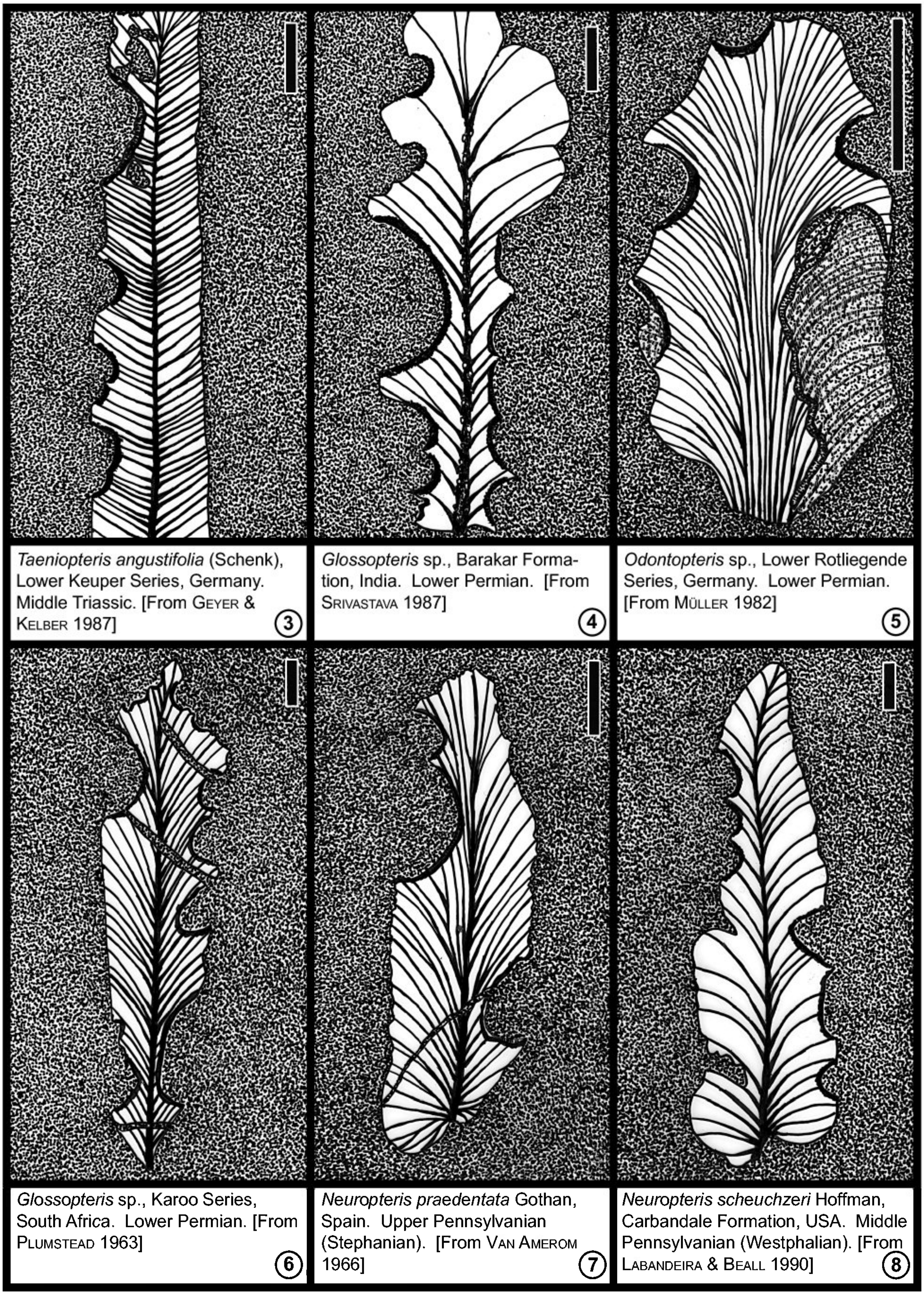
Although evidence from mouthpart structure is crucial for linking DTs to hexapod clades, there are difficulties in achieving satisfactory taxonomic specificity of hexapod herbivores in this approach. Nevertheless, there is the potential for providing an ecological history of terrestrial and aquatic plant-hexapod associations, with variable specificity of hexapod culprit clades. What is clear from the available evidence to date is the ubiquity of convergent feeding styles in time and space, regardless of "ephemeral" plant hosts and hexapod herbivores. Thus, FFGs represent a fixed number of ways that hexapods consume land and aquatic plant tissues that are independent of continual turnover of plant hosts and hexapod herbivores. For the terrestrial realm, most of these FFGs were established during the Late Pennsylvanian and all were present in the early Late Triassic, at which time the herbivores of land plants became trophically modern.

Tab. 1. Floras providing most plant-arthropod associational data for Figs. 1, 2, 49 and 50 of this contribution.

Informal Name	Locality	Stratigraphic Placement	Time Interval	Major References & Text Figures
Chinle	Petrified Forest National Park, Arizona, USA	Chinle Formation	Late Triassic (Norian)	WALKER 1938; ASH 1997, 1999, 2000, 2005; ASH & SAVIDGE 2004; CREBER & ASH 2004
Molteno	Karoo Basin, KwaZulu-Natal, Eastern Cape and Northern Cape, South Africa	Molteno Formation	Late Triassic (Carnian)	ANDERSON & ANDERSON 1985, 2003; SCOTT et al. 2004; LABANDEIRA 2005; *Figs. 25–42*
Keuper	Wasselonne, Bas-Rhine; Schleerieth and Ochsenfurt, Franconia, Germany	Lower Keuper and Lettenkohle Formations	Middle Triassic (late Ladinian)	LINCK 1949; ROSELT 1954; GEYER & KELBER 1987; KELBER 1988; GRAUVOGEL-STAMM & KELBER 1996; *Fig. 3*
Grès à Voltzia	Grès à Voltzia, northern Vosges Mountains, France	Bundsandstein Formation	Middle Triassic (lower Anisian)	GRAUVOGEL-STAMM & KELBER 1996
Clouston Farm	Colenso, KwaZulu-Natal, South Africa	Estcourt Formation	Permian (Changhsingian)	Prevec & Labandeira unpubl. data
Bowen Basin	Bowen Basin, Queensland Australia	Bandanna Formation (Rangal Coal Measures)	Permian (Wuchiapingian)	MCLOUGHLIN 1994a,b
Cooyal	Cooyal, Sydney Basin, New South Wales, Australia	Upper Illawarra Coal Measures	Late Permian	HOLMES 1995
Vereeninging	Vereeninging, Gauteng, South Africa		Middle Permian (?Capitanian)	PLUMSTEAD 1963; *Fig. 6*
Shihhotse	Taiyuan City, Shanxi, China	Shihhotse Formation	Early–Late Permian (Kungurian–Roadian)	GLASSPOOL et al. 2003
Minas do Leão	Minas do Leão, Rio Grande do Sul, Brazil	Irati Formation	Early–Late Permian (Kungurian–Roadian)	ADAMI-RODRIGUES & IANNUZZI 2001; ADAMI-RODRIGUES et al. 2004a,b
Faxinal	Faxinal and Morro do Papaléo, Rio Grande do Sul, Brazil	Rio Bonito Formation	Early Permian (Artinskian)	ADAMI-RODRIGUES & IANNUZZI 2001; ADAMI-RODRIGUES et al. 2004a,b
Barakar	Ranigang Coalfield, West Bengal, India	Barakar Formation	Early Permian (Artinskian)	SRIVASTAVA 1987; *Fig. 4*
Taint	Baylor County, Texas, USA	Waggoner Ranch Formation	Early Permian (Artinskian)	BECK & LABANDEIRA 1998
Coprolite Bone Bed	Archer County, Texas, USA	Nocona Formation	Early Permian (Sakmarian)	GREENFEST & LABANDEIRA 1997; LABANDEIRA & ALLEN 2007
La Magdalena	La Magdalena Coalfield, León, Spain	[formation not reported]	Pennsylvanian (Gzhelian)	AMEROM 1966; CASTRO 1997; *Fig. 7*
Calhoun Coal	Illinois Basin, Berryville, Illinois, USA	Mattoon Formation	Pennsylvanian (Kasimovian)	LABANDEIRA & PHILLIPS 1996a,b, 2002; LABANDEIRA et al. 1997; *Figs. 13–24*
Mazon Creek	Mazon Creek, Will and Grundy Counties, Illinois, USA	Carbondale Formation	Pennsylvanian (late Moscovian)	SCOTT & TAYLOR 1983; LABANDEIRA & BEALL 1990; SCOTT et al. 1992; *Fig. 8*
“Coal Measures”	Northumberland and other north-central localities, UK	Coal Measures	Pennsylvanian (middle Moscovian)	THOMAS 1969; AMEROM 1973; MÜLLER 1982; CHALONER et al. 1991
Sydney Basin	Sydney Basin, New South Wales, Australia	McInnes Formation	Mississippian (early Serpukhovian)	Labandeira & Iannuzzi unpubl. data
Gaspé	Gaspé, Québec, Canada	Battery Point Formation	Devonian (Emsian)	TRANT & GENSEL 1985; BANKS & COLTHART 1993; HOTTON et al. 1996; HUEBER 2001
Rhynie Chert	Aberdeenshire, Scotland, UK	Dryden Flags Formation (includes the Windyfield Chert)	Devonian (Pragian)	KIDSTON & LANG 1921; KEVAN et al. 1975; SHEAR & SELDEN 2001; HABGOOD 2004; *Figs. 9–12*
Ludford Lane	Ludford Lane, Perton Lane, Wales, UK	Downton Castle Limestone	Silurian (Prídolí)	EDWARDS et al. 1995; EDWARDS 1996



Figs. 1–2. Geochronology of terrestrial plant-arthropod herbivore associations during the Late Silurian to Late Triassic interval. **1**: The early geochronologic distribution of DTs from only compression floras, listed at near left, but also including other important occurrences that range from Late Mississippian to Late Triassic in age. Damage types (DTs) are listed numerically by functional feeding group (FFG) at top and each occurrence on a flora is designated as a thick horizontal bar. Major extinction events occur at the ends of the Middle Pennsylvanian (mid-late Penn. event) and terminal Permian (P-T event). The geochronologic positions of floras are fitted with the best stratigraphic data available and some may be approximate, such as Vereeniging and Barakar. DTs are after WILF & LABANDEIRA (1999) and LABANDEIRA et al. (2002b). The damage-type designation "A" following "121" is not formally described. **2**: Distribution of FFGs for the earliest well-preserved terrestrial biotas, consisting of compression and permineralized floras. Included under "Rhynie Chert" is the nearby, penecontemporaneous Windyfield chert deposit. Large arrows at far left indicate the three most important Paleozoic floras for which there are hexapod or other arthropod associational data, herein illustrated: lower arrow, Dryden Flags Formation (Figs. 9–12); middle arrow, Calhoun Coal of the Mattoon Formation (Figs. 13–25); upper arrow, Molteno Formation (Figs. 25–44). See Tab. 1 for details of all floras listed at left. Abbreviations: Sil., Silurian; Penn., Pennsylvanian; E., Early; M., Middle; L., Late; Skel., Skeletonization; Pred., Predation; P&S, Piercing-and-sucking. Geochronology after GRADSTEIN & OGG (2004). [Original illustration]



Taeniopteris angustifolia (Schenk), Lower Keuper Series, Germany. Middle Triassic. [From Geyer & Kelber 1987] ③

Glossopteris sp., Barakar Formation, India. Lower Permian. [From Srivastava 1987] ④

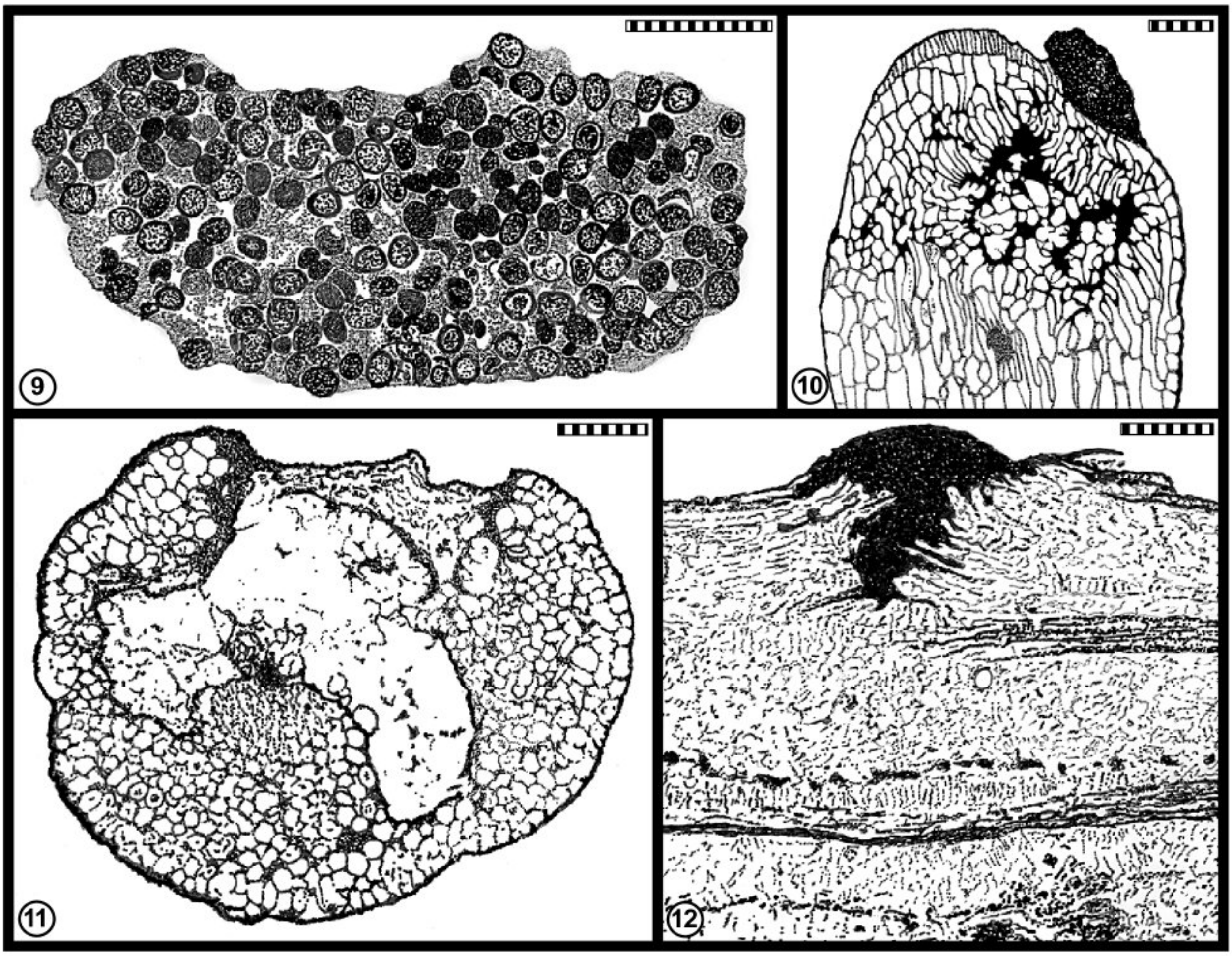
Odontopteris sp., Lower Rotliegende Series, Germany. Lower Permian. [From Müller 1982] ⑤

Glossopteris sp., Karoo Series, South Africa. Lower Permian. [From Plumstead 1963] ⑥

Neuropteris praedentata Gothan, Spain. Upper Pennsylvanian (Stephanian). [From Van Amerom 1966] ⑦

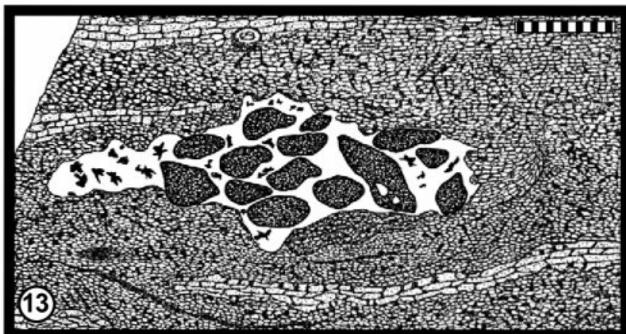
Neuropteris scheuchzeri Hoffman, Carbandale Formation, USA. Middle Pennsylvanian (Westphalian). [From Labandeira & Beall 1990] ⑧

Figs. 3–8. Examples of hexapod herbivore margin feeding (DT12), the most abundantly preserved DT in late Paleozoic and Triassic floras. Margin feeding is preserved especially on cycadophyte, glossopterid and medullosan leaves that range in age from the younger Middle Triassic (**3**) through the Permian (**4–6**), Late Pennsylvanian (**7**) and into the youngest Middle Pennsylvanian (**8**). Recent evidence indicates that this DT now extends to the early Late Mississippian (R. Iannuzzi & C. Labandeira unpubl. data). Solid scale bar = 1 cm. [Original illustration, redrawn from cited sources]



Figs. 9–12. Spectrum of herbivore plant-arthropod associations from the Early Devonian (~ 408 Ma) Dryden Flags Formation, near Edinburgh, in southeastern Scotland, U.K., showing examples from the Windyfield chert (**9**) and coeval, nearby Rhynie chert (**10–12**) localities. **9**: A coprolite assigned to the ichnotaxon *Lancifaex simplex* containing a monospecific population of a laevigate spore type within a matrix of amorphous organic matter, indicating palynivory. Redrawn from Habgood et al. (2004: fig. 3A); slide RC-463-A. **10**: Pith boring in the axis of the rhyniophyte *Aglaophyton major* (oblique section?) showing cortical tissue with hypertrophic cells and an opaque intercellular material. Redrawn from Kevan et al. (1975: plt. 54, fig. 3); slide V.57833. **11**: Different view of a pith boring in *A. major* showing overall structure and internal tunnel lining, but lacking the extensive reaction tissue shown in Fig. 10. Redrawn from Kevan et al. (1975: plt. 54, fig. 2); slide V.57833. **12**: Lesion filled with opaque substance in *A. major*, reaching the central vascular tissue seen at center-right. This damage was probably made by a piercing-and-sucking arthropod; elongate structures filled with black material along the lesion wall may represent individual stylet probes. Redrawn from Kevan et al. (1975: plt. 54, fig. 1); slide V.57834. Striped scale bar = 0.1 cm. [Original illustration, redrawn in pen and ink from cited sources]

Figs. 13–24. Spectrum of plant-hexapod and plant-mite associations, including detritivory and herbivory, from the Late Pennsylvanian (~ 303 Ma) Calhoun Coal Member of the Mattoon Formation, Illinois Basin, near Berryville, in southeastern Illinois, U.S.A. **13**: Detritivore boring, probably hexapodan, in stem ground tissue (parenchyma) of the marattialean tree fern *Psaronius chasei*, with in situ mesocoprolites (USNM, BV11-Abot, slide 497493). **14**: Oribatid mite boring in a *P. chasei* rootlet in which aerenchyma tissues have been excavated (USNM, BV71-Dbot, slide 500995). **15**: An example of oribatid mite coprophagy of an hexapod macrocoprolite, shown by gallery construction with in situ microcoprolites (USNM, BV16-Ftop, slide 497461). **16**: Hexapod detritivore macrocoprolite of *Psaronius* sp. stem tissues showing the indigestible nature of gum-sac cells (black areas) and complete digestive processing of surrounding parenchyma (USNM, BV49-Dtop, slide 499146). **17**: Hexapod herbivore macrocoprolite containing considerable foliage of the arborescent sphenopsid *Calamites* sp. (USNM, BV68-Dtop, slide 497453). **18**: Hexapod herbivore macrocoprolite containing abundant uniseriate trichomes of the medullosan pteridosperm *Alethopteris* (USNM, BV42-Bbot, slide 501003). **19**: Macrocoprolite made by an hexapod palynivore, consisting almost entirely of *Psaronius* sp. tree-fern spores (*Convolutispora* sp. or *Apiculatosporis* sp.) and associated sporangial tissues (BV9-Dtop, slide 499151). **20**: Hexapod produced macrocoprolite consisting almost entirely of *Florinites* sp. cordaitalean pollen (USNM, BV20-Bbot, slide 497523). **21**: A ruptured boring in *Psaronius* sp. root aerenchyma with reaction tissue indicated by darker shading (USNM, BV79-Ctop, slide 499065). **22**: An hexapod boring of trunk ground tissue (parenchyma) from a *P. chasei* trunk, assigned to the ichnotaxon *Pteridoscaphichnos psaronii* (Labandeira & Phillips 2002) (BV79-Ctop, slide 499065). **23**: Two palaeodictyopteran insect stylet tracks on a *P. chasei* frond petiole illustrating consumption of xylem and phloem cell protoplasts from a feeding pool (at lower-right) and parenchymatic reaction tissue surrounding both stylet tracks (indicated by darker shading) (UIUC, BV8227-Bbot, slide 22736). **24**: Holometabolous insect gall of a *P. chasei* tree-fern frond petiole assigned to the ichnotaxon *Pteridotorichnus stipitopterii* (Labandeira & Phillips 2002), demonstrating the presence of a chamber surrounded by anomalous nutritive tissue and distinctive particulate coprolites of inner parenchyma (UIUC, BV31272-Btop, slide 22397). All specimens are from carbonate-permineralized coal balls. Figures are pen and ink drawings from enlarged photographic prints. Depository abbreviations: USNM, National Museum of Natural History, Washington D.C., U.S.A.; UIUC, University of Illinois at Urbana-Champaign, Illinois, U.S.A.. Scale bars: striped = 0.1 cm; dotted = 0.01 cm. [Original illustrations]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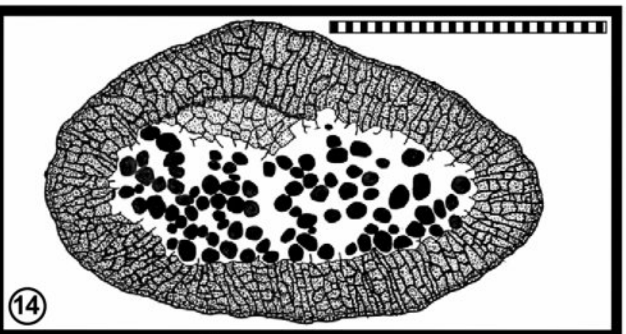
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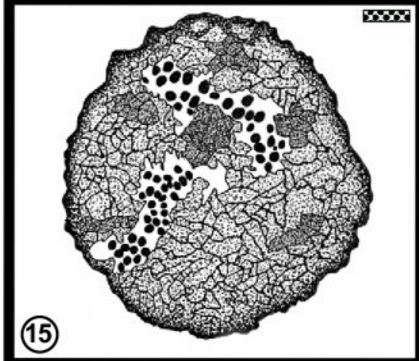
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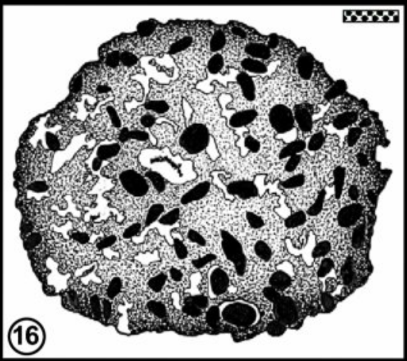
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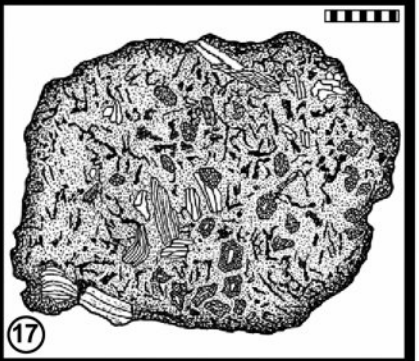
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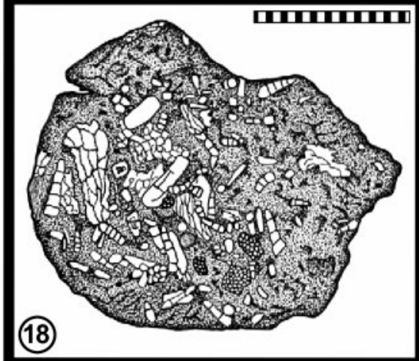
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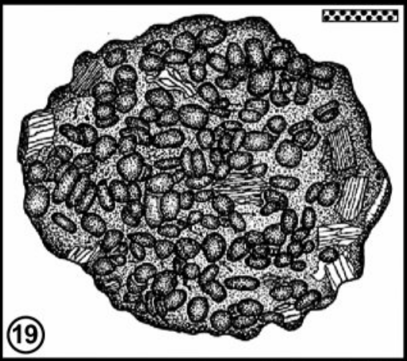
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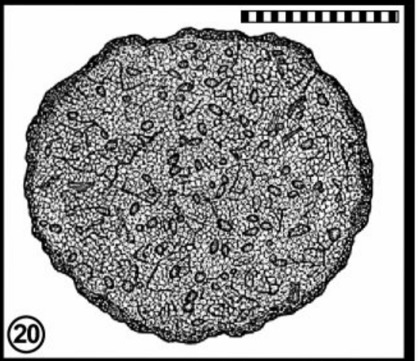
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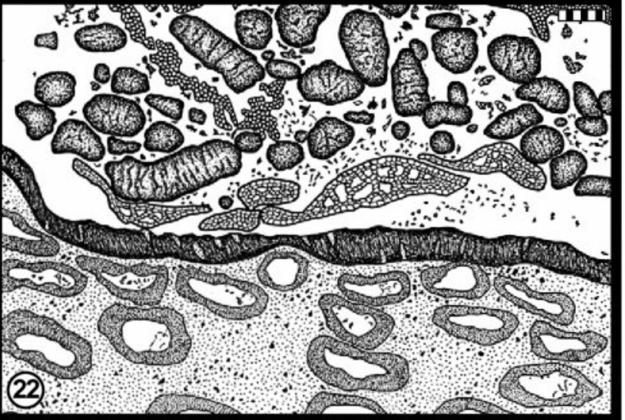
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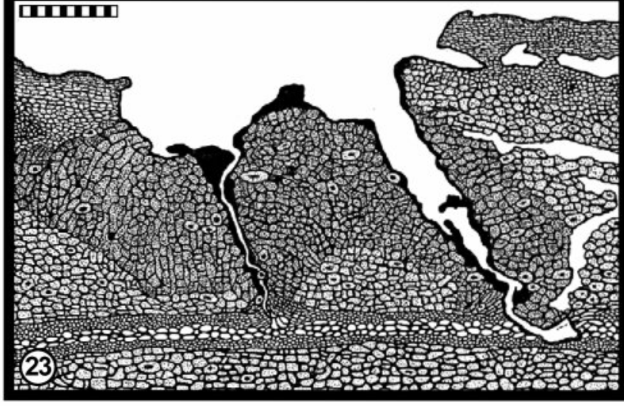
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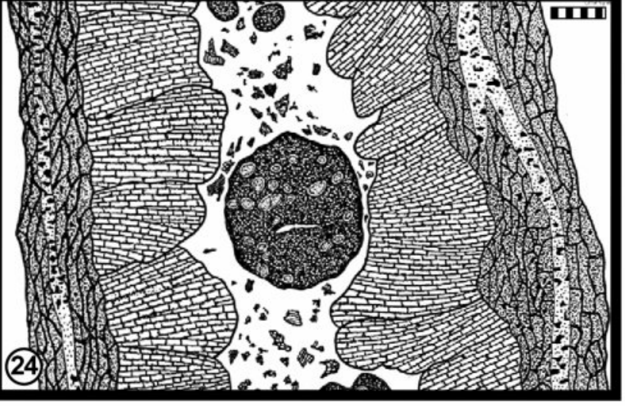
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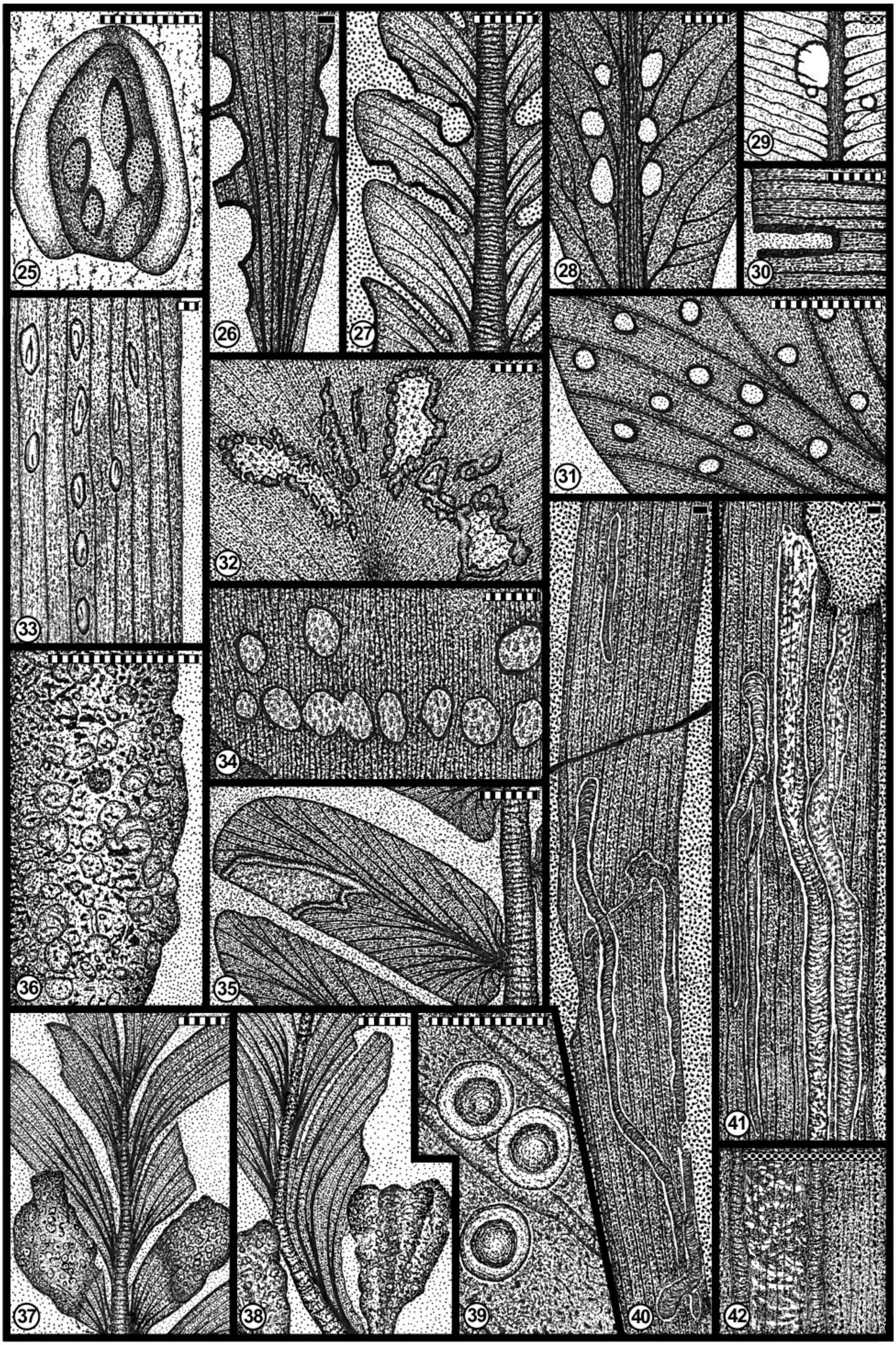
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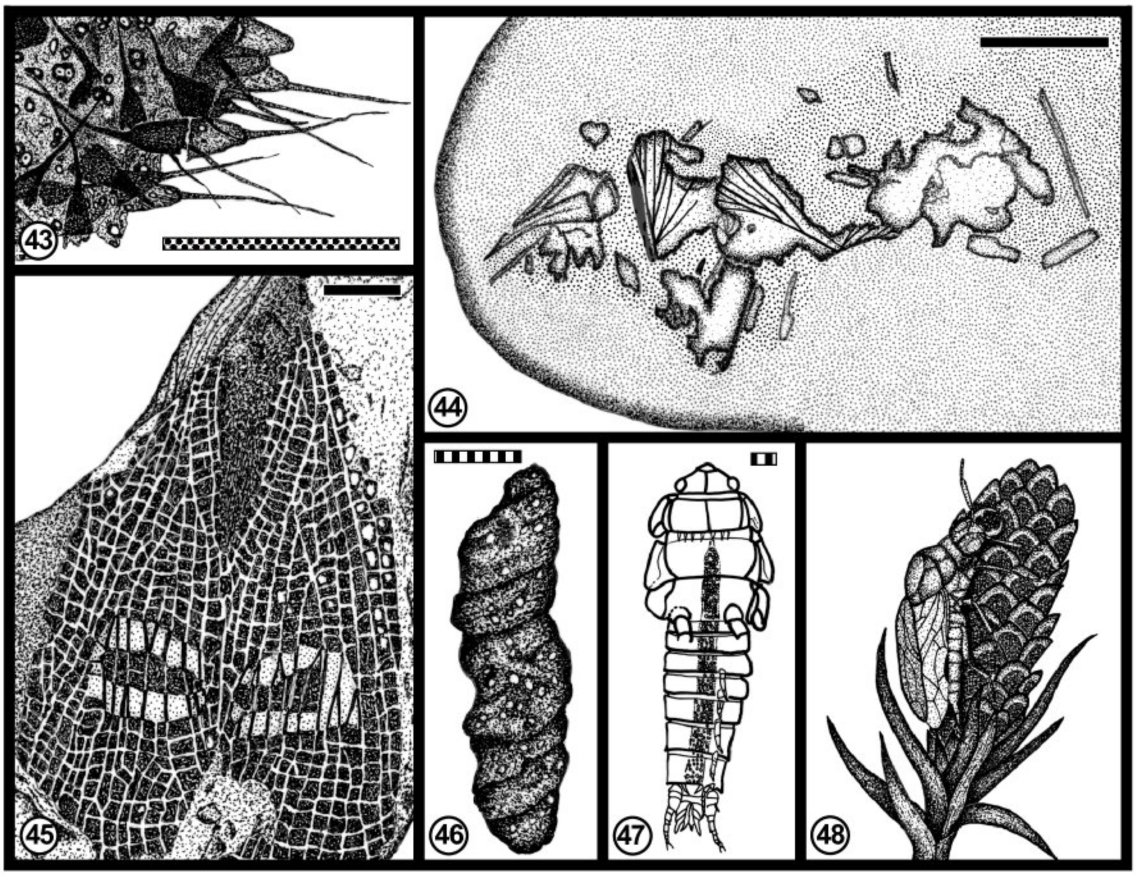

Figs. 43–48. Late Paleozoic evidence for predation (**43–45**) and palynivory (**46–48**). **43**: A fossil spider spinneret showing a cluster of attached and detached spigots, from the Middle Devonian (Givetian) of Gilboa, New York, U.S.A. (redrawn from Shear et al. 1989). **44**: A relatively large, probably odonatopteran coprolite containing remains of a dictyopteran, including wings, legs and an acuminate ovipositor at left. This specimen is from the late Middle Pennsylvanian of Mazon Creek, Illinois, U.S.A. (from Labandeira 2002b; FMNH PE 54114). **45**: From the same locality as Fig. 44, the insect *Protodiamphipnoa woodwardi* ("Protorthoptera": Cnemidolestidae), with prominent eyespots on forewings (redrawn from Carpenter 1969). **46**: A fusiform coprolite containing early land-plant spores from the Lower Devonian (Lochkovian) of Wales, U.K. (redrawn from Edwards et al. 1995; NMW 94.60G.18). **47**: A terrestrial insect nymph (Diaphanopterodea) from the same locality as Fig. 46, showing gut contents of pteridophyte spores (from Kukalová-Peck 1987). **48**: Reconstruction at approximately life-size of a Late Triassic conifer-insect association from Eurasia. The pollinivorous insect is *Archexyela smilodon* Rasnitsyn (Hymenoptera: Xyelidae), redrawn from an original by A.G. Ponomarenko (Rohdendorf & Rasnitsyn 1980). Depository abbreviations: FMNH, Field Museum of Natural History, Chicago, U.S.A.; NMW, National Museum of Wales, U.K. Scale bars: solid = 1.0 cm; striped = 01. cm, dotted = 0.01 cm.

Figs. 25–42. Spectrum of plant-hexapod and plant-mite associations (except for Fig. 35) from the Late Triassic (~ 226 Ma) Molteno Formation of the Karoo Basin in South Africa. Based on a preliminary survey, the illustrated plant damage types (DTs) listed below are assigned to the following functional feeding groups (FFGs): seed predation (DT73), external foliage feeding (DTs 1, 2, 12, 15, 30), galling (DT70), piercing-and-sucking (DT77), leaf mining (DT71), the nonfeeding but analogous FFG of oviposition (DTs 72, 108), and probable fungal or bacterial lesions (DT75). **25**: Seed predation (DT73) on the ginkgoalean platysperm seed *Avatia bifurcata* (Aasvoëlberg locality [Aas 411], BP/2/47798). **26**: Cuspate margin feeding (DT12) on the matatiellalean ginkgoopsid pinnule *Dejerseya lunensis* (Little Switzerland locality [Lit 111], PRE/F/22184). **27**: Cuspate and trenched and margin feeding (DTs 12, 15) on a pinnule of the umkomasialean peltasperm *Dicroidium crassinervis* (Kapokkraal locality [Kap 111], PRE/F/17597a). **28**: Hole feeding (DT50) on the gnetopsid nataligmalean leaf *Gontriglossa verticilliata* (Umkomas locality [Umk 111], PRE/F/465). **29**: Hole feeding (DTs 1, 2) on a leaf of the gnetopsid fraxinopsialean *Yabiella mareyesiaca* (Hlatimbe Valley [Hla 213], PRE/F/1207b). **30**: Slot-like trenched feeding (DT15) on the broadleaved voltzialean conifer *Heidiphyllum elongatum* (Aasvoëlberg locality [Aas 411], PRE/F/12625b). **31**: Small hole feeding (DT1) on unidentified foliage (Kapokkraal locality [Kap111], PRE/F/16344b). **32**: Polylobate surface abrasion (DT30) on *Dicroidium odontopteroides* (Kapokkraal locality [Kap111], PRE/F/17586). **33**: Oviposition insertions (DT76) on *H. elongatum* (Aasvoëlberg locality [Aas 411], PRE/F/12639). **34**: Oviposition scars (DT72) on the equisetalean stem *Equisetum nuwejaareensis* (Aasvoëlberg locality [Aas 411], PRE/F/22748). **35**: Probable fungal or bacterial lesion (DT75) on unidentified foliage (Kapokkraal locality [Kap 111], PRE/F/17579). **36**: Enlargement of a mature mite gall (DT70) on *D. crassinervis* (Aasvoëlberg locality [Aas 411], PRE/F/12387b). **37**: Two intermediate-stage mite galls (DT70) on pinnules of *D. crassinervis* (Aasvoëlberg locality [Aas 411], PRE/F/21908b). **38**: Two mature mite galls (DT 70) on pinnules of *D. crassinervis* (Aasvoëlberg locality [Aas 411], PRE/F/12392). **39**: Scale marks (DT77) on the stem of the equisetalean *Balenotheca linearifolia* (Umkomas locality [Umk 111], PRE/F/220a). **40**: Three elongate leaf mines (DT71), one aborted, on *H. elongatum* (Little Switzerland [Lit 111], PRE/F/5676). **41**: Four leaf mines (DT71) on a *H. elongatum* leaf (Little Switzerland [Lit 111], PRE/F/5709). **42**: Enlargement of leaf mine (DT71) on a *H. elongatum* leaf, showing particulate frass (PRE/F/5342). Taxonomy is after Anderson & Anderson (1983, 1989, 2003). All specimens are compressions or impressions on shale or mudstone. Figures are pen and ink drawings from enlarged photographic prints. Depository abbreviations: BP, Bernard Price Institute of the University of the Witswatersrand, Johannesburg, South Africa; PRE, South African National Biodiversity Institute in Pretoria. Scale bars: solid = 1 cm; striped = 0.1 cm; dotted = 0.01 cm. [Original illustrations]

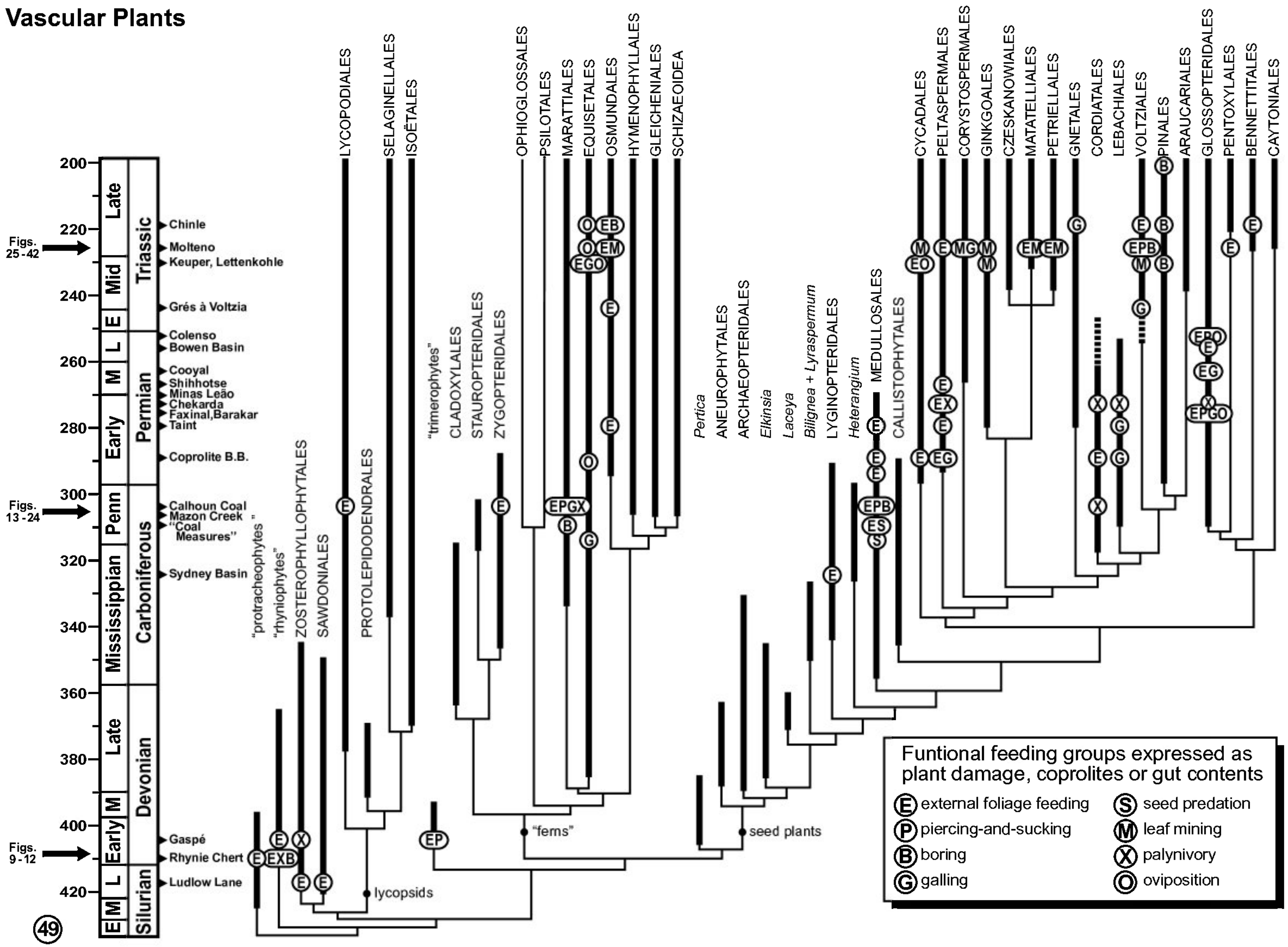

Fig. 49. Clades of vascular plants through the later Paleozoic and Triassic, indicating the occurrence of arthropod (almost entirely hexapod) mediated damage for the 20 or so biotas, most of which are listed in Fig. 1 (also see Tab. 1). Conventional clades are in upper case or italics if genera are used as exemplars; paraphyletic clades are in lower case and in quotes. Functional feeding groups (FFGs) are defined in LABANDEIRA (1998a, 2002a). These attributions are not exhaustive. Clade ranges after KENDRICK & CRANE (1997), ROTHWELL & SERBET (1994), and ANDERSON et al. (in press); phylogeny after KENDRICK & CRANE (1997), PRYER et al. (2004a,b), and HILTON & BATEMAN (2006). Geochronologic time scale is from GRADSTEIN et al. (2004); see Fig. 1 for abbreviations. [Original illustration]

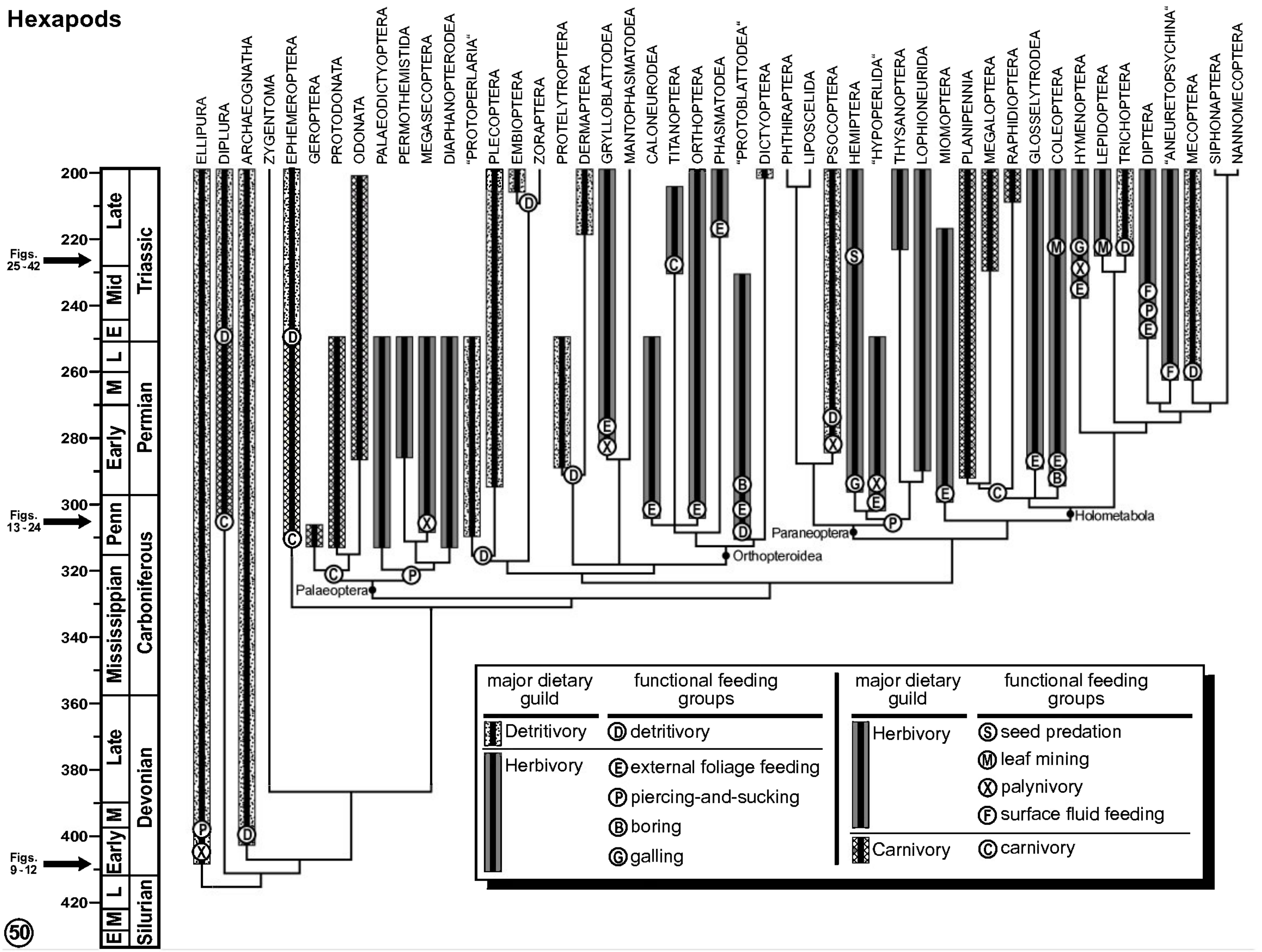

Fig. 50. Clades of Hexapoda through the later Paleozoic and Triassic, indicating the occurrence of major dietary guilds (detritivory, herbivory and carnivory) and major herbivore functional feeding groups. The position of the 20 or so biotas listed in Figs. 1 and 49 constitute most of the plant-damage data inferred for the various clades. These attributions are not exhaustive. Note the origination of seven clades during the earliest Pennsylvanian and the extinction of nine clades at the P-T event. Paraphyletic clades are in quotes. Clade ranges are after Labandeira (1994) and updates, Rasnitsyn & Quicke (2002), and Grimaldi & Engel (2005); phylogeny is modified after Grimaldi & Engel (2005). Relationships among some clades of ordinal rank are controversial, as is the Paleozoic and Mesozoic range of the Grylloblattodea. Geochronologic time scale is from Gradstein et al. (2004). [Original illustration]

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