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The Four Phases of Plant-Arthropod Associations in Deep Time

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ABSTRACT

Vascular-plant hosts, their arthropod herbivores, and associated functional feeding groups are distributed spatiotemporally into four major herbivore expansions during the past 420 m.y. They are: (1) a Late Silurian to Late Devonian (60 m.y.) phase of myriapod and apterygote, hexapod (perhaps pterygote) herbivores on several clades of primitive vascular-plant hosts and a prototaxalean fungus; (2) a Late Mississippian to end-Permian (85 m.y.) phase of mites and apterygote and basal pterygote herbivores on pteridophyte and basal gymnospermous plant hosts; (3) a Middle Triassic to Recent (245 m.y.) phase of mites, orthopteroids (in the broadest sense) and hemipteroid and basal holometabolan herbivores on pteridophyte and gymnospermous plant hosts; and (4) a mid Early Cretaceous to Recent (115 m.y.) phase of modern-aspect orthopteroids and derived hemipteroid and holometabolous herbivores on angiospermous plant hosts. These host-plant and herbivore associations are mediated by seven functional feeding groups: a) external foliage feeding, b) piercing-and-sucking, c) boring (Phase 1 origins); d) galling, e) seed predation, f) nonfeeding oviposition (Phase 2 origins); and leaf mining (early Phase 3 origin). Within about 20 m.y. of each herbivore expansion, there is a biota that expresses the nearly full spectrum of later plant-arthropod associations. These four associational phases may be linked to the paleoclimatologic variables of greenhouse/icehouse cycles and atmospheric O_2 and CO_2 levels by uncertain causes, although some relationship probably is present. The 7 functional feeding groups persist through most of the sampled interval but harbor host-plants and arthropod herbivores that are spatiotemporally ephemeral. Poor understanding of associations in Phases 1 to 3 is attributed to disproportionate focus on the angiosperm and holometabolan insect associations of Phase 4.

KEYWORDS | **Plant-insect-associations. Herbivory Fossil-record. Land plants. Insects. Paleoclimate.**

INTRODUCTION

The major macroscopic source for biodiversity on the planet is land plants and arthropods (Wilson, 1992; Schoonhoven et al., 2005). These two hyperdiverse clades, and to some extent, fungi, historically have provided the basic evolutionary history and ecological structure to continental (terrestrial + fresh water) ecosystems. Nowhere is the combination of taxonomic diversity and ecological richness better demonstrated than the varied plant-insect associations that have been documented for the fossil record during the latest wave of major terrestri-

alization that commenced about 420 m.y. ago, during the Late Silurian (Labandeira, 2005a). This major invasion of terrestrial environments has continued unabated to the Recent and has experienced a dramatic expansion in taxonomic speciosity, major clade diversity, biomass abundance, biogeographic colonization, and ecologic richness (Labandeira 2002a). Although these five measures are inextricably linked, it is ecological richness that provides the single most effective way of assessing how terrestrial ecosystems evolve in deep geologic time (Vermeij, 2004). In particular, it is an examination of plant-insect associations—which provides the paleobiological evidence for the fundamental interorganismic links of species within food webs, communities, and ecosystems—that is the central focus of this study.

The ecology of plant-insect associations is a significant aspect of modern ecological research, as illustrated by sections of ecological journals devoted to this topic. However, the intensity and broad scope of the study of modern plant-insect associations has not been matched by a parallel examination of the fossil record (Labandeira, 2005b). This disconnect is attributable mainly to an overwhelming paleobiological focus on the description, classification, and phylogenetic analyses of taxa, rather on the paleoecological associations of plants and arthropods. Recently, however, there has been a gradual and sustained, albeit limited, trend toward examination of plant-insect associations in the fossil record. These studies are characterizable into: (1) studies of a specific host plant interaction with an insect herbivore (Amerom and Boersma, 1971; Zhou and Zhang, 1989; Waggoner and Poteet, 1996), typically involving one or perhaps a few associations; (2) the examination of a particular insect herbivore functional feeding group, such as leaf mining, on multiple hosts within a flora of interest (Crane and Jarzembowski, 1980; Lang et al., 1995); or alternatively (3) the comparatively rare assessment of multiple herbivore associations on a single host-plant genus or species, such as Early Devonian *Psilophyton* DAWSON 1859 (Trant and Gensel, 1985; Banks and Colthart, 1993) or Late Pennsylvanian *Psaronius chasei* MORGAN 1959 (Labandeira, 1998c; Labandeira and Phillips, 1996a, 1996b); and (4) the comprehensive study typically of an entire flora and all of its herbivore associations, replete with a multitude of plant hosts and herbivore damage types. This fourth approach of evaluating bulk floras has variously focused on general qualitative examinations (Straus, 1977; Scott et al. 1985, Stephenson and Scott, 1992; Grauvogel-Stamm and Kelber, 1996; Ash, 1997; Castro, 1997; Glasspool et al., 2003), quantitative use of presence-absence data such as Scott and Taylor (1983) from a comparatively limited number of specimens representing a single plant-host taxon, to diverse bulk floras with explicitly described damage types (Labandeira et al., 2002a; Wilf and Labandeira, 1999; Wilf et al., 2005) or quantitative assessments of herbivorized versus original surface area (Beck and Labandeira, 1998; Adami-Rodrigues et al., 2004b), similar to examinations of extant plants (Wint, 1983; Coley and Barone, 1996). To date, there have been a sufficient number of such studies regionally and from the latest Silurian to the Pleistocene-Holocene boundary that a global data set now can be assembled and examined for coarse-grained patterns involving vascular plants, herbivorous arthropods, and their ecological associations. The results of these data provide the broadest view of how plant-arthropod associations have appeared, expanded, and contracted in terrestrial environments, resulting in the bewildering ecological richness of today (Wilson, 1992).

Although the data provided herein are comparatively coarse, it is my intention to provide a plant-arthropod associational baseline for Phanerozoic terrestrial ecosystems, by which finer patterns, involving taxonomically more circumscribed plant hosts and arthropod herbivores, can be further elucidated. In parts of this temporal-taxonomic-associational matrix where preservational potential is high and intervals of geologic time are relatively short, more taxonomically circumscribed plant-host clades, or lineages, can be specified and investigated for the evolution of their component communities of arthropod herbivores (Root, 1973; Futuyma and Mitter, 1996). As an alternative to this lineage-by-lineage "vertical" approach, a "horizontal" approach would examine the topology of a herbivore radiation or demise, such as the geochronologically sudden colonization of plant-host lineages by clades of arthropod herbivores, leading to particular types of stereotyped associations or specified lineages of insect gallers or leaf miners (Farrell, 1998; Wilf et al., 2000; Cook et al., 2002; Farrell and Sequeira, 2004). Fossil studies have the potential to provide paleobiological ground-truthing, such as calibration rates of colonization or extinction by comparing occurrences of taxa to known time intervals, or tests of evolutionary hypotheses regarding the origin and evolution of plant-insect associations (Fox, 1988; Boucot, 1990; Jermy, 1993; Farrell and Mitter, 1993; Thompson, 1994; Price, 1997; Vermeij, 2004; Schoonhoven et al., 2005). It should be noted that historically the plant host (paleobotanical), arthropod herbivore (paleoentomological), and associational (paleoecological) fossil records have been considered separate (Labandeira, 2002a), and have had minimal cross links for understanding how plants and arthropods actually have interacted in deep geologic time.

METHODS, DATA STRUCTURE, AND RATIONALE

This is the first compilation of published or otherwise personally observed associational data from the fossil record to provide plant hosts, types of associations, and

insect herbivores that are partitioned into discrete slices of time. The associational part of these data is expressed by the major types of feeding, known as functional feeding groups (Coulson and Witter, 1984; Labandeira, 1998a; Wilf and Labandeira, 1999). The plant-host taxa generally are provided at the conventionally accepted ordinal rank and the inferred arthropod herbivores are delimited by ordinal and superordinal ranks. The 7 functional feeding groups of plant-arthropod associations are a) external foliage feeding, b) piercing-and-sucking, c) boring, d) leaf mining, e) galling, f) seed predation, and g) oviposition. The first six are distinctive feeding strategies; the last one is not a feeding type, but rather a distinctive egg-laying strategy that involves endophytic insertion of eggs into plant tissues by a lancet-like device, the ovipositor (Wesenberg-Lund, 1913), and thus is included for completeness since it has a significant fossil record of plant damage (Béthoux et al., 2004). This examination of the 6 functional feeding groups and oviposition is supplemented by an earlier, separate study of palynivory and nectarivory (Fig. 1; Labandeira, 2000). The additional functional feeding groups of palynivory and nectarivory (surface fluid feeding) are not considered further in this study. The plant taxa and phylogenetic framework to which the 7 associations were assigned is based mostly on the recent work of Anderson et al. (in press) and Hilton and Bateman (2006).

A context for this contribution is provided by several studies of both plant diversity (Knoll and Niklas, 1987; Niklas et al., 1985) and insect diversity (Labandeira and Sepkoski, 1993; Jarzembowski and Ross, 1996; Dmitriev and Ponomarenko, 2002) through time that provide broad patterns of major clade origination, turnover and extinction during the past 420 m.y., based on taxa that are assumed to be or are monophyletic from then-current evaluations (See Labandeira [2005a] for the validity and indispensability of the taxic approach in understanding major patterns of insect diversity through time). Although there has been discussion regarding the more specific and focused associational relationships of these two hyperdiverse and interacting clades through time (Howe and Westley, 1988; Jolivet, 1998; Shcherbakov, 2000; Vermeij, 2004; Schoonhoven et al., 2005), modest attempts have demonstrated mostly anecdotal evolutionary patterns (Willemstein, 1987; DiMichele and Hook, 1992; Scott et al. 1992; Labandeira, 2002a; Zherikhin, 2002a, 2002b). This contribution adds to these studies by providing: (1) documentation of the major plant lineages through time and identification of particular, ecologically dominant host-plant clades; (2) a record of major arthropod herbivore lineages through time (myriapods and especially mites and hexapods), including their intervals of dominance; (3) determination of the temporal distribution of the basic functional feeding groups based principally on arthropod-mediated damage on plants; (4) a temporal framework in which these three records are geochronologically related, including recent absolute-age calibrations of the geologic time scale and stage-level correlations of relevant strata; and (5) a preliminary assessment of the role between global phases of herbivory and environmental variables such as atmospheric oxygen abundance and surface temperature.

Initial evaluation of the data was done by recording only those publications that had explicit and compelling photographic documentation. Personal observation by the author of unpublished plant-insect associational data also was included. Published and observational data included in the data base (see Appendix at www.geologica-acta.com) required demonstration of herbivory, often using multiple criteria, as opposed to detritivory (Labandeira, 1998a; Scott and Titchener, 1999). For most functional feeding groups, one or more of the following four criteria were present (Labandeira, 1998a). First, the presence of callus or other types of reaction tissue induced by trauma to a live plant should be demonstrated (Tovar et al., 1995). A second line of evidence, particularly for external foliage feeding, is the presence of micromorphological structures such as veinal stringers, necrotic tissue flaps, and contiguous cuspules within larger excisions that are caused by mandibulate chewing, or other features that indicate active feeding (Gangwere, 1966; Kazikova, 1985; Araya et al., 2000). Third is the presence of stereotyped feeding patterns that are consistent with known modern feeding types (Bodnaryk, 1992; Puplesis, 1994; Heron, 2003). The resulting plant-host damage types involve both a single, unique pattern by a host-specialist clade as well as a pattern that is convergently arrived at by different, often host-generalist, clades (see discussion in Labandeira et al. 2002a). Last, within diverse floras, distinctive plant-host specificity patterns and the targeting of particular tissue types can reveal herbivory that would not be expected from physically induced leaf injury such as wind damage or particle impact abrasion (Katterman, 1990; Vincent, 1990). In certain instances, criteria included links to known, highly distinctive, extant damage types (Opler, 1973), sometimes involving both conspecific larval and adult instars on the same host-plant species (Wilf et al., 2000). Collectively or singly, these four criteria effectively segregated herbivory from detritivory in almost all cases. Only in the case of boring in wood, was there often an absence of evidence for consumption of live tissue. However, since many holometabolous insect wood-borers live in live cambial tissue but also bore through dead secondary xylem, borings were included whose diameters indicate production by beetles or other holometabolous larvae. Excluded were borings attributed to detritivorous arthropods, such as termite galleries and all small diameter oribatid mite borings (Hueber and

Galtier, 2002), unless there was separate evidence for plant response tissues. Some groups of termites and mites are herbivorous (Krantz and Lindquist, 1979; Waller and La Fage, 1987), although their activities are more appropriately registered in the fossil record from the evidence of plant damage attributed to external foliage feeders or as identifiable contents of coprolites.

After herbivory was established by scrutiny of illustrated examples from the paleoecological literature, as well as personally examined material, these data were included in the Appendix (www.geologica-acta.com). The Appendix was partitioned into four subsets, each defined by the temporal ranges of major host-plant and plant-feeding arthropod clades. In particular, these separations into four principal intervals were based on a combination of: (1) temporal ranges of major dominant plant-host and arthropod-herbivore clades in the fossil record, (2) extinction or other major turnover events, whether of many individual clades or entire biotas, and (3) occasional intervals of ecologically distinctive associations not present in earlier or later biotas (Knoll and Niklas, 1987; Labandeira and Sepkoski, 1993; Stewart and Rothwell, 1993; Labandeira, 2002a).

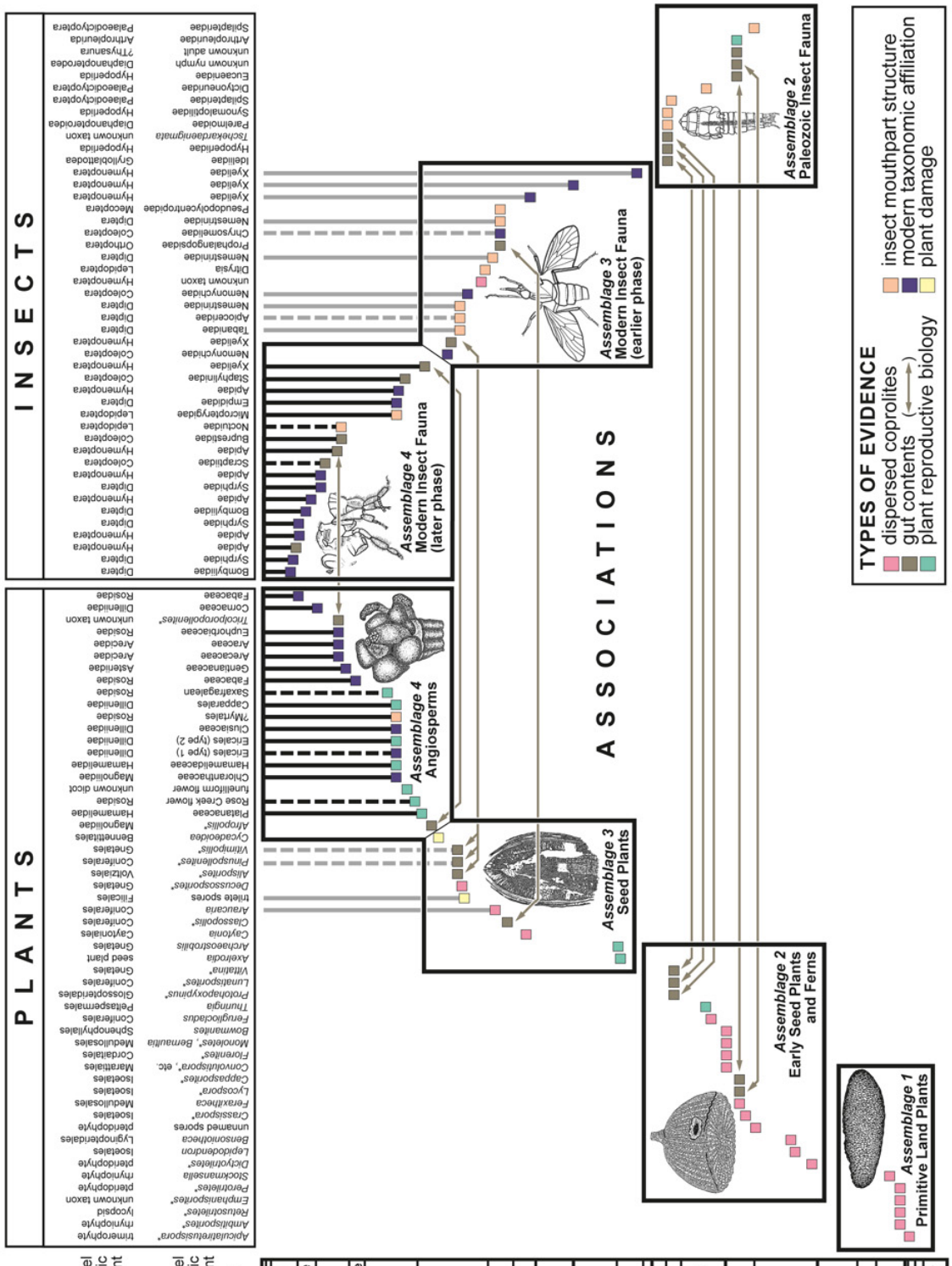
The relevant literature on fossil plant-insect associations was extensively but not exhaustively surveyed. In those instances where there were multiple duplicative literature citations documenting the same association or set of associations, only the most comprehensive or recent source, or both, were used. Occurrence data from this search (Appendix; www.geologica-acta.com) represents a 420 m.y. interval from the latest Silurian to the latest Pleistocene, and resulted collectively in 181 biotas possessing 424 separate associations. These biotas were allocated to 54 distinct, five-million-year bins of time based on age dates or stage-level correlations of each biota. These biotas range from a single association between a plant host and its arthropod herbivore (Karpiński, 1962; Amerom, 1966; Opler, 1982) to a few extensively studied biotas that contain numerous clades of damaged plant hosts, several types of associations, and a variety of inferred insect herbivores (Grauvogel-Stamm and Kelber, 1996; Ash, 1997; Wilf and Labandeira, 1999; Scott et al., 2004). However, for those specific host-plant taxa that harbored five or more functional feeding groups, a cutoff of four was used per cell for graphical clarity in figures 3-6. Collectively, most of the data qualitatively occurred between the two end-members of single occurrences and descriptions of multitudinous associations from a single, diverse biota.

The data (Appendix; www.geologica-acta.com) represent 60 major clades of tracheophyte plants that have been considered typically at an ordinal taxonomic rank, with the exception of higher-ranked Devonian plant lineages (Rothwell and Serbet, 1994; Hilton and Bateman, 2006). For reasons of completeness, particularly as it relates to the origin of the borer functional feeding group, a "woody" Devonian clade of massive, lignified fungi (*Prototaxites*) was added to the host list. For arthropod herbivores, which are dominantly insects, 18 major clades were included, which traditionally have been allocated to ranks from order to superorder. These clades of plant hosts and insect herbivores interacted with each other through 7 plant-arthropod functional feeding groups. The quality of assignments for these three elements was best for functional feeding groups, whose assignments were obvious; of high but somewhat lesser reliability was identification of the plant hosts; and the least reliable overall were the inferred insect herbivores, which occasionally lacked diagnostic plant-damage evidence that would confidently assign the potential culprit to a particular myriapod, mite, or insect clade.

TEMPORAL PATTERNS OF HERBIVORY

The temporal distribution of plant hosts, associations, and arthropod herbivores resulted in four distinctive herbivore expansion phases, paralleling in timing the previously identified "evolutionary assemblages" for palynivory and nectarivory (Labandeira, 2000; Fig. 1). Defining features of these assemblages are: (1) a temporally constrained and taxonomically distinctive suite of plant host-clades typically at the ordinal rank, (2) a similarly juxtaposed assemblage of arthropod herbivore clades that consumed or otherwise interacted with plant-host clades, and (3) the presence of a diverse, abundant, preservationally exceptional and associationally rich biota

FIGURE 1 | **A matrix of vascular plants, insects, and their associations for palynivory and pollination, placed in geochronological context. This matrix details the four evolutionary assemblages of palynivores, nectarivores, pollinators, and their host plants that are distinct at the highest taxonomic levels, discussed in Labandeira (2000). Fossil plant and animal taxa at top are those that display evidence for plant-insect associations, based on direct or indirect evidence from dispersed coprolites, gut contents, plant reproductive biology, insect mouthpart structure, plant damage, and modern taxonomic affiliation. Thin horizontal connectors are well-supported associations from identified insects with known plant palynomorphs as gut contents. Plant taxa with asterisks (*) are spores or pollen; a few Paleozoic taxa refer to form-genera of plant organs with known whole-plant taxonomic attributions. Taxa persisting to the present are indicated by bold vertical links, solid for Assemblages 3 and 4, respectively. The arthropod culprits of Assemblage 1 remain unknown and probably include arthropods other than insects, such as myriapods. This compilation includes the most prominent studies and is not complete. Modified from Labandeira (2000) to conform to recent changes of the geologic time scale (Gradstein et al., 2004); the two, topmost intervals of time of the Neogene are, from oldest to youngest, Pliocene and Pleistocene. Abbreviations: Miss.: Mississippian (or Early Carboniferous); Penn.: Pennsylvanian (or Late Carboniferous).**


PLANTS
INSECTS
ASSOCIATIONS
higher-level taxonomic assignment
lower-level taxonomic assignment
Epoch
Period
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Neog
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Cretaceous
Jurassic
Triassic
Permian
Carboniferous
Devonian
Silurian
Miocene
Oligocene
Eocene
Paleocene
Late
Early
Middle
Lopingian
Guadalup.
Cisuralian
Penn.
Miss.
Ludlow
Wenlock
Llandovery
0
50
100
150
200
250
300
350
400
Assemblage 1
Primitive Land Plants
Assemblage 2
Early Seed Plants and Ferns
Assemblage 3
Seed Plants
Assemblage 4
Angiosperms
Assemblage 2
Paleozoic Insect Fauna
Assemblage 3
Modern Insect Fauna (earlier phase)
Assemblage 4
Modern Insect Fauna (later phase)
TYPES OF EVIDENCE
dispersed coprolites
gut contents
plant reproductive biology
insect mouthpart structure
modern taxonomic affiliation
plant damage

early within the development of each of the four expansion phases. These biotas provide excellent examples of associational richness within each expansion phase, and can be considered as a "flagship" biota to which others within the same expansion phase can be compared (Table 1).

Herbivory in the Earliest Terrestrial Ecosystems

A controversial issue regarding the trophic structuring of early land-based ecosystems is the role of detritivores versus herbivores in channeling the primary production of land plants into the food web. An early view was that early land ecosystems were scaled-down or otherwise simple versions of extant ecosystems, containing the full compliment of major trophic groups, including herbivores. An alternative view is that the earliest ecosystems either lacked herbivores or the consumption of live plant tissues was insignificant (Shear and Selden, 2001; Habgood et al., 2004). Given the evidence, principally from coprolites and plant damage from several major Late Silurian–Middle Devonian biotas, the truth is somewhere in between, with detritivory and palynivory dominant and herbivory and carnivory subordinate. The earliest herbivory was a consequence of a few modes of feeding, but qualitatively much less than that of the subsequent Carboniferous (Labandeira, 2002a). This conclusion is based on the sparse occurrence of insect-mediated plant lesions or borings during the Late Silurian and Devonian (Labandeira, 1998a). The tracking of plant organs and the first instance of herbivory on them has a bimodal distribution (Fig. 2), suggesting a geologically earlier targeting of stems and spores but a delayed attack on roots, leaves, wood and seeds that was launched during the Late Mississippian–Middle Pennsylvanian (Iannuzzi and Labandeira, unpubl. data). Although many recognize herbivory in the early land plant record, a dissenting view holds that some of these damaged tissues were either mediated by abiological agents or may not constitute herbivory (Shear and Selden, 2001). There have been a significantly greater number of relevant studies of Pennsylvanian-age, when compared to Mississippian-age, floras (DiMichele and Hook, 1992), in addition to the fact that the Pennsylvanian is about one-third the duration of the Mississippian. Both of these factors may account for an intrinsically deficient record of herbivory during the Mississippian.

Another issue is what constitutes 'herbivory?' The long-standing view of insect ecologists is that herbivory is the '…consumption by animals of any plant parts, including foliage, stems, roots, flowers, fruits or seeds' (Schowalter, 2000). An alternative concept of herbivory is that only consumption of the vegetative parts of the plant constitutes herbivory, and that seeds, spores and pollen and possibly roots are an exception because they are either too nutritionally rewarding or too difficult to access for digestion (Shear and Selden, 2001). However, vegetative parts of a plant also represent continua between less digestible tissues (e.g. vascular strands) to tissues with greater nutritional value (e.g. mesophyll). Additionally, pollen and spore protoplasts are accessible by a variety of insects that extract their contents by a range of processes without subjecting the exterior grain walls to physical breakage (Scott et al., 1985; Oliveira et al., 2002). Thus, consumption of all live plant tissues is considered as herbivory, whereas the feeding on dead plant, fungal, and animal tissues is considered detritivory. It is this latter definition, proposed by ecologists, which provides the context for the initial herbivory on land (Figs. 1 to 3), as represented by Herbivore Expansions 1 and 2.

Temporal Lags between the Origin of Plant Tissues and their Herbivory

The Paleozoic fossil record of arthropod use of vascular plant tissues is one of plant-host histological diversification up to the Pennsylvanian, with minor to major temporal lags between the time of anatomical origin of particular tissues and the time of origin of their herbivore consumption (Fig. 2). In some cases during the Late Silurian to Early Devonian there was relatively sudden and early colonization by palynivorous herbivores of sporangia and their spores (Figure 1; Edwards et al., 1995; Habgood et al., 2004) by piercer-and-suckers of stems (Figure 2; Kevan et al., 1975; Banks and Colthart, 1993), and wood precursor tissues in the form of borings within the hardened basidiomycete fungus *Prototaxites* DAWSON 1859 (Hotton et al., 1996.). By contrast, subsequently derived tissues, occurring in organs such as roots, leaves, and seeds, originate from the later Early to Late Devonian, yet do not exhibit evidence for earliest herbivory until the Late Mississippian, representing lags from ~ 50 to 100 m.y. This latter herbivory event initiates Herbivore Expansion Phase 2, which includes folivory (Iannuzzi and Labandeira, unpubl. data), a second expansion of boring into the true wood of lignophyte vascular plants (Dunn et al., 2003), seed predation (Jennings, 1974), and roots (Labandeira, 2001). A similar lag also is evident at the commencement of Herbivore Expansion 3, in which the earliest example occurs from the early Middle to early Late Triassic, postdating the prior presence of relevant plant-host clades by several million years, especially true for the Karoo Basin of South Africa (Scott et al., 2004; Labandeira and Anderson, 2005.). Similarly, but perhaps more muted, was herbivore response that has been noted for the aftermath of the end-Cretaceous extinction within Herbivore Expansion 4, in which herbivore levels and richness during the latest Cretaceous were not reached until the Paleocene/Eocene boundary, some 10 m.y. after the extinction event (Wilf et al., 2001; Labandeira et al., 2002b). The existence of these lags between the initial

TABLE 1 | **Salient featuresof the four phases of herbivore expansion (excluding palynivory and nectarivory).**

Herbivore expansion phase, interval, and duration	Major host-plant-clades[1]	Major arthropod herbivore clades[1]	Early flagship biotas	Functional feeding groups	Number of associations	Number of biotas investigated	Number of 5 m.y. intervals
1. 420–360 Ma (~60 m.y.)	protracheophytes, trimerophytes, rhyniopsids, lycopsids, zosterophylls, pteridophytes, prototaxales[2]	myriapods, apterygotes	Rhynie	3	10	5	5
2. 335–251 Ma (~ 85 m.y.)	pteridophytes, stem spermatophytes, (crown spermatophytes)	myriapods, mites, apterygotes, palaeodictyopteroids[3] "prot-orthopteroids"	Calhoun	7	57	31	14
3. 245 Ma–present (245 m.y.)	pteridophytes, crown spermatophytes, (stem spermatophytes)	mites, orthopteroids, hemipteroids, early or plesiomorphic holometabolan clades	Molteno	8	95	56	33
4. 115 Ma–present (115 m.y.)	angiosperms, (pteridosperms), (conifers)	orthopteroids, hemipteroids, late or apomorphic holometabolan clades	Dakota	8	263	88	22

[1]See text for listing of subclades within these groups; parentheses indicate a subdominant clade of plant hosts; groups in quotes are paraphyletic.

[2]A columnar basidiomycete fungus (Hueber, 2001).

[3]A monophyletic clade united by unique mouthpart construction and consisting of the subclades Palaeodictyoptera, Megasecoptera, Diaphanopterodea and Dicliptera (Grimaldi and Engel, 2005).

appearance of available tissues and their initial consumption by arthropod herbivores may be a general feature of the plant-arthropod associational record.

Herbivore Expansion 1: Late Silurian to Mid-Carboniferous

Records of Herbivore Expansion 1 (Fig. 3), which persisted for about 60 m.y., originate from the coastlines of Euramerica (Appendix; www.geologica-acta.com). This phase consists of 5 examined biotas, each occurring in a five-million-year interval, but clustered toward the latest Silurian and Early Devonian. Three functional feeding groups (excluding palynivory; see Labandeira, 2000) and 10 discrete associations are present (Figs. 1 and 3; Table 1). Dominant host plants consist of basal clades of vascular plants, namely protracheophytes, trimerophytes, rhyniopsids, lycopsids, zosterophylls and pteridophytes, but also the massive basidiomycete *Prototaxites* (Hueber, 2001). Herbivorous arthropods probably were myriapods (diplopods and arthropleurids), mites, and to a lesser extent apterygote hexapods and possibly true insects. Four plant-arthropod associations are represented. These associations are external feeding (Trant and Gensel, 1985) and piercing-and sucking (Kevan et al., 1975; Banks and Colthart, 1993), both on photosynthetic tissues of stems; boring in the cortical and medullary tissues of the indurated axial organs of *Prototaxites* and piths of land plants (Kidston and Lang, 1921; Hueber, 2001); and palynivory of spores and sporangia (Edwards et al., 1995; Habgood et al., 2004; Figs. 1 to 3). The dominantly targeted plant host appears to be the Rhyniopsida. The dominant herbi-

vore group may have been subgroups of myriapods. The most pervasive association is external feeding on photosynthetic tissues. These sparse data document the relatively early origin of herbivory in terrestrial habitats within predominantly detritivore ecosystems (Labandeira, 2005a), and provide a reasonable spectrum of feeding types involved in the consumption of several available tissue types from primitive vascular-plants. Tissues or parts of organs that originated later during the Devonian, such as leaves for folivorous external feeders, wood for borers

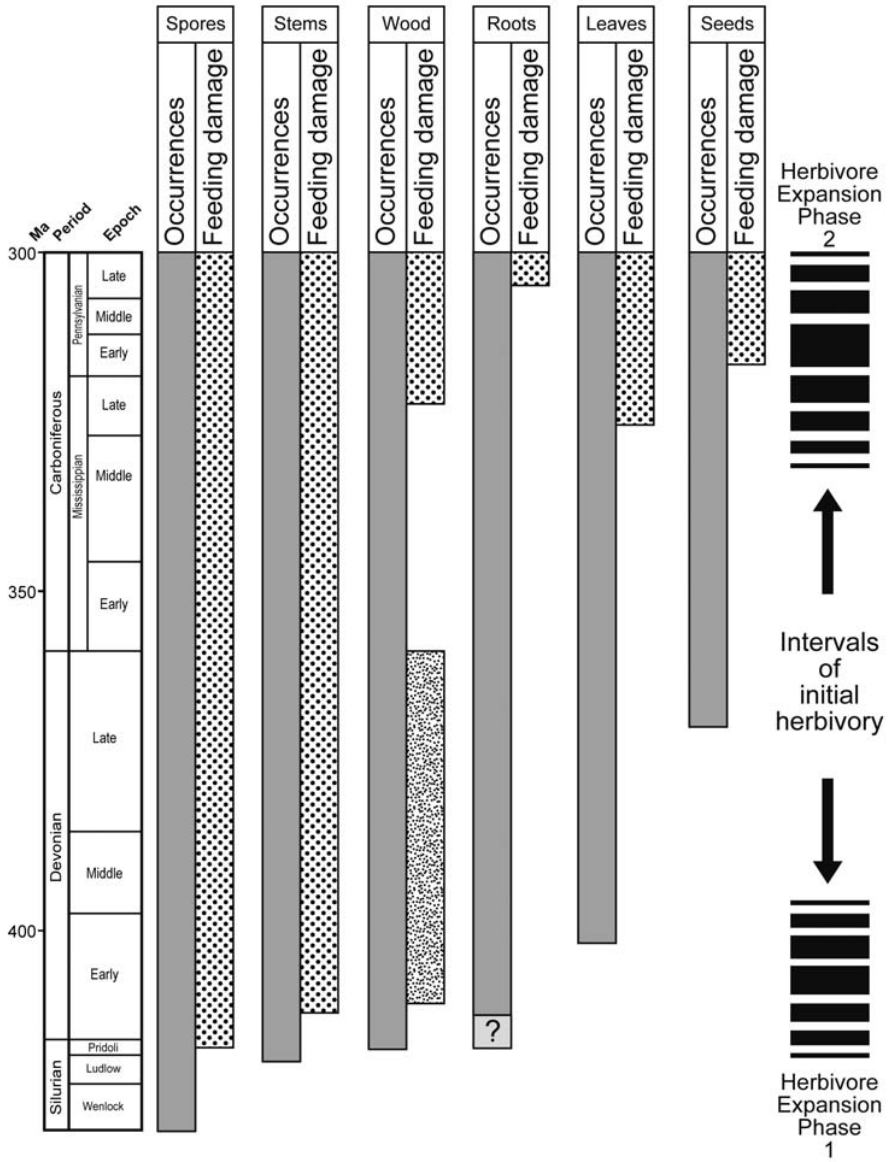


FIGURE 2 | **Occurrence data provided for the first appearance and initial herbivore colonization of six organ or tissue types. Colonization of Herbivore Expansion 1 includes consumption of spores (Edwards et al., 1995; Edwards, 1996; Habgood et al., 2004); consumption of stem tissues by both external feeders (Kevan et al., 1975; Trant and Gensel, 1985; Banks and Colthart, 1993) and by piercer-and-suckers (Kevan et al., 1975; Banks and Colthart, 1993); and borers of "woody" tissues in the form of lignified cortical and medullary tissues, depicted in Fig. 7. Borings occurred initially in vegetative portions of the massive basidiomycete fungus *Prototaxites* DAWSON 1859 (Hueber, 2001) that bear borings (Arnold, 1952; Hotton et al., 1996; Hueber, 2001; Labandeira pers. observ.), shown by the finely stippled Devonian pattern, and later as Late Mississippian and Pennsylvanian borings in plant hosts (Dunn et al., 2003), shown in the coarsely stippled pattern. These three latter functional feeding groups, and their plant hosts and inferred insect herbivores, are shown in Fig. 3. Note that *Prototaxites* is a fungus (Hueber, 2001), but served as an initial host for borers of lignified tissues, a functional feeding group that later may have independently re-evolved on lignophyte plants by a different arthropod clade. Herbivore Expansion 2 commences during the later Mississippian, and contains a second invasion of borings in indurated tissues (Dunn et al., 2003), this time on lignophytic seed plants (Kenrick and Crane, 1997). Additionally, there is evidence for the initial herbivory on leaves, or external foliage feeding (Iannuzzi and Labandeira, unpubl. data), initial seed predation (Jennings, 1974), and initial root feeding (Labandeira, 2001). Root feeding is very poorly documented in the fossil record, and is not included in any figure as a distinct functional feeding group.**

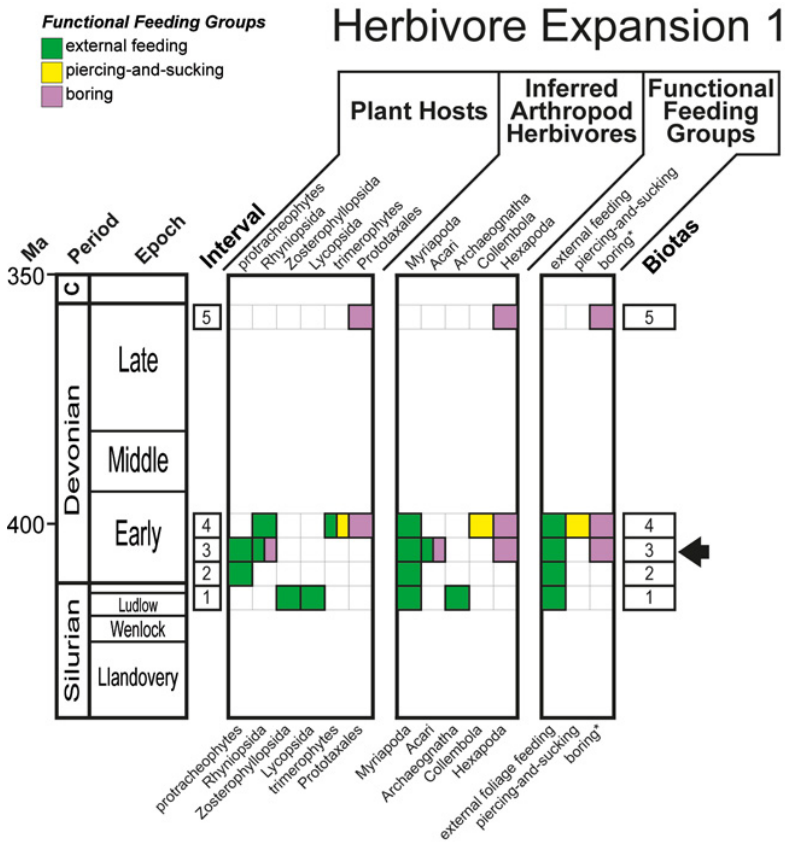


FIGURE 3 | **Herbivore Expansion 1. Illustrated is the distribution of functional feeding groups within specified biotas (at right), on accompanying plant hosts within specified five-million-year intervals (at left). Inferred insect herbivores are provided in a middle panel that link functional feeding groups with plant hosts within each binned interval. Color symbols for functional feeding groups (basic associations) are at upper-left, and apply throughout the chart to inferred insect herbivores and plant hosts for each successive 5-million-year interval ranging from the Late Silurian to Late Devonian. Arrow indicates the "flagship" associational biota for Expansion Phase 1, the silica permineralized Rhynie and Windyfield Cherts of Scotland; United Kingdom. See Fig. 1 for the distribution of a fourth functional feeding group, palynivory, not displayed herein. Plant-host clades are from Kenrick and Crane (1997); arthropod-herbivore clades are from Wheeler et al. (2004). Geologic time scale is after Gradstein et al. (2004). See Appendix at www.geologica-acta.com, Table 1, and text for additional details. Abbreviation: C: Carboniferous; uppermost stage of the Silurian is Přídolí.**

on more massive plant trunks, or seeds for seed predators, were not consumed until the beginning of Herbivore Expansion 2.

The early "flagship" biota for Herbivore Expansion 1 is the permineralized Rhynie and Windyfield Cherts from southern Scotland, of Early Devonian (Pragian) age (Trewin and Rice, 2004). These deposits are part of the Dryden Flags Formation, and are interpreted as preserved siliceous hot springs within a region of lacustrine and fluvial sedimentary environments (Trewin, 1994; Habgood et al., 2004). The associated biota consists of early land plants, a relatively diverse assemblage of freshwater and especially terrestrial arthropods, and a modest number of plant hosts and arthropod associations.

Herbivore Expansion 2: Mid Carboniferous to the Permo-Triassic Boundary

The earliest expression of Herbivore Expansion 2 (Fig. 4) is documented from two occurrences during the Late Mississippian. The older example is the earliest occurrence of external foliage feeding (Iannuzzi and Labandeira, unpubl. data), about 6 million years prior to the sudden and major increase in the taxonomic diversity of winged insects at the Mississippian-Pennsylvanian boundary (Brauckmann et al., 1995). The other consists of borings in plant axial tissues from slightly younger strata (Dunn et al., 2003). Notably, both occurrences are on pteridosperm taxa. Documentation for Phase 2, which lasted approximately 85 m.y., principally originates from Euramerica during the Early Pennsylvanian to mid Early Permian, particularly the interior peat-bearing basins in the eastern United States and western Europe and from Gondwanaland during the mid Early Permian to the latest Permian, especially the Karoo Basin of South Africa, the Sydney and Bowen Basins of Australia, and the Paraná Basin of east-central South America (Appendix; www.geologica-acta.com). This phase of distinctive herbivory documents 6 functional feeding groups (only leaf mining is absent), representing 57 separate associations from 31 biotas that occur among 14 five-million-year intervals. Palynivory is not included in this tabulation (Labandeira 2000). The dominant host plants consist of pteridophytes, mostly stem spermatophytes (seed plants), and to a lesser extent crown spermatophytes (sensu Hilton and Bateman, 2006) (Table 1; Figs. 1 and 4). Herbivorous arthropods are significantly more varied than those of Phase 1, and consist principally of myriapods, mites, and particularly paleopterous and neopterous insects, the latter two of which predominantly consist, respectively, of the monophyletic paleodictyopteroids and the paraphyletic

"protorthopterans." The plant-host clades that were most targeted overall by herbivorous arthropods were medullosan pteridosperms during the Pennsylvanian and Early Permian in Euramerica, and glossopterid pteridosperms throughout the Permian in Gondwana. Subordinately, Euramerican lyginopterid pteridosperms were attacked during the Pennsylvanian and cordaites in biogeographically disparate sites during the Late Pennsylvanian and Early Permian. One of the major trends of Herbivore Expansion 2 during the Pennsylvanian and Early Permian is the launching of herbivory on medullosan pteridosperms in Euramerica, which exhibits by far the greatest amount of herbivore-mediated damage, especially external foliage feeding, of any contemporaneous plant clade, both in terms of herbivorized pinnule area and frequency of attack (Greenfest and Labandeira, 1997; Beck and Labandeira, 1998; Labandeira, 2001). This phenomenon occurs both in compression floras, representing fluvial subenvironments, and peat-substrate wetland environments (Labandeira, 2001). In a similar way glossopterids were preferentially targeted during the Permian in Gondwana (Plumstead, 1963; Holmes, 1995; Adami-Rodrigues et al., 2004a). An interesting pattern is the relatively balanced distribution of all 6 associations (Fig. 4), with the exception of overall dominance by external foliage feeding.

The Calhoun Coal, from southeastern Illinois, U.S.A., of early Late Pennsylvanian (Kasimovian) age, is a member of the Mattoon Formation, and is a calcite permineralized coal-ball deposit representing a peat-swamp forest dominated by marattialean tree-ferns and subordinately by medullosan seed ferns (Labandeira, 2001). No known arthropod fauna has been found from this deposit, attri-

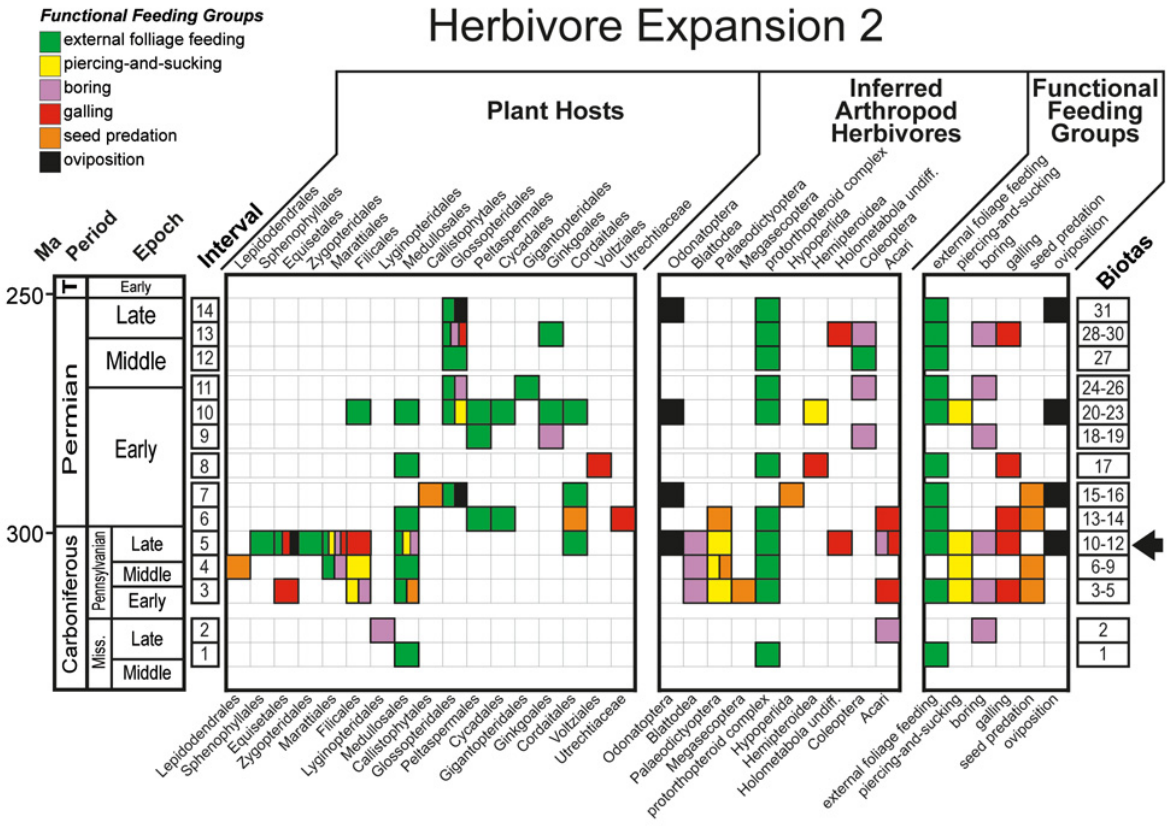


FIGURE 4 | **Herbivore Expansion 2. Illustrated is the distribution of functional feeding groups within specified biotas (at right), on accompanying plant hosts within specified five-million-year intervals (at left). Inferred insect herbivores are provided in a middle panel that link functional feeding groups (basic associations) with plant hosts within each interval. Color symbols for functional feeding groups are at upper-left, and apply throughout the chart to inferred insect herbivores and plant hosts for successive 5-million-year intervals ranging from the Late Mississippian (Early Carboniferous) to Late Permian. Arrow indicates the "flagship" associational biota for Expansion Phase 2, the carbonate permineralized Late Pennsylvanian (Late Carboniferous) Calhoun Coal of Illinois, U.S.A. See Fig. 1 for the distribution of an additional functional feeding group, palynivory, not displayed herein. Plant-host clades are from Rothwell and Serbet (1994) and especially Hilton and Bateman (2006); arthropod-herbivore clades are from Coddington et al. (2004) and especially Willmann (2004), except for the "protorthopteroid complex" which is either paraphyletic or monophyletic in the sense that the group is used herein. The Palaeodictyopteroidea is considered to be monophyletic, united with distinctive mouthpart characters, and consists of the subclades Palaeodictyoptera, Megasecoptera, Diaphanopterodea and Dicliptera (Grimaldi and Engel, 2005). Geologic time scale is after Gradstein et al. (2004). See Appendix at www.geologica-acta.com, Table 1 and text for additional details. Abbreviation: T: Triassic.**

butable to the apparent lack of chitin preservation. Nevertheless, the superb anatomical preservation of plant tissues in the Calhoun Coal has resulted in the most diverse assemblage of plant-insect associations for any known deposit of Herbivore Expansion 2 (Labandeira and Phillips, 1996a, 1996b, 2002). Evidence for insect-mediated herbivory is principally from varied types of anatomically preserved endophytic and exophytic plant damage that reveal details such as mouthpart stylet tracks, callus and other types of reaction tissue such as those from stylet tracks and galls, and diverse populations of coprolites whose contents preserve pollen, spores, and vegetative tissues assignable to both plant-host tissues and taxa. This evidence allows identification at the species level of almost all interacting host plants (Labandeira, 1998a, 1998c).

Although this account is concerned principally with plant-herbivore associations, the pattern of Paleozoic detritivore associations also expresses a significant expansion coincident with the second phase of herbivory. Commencing during the Middle Mississippian (Visean), particularly in Euramerican floras, there is a major increase of oribatid mite detritivory in a variety of host-plant and environmental settings (Rex, 1986; Scott, 1977; Scott et al., 1992; Labandeira et al., 1997; Tomescu et al., 2001), mixed with limited evidence for herbivory (Dunn et al., 2003). This degradation of a wide variety of Middle Mississippian plant tissues continued throughout the Paleozoic and was extensively supplemented during the later Mesozoic by clades such as termites and wood roaches (Labandeira et al., 1997; Nalepa et al., 2001).

Herbivore Expansion 3: Middle Triassic to Recent

The lower boundary of Herbivore Expansion 3 (Fig. 5) is probably the end-Permian event, coupled with major floral turnover during the Late Permian. The earliest evidence for Herbivore Expansion 3 is found in three principal regions during the Middle Triassic, but continues through the early Late Triassic. They are the southwestern United States (Walker, 1938; Ash, 1997, 2000, 2005), Western Europe (Linck, 1949; Roselt, 1954; Grauvogel-Stamm and Kelber, 1996), and the Karoo Basin of South Africa (Anderson and Anderson, 1989; Scott et al., 2004). This worldwide pattern extends into the Mesozoic and is supplemented with deposits from all continents. Herbivore Expansion 3 contains the full modern compliment of 7 functional feeding groups (Figs. 1 and 5; Table 1) that provide 95 distinct associations from 56 biotas that represent 33 five-million-year intervals. (Palynivory and surface fluid feeding are excluded from Fig. 5; Labandeira, 2000). Notably, unlike the other three major assemblages of plant-insect associations, Herbivore Expansion 3 has the longest persistence in geologic time, lasting for about 245 m.y. from the Middle Triassic to the Recent. It is likely that many of the Late Cretaceous to Neogene associations of Herbivore Expansion 4 were laterally transferred from angiosperm hosts onto the gymnospermous hosts of Herbivore Expansion 3, and thus are temporally distinct from the more ancient, Mesozoic associations such as those detailed by Farrell (1998).

The dominant host plants of Herbivore Expansion 3 are pteridophytes, crown spermatophytes, and, to a lesser extent, stem spermatophytes, the latter of which were experiencing replacement by more derived gymnospermous clades. Herbivorous arthropods comprise principally mites, orthopteroids (Orthoptera, Holophasmatodea), hemipteroids (Lophioneurida, Thysanoptera, Auchenorrhyncha, Sternorrhyncha) and early or otherwise plesiomorphic holometabolan clades (such as Archostemata, Nemonychidae, Belidae, Symphyta, Aneuretopsychina (sensu Rasnitsyn and Kozlov, 1991), Nemestrinidae, Archaeolepidae, Micropterygidae and Agathiphagidae). There is a distinctive evolution of major host-plant use by herbivores within Phase 3, beginning with a variety of ginkgoopsids, peltasperms, broadleaved voltzialean (e.g. *Heidiphyllum*) and podocarpalean (Podocarpaceae + Araucariaceae) conifers, and perhaps pteridophytes that were colonized during the Middle to early Late Triassic by all functional feeding groups (Anderson and Anderson, 1985; Grauvogel-Stamm and Kelber, 1996; Ash, 1997). This diversification was followed during the Jurassic to Early Cretaceous by a shift to a variety of cycads, non-voltzialean conifers, bennettitaleans and pentoxylaleans that were colonized by borers and subordinately by seed predators. Probable culprits for some of these associations include principally beetles (Crepet, 1974), such as the Obrieniidae (Klavins et al., 2005) and Nitidulidae (Nishida and Hayashi, 1996). Late Cretaceous to Neogene occurrences emphasize the conifer order Pinales (including "cupressoid" families) in which boring and seed predation virtually are the only remaining major associations (Fig. 5). The dominant insect herbivore taxon throughout Herbivore Expansion 3 is the Coleoptera, early Triassic occurrences of which emphasize external leaf mining, external foliage feeding, and especially boring on many broadleaved gymnospermous clades. Subsequently, there was the re-emergence of seed predation, and especially wood boring by saproxylic coleopterans during the Lower Cretaceous on pinaceous conifers (Jarzembowski, 1990; Falder et al., 1998; Ratzel et al., 2001). These clades, particularly the Curculionoidea, were involved in the recolonization of xylic substrates in pinaceous conifers and included invasion of cambial tissues. During the Neogene the emergence of galling Diptera, principally Cecidomyiidae (Labandeira, 2005c), supplemented existing associations. Throughout Phase 3, odonatopterans evidently oviposited in pteridophytes and a restricted variety of

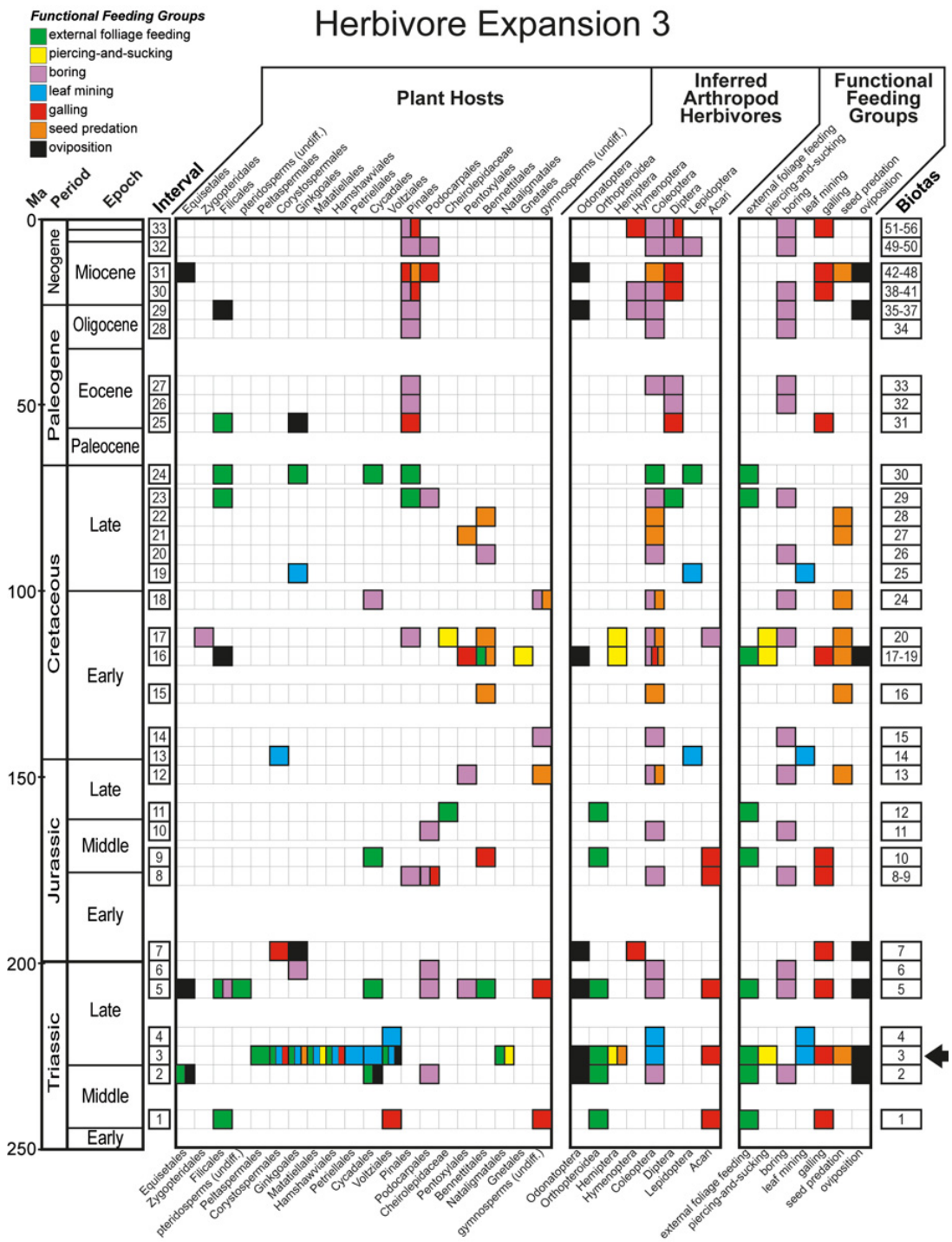


FIGURE 5 | **Herbivore Expansion 3. Illustrated is the distribution of functional feeding groups within specified biotas (at right), on accompanying plant hosts within specified five-million-year intervals (at left). Inferred insect herbivores are provided in a middle panel that link functional feeding groups (basic associations) with plant hosts within each interval. Color symbols for functional feeding groups are at upper-left, and apply throughout the chart to inferred insect herbivores and plant hosts for successive 5-million-year intervals ranging from the early Middle Triassic to the Recent. Arrow indicates the "flagship" associational biota for Expansion Phase 3, the compression Late Triassic Molteno Formation of South Africa. See Fig. 1 for the distribution of additional feeding groups, palynivory and nectarivory, not displayed herein. Plant-host clades are from Rothwell and Serbet (1994), Anderson et al. (in press) and especially Hilton and Bateman (2006); arthropod-herbivore clades are from Coddington et al. (2004) and especially Willmann (2004), with "Orthopteroidea" synonymous with his "Polyneoptera". Geologic time scale is after Gradstein et al. (2004); the two, topmost intervals of time of the Neogene are, from oldest to youngest, Pliocene and Pleistocene. See Appendix at www.geologica-acta.com, Table 1 and text for additional details.**

gymnospermous seed plants. Evidence for piercing-and-sucking is rare.

The Molteno Formation is of Late Triassic (Early Carnian) age that yields compression fossils of diverse plants and insects that geographically span much of the Karoo Basin of South Africa, and has been extensively examined since the late 1960's (Anderson and Anderson, 1983, 1985, 1989, 2003; Scott et al., 2004). This "flagship" deposit for Herbivore Expansion 3 contains about 100 anthropogenically unbiased and censused localities representing an estimated 180,000 plant-organ specimens (overwhelmingly leaves and seeds), many of which provide clear and abundant evidence for external foliage feeding, piercing-and-sucking, leaf mining (earliest known occurrence), galling, seed predation, and oviposition (Anderson and Anderson, 1989, 2003; Scott et al., 2004; Labandeira and Anderson, 2005). The major plant-host clades include sphenophytes, filicalean ferns, voltzialean conifers, peltasperms, cycads, subclades of ginkgoopsids that include ginkgoaleans, as well as pentoxylaleans, and gnetopsids (Anderson and Anderson, 2003; Anderson et al., in press; Hilton and Bateman, 2006). Several major habitats have been reconstructed from the floristic data: *Dicroidium* riparian forest (two types), *Dicroidium* woodland, *Sphenobaiera* woodland, *Heidiphyllum* thicket, *Equisetum* marsh, and a fern–*Kannaskoppifolia* meadow (Anderson et al., 1998; Anderson and Anderson, 2003). These taxonomic and community-level data indicate a diverse, ecologically heterogeneous ecosystem of several million years duration with extensive associations among insect herbivores (Scott et al., 2004; Labandeira and Anderson, 2005). The Molteno Formation overwhelmingly contains the most diverse associations of any deposit from Herbivore Expansion 3, and was present within 20 m.y. of commencement of the phase. The absence of any subsequent Jurassic or earliest Cretaceous biota with equivalent levels of associations as the Molteno is anomalous, and may be attributable to a poor fossil record or an intrinsic decrease in associational complexity in most ecosystems.

Herbivore Expansion 4: Mid Lower Cretaceous to Recent

The most recent and intensively studied phase of arthropod herbivory on vascular plants is Herbivore Expansion 4 (Fig. 6). This phase is synonymous with the angiosperm radiation, and their herbivore associations are predominantly with more apomorphic clades of hemipteroid and holometabolous insect orders. The 115 m.y. duration of this phase parallels the last half of Herbivore Expansion 3, although their temporal overlap suggests evolutionary host switching of herbivores to and from plant-host clades of both major expansions. This phase of herbivory contains 7 functional feeding groups representing 262 associations from 89 biotas among 22 five-million-year intervals. Palynivory and surface fluid feeding are excluded from the listed functional feeding groups (Labandeira, 2000). The primary data documenting Herbivore Expansion 4 is worldwide in origin, although the greatest concentrations of localities are in Western Europe and North America, primarily because of greater paleontological examination rather than a necessarily richer record. The relatively compact but even distribution of taxa and associations during this phase resembles that of Herbivore Expansion 2 of the late Paleozoic rather than that of the earlier and contemporary phase of Herbivore Expansion 3, the latter of which is twice as long-lived and displays a more open matrix of colonized plant-hosts, their herbivores and associations (Figs. 5 to 7). Interpretations of this latter pattern are that it either reflects a real biological signal, or alternatively represents an absence of investigation, particularly for the Jurassic and Early Cretaceous.

Twenty-eight orders of angiosperms, including a significant number of unassignable taxa, constitute the plant hosts for Herbivore Expansion 4. Nine identifiable plant-host orders have the most occurrences (Fig. 6), all of which bear the full or almost full spectrum of functional feeding groups and colonization by the major groups of arthropod herbivores. However, there is a threefold, successive pattern of insect colonization of families within each of these orders. First, the Laurales (Lauraceae, Chloranthaceae) and Proteales (Platanaceae, Trochodendraceae) have among the earliest occurrences but also have the most persistent record of colonization, well into the late Neogene. Second, the Saxifragales (Cercidiphyllaceae, Hamamelidaceae) represents a subsequent, later Cretaceous to mid-Eocene colonization. Third, the remaining six orders—Malpighiales (Malpighiaceae, Euphorbiaceae, Salicaceae), Fabales (Fabaceae sensu lato), Rosales (Rosaceae, Ulmaceae, Celtidaceae, Moraceae), Fagales (Fagaceae, Betulaceae, Juglandaceae, Myricaceae), Sapindales (Sapindaceae, Anacardiaceae, Rutaceae), and Ericales (Ericaceae, Theaceae, Sapotaceae)—have late Paleocene to Recent patterns of exploitation by arthropod herbivores that are represented by all functional feeding groups. The principal arthropod clades of interacting herbivores are orthopteroids (Orthoptera, Phasmatodea), crown-group hemipteroids (especially Sternorrhyncha and Heteroptera), and principally crown-groups of holometabolous insects (Polyphaga, Formicidae, Apoidea, Ditrysia, Cyclorrhapha). Notably, the density of functional feeding groups is more intense for Herbivore Expansion 4 than any of the three preceding or contemporaneous phases, and no particular dietary mode is dominant. Additionally, there is more partitioning of individual plant clades by multiple functional feeding groups and arthropod herbivores. For individual

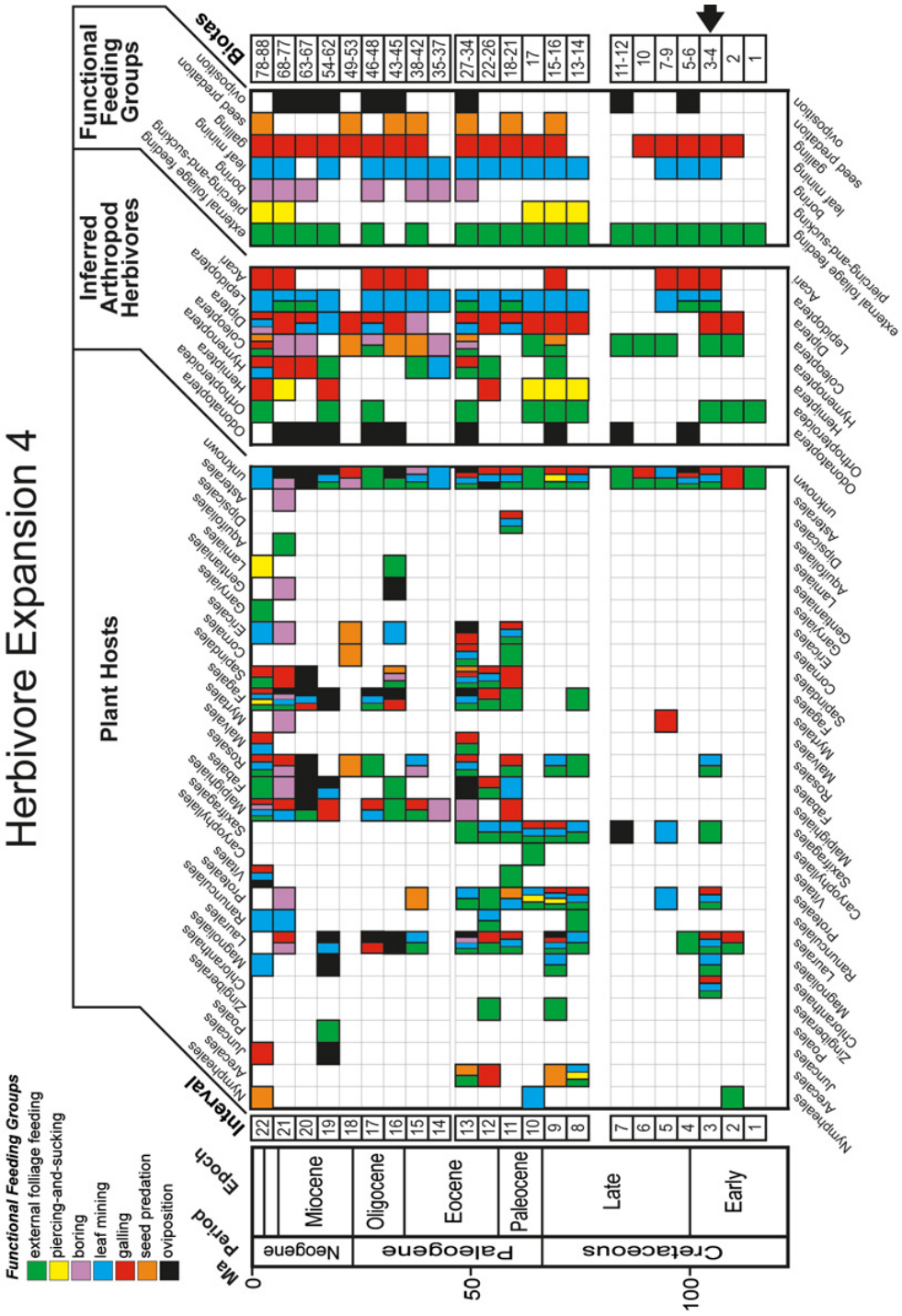


FIGURE 6 | **Herbivore Expansion 4. Illustrated is the distribution of functional feeding groups within specified biotas (at right), on accompanying plant hosts within specified five-million-year intervals (at left). Inferred insect herbivores are provided in a middle panel that link functional feeding groups (basic associations) with plant hosts within each interval. Color symbols for functional feeding groups are at upper-left, and apply throughout the chart to inferred insect herbivores and plant hosts for successive 5-million-year intervals ranging from the mid Early Cretaceous to the Recent. Arrow indicates the "flagship" associational biota for Expansion Phase 4, the compression latest Early Cretaceous Dakota Formation of Kansas, U.S.A. See Fig. 1 for the distribution of additional functional feeding groups, palynivory and nectarivory, not displayed herein. Plant-host clades are from Soltis and Soltis (2004); arthropod herbivore clades are from Coddington et al. (2004) and especially Willmann (2004), with "Orthopteroidea" synonymous with his "Polyneoptera". Geologic time scale is after Gradstein et al. (2004); the two, topmost intervals of time of the Neogene are, from oldest to youngest, Pliocene and Pleistocene. See Appendix at www.geologica-acta.com, Table 1 and text for additional details.**

functional feeding groups, external foliage feeding (Straus, 1977), leaf mining (Kozlov, 1988; Labandeira et al., 1994), galling (Scott et al., 1994) and oviposition (Hellmund and Hellmund, 2002b) have the greatest throughput and are present from the beginning of the angiosperm radiation. Curiously, piercing-and-sucking, boring and seed predation are relatively delayed, collectively appearing from the later Late Cretaceous to the middle Eocene. These patterns also occur on the unassigned plant hosts, which could represent a random sample of available plant hosts because of their uncertain and variable taxonomic affinities.

The Dakota Fm, the "flagship" biota for the Herbivore Expansion 4, spans the Early to Late Cretaceous boundary (late Albian to mid Cenomanian), and encompasses fluvial, deltaic and other terrestrial deposits bordering the east and west sides of the midcontinental seaway that extended from the Arctic Ocean to the Gulf of Mexico (Brenner et al., 2000; Wang, 2002). Sites from Kansas and Nebraska, U.S.A., of late Albian age (~103 Ma) represent coastal swamp, flood plain lake, and ox-bow channel deposits, and contain the earliest, highly diverse, abundant, and well preserved associations with angiosperms during their initial ecological radiation across a variety of lowland environments (Doyle and Hickey, 1976). The Dakota Formation probably has in excess of 300 species of vascular plants (Wang 2002) and many remain undescribed. Plant-insect associations from this important deposit have only recently been investigated (Stephenson, 1991; Scott et al., 1994; Labandeira et al., 1994; Labandeira, 1998b), but contain the earliest occurrences of leaf mines and among the earliest galls and external foliage feeding of any early angiosperm flora. There are virtually no insect body fossils.

Synchronicity of Herbivore Expansion Phases with Environmental Change?

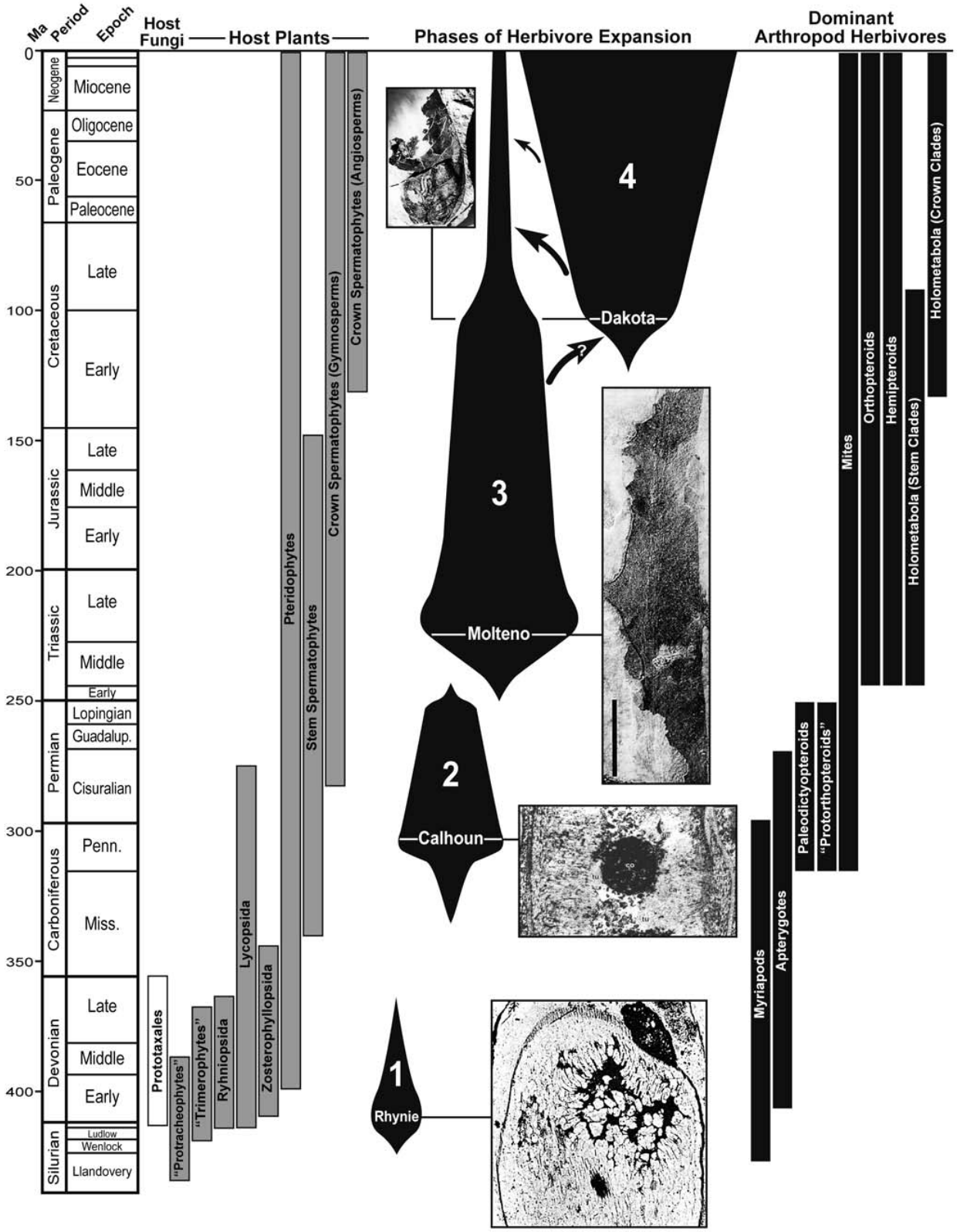
An obvious issue is whether the temporal distribution of the four herbivore expansion phases (Fig. 7) matches major cycles or otherwise aperiodic intervals of environmental change, such as paleoclimatologic shifts (Fig. 8). Three evident phenomena—greenhouse/icehouse cycles and associated global temperature and fluctuations in both atmospheric O_2 and CO_2 content—may have possible links with the four phases of herbivore expansion. These possible relationships could be mediated by an effect on underlying vegetation as a resource for arthropod herbivores. Data for establishing a greenhouse/icehouse world are from Frakes et al. (1992) and global temperatures are from Scotese (2005). Atmospheric O_2 levels are based on the sediment abundance model (Berner et al., 2000, 2003; Falkowski et al., 2005; see also Lenton, 2001). Atmospheric CO_2 levels are inferred from the data of Cornette et al. (2002), based on the ratio of historical CO_2 to recent CO_2, presented in Berner and Kothavala (2001). These data and their relationship to the four herbivore expansion phases are plotted in Fig. 8.

Herbivore Expansion 1 occurs from the Late Silurian to the Early Mississippian and is linked to a distinct combination of primitive, terrestrial vascular plant and arthropod clades. The earlier part of Phase 1 is associated with a greenhouse world that was gradually transformed midway to an icehouse world. Additionally, there are initially stable, high O_2 levels (22.5% to 25%) during the Late Silurian and Early Devonian that subsequently plummet to 13% by the early Late Devonian, compared to present value of 21%. Very elevated but highly fluctuating CO_2 levels characterize Phase 1 during the early to middle Devonian, but are followed by a sharp decline to modern levels during the Early Mississippian.

After an Early Mississippian hiatus occurring prior to Herbivore Expansion 2 (Ward et al., in press), there is a resurgence of herbivory during the Late Mississippian to the Permo Triassic boundary, similar to the previous phase by occupying a strong greenhouse world. Moreover, Phase 2 occurs during a broad, unimodal distribution of elevated atmospheric O_2 levels, starting with relatively depressed concentrations (~ 17 %), reaching an unprecedented peak of 31% during the Early Permian (but see Lenton, 2001), and decreasing to approximately current levels at the Permian-Triassic boundary. This decrease may explain major turnover of Permian plant clades. Atmospheric CO_2 was consistently low, comparable to modern levels throughout the Carboniferous and Permian, but experienced a sharp rise during the Triassic, in which there may have been a reorganization of the global carbon cycle, and thus resetting the CO_2 level at higher values (Berner, 2002).

Herbivore Expansion 3, from the Middle Triassic to the Recent, originates during an icehouse world and evolves into the anomalous greenhouse world of the Jurassic to mid Cretaceous, in which there evidently is latitudinal cooling but no polar icecaps. Atmospheric O_2 content during Phase 3 reaches its lowest levels of the past 420 m.y., fluctuating from 12.5 to 19% for Early Triassic to Middle Jurassic, only to remain flat (17% to 19%) for about a 100 m.y. interval from the Late Jurassic to mid Cretaceous, and rising during the past 50 m.y. to somewhat higher than present levels (23% to 21%). By contrast, atmospheric CO_2 levels are elevated at ~ 5% throughout the Triassic (Berner, 2002), followed by a modest increase to higher levels of ~ 9% during the Middle Jurassic, and thenceforth steadily declining to approximately the 0.035% preindustrial value of today.

Herbivore Expansion 4 occurs from the mid Early Cretaceous to the Recent. Unlike the initial part of Phase


Ma
Period
Epoch
Host Fungi
Host Plants
Phases of Herbivore Expansion
Dominant Arthropod Herbivores
0
50
100
150
200
250
300
350
400
Neogene
Paleogene
Cretaceous
Jurassic
Triassic
Permian
Carboniferous
Devonian
Silurian
Miocene
Oligocene
Eocene
Paleocene
Late
Early
Late
Middle
Early
Late
Middle
Early
Lopingian
Guadalup.
Cisuralian
Penn.
Miss.
Late
Middle
Early
Ludlow
Wenlock
Llandovery
Prototaxales
"Protracheophytes"
"Trimerophytes"
Ryhniopsida
Lycopsida
Zosterophyllopsida
Pteridophytes
Stem Spermatophytes
Crown Spermatophytes (Gymnosperms)
Crown Spermatophytes (Angiosperms)
1
Rhynie
2
Calhoun
3
Molteno
4
Dakota
?
Myriapods
Apterygotes
Paleodictyopteroids
"Protorthopteroids"
Mites
Orthopteroids
Hemipteroids
Holometabola (Stem Clades)
Holometabola (Crown Clades)

3, Phase 4 commences during a greenhouse world, and similarly evolves into a subsequent icehouse world of the Paleogene and Neogene. Unlike Phase 3, however, earlier Phase 4 associations occurred during somewhat depressed but stable O_2 levels (18% to 17%), peaking at 23% at 30 Ma (early Oligocene), and then declining but remaining high, reaching levels of 21% O_2 today. Atmospheric CO_2 levels begin with levels of ~ 7% during the Early Cretaceous, followed by a steady decline to the preindustrial values of 0.035%.

There is limited evidence that these three paleoclimatologic indicators have a rational, predictive combination of a greenhouse/icehouse switch that is linked to values of atmospheric O_2 and CO_2 (Veizer et al., 2000). However, it is not clear what the proximal cause is between the apparent synchrony of these three paleoclimatologic variables and each of the four herbivore expansion phases (Fig. 8). For example, the role of paleogeography remains unknown. It is known, though, that all phases except for Phase 3 began during periods of globally warm temperatures. One possibility is that these atmospheric variables have direct physiologic consequences on the selection and turnover of particular plant clades globally, which in turn elicit an associational response from selected clades of insect herbivores. The Early Cenozoic Thermal Maximum may be more a temporally restricted example of this phenomenon (Wilf et al., 2001). It remains untested whether a unique, combined signal of these three (or perhaps other) paleoclimatologic variables is explainable by plant or insect physiology (Lincoln et al., 1993; Graham et al., 1995), and if there is a trigger which resulted in phases of unique or augmented plant-insect associations. Modern studies from the experimental physiology of plants (Graham et al., 1995; Whittaker, 2001) and insects (Bartholomew and Casey, 1977; Loudon, 1988; Nicolas and Sillans, 1989; Hagner-Holler et al., 2004) that are subjected to fluctuating levels of O_2 and CO_2 may be relevant.

DISCUSSION

This compilation and the resulting matrices depicting the ecological associations of host plants and their insect herbivores in the fossil record have provided some basic macroevolutionary patterns. One is the presence of several fixed and persistent functional feeding groups of arthropod herbivores since they originated during the Late Paleozoic, or Triassic in the case of leaf mining. By contrast, the specific plant and arthropod occupants of these associations are ephemeral in time and space. Membership volatility is attributable to clade turnover of plants and their herbivore arthropods, as well as associated fungi, and perhaps other interacting organisms. This turnover provides a dynamic context to the evolution of not only associations among specific biotas within each of the four herbivore expansions, but also among each of the four major phases. Additionally, comparisons of the biogeography of these associations within and among penecontemporaneous floras of each phase may record the emergence and evolutionary radiation of arthropod herbivore clades. A potential example of hemispherical extent would be Gondwanan floras occurring in the same paleocontinental and similar basinal settings from Southern Africa, South America, Australia, India and Antarctica during the end of pteridophyte- and glossopterid dominated Herbivore Expansion 2, and the beginning of more diverse floras that were dominated by ginkgoopsid, voltzialean conifer, cycadophyte and gnetopsid taxa of Herbivore Expansion 3 (Fig. 7). It remains unknown whether similar plant hosts across the broad supercontinent of Gondwana shared similar herbivores in distant basins within each of these two phases, or if they evolved geographically distinctive suites of herbivores. A related issue is whether there is persistence of taxonomically conservative lineages of plant hosts and their insect herbivores through time, particularly among the preangiospermous portion of Herbivore Expansion 3 to the Recent. Such associational longevity may address whether some associations of today are truly ancient in origin (Farrell, 1998; Powell et al., 1998).

FIGURE 7 | **Summary of herbivore expansion phases in Phanerozoic continental environments. This figure is a condensation of, from left to right, plant host, plant-insect associational, and inferred insect herbivore patterns provided in figures 3 to 6. At left are major plant-host clades, based on classifications from Kenrick and Crane (1997), Rothwell and Serbet (1994), Judd et al. (1999), Soltis and Soltis (2004), Pryer et al. (2004) and Anderson and Anderson (2003). At right are the dominant arthropod herbivore clades that are based on classifications from Wheeler et al. (2004), Coddington et al. (2004), and Willmann (2004). An exception is the major fungal clade, Prototaxales, at far left. At center are the four, major expansion phases, based on associations from the literature, each of which has a "flagship" biota early in its development (Table 1). They are, from bottom to top: the first is Herbivore Expansion 1, with an axis of the rhyniopsid *Rhynia gwynne-vaughanii* KIDSTON and LANG 1917 containing a stem boring, from the Rhynie Chert (Early Devonian, Early Pragian) of Scotland (Kevan et al., 1975). Second is Herbivore Expansion 2, with a gall in the rhachis tissues of the marattialean fern *Psaronius chasei* MORGAN 1959, from the Calhoun Coal (Late Pennsylvanian, Kasimovian) of the Illinois Basin, Illinois, U.S.A. (Labandeira and Phillips, 2002). Third is Herbivore Expansion 3, with external foliage feeding on the matatiellalean ginkgoopsid *Dejerseya lunensis* (JOHNSTON) ANDERSON and ANDERSON 1989, from the Molteno Formation (Late Triassic, Carnian) of the Karoo Basin of South Africa (Scott et al., 2004). Last and fourth is Herbivore Expansion 4, with a leaf mine on the protealean (platanoid) *Sapindopsis beekeria* WANG 2002 from the Dakota Formation (Early Cretaceous, late Albian) of Kansas, U.S.A. (Labandeira et al., 1994; Wang, 2002). The absolute widths of each bubble do not necessarily conform to the absolute diversity of associations, but the relative distributions of widths among the four phases indicate relative importances. At right are major groups of interacting arthropod herbivores, namely clusters of clades that consist of myriapods, mites, and several insect lineages (Labandeira, 1994; Rasnitsyn and Quicke, 2002). Geologic time scale after Gradstein et al. (2004); the two, topmost intervals of time of the Neogene are, from oldest to youngest, Pliocene and Pleistocene.**

One observation that contextualizes this study involves the overwhelming focus by biologists on associations between angiosperms and holometabolous insects. This singular emphasis involves documentation of numerous associations and co-radiations between these currently hyperdiverse clades (Grimaldi, 1999; Grimaldi and Engel, 2005). This predilection is reasonable, as the overwhelming majority of extant associations available for study involve angiosperms and holometabolous insects from Herbivore Expansion 4. Those that may have survived from Herbivore Expansion 3 occur on conifers, cycads and possibly gnetaleans (Burdick, 1961; Norstog, 1987; Kato and Inoue, 1994) that have geographically unique or relictual distributions. Apparently, there are no extant associations from herbivore Expansions 1 and 2. This "angiocentrism" has clouded our understanding of the deeper history of plant-insect associations by limiting our understanding of how extinct host-plants and their insect herbivores have associated at deeper macroevolutionary timescales.

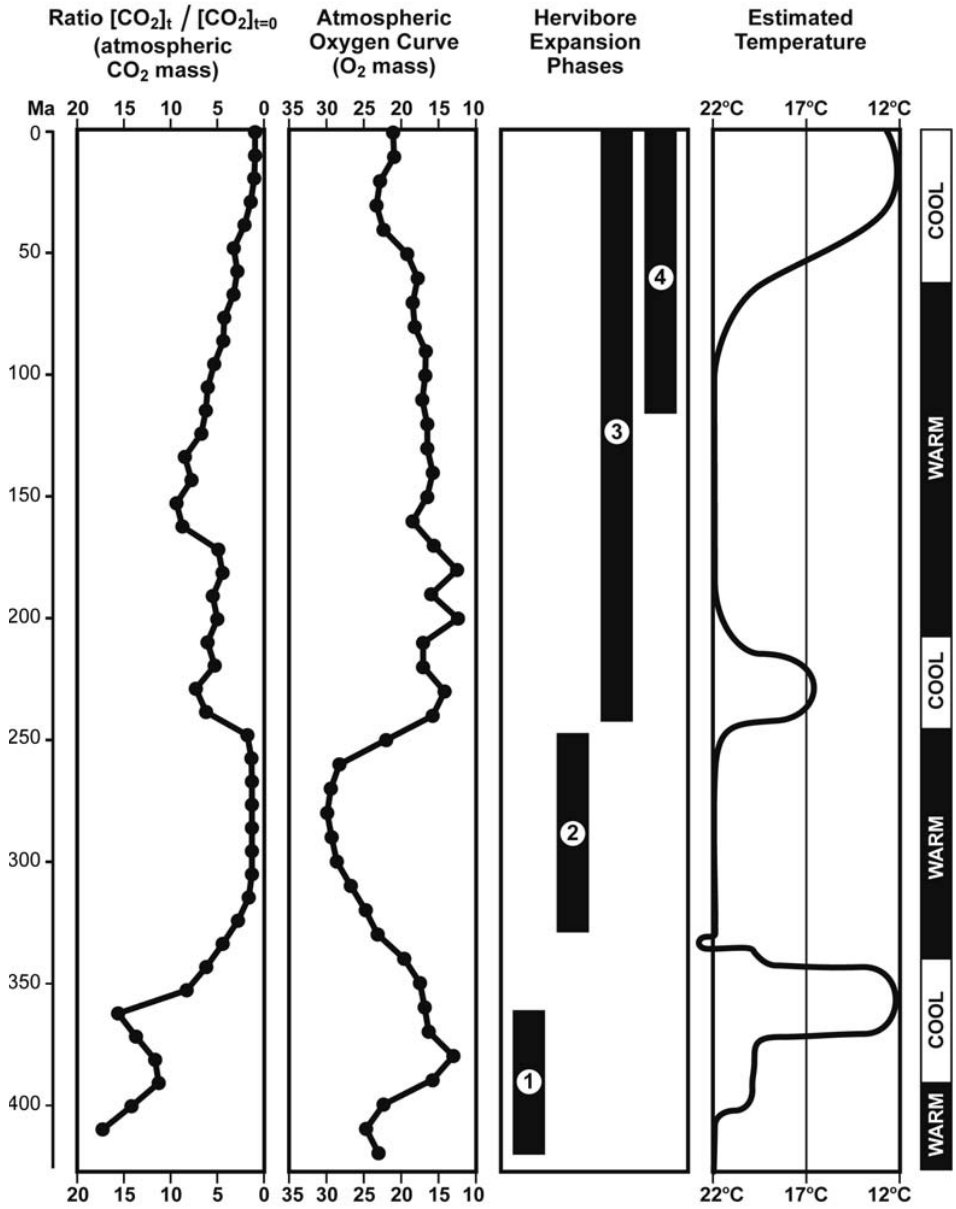


FIGURE 8 | **The relationship of Late Silurian to Recent physical variables—atmospheric O_2 and CO_2 content, and average global temperatures—with that of the four herbivore expansion phases, as determined by the fossil history of plant-insect associations. Atmospheric CO_2 ratios are from Berner and Kothavala (2001); atmospheric O_2 percentages from Falkowski et al. (2005) and Ward et al. (in press); average global temperature from Scotese (2005); and greenhouse/icehouse cycles are from Frakes et al. (1992).**

Current ecological studies of plant-arthropod associations thus focus overwhelmingly on plant-host taxa that are crown spermatophytes (angiosperms) and on insect herbivore taxa that are clades of crown-group Holometabola ("phytophagan" beetles, cyclorrhaphan flies, ditrysian moths, and aculeate hymenopterans) and to a lesser extent Hemipteroidea (especially sternorrhynchans and phytophagous bugs such as Lygaeidae, Coreidae, and Miridae; Fig. 7). Paleobiologically, this is a rather atypical situation, historically confined to the last fourth of the history of plant-arthropod associations. A retreat to Herbivore Expansion 3 would reveal taxa in which the crown spermatophytes of the time were various gymnospermous clades (several lineages of ginkoopsids, voltzialean and cheirolepidaceous conifers, peltaspermaleans, pentoxylaleans, bennettitaleans) and their arthropod herbivores were more basally positioned clades of holometabolous insects (polyphagan coleopterans, brachyceran flies, aneuretopsychid mecopterans, micropterygid to monotrysian lepidopterans, symphytan hymenopterans) and hemipteroids (thysanopterans, lophioneurids, sternorrhynchans, auchenorrhynchans). Would the partitioning and use of plant-host taxa be the same as those for Herbivore Expansion 4? Retreat yet one more phase to that of Herbivore Expansion 2, and the landscape of host plants then consisted of pteridophytes (especially marattialean ferns) and stem spermatophytes (dominantly medullosan and glossopterid pteridosperms and cordaitalean conifers), and the dominant phytophagous clades of arthropod herbivores were mites, apterygotes, paleodictyopteroids and a diverse assemblage of primitive "protorthopteroid" insects. How would the herbivore component community on a host plant dominant within Phase 2 compare ecologically with a component community of today's Phase 4? More specifically, could the varied associations seen among the Herbivore Expansion 4 be an ecologically similar or repackaged version of those from Herbivore expansions 2 or 3, but with different players?

CONCLUSIONS

Although this study is only a first attempt to understand the broad patterns of plant-arthropod associations in deep time, five conclusions are made. These conclusions can be considered as hypotheses that should engender additional analyses and testing though the gathering of additional data at finer spatiotemporal scales.

1. The fossil record of plant-insect associations can be organized into four, major, temporal phases. Each of these phases has a unique spectrum of major interacting clades of vascular-plant hosts and arthropod (overwhelmingly insect) herbivores.

2. Each herbivore expansion phase is typified by an early biota of exceptional associational richness that establishes most of the broad limits for subsequent associations and their modifications. This early expression, represented by a "flagship" biota, can be considered ecologically either as a rebound from an earlier event characterized by the demise of the previous herbivore expansion phase, or alternatively the origination of a fundamentally new major clade of host plants and insect herbivores without linkage to a causative environmental perturbation.

3. There are qualitative links between each of the herbivore expansion phases and three paleoclimatologic variables (greenhouse or icehouse world and atmospheric O_2 and CO_2 levels). However, no consistent or predictive pattern emerges that can explain the specific relationship between these paleoclimatologic variables and a particular herbivore expansion phase.

4. Associations persist through geologic time whereas the occupants of those associations are spatiotemporally constrained. This suggests that the several modes of arthropod feeding on vascular plant tissues are fixed, constrained possibly by plant tissue architecture and arthropod mouthpart structure, and thus displays extensive taxonomic and functional convergence.

5. An "angiocentric" focus on Herbivore Expansion 4 (angiosperms vs. crown holometabolans and hemipteroids) has had the effect of de-emphasizing patterns and processes of plant-arthropod associations during the preceding 300 million years. In particular, more understanding of herbivore expansions 1 through 3 is needed to comprehend the full breadth of how vascular plants and their arthropod herbivores historically have monopolized life on land.

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APPENDIX

Register of biotas for Figures 3 to 6

Herbivore Expansion 1

Biota	Locality	Stratigraphic placement	Time interval	Major references
1	Ludford Lane, Perton Lane, Welsh Borderland U.K.	Downton Castle Limestone	Silurian, Přídolí	Edwards et al. 1995; Edwards 1996
2	Brown Clee Hill, Welsh Borderland, Wales, U.K.	Old Red Sandstone, *micr-ornatus-newportensis* Spore Biozone	Devonian, Lochkovian	Edwards et al. 1995; Edwards 1996
3	Rhynie Chert, Aberdeen-shore, Scotland, U.K.	Dryden Flags Formation	Devonian, Pragian	Kidston and Lang, 1921; Kevan et al. 1975; Shear and Selden 2001; Habgood et al. 2004
4	Gaspé, Quebec, Canada	Battery Point Formation	Devonian, Emsian	Trant and Gensel 1985; Banks and Colthart 1993; Hotton et al. 1996; Hueber 2001; Labandeira, pers. observ
5	Kettle Point, Ontario, Canada	Huron Shale	Devonian, Famennian	Arnold 1952; Hueber 2001

Herbivore Expansion 2

Biota	Locality	Stratigraphic placement	Time interval	Major references
1	Sydney Basin, New South Wales, Australia	McInnes Formation	Mississippian, earliest Serpukhovian	Iannuzzi and Laban-deira, unpubli. data
2	White River, Washing-ton Co., Arkansas, U.S.A.	Fayetteville Formation	Mississippian, Serpukhovian	Dunn et al. 2003
3	Jackson Co., Illinois, U.S.A.	Caseyville Formation	Pennsylvanian, Bashkirian	Jennings 1974
4	Northumberland, England, U.K.	Coal Measures, below the Ashlington Marine Band	Pennsylvanian, late Bashkirian to early Moscovian	Thomas 1969; Amerom 1973
5	North-central England, U.K.	Coal Measures, below and above the Catharina Seam	Pennsylvanian, Moscovian	Holden 1910, 1930; Chaloner et al. 1991
6	Méricourt, Arras, France	"Assise de Bruay" unit	Pennsylvanian, middle Moscovian	Amerom and Boersma 1971
7	Zwickau, Germany	"Hellgrauer Schieferton"	Pennsylvanian, late Moscovian	Müller 1982
8	Saline and Gallatin Cos., Illinois, U.S.A.	Carbondale Formation, (Herrin Coal)	Pennsylvanian, late Moscovian	Labandeira and Phillips 2002
9	Mazon Creek, north-central Illinois, U.S.A.	Carbondale Formation, (Francis Creek Shale)	Pennsylvanian, late Moscovian	Scott and Taylor 1983; Labandeira and Beall 1990; Scott et al. 1992

10	Berryville, Lawrence Co., Illinois, U.S.A.	Mattoon Formation (Calhoun Coal)	Pennsylvanian, Kasimovian	Lesnikowska 1990; Labandeira and Phillips 1996a, 1996b, 2002; Roßler 2000; Labandeira, pers. observ.
11	La Magdalena Coalfield, León, Spain	[formation not reported]	Pennsylvanian, Gzehlian	Amerom 1966; Castro 1997
12	Graissessac, Hérault, France	"…between the Grand Pas and Burelle Coal Seams…"	Pennsylvanian late Gzhelian	Béthoux et al. 2004
13	Saar-Nahe Basin, Germany	Lower Rotliegende	Carboniferous-Permian boundary	Florin 1945; Meyen 1984; Kerp 1988; Zherikhin, 2002a
14	Chunya, Siberia Russia	[formation not reported]	latest Carboniferous	Sharov 1973; Zherikhin 2002a
15	Pingquan, Hebei Province, China	Taiyuan Formation	Permian, Asselian	Hilton et al. 2001, 2002
16	Faxinal and Morro do Papaléo, Rio Grande do Sul, Brazil	Rio Bonito Formation	Permian, Artinskian/Kungurian	Guerra-Sommer 1995; Adami-Rodrigues et al. 2004a, 2004b
17	Coprolite Bone Bed, Archer Co., Texas, U.S.A.	Nocona Formation	Permian, Sakmarian	Greenfest and Labandeira 1997
18	Chemnitz, Erzgebirge Basin, Sachsen, Germany	Leukersdorf Formation, "Zeisgwald-Tuff-Horizontes"	Lower Permian	Roßler1996
19	Gaines Co., Texas, U.S.A.	Clear Fork Group	Permian, late Artinskian	DiMichele et al. 2000
20	Ranigang Coalfield, West Bengal, India	Barakar Formation	Permian, Artinskian/Kungurian	Srivastava 1987
21	Taint, Baylor Co., Texas, U.S.A.	Waggoner Ranch Formation	Permian, Artinskian	Beck and Labandeira 1998
22	Chubut, Argentina	Río Genoa Formation	Lower Permian	Cúneo 1987
23	Minas do Leão, Rio Grande do Sul, Brazil	Irati and Serra Alta Formations	Permian, Kungurian/Roadian	Adami-Rodrigues and Iannuzzi 2001; Adami-Rodrigues et al. 2004a
24	Taiyuan City, Shanxi, Province, China	Shihhotse Formation	Permian, Kungurian /Roadian Boundary	Glasspool et al. 2003
25	King Co., Texas, U.S.A.	Blaine Formation	Permian, ?Roadian	DiMichele et al. 2004
26	Vereeniging, Gauteng, South Africa	Vryheid Formation	Permian, ?Roadian	Plumstead 1963; Amerom 1966
27	Cooyal, Sydney Basin, Australia	Upper Illawarra Coal Measures	Late Permian	Holmes 1995
28	Ranigang Coalfield,	Ranigang Formation	Late Permian	Srivastava 1996; Banerjee and Bera 1998
29	Northern Prince Charles Mountains, East Antarctica	Bainmedart Coal Measures	Late Permian	Weaver et al. 1997
30	Bowen Basin, Queensland, Australia	Rangal Coal Measures, Bandanna Formation	Permian, Wuchiapingian	McLoughlin 1994a, 1994b
31	Clouston Farm, KwaZulu-Natal, South Africa	Estcourt Formation	Permian, Changhsingian	Labandeira and Prevec, unpubl. data

Herbivore Expansion 3

Biota	Locality	Stratigraphic placement	Time interval	Major references
1	Grès-à-Voltzia, northern Vosges Mtns., France	Bundsandstein Formation	Triassic, Lower Anisian	Grauvogel-Stamm and Kelber 1996
2	Wasselonne, Bas-Rhine, France; Schleerieth and Ochsenfurt, Franconia, Germany	Lettenkohle and Lower Keuper Formations	Triassic, Upper Ladinian	Linck 1949; Roselt 1954; Geyer and Kelber 1987; Kelber 1988; Grauvogel-Stamm and Kelber 1996
3	Karoo Basin: KwaZulu-Natal, Eastern Cape and Northern Cape Provinces, South Africa	Molteno Formation	Triassic, Carnian	Anderson and Anderson 1989; Scott et al. 2004; Labandeira and Anderson 2005
4	Sydney Basin, New South Wales, Australia	Blackstone Formation	Triassic, Carnian	Tillyard 1922; Rozefelds and Sobbe 1987
5	Petrified Forest National Park, Arizona, U.S.A.	Chinle Formation	Triassic, Norian	Walker 1938; Ash 1997, 1999, 2000, 2005; Ash Savidge 2004; Creber and Ash 2004
6	Xiniguá, Rio Grande do Sul, Brazil	Santa Maria Formation	Triassic, Norian	Minello 1994
7	Küfner, Bavaria, Germany	"Pflanzensandstein"	Jurassic, Hettangian	Weber 1968; Van Konijnenburg-Van Cittert and Schmeißner 1999
8	Yima, Henan Province, China	Yima Formation	Jurassic, Toarcian to Aalenian	Zhou and Zhang 1989
9	Murlipahar, Bihar, India	Dubrajpur Formation	Jurassic, Aalenian	Vishnu-Mittre 1957; Sharma and Harsh 1989
10	Yorkshire, northern England, U.K.	Scarborough Formation	Jurassic, Bajocian	Harris 1942; Alvin et al. 1967; Scott et al. 1992
11	Jaramillo, Santa Cruz Province, Argentina	La Matilde Formation	Jurassic, Callovian to Oxfordian	Genise and Hazeldine 1995
12	Mikhailovka, Chayan District, Kazakhstan	Karabatsu Formation	Jurassic, Kimmeridgian	Rasnitsyn and Krassilov 2000
13	Steiner, Mt. Ellen, and East McElmo Creek localities, Western Interior, U.S.A.	Morrison Formation	Jurassic Tithonian	Tidwell and Ash 1990; Tidwell and Medlyn 1992; Dayvault and Hatch 2003
14	Clack Island, northern Queensland, Australia	Battle Camp Formation	Latest Jurassic to earliest Cretaceous	Rozefelds 1988a
15	Crowborough, East Sussex, England, U.K.	Waldhurst Clay or Ashdown Formation	Cretaceous, late Berriasian to middle Valanginian	Jarzembowski 1990
16	Przenosza, Limanowa District, Poland	?Verovice Shale	Cretaceous, ?Barremian	Reymanówna 1960, 1991
17	Makhtesh Ramon, Negev, Israel	Hatira Formation	Lower Aptian	Krassilov et al. 2004b
18	Chunakhal and Hiranduba, Jharkhand State, India	Rajmahal Formation (Intertrappean Beds)	Cretaceous, Aptian/Albian boundary	Banerji 2004
19	Amarjola, Bihar State, India	[formation not reported]	Lower Cretaceous	Bose 1968

20	Glen Rose, Somervell Co., Texas	Glen Rose Formation	Aptian/Albian boundary	Watson 1977
21	Yuleba, Queensland, Australia	Mooga Sandstone	Lower Cretaceous	Tidwell and Rozefelds 1991
22	Hokodz, northwestern Caucasus Region, Russia	*Diadochoceras nodosocostatum* and *Acanthoplites bigoureti* Zone	Cretaceous, upper Albian	Falder et al. 1998; Ratzel et al. 2001
23	Blackhawk, Black Hills South Dakota, U.S.A.	"Sandstones"	Lower Cretaceous	Wieland 1906; Delevoryas 1968; Crepet 1974; Crowson 1976
24	Valcheta, Rio Negro, Argentina	[formation not reported]	Late Cretaceous	Andreis et al. 1991; Genise 1995
25	Nammoura, Mont-Liban District, Lebanon	"Namoura Plattenkalk"	Cretaceous, Cenomanian	Krassilov and Bacchia 2000
26	Shuparo Lake, Hokkaido Japan	Yezo Group	Cretaceous, Cenomanian to early Santonian	Saiki and Yoshida 1999
27	Ohyubari, Hokkaido Japan	Yezo Group	Cretaceous, Late Turonian to Early Campanian	Nishida and Hayashi 1996
28	Brannen Lake, Vancouver Island, British Columbia, Canada	Haslam Formation	Cretaceous, lower Campanian	Stockey and Rothwell 2003
29	Big Cedar Ridge, Wyoming, U.S.A.	Meeteetsee Formation	Cretaceous, early Maastrichtian	Wing et al. 1993; Labandeira et al. 1995
30	Williston Basin, southwestern North Dakota, U.S.A.	Hell Creek Formation	Cretaceous, late Maastrichtian	Labandeira et al. 2002a, 2002b
31	Republic, Ferry Co., Washington, U.S.A.	Klondike Mountain Formation	Paleogene, Ypresian	Labandeira, pers. observ.
32	Baltic amber; Baltic Region, northern Europe	Prussian Formation	Paleogene, Lutetian	Conwenz 1890
33	Geodetic Hills, Axel Heiberg Island, Nunavut, Canada	Buchanan Lake Formation	Paleogene, Lutetian	Labandeira et al. 2001
34	Dynów, Skole Nappe, Outer Carpathians, Poland	Kliwa Sandstone	Paleogene, Rupelian	Rajchel and Uchman 1998
35	Klepzig, Germany	"lignite"	Paleogene, middle Oligocene	Linstow 1906
36	Rott, Schwaben, Germany	"porcellanite"	Paleogene, Chattian	Hellmund and Hellmund 1991
37	Freilendorf, Hessen, Germany	"lignite"	Paleogene Chattian	Roselt and Feustel 1960
38	Southern Limburg, Netherlands	[formation not reported]	Neogene, late Miocene	Süss 1979, 1980
39	Szentgal, Hungary	"lignite"	Neogene, Tortonian	Dudich 1961
40	Konin, Poland	"lignite"	Neogene, Tortonian	Madziara-Borusiewicz 1970
41	Düren, Nordrhein-Westfalien, Germany	"lignite"	Neogene, ?early Miocene	Möhn 1960
42	Bohemia, Czech Republic	[formation not reported]	Neogene, ?early Miocene	Engelhardt 1876

43	Wieliczka, Poland	Salzstocke Formation	Neogene, ?early Miocene	Zablocki 1960
44	Clarkia, Latah Co., Idaho, U.S.A.	Latah Formation	Neogene, middle Miocene	Lewis 1985, Lewis et al. 1990b
45	Emerald Creek 1, Benewah Co., Idaho, U.S.A.	Latah Formation	Neogene, middle Miocene	Lewis et al. 1990b
46	Emerald Creek 2, Shoshone Co., Idaho, U.S.A.	Latah Formation	Neogene, middle Miocene	Lewis et al. 1990b
47	Oviatt Creek, Clearwater Co., Idaho, U.S.A.	Latah Formation	Neogene, middle Miocene	Lewis et al. 1990b
48	Juliaetta, Nez Perce Co., Idaho, U.S.A.	Latah Formation	Neogene, middle Miocene	Lewis et al. 1990a
49	Jasper Creek, Yellowstone National Park, Wyoming, U.S.A.	[formation not reported]	Neogene, Messinian	Brues 1936
50	Guntramsdorf, Austria	"Congeriensand"	Neogene, lower Pliocene	Abel 1933
51	Königsbruck, Alsace, France	[formation not reported]	Neogene, middle to upper Pliocene	Geissert et al. 1981
52	Peary Land, northern Greenland, Denmark	Kap København Formation	Neogene, Pliocene/Pleistocene Boundary	Böcher 1995
53	Scarborough, Ontario, Canada	interglacial clays	Neogene, Pleistocene	Scudder 1900
54	Washington, District of Columbia, U.S.A.	unconsolidated sediment	Neogene, Pleistocene	Berry 1924; Gagné 1968
55	Santa Cruz Island, California, U.S.A.	Santa Cruz Island Formation (alluvial deposits)	Neogene Pleistocene	Chaney and Mason 1934
56	Near Fairbanks, Alaska, U.S.A.	Goldstream Formation	Neogene, late Pleistocene	Péwé et al. 1997

Herbivore Expansion 4

Biota	Locality	Stratigraphic placement	Time interval	Major references
1	Kiowa Co., Kansas, U.S.A.	Cheyenne Formation	Cretaceous, lower to middle Albian	Stephenson 1991
2	Stump Neck, Maryland, U.S.A.	Patapsco Formation	Cretaceous, middle to upper Albian	Hickey and Doyle 1977; Larew, 1992
3	Quantico, Virginia, U.S.A.	Potomac Group, unassigned	Cretaceous, middle to upper Albian	Upchurch et al. 1994
4	Rose Creek, Hoisington, Linnenberger Ranch, and Acme localities, Kansas and Nebraska, U.S.A.	Dakota Formation	Cretaceous, late Albian	Stephenson 1991; Labandeira et al. 1994; Labandeira 1998b; unpubl. data
5	Cumberland, Lincoln Co., Wyoming, U.S.A.	Frontier Formation (lower)	Cretaceous, early Cenomanian	Stephenson 1991
6	Tumbler Ridge, east-central British Columbia, Canada	Dunvegan Formation	Cretaceous, early Cenomanian	Crabtree 1987

7	Vyserovice, Lidice, Kounice and other localities, Bohemia, Czech Republic	Perucer Formation	Cretaceous, middle Cenomanian	Frič 1882, 1901; Stephenson 1991
8	Karatau, Kzyl Dzhar Region, Kazakhstan	Beleutinskaya Formation	Cretaceous, Turonian	Kozlov 1988
9	Gerofit, Negev, Israel	Gerofit Formation	Cretaceous, middle Turonian	Krassilov et al., 2004a
10	Cumberland, Lincoln Co., Wyoming, U.S.A.	Frontier Formation (upper)	Cretaceous, late Turonian	Knowlton 1917; Crabtree 1987
11	"Oilfield Coulee", Madison, Co., Montana, U.S.A.	Two Medicine Formation	Cretaceous, lowermost Campanian	Crabtree 1987
12	Gaillard, Crawford Co., Georgia, U.S.A.	Gaillard Formation	Cretaceous, late Santonian	Lupia et al. 2002
13	Big Cedar Ridge, northwest Wyoming, U.S.A.	Meeteetsee Formation	Cretaceous, early Maastrichtian	Wing et al. 1993; Labandeira, pers. observ.
14	Bisti Badlands, New Mexico, U.S.A.	Fruitland Formation	Cretaceous, late Campanian	Tidwell et al. 1981
15	Valcheta, Rio Negro, Argentina	[formation not reported]	Late Cretaceous	Andreis et al. 1991; Genise 1995
16	Williston Basin, southwestern North Dakota, U.S.A.	Hell Creek Formation	Cretaceous, late Maastrichtian	Wilf et al. 2000; Labandeira et al. 2002a, 2002b
17	Williston Basin, southwestern North Dakota, U.S.A.	Fort Union Formation (lower)	Paleogene, Danian	Labandeira et al. 2002a, 2002b
18	Various localities, northern Western Interior, Wyoming, Montana, Utah, U.S.A.	Fort Union Formation (upper)	Paleogene, Selandrian to Thanetian	Wilf and Labandeira 1999; Wilf et al. 2001
19	Cold Ash, Berkshire, U.K.	Woolwich and Reading Beds	Paleogene, Thanetian	Crane and Jarzembowski 1980
20	Damalgiri, Meghalaya State, India	Tura Formation	Paleogene, Thanetian	Srivastava et al. 2000
21	Almont, North Dakota, U.S.A.	Sentinel Butte Formation	Paleogene, Thanetian	Crane et al. 1990
22	Foster Gulch, Carbon Co., Montana, U.S.A.	Fort Union Formation (upper)	Paleogene, early Ypresian	Lang 1996
23	Puryear, Henry Co., Tennessee, U.S.A.	Wilcox Formation	Paleogene, Ypresian	Berry 1923; Brooks 1955; Wittlake 1969
24	Sourdough Flora, Sweetwater Co., Wyoming, U.S.A.	Wasatch Formation	Paleogene Ypresian	Wilf et al. 2000, 2001, 2005
25	Laguna del Hunco, Chubut Province, Argentina	La Huitrera Formation	Paleogene, Ypresian	Wilf et al. 2005
26	Dubois, Park Co., Wyoming, U.S.A.	Wind River Formation	Paleogene, late Ypresian	Hickey and Hodges 1975
27	Bonanza, Uintah Co., Utah, U.S.A.	Green River Formation	Paleogene, Lutetian	Wilf and Labandeira 1999; Wilf et al. 2001, 2005

28	Darmstadt, Hessen, Germany	Messel Formation	Paleogene, Lutetian	Kinzelbach 1970; Straus 1976; Barthel and Rüffle 1976; Collinson 1990; Schaarschmidt 1992; Hellmund and Hellmund 1998
29	Geiseltal, Halle, Sachsen-Anhalt, Germany	Mittelkohle Formation	Paleogene, Lutetian	Mai 1976
30	Republic, Ferry Co., Washington, U.S.A.	Klondike Mountain Formation	Paleogene, Lutetian	Wolfe and Wehr 1987; Lewis 1992; Lewis and Carroll 1991; Pigg et al. 2001; Labandeira 2002b
31	Bonanza, Uintah Co., Utah, U.S.A.	Green River Formation	Paleogene, Lutetian	Wilf et al. 2001, 2005
32	Eckfeld, Manderscheid, Rheinland-Pfalz, Germany	Maar Formation	Paleogene, Lutetian	Wilde and Franken-häuser 1998
33	Baltic amber; Baltic Region, northern Europe	Prussian Formation	Paleogene, Lutetian	Wappler and Engel 2003
34	Prineville, Crook Co., Oregon, U.S.A.	Clarno Formation	Paleogene, Rupelian	Chaney 1927; Gregory 1969
35	Holley, Crook Co., Oregon, U.S.A.	Eugene Formation	Paleogene, Bartonian	Gregory 1968
36	Bournemouth, East Dorset, England, U.K.	Branksome Sand Formation (including Bournemouth Fresh Water Beds)	Paleogene, Bartonian	Stephenson 1991; Lang et al. 1995
37	White Lake Basin, British Columbia, Canada	[unreported formation]	Paleogene, Bartonian	Freeman 1965
38	Kennedy Range, West Australia, Australia	Merlinleigh Sandstone	Paleogene, ?Priabonian	McNamara and Scott 1983
39	Amethyst Mountain, Park Co., Wyoming, U.S.A.	[formation not reported]	Paleogene, ?Priabonian	Süss and Müller-Stoll 1980
40	Comstock, Douglas Co., Oregon, U.S.A.	Comstock Formation	Paleogene, Priabonian	Sanborn 1935
41	Florissant, Park Co., Colorado, U.S.A.	Florissant Formation	Paleogene, Priabonian	Cockerell 1908a, 1908b, 1910; Opler 1982; Meyer 2003
42	Anglesea, Victoria, Australia	[formation not reported]	Paleogene, Priabonian	Rozefelds 1988b
43	Vargem, Grande do Sul, São Paulo, Brazil	Tremembé Formation	Paleogene, Rupelian	Martins-Neto 1989, 1998
44	La Porte, Plumas Co., California, U.S.A.	?Ione Formation	Paleogene, Rupelian	Potbury 1935
45	Seifhennersdorf, Sachsen, Germany	"Kuclin" diatomite	Paleogene, middle Oligocene	Hellmund and Hellmund 1996
46	Wind brickyard, Baromállás, Hungary	[formation not reported]	Paleogene, Chattian	Ambrus and Hably 1979
47	Ruby River, Madison Co., Montana, U.S.A.	Renova Formation	Paleogene, Chattian	Becker 1965, 1969; Lewis 1976
48	Rott, Schwaben, Bayern, Germany	Köln Formation	Paleogene, Chattian	Heyden 1862; Sittig 1927; Hellmund and Hellmund 1991

49	Simojovel, Chiapas, Mexico	Baluntun Formation	Neogene, Aquitanian	Poinar and Brown 2002
50	Most, Czech Republic	"Main Brown Coal Seam"	Neogene, Aquitanian	Mikuláš et al. 1998
51	Düren, Nordrhein-Westfalien, Germany	"Flöz Garzweiler"	Paleogene, Aquitanian	Schmidt et al. 1958
52	Mainz and Petersburg, Rheinland-Pfalz, Germany	Hydrobia Limestone	Neogene, Aquitanian	Schmidtgen 1938
53	Osieczow, Poland	"Quadersandstein formation"	Neogene, Aquitanian	Karpiński 1962; Radwanski 1977
54	Oeningen, Baden, Switzerland	"Stinkschiefer"	Neogene, ?early Burdigalian	Heer 1853; Mädler 1936
55	Berzdorf (Sachsen), Germany	Toneisensteinblock Formation	Neogene Burdigalian	Hellmund and Hellmund 2002a, 2002b
56	Ribesalbes, Castellón, Spain	[formation not reported]	Neogene, Lower Miocene	Peñalver and Martínez-Delclòs 1997; Peñalver and Martínez-Delclòs 2004
56a	Bellver de Cerdaña	[formation not reported]	Neogene, Upper Miocene	Martínez-Delclòs 1996
57	Rubielos de Mora, Teruel, Spain	[formation not reported]	Neogene, Lower Miocene	Peñalver and Martínez-Delclòs 1997
58	Seed site 64, Sioux Co., Nebraska, U.S.A.	Sheep Creek Formation	Neogene, Burdigalian	Thomasson 1982
59	Salhausen, Hessen, Germany	Braunkohle Formation	Neogene, late Burdigalian	Hellmund and Hellmund 2002a, 2002b
60	Randecker Maar, Stuttgart, Baden-Württemburg, Germany	Dysodil Formation	Neogene, late Burdigalian	Hering 1930; Hellmund and Hellmund 2002b
61	Stinking Water Harney Co., Oregon, U.S.A.	Astoria Formation	Neogene, Langhian	Opler 1973; Waggoner 1999
62	Gilliam Springs, Washoe Co., Nevada, U.S.A.	[formation not reported]	Neogene, early Langhian	Waggoner and Poteet 1996
63	Linqu, Shandong, China	Shanwang Formation	Neogene, Langhian or Serravallian	Guo 1991
64	Upper Goldyke, Cedar Mtns., Nevada, U.S.A.	[formation not reported]	Neogene, Langhian	Opler 1973
65	Trout Creek, Oregon, Stewart Valley and Buffalo Canyon, Nevada, U.S.A.	Buffalo Canyon Formation and others of similar age	Neogene, Langhian	Opler 1973
66	Clarkia, Shoshone Co., Idaho, U.S.A.	Latah Formation	Neogene, Tortonian	Knowlton, 1926; Opler 1973; Lewis 1985
67	Albertine Rift Valley, Uganda	Nkondo Formation	Neogene, Tortonian	Nel 1994
68	Aldrich Station, Nevada, U.S.A.	[formation not reported]	Neogene, late Serravallian	Opler 1973
69	Southern Idaho, U.S.A.	Trapper Creek Formation	Neogene, Tortonian	Liebhold et al. 1982
70	Wüstensachsen, Hesse, Germany	Lettengraben Formation	Neogene Tortonian	Müller-Stoll 1989

71	Table Mountain, Tuolumne Co., California, U.S.A.	Mehrten Formation	Neogene, Tortonian	Condit 1944
72	Paris Basin, France	[formation not reported]	Neogene, late Miocene	Brues 1936
73	La Cerdaña, Lérida, Spain	"Unit C of lower Neogene unit"	Neogene, late Miocene	Diéguez et al. 1996; Barrón et al. 1999
74	Nagano and Gumma Prefectures, Japan	"Kabutiowa Plant Bed"	Neogene, late Miocene	Kuroko 1987
75	Douglas Co., Washington, U.S.A.	[formation not reported]	Neogene, late Miocene	Hoffman 1932
76	Egweil, Württemburg, Germany	"Sußwassermolasse"	Neogene, late Miocene	Selmeier 1984
77	Mikófalva, Hungary	[formation not reported]	Neogene, Messinian	Süss and Müller-Stoll 1975
78	Willershausen, Thuringia, Germany	"lacustrine clay sediments"	Neogene, early Pliocene	Kernbach 1967; Heie 1967; Steinbach 1967; Straus 1967, 1977
79	Chuizbaia, Maramureş northwestern Romania	Diatomit-Schiefer	Neogene, early Pliocene	Givulescu 1984
80	Brun-Vösendorf and Laaer Berg, Austria	[formation not reported]	Neogene, early Pliocene	Berger 1949, 1953 Straus 1967, 1977
81	Neu-Isenburg, Hessen, Germany	"Tonscholle"	Neogene, Pliocene	Rietschel 1983
82	Wetterau, Hesse, Germany	"lignite"	Neogene, Pliocene	Greiling and Schneider 1973
83	Santa Rosa, Sonoma Co., California, U.S.A.	Sonoma Formation	Neogene, middle Pleistocene	Axelrod 1944
84	Vitošov, Czech Republic	"karst breccia"	Neogene, Pleistocene	Mikuláš et al. 1998
85	Beceite, Teruel, Spain	travertine deposits	Neogene, Pleistocene	Peñalver et al. 2002
86	Königsburg, Alsace, France	"lignite"	Neogene, middle to late Pliocene	Geissert et al. 1981
87	Birtley, Durham, England, U.K.	unconsolidated peat	Neogene, late Pleistocene	Heslop-Harrison 1926
88	Rancho La Brea, Los Angeles Co., California, U.S.A.	asphaltum	Neogene, late Pleistocene	Larew 1987