

Chapter 2 The history of associations between plants and animals

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2.1 Introduction

Ever since the greening of a strip of equatorial coastline that fringed tropical oceans approximately 425 Ma, plants and animals have been extending their ecological reach on land. Today their terrestrial representatives constitute the overwhelming bulk of macroscopic diversity on the planet, and occur in profusion in virtually all terrestrial habitats. The earth's land surface today is fundamentally an abode for vascular plants and five major groups of macroscopic animals: nematodes, gastropods, onychophorans, arthropods and vertebrates. Two subgroups of this menagerie—seed plants and insects—contribute the preponderance of this diversity, and overwhelmingly outnumber in species all other groups combined. Virtually all terrestrial life is affected in some way by their myriad associations.

The origin and evolution of associations between vascular plants and animals has a rich but undervalued fossil history. This history has been integrated into biological and palaeobiological perspectives, each of which has explored the deep historical dimension of vascular plant and animal associations. The empirical data underlying both of these approaches will be interpreted in this chapter within a context of such theoretical questions as the initial launching of herbivory on land; the origin and early expansion of major ecological associations; the establishment of modern associations and the survival of ancient relationships; and the roles of taxonomic extinction, ecological convergence and escalation in long-term patterns of herbivory. Both palaeobiological and biological approaches have unique strengths and liabilities that include the varied uses of uniformitarianism, the quality of fossil evidence for inferring past associations, the role of combining phylogenetic and ecological data

in estimating the duration of associations, and limitations on the use of modern ecological analogues for correctly interpreting fossil material. In this context I have chosen three ecomorphological units—functional feeding groups, dietary guilds and mouthpart classes—as yardsticks to anchor much of the discussion of the fossil record. Emphasis will also be placed on results from varied phylogenetic studies for inferring the history of associations between plant hosts and their animal herbivores. A glossary of technical terms is shown in Box 2.3 at the end of the chapter (p. 73).

2.2 Why study plant–animal associations of the past?

The evolutionary history of biodiversity is essentially a chronicle of species interactions; species do not occur in splendid isolation. This precept suggests that an understanding of the history of life and the generation of biodiversity must include an examination of when, how and why organisms have associated during geological time. By contrast, the overwhelming effort in palaeobiology and biology has concentrated on examinations of isolated species in time and space. As indicated by Price in Chapter 1, there has been a growing realization that comprehending associations locked within a biota is considerably more than the sum of constituent species lists, and alternatively requires placing associations in an evolutionary context (Price 1997). Early efforts at unravelling these associations focused on gross correlations between the taxonomies of plant hosts and their insect herbivores (Ehrlich & Raven 1964), followed by more refined hypotheses (e.g. Funk et al. 1995), demonstrating that cycles of adaptations of plant defence and reciprocal counter-adaptations of herbivore attack resulted in the long-term

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improvement of individuals towards coping with decreasing odds of survival. Curiously, this research did not influence palaeobiology.

By contrast, the escalation hypothesis of Vermeij (1987) was proposed from an evaluation of the fossil record of marine invertebrates. Vermeij's formulation describes escalation as the increasing adaptiveness of lineages through time resulting from successively higher levels of selection pressure by predators on prey. It differs from various coevolutionary hypotheses by (1) a focus on the adaptation of evolving species to a changing environment rather than through interbiotic associations, and (2) the primacy of antagonistic associations such as predation over less antagonistic associations such as mutualism. The escalation hypothesis was a logical extension of the Red Queen hypothesis proposed earlier (Van Valen 1973), in which an adaptation in one species affected the relative non-adaptedness of other species, resulting either in the simultaneous improvement of interacting species or their marginalization through extinction or relegation to safer marginal environments.

Until recently, palaeobiology never developed a methodology to extensively test trends in the fossil record resulting from patterns seen in modern plant–insect associations. Rather than investigation of mutualisms or other modes of accommodation, overt predation has been the centre of study. Much of this reluctance is attributable to criticisms regarding a poor fossil record, the inability of fossils, if found, to illuminate relevant questions of phylogeny, or perceived limitations in the interpretation of evidence from plant–insect associations (Farrell & Mitter 1993; Shear & Kukulová-Peck 1990). Nevertheless there is an informative and interpretable record that has been documented and used productively. This is particularly true for well-preserved deposits that provide unique windows into the past (Crepet 1996; Labandeira 1998a). In particular, examination of fossil plant–insect associations is essential for testing hypotheses regarding the macroevolutionary dynamics of plants and their insect associates. These data are the source for patterns, especially temporal trends, that can support or refute hypotheses originating from modern ecological studies (Coley 1999).

2.2.1 Associations and time

An association is an ecological relationship that occurs indirectly or directly among two or more participants that use a resource in a repeatable or otherwise stereotyped

or predictable way. Associations range from antagonistic interactions such as predation or parasitism, to neutral relationships such as commensalism, to the collectively beneficial arrangements of various mutualisms. Feeding or feeding-related processes constitute the bulk of known relationships between plants and animals, and thus an association is conceived as an available food resource 'niche' that is variably occupied by different hosts and consumers in time and space. An instructive example are marattialean ferns and their insect herbivores, both of which underwent a complete taxonomic turnover during the 300 million years since the Late Pennsylvanian (see p. xii for a time scale). During the Late Pennsylvanian almost all the fundamental ways that insects consume land plants were established—chewing, piercing and sucking, galling, boring, and consumption of spores and prepollen (Labandeira 1998a). Only leaf-mining was apparently absent. These basic feeding styles, or functional feeding groups, also occur in the modern descendants of marattialean ferns, albeit by herbivores from lineages that have evolved more recently than the late Palaeozoic. In a similar context, Lawton and colleagues (1993) provide an example from the modern herbivores of the cosmopolitan bracken fern, in which continental geography rather than geological time is examined. They conclude that the current insect herbivores of bracken are highly variable globally, often with phylogenetically disparate insect taxa occupying the same functional feeding group on different continents, and in some regions particular functional feeding groups may be occupied by multiple taxa or even remain vacant. The salient point is that while plant hosts and their varied insect herbivores evolve and are constantly replaced in time and space, their associations nonetheless remain constant. A Palaeozoic palaeodictyopterid insect imbibing vascular tissue sap from a marattialean tree fern is functionally playing the same role as an aphid today feeding on the same tissues in an angiosperm (Labandeira & Phillips 1996). An appropriate analogy is a soccer team in which the positions remain the same but players occupying these positions are periodically rotated, retired and recruited.

2.2.2 Theoretical issues about the origin and evolution of associations

Four basic questions have been identified that are of interest to palaeobiologists and biologists. All are united by explicit reference to geological time, which provides the

chronometer by which long-term trends and processes are calibrated and ultimately interpreted.

2.2.2.1 *How were plant–animal associations launched during the Palaeozoic?*

Three hypotheses have been proposed for assessing how ecological units, such as functional feeding groups, dietary guilds and mouthpart classes, expand in macro-evolutionary time (Strong et al. 1984). The first hypothesis, the ecological saturation hypothesis (ESH), advocated by palaeobiologists, maintains that the total number of ecological positions, or roles, has remained approximately constant through time after an initial exponential rise (Fig. 2.1a). Thus taxa enter and exit the ecological arena of the local biological community (Box 2.1), but their associations or roles remain virtually level. By contrast, the expanding resources hypothesis (ERH) is favoured by biologists and states that there is a gradual increase in food resources and availability of niches through time, such that the current high level of exploitation is a geologically recent phenomenon (Fig. 2.1b). Last, the intrinsic trend of diversification hypothesis (ITDH), suggested by Schoonhoven et al. (1998), holds that the long-term patterns of ESH and ERH vary among groups of organisms (Fig. 2.1c). This view would imply that the proportion of occupied ecological roles has a globally disjunct pattern according to group, time and space. Of these, the data currently favors ESH, if one assumes that the ecological clock was set during the Pennsylvanian and the previous fossil record is too poor for analysis. The ITDH could be evaluated on a group-by-group basis, if the temptation is avoided to time-average the proportion of occupied ecological roles across all groups worldwide.

2.2.2.2 *What is the role of extinction?*

The fossil record of life on land is replete with major and minor episodes of mass extinction that correspond to rates of taxal mortality significantly above the background level (Raup & Sepkoski 1982). Major events include the two devastating ones at the ends of the Permian and the Cretaceous Periods, and less intense events such as the ends of the Middle Pennsylvanian, Late Triassic and Eocene Epochs (Boulter et al. 1988; Labandeira & Sepkoski 1993). Thus a basic question regarding the extinction record of major terrestrial organisms is whether the post-event evolutionary clock was reset, either by plants

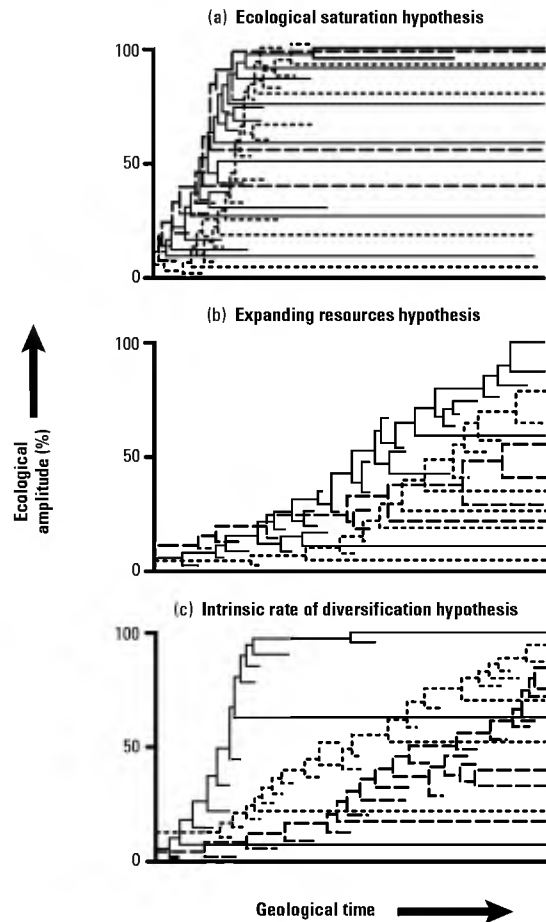


Figure 2.1 The three principal hypotheses for the ecological origin and development of plant–insect associations. Ecological amplitude is a measure of the amount of occupied ecological space, calibrated to the present as equalling 100%. Proxy measurements of ecological amplitude, relevant to plant–insect associations, include functional-feeding groups or dietary guilds or mouthpart classes (see Figs 2.6, 2.16 and 2.17). The ecological saturation hypothesis (a) has been principally advocated by palaeobiologists, and has been supported by Raup (1972) and Behrensmeier et al. (1992). The expanding resources hypothesis (b) has been mainly propounded by biologists, including Strong et al. (1984). The intrinsic rate of diversification hypothesis (c) is group-specific and has been proposed by Schoonhoven et al. (1998).

becoming unavailable for consumers or the absence of animal associates that can contribute to plant survival through mutualisms such as pollination, seed dispersal or defence from herbivores? Also, what are the consequences for species and their associations when entire

Box 2.1 Plant–animal associations in the context of past biological communities

Biotic communities are local assemblages of trophically linked species, some members of which enter into highly intimate associations. These communities, as well as their myriad constituent plant–animal associations, possess distributions in space and time (Fig. 1) that include extinction (a), re-evolution (b), coalescence (c), complex patterns of extinction, coalescence and persistence (d), persistence (e) and relatively recent origination (f). A uniformitarian approach—where ‘the present is the key to the past’—works best for the more recent portion of the biota whereas more ancient examples are likely to have occurred under processes and conditions without recent analogues, necessitating non-uniformitarian approaches.

Although communities evolve, certain highly associated or coevolved constituents may indeed persist unchanged for long geological stretches (Labandeira et al. 1994; Wilf et al. 2000), even though there is evidence that some commu-

nities of today are not analogous to communities even of the very recent past. An intimately coupled association between a host-plant lineage and its insect herbivore lineage may provide a rare opportunity of persistence in the face of species turnover within a community. By contrast, ecologically malleable or geologically fleeting associations, such as ungulate grazers and grasses, are uninformative, if for no other reason than taxal turnover rates are high when compared to plants and their insect taxa (Labandeira & Sepkoski 1993).

Some of the best evidence for modern plant–arthropod associations in the fossil record involves well-preserved angiosperm leaves in Cenozoic deposits with highly stereotyped insect damage, particularly leaf mines and galls (see p. xii). For leaf miners, Opler (1973) has documented modern, genus-level associations for both host plant and insect leaf miners that extends to the early Miocene (20 Ma). Another

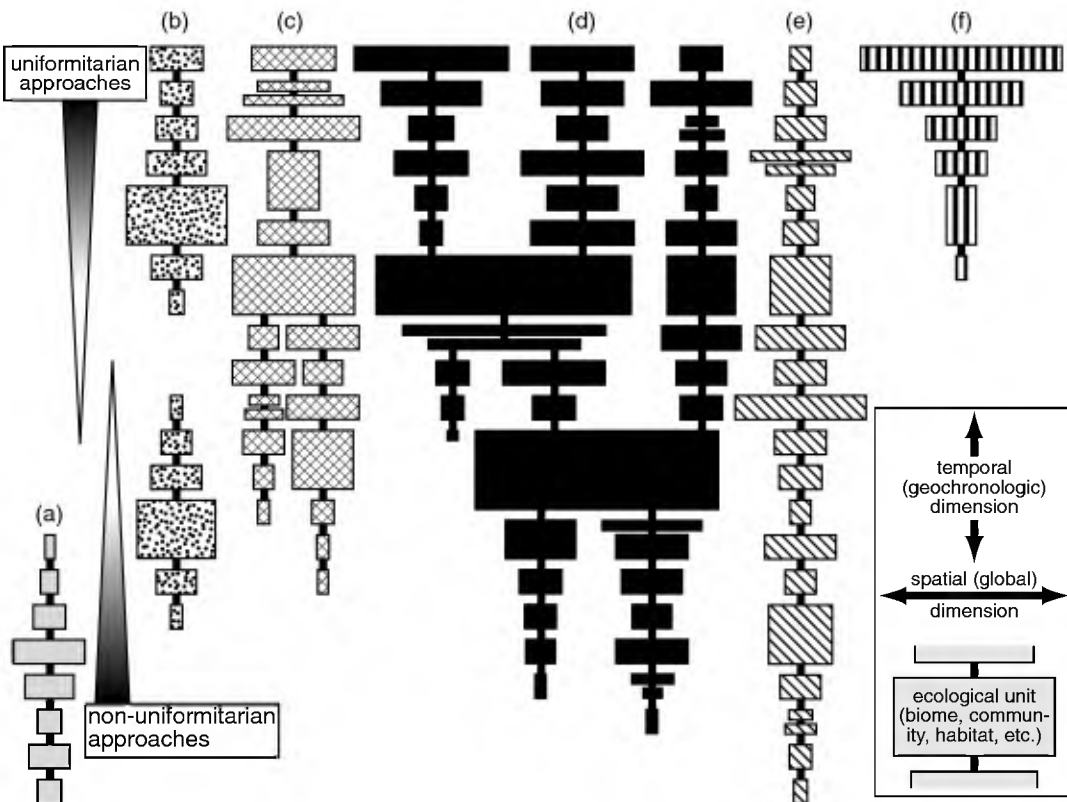


Figure 1

Box 2.1 continued

direct type of evidence was provided by O'Dowd et al. (1991), who isolated mites and their domatia on angiosperm hosts from the middle Eocene of Australia. Opting for a more indirect approach, Moran (1989) combined biogeographical and palaeobotanical data with successful host transfer experiments between North American and Chinese aphids, indicating that the aphid/sumach/moss life cycle was established by the early Eocene (48 Ma). She concluded that complex multispecies life histories may result from ancient evolution-

ary commitments, allowing a role for historical constraints. However, these older associations are more difficult to track because they are rarer in the fossil record and in the modern biota (Farrell & Mitter 1993) and because increased resolution and phylogenetic scope is needed to detect a weaker signal among extant lineages. In most instances the biological communities in which these older associations occurred are gone or otherwise transformed (Fig. 1), indicating that when they persist today, they occur as relicts.

communities are devastated? Tentative data indicate that major floral extinction results in a trophically cascading response that affects insect herbivores. This occurred during the Middle to Late Pennsylvanian extinction (Labandeira 1998a), dramatically during the terminal Permian event (Labandeira & Sepkoski 1993) and there is evidence now for a significant turnover in insect herbivore types at the Cretaceous–Tertiary (K/T) boundary (Labandeira et al. 2002), based on plant–insect associational data where previously no extinction was detectable from family-level analyses of body fossils (Labandeira & Sepkoski 1993; Fig. 2.2). Given the taxonomic turnover of vascular plants and herbivorous insects and yet the survival of persistent ecological associations, the phenomenon of ecological convergence is an important long-term pattern, as exemplified by marattialean ferns and their herbivores mentioned above. However, other options are possible, such as the geographical restriction of associations to small refuges and their subsequent expansion and colonization of much larger regions when conditions become favourable.

2.2.2.3 Do animals track the environment and plants during geological time?

One of the most pronounced patterns in the distribution of organisms is their overall greater diversity in the tropics than at higher latitudes (Blackburn & Gaston 1996). This pattern is particularly dramatic for insects and their vascular plant associates, and has been documented for bulk defoliation values for local floras or single plant species (Coley & Barone 1996). Insect herbivores typically demonstrate greater removal rates of leaf area in the tropics when compared to higher latitudes. For example, leaf-mining diversity is elevated in tropical regions where centres of diversity exist for several groups (Powell et al.

1999), a trend that parallels wood-boring insect diversity based on species distribution lists. By contrast, galling insects peak at warm-temperate to subtropical xeric latitudes where they are associated with dry, sclerophyll vegetation (Fernandes & Lara 1993). These latitudinal trends are mirrored by altitudinal transects, although notable exceptions are aphids (Dixon 1998) and bees (Michener 1979), which have their greatest diversities at temperate latitudes.

These latitudinal patterns are associated with important trends in climate, including temperature, precipitation and seasonality. Such trends also can be tracked by keeping latitude stationary and varying temporal context such that changes in global climate can be observed vertically in a stratigraphic section containing a taxonomically characterized and well-preserved record of plant fossils. Using this approach, Wilf and Labandeira (1999) studied the Early Cenozoic Thermal Maximum in the Greater Green River Basin of Wyoming, USA, during an interval of a 7°C to 9°C rise in mean annual temperature and representing a shift from temperate to subtropical vegetation during the latest Palaeocene (56 Ma) to Early Eocene (53 Ma) interval. Major vegetational changes were documented during this period, as well as differences in the intensity and spectrum of insect-mediated damage on each plant species in before and after floras (Fig. 2.3). A significant trend was the increased intensity and spectrum of insect damage on poorly defended, fast-growing species, such as members of the birch family. This indicated the pre-eminence of a herbivore-accommodating, weed-like defence strategy under the subtropical conditions of the early Eocene, a pattern that was absent during the much cooler latest Palaeocene. This study demonstrates that the fossil record can be used to test long-term predictions of hypotheses based on ecological studies of extant organisms.

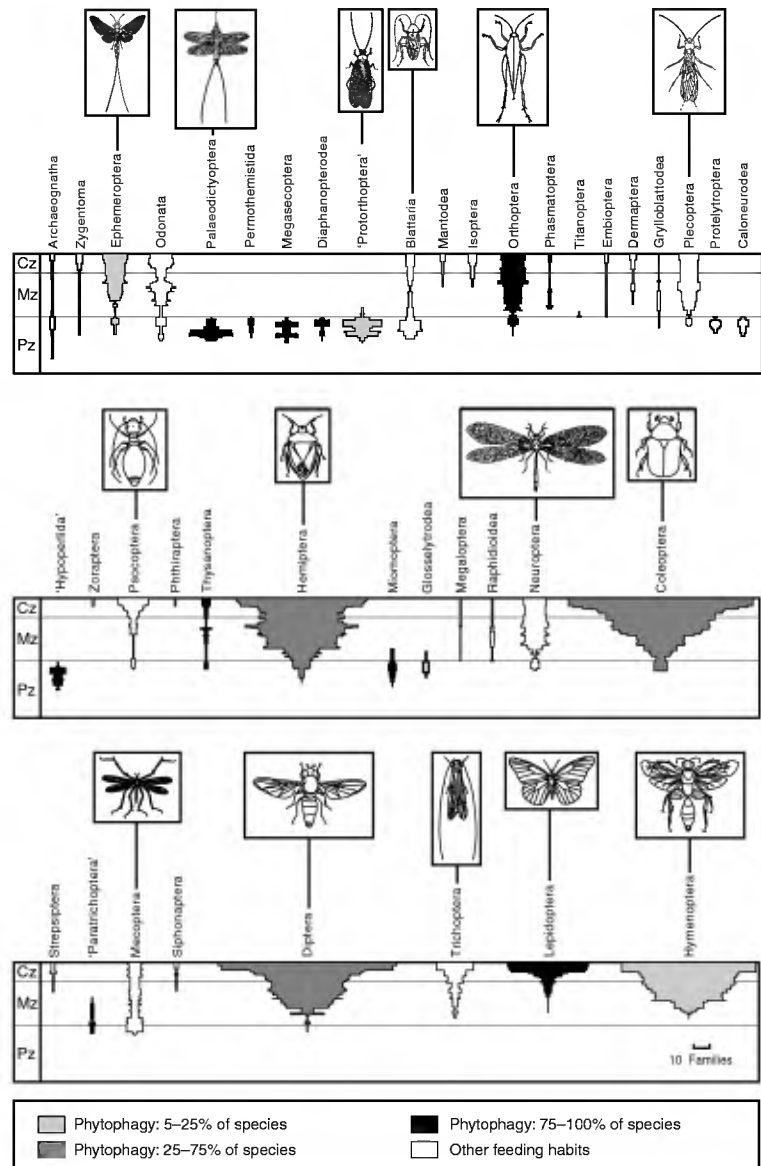


Figure 2.2 Geochronological changes in family-level diversity of major insect clades, categorized by phytophagous dietary preferences. (Modified from Labandeira and Sepkoski 1993.)

2.2.2.4 Applying inverse uniformitarianism: is the past the key to the present?

Catastrophism holds that geologically rapid, global upheavals have been the major influence on the history of life. By contrast, uniformitarianism, which has largely supplanted catastrophism, embodies two distinctive aspects (Gould 1965). One is methodological uniformitarianism, in which the fundamental laws of the modern physical world apply to the past, and the other is substan-

tive uniformitarianism, which states that the rates and conditions of current existence are also applicable to the past. Of these two distinct concepts, methodological uniformitarianism is largely unassailed, but substantive uniformitarianism has not withstood close scrutiny (Ager 1993). Indeed, multidisciplinary evidence from various geological disciplines, particularly those applied to the earlier part of the fossil record, indicate that the more ancient the ecosystem, the less it resembles the present. Consequently uncritical application of present-day material

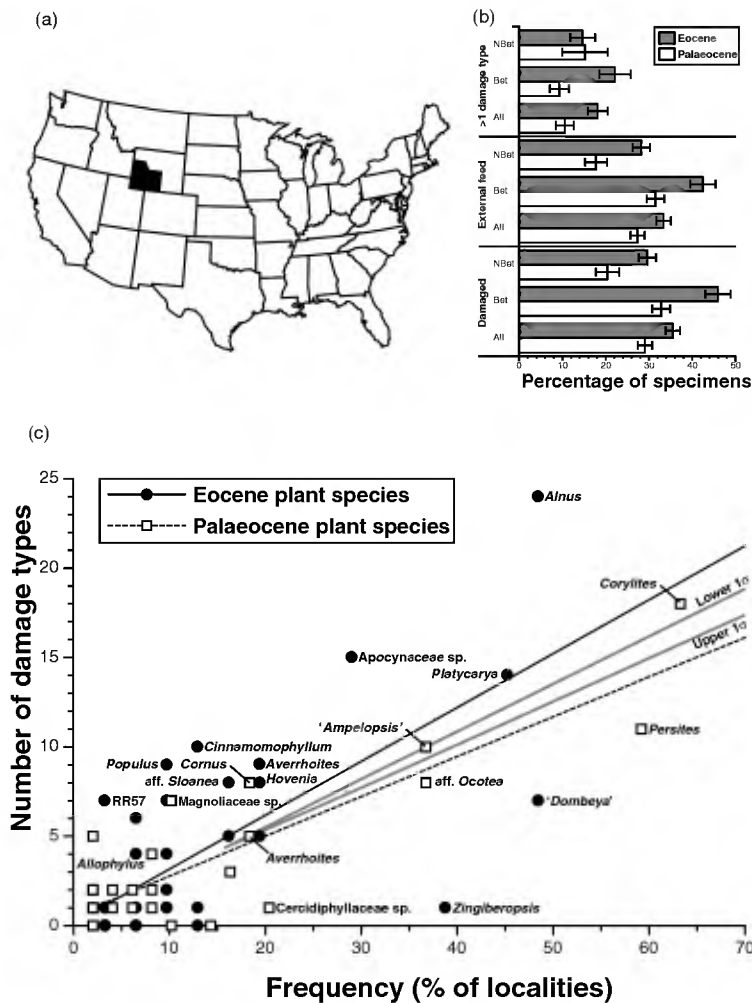


Figure 2.3 A study by Wilf and Labandeira (1999) showing the response of plant–insect associations to the Early Cenozoic Thermal Interval (ECTI), an interval of elevated global warming. A greater variety of insect damage per host species and increased attack frequencies characterize early Eocene plants, occurring under considerably warmer conditions, as compared to earlier late Palaeocene plants. In addition, herbivory is elevated for both late Palaeocene and early Eocene members of the Betulaceae (birch family), a group of fast-growing plants with minimal herbivore defences. (a) Sampling areas are indicated by black polygons. (b) Damage census data for Late Palaeocene and Early Eocene leaves, illustrating the greater percentage of specimens with damage from early Eocene sites. From bottom to top: leaves with any insect damage, leaves externally consumed, and the percentage of damaged leaves bearing more than one damage type. These categories are each analysed separately for all leaves (All), Betulaceae only (Bet) and taxa other than Betulaceae (NBet). (c) Diversity of insect damage for each plant–host species (vertical axis), plotted against the percentage of localities (49 late Palaeocene and 31 early Eocene) at which species occur (horizontal axis). Each data point is one species; many data points overlap at the lower left; survivors are plotted twice. Grey lines show divergence of 1 standard deviation (68%); confidence intervals are for two regressions. This graph shows the higher percentage of localities with more damage types from the early Eocene.

conditions and rates of change to the distant past may not be valid, and the maxim ‘the present is the key to the past’ may be inappropriate in many instances.

In the context of long-term development of ecosystems and species interactions, the role of very different past conditions for establishing general adaptation and the successful early incumbency of a group is an important guide for understanding its present condition. This grants legitimacy to an inversion of the uniformitarian principle in that ‘the past is the key to the present.’ As a result, the extent to which substantive uniformitarianism can be extended to the past is debatable. It is generally agreed that the further one delves into the past, eventually a threshold is reached whereby extension of modern conditions be-

comes unreliable (Box 2.1, Fig. 1). It should be stressed that the biological context of plant–animal associations is the local ecological community, which is a spatiotemporally interacting group of organisms that is governed both by external changes in the physical environment and the evolving internal biological integration of its constituents. Depending on the extent of species-level turnover that has occurred, these communities are amenable to greater or lesser application of uniformitarian principles.

2.3 The geochronological context

An appreciation of the history of plant–animal associations involves knowledge of the evolution of terrestrial

life. This includes how life colonized the land, processes of fossilization, and biases in the preservation of organisms and past environments. While the terrestrialization of life is a relatively recent event, it has parallels with much earlier episodes of the diversification of marine life, which also resulted in the rapid colonization of vacant but habitable space.

2.3.1 The geological time-scale and important events

The Earth is about 4.6 billion years old, and life originated soon thereafter, according to diagnostic carbon isotopic signatures in sedimentary rocks dated at 3.8 billion years (see p. xii for time scale). The earliest microfossils are 3.5 billion years old, and macroscopic biotic structures resembling prokaryotic algal accumulations occur at 3.0 billion years. Eventually free oxygen accumulated in the atmosphere, reaching levels that became metabolically threatening to prokaryotic life, although mechanisms were evolved to ward off the initial biocidal effect of an oxidative environment. The earliest eukaryotes are algae documented from rocks of 2.2 billion years, for which distinctive geochemical evidence is present by 1.7 billion years; by contrast, the earliest known identifiable animal occurs in 0.9 billion-year-old sediments. The distinctive multicellular Ediacarian fauna occupied shallow marine environments worldwide, occurring from 0.565 to 0.545 billion years ago, immediately prior to the metazoan diversification event during the earliest Cambrian. Multicellular, skeletonized animals, including arthropods, mark the beginning of the Palaeozoic Era. The earliest tangible evidence for terrestrial life is Late Silurian, although suspiciously terrestrial fossils are known earlier from marginal marine deposits.

The earliest terrestrial biota is Late Silurian (approximately 425 Ma) from the United Kingdom and intriguingly contains evidence for plant–animal associations from coprolites deposited by an animal consuming spores and vegetative tissues (Edwards et al. 1995). More recent Early to Middle Devonian biotas that contain insects and their close relatives, as well as evidence for associations with plants, are documented from the Rhynie Chert of Scotland, at Gaspé, Quebec, and at Gilboa, in New York state (Shear & Kukalová-Peck 1990). A 55-million-year gap occurs during the Middle Devonian to the Mississippian/Pennsylvanian boundary during which terrestrial floras are modestly represented but the arthropod record

essentially ceases, only to resume in profusion in the Early Pennsylvanian. During this interval the earliest tetrapods are documented from Greenland in strata of latest Devonian age. A smaller gap, though with very limited arthropod but modest vertebrate occurrences, occurs from the Late Permian to the Middle Triassic, straddling the end-Palaeozoic extinction. The Palaeozoic land biota consisted of clades that are extinct or highly diminished in diversity, by comparison to Mesozoic biotas, which typically harbour precursors of modern lineages. The K/T mass extinction, less severe than that at the end of the Palaeozoic, was responsible for the demise of some important higher-level groups such as rudistid clams, ammonites, dinosaurs, and many seed-plant and insect lineages. Since the expansion of angiosperms during the Middle Cretaceous, animal herbivory has continued unabated, marked by an end-Cretaceous extinction, subsequent reduction in Palaeocene associations, and a rebound during the latest Palaeocene to Early Eocene prior to the diversification of mid-Cenozoic grasslands.

2.3.2 Taphonomic filters and fossil deposits

Taphonomy is the study of the physical, chemical and biotic events that affect organisms after death, including pre-burial, burial and post-burial processes that transform the original living community into an entombed death assemblage that may be encountered by palaeobiologists many aeons later. The fidelity to which the preserved assemblage actually resembles the source community is an issue in discussions of the quality of the fossil record (Behrensmeyer et al. 1992).

Terrestrial *Lagerstätten* deposits occur episodically in the fossil record and are spatiotemporally separated from each other by extensive barren strata (Box 2.2). Nevertheless they represent particularly informative glimpses into once-living, diverse assemblages, and constitute most of our knowledge of many organismic groups and their past environmental settings. They provide virtually all of the documentation for associations between plants and animals. Most *Lagerstätten* are fine-grained, stratified deposits that contain two-dimensional compression fossils that originate from lake, deltaic or river-associated environments. Permineralized deposits, featuring three-dimensional impregnation of fossils typically by carbonate, silica or phosphate, are rarer but include fossils such as coal balls and petrified wood. Amber deposits, like compressions in shales and other fine-grained sedimentary

Box 2.2 *Lagerstätten* and modes of preservation

Through centuries of fossil exploration it has become clear that there are two basic, albeit intergradational, modes of fossil preservation. The most commonly encountered mode is that of fossil deposits whereby organisms with resistant hard parts survive, mostly skeletonized invertebrates in marine deposits and bone-bearing vertebrates in terrestrial deposits. Plant leaves and insect wings as compression or impression fossils are typically encountered in such deposits of mediocre preservation (Fig. 1, *right*).

A very different and special mode of preservation is known as a *Lagerstätte* (plural, *Lagerstätten*) which is an

extraordinarily well-preserved fossil deposit that merits considerable scientific interest. Many deposits with superb preservation of plant–animal associations – such as the post-Devonian grey arrows in the time scale on p. xii – are *Lagerstätten* characterized by anatomically spectacular detail resulting from entombment under special conditions of rapid burial and chemical sealing, followed by minimal subsequent decay, usually under anaerobic conditions. Such fossils are characterized by greater than usual resolution of fossil anatomy (Fig. 1, *left*). Postmortem alteration within more typical deposits includes chemical changes of fossil skele-

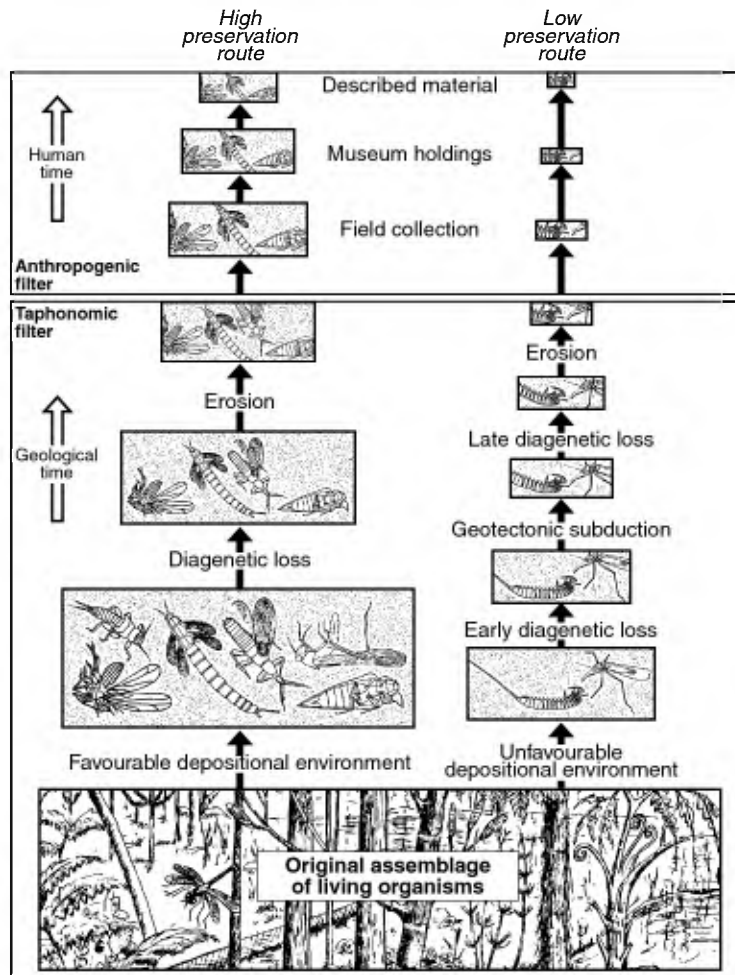


Figure 1

Box 2.2 continued

tons by mineral replacement or removal by ground water, mineralic phase recrystallization under conditions of elevated temperature or pressure, and sediment compaction. A major source of taphonomic loss is erosion from initial deposition in areas of high elevation that have become uplifted. Degradation of the fossil record occurs in geotectonically active regions where there is faulting, folding or magnetic intrusion.

Geographically, much of the terrestrial fossil record has been obliterated by tectonism and erosion. Geotectonic subduction and associated magmatism at leading edges of continental plates, where they abut with the denser crust of oceanic plates, has resulted in physical removal of transported terranes and the diagenetic alteration of remaining land

masses such that fossil biotas are unrecognizable. For areas of montane uplift in continental interiors there has been accelerated erosion of the sedimentary record. Ironically, major crater-impact structures that destroy the previous sedimentary record also act as subsequent, long-term sediment traps, often containing spectacular *Lagerstätten* (Crepet 1996). By contrast, oceanic islands are geologically ephemeral and undergo either geotectonic subduction or eustatic subsidence and become inundated (Wagner & Funk 1995). The geologically permanent continental centres of lowland equatorial latitudes are frequently unavailable for exploration because of the destructive effect of vegetation on surface exposures. Similarly, present-day polar latitudes are covered by permanent ice caps and are inaccessible.

rocks, are also important, although the oldest dated amber with insect inclusions is approximately 125 Ma, representing only the last 30% of terrestrial plant and arthropod history, useful mostly for the earlier evolution of extant clades. Lake deposits, by contrast, have the greatest geochronological persistence, extending about 280 million years, into the Late Palaeozoic, and are critical for discerning premodern plant–animal associations. Special trap deposits such as fissure fills and asphalt pools are unique ephemeral environments generally confined to the Late Caenozoic (Labandeira 1999).

2.4 Approaches towards the study of past associations

The use of two types of approaches—phylogenetic versus ecological, and palaeobiological versus biological—collectively demonstrate much promise for integrating complementary ways for understanding the origin and evolution of plant–animal associations.

2.4.1 When phylogeny matters: mapping ecological attributes onto clades

A central goal of biology is to establish as accurately as possible an explicit relationship among organisms, using methodology that minimizes ad hoc assumptions and is consistent with an understanding of their molecular and morphological structure and occurrence in the fossil record (Funk & Brooks 1990; Fox et al. 1999). A cladogram that is well corroborated by available and diverse

evidence can be considered as a hypothesis of organismic relationships (Funk & Brooks 1990), but equally as a starting-point for testing ecological concepts derived from other, fundamentally different, types of data (Grandcolas 1997). For plant–insect associations, ecologically coupled and putatively related herbivore taxa can be mapped onto a phylogeny of their constituent, uniquely derived (monophyletic) plant hosts (Brooks & Mitter 1984). The degree to which there is a phyletic association between a monophyletic clade of host plants and a monophyletic or otherwise clade of their insect herbivores can be evaluated statistically for congruence. Degrees of coordinated association between host plants and their insect herbivores have been documented, ranging from parallel cladogenesis approaching one-for-one matches between host and herbivore (Roderick 1997; Farrell & Mitter 1998) to looser arrangements (Janz & Nylin 1998) to diffuse associations where weak or anecdotal evidence supports occasional associations between related host plants and their related insect herbivores (Armbruster 1992). Typically, estimates for the divergence of radiations of plant or herbivore clades are pegged to a molecular clock, sometimes calibrated to relevant fossil occurrences of plant hosts or insect herbivores, or are linked to biogeographic events (Funk et al. 1995; Janz & Nylin 1998).

Less resolved phylogenetic data, without explicit congruence of host and herbivore clade topology at the species level, can be used for ascertaining the degree of relationship between plants and their presumed animal associates. There are two common techniques that have

exploited comparative ecological or temporal data to determine whether one of two or more clades have promoted taxonomic diversification (Mitter et al. 1988). The first technique is whether a key ecological trait, usually a synapomorphy, which was unique to the early phylogeny of one of two sister-groups, has also been associated with significantly greater taxonomic diversity (Coddington 1988). Examples of such a sister-taxon comparison is the study by Mitter and colleagues (1988) which demonstrated, in an overwhelming number of pair-wise contrasts, that herbivorous clades are more diverse than their non-herbivorous sister-clades, and the examination by Dodd and colleagues (1999) that biotically pollinated angiosperm families are more diverse than their abiotically pollinated sister-clades. Also illustrating this method is the study by Farrell et al. (1991), who concluded that increased taxonomic diversity occurs in those plant sister-lineages that singularly possess latex-canal defences to resist insect herbivory. An opposite conclusion was obtained by Wiegmann et al. (1993) when examining whether carnivorous parasitic insects were more diverse than their non-parasitic sister-lineages.

The second technique determines if there is a preferred pattern of appearance in the fossil record of specific related or unrelated clades possessing predicted ecological characters associated with increased taxonomic diversity. An application of this method is the appearance of certain insect-related floral structures in several angiosperm lineages during their Cretaceous ecological expansion, indicative of the acquisition of particular pollination styles or 'syndromes' (Crepet & Friis 1987). On balance, these clade comparisons for detection of the presence or timing in the appearance of clade attributes can provide strong evidence indicating whether particular associations, such as generalized herbivory, pollination or seed-dispersal syndromes, have been associated with increased species-level diversification.

2.4.2 Non-phylogenetic data: measures of herbivore impact and specificity

Not all insights on past plant–insect associations are derivable only from phylogenetic analyses of modern taxa. According to Wing & Tiffney (1987: 204), 'it is possible to infer past ecological interactions through morphological analogies with extant organisms and systems. Such inferences can be made independent of systematic affinity, and permit us to escape the potential

trap of assuming ecological features and community structure on the basis of the taxonomic affinities of the organisms in question.' These inferences apply to the more distant fossil record, and recognize the validity of methodological uniformitarianism. Accordingly, the fossil record becomes an independent source of direct inference, principally as a repository of animal-mediated damage to fossil plants. These types of records not only extend biological data derived from modern descendant taxa (Moran 1989; O'Dowd 1991), they also provide primary associational data from the fossil record that record the role of plants and insects in past ecosystems. Such data includes the intensity of herbivore attack, levels of host specificity in particular floras, and the temporal trend of herbivore pressure on bulk floras or on component communities of plant lineages (Futuyma & Mitter 1996). Such data, as well as fossil documentation of the spectrum of recognizable damage types (Stephenson 1992; Wilf & Labandeira 1999), have established trends regarding the spectrum and intensity of herbivore pressure through time.

2.4.3 Palaeobiological approaches

The source of primary data for palaeobiology is fossil material whereas for biology it is information from modern organisms. The boundary between these two disciplines typically relies on whether the preponderance of the research is centred on fossil versus extant material, and is occasionally fuzzy. Figure 2.4 is a summary of the published literature, and reveals that palaeobiological approaches are applicable to the entire 425-million-year terrestrial fossil record whereas biological approaches are generally restricted to the past 150 million years, except for the extension of modern mouthpart classes to the entire fossil record and the assignment of Permian dates for the origin of feeding strategies in a few phylogenetic analyses. A perusal of all 12 types of data reveals a few glaring gaps, notably the Middle Devonian to latest Mississippian, the Permo-Triassic boundary interval and the Late Triassic through Late Jurassic. As expected, the fossil record improves towards the present in terms of the frequency of deposits and the greater percentage of plant/animal associations that are recognizably modern. This phenomenon, termed 'the pull of the Recent' when initially described for taxonomic data (Raup 1972), reflects the increase in quality of fossil assignments during the more recent past.

This evidence for the associations between plants and insects, and to a lesser extent mites, has been partitioned into three types of ecological data: functional feeding groups, dietary guilds and mouthpart classes. Each of these three ecomorphological units is defined by the type of relationship existing between the insect consumer and the consumed food. Functional feeding groups are defined according to *how their food is consumed*, and includes types such as external foliage-feeding and leaf-mining. Dietary guilds are delimited by *what type of food is consumed* and consist of herbivores on live tissue and detritivores consuming decaying litter. In some instances entire organisms are consumed, such as many algae, spores and seeds, while in other cases whole organs with multiple tissues are eaten, such as roots, twigs or leaves, and in other examples a single or a few tissues are consumed, such as sap, cambium or secretory gland products. Mouthpart classes, by contrast, are classified by *what type of structural apparatus is used* to consume food. Mouthpart classes have been defined from the results of a phenetic analysis of modern insects and their relatives, in which 34 distinctive clusters were elucidated (Labandeira 1997), almost all of which were recognized independently in classic morphological studies (Chaudonneret 1990). Mouthpart classes are grouped into broader groupings by shared structural features. These three ecomorphological units provide a vital ecological component to the history of insects and plants independent of taxonomy. Each displays considerable ecological convergence in time and space.

2.4.3.1 Types of evidence for arthropod and plant associations

A full appreciation of the fossil associational record requires an evaluation of the five major types of qualitative evidence: plant reproductive biology, plant damage, dispersed coprolites, gut contents, and insect mouthparts. There are two major preservational modes that are relevant to assessments of evidence type. Two-dimensional compressions are good for preserving flat organs, particularly leaves and floral structures, and are ideal for detecting gut contents and plant damage, such as external foliage-feeding and leaf-mines. By contrast, three-dimensional permineralization and transformation into charcoal preserve structures such as twigs and seeds, and are prone to preserve spheroidal coprolites and thickened plant damage produced by piercers-and-suckers, gallers and

borers. Collectively, these five types of evidence range from the direct, 'smoking gun' of gut contents, where the consumer and consumed are typically identifiable, to the more remote and circumstantial evidence of floral reproductive biology and mouthparts, where inferences are based on functional understanding, usually from modern analogues. Plant damage and dispersed coprolites are within the middle of this continuum, and represent high resolution of targeted plants but poor definition of the insect culprits. The spatiotemporal distribution of these types of evidence is highly variable in the fossil record: compressions provide broad-scale data, although less frequent permineralization can document in considerable detail the plant-damage structure, especially histological features important for inferring the plant-host's response to particular types of herbivory (Labandeira & Phillips 1996). Amber has been minimally used in this context.

The fossil history of these five qualitative types of evidence is illustrated in Fig. 2.5. Each horizontal bar represents a *Lagerstätten*, placed in relative geochronological order, and containing multiple but not all of the five types of evidence for plant–insect associations. In such deposits each type of evidence, when present, provides data that links plant–insect associations to the separate plant and insect fossil records. Assembly of this evidence from the available associational, plant and insect fossil records reveals a solution to a larger puzzle that addresses the trophic network within each of these ancient ecosystems.

2.4.3.1.1 Plant reproductive biology (Fig. 2.4f)

Evidence for arthropod associations from plant reproductive biology originates from a wide variety of deposits through time. One of the earliest examples are megaspores possessing long appendages with grapnel-like terminal hooks from the Late Devonian of England (Kevan et al. 1975) and the Mississippian of Egypt, interpreted as structures for dispersal by arthropods. In coal-swamp forests of Late Pennsylvanian age, medullosan seed ferns bore unusually large prepollen, which considerably exceeded the range for wind-dispersed pollen, implicating insects as transport agents (Taylor & Millay 1979). This inference of arthropod transport of prepollen is buttressed by piercing-and-sucking damage of male organs that contain the same prepollen type (Labandeira 1998a) and the probable presence of this same prepollen type in dispersed coprolites. All three disparate types of evidence occur in

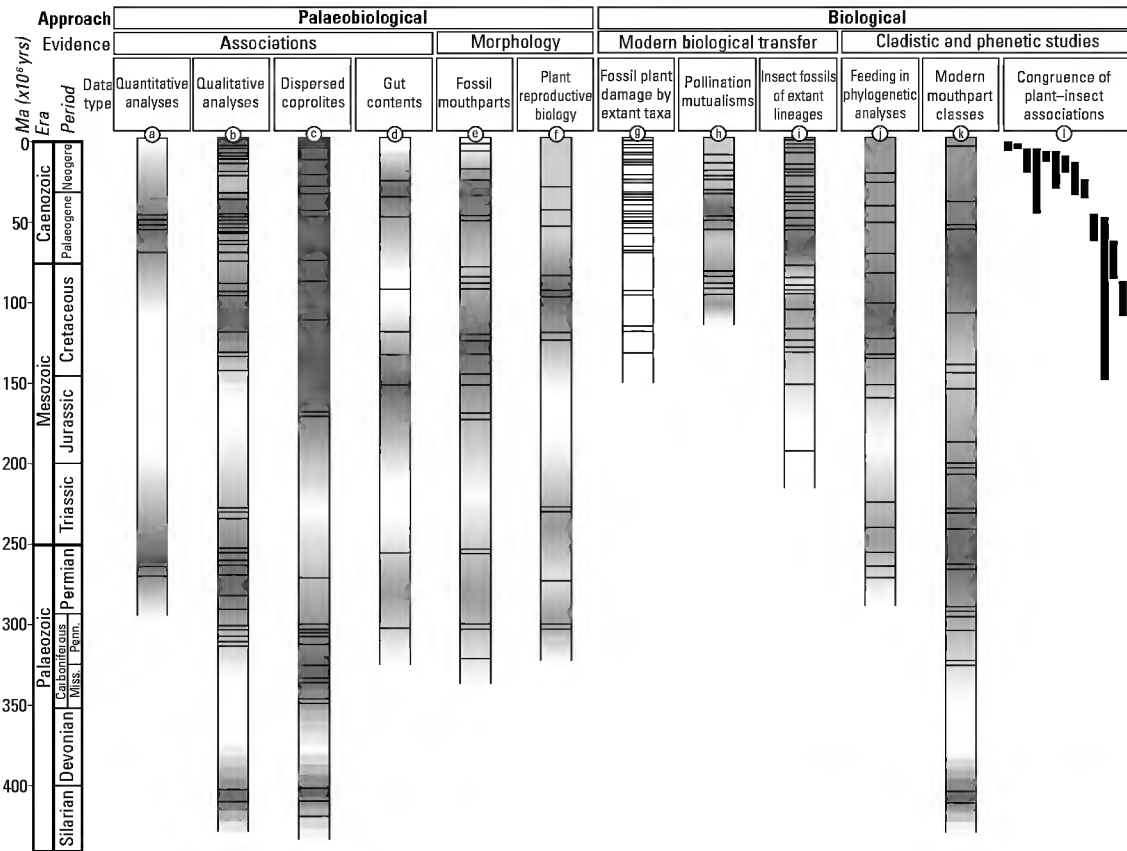


Figure 2.4 Summary of palaeobiological versus biological approaches in examinations of the temporal dimension of plant–animal associations. The types of data and their categorization at the top are a representative sample of the literature. The data of fossil occurrences are horizontal lines within vertical bars. Palaeobiological approaches typically span the terrestrial Phanerozoic record, but there are important earlier Palaeozoic and mid-Mesozoic gaps. By contrast, biological approaches, with the exception of modern mouthpart classes and perhaps feeding inferences in phylogenetic analyses, best describe the Cretaceous and Caenozoic, and are approximately equivalent to the duration of most of the larger extant clades. Abbreviations: Sil. = Silurian, Miss. = Mississippian, Penn. = Pennsylvanian, Neog. = Neogene.

Palaeobiological approaches (a to f), are given as follows: (a), quantitative analyses; (b), qualitative analyses; (c) dispersed coprolites; (d) gut contents; (e) fossil insect mouthparts; and (f) fossil plant reproductive biology. Biological approaches are partitioned as follows: (g), assignment of highly stereotyped damage in the fossil record to extant taxa; (h), the extension of modern pollination mutualisms by reference to diagnostic plant and insect morphological attributes in fossils; and (i), inferences of plant–insect associations based solely on insect fossils of modern lineages and modern ecological affiliations, biogeographical patterns or other supportive biological data. Assessments from phylogenetic analyses of the time of origin of plant-related feeding attributes (j) are typically approximate, and midpoints have been assigned to time interval estimates from the literature. Data for the geochronological extension of modern mouthpart classes are provided in (k). A brief survey of analyses demonstrating congruent associations between plants and insects constitutes a sample of 13, each of which provides estimates for the origin of subclades (l). Data for each horizontal line within the vertical columns, including deposit, age, locality and literature source, will be found in the Appendix.

the same deposit, the Calhoun Coal of Fig. 2.5e. The same plant bore butternut-sized seeds containing abundant and nutrition-laden megagametophytic tissue surrounded by a thick woody layer; – promising candidates for vertebrate endozoochory, although a credible disperser remains elusive.

Like some seed ferns, some Palaeozoic cycadophytes in somewhat younger, Early Permian deposits possessed leaves that had prominent glandular hairs, considered by some as deterrents to herbivory (Beck & Labandeira 1998). In contrast, closely related or conspecific fructifications bore similar glands among their seeds that have

been considered as inducements for pollinating insects. The occurrence of a pollination drop mechanism in many of these seed plants, accompanied by a tubular micropyle leading to a basal pollen chamber, is similar to that in extant conifers (Tomlinson et al. 1991) and cycads (Norstog & Nicholls 1997), and may have been a source of nutrition for surface fluid-feeding and pollinating insects. A modification of this attraction mechanism, involving accumulation of fluid from specialized tissue into a depression encircling the seed apex, has been proposed for the Early Permian conifer *Fergliocladius* (Archangelsky & Cuneo 1987).

The micropyle-pollination drop mechanism also occurred among Mesozoic seed plants, including Late Triassic 'gnetophytes' (Cornet 1996) and Early Cretaceous bennettitaleans. However, it is among Middle Cretaceous deposits from the USA Atlantic Coastal Plain and southern Sweden, representing the early angiosperm radiation, that a variety of flowers and fruits have yielded important discoveries regarding the early history of modern types of pollination. This material consists of small, intact reproductive material preserved as charcoallified structures containing remarkably preserved, three-dimensional anatomy and external structure, frequently with in situ pollen and ovular contents. Beetle, fly, and bee styles of pollination have been recognized during this interval, including mid-Cretaceous pollination by anthophorid bees, as evidenced by the presence of oil-secreting nectaries of guttifer flowers (Crepet 1996). Similar types of analyses from Late Palaeocene to middle Eocene compression material have revealed associations between highly faithful insects and modified angiosperm inflorescences, including bee pollination of leguminous brush blossoms. It is notable that these abundant and distinctive floral features indicate the presence of insect pollination styles in the absence of body-fossil support: for example, only one documented bee body-fossil is known from the Cretaceous.

2.4.3.1.2 Plant damage (Fig. 2.4b)

Of all types of evidence for plant–arthropod associations, plant damage has the most extensive fossil record, occurring in the widest variety of *Lagerstätten* deposits from the Early Devonian to the late Caenozoic (Box 2.2). Most functional feeding groups are revealed predominantly by plant damage; for surface fluid feeding, pollination and aquatic feeding the evidence principally originates from plant reproductive structure, gut contents and insect

mouthparts. The earliest occurrences of plant damage are Early Devonian silicified stems of primitive vascular plants from the Rhynie Chert of Scotland (Kevan et al. 1975) and at Gaspé and Campbellton, eastern maritime Canada (Banks & Colthart 1993). During the Late Pennsylvanian of Euramerica, carbonate coal-ball permineralizations predominate, originating from extensive equatorial wetlands that contain tissues damaged by external feeders, borers, gallers and piercers-and-suckers (Labandeira 1998a). Permian carbonate and silica permineralizations containing oribatid mite and insect-sized borings are documented for glossopterid and other seed-plant woods, mostly from Gondwanaland continents (Weaver et al. 1997). Much of the subsequent permineralized fossil record contains insect borings and seed predation in silicified material. Permineralized material in Mesozoic deposits overwhelmingly contains beetle borings in gymnospermous wood. By contrast, a more diverse plant-damage spectrum occurs in Caenozoic deposits, typically in angiospermous woods and seeds, and includes damage by termites, ants and wasps, flies and especially beetles, many identifiable at the family or genus level. The fossil record of permineralized plant damage is largely decoupled from the compression/impression fossil record and each documents the history of different functional feeding groups.

The fossil record of plant damage from compressions and impressions is more persistent and abundant than that of permineralizations. The earliest major deposits are latest Pennsylvanian to Early Permian, representing riparian or estuarine deposits close to sea level or as humid settings marginal to peat accumulations (Labandeira 1998a). All major Palaeozoic plant taxa are represented in these deposits, including sphenopsids, ferns, seed ferns (such as medullosans, glossopterids and giantopterids), cordaites, conifers and cycadophytes. By the Late Triassic there is a shift towards feeding on advanced fern and seed-fern clades, conifers and bennettitaleans, documented in floras from the south-western USA (Ash 1997) and western Europe (Grauvogel-Stamm & Kelber 1996). Although evidence for plant damage in Jurassic and earlier Cretaceous floras is poor (Fig. 2.4b), the record becomes more informative for floras of mid-Cretaceous age where there is considerable evidence for diverse and abundant herbivory (Stephenson 1992; Labandeira et al. 1994) coincident with the ecological expansion of angiosperms. After the K/T extinction, there is depauperate representation of plant damage in Palaeocene floras (Labandeira

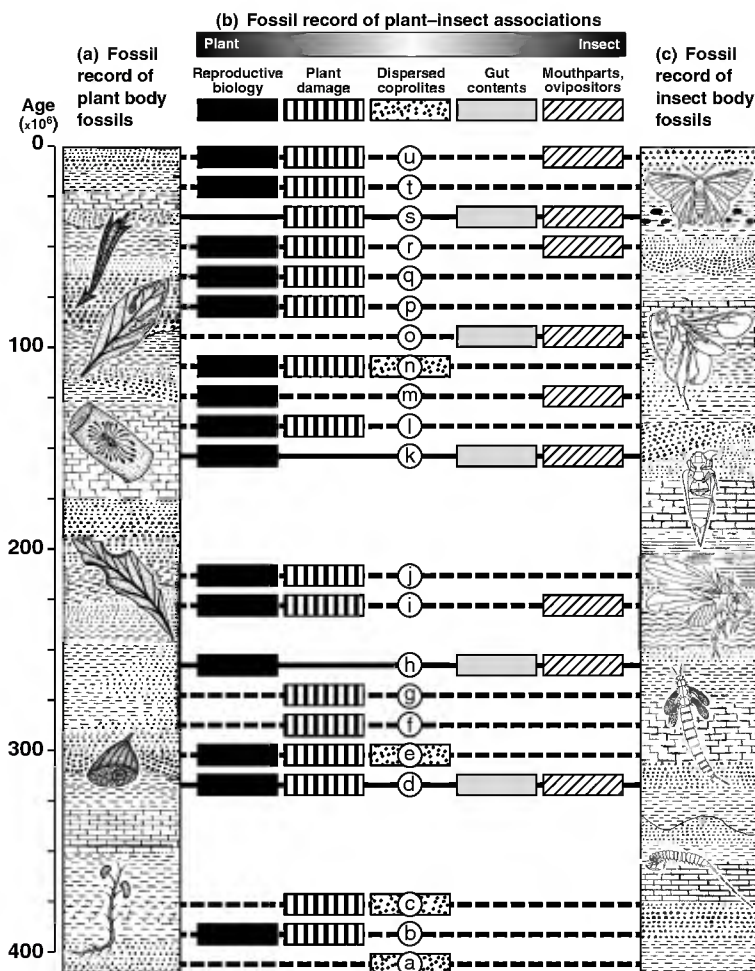


Figure 2.5 Types of evidence for plants, insects and their associations for 21 biotas, a small but representative sample selected from the fossil record and documented from the literature. The fossil record of plant–insect associations (centre panel with links) consists of one to four of the five major categories of evidence for plant–insect associations that have been used to establish direct (solid lines) to indirect links (dashed lines) between plants and insects. These types of evidence range from those centred primarily on the plant (reproductive biology) to those concentrating on both plant and insect (dispersed coprolites) to those focusing on insect structures (mouthparts and ovipositors). These biotas are not a complete inventory but represent most of the best-case examples, placed in geochronological order and approximately pegged to their absolute ages (left).

Each biota is identified by a circled letter and are from oldest to youngest: (a) Downton Castle Formation and Ditton Group, Late Silurian and Lower Devonian; (b) Rhynie Chert, Lower Devonian; (c) Battery Point Formation, Lower Devonian; (d) Carbondale Formation, Middle Pennsylvanian; (e) Mattoon Formation, Late Pennsylvanian; (f) La Magdalena coalfield, Late Pennsylvanian; (g) Waggoner Ranch Formation, Early Permian (Artinskian); (h) Koshchevo Formation, Early Permian; (i) Upper Buntsandstein and Lower Keuper Formations, Middle Triassic; (j) Chinle Formation, Late Triassic; (k) Karabastau Formation, Late Jurassic; (l) Wealden Formation, Early Cretaceous; (m) Yixian Formation, Early Cretaceous; (n) Kootenai Formation, Early Cretaceous; (o) Santana Formation, Early Cretaceous; (p) Dakota Formation, earliest Late Cretaceous; (q) Hell Creek and Fort Union Formations, latest Cretaceous to earliest Palaeocene; (r) Klondike Mountain Formation, middle Eocene; (s) Baltic amber, late Eocene; (t) Passamari Formation, late Oligocene; (u) the Störungszone, Pliocene. See the Appendix for additional locality details and references.

et al. 2002), after which the plant damage record improves considerably from the early Eocene on (Wilf & Labandeira 1999), and continues thereafter in deposits from intracontinental basins (Schaal & Ziegler 1992; Stephenson 1992).

2.4.3.1.3 *Dispersed coprolites* (Fig. 2.4c)

For sheer quality of preservation and abundance of deposits containing matrix-dispersed coprolites, the Pennsylvanian is the single most important taphonomic window worldwide. Euramerican coal-balls of Pennsylvanian age were deposited as nodular accumulations of plant organs with spectacular histological resolution, revealing peat-litter horizons that contain plant organs and interspersed coprolites with identifiable tissues from major plant taxa (Behrensmeyer et al. 1992). These coprolites range in size from those of oribatid mites (50 to 200 µm in length) to those of large mandibulate insects and perhaps millipedes (10⁴ µm in length), and represent detritivorous and herbivorous consumption of almost all accessible plant tissues, including root, stem and foliar parenchyma, epidermis, xylem and phloem, and spores and pollen. There also is evidence for detritivorous wood-boring and coprophagy, principally by mites (Labandeira et al. 1997). The presence of such rich data for inferring Pennsylvanian arthropod diets is attributable to a carbonate matrix forming in situ permineralization which preserves the cellular detail of plants. Unfortunately such a wealth of dietary data is difficult to attribute to particular arthropod culprits since the taphonomic processes that are ideal for retention of plant-tissue detail are apparently inhospitable to the preservation of arthropod chitin.

Arthropod coprolite assemblages are found in other fossil deposits, including some of the earliest known plant communities in the United Kingdom and the littoral of north-eastern North America (Edwards et al. 1995). They are typically found as ellipsoidal, spheroidal or even spiral to somewhat flattened coprolites bearing spores and vegetative tissues. Assemblages of large dispersed coprolites containing dominantly sporangial tissues and lesser amounts of conspecific vegetative tissue are known from the Early Mississippian to Early Permian. After the Palaeozoic, dispersed, frequently pollen-containing, coprolites occur in mid-Cretaceous sediments containing charcoalfied flowers and vegetative tissues. In addition, an increasingly rich record of herbivorous dinosaur coprolites is known from the Late Triassic to Late Cretaceous, including finds often with identifiable plant organs

from the Western Interior of North America (Chin & Gill 1996), the United Kingdom and India (Nambudiri & Binda 1989). These coprolites are typically composed of calcium phosphate, although younger coal-like versions are known from mammals at several Caenozoic deposits, including the middle Eocene lake at Messel in Germany (Schaal & Ziegler 1992). Avian and mammalian mummified dung has been recorded in cave deposits from extinct Quaternary herbivores, particularly from biotas such as Hawaii and the Balearic Islands (James & Burney 1997; Alcover et al. 1999), but also continental interiors (Thompson et al. 1980).

2.4.3.1.4 *Gut contents* (Fig. 2.4d)

Although gut contents are the rarest type of evidence for plant–animal associations in the fossil record, they are the most informative, since the taxonomic identities of both the consumed plant and the herbivore consumer are typically available. Gut contents of plant material are found in both the arthropod and vertebrate fossil records, and provide valuable dietary information that can verify evidence from insect mouthparts, vertebrate dentition and even plant reproductive biology. The most renowned site for gut contents is the Early Permian deposit at Chekarda, in the Ural Mountains of Russia, in which hypoperlid insect taxa previously presumed to be pollinivores based on mouthpart morphology, were subsequently discovered to contain gut contents of predicted seed-plant prepollen and pollen (Krassilov & Rasnitsyn 1999). This site has yielded additional insect taxa from other major clades, including Grylloblattida and Psocoptera, that variously bore monospecific to multitaxal pollen assemblages from seed-fern, cordaite and walchian conifer source plants (Krassilov & Rasnitsyn 1999). Three other sites where insect gut contents have been preserved are Karatau, from the Late Jurassic of south-eastern Kazakhstan, where grasshoppers consumed the pollen of an extinct family of conifers; the Early Cretaceous of Baissa, Russia, featuring xyelid sawfly guts containing pinalean conifer and similar seed-fern pollen; and Santana, from the Early Cretaceous of north-eastern Brazil, in which another xyelid sawfly species consumed apparently angiosperm pollen (Krassilov & Rasnitsyn 1999). Caenozoic insect-gut contents occur in more recent settings, such as the middle Eocene Messel deposit of Germany, late Eocene Baltic amber and early Miocene Dominican amber (Schaal & Ziegler 1992).

Vertebrate gut contents are rarer than those of insects.

The geologically earliest, well-documented example are sizable conifer ovules and associated gizzard stones in a food bolus from the stomach region of a pareiasaur (Munk & Sues 1993). Occasional gut contents have also been found in stomach cavities within dinosaurs skeletons, such as conifer needles and unascrbed fruits in the Late Cretaceous Canadian ornithopod *Trachodon*. The most spectacular discovery to date has been an abundance of gut contents in numerous plant-associated avian and mammalian taxa from the middle Eocene oil shales at Messel, including foliar remains in the rodent *Ailuravus* and foliar material and grape seeds in the early horse *Propalaeotherium* (Schaal & Ziegler 1992).

2.4.3.1.5 Mouthparts and feeding mechanisms (Fig. 2.4e)

The body-fossil record of animal mouthparts is sporadic but is controlled by the dominant *Lagerstätten* representing a diversity of taphonomic modes. Although geologically more recent amber deposits perhaps offer the best resolution of insect mouthpart structure, other preservational types, including silica permineralization, ironstone nodules and especially fine-grained compression deposits offer valuable data, particularly in the older fossil record (Shear & Kukulová-Peck 1990; Labandeira 1999). In several permineralized and compression deposits mouthpart structure can reveal considerable detail of robust individual elements, but also details of the setation and lobation for less sclerotized elements and the construction of multi-element mouthpart complexes (Labandeira 1997). A related, alternative approach is based on geochronological extensions into the fossil record of modern mouthpart classes. This tack, detailed in Section 2.4.3.4, provides a parallel system of inferring the history of mouthpart types.

Studies of fossil vertebrate chewing have focused on biomechanical analyses, as compared to the more descriptive documentation of arthropod mouthparts that are typically based on modern descendants. Within vertebrates, the relatively early origin of herbivory has been advanced from reconstructions of jaw movement, tooth-shearing planes and dental microwear striations for Permian synapsids and reptiles (Hotton et al. 1997; Sues & Reisz 1998). These have also been applied to a wide variety of herbivorous dinosaurs and other reptile-grade groups (Farlow 1987; Weishampel & Norman 1989). In particular, considerable effort has been directed towards understanding the complex mechanics of ornithopod and ceratopsian chewing (Weishampel & Norman 1989; Sereno 1999) as well as the processing of large quantities

of high-fibre food by tooth-poor sauropods (Bakker 1986; Farlow 1987). The chewing mechanics of early Caenozoic mammalian taxa have been examined for multituberculates, primates and other mammals, although much of this inference relies on research from modern descendants (Rensberger 1986).

2.4.3.2 Insect functional feeding groups

Functional feeding groups can be sorted into 14 basic ways that insects access food (Fig. 2.6). The concept of the functional feeding group was formalized initially from ecological studies of freshwater insects (Cummins & Merritt 1984), although the concept has also been used informally to refer to the varied feeding modes of terrestrial insects (Lawton et al. 1993). Functional feeding groups, like mouthpart classes, are ancient and originated independently multiple times within unrelated insect clades (Cummins & Merritt 1984; Labandeira 1997).

2.4.3.2.1 External foliage feeding (Fig. 2.7)

External foliage-feeders comprise the larval and adult stages of mandibulate insects that consume the entire or partial thickness of live leaf tissue from the outside. Several major subtypes of external foliage-feeding are recognized, namely margin-feeding, characterized generally by semicircular excavations of leaf-margin removal; hole-feeding, whereby interior circular or polygonal portions of the leaf are excised; and skeletonization, which features consumption of a non-marginal part of a leaf with venation remaining, often as a latticework of fine or coarser veinlets. Bud-feeding is a specialized type of external foliage-feeding that is caused by a larva tunnelling through imbricate leaf blades that are folded within a bud, leaving a characteristic pattern of symmetrical holes once the young leaf has unfurled. Free-feeding is an extreme type of external foliage-feeding whereby most of the leaf is consumed, with only major veins and occasional flaps of leaf tissue remaining. These basic types of external foliage-feeding and their geochronologies are illustrated in Fig. 2.6, and are compared to generalized feeding, equivalent to consumption of dead foliar tissue. In well-preserved Cretaceous and Caenozoic angiosperm-dominated floras, there are approximately 30 distinct damage types of external foliage-feeding, ranging from generalized bite-marks on margins to highly stereotyped and often intricate patterns of slot-hole feeding; earlier floras have fewer recognizable types of damage. Most

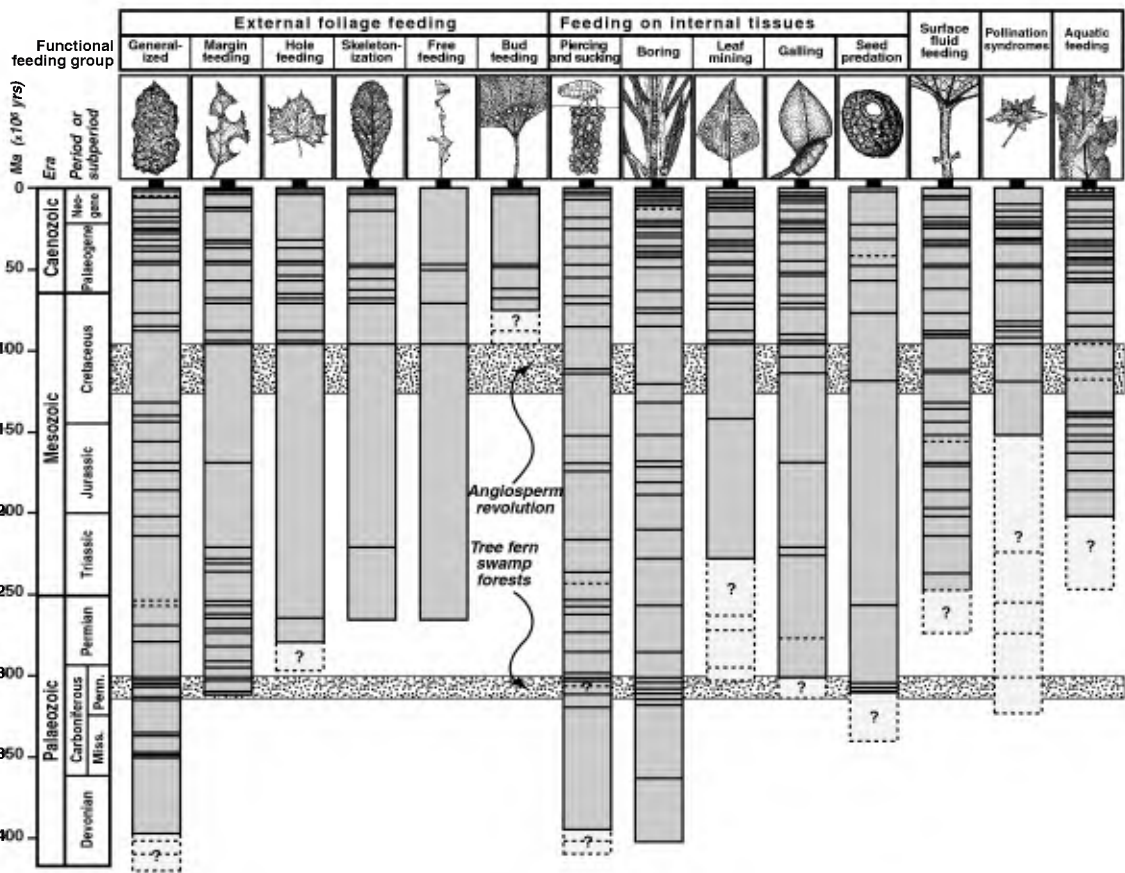


Figure 2.6 The fossil record of plant-associated insect functional-feeding groups. Horizontal lines on each vertical bar represents a datum collected from the literature of fossil plant–insect associations, and to a lesser extent, the fossil record of relevant plant and insect occurrences. Solid horizontal lines are well-supported data; dotted horizontal lines indicate probable or possible occurrences. Darker vertical bars encompassing the horizontal lines represent the geochronological duration of each functional-feeding group; less compelling earlier occurrences are indicated by lighter shading and question marks. Each functional-feeding group is included within a more inclusive feeding category based on terrestrial versus aquatic and internal versus external feeding modes. Pollination syndromes are from plant-reproductive and insect structural features that indicate associations, particularly mutualisms; they include interactional features that transcend the mere consumption of spores and pollen. Included under ‘borings’ are Early and Late Devonian tunnels and galleries in the ‘woody’ stroma of *Prototaxites*, a large, enigmatic, lignin-bearing fungus. For delimitation of functional-feeding groups see Coulson and Witter (1984) and Cummins & Merritt (1984). Abbreviations: Miss. = Mississippian; Penn. = Pennsylvanian; Neog. = Neogene. Documentation is available in the Appendix in figure captions for functional feeding groups (Figs. 2.7–2.13 and 2.15).

extant taxa of external foliage-feeders are immatures and adults of almost all species of Orthoptera, Phasmatodea and Lepidoptera, and a lesser percentage of Coleoptera and Hymenoptera. Palaeozoic external foliage-feeders were probably the Protorthoptera, Paratrachoptera and some Hypoperlida (Fig. 2.2).

Although generalized detritivory extends to the Early Devonian, based on dispersed coprolites, there also is evidence for external chewing on stems, based on plant damage with response tissue (Fig. 2.7a,b). Leaves were a subsequent development, and the fossil record

documents margin-feeding of foliage during the Middle Pennsylvanian (Labandeira 1998a). Hole-feeding, skeletonization and free-feeding were present during the Early Permian as well (Fig. 2.7c–h), although earlier origins are likely. Early external foliage-feeders were preferentially targeting diverse seed-ferns with fern-like foliage, large foliose leaves of gigantopterids, and to a much lesser degree ferns and cycadophytes; conifers were virtually free from attack. These functional feeding groups reappear on Middle and Late Triassic vegetation (Grauvogel-Stamm & Kelber 1996; Ash 1997), principally on ferns, but are

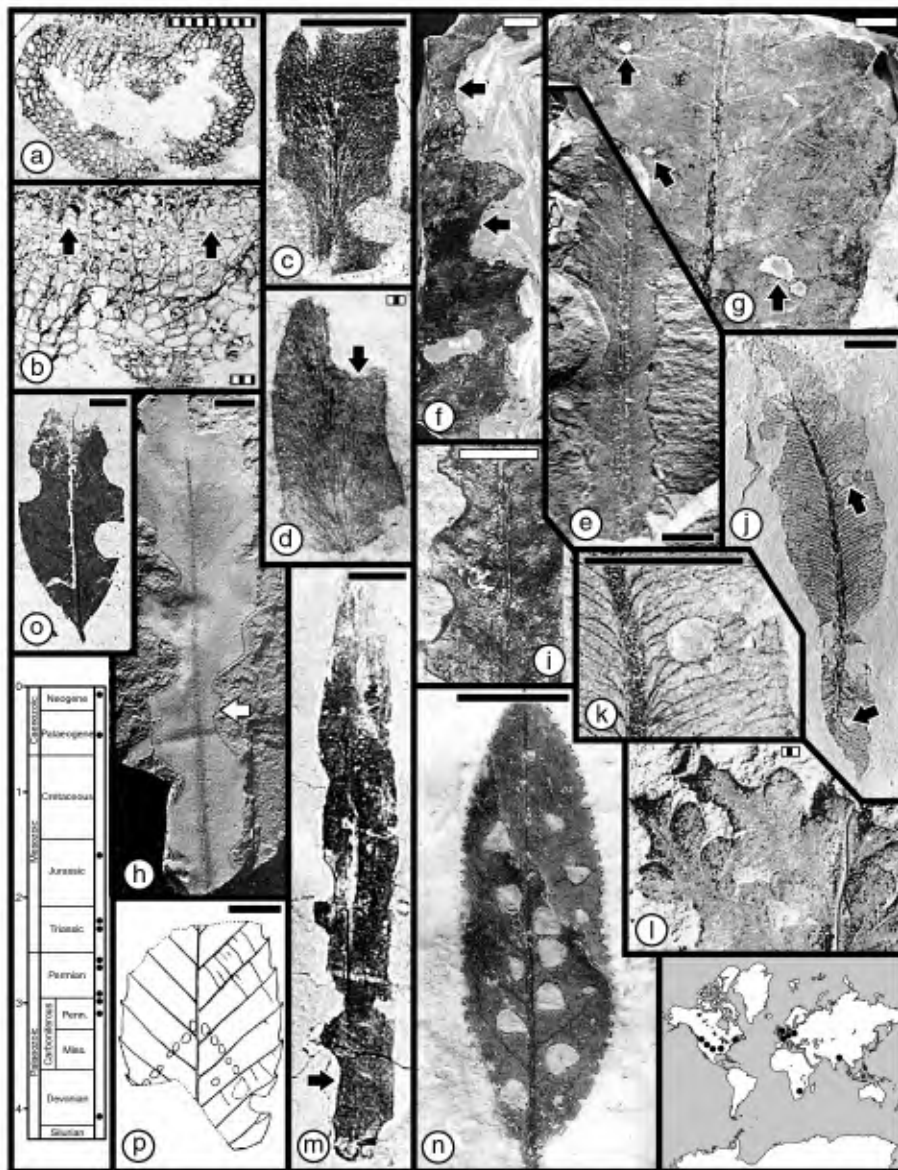


Figure 2.7 The fossil history of insect external foliage-feeding. (a) Transverse section of a permineralized specimen of a Lower Devonian trimerophyte, showing cortical collenchyma and wound response at top; inner tissues missing. (b) Detail of wound response tissue in (a), indicated by arrows, suggesting surface grazing. (c) A pinnule of a Middle Pennsylvanian seed-fern displaying cusped margin-feeding excisions. (d) A Late Pennsylvanian seed-fern exhibiting a bite mark (arrow) attributable to an external feeder. (e) A Lower Permian specimen of a seed-fern leaf showing extensive, scalloped, margin-feeding (arrow). (f) A Lower Permian cycadophyte displaying extensive margin-feeding (arrows). (g) From the same deposit as (f) is a gigantopterid plant displaying hole-feeding and surrounding necrotic blotches (arrows). (h) Specimen of an Upper Permian seed-fern showing cusped excavations (arrow) along the leaf margin and extending almost to the midrib. (i) Short leaf segment of a Middle Triassic cycadophyte leaf, showing three serial, cusped excavations that have projecting veinal stringers. (j) Leaf fragment of the Upper Triassic filicalean fern showing margin- and hole-feeding traces (arrows). (k) Detail of hole-feeding trace in the upper part of (j), exhibiting a reaction rim. (l) Cusped margin-feeding on a probable seed-fern from the same provenance as (j). (m) A Middle Jurassic cycad leaf exhibiting margin-feeding. (n) An unidentified angiosperm leaf with hemispheric- to deltoid-shaped feeding holes between secondary veins, from the middle Eocene. (o) Damage by an adult leafcutter bee (*Megachilidae*) on a middle Eocene rosaceous leaf. (p) Insect bud-feeding on a lower Pliocene chestnut leaf. Scale bars for this and succeeding figures: crosshatched = 10 cm, solid = 1 cm, dotted = 0.01 cm (100 μ m), and back-slashed = 0.001 cm (10 μ m). Additional locality data and source references can be found in the Appendix.

poorly documented in Jurassic and Early Cretaceous deposits (Figs. 2.4, 2.6, 2.7i–m). New foliage types of mid-Cretaceous angiosperms were heavily attacked by external feeders, but also leaf-miners and galls (Stephenson 1992). Bud-feeding can be traced to the Late Cretaceous and so far has only been found on angiosperms (Fig. 2.7p). This intensification and diversification of external foliage-feeding continued until the K/T extinction, after which floras had generalized and lower levels of damage (Labandeira et al. 2002) until the Palaeocene to Eocene transition, after which many modern damage types are recognizable (Fig. 2.7n,p; Wilf & Labandeira 1999).

2.4.3.2.2 *Piercing and sucking* (Fig. 2.8)

Piercing-and-sucking insects possess specialized mouthparts composed typically of one or two pairs of stylets for penetrating plant tissues and include accessory structures such as a muscle-controlled cibarial pump for creating suction for sap uptake. Piercers-and-suckers exhibit a unique combination of feeding on internal tissues while they are stationed external to the attacked plant organ. These invasive feeders typically target one of three vascular plant tissues—xylem, phloem or mesophyll—and they leave a characteristic pattern of internally and externally evident plant damage (Johnson & Lyon 1991). This type of plant damage has been found in Early Devonian deposits, although evidence for this type of feeding is rare and generally requires three-dimensionally preserved permineralized material. Thus there are a limited number of examples from the fossil record, most of which are Devonian (Kevan et al. 1975; Banks & Colthart 1993) and Pennsylvanian in age (Labandeira 1998a; Labandeira & Phillips 1996), with sporadic occurrences thereafter. Compelling evidence for the presence of piercing-and-sucking damage includes stylet tracks in plant tissue, frequently expressed as multiple radiating probes from a point of origin on the surface; the presence of a stylet terminus indicating the target tissue, with or without a feeding pool; disruption of surrounding, often parenchymatous tissue showing abnormal cellular development; and the presence of typically opaque, acellular material sheathing the stylet track or feeding pool (Labandeira & Phillips 1996). Two-dimensional surface views of punctures in compression material are less informative, revealing only a central perforation and a thickened, surrounding callus or other reaction tissue (Fig. 2.8l).

Insect groups responsible for piercing and sucking have changed significantly through time. They range from

unknown Devonian microarthropods (Fig. 2.8a–e) to four orders of later Palaeozoic palaeodictyopteroids (Fig. 2.8f–k; Carpenter 1971; Labandeira & Phillips 1996), which in turn were replaced by basal lineages of Hemiptera and Thysanoptera during the mid-Permian. After the demise of palaeodictyopteroids by the terminal Permian extinction, hemipteran and thysanopteran clades extended their ecological reach of feeding styles onto diverse vascular plants (Fig. 2.8l). Currently these two groups are the predominant piercing-and-sucking herbivores, although proturans, springtails and several families of beetles are also represented, many of which feed on fungal hyphae, algal filaments and mosses (Crowson 1981; Verhoef et al. 1988).

2.4.3.2.3 *Boring* (Fig. 2.9)

Arthropod borers construct tunnels through hard plant tissues, especially wood, but also bark, collenchyma and sclerenchyma. Additionally, the hard, chitinous basidiocarps of some fungi are bored in much the same manner as wood. Boring is overwhelmingly done by oribatid mites, termites and holometabolous insect larvae, the latter two of which bear mandibulate mouthparts for macerating or shredding indurated tissue into smaller particles that may be digested and voided as faecal pellets. These pellets are often formed into internal tunnel coatings or packed as undigested frass behind the advancing borer. Some mites and insects are known to possess a special gut microbiota responsible for the digestion of lignin and other structural polysaccharides found in wood and similar tissues that are typically resistant to enzymatic breakdown (Wilding et al. 1989). By contrast, other insect groups form a mutualism by supplying wood fragments and frass as a substrate, and feeding on portions of the resulting fungi for their nutrition. Modern borers are predominantly termites and larval beetles which variously bore through heartwood, cambium and bark (Crowson 1981). The larval wood-borers of other holometabolous insects include fungus gnats and leaf-miner flies among the Diptera, ghost moths, clearwing moths, carpenter worms and cutworms among the Lepidoptera, and the common sawflies, horntails, wood wasps and carpenter ants among the Hymenoptera (Johnson & Lyon 1991), many of which are cambium- or pith-borers that consume softer tissues. Insect borers inhabit wood in live or dead plants whereas oribatid mite borers almost always occur in dead wood and construct tunnels whose diameters are minimally an order of magnitude narrower.

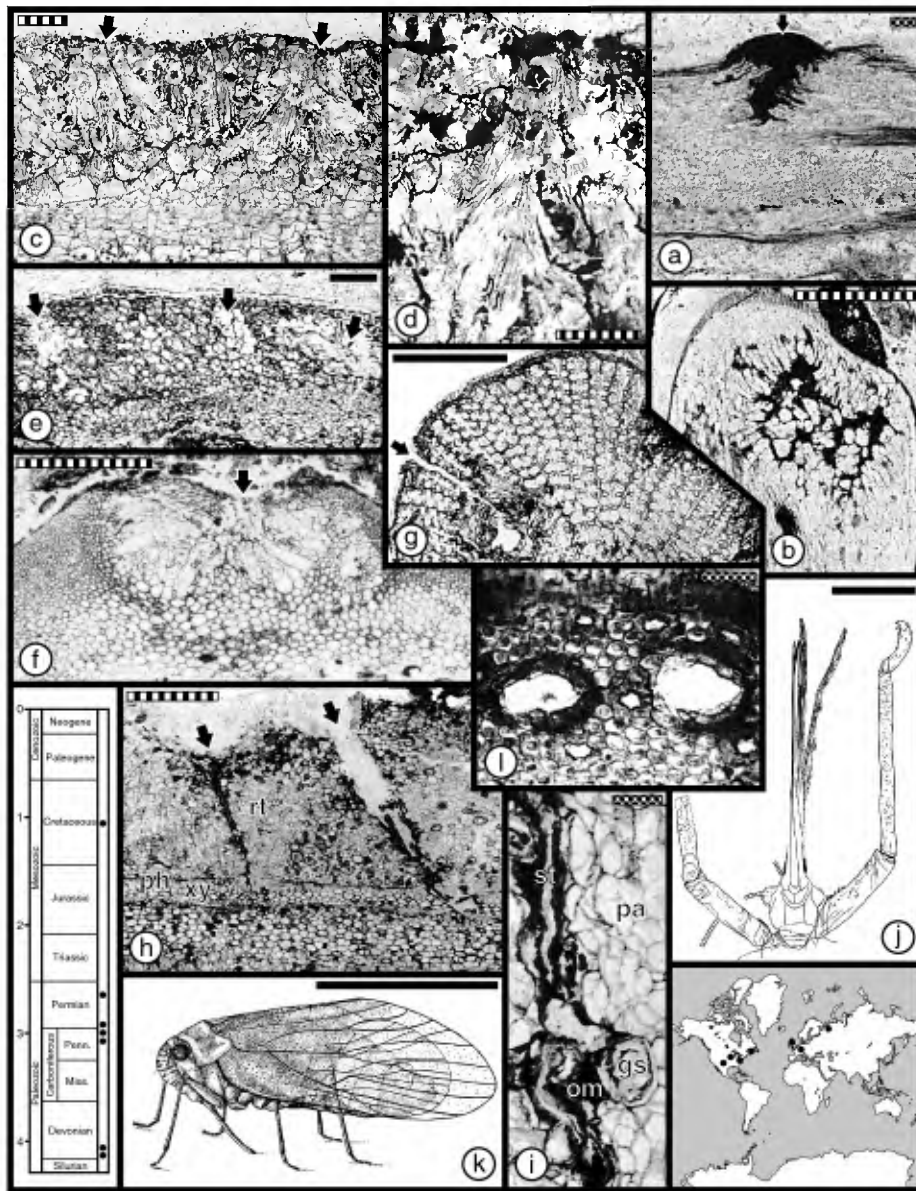


Figure 2.8 The fossil history of piercing-and-sucking. (a) An oblique, longitudinal section of an axis of a Lower Devonian rhyniophyte showing a lesion plugged with opaque material and extending to subjacent vascular tissue. (b) Another Lower Devonian axis in transverse section, displaying hypertrophied cortical cells and associated opaque material. (c) A specimen of the Lower Devonian trimerophyte, exhibiting three sites of piercing (arrows). Below each puncture site is a cone of lysed subepidermal tissue that is floored by unaltered periderm tissue. (d) Detail in (c), showing an enlarged cone of lysed tissue with radiate stylet tracks and damaged epidermal cells at the top. (e) Three piercing wounds on a Lower Devonian trimerophyte, eliciting a light-hued response periderm (arrows). (f) Damage to a Middle Pennsylvanian fern petiole, probably by an insect with styletate mouthparts, showing disorganized tissues enveloping the puncture wound. (g) A stylet track with terminal feeding pool, surrounded by reaction tissue, in a seed-fern prepollen organ from the Late Pennsylvanian. (h) Two stylet tracks targeting vascular tissue (*xylem* and *phloem*) of a Late Pennsylvanian marattialean fern. The right track, approximately 3 mm long, is sectioned lengthwise and shows surrounding reaction tissue (*rt*) and a terminal feeding pool. (i) Detail of the left stylet track in (h), showing stylet track (*st*), surrounding opaque material (*om*), penetration of undifferentiated parenchyma (*pa*) and avoidance of large gum-sac cells (*gs*). (j) Head and 3.2 cm-long stylete mouthparts of the Lower Permian palaeodictyopterid insect, *Eugereon*. (k) Reconstruction of the Lower Permian early hemipteran, *Permocicada*. (l) Two stylet probes, with surrounding rims of opaque material, on a Lower Cretaceous cheirolepidiaceus conifer. See Fig. 2.7 for scale-bar conventions; additional locality data and source references can be found in the Appendix.

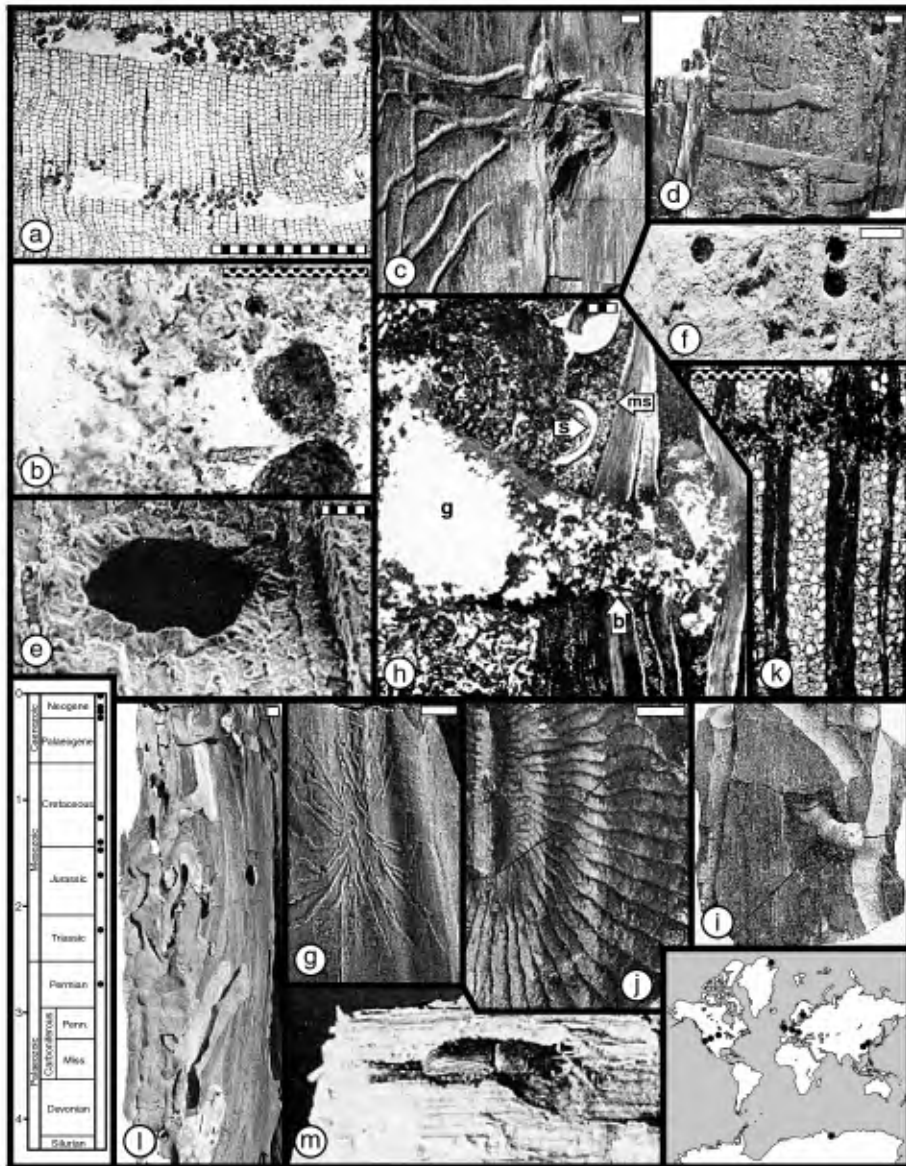


Figure 2.9 The fossil history of borings. (a) Oribatid mite borings in Late Permian gymnospermous wood. (b). Enlarged region of a boring in (a), showing ellipsoidal coprolites and associated undigested frass. (c) Insect (probably beetle) borings in cambium of a Late Triassic conifer. (d) Cambium borings in a conifer as in (c), but fabricated by a different insect species. (e) Scanning electron micrograph of a probable beetle boring in Middle Jurassic coniferous wood, healed by parenchymatous tissue. (f) Late Jurassic beetle borings in gymnospermous wood, assignable to the family Cupedidae. (g) A bark-beetle cambium boring in an unnamed, Early Cretaceous conifer. (h) Probable beetle invasion of the androecium of a Lower Cretaceous bennettitalean, showing consumption of synangial-associated tissues (s, synangium), a gallery (g) and an exit or entry tunnel (b) across the microsporophyll (ms) which are bract-like, enveloping structures. (i) A late Oligocene or early Miocene longhorn-beetle boring in unknown wood. (j) A bark-beetle cambium boring in unknown wood of middle Miocene age. (k) An upper Miocene dipteran cambium miner (Agromyzidae) in sycamore wood, displaying tissue damage at the top. (l) A late Pliocene boring of a longhorn beetle in larch (Pinaceae) wood. (m) The bark-beetle *Eremotes* within a boring of unknown Holocene wood. See Fig. 2.7 for scale-bar conventions; additional locality data and source references can be found in the Appendix.

The earliest examples of borers in terrestrial ecosystems are undescribed three-dimensional networks in living tissues of massive lignified fungi from the Early and Late Devonian of eastern North America. These specimens are assigned to *Prototaxites*, now considered a columnar, polypore-like basidiomycete. During the subsequent Mississippian microarthropod-size coprolites are known within plant tissues, but it is from coal-swamp forests during the Pennsylvanian that extensive evidence has been recorded for detritivorous oribatid mite tunnels in a variety of hard plant tissues (Labandeira et al. 1997), particularly cordaite and calamite wood, but also fleshy leaf cushions of arborescent lycopods, other coprolites and seed-fern pinnules. During the Permian there is limited evidence for oribatid mite damage in conifer and seed-fern woods (Fig. 2.9a,b), as well as the earliest appearance of insect-size borings (Weaver et al. 1997). During the Late Triassic to Early Cretaceous various borings assigned to beetles have been documented from a variety of woods and pithy tissues that include conifers, seed ferns and Bennettitaleans (Fig. 2.9c–f,h). The earliest bark-beetle damage is probably Early Cretaceous (Fig. 2.9g), and diverse damage has been described from the Late Cretaceous of Argentina. During the Cenozoic, recognizably modern groups are documented, including most of the modern taxa mentioned above (Fig. 2.9i–m; for a review see Labandeira et al. 1997).

2.4.3.2.4 Leaf-mining (Fig. 2.10)

Leaf-miners are mobile consumers of soft foliar tissue that do not elicit a major histological response. They are the larvae of holometabolous insects (Connor & Taverner 1997) and rarely mites; the former exhibiting a characteristic ontogenetic pattern beginning with an oviposition site containing an egg either embedded in leaf tissue or laid on the surface. This is followed by larval consumption of a particular tissue layer from which a characteristic frass trail is produced, frequently terminating in an enlarged, terminal chamber used for pupation (Frost 1924). In serpentine miners the frass trail is centrally positioned within a mine that becomes enlarged step-wise as the larva moults and increases in size, and may eventually assume a distinctive trajectory or shape immediately prior to pupation. Blotch mines are seemingly less structured externally, although the frequently obscured frass pattern, the specificity of the plant host and its tissue type, and the mine location on the leaf can be equally stereotyped. Modern leaf-miners comprise the larvae of the four major

holometabolous orders: Coleoptera, Diptera, Lepidoptera and Hymenoptera (Hespenheide 1991; Connor & Taverner 1997). Coleopteran leaf-miners occur in seven families, each representing an independent origin (Crowson 1981; Hespenheide 1991). Dipteran leaf-miners also occur sporadically throughout the order, evolved at least seven times, and include more basal members such as crane flies, aquatic midges and root gnats as well as more advanced members such as hover flies, fruit flies, and especially leaf-miner flies (Frost 1924). Within the Hymenoptera fewer than 100 leaf-mining species are known even though this life-habit evolved six times, all occurring within the sawfly superfamily Tenthredinoidea (Connor & Taverner 1997). The Lepidoptera overwhelmingly contains the majority of leaf-mining species, but unlike other orders characterized by multiple originations of relatively derived taxa from external feeders, the mining habit in moths probably originated once and is a primitive feature for the order (Kristensen 1997; Powell et al. 1999). The most basal lepidopteran lineage is similar to Mesozoic forms occurring in deposits as old as the Early Jurassic, whose larvae are mandibulate external feeders. Apparently leaf-mining originated in the next derived clade, the Heterobathmiidae, and was retained plesiomorphically during subsequent major cladogenetic events, although many lineages evolved external feeding as a secondary life-habit (Kristensen 1997; Connor & Taverner 1997).

Leaf-mining may be one of the few herbivore functional-feeding groups that originated during the Mesozoic, as Palaeozoic examples are currently unconvincing either histologically as permineralized sections or as foliar surface compressions with diagnostic features (Labandeira 1998a). Suspect Palaeozoic occurrences include U-shaped interveinal areas on seed-fern pinnules of Middle Pennsylvanian to Early Permian *Macroneuropteris* from several Euramerican localities that could be indicative of mining activity (Fig. 2.10a). Although these necrotic zones resemble blotch mines, no requisite anatomical evidence is present. Similarly, short sinusoidal features on pinnules of the seed-fern *Autunia* may be mines (Müller 1982) although they lack frass trails, discrete step-wise width expansions and terminal chambers. The earliest reliably identifiable leaf-mine was initially attributed to a nepticuloid lepidopteran, originates from the Jurassic/Cretaceous boundary of northern Australia, and occurs on the seed-fern *Pachipteris* (Fig. 10b,c). This occurrence (Rozefelds 1988) suggests that at least one

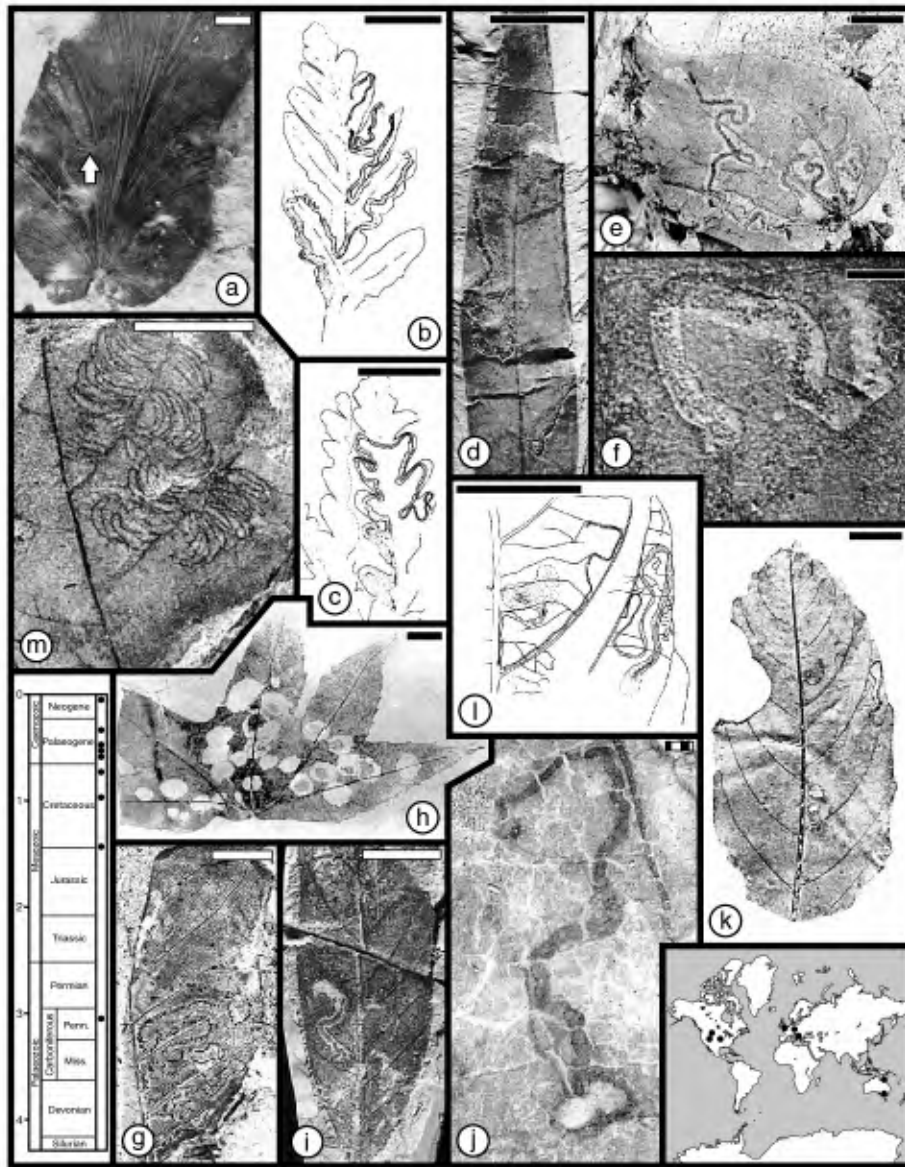


Figure 2.10 The fossil history of leaf-mining. (a) Possible U-shaped blotch mine on a Middle Pennsylvanian seed-fern leaf. (b) A holometabolous serpentine leaf-mine on a latest Jurassic to earliest Cretaceous corystosperm seed-fern. These leaf-mines antedate the earliest documented angiosperms by approximately 15 million years. (c) Another serpentine leaf-mine on a different corystosperm leaf, from the same deposit as (b). (d) A mid-Cretaceous serpentine leaf-mine produced by a moth (Gracillariidae) on a primitive dicot, showing oviposition site, frass trail and pupation chamber. (e) A Late Cretaceous serpentine leaf-mine of a nepticulid moth (Nepticulidae) on a katsura tree leaf (Cercidiphyllaceae). (f) Detail of leaf mine in (e), showing a medial frass trail of particulate coprolites. (g) Portion of an early Eocene mahogany leaflet (Meliaceae) with a serpentine, frass-bearing leaf-mine of a moth (Gracillariidae). (h) Middle Eocene circular leaf-mines of fairy moths (Incurvariidae) on a sycamore-like leaf (Platanaceae). (i) A middle Eocene dicotyledonous leaf bearing a serpentine leaf-mine assignable to the Lepidoptera, probably Nepticulidae. (j) Detail of leaf-mine in (i), showing complete developmental progression from oviposition to pupation. (k) A late Eocene leaf of Lauraceae exhibiting a serpentine lepidopteran mine (Nepticulidae). (l) Camera lucida enlargements of two mines in (k). (m) An upper Miocene dipteran blotch mine (Agromyzidae) on a leaf of Lauraceae. See Fig. 2.7 for scale-bar conventions; additional locality data and source references can be found in the Appendix.

lineage of holometabolous leaf-mining insects was selectively mining seed-fern hosts significantly before the earliest documented angiosperms (Labandeira et al. 1994; see also Powell et al. 1999). During the Middle Cretaceous ecological radiation of angiosperms several leaf-mining lineages of insects became associated with foliar tissues of principally primitive dicotyledonous angiosperms (Fig. 2.10d,e). This expansion of plant/insect associations, at least in North America, was disrupted by the K/T extinction (Labandeira et al. 2002), but slowly rebounded thereafter (Fig. 2.10f–m).

2.4.3.2.5 *Galling* (Fig. 2.11)

An arthropod gall is an atypically enlarged plant structure that is endophytically induced by a larval or nymphal arthropod, and results in the production of certain nutrient-rich tissues that are eventually consumed. Galls are three-dimensional, conspicuous, often externally hardened structures that can occur on any plant organ and represent the metabolic control of host-tissue production by the encapsulated mite, hemipteroid nymph or holometabolous larva (Shorthouse & Rohfritsch 1992). The galling life-habit originated independently numerous times and includes tarsonemoid and eriophyoid mites; and numerous lineages of Thysanoptera (thrips), Hemiptera, Coleoptera, Diptera, Lepidoptera and Hymenoptera (Shorthouse & Rohfritsch 1992). Insect gallers are highly tissue- and host-specific. Although about 80% of extant galls occur on leaves, the fossil record of galls indicates that the earliest known galls were found on stems or petioles—an ancient feeding mode rooted in Pennsylvanian coal-swamp forests and probably derived from insect borers (Labandeira 1998a).

These earliest, anatomically documented galls occurred on frond petioles of arborescent marattialean ferns (Fig. 2.11c,d) and probably the terminal shoots of calamitalean sphenopsids (Fig. 2.11a,b). Evidence for Permian galls is sparse and unconvincing. Nevertheless there are well-documented examples of spindle-shaped thickenings of branchlets from two taxa of voltzialean conifers from the Middle Triassic of western Europe (Fig. 2.11e). In addition an undetermined gymnosperm from the Late Triassic of the south-western United States bears spheroidal mite-sized galls on leaves (Fig. 2.11f,g). Similar but somewhat larger mite-sized, foliar galls have been recorded on a Middle Jurassic bennettitalean leaf (Fig. 2.11h). After a hiatus of about 65 million years, galls reappear in the fossil record, but now on angiosperms, and

sparingly from the earlier Middle Cretaceous of the eastern United States, later becoming abundant on various taxa from the Dakota Formation of Kansas and Nebraska. Foliar galls from a diversity of Dakota angiosperms occur on midribs, other major veins, petioles and non-veinal leaf-blades, and thus present a modern spectrum of foliar gall types. Subsequent Cretaceous and Caenozoic gall types are elaborations of this theme (Fig. 2.13i–m; Scott et al. 1994), although there is an apparent extinction of certain gall types at the K/T boundary. During the Caenozoic distinctive gall morphologies are occasionally discovered that are very similar to modern gall taxa and their hosts, including the gall wasp *Antron* on oak, and the gall midge *Thecodiplosis* on bald cypress (Fig. 2.11j,m). Fossil galls are found in compression and permineralized deposits (Larew 1992), rarely in amber, and are best preserved in carbonate-permineralized coal-balls where histological detail is similar to the anatomical sections of modern galls (Fig. 2.11c,d).

2.4.3.2.6 *Seed predation* (Fig. 2.12)

Insects preying on seeds typically penetrate hardened tissues to reach target food reserves, particularly endosperm or other analogous tissues essential for sporophyte survival. Palaeodictyopteroids have been implicated as Palaeozoic seed predators (Shear & Kukalová-Peck 1990), although present-day seed predators include seed bugs, seed beetles, weevils, seed-chalcid wasps and oecophorid moths. Ants are probably the foremost plant associates that use seeds mutualistically, only serving a role in seed dispersal. The fossil record of seed predation extends to the Middle Pennsylvanian in the form of punctured spores and three-dimensional seeds of seed-ferns bearing plugs indicating the presence of a borer (Fig. 2.12a,d), and especially cordaite seeds with circular drill holes that correspond to the width of certain co-occurring palaeodictyopteran beaks (Fig. 2.12b,c). Gingkophyte seeds were used to construct caddisfly cases in Early Cretaceous lake deposits of Mongolia (Fig. 2.12e), and borer damage in dicotyledonous seeds from the Late Cretaceous of Argentina are similar to modern seed-beetle predation (Fig. 2.12f). The Caenozoic has produced a richer record of seed predation, including small holes in seeds of the citrus and legume families (Fig. 2.12g–j).

2.4.3.2.7 *Surface fluid-feeding* (Fig. 2.13)

Whereas pollinators consume fluids associated with flowers and are involved in pollen transfer, surface fluid-

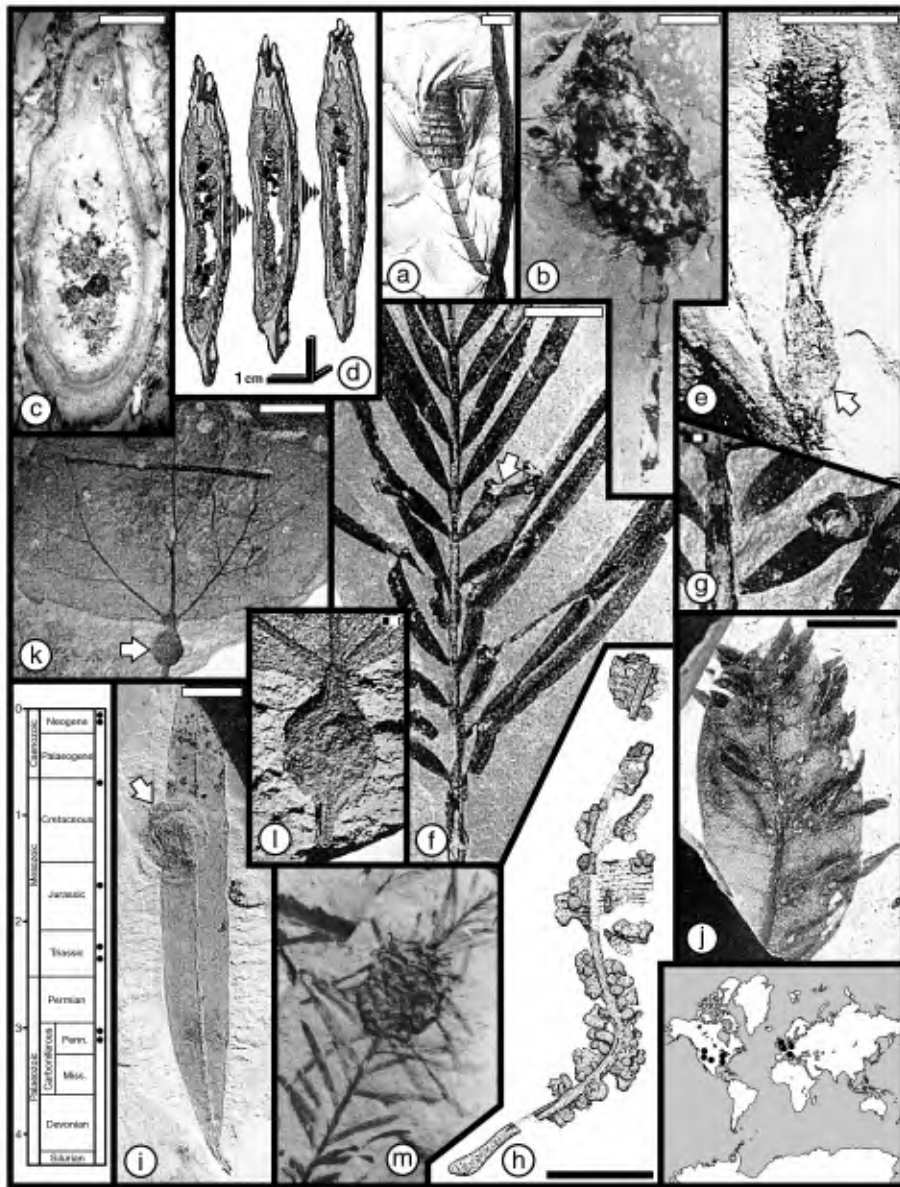


Figure 2.11 The fossil history of galling. (a) A probable Middle Pennsylvanian gall on the terminus of a sphenophyte shoot. (b) A Middle Pennsylvanian 'fructification' reinterpreted as a probable stem gall. (c) A Late Pennsylvanian gall of a holometabolous insect on the rachis of an arborescent marattialean fern. Note barrel-shaped coprolites and frass in the central lumen, and surrounding tufts of hyperplasic and hypertrophic parenchyma. (d) Three-dimensional reconstruction of the same gall type in (c), from the same deposit. (e) An aborted cone of a Middle Triassic voltzialean conifer showing a basal stem expansion interpreted as a gall. (f) Round, oval and deltoid leaf galls on an enigmatic Upper Triassic gymnosperm, expressed as swellings typically occurring about 1 to 1.5 cm from the base of the leaf. (g) Enlargement of a gall in (f) (arrow), showing a deltoid shape and extension beyond the leaf margin. (h) Abundant, bulbous galls on the leaf of a Middle Jurassic bennettitalean, occurring in clusters and preserved three-dimensionally. (i) A large spheroidal gall on a Late Cretaceous angiosperm leaf, similar in form to those produced by gall wasps (Hymenoptera, Cynipidae). (j). Cynipid spindle galls on the leaf of a middle Miocene oak. These distinctive galls are most similar to those of the extant gall wasp *Antron clavuloides*, which parasitizes oaks. (k) A petiolar gall, attributed to a gall aphid, on an upper Oligocene cottonwood leaf. (l) Enlargement of the gall in (k), showing a characteristic stem expansion. (m) A cone-mimicking gall of a gall-midge dipteran on a middle Miocene bald cypress, a swamp-dwelling conifer. See Fig. 2.7 for scale-bar convention; additional locality data and source references can be found in the Appendix.

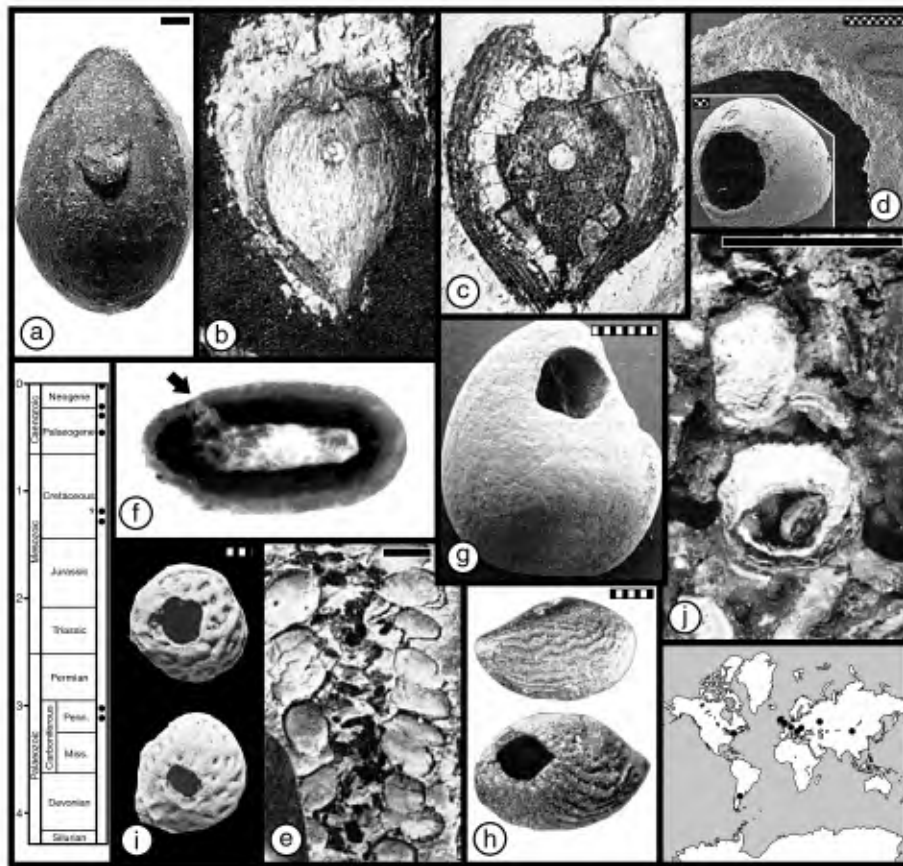


Figure 2.12 The fossil history of seed predation. (a) A sandstone cast of a Pennsylvanian seed displaying a plug infilling a presumptive hole in the seed coat. (b) External surface of a Middle Pennsylvanian cordaitalean seed. The culprit is probably a palaeodictyopterid insect in the same deposit possessing a beak width matching the hole diameter. (c) A similarly bored seed from the same deposit, in longitudinal section. (d) A boring in a Middle Pennsylvanian lycopsid megaspore, showing the entire spore (inset) and a detail of the bored margin. (e) A caddisfly case of ginkgophyte seeds from the Lower Cretaceous. (f) Longitudinal section of a permineralized dicotyledonous seed or fruit from the probable Upper Cretaceous, showing a boring assigned to the trace-fossil genus *Carpoichnus*, with exit hole at arrow. (g) A middle Eocene seed of the citrus family (Rutaceae) with an insect exit hole. (h) Pristine (top) and bored (bottom) seeds of another type of citrus family seed, from the early Oligocene. (i) Bored early Miocene stone fruits of a hackberry fruit (Ulmaceae), assigned to the trace-fossil genus *Lamniporichnus*. This damage is typical of weevils. (j) Additional damage of another hackberry fruit, from a Pleistocene hot-spring deposit. See Fig. 2.7 for scale-bar conventions; additional locality data and source references can be found in the Appendix.

feeders have a broader range of imbibed fluids that are produced by plants and many are not necessarily involved with pollination. Common foods for surface fluid-feeders originate from all major vascular plant groups and include floral and extra-floral nectaries, sap flows, exposed subdermal tissue and resulting fluids, the products of guttation, honeydew from sap-sucking insects and deliquescent fungal fruiting bodies (Fahn 1979; Setauda 1995). Surface fluid-feeders are a diverse assemblage of insects from overwhelmingly adult stages that bear a variety of mouthpart mechanisms for imbibing fluid food. The

most common types of fluid uptake are sponging in caddisflies and flies, siphoning in lepidopterans and beetles, and various combinations of lapping, sponging and siphoning among those hymenopterans bearing a retractile maxillolabial apparatus (Chaudonneret 1990; Labandeira 1997; Jervis & Vilhelmsen 2000). Surface fluid-feeders are traceable to the Early Triassic, coincident with the early radiation of basal Diptera and other holometabolous insects (Wootton 1988; Krzemiński 1992), although they probably have Palaeozoic roots (Fig. 2.6). Most of the evidence for surface fluid-feeding

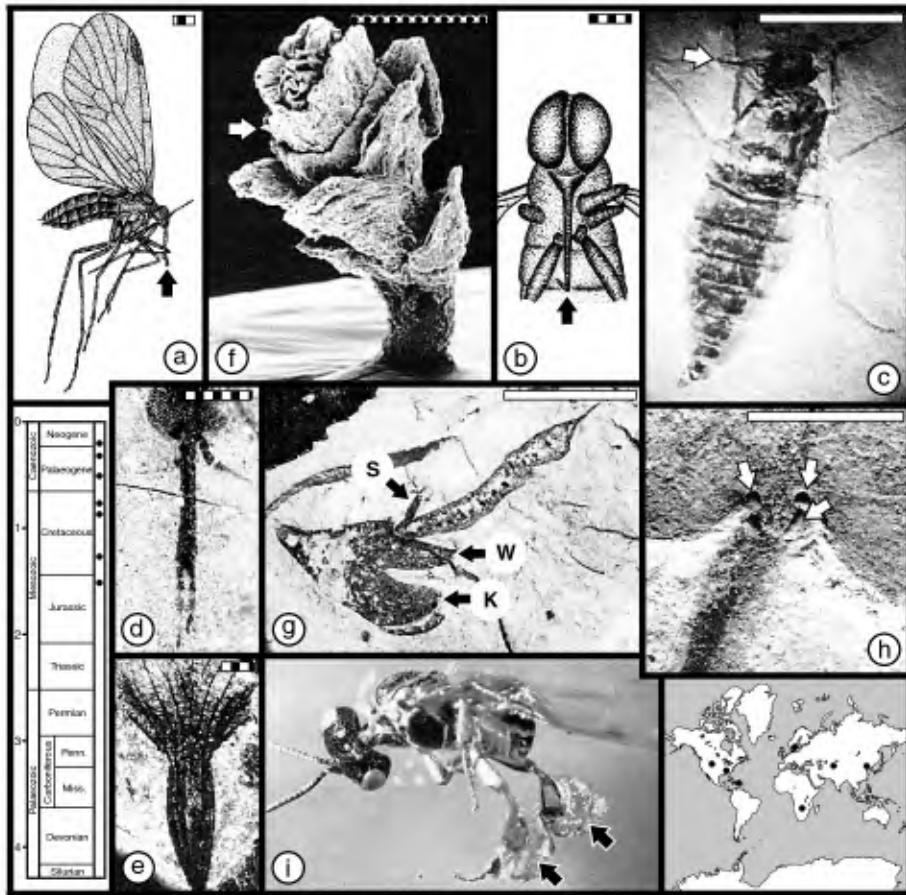


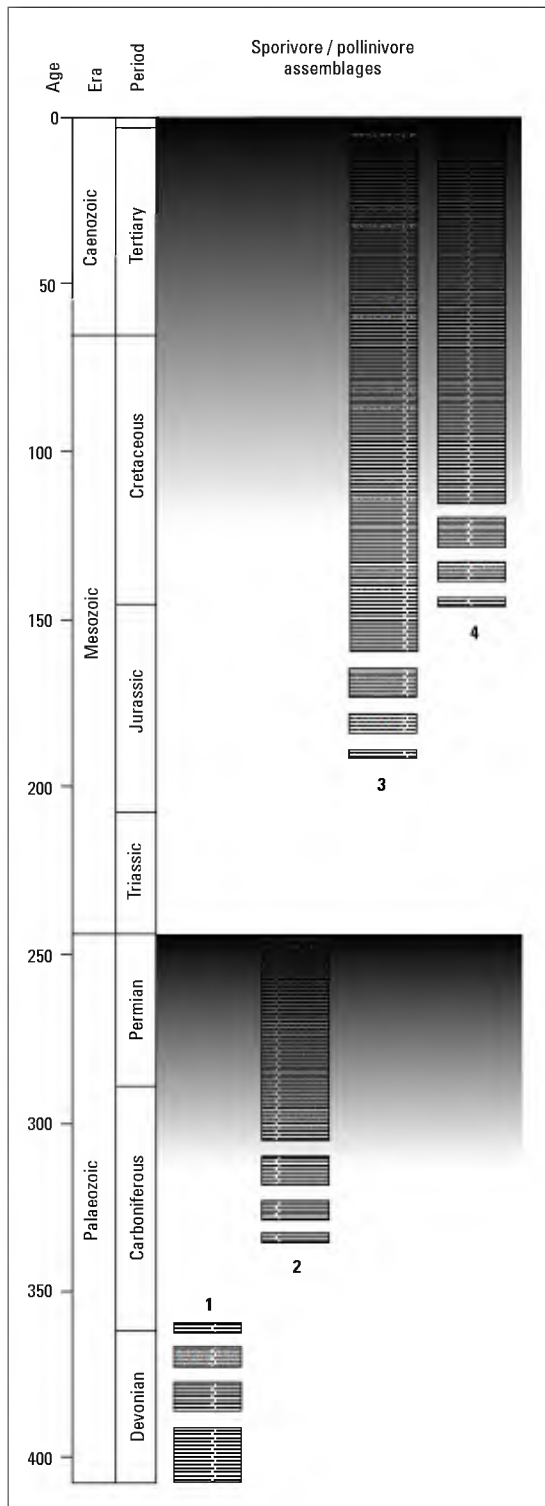
Figure 2.13 The fossil history of surface fluid-feeding. (a) The Late Jurassic scorpionfly *Pseudopolycentropus latipennis*, with elongate mouthparts (arrow), redrawn from a camera lucida sketch in Novokshonov (1997). (b) Head and mouthparts (arrow) of the tanglevein fly *Protneumestrius rohdendorfi*, of the family Nemestrinidae, from the same provenance as (a). (c) Another tanglevein fly *Florinestrius pulcherrimus*, from the Early Cretaceous of western Liaoning, China. Note elongate mouthparts (arrow) which are similar in form to extant nectar-feeding nemestrinids. (d) Head and mouthparts of the mid-Cretaceous crane fly *Helius botswanensis* (Tipulidae), some extant descendants of which feed on flowers. (e) From the same deposit as (d) is a funnel-shaped flower consisting of fused petal bases and a deep throat, indicative of insect pollination. (f) Scanning electron micrograph of a small charcoalified flower showing a nectary disk (white arrow) above the region of petals, from the Late Cretaceous. (g) A showy, bilaterally symmetrical, papilionoid flower (Fabaceae) from the Palaeocene to Eocene boundary, exhibiting an upper banner petal (s), two lateral wing petals (w) and bottom keel petals (k), associated with bee pollination. (h) Extra-floral nectaries (arrows) at the junction of the leaf blade and petiolar base of a cottonwood (Salicaceae), from the uppermost Eocene and suggestive of an ant/plant interaction. (i) A worker of the early Miocene stingless bee *Proplebia dominicana* (Apidae) bearing conspicuous resin balls (arrows) attached to hind-leg corbiculae. See Fig. 2.7 for scale-bar conventions; additional locality data and source references can be found in the Appendix.

comes from insect mouthparts of body fossils from compression deposits (Fig. 2.13a,b–d) although various plant secretory tissues, including nectaries, floral oil glands and resin-secreting glands, suggest their presence (Fig. 2.13e–i).

2.4.3.2.8 Pollination (Figs 2.14 and 2.15)

The present associations between animals and plants are

perhaps nowhere highlighted more than by the varied pollination mutualisms which mediate the advantages of outcrossing in plants with the availability of accessible food resources to insects. These plant products include pollen, nectar and oils for nutrition, but floral structures also serve as mating sites and shelter (Proctor et al. 1996). Extant pollinators of angiosperms include members from virtually every major insect order, but notably



Thysanoptera, Coleoptera, Lepidoptera, Diptera and Hymenoptera. The mutually beneficial reward system that is the essence of pollination can be extended to the mid-Mesozoic, with the best examples being bennettitaleans and especially cycads, based on a variety of fossil and modern evidence (Norstog & Nicholls 1997; Windsor et al. 1999). In fact, the presence of extant cycad–beetle pollination associations, coupled with the fossil histories of cycads and their pollinators, indicate that the origin of some host-specific mutualisms occurred independent of and before the appearance of flowering plants (Farrell 1998; Windsor et al. 1999), particularly from the perspective that modern cycad families extend to the interval from the Late Jurassic to the Middle Cretaceous (Kvacek 1997; Norstog & Nicholls 1997; Artabe & Stevenson 1999).

The fossil record reveals four distinctive, temporal assemblages of spore and pollen consumption based on taxonomic affinities of source plants and their spore and pollen consumers (Labandeira 1998b; Fig. 2.14). The earliest assemblage consists of Late Silurian to Early Devonian spore-rich, dispersed coprolites (Fig. 2.15a,b), although there is no direct evidence of trophically linked arthropods. The second assemblage, Middle Pennsylvanian to Permian in age, consists of orthopteroid and hemipteroid insects associated with pteridophytes and early seed plants, evidenced by dispersed coprolites and gut contents (Fig. 2.15c–h). Evidently this assemblage was extinguished by the end-Permian mass extinction and was succeeded by the third phase during the earlier Mesozoic (Fig. 2.15i–m), dominated by advanced seed-plant hosts and orthopteran and basal holometabolan lineages (Krassilov & Rasnitsyn 1999). Present-day survivors include cycads and their weevil pollinators (Norstog & Nicholls 1997). The fourth, most recent assemblage (Fig. 2.15n–r) began during the mid-Cretaceous and comprises angiosperms and more derived holometabolan lineages (Crepet & Friis 1987). Assemblages 3 and 4 are associated with pollination ‘syndromes’, and it is likely that

Figure 2.14 The four distinctive assemblages of fossils representing insect consumption of spores, pollen or nectar, based on a variety of evidence, including that illustrated in Figures 2.15 and 2.17. Assemblages 3 and 4 include prominent pollination mutualisms; assemblage 2 is probably associated with pollination mutualisms; and assemblage 1 lacks known arthropod culprits. The presence and intensity of background shading indicates the probable duration and pervasiveness of pollination. (Modified from Labandeira 1998b.)

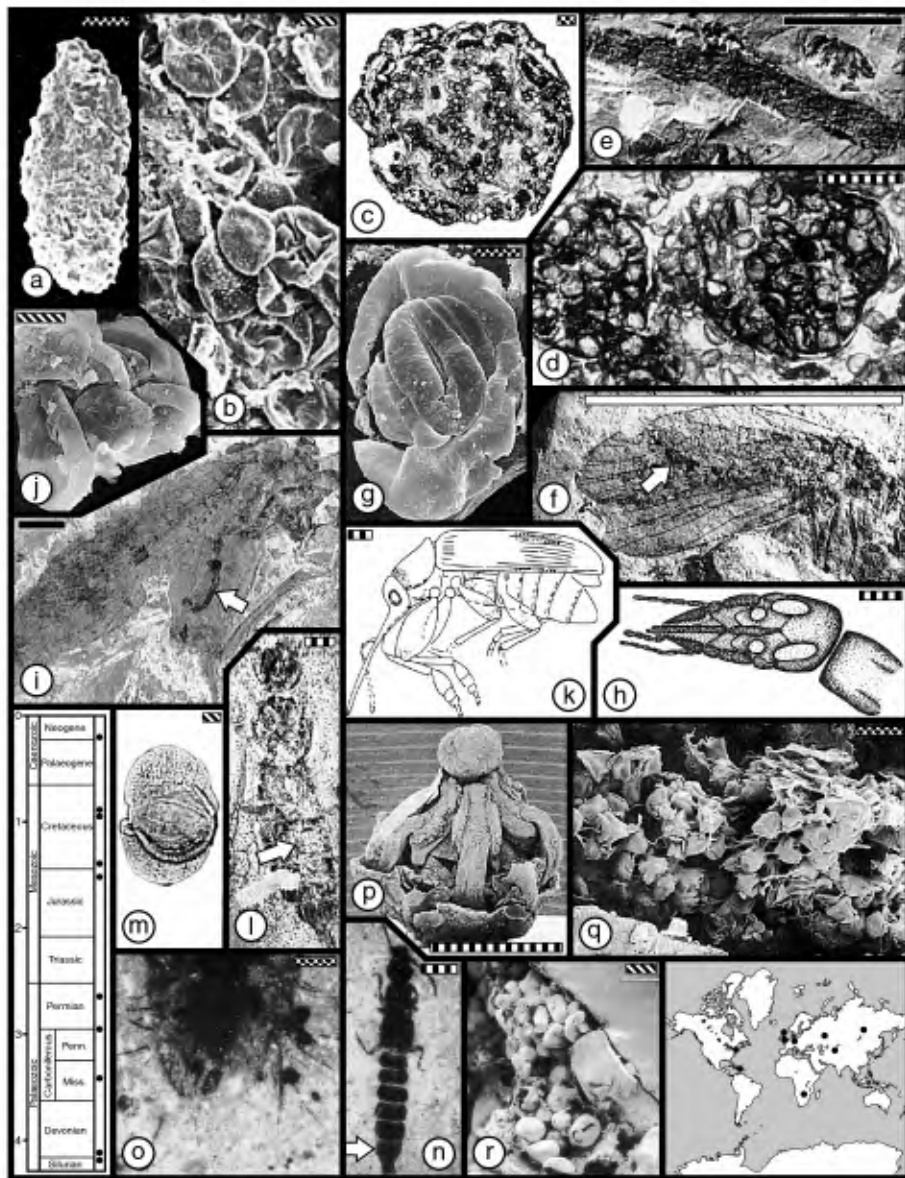


Figure 2.15 The fossil history of spore and pollen consumption, and pollination. (a) An elliptical, somewhat flattened coprolite containing plant cuticle and mostly spores, from the Late Silurian. (b) Contents of a Lower Devonian coprolite containing abundant vascular plant spores. (c) Sporangial fragments and isolated spores of the Mississippian-age coprolite *Bensoniotheca*, attributed to a lyginopterid seed-fern. (d) Two relatively intact sporangia in a *Bensoniotheca* coprolite from the same provenance as (c). (e) The latest Pennsylvanian or earliest Permian coprolite *Thuringia*, consisting of the digested remnants of a seed-fern prepollen organ. (f) The hypoperlid insect from the Lower Permian, containing a plug of pollen (arrow) preserved in its gut. (g) Detail of a *Lunatisporites*-type pollen grain extracted from (f), attributable to a voltzialean conifer. (h) Reconstruction of the head and mouthparts of another hypoperlid insect with pollinivorous habits from the same provenance as (f). (i) A Late Jurassic grasshopper with an arrow indicating a bolus of pollen in its intestine. (j) A cluster of digested *Classopollis* pollen from a cheirolepidiaceae conifer, extracted from the gut of (i) below. (k) A nemomychid weevil from the same provenance as (i), showing a long, decurved rostrum. (l) A Lower Cretaceous xyelid sawfly bearing well-preserved gut contents of pollen (arrow). (m) A pollen grain of *Pinuspollenites*, from a pinalean conifer, found in the sawfly gut in (l). (n) A rove beetle from the Late Cretaceous, displaying pollen transportation (arrow). (o) Enlargement of terminal abdominal region of (n), showing pollen grains trapped among hairs. (p) Lateral view of an Upper Cretaceous charcoalified flower belonging to the Ericales/Theales angiosperm complex. (q) Contents of an anther from the same taxon as (p), displaying the characteristic network of viscin threads, implying a pollinator mutualism. (r) A clump of two types of pollen from the external abdominal surface of a lower Miocene stingless bee, revealed by scanning electron microscopy. See Fig. 2.7 for scale-bar conventions; additional locality data and source references can be found in the Appendix.

Assemblage 2 was too, based on circumstantial evidence such as plant reproductive structure mentioned previously (Labandeira 1998a). Compression-type preservation provides the best evidence for pollination, although this mutualism is the most difficult to demonstrate of all functional feeding groups because of the very indirect nature of the evidence for plant entomophily and insect pollen transfer.

2.4.3.2.9 *Aquatic feeding*

Three distinctive modes of insect feeding in aquatic ecosystems—scraping, shredding and filtering—each represent a different solution to acquiring plant food that has a varied size-range and spatial distribution within freshwater habitats. Scrapers remove substrate-attached algae and associated material by specialized mouthparts that often include blade-like mandibles (Cummins & Merritt 1984). Scrapers that graze on algal film surfaces of mineralic and organic surfaces include Ephemeroptera, Hemiptera, Trichoptera, rare Lepidoptera, and especially Coleoptera and Diptera, most members of which feed in essentially in similar ways (Cummins & Merritt 1984). Shredders comminute dead and live plant material, including wood, in much the same way as terrestrial external foliage-feeders and borers, typically ingesting plant tissues as coarse particulate organic matter. Shredders are principally represented by members of Trichoptera, Coleoptera, Diptera and subordinately Plecoptera and Ephemeroptera. Filterers collect suspended particulate matter, including phytoplankton, by active sieving or passive screening by means of labral fans or mouthpart-associated brushes. Filterers prominently include larval Diptera, but are found sporadically in other aquatic insect groups. These three modes of aquatic feeding are the principal ways of incorporating dead and live plant material into higher trophic levels within aquatic ecosystems. Much of this material exists in the form of particulate plant detritus, and algae and microbes as part of substrate-attached films.

Insect aquatic feeding has a Permian origin, based on the inferred presence of aquatic immature stages of terrestrial adults recovered from several deposits. Most of these lineages with Permian representatives presumably had aquatic immatures that were predaceous in lotic environments, including Odonata, Megaloptera and Coleoptera (Kukalová-Peck 1991; Wootton 1988). However, there is also sparse fossil evidence for contemporaneous ephemeropteran and plecopteran naiads as detritivores (Kukalová-Peck 1991). Evidence for elevated detritivory

and herbivory in aquatic ecosystems increased during the Middle to Late Triassic, marked by the radiation of nematocerous Diptera (Shcherbakov et al. 1995), including lineages with aquatic stages, based on information from Early Jurassic occurrences, modern ecological associations and rarely preserved Triassic larvae. This interval documents the earliest known appearance of scrapers and shredders (Fig. 2.6). These early aquatic faunas were preserved in Middle to Late Triassic lacustrine faunas from the eastern United States, France and central Asia (Krzeminski 1992; Shcherbakov et al. 1995). They signal the early invasion and trophic partitioning of lotic habitats, including the neuston zone, water column and benthos, which was followed by expansion into lentic habitats during the Early Jurassic (Wootton 1988). This pattern of increasing food exploitation and partitioning, including the use of aquatic macrophytes, wood, phytoplankton and substrate-encrusting algae, continued into the Cretaceous (Ponomarenko 1996), during which the modern spectrum of aquatic feeding styles was established.

2.4.3.3 *Insect dietary guilds*

Dietary guilds are defined by what an insect consumes and are more phylogenetically labile than a functional feeding groups. Particular types of herbivory have originated from a few to undoubtedly hundreds of times among unrelated insect lineages. For example, the consumption of pollen has been considered a plesiomorphic feature in certain holometabolous insects because of shared, functionally similar mouthpart features in basal Coleoptera, Hymenoptera, Lepidoptera and perhaps related clades (Vilhelmsen 1996). However, pollinivory, with no implication for pollination, also occurs sporadically among numerous phylogenetically disparate groups of recent insects. This evidence is based principally on gut contents, observations of pollen extensively investing surfaces of mouthpart elements and functional morphology. Pollinivores include Collembola, katydids, three families of thrips, several lineages of beetles, several lineages of flies, bees, sphecids and vespids wasps, even two families of butterflies, and other groups not typically associated with pollen consumption (Proctor et al. 1996; Gilbert & Jervis 1998). As discussed previously, fossil pollen-feeders extend this list to orthopterans, hypoperlids, grylloblattodeans, booklice and xyelid sawflies. Other diets can be cited, such as meristematic stem tissue (cambium) or seeds, reinforcing a view that dietary convergence is ubiquitous and results from the opportunistic nature

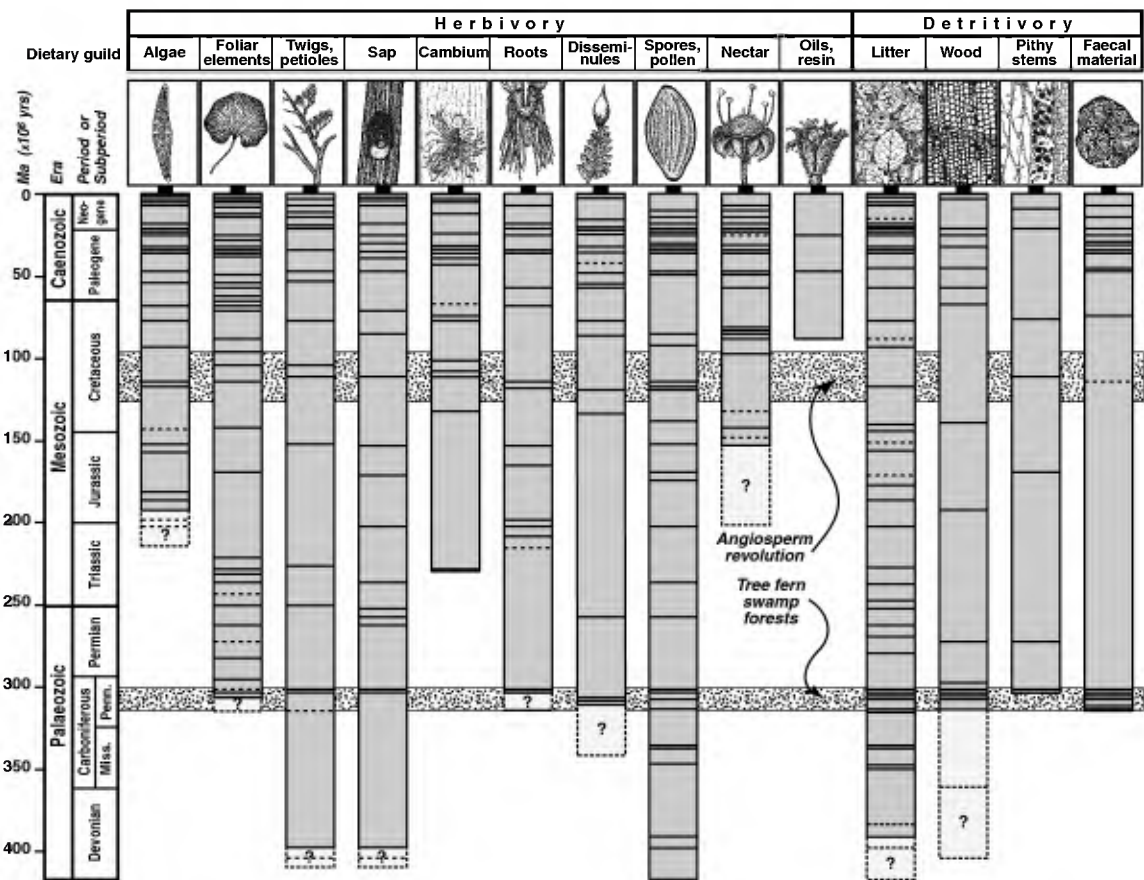


Figure 2.16 The fossil record of plant-associated insect dietary guilds. Horizontal lines on each vertical bar represents a datum collected from the literature of fossil plant–insect associations, and the fossil record of relevant plant and insect occurrences. Solid horizontal lines are well-supported data; dotted horizontal lines indicate probable or possible occurrences. Darker vertical bars surrounding the horizontal data lines represent the geochronological duration of each dietary group; less compelling earlier occurrences are indicated by lighter shading and question marks. Dietary guilds are consolidated into herbivory or consumption of live plant tissue (left), and detritivory or consumption of dead plant tissue (right). Herbivory of spores and pollen refers to evidence for consumption only, and excludes other types of evidence for pollination syndromes detailed in Fig. 2.8. The category ‘disseminules’ refers to fruits, seeds and analogous reproductive structures. The consumption of wood includes the lignified and hardened tissues of the polypore-like basidiomycete during the Devonian. For delimitation of dietary guilds see Slansky and Rodriguez (1987) and references there. Abbreviations: Miss. = Mississippian; Penn. = Pennsylvanian; Neog. = Neogene.

of insect feeding as exploitable food resources become available in time and space (Simpson & Neff 1983; Lawton et al. 1993).

The history of arthropod feeding on plants began during the Late Silurian to Early Devonian, characterized by coarse dietary subdivision of food into its three elemental forms: solid, particulate and fluid (Fig. 2.16, bottom). Litter detritus and live solid food like stem tissues were undoubtedly eaten by several types of microarthropods, including collembolans, archaeognathans and mites, and possibly myriapods such as millipedes and arthropleuroids.

In addition there was consumption of woody fungal tissues by unknown arthropod borers. Evidence for fluid-feeding on plant sap originates from plant damage interpreted as stylet-track damage (Banks & Colthart 1993; Labandeira & Phillips 1996) and associated wound responses (Kevan et al. 1975). Lastly, the oldest of these most fundamental of feeding modes—consumption of particulate matter—is documented from the Late Silurian of England (Edwards et al. 1995) and is revealed by spore-packed spindle-shaped coprolites that indicate the wholesale consumption of spores and perhaps entire

sporangia by undetermined arthropods. Thus the chewing of plant organs, the piercing of tissues for sap consumption, sporivory and the boring of hard fungal tissues are the most ancient arthropod diets on land.

By the close of the Pennsylvanian, the expansion of arthropod herbivory had invaded all plant organs and virtually all plant tissues (Fig. 2.16, lower horizontal bar). This expansion of dietary breadth provided a modern cast to the spectrum of insect diets. The best qualitative data comes from the Late Pennsylvanian Calhoun Coal Flora of Illinois. Targeted tissues included xylem and phloem, petiolar parenchyma, root epidermis, sporangial and pre-pollen organ tissues, and wood (Labandeira 1998a). The first evidence for faecal consumption (coprophagy) is also present, with oribatid mites implicated (Labandeira et al. 1997). By the Late Triassic, cambial tissues were added to this inventory but the invasion of lotic and probably lentic aquatic ecosystems by consumers of substrate-attached and suspended algae was also important (Wootton 1988, Ponomarenko 1996). Later, nectarivory became a staple for surface fluid-feeding and pollinating insects, undoubtedly linked to the diversification of advanced seed plants that included the presence of extra-floral nectaries and a transfer in function of the pollination drop mechanism. Last, with the ecological expansion of flowering plants during the mid-Cretaceous (Fig. 2.16, upper horizontal bar), there is documentation for the consumption of oils, supported by highly distinctive floral features in plant taxa related to modern guttifer and malpighia families (Crepet 1996) that are often pollinated today by bees. In summary (Fig. 2.16), while the overwhelming bulk of the 14 plant-associated diet types was in place during the Late Pennsylvanian, it was followed by the addition of 4 novel diet types during the Mesozoic in conjunction with the establishment of freshwater ecosystems and the diversification of advanced seed plants.

2.4.3.4 Insect mouthpart classes

Mouthpart classes, the third ecomorphological unit that will be considered, occur as body fossils and thus provide a direct record of the feeding apparatus insects have used to consume food. While there are some spectacular examples of insect body fossils from *Lagerstätten* that bear well-preserved mouthparts, the historical record of mouthparts is sporadic. However, a complementary method was devised to infer the fossil history of insect mouthpart classes (Labandeira 1997).

Six conclusions have come from a study of the geochronological history of insect mouthparts (Labandeira 1997). The first is that there are 34 fundamental, modern mouthpart types, although subsequently 2 additional (and plant-associated) mouthpart types have been recognized in the Palaeozoic (Fig. 2.17). Of these mouthpart types, about half are associated with plants in major ways. Second, about half the mouthpart classes have originated multiple times when evaluated at coarser taxonomic levels, some several times, thus providing a major role for morphological convergence in the generation of mouthpart morphology and innovation (Cummins & Merritt 1984; Labandeira 1997). Third, there are moderate to strong associations between mouthpart class and general dietary features, such as the form of the food and dietary preferences. Fourth, whereas taxonomic diversity is best characterized as a semi-exponential rise with constant and ever-increasing accretion of taxa towards the present, mouthpart class diversity is logistic and has essentially stabilized since the mid-Mesozoic (Fig. 2.18). Because of this dynamic decoupling, mouthpart data tend to support ecological saturation rather than expanding resources (Labandeira 1997), although there is a modest time lag for mouthpart class accumulation into the earlier Mesozoic. Similar data from functional feeding groups and dietary guilds independently buttress this conclusion. Fifth, a recurring pattern has been the serial derivation of fluid-feeding from generalized mandibulate insects, principally through unique co-optations of mouthpart regions and associated elements to produce haustellate structures such as the lepidopteran siphon, the dipteran sponging labellum and the hymenopteran maxillolabiate apparatus (Chaudonneret 1990; Jervis & Vilhelmsen 2000). Last, there are five major phases present in the temporal distribution of mouthpart classes, each associated with the relatively rapid origination of structural novelty.

From what is known of a sparse Late Silurian to Middle Devonian arthropod record and the phylogenetic relationships among extant basal lineages of hexapods, four or perhaps five ancient mouthpart classes characterize the first phase of mouthpart evolution (Fig. 2.17: 1–4, ?22; Labandeira 1997). Hexapods and possibly some myriapods possessed these 4 or 5 mouthpart types that were collectively responsible for chewing and piercing dead and live plant tissue, as well as boring through hard fungal tissues. By the Late Pennsylvanian, the second phase of mouthpart evolution was underway, through the addi-

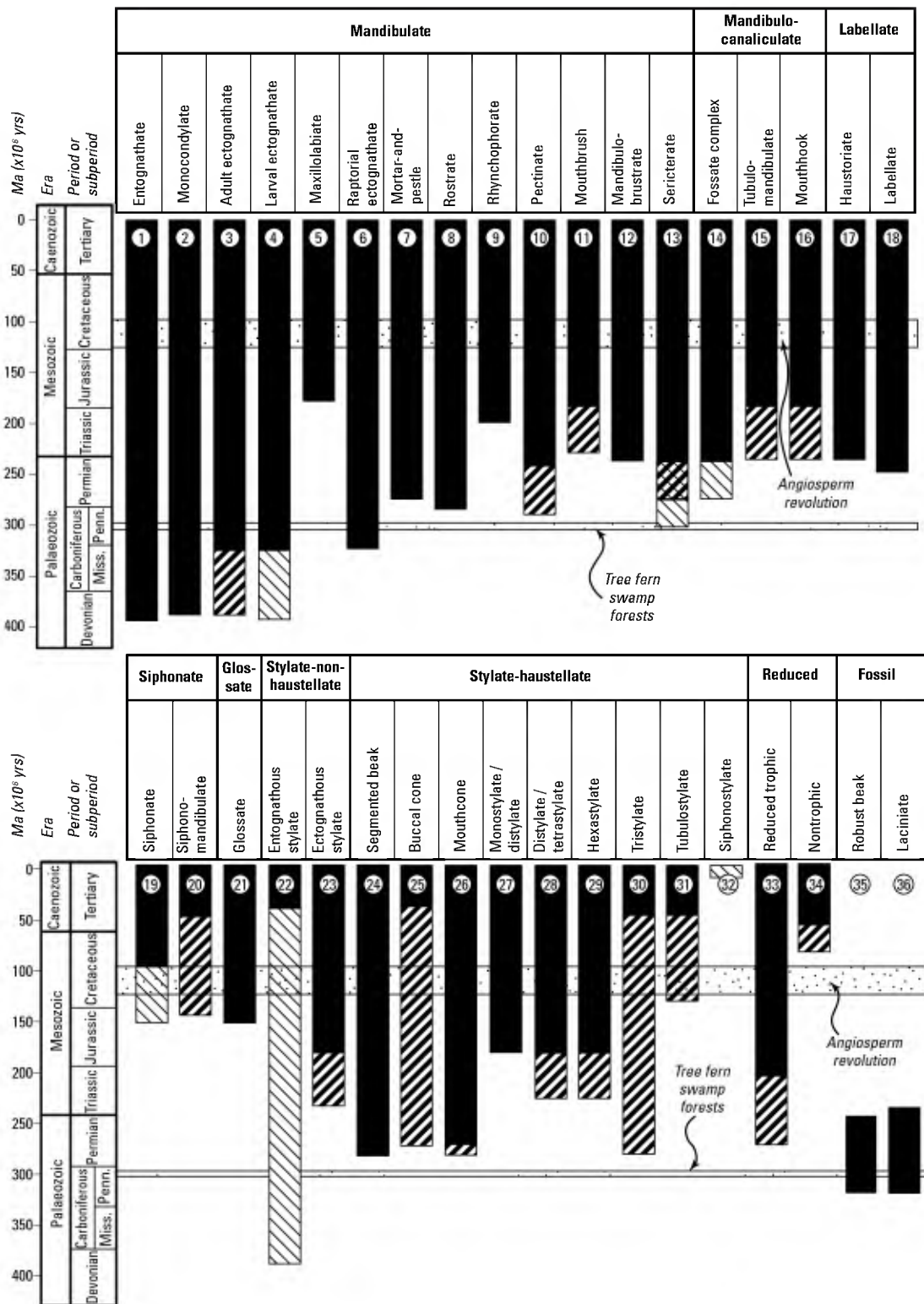


Figure 2.17 The fossil record of insect mouthpart classes. The figure is from Labandeira (1997). Solid black segments of vertical bars indicate presence of a mouthpart class evidenced as body fossils in well-preserved deposits; heavy slashed segments indicate presence based on sister-group relationships when one lineage of a pair occurs as fossils and the sister lineage, whose modern representatives bear the mouthpart class in question, is inferred to have been present. The lightly slashed segments indicate more indirect evidence for presence, such as trace fossils, and the occurrence of a mouthpart class in one life-stage of a species (e.g. adult) when the mouthpart class of interest is inferred to have been present in another life-stage that lacks a fossil record (e.g. larva). Abbreviations: Devon. = Devonian, Carbonif. = Carboniferous, Miss. = Mississippian, Penn. = Pennsylvanian, Perm. = Permian, Trias. = Triassic, Caenoz. = Cenozoic.

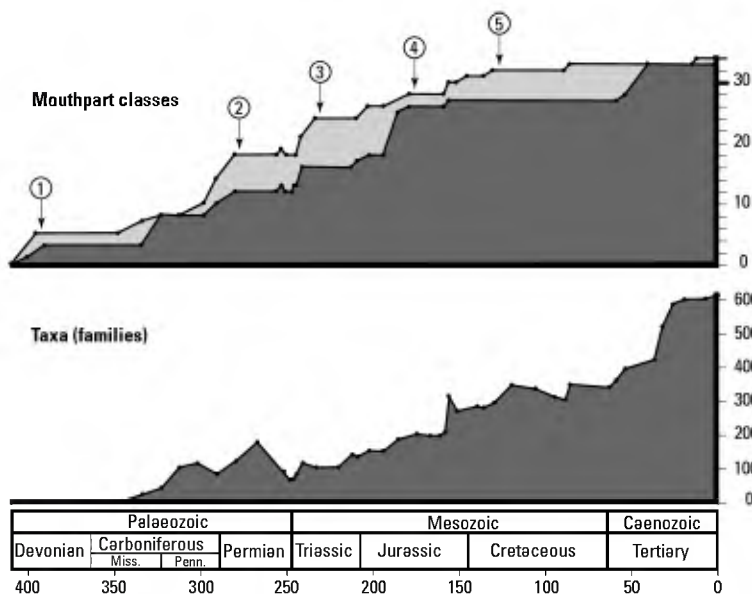


Figure 2.18 Comparison of mouthpart class diversity (upper panel) and family-level taxonomic diversity (lower panel) since the Early Devonian (from Labandeira 1997). Data for both graphs are resolved at the stage level, shown at the bottom sequentially as data points but included in the upper panel to reflect diversity changes. For mouthpart diversity, the darker pattern indicates strong evidence for presence (equivalent to the black portions of bars in Fig. 2.17) and the lighter pattern indicates less reliable evidence (corresponding to slashed patterns of bars in Fig. 2.17). Arrowed numbers refer to the five phases of mouthpart class diversification discussed in the text. Mouthpart data are an updated version of Labandeira (1990); taxonomic data are from Labandeira and Sepkoski (1993).

tion of several mouthpart classes involved in herbivory, including two Palaeozoic-only classes involved in fluid-feeding and spore and pollen consumption, and probably the mouthparts of larval holometabolans (Fig. 2.17: 7, 8, 10, 14, 24–26, 30, 33; Labandeira 1997, 1998a). By contrast, the third phase of the Early Permian marked a great increase in mouthpart innovation, represented by sap-feeding mouthpart classes from the hemipteroid radiation, and early occurrences of a diverse suite of mouthparts borne mostly by early holometabolous lineages. The presence of morphologically distinct and ecologically separate larval and adult stages associated with holometabolous development resulted in the generation of 7 mouthpart classes (Fig. 2.17: 4, 11–16). This major structural innovation offered for the first time the presence of 2 distinctive mouthpart classes and feeding strategies encompassed by the same biological species.

The fourth and most expansive phase is attributable mostly to the radiation of basal groups of Diptera and Trichoptera during the Late Triassic to Early Jurassic (Shcherbakov et al. 1995). These groups provided new mouthpart classes involved in the invasion of freshwater habitats by larvae (Fig. 2.17: 5, 9, 11, 12, 15–18, 23, 27–29), and the increasing reliance on exposed and tissue-enveloped fluid food by adults. The emergence of advanced lineages of seed plants was exploited by highly stereotyped mouthparts borne by adult weevils and small

parasitic wasps, involving the chewing of hardened tissue and the extraction of surface fluids respectively. Stylate penetration of vascular plant tissues and algal and fungal filaments by several independent lineages of small beetles presumably occurred during this interval. Mouthpart types appearing during the fifth phase, from the Late Jurassic to Early Cretaceous, were involved in fluid-feeding on various plant exudates, including nectar (Fig. 2.17: 19–21, 31, 34). When expressed as a diversity curve spanning the past 400 million years, there is a linear but stepped rise in mouthpart class diversity from the Early Devonian to the Early Jurassic, where it reached a plateau, followed by only a few subsequent additions (Fig. 2.18). Thus virtually all basic mouthpart innovation, including plant-associated mouthpart classes, was established prior to the angiosperm ecological expansion during the Middle Cretaceous, suggesting that mouthpart classes are attributable to basic associations with seed plants, or vascular plants of the more remote past, rather than the relatively late-appearing angiosperms (Labandeira & Sepkoski 1993).

2.4.3.5 Quantitative analyses

Quantitative analyses of herbivore damage of leaf floras is currently the only way of measuring the intensity of herbivory through time, provided that analysed assemblages are well preserved, sufficiently diverse, abundant and

comparable to analogous modern studies. An essential goal in such quantitative analyses is evaluation of the amount of damage inflicted by insects on past floras, as measured by the amount of herbivorized surface area and the frequency of attack of leaves. Site-specific, time-averaged floras, a veritable given in the fossil record, are ideal for providing bulk values for the long-term examination of herbivory in the fossil record and for comparisons with modern floras (Coley & Barone 1996). Although the application of this approach to the fossil record is still in its infancy (Fig. 2.4a), it shows promise for resolving such basic questions as the origin of substantive herbivory during the late Palaeozoic in a variety of environments (Labandeira 1998a). Thus vegetation from an identifiable and geochronologically persistent environment, preserved as taphonomically equivalent deposits, can be tracked vertically through time regardless of taxonomic turnover in the resident host plants or insect herbivores. Variations in foliar attack frequencies and levels of herbivore leaf-area removal, host specificity and insect damage-type spectra provide the basic data for deducing the role of insect herbivores in plant community evolution. A more focused approach can be applied to the component community of a particular plant taxon or lineage through time, in which changes in herbivore type, feeding intensity and plant-host specificity, in response to long-term environmental perturbations, is tracked through time. This latter approach could provide rare, crucial data for evaluating the long-term origin, persistence or extinction of insect associates of particular plant taxa. Many associations between plants and insects are evolutionarily very conservative and ancient (Funk et al. 1995; Futuyma & Mitter 1996; Farrell 1998). If host-plant damage patterns of these ancient lineages are recognizable, a direct palaeobiological dimension can supplement various congruence studies that establish estimates of the origin times for plant-hosts and their insect herbivores.

2.4.3.6 Substrates for insect oviposition and shelter

Although mouthparts are the primary structure by which insects interact with plants, ovipositors also are important (Fig. 2.19). Plant-piercing ovipositors for the insertion of eggs into plant tissues occur in Orthoptera, Hemiptera, Coleoptera, Lepidoptera and Hymenoptera, among others, and are frequently characterized by lateral compression of valves and ridged or sawtooth ornamentation. Ovipositors also are present in exclusively predaceous

dragonflies and in exclusively fossil groups such as the Palaeodictyopteroidea and Hypoperlida (Fig. 2.19a,b), which were predominantly used for penetrating plant tissues. Damage to stem and foliar tissues can be externally distinctive (Fig. 2.19c–j), resulting in a characteristic pattern of linear to crescentic rows of ovate, highly patterned, slit-like scars that elicit a reaction tissue response. The evidence for fossil oviposition originates from plant damage (Grauvogel-Stamm & Kelber 1996) and ovipositor structure (Kukalová-Peck 1991).

Arthropods have used plants extensively for shelter probably since the Early Devonian (Kevan et al. 1975). In many instances the use of a domicile is synonymous with endophytic feeding modes such as leaf-mining, galling, and boring, whereas in other contexts shelter is provided externally by insects such as rollers, tiers and tent-makers, or by case-makers such as bagworms, shield-bearers or caddisflies. These latter types of shelter are seldom identified in the fossil record, except for caddisfly cases fabricated from plant materials, which occur as trace fossils from the later Mesozoic of Eurasia, and in such Cenozoic deposits as the Miocene Latah biota of the Pacific Northwest. Ant–plant mutualisms are poorly documented in the fossil record, and there are no documented cases of aperturate inflated thorns, galleried fern tubers or excavated pithy stems serving as ant domiciles (see also Mueller et al. 1998). Extra-floral nectaries on the petiole of an Oligocene cottonwood leaf (Fig. 2.13h), almost identical in position and structure to ant-tended nectaries on an extant descendant, is the only example indicating past ant–plant mutualisms. Mite leaf domatia, however, have been found in Eocene deposits of Australia, with entombed mites residing in vein-axil pouches (O'Dowd et al. 1991). Last, a surprising pattern is the depauperate representation of sheltered insect eggs on plant surfaces, though they have been described from Permian *Glossopteris* leaves, Middle Triassic horsetail stems and Jurassic fern fronds (e.g. Grauvogel-Stamm & Kelber 1996).

2.4.3.7 The fossil record of vertebrate associations with plants

The amount of live plant tissue assimilated by arthropods is significantly greater than that of vertebrates in virtually all biomes except grasslands (Crawley 1983). The fossil evidence indicates that this arthropod dominance has probably been the case since the establishment of the earliest terrestrial ecosystems. In fact, it was not until the lat-

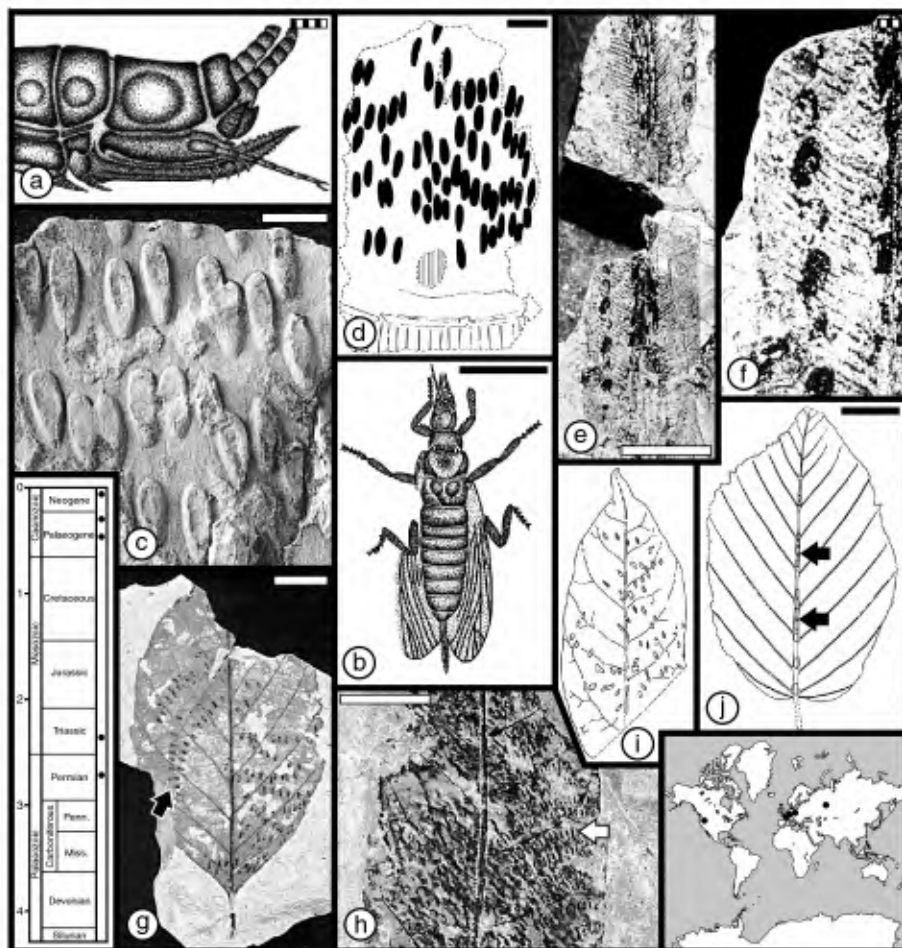


Figure 2.19 The fossil history of oviposition. (a) Reconstruction of the terminal abdominal region of a female diaphanopterodean from the Lower Permian, illustrating a vertically compressed, sawtooth ovipositor used for inserting eggs into plant tissues. (b) A pollinivorous hypoperlid insect from the same provenance as (a). Note the pronounced, flattened ovipositor that was probably used for the endophytic insertion of eggs. (c) Elongate-oval oviposition scars on a Middle Triassic horsetail. (d) Camera lucida drawing of a leaf sheath from another Middle Triassic horsetail species, showing dense, elongate-oval oviposition scars arranged in a zigzag pattern. (e) Probable insect eggs in or on a Middle Triassic cycadophyte leaf. (f) Enlargement of oval oviposition scars in (e) linearly and obliquely placed between the midrib and margin. (g) Oviposition scars of odonatan eggs, inserted as eccentric arcs (arrow) on a middle Eocene alder leaf (Betulaceae). (h) Oviposition scars on an unidentified middle Eocene leaf, similar to and approximately contemporaneous with those of (g), and presumably produced by an odonatan. The arrow refers to an arcuate row of scars. (i) An upper Miocene angiosperm leaf probably of the walnut family, showing odonatan oviposition scars typical of the Coenagrionidae. (j) A middle Oligocene leaf of hornbeam (Betulaceae) exhibiting petiolar oviposition scars (arrows) typical of the odonatan family Lestidae. See Fig. 2.7 for scale-bar conventions; additional locality data and source references can be found in the Appendix.

est Devonian that vertebrates emerged on land (Marshall et al. 1999), for which evidence indicates obligate carnivory. The radiation of early amphibians and reptiles that started during the Mississippian continued into the Pennsylvanian (Behrensmeyer et al. 1992). Direct evidence for vertebrate herbivory does not occur until the latest Penn-

sylvanian to earliest Permian (Weishampel & Norman 1989; Sues & Reisz 1998), about 100 million years after it appeared among mid-Palaeozoic arthropods.

Compared to arthropods, vertebrates are large, typically occur in low abundance in deposits, and possess a very different mechanical apparatus for processing food. For

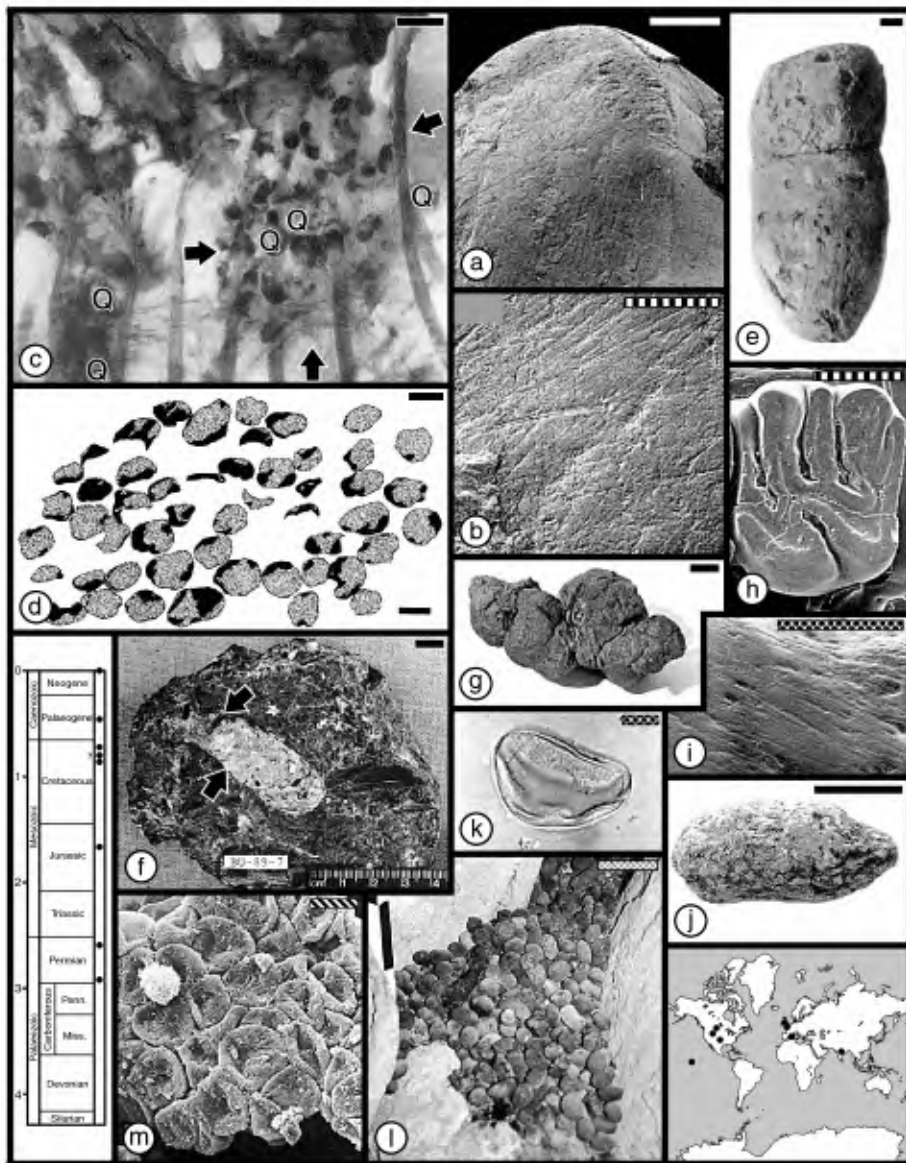


Figure 2.20 The fossil history of plant–vertebrate associations. (a) A crown of a ‘molariform’ cheek tooth from *Diadectes*, a high-fibre herbivore from the latest Pennsylvanian. (b) Detail of striations in (a) on the wear facet parallel to the long axis of the jaw. (c) Gut contents of the Upper Permian pareiasaur *Protosaurus speneri*, illustrating a food bolus (delimited by arrows) that contains conifer ovules (dark circular or hemispherical structures) and quartzose gizzard stones (*Q*). (d) A cluster of small, loose pellet-like coprolites attributed to a Middle Jurassic ornithomimid dinosaur, each containing abundant bennettitalean leaf cuticle. (e) A Late Cretaceous, herbivorous dinosaur coprolite, showing constrictions and resembling the segmented faeces of extant herbivorous mammals. (f) A Late Cretaceous, herbivore coprolite with two back-filled burrows (one at upper arrow) within a dark groundmass composed of comminuted xylem fragments, and the other light-coloured (lower arrow) packed with intermixed sediment and dung. Both burrows are inferred to have been made by dung beetles (Scarabaeidae), based on burrow patterns. (g) A serpentine dinosaur coprolite displaying conifer twigs, from the Upper Cretaceous. (h) An upper molar of the Eocene rodent *Thalermys headonensis*, a herbivorous browser; note the broad shelf for seed grinding. (i) A rodent from the late Eocene, with subparallel microwear scratches and pits on upper deciduous molars, suggesting consumption of indurated food. (j) A Holocene coprolite from an extinct folivorous duck of Hawaii. (k) A monolet fern spore from another coprolite from the same locality in (j); ferns were a major component of the diet of this herbivore. (l) A heap of coprolites from an extinct goat-like bovid, found in a Holocene cave. (m) Pollen of the box family (Buxaceae) from coprolites of the bovid mentioned in (l), its major dietary constituent. See Fig. 2.7 for scale-bar conventions; additional locality data and source references can be found in the Appendix.

this reason, the vertebrate fossil record of associations with plants is dominated by coprolites and features of the chewing apparatus (Fig. 2.20). A consequence of large vertebrate size is that consumption of plant organs is frequently complete and not partial as it is among arthropods, leaving minimal evidence from leaves, seeds and other wholly-consumed items. Also, the rarity of vertebrates when compared to arthropods may result in an underestimate of vertebrate importance in their interactions with plants. Lastly, the vastly different and relatively simple construction of vertebrate chewing apparatus, as opposed to arthropod mouthpart complexes, has allowed for inferences in vertebrate food consumption that have stressed the biomechanics of the jaws and associated muscles (Weishampel & Norman 1989), microstructural details of tooth surfaces (Collinson & Hooker 1991) and digestive physiology (Farlow 1987).

2.4.3.7.1 Late Palaeozoic herbivores

At the end of the Palaeozoic, at 245 Ma, three major amniote clades were established on land: synapsids, parareptiles and reptiles, each constituting a significant diversity of lineages (Sues & Reisz 1998). Seven of these lineages possessed herbivorous Permian members with high-fibre diets: diadectomorphs, caseids, edaphosaurs, dinocephalians and anomodonts within the Synapsida; pareiasaurs within the Parareptilia; and captorhinids within the Reptilia. These forms exhibited overwhelmingly large, barrel-shaped thoraces that apparently housed extensive digestive tracts for fermentative degradation of cellulose-rich plant matter by microorganisms. This feature was associated with a posterior expansion of the skull for the accommodation of extensive musculature for jaws closure in the processing plant material. Depending on the lineage, herbivore innovations in dentition included the modification of molariform teeth into transversely expanded grinding or crushing surfaces (Fig. 2.20a,b), the presence of additional rows of teeth in both the upper and lower jaws, or replacement of the teeth by a keratinous beak (Sues & Reisz 1998). Rare finds of gut contents in some fossil skeletons have provided direct evidence for diets, such as conifer and seed-fern seeds in the Late Permian diapsid reptile *Protorosaurus* (Fig. 2.20c; Munk & Sues 1993). These discoveries, in concert with current understanding of seed-fern reproductive biology, indicate that seeds may have been an important dietary component for some large tetrapods (Tiffney 1986).

Anamniote batrachosaurs, which diversified during

the Mississippian, have been considered to be omnivores that supplemented their diet with low-fibre plant material (Hotton et al. 1997). However, the best evidence for the earliest plant-feeding vertebrates are the diadectomorphs from the latest Pennsylvanian of North America and Europe (Sues & Reisz 1998), considered as either amniotes or their close relatives (Laurin & Reisz 1995). These taxa bear jutting incisors and a transversely expanded battery of molariform teeth. The unrelated sail-backed *Edaphosaurus* occurs in deposits of similar age and bears additional rows of blunt teeth in both jaws and a disproportionately large, cylindrical trunk when compared to other coexisting vertebrates, strongly indicating high-fibre herbivory. Other Early Permian reptile lineages bear similar features, although it is during the Late Permian that these lineages evolved herbivory, especially dinocephalian and anomodont diapsids in mesic to xeric environments. For dinocephalian diapsids, considerable remodelling of jaw closure musculature and their sites of insertion allowed for articular flexibility in jaw movement, easing the cropping and powerful processing of fibrous plant matter. In a review of Palaeozoic tetrapod herbivory, Sues and Reisz (1998) concluded that two herbivore types evolved during the Late Pennsylvanian to Late Permian: those bearing higher-crowned and leaf-shaped teeth occurring on the external jaw margin, used for shearing and puncturing plant tissue elements; and those bearing crushing to grinding dentitions where occlusion of horizontal tooth surfaces physically degraded plant material.

2.4.3.7.2 Dinosaurs and Mesozoic herbivory

An interesting aspect of Palaeozoic tetrapod herbivores is that they were uniformly short-necked and short-limbed browsers that cropped plant material within a metre to perhaps 2 metres of the ground surface. This trend continued with surviving diapsid and synapsid lineages from the end-Permian extinctions into the Late Triassic, at which time basal dinosaur lineages began their diversification into virtually all major terrestrial feeding niches (Fig. 2.21). Early members of this radiation were prosauropod dinosaurs with elongate necks and probable tripodal stances that increased the browse height several times. This fundamental shift to high-browsing prosauropods, accentuated in the Jurassic with the emergence of much larger quadrupedal sauropods browsing up to 12 metres (Bakker 1986), occurred in concert with a shift from an earlier flora of mostly seed-ferns to a later

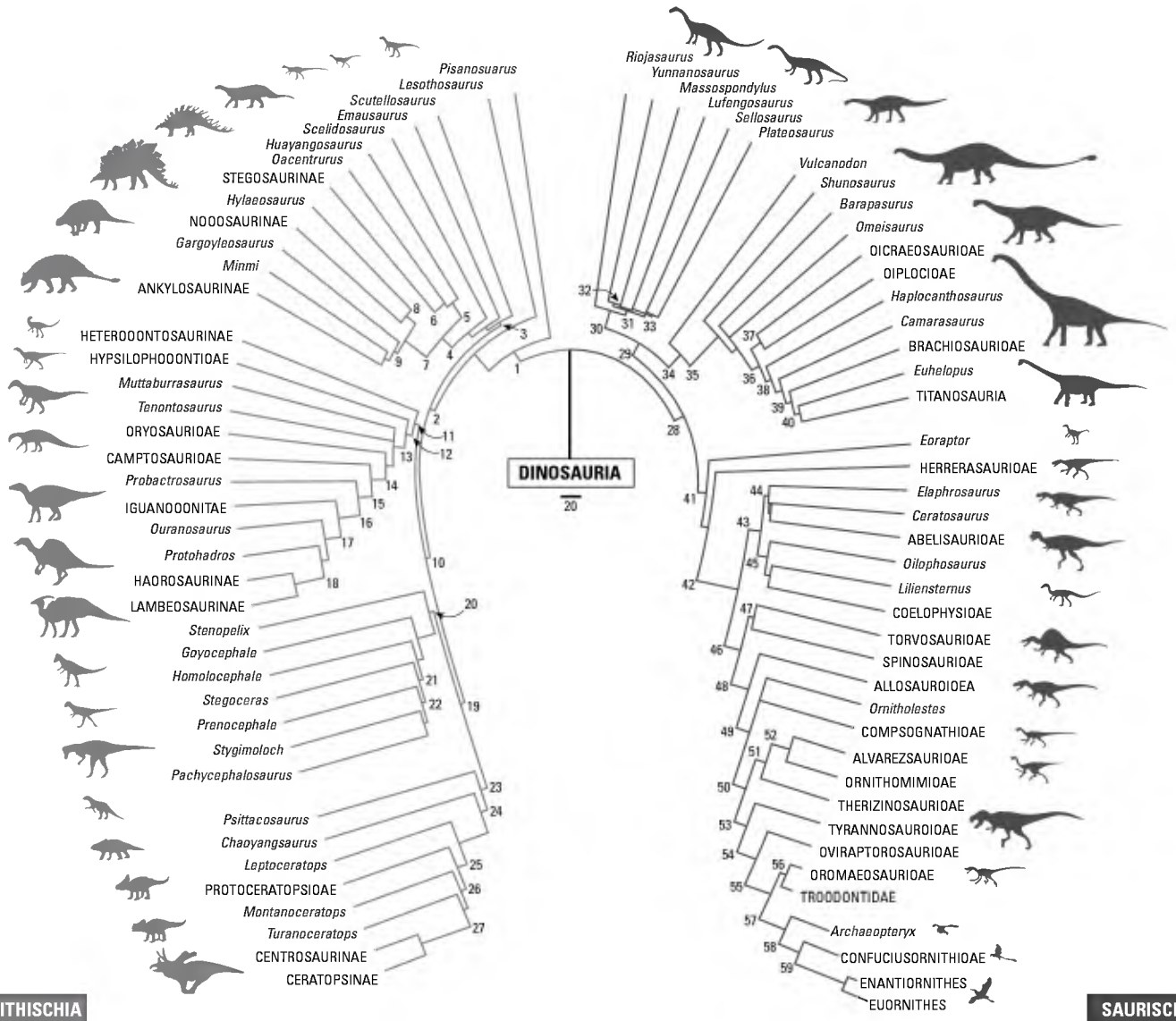


Figure 2.21 Phylogeny of the Dinosauria, showing the relationships among ornithischians (left) and saurischians (right). Plant-feeding clades are the Ornithischia at left and Sauropodomorpha at upper right. For more details, see Sereno (1999), from which this figure is taken. Thickened internal branches are scaled to reflect the number of supporting synapomorphies (scale bar equals 20 synapomorphies). Numbered nodes are as follows, with normal and bold type indicating stem- and node-based taxa respectively: 1, Ornithischia; 2, **Genasauria**; 3, Thyreophora; 4, **Eurypoda**; 5, Stegosauria; 6, Stegosauridae; 7, Ankylosauria; 8, Nodosauridae; 9, Ankylosauridae; 10, Neornithischia; 11, **Ornithopoda**; 12, Euornithopoda; 13, Iguanodontia; 14, **Ankylopollexia**; 15, Styracosterna; 16, **Hadrosauriformes**; 17, Hadrosauroidae; 18, **Hadrosauridae**; 19, Marginocephalia; 20, Pachycephalosauria; 21, **Pachycephalosauridae**; 22, Pachycephalosaurinae; 23, Ceratopsia; 24, Neoceratopsia; 25, **Coronosauria**; 26, Ceratopsoidea; 27, **Ceratopsidae**; 28, Saurischia; 29, **Sauropodomorpha**; 30, Prosauropoda; 31, **Plateosauria**; 32, Massospondylidae; 33, Plateosauridae; 34, Sauropoda; 35, Eusauropoda; 36, **Neosauropoda**; 37, Diplodocoidea; 38, Macronaria; 39, **Titanosauriformes**; 40, Somphospondyli; 41, Theropoda; 42, **Neotheropoda**; 43, Ceratosauria; 44, Ceratosauroidae; 45, Coelophysoidea; 46, Tetanurae; 47, **Spinosauroidae**; 48, **Neotetanurae**; 49, Coelurosauria; 50, **Maniraptoriformes**; 51, Ornithomimosauria; 52, Ornithomimidae; 53, Tyrannoraptora; 54, **Maniraptora**; 55, Paraves; 56, **Deinonychosauria**; 57, **Aves**; 58, Ornithurae; 59, **Ornithothoraces**. Silhouettes are not drawn to scale.

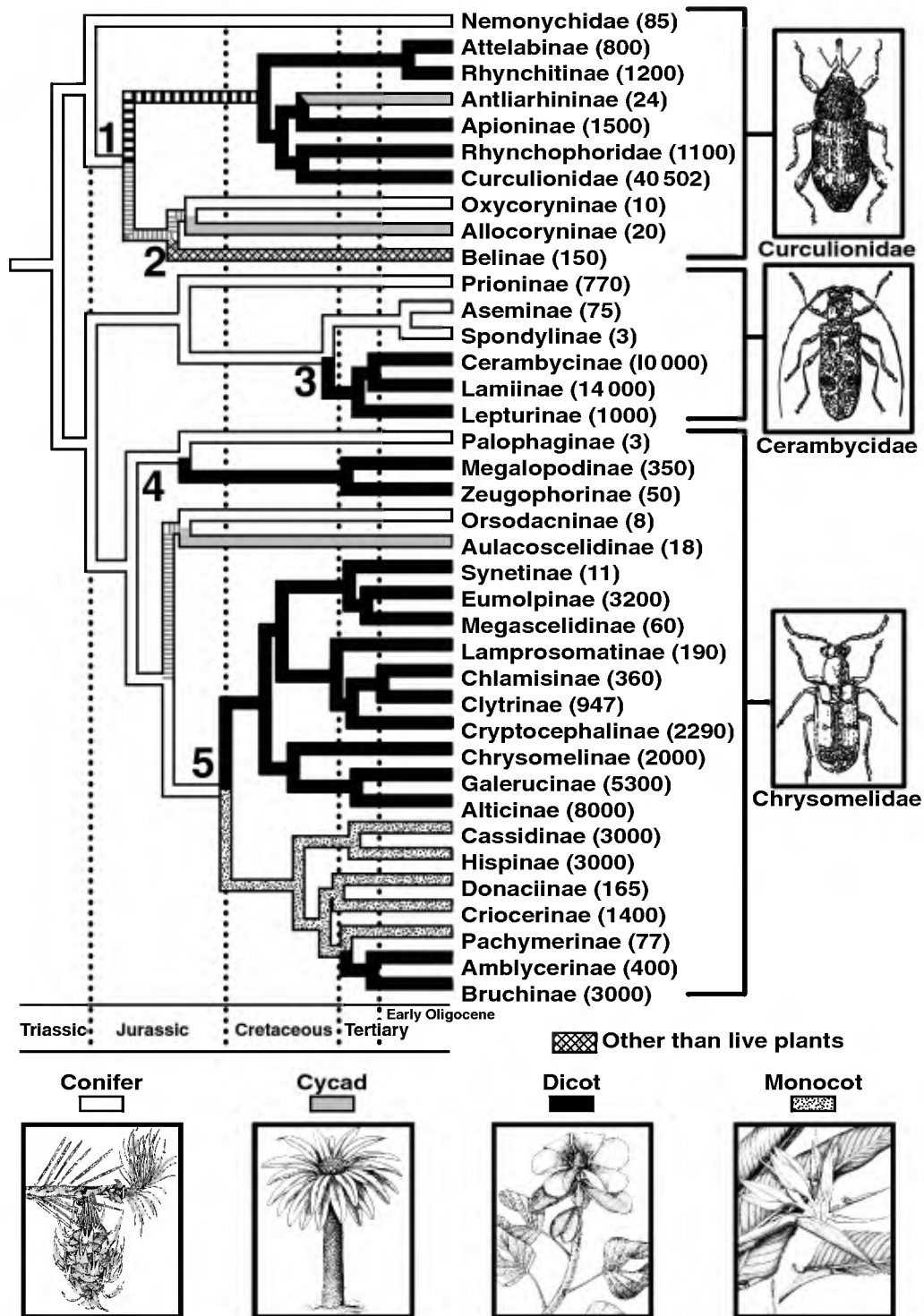


Figure 2.22 The history of plant–host associations in the beetle clade Phytophaga (from Farrell 1998). The Phytophaga consists of weevils, longhorn beetles and leaf beetles (upper right insets), and their seed-plant hosts are characterized broadly (bottom insets) as conifer and cycad gymnosperms and dicot and monocot angiosperms. When plant–host use is mapped onto the phylogeny of major Phytophaga clades, there is a pattern of more primitive beetle lineages using primitive seed plants whereas the more advanced beetle lineages are using advanced seed plants. The five most parsimonious origins of angiosperm associations are numbered. Calibration of each beetle clade’s age is provided from fossil occurrences; an estimate of the species-level diversity of each clade is given in parentheses. See Farrell (1998) for additional details.

flora dominated by towering, pole-like conifers. During the Cretaceous the intensified and more specialized cropping of vegetation by low browsers is consistent with angiosperm survival strategies such as rapid regeneration of foliar units, quick recolonization of disturbed habitats and the evolution of seed-dispersal syndromes (Wing & Tiffney 1987).

Dinosaur coprolites offer a direct avenue for inferring herbivory, although their presence in the fossil record is rare. These large, often phosphatized, structures, range from 2 to 10 cm in diameter and up to 15 cm or somewhat more in length (Thulborn 1991). The shapes of dinosaur coprolites are variable, and most have a pinched-off end, formed by a cloacal sphincter muscle, whereas others are flattened, presumably resulting from impact with the ground from a significant vertical drop (Thulborn 1991). The contents of these coprolites range from bennettitalean seeds, seed-fern pollen, ginkgo foliage and fern fronds among earlier occurrences, to conifer twigs, angiospermous fruits and distinctive angiosperm pollen in later occurrences, some of which have been modified by dung-beetle nest construction (Chin & Gill 1996). A related feature is gizzard-stone concentrations associated with the gut regions of dinosaur skeletons (Bakker 1986), indicating digestive degradation of plants akin to some herbivorous birds. Lastly, gut contents of dinosaurs have been described, such as a Late Cretaceous *Trachodon* containing conifer shoots and abundant small fruits and seeds. These data indicate that Late Triassic to Early Cretaceous dinosaurs typically consumed high-fibre vegetation that relied on physical digestive breakdown, whereas during the Late Cretaceous there was greater specialization, particularly by dentally sophisticated ornithomimids on angiosperm foliage and seeds (Wing & Tiffney 1987).

The basic dental modifications for processing high-fibre vegetation that were present during the Permian continued into the Triassic. These feeding modes required considerable oral processing and mastication of food with relatively simple up-and-down (orthal) strokes for slicing, pulping or puncture-crushing of food items in an approximate vertical plane (Weishampel & Norman 1989). In addition, fore-and-aft protraction and retraction for movement of the lower jaw was an efficient mechanism for grinding fibrous food. Othal puncture-crushers did not survive the Triassic, and some othal slicers receded into relative obscurity. By contrast, another replacement, the ceratopsians, elaborated slicing through extensive

contact surfaces and the possession of a keratinous beak. Othal pulpers were replaced by stegosaurs, pachycephalosaurids, ankylosaurs and segnosauroids, all of which persisted into the Late Cretaceous; fore-and-aft grinders such as Triassic and Early Jurassic dicynodonts and tritylodonts were succeeded by Late Jurassic to early Tertiary multituberculates. During the Late Triassic to Early Jurassic, prosauropods pioneered the gut processing of vegetation. They were superseded by sauropods during the Middle Jurassic, characterized by slow and heat-generating fermentation of gut compost (Farlow 1987). Other than gut processors, the most significant innovation of Mesozoic food-processing were the transverse grinders (Weishampel & Norman 1989), developed by Late Triassic to Early Jurassic heterodontosaurids, and elaborated especially by the hadrosaurs. For hadrosaurs, there was increased rotation of the upper jaws, shear surfaces were approximately 45° from horizontal, and the dental battery was closely packed with teeth bearing broad contact surfaces (Serenó 1999)—a feature convergent on the transverse chewing stroke of herbivorous mammals.

2.4.3.7.3 *Caenozoic patterns of mammalian herbivory*

Following the end-Cretaceous demise of dinosaurs (Serenó 1999), there was a Palaeocene interval with low vertebrate diversities that characterized all known ecosystems that have been studied to date. New mammalian clades and some surviving from the Cretaceous diversified during this recovery phase and established associations among plants and other organisms. Although Palaeocene mammalian faunas have a comparatively sparse fossil record, they comprise small-sized members of lineages that gradually increased in body mass. By Eocene times a clearer picture had emerged regarding the associations between taxa stemming from the basal eutherian radiation and modern-aspect plant taxa. One particularly renowned deposit documenting many of these associations is the Messel Oil Shale in Germany (Schaal & Ziegler 1992), of middle Eocene age (48 Ma). This *Lagerstätten* has provided extensive data on superbly preserved gut contents, including histological detail of plant tissues such as leaves, pollen and seeds, in addition to the presence of dental microstructure, dispersed vertebrate coprolites and frequent soft-part anatomy. Less spectacular but coeval deposits from England provide evidence from tooth shape and dental microwear patterns that indicate primate and rodent fruit consumption (Fig. 2.20h,i),

including the probable hoarding of nuts (Collinson & Hooker 1991). During this interval there is the earliest evidence for modern mammalian seed-dispersal syndromes (Tiffney 1986), which was preceded during the earlier Eocene by the evolution of relatively large fruits with thick and fleshy outer tissues.

While Palaeocene to middle Eocene mammalian herbivores were dominated by small to medium-sized forms consuming fruit, seeds and leaves, later herbivores were much larger, and invaded the browsing and eventually grazing adaptive zones (Wing & Tiffney 1987). This shift is related to the mid-Cenozoic origin of savanna and grassland biomes concomitant with the ecological spread of grasses. The oldest grasses reliably documented in the fossil record occur at the Palaeocene/Eocene boundary (Crepet & Feldman 1991), although the earliest evidence for a grassland-adapted mammalian fauna is from the middle Oligocene of Mongolia (Behrensmeyer et al. 1992). By the late Miocene, woodland savanna and grasslands were present, exemplified by the diverse Siwalik Fauna on the Indian subcontinent, which included browsing and grazing ungulates. Towards the late Miocene, there was a major worldwide transition from browsers with low-crowned molars to grazers with high-crowned molars. This shift is associated with increasing aridity and an upturn in the abundance of plants from the legume, goosefoot and sunflower families (Behrensmeyer et al. 1992). Although grasses contain considerable silica in their leaves that render folivory an abrasive proposition, the presence of an ever-growing basal meristem probably allowed for a significant increase in herbivore biomass when compared to browsed temperate forest.

Recent technological innovations in the detection of carbon isotopic fractionation in the fossil record has spurred research on determining the diets of later Cenozoic herbivorous mammals (Barrick 1998). This research is based on the fortuitous presence of two basic trajectories by which vascular land plants photosynthetically process the ^{13}C isotope of carbon—the C3 pathway (Calvin Cycle) typical of almost all arborescent plants, herbs and cool-temperate grasses, and the C4 pathway (Hatch–Slack Cycle) characteristic of warm-temperate to tropical grasses. Each of these two suites of plants process ^{13}C such that in C3 plants the ^{13}C isotope is preferentially depleted whereas in C4 plants the same isotope is preferentially enriched. Mammals that ingest assemblages of C3, C4 or a mixed assemblage of plants will deposit in their tooth enamel and bone protein isotope values that will reflect either of these end-member values or an inter-

mediate value for mixed diets. These teeth and bone values can be measured as fossils not only to determine their past diets, but also to assess whether they were grazers or browsers, given supplemental palaeobotanical and palaeoenvironmental knowledge. In addition, recent refinements in measurement have revealed that short-term seasonal to longer-term palaeolatitudinal patterns of herbivory can be ascertained as well. Examples include Cerling and colleagues (1997) who documented the worldwide shift from C3 to C4 plants during the late Miocene (8 to 6 Ma) based on analyses of ^{13}C in the teeth of megafauna from a variety of continents. A more detailed study involved the use of variable distributions of ^{13}C within both C3 and C4 plants, as well as dental microwear striations, to infer that the extinct South American mammal *Toxodon* was not a grazer but fed predominantly on aquatic C4 vegetation in non-forested areas (Barrick 1998).

2.4.3.7.4 Quaternary extinctions

During the Pleistocene (2.65 Ma to 11 000 yr BP), much of the planet underwent severe climatic perturbations from five major episodes of continental and associated alpine glaciation. Continental faunas were considerably reorganized during and after this interval in terms of the dominance and composition of species, at least in North America (Graham 1986). The last reorganization event is associated with significant vertebrate extinction, sea-level rise and major climatic change. This great megafaunal extinction, centred approximately 11 000 yr BP, occurred worldwide, although it was ameliorated in Africa. Much evidence now supports a view that continental species did not respond as cohesive assemblages to these major environmental shifts, but rather individually, supported by vertebrate, pollen and generalist insect distributions (Graham 1986; Overpeck et al. 1992; Coope 1995). An important exception to this trend are insects with high host specificity, which responded differently, retaining ancestral plant associations to the present (Labandeira et al. 1994; Farrell 1998; Wilf et al. 2000) or becoming extinct. Herbivorous mammals have less obligate dependence on plant species (Crawley 1983) and thus exhibit greater dietary flexibility during times of major environmental stress. However, there was a great megafaunal extinction, attributable variously to severe range contraction and environmental degradation or anthropogenic overkill (Thompson et al. 1980; Graham 1986). This extinction event is well illustrated on islands, where severe species reductions occurred during the latest Pleis-

tocene and Holocene (Steadman 1995). Two notable examples of extinctions occurring around 4000 yr BP have been deduced primarily from well-preserved coprolitic and skeletal material in island caves. First is the herbivorous swan-like duck *Thambetochin chauliodous* from the Hawaiian Islands, which fed almost exclusively on ferns (Fig. 2.20j,k); the second is the goat-like *Myotragus balearicus* from the Mediterranean Balearic Islands, which fed dominantly on alkaloid-laden boxwood (Fig. 2.20l,m). Both examples provide evidence of unusual feeding specializations and associated coprolites that demonstrate highly plant-specific diets, rendering these taxa susceptible to extinction during periods of major environmental change.

2.4.4 Biological approaches

The traditional method of using modern biology to understand past plant–animal associations is to assign a known ecological association to an insect-damaged fossil plant that exhibits recognizable and stereotyped insect damage. This procedure of ecological transfer is based on a uniformitarian approach and is typically available for Caenozoic and some Late Cretaceous taxa. The two most prominent uses of this method are identification of stereotyped herbivore damage on plant organs (Fig. 2.4g) and evaluation of suites of distinctively specialized floral characters indicative of unique pollinator presence (Fig. 2.4h). A third use involves the simple presence in *Lagerstätten* of insect body fossils from extant lineages with known ecologies (Fig. 2.4i).

The major alternative way of inferring the history of plant–animal associations using a biological approach is to take advantage of insect or plant phylogeny and identify those nodes which reveal character states that have direct correlates to feeding strategies (Fig. 2.4j). One such type of study is to ascertain the time of origin of particular character states (synapomorphies) on a cladogram that reveal features such as digestive physiologies or alimentary structures. A second methodology employs a phenetic classification of an ecomorphological feature in a group of modern animals of importance to plant–animal associations. The fundamental structural entities of this classification are then mapped onto the phylogenies that bear them, and are subsequently tracked geochronologically by established phylogenetic relationships calibrated by known fossil occurrences (Labandeira 1997). Such studies can provide minimum geological dates for the origin of feeding strategies, including types of herbivory

(Fig. 2.5k). Lastly, assessment of phylogenetic congruence between plant hosts and their animal herbivores, combined with age estimates for the times of origin of their radiations, is also a powerful way of using phylogenies to infer the history of associations (Fig. 2.5l).

2.4.4.1 Transfer ecology from extant descendants of fossil-bearing lineages

Knowledge of modern autecology frequently has been used to infer the life-habits of fossil representatives that have modern descendants (Behrensmeyer et al. 1992). This equivalence is based on three assumptions, namely that a close genealogical relationship exists between the extinct and extant taxa, that there has been minimal ecological change separating the taxa during the intervening time, and that the extant taxon has not been ecologically restricted relative to that of its extinct antecedent (Behrensmeyer et al. 1992). The applicability of transfer ecology is also dependent upon whether the ecologies of documented modern representatives are known well enough, if at all, to comment on the fossil taxa. Perhaps the most serious limitation on the applicability of transfer ecology is whether the time interval separating the past from present taxa is not excessively long so as to invalidate uniformitarian argumentation. In practice, this means that transfer ecology is reasonably sound for lineages that occur in the later Caenozoic, and is applicable to the earlier Caenozoic and later Mesozoic for those lineages that either represent ancient associations or are found in environments and exhibit sufficiently stereotyped morphologies or life-habits for them to be compared to more distantly related extant taxa, but still encompassed taxonomically by the same and more inclusive recent clade. It should be noted that varied evidence indicates that ancient associations between herbivorous insects and their plant hosts should be expected in the fossil record. This prediction is buttressed by studies of genetic variation and physiology that demonstrate pronounced plant-host conservatism in many herbivorous insects (Futuyma & Mitter 1996), the absence of evidence for insect extinction during the Pleistocene glaciations, the most climatically punishing period of the Caenozoic (Coope 1995), and the comparatively long geochronological longevities of insect families when compared to other terrestrial taxa (Labandeira & Sepkoski 1993).

Transfer ecology has been used extensively for body-fossil data, and much less employed for plant–animal associations. In some instances there are excellent matches

between a fossil plant–insect association and a particular diagnostic syndrome of herbivore-mediated damage occurring today on the same or a similar host plant (Opler 1973; Wilf et al. 2000). For some palaeoecological data, transfer ecology based on plant–animal associations is more informative than those of the body fossils, since the ecologies are literally preserved in an associational context, such as moth leaf-mines or bark-beetle borings. In fact, such inference from body-fossil morphology or taxonomic identity alone is more difficult, and for many groups such as pollinator and leaf-miner lineages, the trace-fossil record is richer and more ecologically informative than the corresponding body-fossil record.

2.4.4.2 Inferences about feeding from phylogenetic analyses of clades

There are three basic methods for ascertaining the macroevolutionary history of plant–animal associations that employ either a phylogenetic analysis only or a combination of a phylogenetic and phenetic analysis of ecomorphological data. The first method is to locate on a clade those synapomorphies that record relevant feeding characters. The branching sequence of feeding-related characters on a clade can provide data for inferring the relative temporal distribution of feeding strategies. If it is possible to peg these data to a geochronology, then ‘absolute’ ages also can be inferred. The second method is to map non-phylogenetic ecological attributes onto independently established phylogenies to determine the taxal distribution and times or origin of, for example, feeding types. In these analyses, ecological attributes are logically separate from characters used in phylogeny reconstruction and are thus analysed independently by a variety of techniques or are simply recorded as attributes onto clade taxa. Examples include the evolution of dung use in scarab beetles (Cambeffort 1997) and the evolution of the blue and ultraviolet components of colour vision within Hymenoptera prior to the advent of angiosperms (Chittka 1996). An application of this method employs a multivariate phenetic analysis of the ecological data, followed by mapping the resulting phenetic classification onto cladograms or phylograms based on modern taxa (Labandeira 1997), discussed previously. The detection of ecological convergence in attributes is a central goal of such methods.

A third method of investigating the macroevolutionary history of plant–animal associations is analysis of charac-

ter-state evolution within the context of a cladogram, using a variety of techniques. One example is multivariate analyses of phylogenetic and ecological distance matrices to ascertain if and to what extent ecological attributes are associated with phylogeny (Pagel 1999). One of these approaches, used by Gilbert and colleagues (1994) to elucidate the evolution of diet in larval syrphid flies, combines cladistic analysis with ahistorical techniques typically used in ecology. Moreover, depending on the question being asked, one can test for whether phylogeny influences an ecological trait of interest or whether phylogeny and ecological traits co-vary. Since these techniques use phylogenies directly or as part of a combined study, a historical component can now be added to plant–animal associations derived exclusively from modern data. Much of the motivation in such analysis is to search for a common pattern among convergent characters (Coddington 1988) and to evaluate the role of environmental variables and phylogeny in the production of functionally equivalent morphologies. Ecological convergence and the exploration of character change can also be investigated using plant hosts, in addition to the examples of animal herbivores mentioned previously. Such an example is Crisp’s (1994) analysis of floral features from a tribe of Australian legumes to determine the origin of bird-pollination syndromes. In summary, analyses of plant- or animal-associated character-state evolution in the context of a cladogram considers ecological convergence as a phenomenon of immense interest demanding explanation, unlike its characterization as a problem in phylogenetic analyses.

2.4.4.3 Phylogenetic congruence of plant hosts and their insect herbivores

The history of observations and theories supporting the idea of mutual phylogenetic association originated along several parallel tracks from 1860 to 1920. During this formative interval, studies on plant and pollinator co-specialization, mimicry (e.g. Darwin 1877), and similarities between co-associated animals and parasite taxa both within and among biogeographic regions, led to a view that specialization could occur among multiple species, causing unidirectional effects on one partner or even bilateral consequences. Although early researchers recognized a conserved phylogenetic pattern of specificity between insects and their host plants, the seminal break occurred in Ehrlich and Raven’s (1964) paper in which

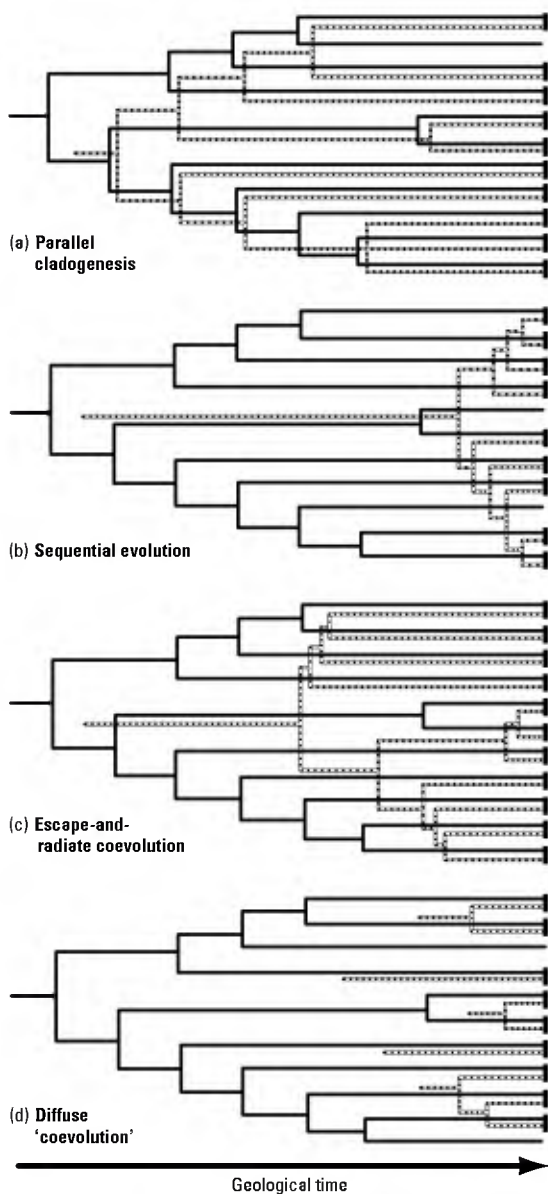
these phylogenetic constraints were placed in an explicit theoretical context that later became known as escape-and-radiate evolution (Schoonhoven et al. 1998). Ehrlich and Raven's (1964) thesis was based on adversity, borrowed from earlier studies of animals and their host parasites (Thompson 1994), unlike Janzen's (1966) subsequent investigations, which considered the associations between leguminous trees and their ant associates to be true mutualisms. Continued and ever-expanding research in the field of plant–animal associations in general and plant–insect associations in particular—such as the fig and figwasp, yucca and yucca moth, and milkweed and milkweed beetle systems—has resulted in a large literature and increasing investigation of congruence between host–plant lineages and their associated insect herbivore lineages. An exciting study is Farrell's (1998) analysis of subfamily relationships within the highly diverse and herbivorous clade Phytophaga, consisting of leaf beetles, longhorn beetles and weevils (Fig. 2.22). Farrell's study demonstrated that the most basal and fundamental splits within this clade are ancient associations with pre-angiospermous seed plants (cycads and conifers) of the Jurassic, and that more recently evolved diversification is associated with lower-level taxa radiating in parallel with the angiosperm ecological expansion. Of those congruence studies that have provided time estimates for the origin of such associations, 13 are displayed in Fig. 2.41. If representative, these studies indicate that there are two clusters for dates of origin: one concentrated in the later Caenozoic, and the other during the later Cretaceous. This bimodal distribution is consistent with independent evidence gleaned from the fossil record, and is attributable to a major spurt of herbivore diversification coinciding with the mid-Cretaceous ecological expansion of angiosperms, succeeded by the extirpation of many specialized associations at the K/T boundary, followed by gradual rebound to Late Cretaceous levels during the earlier Cenozoic (Wilf & Labandeira 1999; Labandeira et al. 2002).

Currently, four major hypotheses account for the origin of plant–insect associations (Schoonhoven et al. 1998; Thompson 1999c). These hypotheses are distinguished principally by the extent of reciprocal genetic selection of one partner on the other, and by the relative timing of events by which a herbivore clade becomes associated with a plant clade (Fig. 2.23). Parallel cladogenesis, or phylogenetic tracking, is an association typically characterized by a one-to-one match between host and herbi-

vore (Fig. 2.23a; Mitter & Brooks 1983). Although there is simultaneous speciation of host and herbivore, it is not caused by coevolutionary genetic feedback. An example is *Nesosydne* planthoppers on Hawaiian silverswords, members of the sunflower family (Roderick 1997). By contrast, sequential evolution (Jermy 1984) indicates that hosts and herbivores lack reciprocal selection and thus do not coevolve. Host lineages undergo phases of diversification independent of herbivore association, and are subsequently, often much later, colonized by herbivores. An example is *Ophraella* leaf beetles on North American hosts of the sunflower family (Fig. 2.23b; Funk et al. 1995). Alternatively, the escape-and-radiate hypothesis (Ehrlich & Raven 1964) invokes a more complex series of events in which mutant plant-host species evolve chemical or physical defences from their herbivores, allowing diversification in enemy-free space. Novel herbivore populations subsequently breach those plant defences, radiate onto the host lineage and colonize individual plant species as descendant herbivore populations become specialized. Later, a plant-host species develops another round of anti-herbivore defence, escaping herbivory but eventually becoming colonized as the process of escape and radiation is repeated. This process is driven by host defences and herbivore counter-defences, and there is not necessarily a one-for-one match between host and herbivore on individual host species. An example is *Tetraopes* longhorn beetles on North American milkweeds (Fig. 2.23c; Farrell & Mitter 1998). Lastly, diffuse coevolution, including diversifying coevolution (Thompson 1994, 1999), is a hypothesis that includes several mechanisms in which herbivore populations specialize on plants based on local processes of reciprocal adaptation, but result in patterns that are not typically phylogenetically congruent. An example is bee pollinators of *Dalechampia* vines (Armbruster 1992), members of the spurge family, in which there is a mixture of limited clade congruence and isolated colonization (Fig. 2.23d). Current evidence favours sequential evolution, although there are several well-established cases of parallel cladogenesis and escape-and-radiate evolution. Diffuse coevolution is difficult to evaluate because of the plurality of mechanisms involved.

2.4.5 Complementarity of both approaches

Palaeobiological and biological approaches both address the same questions regarding the spatiotemporal patterns and processes involved in plant–animal associations.



Their distinction principally involves one of scope: palaeobiological approaches have been primarily concerned with the temporal scale of associations variably preserved in the fossil record whereas biological approaches have investigated the spatial wealth and intricacy of associations occurring today. Each approach presents a unique take on reliability of evidence, what constitutes

Figure 2.23 Four major hypotheses regarding the evolution of plant–insect associations (Schoonhoven et al. 1998; Thompson 1999d). See text for additional explanation. Examples are idealized, although case-studies may be consulted from the literature indicated. Plant hosts are deployed as black lines, insect herbivores are dashed lines; terminal black rectangles indicate an extant host plant/insect herbivore association. (a) Parallel cladogenesis, or phylogenetic tracking (Mitter & Brooks 1983); for example, *Nesosydne* planthoppers on Hawaiian silverswords (Roderick 1997). (b) Sequential evolution (Jermy 1984); for example, *Ophraella* leaf beetles on North American asteraceous hosts (Futuyma et al. 1995). (c) The escape-and-radiate hypothesis (Ehrlich & Raven 1964); for example, *Tetraopes* longhorn beetles on North American milkweeds (Farrell & Mitter 1998). (d) Diffuse coevolution, including diversifying coevolution (Thompson 1994); for example, bee pollinators of euphorbiaceous *Dalechampia* vines (Armbruster 1992).

direct versus indirect observation, varying ways of inferring deep geological time and a spectrum of methodologies for assessing the history of plant–animal associations.

One context that clouds the distinction between palaeobiological and biological approaches is the quality of evidence. Fossils that include slabs of compression imprints, permineralized tissue or amber can be compared to modern material such as pressed plants in herbaria, insects in alcohol vials or mounted on pins and histological sections of damaged plants. The view that modern material is markedly better-preserved than fossil material is certainly true in the aggregate, but permineralized material, amber and even compressions do offer surprises. For example, permineralized plant tissues from coal-ball floras of Middle and Late Pennsylvanian age often display histological detail similar to microtomed sections of modern embedded plant tissues. Amber contains details of surface ornamentation, setation, genitalia and other key characters that allow taxonomic resolution within a systematic context of extinct and modern taxa. Compression fossils, typically considered as substandard for detection of important diagnostic characters, often present features in *Lagerstätten* that reveal considerable plant-associational data, including mouthpart and ovipositor structure, habitus and important structures such as distinctive hair, surface ornamentation and gut contents. In addition, compression and permineralized material is virtually our only source of ecological data for leaf-mines, galls, borings and other stereotyped feeding patterns, and often provide taxonomically highly-resolved associational data not available from other preservational modes such as

amber. Admittedly these data provide an inadequate inventory of the totality of past associations, but they are robust at higher taxonomic and ecological scales (Figs 2.4, 2.6, 2.16–2.18). Conversely, the extant insect fauna also is poorly understood at lower taxonomic and ecological scales. Estimates of the true species-level abundance of insects indicate that a significant number of modern plant–insect associations are unknown at lower latitudes, and others that are known are typically gleaned from evidence representing either adult or immature phases, but not both. Issues of sampling completeness, variable coverage and attribution of known plant damage to insect hosts afflicts fossil and modern material alike, both of which provide a small representation of true associational diversity in time and space. Perhaps the greater inventory of

modern plant–animal associations is balanced by the greater temporal breadth of associations documented in the fossil record.

Increasingly both approaches have supplemented each other and their interface is becoming fuzzy (Fig. 2.4). Biological approaches have gradually relied on the fossil record to calibrate plant–host and animal–associate phylogenies whereas palaeobiologists have begun to test evolutionary and ecological hypotheses based on modern associational data. The fossil record has even been used as primary data for understanding how insect herbivores respond to palaeoclimatically induced vegetational change. This mutual dependence of palaeobiological and biological associational data will only increase in the near future.

Box 2.3 Glossary

assemblage A group of fossil organisms occurring in a deposit, without any implication of contemporaneous biological association, as in a modern community.

biomechanics The study of the mechanisms by which organisms function, usually investigated by mathematical modelling of how organismic structure responds to external perturbation.

body fossil A fossil consisting of its physical remains or its mineralic alteration, rather than the activity of the organism expressed as a trace fossil, such as plant damage or coprolites.

catastrophism The doctrine that past geological paroxysms, such as relatively sudden climatic change and tectonism, has had a major impact on the course of the history of life.

cladogram A diagrammatic depiction of branching phylogenetic relationships, which lists key characters (synapomorphies) that define particular taxa.

coal-ball A globular, concretionary fossil permineralized by carbonate minerals, occurring in coal seams or adjacent strata, and preserving fossil plants, often with superb detail of tissues.

community A group of organisms representing various species that co-occur in the same spatial habitat and are linked trophically such that they form a web of interdependent associations.

component community A plant species and all of its dependent organisms, including herbivores, pathogens, fungi and all trophically dependent predators, parasitoids and parasites.

compression Fossil preservation of an entombed organism on a bedding surface, represented by a carbon film, and often

as flattened resistant tissue such as plant cuticle or insect chitin.

convergence The independent evolution of structural or functional similarity in two or more unrelated lineages that is not based on genotypic similarity; homoplasy.

domatium A region on a leaf—usually a pit, flap or hollowed area—typically located at the angle of two major veins, serving as lodging for mites or insects.

ecomorphological feature An organismic attribute characterized by ecological or structural criteria, often contrasted to clades on which such features are frequently mapped or contrasted.

entomophily The pollination of seed plants by insects, as opposed to other organisms or physical agents such as wind or water.

escalation The hypothesis that, because of the greater intensity of selection within a habitat through macroevolutionary time, lineages must become successfully better adapted to exist.

geotectonic Broad, regional processes, related directly or indirectly to the planet's tectonic plates, that deform or otherwise affect the earth's crust.

holometabolous Possessing a complete developmental transformation in insects, consisting of the separate and distinctive sequence of egg, larval, pupal and adult stages.

impression A mode of fossilization in which the flattened imprint of an organism forms on a bedding surface, without the preservation of original organismic tissue.

individualistic response The reaction of organisms to profound ecological change by species-specific abiotic and

Box 2.3 continued

biological preferences rather than community-wide readjustment.

isotope geochemistry The study of the relative abundances of isotopes in sediments to determine environmental conditions of the past, including salinity and especially climate.

macroevolutionary Evolutionary processes viewed from the perspective of geological time, such as the origin of higher taxonomic categories, and attributable either to the prolonged accumulation of microevolutionary processes or the operation of hierarchically different processes during species formation.

megafauna A large-statured, continental vertebrate fauna associated with the Quaternary, whose extinction around 11000 BP is associated with climatic deterioration or anthropogenic overkill.

molecular clock hypothesis The idea that point mutations occur at a sufficiently regular rate to permit the dating of phylogenetic sister-taxa.

pollination drop mechanism A type of gymnosperm pollination in which a mucilaginous drop exuded from the ovular micropyle traps and detains pollen grains in a pollen chamber, resulting in pollen germination and subsequent fertilization.

prepollen Fossil pollen grains that function as pollen but morphologically resemble spores in that they bear trilete marks and germinate proximally.

pull of the recent The inherent bias in the fossil record attributable to greater representation of more recently deposited sediments than those deposited in the more remote past.

radiation The geologically rapid, evolutionary divergence of lineage members into a variety of adaptive types, frequently with differentiation of taxa in the use of resources or habitats.

syndrome A controversial concept that defines discrete types of biotic associations, especially pollination and seed dispersal, based on symptoms and structural features that characterize the dispersed plant and the dispersing animal.

time-averaging The incorporation, either within a deposit or among adjacent successive deposits, of material representing different instantaneous occurrences in time, resulting in the averaging of more discrete and shorter-term evolutionary processes or events.

trace fossil A type of behavioural evidence for life of the past, consisting of animal-mediated plant damage, coprolites, tracks, trails and burrows that occur in the fossil record.

transfer ecology The use of the ecological attributes of modern taxa to understand the palaeoecology of phylogenetically related, extinct taxa.

uniformitarianism The principle that there are inviolable laws of nature that have not changed during the course of time.

Appendix

Supplementary information for Chapter 2

This Appendix contains additional material for Chapter 2, 'The history of associations between plants and animals', by Conrad C. Labandeira. It is intended to contain more detailed explanations of some of the figures appearing in that chapter and supplements the captions that appear with the figures.

Fig. 2.3 A study by Wilf and Labandeira (1999) showing the response of plant–insect associations to the Early Cenozoic Thermal Interval (ECTI), an interval of elevated global warming. A greater variety of insect damage per host species and increased attack frequencies characterize Early Eocene plants, occurring under considerably warmer conditions compared to earlier Late Palaeocene plants. In addition, herbivory is elevated for both Late Palaeocene and Early Eocene members of the Betulaceae (birch family), a group of plants that are readily located by herbivores (Feeny 1976). (a) Sampling areas indicated by black polygons. (b) Damage census data for Late Palaeocene and Early Eocene leaves. From bottom to top: leaves with any insect damage, leaves externally consumed and the percentage of damaged leaves bearing more than one type of damage. These categories are each analysed separately for all leaves (**All**), Betulaceae only (**Bet**) and taxa other than Betulaceae (**NBet**). Error bars are one standard deviation of binomial sampling error; see Wilf and Labandeira (1999) for details of sample size, leaf area examined and locality information. (c) Diversity of insect damage for each plant–host species (vertical axis) plotted against the percentage of localities (49 Late Palaeocene and 31 Early Eocene) in which the species occurs (horizontal axis). Each data point is one species; many data points overlap at the lower left; survivors are plotted twice. Grey lines show divergence of 1 standard deviation (68%) confidence intervals for the two regressions. See Wilf and Labandeira (1999) for details of regressions and coefficients of determination.

Fig. 2.4 Summary of palaeobiological versus biological

approaches in examinations of the temporal dimension of plant–animal associations. Palaeobiological approaches rely extensively on fossil material and extinct taxa for inferences regarding past plant–animal associations; biological approaches deduce past associations from extant taxa, often with known biologies. This distinction is occasionally unclear, but the separation proposed here approximates the differing subject material or methodologies between the two subdisciplines. The types of data and their categorization are presented at the top and are a representative sample of the literature. The geochronological placement of the data is provided as horizontal lines within vertical bars. Palaeobiological approaches typically span the terrestrial Phanerozoic record, but there are important earlier Palaeozoic and mid-Mesozoic hiatuses. By contrast, biological approaches, with the exception of modern mouthpart classes and perhaps feeding inferences in phylogenetic analyses, best describe the Cretaceous and Cenozoic, and are approximately equivalent to the duration of most lower-level extant clades. Abbreviations: Sil. = Silurian, Miss. = Mississippian, Penn. = Pennsylvanian, Neog. = Neogene.

For palaeobiological approaches, data for quantitative analyses (a) are the following, with geological stages in parentheses from oldest to youngest (see Harland et al. 1990 for nomenclature). From the Lower Permian of north-central Texas, the Coprolite Bone Bed flora (Sakmarian) (Greenfest & Labandeira 1998), the Brushy Creek flora (Artinskian) and the Taint flora (Artinskian) (Beck & Labandeira 1998); the Meeteetsee flora from the Upper Cretaceous (Maastrichtian) of north-western Wyoming (Labandeira et al. 1995); several floras from the Palaeocene to Eocene transition from south-western Wyoming (Wilf & Labandeira 1999); and from the Middle Eocene (Lutetian), the Republic flora from north-eastern Washington state (Palmer et al. 1998) and the Green River flora from eastern Utah (Wilf et al.,

2001). Compendia of data for qualitative analyses (b) and dispersed coprolites (c) are provided in Labandeira (2002). Data for gut contents (d) are, from oldest to youngest: Mazon Creek, from the Middle Pennsylvanian (Moscovian) of north-central Illinois; Chekarda, from the Lower Permian (Kungurian) of the Perm Region, Russia; Karatau, from the Upper Jurassic (Kimmeridgian) of southern Kazakhstan; Baissa, from the Lower Cretaceous (Neocomian) of the Buryat Republic, Russia; Santana, Lower Cretaceous (Aptian) of Ceará, Brazil; Orapa, Upper Cretaceous (Cenomanian) of central Botswana; Messel, from the Middle Eocene (Lutetian) of Germany; Baltic amber, from the Late Eocene (Priabonian) of various localities in northern Europe; and Dominican amber, from the Lower Miocene (Aquitania) of the northern Dominican Republic. See also Figures 2.15 and 2.16, and Labandeira (1998a, 1998b). Data for fossil mouthparts (e) is extensively documented in Labandeira (1990), abridged in Labandeira (1997). Examinations of fossil plant reproductive biology with regard to insect associations (f) are relatively few, and are provided in Labandeira (2002).

For biological approaches, data for the assignment of highly stereotyped damage in the fossil record to extant taxa (g) can be found in Labandeira (2002). The extension of modern pollination mutualisms by reference to diagnostic plant and insect morphological attributes in fossils (h) is also documented in Labandeira (2002). Inference of plant–insect associations based solely on insect fossils of modern lineages and modern ecological affiliations, biogeographical patterns or other supportive biological data (i) occur principally in major *Lagerstätten*. They are, from oldest to youngest: Issyk-Kul from the Lower Jurassic (?Hettangian) of north-eastern Kyrgyzstan; Karatau from the Upper Jurassic (Kimmeridgian) of southern Kazakhstan; from the Lower Cretaceous, Baissa (Neocomian) of eastern Russia, Jezzine amber (Barremian) of Lebanon, Yixian (Barremian) of north-eastern China, Montsec (Barremian/Aptian) of north-western Spain, and Santana (Aptian) of Brazil; from the Upper Cretaceous, Bezzonais and Durtal amber (Cenomanian) of France, Orapa (Cenomanian) of Botswana, Sayreville amber (Turonian) of New Jersey, Taimyr amber (Coniacan or Santonian) of Russia, and Cedar Lake and coeval amber (Campanian) of south-central Canada; from the Palaeogene, the Fur Formation (Thanetian) of Denmark, Hat Creek amber (Ypresian) from southern British Columbia, Green River (Lutetian) from western Colorado

and south-western Wyoming, Messel (Lutetian) from Germany, Angelsea (?Priabonian) of southern Australia, Baltic amber (Priabonian) of northern Europe, Florissant (Priabonian) of Colorado, Ruby River (Rupelian) from south-western Montana, and Aix-en-Provence and associated sites (Chattian) from central France; and from the Neogene are Rott (Aquitania) from Germany, Chiapas amber (Aquitania) from southern Mexico, Dominican amber (?Aquitania) from the northern Dominican Republic; Radaboj (Burdigalian) from Croatia, Latah (Langhian) from northern Idaho, Oeningen (Tortonian) from Switzerland; Randecker Maar (Messinian) from southern Germany, and Willershausen (Piacenzian) from northern Germany.

Assessments from phylogenetic analyses of the time of origin of plant-related feeding attributes (j) are typically approximate, and midpoints have been assigned to time interval estimates from the literature. They are, from oldest to youngest: the origin of the Cicadomorpha (Hemiptera) during the Early Permian by Campbell et al. (1994); an Early Permian origin of the Auchenorrhyncha (Hemiptera) by Sorenson et al. (1995); a Late Permian origin of non-phloem-feeding homopterous Hemiptera by Campbell et al. (1994); the split during the Early Triassic between basal pollinivorous panorpoid lineages into the Hymenoptera and Lepidoptera by Kristensen (1995); basal radiation of phytophagous Sternorrhyncha (Hemiptera) during the Late Triassic by Campbell et al. (1994); Middle to Late Jurassic origin of nectarivorous Apioceridae and Mydidae (Diptera) from area cladograms by Yeates and Irwin (1996); Late Jurassic origin of Cynipoidea (Hymenoptera) by Ronquist (1995); the radiation of earlier lineages of Scarabaeidae (Coleoptera) by Scholtz and Chown (1995); the origin of the Matsucoccidae (Hemiptera) by Foldi (1997); the origin of sporophagous Keroplatidae (Diptera) by Matile (1997); the Early to Late Cretaceous origin of melponine bees by Roubik et al. (1997); the origin of *Urytalpa* (Diptera) plant feeding during the Late Cretaceous by Matile (1997); the commencement of host-plant associations within birdwing butterfly clades (Lepidoptera) during the Cretaceous to Caenozoic transition by Parsons (1996); radiations of more derived scarabaeid clades (Coleoptera) during the earlier Eocene by Scholtz and Chown (1995); the origin and early diversification of *Larinus* weevils (Coleoptera) on thistles by Zwölfer and Herbst (1988); and the origin and early expansion of phytophagous Heliethinae (Lepidoptera) by Mitter et al. (1993). Data

for the geochronological extension of modern mouthpart classes (k) can be gleaned from a compilation in Labandeira (1990), condensed in Labandeira (1997).

From a brief survey of analyses demonstrating congruent associations between plants and insects, a sample of 13 estimates is provided for the origin of subclades (l). These data are, from left (youngest) to right (oldest): an initial time estimate for the colonization of North American Asteraceae by *Ophraella* leaf-beetles (Futuyma & McCafferty 1990); the colonization of Hawaiian silverswords (Asteraceae) by *Nesosdyne* planthoppers (Roderick 1997; Roderick & Metz 1998); the colonization of *Eriogonum* (Polygonaceae) by *Euphyllotes* butterflies (Shields & Reveal 1988); the initial occurrence of *Tetraopes* longhorn beetles on North American milkweed (Asclepiadaceae) hosts (Farrell & Mitter 1998); a subsequent estimate for the colonization of North American Asteraceae by *Ophraella* leaf beetles (Funk et al. 1995); the colonization of plant hosts by ancestral lineages of *Rhagoletis* fruit flies (Diptera) (Berlocher & Bush 1982; Berlocher 1998); the expansion of *Yponomeuta* (Lepidoptera) on Celastraceae, Rosaceae, Crassulaceae and Salicaceae (Menken 1996); the initial colonization of monocots by delphacid plant-hoppers (Hemiptera) (Wilson et al. 1994); the inception of associations between Lamiaceae and *Phyllobrotica* leaf beetles (Farrell & Mitter 1990); the ancestral association between rosid hosts and papilionoid butterflies (Janz & Nylin 1998); a broad estimate for the association between the Chrysomeloidea (longhorn beetles, leaf beetles and weevils) and seed plants (Farrell 1998); the initial association between *Chrysorthenches* moths (Lepidoptera) and conifers (Dugdale 1996); and the ancient colonization of the Malvales by the Carsidaridae (Hemiptera) (Hollis 1987).

Fig. 2.5 Types of evidence for plants, insects and their associations for 21 biotas, a small but representative sample selected from the fossil record. The five major categories of evidence for plant–insect associations range from those centred primarily on the plant (reproductive biology) to those focusing on insect structures that reveal herbivory (mouthparts and ovipositors). The fossil record of plant–insect associations (centre panel with links) is connected to the parallel but mostly separate fossil records of plants (left panel) and insects (right panel). Data provided from the literature illustrate biotas where one to four of the five types of evidence have been used to establish direct to indirect links between plants and insects. These biotas are not a complete inventory but represent best-case

examples, and are placed in approximate geochronological positions, with stage designations in parentheses. They are from youngest to oldest: (a) Downton Castle Formation and Ditton Group, Late Silurian (Pridoli) and Lower Devonian (Lochkovian) respectively, western United Kingdom (Edwards et al. 1995; Edwards 1996); (b) Rhynie Chert, Lower Devonian (Lochkovian) of Rhynie, Scotland (Kidston & Lange 1921; Kevan et al. 1975); (c) Battery Point Formation, Lower Devonian (Pragian) of Gaspé, Quebec (Banks 1981; Labandeira et al. 1988; Banks & Colthart 1993; Hotton et al. 1996); (d) Carbondale Formation, Middle Pennsylvanian (Moscovian) of Mazon Creek, north-western Illinois (Richardson 1980; Scott & Taylor 1983; Shear & Kukalová-Peck 1990; Labandeira & Beall 1990; Labandeira 1997); (e) Mattoon Formation, Late Pennsylvanian (Krevyakinskian) of eastern Illinois (Dilcher 1979; Millay & Taylor 1979; Retallack & Dilcher 1988; Labandeira & Phillips 1996; Labandeira et al. 1997); (f) La Magdalena coalfield, Late Pennsylvanian (Podolskian), of León, Spain (Amerom 1966; Castro 1997); (g) Waggoner Ranch Formation, Early Permian (Artinskian) of north-central Texas (Beck & Labandeira 1998); (h) Koshelevo Formation, Early Permian (Kungurian) of Chekarda, Perm Region, Russia (Becker-Migdisova 1940; Rasnitsyn 1977; Rasnitsyn & Krassilov 1996a, 1996b; Krassilov & Rasnitsyn 1997; Krassilov et al. 1997, 1999; Rasnitsyn & Novokshonov 1997; Novokshonov 1998b; Naugolnykh 1998); (i) Upper Buntsandstein and Lower Keuper Formations, Middle Triassic (Anisian and Ladinian) of western Germany and eastern France (Linck 1949; Kelber 1988; Kelber & Geyer 1989; Grauvogel-Stamm & Kelber 1996); (j) Chinle Formation, Late Triassic (Carnian) of north-western Arizona (Walker 1938; Ash 1997, 1999); (k) Karabastau Formation, Late Jurassic (Kimmeridgian) of Karatau, eastern Kazakhstan (Rohdendorf 1968; Crowson 1981; Arnoldi 1992; Labandeira 1997; Krassilov et al. 1997; Novokshonov 1997); (l) Wealden Formation, Early Cretaceous (Berriasian to Valanginian) of southern England (Jarzembowski 1990); (m) Yixian Formation, Early Cretaceous (Barremian) of western Liaoning, China (Ren 1998; Labandeira 1998b); (n) Kootenai Formation, Early Cretaceous (?Albian) of the Black Hills, South Dakota (Seward 1923; Delevoryas 1968; Crepet 1972, 1974); (o) Santana Formation, Early Cretaceous (Albian) of Ceará, Brazil (Caldas et al. 1989); (p) Dakota Formation, earliest Late Cretaceous (Cenomanian) of Nebraska and Kansas (Basinger & Dilcher

1984; Labandeira et al. 1994; Elliott & Nations 1998); (q) Hell Creek and Fort Union Formations, latest Cretaceous to earliest Palaeocene boundary (Maastrichtian to Danian) of the Williston Basin, south-western North Dakota (Labandeira et al. 2002); (r) Klondike Mountain Formation, Middle Eocene (Lutetian) of Republic, north-eastern Washington (Lewis 1994; Lewis & Carroll 1991; Wehr 1998); (s) Baltic amber, Late Eocene (Priabonian) of northern Europe (Conwentz 1890; Peyerimhoff 1909; Schedl 1947; Willemstein 1980); (t) Passamari Formation, Late Oligocene (Chattian) of Ruby River, south-western Montana (Becker 1965; Lewis, 1972, 1976); (u) the Störungszone, Pliocene (Piacenzian) of Willershausen, Germany (Straus 1967, 1977).

Fig. 2.7 The fossil history of insect external foliage-feeding. Geological stage-level resolution is provided in parentheses. (a) Transverse section of a permineralized specimen of the trimerophyte *Psilophyton dawsonii*, showing cortical collenchyma and wound response at top; inner tissues missing. This specimen is from the Lower Devonian (Pragian) of Gaspé, Quebec (Banks 1981). (b) Detail of wound response tissue in (a), indicated by arrows, suggesting surface grazing (Banks 1981). (c) A pinule of the seed-fern *Paripteris pseudo-gigantea* displaying cusped marginal-feeding excisions, from the Middle Pennsylvanian (Podolskian) of northern France (Amerom & Boersma 1971). (d) The seed-fern *Linopteris neuropteroides*, from the Late Pennsylvanian (Noginskian) of north-western Spain, exhibiting a bite mark (arrow) attributable to an external feeder (Castro 1997). (e) A specimen of the seed-fern leaf *Glossopteris*, showing extensive, scalloped margin feeding (arrow), from the Lower Permian (?Assellian) of north-eastern India (Srivastava 1987). (f) The cycadophyte *Taeniopteris*, from the Lower Permian (Artinskian) of north-central Texas, displaying extensive margin-feeding (arrows) (Beck & Labandeira 1998). (g) From the same deposit as (f) is the gigantopterid *Cathaysiopteris yochelsoni*, displaying hole-feeding and surrounding necrotic blotches (arrows) (Beck & Labandeira 1998). (h) A specimen of the seed-fern *Glossopteris*, showing cusped excavations (arrow) along the leaf margin and extending almost to the midrib, from the Upper Permian of South Africa (Plumstead 1963). (i) A short leaf segment of the cycadophyte *Taeniopteris*, showing three serial, cusped excavations that have projecting veinal stringers (Kelber & Geyer 1989). This specimen is from the Middle Triassic (Ladinian) of western Germany. (j) A leaf fragment of the filicalean fern

Cynepteris lasiophora, showing marginal- and hole-feeding traces (arrows), from the Upper Triassic (Carnian) of north-western Arizona (Ash 1997). (k) Detail of hole-feeding trace in the upper part of (j), exhibiting a reaction rim (Ash 1997). (l) Cusped margin-feeding on the probable seed-fern *Sphenopteris arizonica*, from the same provenance as (j) (Ash 1999). (m) A cycad leaf from the undifferentiated Middle Jurassic of northern England, exhibiting marginal feeding (Scott & Paterson 1984). (n) An unidentified angiosperm leaf with hemispheric- to deltoid-shaped feeding holes between secondary veins, from the Middle Eocene (Lutetian) of western Tennessee (Stephenson & Scott 1992). (o) Damage by an adult leaf-cutter bee (Megachilidae) on a leaf of *Prunus* (Rosaceae), from the Middle Eocene (Lutetian) of north-eastern Washington (Lewis 1994). (p) Insect bud-feeding on the chestnut *Castanea atavia* (Fagaceae) from the Lower Pliocene (Zanclian) of Germany (Berger 1953). Scale bars for this and succeeding figures: crosshatched = 10 cm, solid = 1 cm, striped = 0.1 cm, dotted = 0.01 cm (100 μ), and backslashed = 0.001 cm (10 μ).

Fig. 2.8 The fossil history of piercing-and-sucking. Geological stage-level resolution is provided in parentheses. (a) An oblique, longitudinal section of an axis of the rhyniophyte, *Rhynia*, showing a lesion plugged with opaque material and extending to subjacent vascular tissue (Kevan et al. 1975). This specimen originates from the Lower Devonian (Lochkovian) Rhynie Chert of Scotland. (b) Another *Rhynia* axis from the Rhynie Chert, in transverse section, displaying hypertrophied cortical cells and associated opaque material (Kevan et al. 1975). (c) A specimen of the Early Devonian (Pragian) trimerophyte, *Psilophyton*, from Gaspé, Québec, exhibiting three sites of piercing (arrows) (Banks & Colthart 1993). Below each puncture site is a cone of lysed tissue, on a base of unaltered periderm tissue (Banks & Colthart 1993). (d) Detail of (c), showing an enlarged cone of lysed subepidermal tissue with radiate stylet tracks and damaged epidermal cells at top (Banks & Colthart 1993). (e) Three piercing wounds on an unnamed trimerophyte, eliciting the formation of light-hued response periderm (arrows) (Banks & Colthart 1993). This specimen is from the Lower Devonian (Pragian) of Québec. (f) Damage to a fern (*Etapteris*) petiole, probably by an insect with stylet mouthparts, showing disorganized tissues enveloping the puncture wound. The specimen is from the Middle Pennsylvanian of the eastern United States (Scott & Taylor 1983). (g) A stylet track with terminal feeding pool, sur-

rounded by reaction tissue, on the seed-fern pollen organ *Bernaultia*. This specimen is from the Calhoun Coal of Late Pennsylvanian age from eastern Illinois (Schopf 1948; Millay & Taylor 1979; Retallack & Dilcher 1988; Labandeira 1998a). (h) Two stylet tracks targeting vascular tissue (**xylem** and **phloem**) of the marattialean fern, *Psaronius*, also from the Calhoun Coal of Illinois (Labandeira & Phillips 1996a). The right track, approximately 3 mm long, is sectioned lengthwise, and shows surrounding reaction tissue (**rt**) and a terminal feeding pool. (i) Detail of the left stylet track in (h), showing stylet track (**st**) surrounding opaque material (**om**), penetration of undifferentiated parenchyma (**pa**) and avoidance of large gum-sac cells (**gs**) (Labandeira & Phillips 1996a). (j) The head and 3.2 cm-long stylet mouthparts of the palaeodictyopterid, *Eugereon boeckingi* Dohrn, from the Lower Permian (?Assellian) of Germany (Müller 1978). (k) Reconstruction of the early hemipteran, *Permocicada integra* Becker-Migdisova from the Lower Permian (Wordian) of Russia (Becker-Migdisova 1940). (l) Two stylet probes, with surrounding rims of opaque material, on the cheirolepidiacean conifer *Pseudofrenelopsis*, from the Lower Cretaceous of Texas (Watson 1977). See Figure 2.7 for scale-bar conventions.

Fig. 2.9 The fossil history of boring. Geological stage-level resolution is provided in parentheses. (a) Oribatid mite borings in gymnospermous *Australoxylon mondii* wood, of probable glossopterid or cordaite origin, from the Late Permian of the northern Prince Charles Mountains, Antarctica (Weaver et al. 1997). (b) Enlarged region of a boring in (a), showing ellipsoidal coprolites and associated undigested frass (Weaver et al. 1997). (c) Insect borings in cambium of *Araucarioxylon arizonicum*, from the Late Triassic (Carnian) of Petrified Forest National Monument, Arizona (Walker 1938). These borings were made by unknown beetles. (d) Cambium borings in *Araucarioxylon arizonicum* as in (c), but fabricated by a different insect species (Walker 1938). (e) Scanning electron micrograph of a probable beetle boring in *Protocupressinoxylon* wood, healed by parenchymatous tissue, from the undifferentiated Middle Jurassic of Henan, China (Zhou & Zhang 1989). (f) Beetle borings, assignable to the family Cupedidae, in wood of *Hermanophyton*, a gymnosperm of uncertain affinities (Tidwell & Ash 1990). This material is from the Late Jurassic (Tithonian) of south-western Colorado. (g) A scolytid (bark beetle) cambium boring by a beetle in an unnamed conifer from the Early Cretaceous (Berriasian to Valanginian) of south-

ern England (Jarzembowski 1990; Chaloner et al. 1991). (h) Beetle invasion of the androecium of the bennettitalean, *Cycadeoidea*, showing consumption of synangial-associated tissues (**s**, synangium), a gallery (**g**), and an exit or entry tunnel (**b**) across the microsporophyll (**ms**) which are bract-like, enveloping structures (Crepet 1972). This material is from the Lower Cretaceous (?Aptian) of South Dakota. (i) A cerambycid (longhorn beetle) boring in unknown wood, from the Late Oligocene or Early Miocene (Chattian or Aquitanian) of Germany (Linstow 1906). (j) A scolytid (bark beetle) cambium boring in unknown wood from the Middle Miocene of Shandong, China (Guo 1991). (k) The dipteran cambium miner *Palaeophytobia platani* (Agromyzidae) in sycamore wood (*Platanoxylon*), displaying tissue damage at top, from the Upper Miocene (Tortonian) of Hungary (Süss & Müller-Stoll 1980). (l) A boring of a longhorn beetle (Cerambycidae) in wood of the pinaceous conifer *Larix* (larch), from the Late Pliocene (Piacenzian) of Peary Land, northern Greenland (Böcher 1995). (m) The bark beetle *Eremotes nitidipennis* (Scolytidae) within a boring of unknown wood, from the Holocene of southern Finland (Koponen & Nuorteva 1973). See Figure 2.7 for scale-bar conventions.

Fig. 2.10 The fossil history of leaf-mining. Geological stage-level resolution is provided in parentheses. (a) A possible U-shaped blotch mine on the seed-fern leaf *Neuropteris subauriculata*, from the Middle Pennsylvanian (Moscowian) of Zwickau, Germany (Müller 1982). (b) A holometabolan serpentine leaf-mine on the corytosperm seed-fern *Pachypteris*, from the Jurassic to Cretaceous boundary of northern Queensland, Australia (Rozefelds 1988a). These leaf-mines antedate the earliest documented angiosperms by approximately 15 million years. (c) Another serpentine leaf-mine on a different specimen of *Pachypteris* (Rozefelds 1988a). (d) A serpentine leaf-mine (Lepidoptera: Gracillariidae) on the magnoliid dicot *Densinervum*, showing oviposition site, frass trail and pupation chamber, from the Late Cretaceous (Cenomanian) of Nebraska (Labandeira et al. 1994). (e) A serpentine leaf-mine of *Stigmella* (Lepidoptera: Nepticulidae) on the hamamelid dicot *Cercidiphyllum*, from the Late Cretaceous (Maastrichtian) of Wyoming (Labandeira et al. 1995). (f) A serpentine mine of ?Bucculatricidae on unknown dicot, from the Upper Palaeocene (Thanetian) of England (Crane & Jarzembowski 1980). (g) Portion of a *Cedrela* leaflet (Meliaceae) with a serpentine *Phyllocnistis* leaf-mine (Lepidoptera: Gracillariidae)

bearing a frass trail (Hickey & Hodges 1975). This specimen is from the Early Eocene (Ypresian) of north-western Wyoming. (h) Circular leaf-mines of Lepidoptera (Incurvariidae) on *Macginitiea* (Platanaceae), from the Green River Formation of Bonanza, Utah, of Middle Eocene age (Lutetian) (Labandeira 1998c). (i) An undetermined dicotyledonous leaf bearing a serpentine leaf-mine assignable to the Lepidoptera (?Nepticulidae), from the Middle Eocene of England (Stephenson & Scott 1992). (j) Detail of leaf-mine in (i), showing complete developmental progression from oviposition to pupation (Stephenson & Scott 1992). (k) A leaf of Lauraceae exhibiting a serpentine lepidopteran mine (Nepticulidae), from the Late Eocene (Priabonian) of Victoria, Australia (Rozefelds 1988b). (l) Camera lucida enlargements of two mines in (k) (Rozefelds 1988b). (m) Dipteran blotch mine (Agromyzidae) on *Cinnamomum* (Lauraceae), from the Upper Miocene (Tortonian) of Bosnia (Berger 1949). See Figure 2.7 for scale-bar conventions.

Fig. 2.11 The fossil history of galling. Geological stage-level resolution is provided in parentheses. (a) Probable gall, *Acrobullbillites*, on the stem terminus of the sphenophyte *Asterophyllites longifolius*, from the Middle Pennsylvanian of northern Europe (from Weiss (1876), refigured by Amerom [1973]). (b) The ‘fructification’ *Paracalamostachys spadiceiformis*, reinterpreted as a probable stem gall by Amerom (1973), from the Middle Pennsylvanian of northern England (Thomas 1969). (c) Gall of a holometabolous insect on the rachis of *Psaronius chasei*, a marattialean fern from the Late Pennsylvanian (Krevyakinian) of Illinois (Labandeira & Phillips 1996b). Note the barrel-shaped coprolites and frass in the central lumen, and surrounding tufts of hyperplastic and hypertrophic parenchyma. (d) A three-dimensional reconstruction of the same gall type in (c); same provenance (Labandeira & Phillips 1996b). (e) Aborted cone of the herbaceous voltzialean conifer *Aethophyllum stipulare*, showing a basal stem expansion interpreted as a gall (Grauvogel-Stamm & Kelber 1996). This material is from the Middle Triassic (Anisian) of France. (f) Round, oval or deltoid leaf galls on the enigmatic gymnosperm, *Dechellyia gormanii*, expressed as swellings typically occurring about 1 to 1.5 cm from the base of the leaf (Ash 1997). These galls originate from the Upper Triassic Chinle flora (Carnian), from north-eastern Arizona. (g) Enlargement of a gall in (f) (arrow), showing deltoid shape and extension beyond the leaf margin (Ash 1997). (h) Abundant, bulbous *Wonnacottia* galls on the leaf of a

bennettitalean (probably *Anomozamites nilssoni*), from the Middle Jurassic (Bajocian) of northern England (Harris 1942; Alvin et al. 1967). These galls often occur in clusters and are preserved three-dimensionally. (i) Large spheroidal gall on an angiosperm leaf (Scott et al. 1992), similar in shape and size to those produced by gall wasps (Hymenoptera, Cynipidae), from the Late Cretaceous (Maastrichtian) of Tennessee. (j) Cynipid spindle galls (Hymenoptera) on a leaf of the oak *Quercus hannibali* (Fagaceae), from the Middle Miocene of north-western Nevada (Waggoner & Poteet 1996). These distinctive galls are most similar to those of the extant gall wasp *Antron clavuloides*, which parasitizes *Quercus*. (k) A basal petiolar gall, attributed to a *Pemphigus* gall aphid, on *Populus latior* (Salicaceae), from the Upper Oligocene (Chattian) of Germany (Mädler 1936). (l) Enlargement of a pemphigid gall in (k), showing a characteristic stem expansion (Mädler 1936). (m) A cone-mimicking gall of the cecidomyiid dipteran (*Thecodiplosis*), a gall midge on the conifer *Taxodium* (bald cypress), from the Middle Miocene of northern Idaho (Lewis 1985). See Figure 2.7 for scale-bar conventions.

Fig. 2.12 The fossil history of seed predation. Geological stage-level resolution is provided in parentheses. (a) A sandstone cast of the seed *Trigonocarpus*, from the Pennsylvanian of the United Kingdom, displaying a plug infilling a presumptive hole in the seed coat (Scott et al. 1992). (b) External surface of the cordaitalean seed *Samaropsis* with a hole and surrounding rim, from the Middle Pennsylvanian of Siberia, Russia (Sharov 1973). The culprit may be a palaeodictyopterid insect in the same deposit possessing a beak width approximating the hole diameter. (c) A similarly bored seed from the same deposit, in longitudinal section (Sharov 1973). (d) A boring in a lycopsid *Setosisporites* megaspore, from the Middle Pennsylvanian of Yorkshire, United Kingdom, showing the entire spore (inset) and detail of the bored margin (Scott et al. 1992). (e) A caddisfly case of seeds from the ginkgophyte *Karkenia*, from the Lower Cretaceous of Shin Khuduk (stage unspecified), Mongolia (Krassilov & Sukacheva 1979). (f) Longitudinal section of a permineralized dicotyledonous seed or fruit from the probable Upper Cretaceous (stage unspecified) of southern Argentina, showing a *Carpoichnus* boring (Genise 1995), with exit hole at arrow. (g) A dicotyledonous *Rutaspermum* seed (Rutaceae) with an insect exit hole, from the Middle Eocene (Lutetian) Messel deposit in Germany (Collinson & Hooker 1991). (h) Pristine (top) and bored

(bottom) dicotyledonous seeds of *Zanthoxylum* (Rutaceae) from the Early Oligocene (Rupelian) of Vermont (Tiffney 1980). (i) Bored stone fruits of *Celtis lacunosa* (Fabaceae), assigned to the ichnogenus *Lamniporichnus*, from the Early Miocene (Aquitanian) of the Czech Republic (Mikulás et al. 1998). This damage is typical of weevils. (j) Additional damage of *Celtis*, from a Pleistocene sinter-cemented breccia of the Czech Republic (Mikulás et al. 1998). See Figure 2.7 for scale-bar conventions.

Fig. 2.13 The fossil history of surface fluid-feeding. Geological stage-level resolution is provided in parentheses. (a) *Pseudopolycentropus latipennis*, a scorpion fly with elongate mouthparts (arrow) from the Late Jurassic (Kimmeridgian) of Karatau, Kazakhstan; redrawn from a camera lucida sketch in Novokshonov (1997). (b) Head and mouthparts (arrow) of the tanglevein fly *Protnemestrius rohndendorfi* (Nemestrinidae) from the same provenance as (a), redrawn from a camera lucida sketch in Mostovski (1998). (c) The tanglevein fly *Florinemestrius pulcherrimus* (Nemestrinidae) from the Early Cretaceous (Barremian) of western Liaoning, China. Note elongate mouthparts (arrow) which are similar in form to extant nectar-feeding nemestrinids (Ren 1998). (d) Head and mouthparts of the crane fly *Helius botswanensis* (Tipulidae), extant descendants of which feed on flowers (Rayner & Waters 1991). This specimen is from the Late Cretaceous (Cenomanian) of Orapa, Botswana. (e) From the same deposit as (d) is a funnel flower consisting of fused petal bases and a relatively deep throat, indicative of insect pollination (Rayner & Waters 1991). (f) Scanning electron micrograph of a small charcoalfied flower showing a nectary disk (arrow) above a region of petals from the Late Cretaceous of Skåne, Sweden (Friis 1985). (g) A showy, zygomorphic, papilionoid flower (Fabaceae) exhibiting an upper banner petal (*s*), two lateral wing petals (*w*) and bottom keel petals (*k*), associated with insect, especially bee, pollination (Crepet & Taylor 1985). This specimen comes from Palaeocene to Eocene boundary strata in western Tennessee. (h) Extra-floral nectaries (arrows) at the junction of the leaf blade and petiolar base in *Populus crassa* (Salicaceae) from the uppermost Eocene (Priabonian) of the Florissant lake beds in central Colorado (Pemberton 1992). (i) A worker of the stingless bee *Proplebia dominicana* (Apidae) bearing conspicuous resin balls (arrows) attached to hind-leg corbiculae (Poinar 1992). This specimen is from the Early Miocene (Aquitanian)

Dominican amber deposit of the Dominican Republic. See Fig. 2.7 for scale-bar conventions.

Fig. 2.15 The fossil history of spore and pollen consumption, and pollination. Geological stage-level resolution is provided in parentheses. (a) An elliptical, somewhat flattened coprolite containing plant cuticle and occasional spores, from the Late Silurian (Pridoli) of the United Kingdom (Edwards et al. 1995). (b) Contents of coprolite containing abundant *Streelisporea*, *Aneurospora* and ?*Emphanisporites* spores, from the Lower Devonian (Lochkovian) of the United Kingdom (Edwards et al. 1995). (c) Sporangial fragments and isolated spores of the coprolite *Bensoniotheca*, from the Mississippian (Asbian) of England, attributed to a lyginopterid seed-fern (Rothwell & Scott 1988). (d) Two relatively intact sporangia in a *Bensoniotheca* coprolite from the same provenance as (c) (Rothwell & Scott 1988). (e) The coprolite *Thuringia*, consisting of the digested remnants of a pollen organ referable to the peltasperm seed-fern *Autunia* (Kerp 1988). This specimen is from the Pennsylvanian to Permian boundary of Germany. (f) The hypoperlid insect *Idelopsocus diradiatus* (Family Hypoperlidae), from the Lower Permian (Kungurian) of Chekarda, Russia, containing a plug of pollen (arrow) preserved in its gut (Krassilov & Rasnitsyn 1997). (g) Detail of a *Lunatisporites*-type pollen grain extracted from (f), attributable to a voltzialean conifer (Krassilov & Rasnitsyn 1997). (h) Reconstruction of the head and mouthparts of *Synomaloptila longipennis*, a hypoperlid insect (Family Synomaloptilidae) with pollinivorous habits, from the same provenance as (f) (Rasnitsyn 1977; Labandeira 1997b; Novokshonov 1998a). (i) The prophalangopsid grasshopper *Aboilus*, from the Late Jurassic (Kimmeridgian) Karatau locality of Kazakhstan, with an arrow indicating a bolus of pollen preserved in its intestine (Krassilov et al. 1997). (j) A cluster of digested *Classopollis* pollen from a cheirolepidiacean conifer, extracted from the gut of *Aboilus* in (i) below. (k) The nemomychid weevil *Archaeorrhynchus paradoxopus*, from the same provenance as (i), showing a prolonged and decurved rostrum (Arnol'di et al. 1992). (l) The xyelid sawfly *Ceroxyela dolichocea*, from the Lower Cretaceous (Neocomian) Baissa locality of Russia, with preserved gut contents of pollen indicated by an arrow (Krassilov & Rasnitsyn 1983). (m) A pollen grain of *Pinuspollenites*, from a pinalean conifer, found in the gut of *Ceroxyela* in (l) (Krassilov & Rasnitsyn 1983). (n) A staphylinid beetle, from

the Late Cretaceous (Cenomanian) of Orapa, Botswana, displaying pollen transportation (arrow) (Rayner & Waters 1991). (o) Enlargement of the terminal abdominal region of (n), showing pollen grains trapped among hairs (Rayner & Waters 1991). (p) Lateral view of a charcoalfied flower belonging to the Ericales/Theales complex of dicotyledonous angiosperms, from the Upper Cretaceous (Turonian) of Sayreville, New Jersey (Crepet 1996). (q) Contents of anther from same taxon as (p), displaying the characteristic network of viscin threads, implying a pollinator mutualism (Crepet 1996). (r) A clump of two types of pollen from the external abdominal surface of the stingless bee *Proplebeia dominicana*, revealed by scanning electron microscopy (Grimaldi et al. 1994). This amber specimen is from the Lower Miocene (Aquitania) of the Dominican Republic. See Fig. 2.7 for scale-bar conventions.

Fig. 2.19 The fossil history of oviposition. Geological stage-level resolution is provided in parentheses. (a) Reconstruction of the terminal abdominal region of a female *Uralia* (Diaphanopteroidea), illustrating a vertically compressed, swath ovipositor typical of those used in endophytic oviposition. *Uralia* originates from the Lower Permian (Kungurian) of Chekarda, Perm Region, Russia; redrawn from Kukalová-Peck (1991). (b) The pollinivorous hypoperlid insect *Mycteroptila* (Family Permarhaphidae) from the same provenance as (a). Note the pronounced, flattened ovipositor, which was probably used for endophytic insertion of eggs; redrawn from a camera lucida drawing by Novokshonov (1998a). (c) Elongate-oval oviposition scars on the sphenophyte *Equisetites foveolatus*, from the Middle Triassic (Ladinian) of Germany (Kelber 1988). (d) Camera lucida drawing of a leaf sheath from the sphenophyte *Equisetites arenaceus*, from the Middle Triassic (Ladinian) of Germany, showing dense, elongate-oval oviposition scars arranged in a zigzag pattern (Grauvogel-Stamm & Kelber 1996). (e) Probable insect eggs in or on the cycadophyte, *Taeniopteris angustifolia*, from the Middle Triassic (Ladinian) of Germany (Grauvogel-Stamm & Kelber 1996). (f) Enlargement of oval oviposition scars in (e) linearly and obliquely placed on the *Taeniopteris* leaf between the midrib and margin (Grauvogel-Stamm & Kelber 1996). (g) Oviposition scars of odonatan eggs, inserted as eccentric arcs (e.g. black arrow) on *Alnus* (Betulaceae), from the Middle Eocene (Lutetian) of Republic, Washington State (Lewis & Carroll 1991). (h) Oviposition scars on an unidentified

leaf, similar to and approximately contemporaneous with those of (g), and presumably produced by an odonatan (Schaarschmidt 1992). The white arrow refers to an arcuate row of scars; this leaf is from the Middle Eocene (Lutetian) of Messel, Germany. (i) An angiosperm leaf (?Juglandaceae) showing odonatan oviposition scars typical of the Coenagrionidae, from the Upper Miocene (Messinian) of Randecker Maar, Germany (Hellmund & Hellmund 1996). (j) A leaf of the angiosperm *Carpinus grandis* (Betulaceae) exhibiting petiolar oviposition scars (arrows) typical of the odonatan family Lestidae, from the Middle Oligocene (Chatian) of Germany (Hellmund & Hellmund 1996). See Fig. 2.7 for scale-bar conventions.

Fig. 2.20 The fossil history of plant–vertebrate associations. Geological stage-level resolution is provided in parentheses. (a) Crown of a ‘molariform’ cheek tooth from *Diadectes*, a high-fibre herbivore from the latest Pennsylvanian (Noginskian) of ?Ohio (Hotton et al. 1997). (b) Detail of striations in (a) on the wear facet parallel to the long axis of the jaw (Hotton et al. 1997). (c) Gut contents of the pareiasaur *Protorosaurus speneri*, illustrating a food bolus (delimited by white arrows) that contains conifer ovules (dark circular or hemispherical structures) and quartzose gastroliths (Q) (Munk & Sues 1993). This skeletal material is from the Upper Permian of Hessen, Germany. (d) A cluster of small, loose, pellet-like coprolites attributed to an ornithomimid dinosaur by Hill (1976), each containing abundant leaf cuticle from the bennettitalean *Prilophyllum*, from the Middle Jurassic of northern England (Thulborn 1991). (e) A herbivorous dinosaur coprolite, showing constrictions and resembling the segmented faeces of extant herbivorous mammals (Matley 1941; Thulborn 1991). (f) A herbivore coprolite with two backfilled burrows (one at upper arrow) within a dark groundmass composed of comminuted xylem fragments, and the other light-coloured (lower arrow) packed with intermixed sediment and dung. Both burrows are inferred to have been made by dung beetles (Scarabaeidae), based on extant burrowing patterns; specimen from the Late Cretaceous (Campanian) of Montana (Chin & Gill 1996). (g) A serpentine dinosaur coprolite displaying conifer twigs (arrows), from the Upper Cretaceous (Maastrichtian) of southern Saskatchewan, Canada (Nambudiri & Binda 1989). (h) An upper molar of the rodent *Thalerimys headonensis*, a herbivorous browser, from the Eocene of southern England (Collinson &

Hooker 1991). Note the broad shelf for seed grinding. (i) The rodent *Treposciurus mutabilis*, from the Late Eocene (Priabonian) of England, with sub-parallel microwear scratches and pits on upper deciduous molars, suggesting the consumption of indurated food (Collinson & Hooker 1991). (j) Coprolite of the extinct folivorous moa-nalo, *Thambetochen chauliodous* (Anatidae), from the Holocene of Maui, Hawaii (James & Burney 1997). (k) A monolet fern spore from a coprolite similar to (j); ferns were a major component of the diet of *Thambetochen* (Burney 1997). (l) A heap of coprolites from the extinct goat-like bovid *Myotragus balearicus*, in a Holocene cave from the Balearic Islands, Spain (Alcover et al. 1999). (m) Pollen of *Buxus balearica* (Buxaceae) isolated from coprolites of *Myotragus balearicus* in (l), the major dietary constituent. See Fig. 2.7 for scale-bar conventions.

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