THE ROLE OF INSECTS IN LATE JURASSIC TO MIDDLE CRETACEOUS ECOSYSTEMS

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ABSTRACT: The relationships between insects and other organisms in the Late Jurasic to Middle Cretaceous ecosystems is documented in the fossil record by generalized to highly host-specific vascular plant and insect associations, and to a much lesser extent by plant–fungal–insect and tetrapod–insect associations. Vascular plant and insect associations are essentialy modern during this interval, and consist of external foliage feeding, leaf mining, galling, wood boring, piercing-and-sucking, sporivory and pollinivory, nectarivory, and pollination syndromes. Late Jurassic versions of all these interactions occurred on a diverse repertoire of major gymnospermous plant clades (angiosperms excepted) whereas by the end of the Middle Cretaceous most of these interactions had been transferred onto angiosperms either by descent from gymnospermous ancestors or by direct host transfer. Examples of these host-plant shifts include generalized external foliage feeding, probable host-specific leaf mining, galling, pollinivory, and nectarivory. While most of these associations did not persist to the present, there is evidence that relict, primitive insect lineages survived as intimate herbivores today on host-plant taxa with Late Jurasic to Middle Cretaceous ancestors, notably cycads and primitive dicotyledonous angiosperms.

INTRODUCTION

Terrestrial ecosystems underwent a dramatic transformation during the interval encompassing the Late Jurassic to the Middle Cretaceous. Foremost among this change was the turnover, at the highest taxonomic levels, of plant clades, so that, by the end of the Middle Cretaceous, at 88 Ma, angiosperms had largely replaced other major clades of vascular plants, with the principal exceptions of cool-temperate coniferous forests and local sites rich in ferns or gymnospermous plants (Parker, 1976; Wing et al., 1993). By the end of the Cretaceous, mid–Mesozoic clades such as bennettitaleans, cheirolepidaceous conifers, and several lineages of seed ferns were extinct, and others that have extant representatives, such as gingkoaleans, gnetaleans and cycads, survived at decreased levels of diversity. This shift in ecosystem composition also characterized major tetrapod lineages, notably dinosaurs, in which a Late Jurassic fauna dominant in large sauropods, basal theropod clades, and ornithischian stegosaurids gave way to a Lower Cretaceous fauna of few sauropods, and considerably more ornithischians such as ornithopods (e.g., hypsilophodontids and iguanodontids). Later during the Cretaceous, advanced carnivorous theropods, a plethora of ornithischian groups—especially ceratopsians, hadrosaurs and pachycephalosaurs—diversified and dominated the terrestrial megafauna. This taxonomic shift was perhaps induced by an angiosperm-dominated flora, indicated by dental specialization.

Unlike the important turnover in major plant and tetrapod taxa during this interval, and the drastic pattern of extinction affecting many groups at the terminal Cretaceous, insects had a considerably subtler pattern. Major clades of modern insects (orders to superfamilies) mostly originated during the Triassic, or less commonly were holdovers from the Permian that have persisted to the present, irrespective of major shifts in vascular plant and tetrapod taxonomic composition. The probable exceptions of Mantodea (mantids) and Isoptera (termites) are noteworthy, both which many now consider as subgroups of cockroaches (Grimaldi, 1997; Klass, 1997, 1998; but see Kambhampati, 1996). Unfortunately ecto- and endoparasitic groups such as the Phthiraptera (lice), Strepsiptera (stylopids) and Siphonaptera (fleas) have very poor fossil records and are not known for certain in pre-Cenozoic deposits (Traub, 1980; Kim, 1988; Kathirithamby and Grimaldi, 1993; Poinar, 1995). Nevertheless, many modern insect families originated during the Mesozoic (Labandeira, 1994), although some recent studies indicate that this pattern does not extend to infrafamilial taxa, such as subfamilies and tribes, many Mesozoic examples of which are apparently extinct. (However, see Lawrence [1995] and Rasnitsyn [1997] for examples of recently discovered modern taxa previously known only as extinct fossils).

It is fortunate that, in addition to the insect body-fossil record, there are parallel data of trace fossils—especially vascular plant-and-insect associations, but also rare insect-and-tetrapod interactions. These associational data document the often intricate ecological relationships between insects and vascular plants and less commonly insects and tetrapods. Although limited to well-preserved deposits and spotty in temporal distribution, such data provide a unique glimpse into the minor components of ecosystem structure that is rarely available by more indirect means, such as recent analogs or functional analysis of organismic structures. The scope of such associational data includes plant damage, insect gut contents, floral features tied to insect use, insect mouthpart structure and patterns of hair and setae distribution (vestiture), and special insect structures that accommodate plant products, such as antennal scrobes and leg corbiculae for housing fungal spores and pollen, respectively (Labandeira, 1997, 1998b). These data will be emphasized in this contribution, rather than a descriptive narrative portraying the succession of Late Jurassic to Middle Cretaceous insect faunas. The fundamental, albeit overly ambitious, questions addressed herein is "What were the effects between insects and other organisms during this interval?" and "How did these roles

contribute to the evolving structure of Mesozoic ecosystems?"

THE RELEVANT FOSSIL RECORDS

A perusal of the relevant literature on the associations of fossil insects with other organisms reveals that, like the amount of biomass participating in trophic levels within terrestrial ecosystems, the further the trophic distance from primary production, the less the documentation. Thus, Figure 1 has four times more literature sources and considerably more reliable data on vascular plant–insect associations than it does for insect–tetrapod associations. Because vascular plants are a relatively ubiquitous part of the terrestrial fossil record in terms of frequency of occurrence and abundance, they provide a desirable opportunity for scrutinizing insect interactions during long stretches of geologic time. By contrast, the vertebrate fossil record is significantly more degraded and provides a weak signal for associations with insects. Historically adding to this de-emphasis has been lack of documentation by vertebrate paleobiologists of premortem or postmortem insect damage to bone tissue.

Vascular Plants

Late Jurassic floras are dominated by gymnospermous seed plants, and to a lesser degree pteridiphytes. Some of the best described Late Jurassic plant assemblages are of Kimmeridgian age, from the French Jura Mountains (Barale, 1981) and the lacustrine shales at Karatau, in southeasern Kazakstan (Doludenko and Orlovskaya, 1976). The French material, consistent with a marginal marine lagoonal setting, consists of diverse cycads, bennettitaleans, conifers and ferns, and rare gingkoaleans; the Kazakstani material is dominated by bennettitaleans and conifers, contains subdominant cycads and gingkoaleans, and rare czekanowskialeans. The paucity of well-described Jurassic floras in North America is striking; one of the best documented is the Late Oxfordian to Early Kimmeridgian Monte de Oro flora of north-central California (Vakhrameev, 1988), characterized by mostly cycads and subdominant bennettitaleans and ferns. The vegetation of the Tithonian Morrison Flora from the Rocky Mountains has been reconstructed as widely scattered conifers and more closely-spaced bennettitaleans occurring among cycads and ferns, and rare caytonialean seed ferns and gingkoaleans (Miller, 1987). By contrast, a probable Late Jurassic Nipania Flora from India consists dominantly of pentoxylaleans and conifers, with rare ferns, and notably, bennettitaleans are "conspicuous" by their near absence (Shah, 1977).

Early Cretaceous (Neocomian) macrofloras are almost entirely dominated by gymnospermous and pteridiphyllous plants, although angiospermous pollen is known in paleoequatorial regions at the end of this interval (Brenner, 1976). Angiosperm pollen assemblages, eventually including macrofloral remains, gradually expand poleward throughout the later Early and Middle Cretaceous (Retallack and Dilcher, 1981; Lidgard and Crane, 1990; Drinnan and Crane, 1990). However, most Early Cretaceous floras lack angiosperms—even those as stratigraphically high as the upper Aptian Kootenai Flora of Montana, which was dominated by ferns, caytonialean seed ferns and conifers, with rare Gingko and bennettitaleans. The Koonwarra flora of Australia, of similar age, contains only one angiosperm pollen species out of 62 known taxa (Dettman, 1986),

and one of the earliest known angiosperms has been described as an inflorescence from this deposit (Taylor and Hickey, 1990). Typical of the worldwide floristic heterogeneity of the Early Cretaceous is the well-known Weald Flora of Britain, reconstructed by Batten (1974) and Oldham (1976) as savanna-like vegetation with open forest containing relatively tall conifers and gingkoaleans and arborescent seed ferns of lower-stature, all interspersed among a pteridophyte ground layer.

During the early Albian, angiosperm macrofossils entered the fossil record in some equatorial floras, initially as small-leafed morphs with irregular venation, representing weedy herbaceous or shrubby vegetation (Vakhrameev, 1964; Hickey and Doyle, 1977). During the middle to late Albian, additional large-leafed angiosperms with more ordered venation became more abundant, representing a variety of growth forms in disturbed habitats of riparian communities. By early Cenomanian time, lowland sites were dominated by diverse magnoliid, hamamelid, rosid and other angiosperms (Crabtree, 1987; Lidgard and Crane, 1990), at least in the Northern Hemisphere. The poleward migration of angiosperms from the equator to mid- and high-latitude floras took approximately 20 to 30 million years (Wing and Sues, 1992). The best studied early Middle Cretaceous flora is the Dakota Flora, best preserved in Kansas and Nebraska, collectively consisting of at least 400 species of vascular plants (Dilcher, pers. comm.), including herbs, shrubs and trees.

Tetrapods

Because the focus of this volume is predominantly on the Early and Middle Cretaceous vertebrate assemblages, only brief mention will be made of the Late Jurassic to Middle Cretaceous tetrapod succession. During the Late Jurassic, tetrapod faunas were dominated by gigantic, long-necked sauropods and primitive ornithischians, mostly herbivorous stegosaurs, bipedal camptosaurs and hypsilophodonts, and reptiles such as turtles, sphenodontians and lizards. Some of the earliest lineages of birds and mammals are known from this interval. During the Early Cretaceous, tetrapod faunas became differentiated between the northern and southern hemispheres (Bonaparte, 1990). In the Northern Hemisphere, Late Jurassic assemblages were replaced by ankylosaurs, larger-bodied ornithopods with complex dentition (especially hadrosaurs), the earliest ceratopsians, sphenodontian lepidosaurs, multituberculate mammals, and an early radiation of bird lineages. By contrast, Early Cretaceous assemblages of the Southern Hemisphere contained holdovers such as gigantic sauropods, many endemic taxa, and a rarity of hadrosaurid ornithopods and placental mammals (Bonaparte, 1987; Wing and Sues, 1992). Middle Cretaceous tetrapod faunas were characterized by more diverse and dentally specialized ornithischians and theropods.

Insects

In the context of a Phanerozoic geochronology and a modern taxonomic framework, Late Jurassic to Middle Cretaceous insects have a modern cast. The most profound event during the 400 million year fossil record of insects was the end-Permian extinction and associated earlier Permian replacements, during which there was major taxonomic turnover in insect diversity, and after which was a steep drop in the origination of orders and the commencement of post-Paleozoic family-level originations that constitute the principal insect taxa recognized today

(Labandeira and Sepkoski, 1993; Jarzembowski and Ross, 1996). Thus, the Paleozoic insect fauna is distinct from the post-Paleozoic modern insect fauna at the highest taxonomic levels (Labandeira, 1999b), and those Paleozoic taxa that survived the end-Permian event became a relatively minor component of the modern insect fauna. Of these, three families of the Paleozoic orders Miomoptera and Glosselytrodea survive into the Early Jurassic, one of which, the Polycytellidae, into the Late Jurassic (Labandeira, 1994). The Geraridae of the polyphyletic "Protorthoptera" is recorded in the Middle Triassic, and the paraphyletic stem-groups "Hypoperlida" and "Paratrichoptera" have single families extending into the Middle Triassic and Early Cretaceous, respectively (Labandeira, 1994). The Blattodea sensu Grimaldi (1997) comprises a related assemblage of taxa, including roaches (Blattoidea), termites (Isoptera) and mantids (Mantodea), whose fossil record historically has been difficult to interpret, because pre-Cretaceous roaches bear prominent ovipositors (Vishniakova, 1973), whereas Cretaceous to Recent roaches lack them and deposit eggs in cases known as oöthecae. Related to this issue is the absence of termites and mantids in pre-Cretaceous deposits (but see Hasiotis and Demko, 1996). Although the extension of three Paleozoic-aspect cockroach families into the Late Jurassic to Late Cretaceous suggests prolonged evolutionary stasis, the absence of any oöthecate cockroaches, mantids or termites in pre-Cretaceous deposits indicate that a radiation of these taxa probably occurred during the Late Jurassic.

The insect body-fossil record is relatively rich during the Late Jurassic to Middle Cretaceous (Fig. 1), and is comparable to the coeval vascular plant record and superior to the vertebrate record in abundance and frequency in occurrence of taxa. Insect-yielding deposits during this time interval typically consist either of compressions and impressions occurring as lacustrine fluvial, deltaic, and lagoonal fine-grained, laminated shales and limestones bordering lowland water bodies (Zherikhin, 1978; Sinichenkova and Zherikhin, 1996), or as placer or in situ amber deposits representing woodland and forest environments (Schlee and Glockner, 1978; Grimaldi, 1996). However, these two distinctive and major taphonomic modes are not distributed evenly during this interval (Fig. 1): while fine-grained clastic deposits are globally widespread and abundant, occurring throughout this 70-million-year interval, amber deposits are confined to approximately six well-known deposits in the upper 45-million-year portion of this interval, and essentially sample forested habitats of the Northern Hemisphere. One taphonomically distinctive deposit type that has a geochronologic window occurrence that corresponds almost exactly to the Late Jurassic to Middle Cretaceous are lithographic limestones (Labandeira, 1999a). Lithographic limestones represent lagoonal environments of quiet and brackish water marginal to marine deposits, and include major Lagerstätten such as the Solnhofen Formation of southern Germany (Barthel et al., 1994), Santana Formation of Ceará, northeastern Brazil (Grimaldi, 1990; Maisey, 1991), and the Caliza con Caracéas Formation of northeastern Spain (Martínez-Delclís, 1991a). Notably, these and other major Late Jurassic to Middle Cretaceous deposits—including the Yixian Formation of Liaoning, northeastern China (Ren et al., 1995), Korumburra Group of Victoria, southeastern Australia (Jell and Duncan, 1986), several adjacent localities from southwestern Mongolia (Rasnitsyn, 1986), and the Zaza Formation at Baisa, in Transbaikalian Russia (Rasnitsyn, 1990)—have been explored intensively during the past two decades, resulting in major

increases in understanding of global insect paleobiology. Additionally, there has been continued description of taxa from earlier known deposits such as Karatau in southern Kazakstan, and Magadan in central Russia.

Several major phylogenetic events of insects had a major impact on Late Jurassic to Middle Cretaceous ecosystems and shaped the taxonomic character of the global insect fauna that persists today. These events can be encapsulated by four major radiations transpiring during the Middle to late Jurassic, and another four radiations occurring during the Late Jurassic to Early Cretaceous. The earlier Jurassic events are: (1) the expansion of hemipteran bugs into lotic and lentic aquatic habitats (Popov, 1971), a radiation that postdated the earlier invasion of freshwater by nematocerous Diptera (Wootton, 1988; Labandeira, 1997); (2) the diversification of cucujoid beetle groups, notably plant-feeding chrysomeloid and curculionoid lineages onto gymnospermous plants (Crowson, 1991; Ponomarenko, 1995; Farrell, 1998); (3) the basal radiation of brachycerous fly clades, some of which developed pollination mutualisms, initially with gymnosperms (Labandeira, 1998a), and subsequently on early angiosperms (Dilcher, 1996, but see Ren, 1998a); and (4) the proliferation of parasitoid apocritan wasp clades (Rasnitsyn, 1988a), resulting in taxa that invaded live insect and tetrapod hosts as larvae, and adults that probably were nectar-feeders and assisted the pollination of seed plants and later angiosperms (Hespenheide, 1985; Jervis, et al., 1993).

During the Late Jurassic to Early Cretaceous, there was further co-optation of seed plants in several respects, probably including angiosperms during the later phases of this interval. The previously mentioned radiation of blattodean clades (5) probably resulted in the first example of insect sociality, in termites, and a co-ordinate major invasive of xylic substrates (Wilson, 1971), a phenomenon that was soon followed by the advent of bees (6) which evidently were derived from sphecoid wasps (Brothers, 1975) and subsequently became intimately involved as pollinators of angiosperms; (7) the radiation of major lepidopteran subgroups, involved overwhelmingly in endophytic consumption of gymnospermous and angiospermous seed plants (Thien et al., 1985; Labandeira et al., 1994; Davis, 1994); and finally (8) the multiplication of cyclorrhaphan fly lineages from a brachyceran ancestor (Sinclair, 1994), resulting in penetration of live and dead vertebrate hosts, and the occupation of moist habitats involving decomposing plant and fungal detritus (Oldroyd, 1964). After the conclusion of these important insect radiations sometime during the Middle Cretaceous, the major, insect-related features were essentially established (Jarzembowski, 1995; Labandeira, 1997), with the possible exception of derived modes of insect pollination of angiosperms, which progressed during the Late Cretaceous and Paleogene with the appearance of specialized flowers (Willemstein, 1987; Crepet and Friis, 1997).

ASSOCIATIONS OF INSECTS WITH OTHER ORGANISMS

Much of the paleoecology of insects and other organisms is revealed in the trace-fossil record of insect-mediated damage, both as tissue response to invasive trauma when the host was alive, as well as detritivorous patterns of tissue consumption after death. While the Late Jurassic to Middle Cretaceous fossil record of vascular plant–insect and insect–tetrapod associations is not as bountiful as either the Late Carboniferous or Paleogene intervals (Labandeira, 1999b), there is, nevertheless, sufficient primary evidence for documenting major interactions between insect

culprits and their plant targets (Figs. 1–4). Presently, only a tentative glimpse of associations between insects and their tetrapod hosts is available, primarily ectoparasitism and blood-feeding. Lastly, there are implications in a few of these interactions for the role that fungi played in the mediation of plant decomposition by insects.

Plant–Insect Associations

Insects collectively consume virtually any nutritionally rewarding substance, and nowhere is their dietary repertoire more manifest than in their myriad associations with plants. Most herbivorous insect species on extant vascular plants are mono- or oligophagous (Futuyma and Mitter, 1996), and many of those consume only a particular tissue type, such as the abaxial palisade layer by a leaf-mining moth larva or the consumption by an encapsulated gall midge larva of nutritive tissue that is produced by its host plant (Hering, 1951; Meyer, 1987). These and other interactions, such as external foliage feeding, leave distinctive, often highly stereotyped, patterns of damage on plant organs—features of which are eminently preservable in the fossil plant record (Figs. 2–3). The most useful classification of these damage types is the functional-feeding-group approach, which specifies how the damage was created. Typically encountered

FIGURE 1. Distribution of major insect deposits and associations between insects and plants and insects and reptiles during the Late Jurassic to Middle Cretaceous. Included are deposits and associations resolvable more-or-less to the stage-level placement, and their geochronological positions are approximate in many cases. Insect deposits are designated as striped bars for compressions and as gray bars for amber. Taxal ranges in the center and right panels are solid for well-established occurrences and dotted for unconfirmed data; similarly solid dots represent direct evidence for an association whereas unfilled dots represent indirect evidence. Geochronology is from Harland et al. (1990); taxa are from Cleal (1993a, 1993b) for plants and Benton (1993) for reptiles.

Major insect deposits. Documentation and sources for major insect deposits are: 1, amber from the Raritan-Magothy Fm., Sayreville, New Jersey, USA (Grimaldi et al., 1989); 2, Beleytinskaya Fm., Kizyl Zhar, Kazakhstan (Kozlov, 1988); 3, amber from the Dolganskaya Fm., Agapa, Krasnoyarsk Oblast, Russia (Kalugina, 1992; Szadziewski, 1996); 4, unnamed mudstones at Orapa, Botswana (Rayner, 1993); 5, Steinkohle Fm., Jihocesky Region, Czech Republic (Fritsch, 1882; Fric, 1901); 6, amber from Durtal and Bezonnais, Maine-et-Loire Dept., France (Schlüter, 1978); 7, Olskaya Fm., Magadan, Russia (Zherikin, 1978); 8, Dakota Fm., Kansas and Nebraska, USA (Upchurch and Dilcher, 1990; Labandeira et al., 1994); 9, Khetana, northeastern Russia (Ponomarenko, 1995); 10, Dalzai Fm., Jilin Prov., China (Lin, 1994); 11, Mogotuinsk Fm., Manlay, Omnogovy Region, Mongolia (Kalugina et al., 1980); 12, Crato Fm., Ceará State, Brazil (Grimaldi, 1990; Maisey, 1991); 13, Glushkovo Fm., Unda and Daia, Chita Prov., Russia (Kovalev and Mostovski, 1997); 14, Koonwarra Bed, Leongnatha, Victoria Prov., Australia (Jell and Duncan, 1986); 15, Khurlit Fm., Bon Tsagan, Bayan-Khongor Aimak, Mongolia (Rasnitsyn, 1991); 16, amber from Chosi, Chiba Prefect., Japan (Fujiyama, 1994); 17, Gurvan-Eren Fm., Bulgan Aimak, Mongolia (Rasnitsyn, 1988b); 18, Turga Fm., Semen, Chita Region, Russia (Eskov and Zonshtein, 1990); 19, amber from Golling, Austria (Borkent, 1997a); 20, Upper Weald Clay, Surrey, Britain (Jarzembowski, 1991); 21, Laiyang Fm., Shandong Province, China (Lin, 1994); 22, Calizas de la Huérguina, Las Hoyas, Cuenca, Spain (Martínez-Delclís and Nel, 1994); 23, Lower Weald Clay, Sussex, Britain (Jarzembowski, 1991); 24, amber from Jezzine and Dar-el-Baidha, Lebanon (Schlee and Dietrich, 1970); 25, Vinkinskaya Fm., Bolboia and Urtuya, Priarguisk Region, Russia (Rasnitsyn, 1990); 26, Zaza Fm., Baisa, Buryat Prov., Russia (Rasnitsyn, 1986); 27, Schouchang Fm., Zhejiang, China (Lin, 1994); 28, Waldhurst Clay, Britain (Jarzembowski, 1990); 29, Caliza con Caracéas Fm., Montsec, Lleida Prov., Spain (Martínez-Delclís, 1991a, 1991b); 30, Purbeck Beds, Dorset, England (Allen and Wimbledon, 1991); 31, Khotont, Ara-Khangai Aimak Mongolia (Lukashevich, 1996); 32, Ulan-Ereg Fm., Khoutin, Central Gobi Aimak, Mongolia (Ponomarenko, 1997); 33, Yixian Fm., Liaoning Prov., China (Ren et al., 1995); 34, Dabeagou Fm., Hebei Prov., China (Lin, 1994); 35, Solnhofen Plattenkalk, Bavaria, Germany (Lambkin, 1994); 36, Todlito Fm., Warm Springs, New Mexico (Bradbury and Kirkland, 1968); 37, Nusplinger Plattenkalk, Westerberg, Germany (Schwiegert et al., 1996); 38, Karabastau Fm., Karatau, Chiment Oblast, Kazakhstan (Rohdendorf, 1968a); 39, Udinskaya Fm., Mogzon, Chitinskaya Oblast, Russia (Kalugina and Kovalev, 1985). See also Rohdendorf (1957) Zherikhin (1978), Kalugina and Kovalev (1985), Rasnitsyn (1990) and Lin (1994) for additional Eurasian locality information.

Plants. Occurrences of insect associations on major vascular plant clades from the Late Jurassic to the Middle Cretaceous interval, documented from the literature. Sources for insect-plant associations are: A, external feeding on fern foliage (Labandeira and Dilcher, 1993); B, stem borings in the fern Tempskya (Seward, 1924); C, coprolites with fern spores (Kampmann, 1983); D, nepticuloid leaf-mines on Pachypteris (Rozefelds, 1988); E, stem borings on Hermanophyton (Tidwell and Ash, 1990); F, inferred life-habit attributes of fossil chrysomelid and curculionoid beetles consistent with associations in co-occurring cycads (Crowson, 1991; Ponomarenko, 1995); G excavated galleries with frass within cones of Cycadeoidea (Delevoryas, 1968; Crepet, 1974); H, bennettitalean pollen (Vitimipollis) in the gut of a xyelid sawfly (Krassilov and Rasnitsyn, 1983); I, probable insect removal of the ovuliferous layer within the receptacle of a Williamsonia cone (Bose, 1968; Crowson, 1991); J, mouthpart structure of several brachyceran fly taxa consistent with nectaring on co-occurring gnetaleans (Nartshuk, 1996; Labandeira, 1998a; but see Ren, 1998a); K, earlier brachyceran flies with mouthpart structure consistent with nectaring on gnetaleans (Rohdendorf, 1968; Labandeira, 1997, 1998a); L, lepidopteran mines of Nepticulidae on Platanaceae, Cercidiphyllaceae and Trochodendraceae (Kozlov, 1989; Donner and Wilkinson, 1989); M, co-occurrence of insects bearing elongate mouthparts and probable pollen-laden vestiture with funnel-shaped flowers (Rayner, 1991, 1993); N, leaf mines on various dicots (Fritsch, 1882; Fric, 1901); O, lepidopteran mines of Nepticulidae and Gracillariidae on magnoliid and hamamelid dicots (Labandeira et al., 1994); P, foliar gall on "Sassafras" (Hickey and Doyle, 1977); Q, foliar gall on Pabiana (Upchurch et al., 1994); R, winteraceous pollen (Afropollis) in the gut of an xyelid sawfly (Caldas et al., 1989); S, caddisfly case constructed from Karkenia seeds (Krassilov and Sukacheva, 1979); T, probable stylet punctures on the cuticle of Pseudofrenelopsis (Watson, 1977); U, the nemonychid weevil Libanorhinus associated with co-occurring Araucariaceae, based on life-habits of extant descendants (Kuschel and Poinar, 1993); V, conifer pollen (Alisporites, Pinuspollenites) in the gut of a xyelid sawfly (Krassilov and Rasnitsyn, 1983); W, wood boring of a bark beetle on conifer wood (Jarzembowski, 1990); X, Classopollis conifer pollen in the gut of the hagloid orthopteran Aboilus (Krassilov et al., 1997a, 1997b); Y, borings in female cones of Araucaria (Stockey, 1978; Crowson, 1991; Farrell, 1998), although geochronologic placement is uncertain. See Figures 2 and 3 for additional details.

Reptiles. Occurrences of insect associations on principal terrestrial reptile clades from the Late Jurassic to Middle Cretaceous interval, documented from the literature. Sources for insect-reptile associations are: A, the unassigned insect Saurophthirodes presumably an ectoparasite on pterosaurs (Ponomarenko, 1986); B, the unassigned insect Saurophthirus presumably also an ectoparasite on pterosaurs (Ponomarenko, 1976); C, insect (?dermestid) borings in sauropod and theropod bones (Laws, 1996; Hasiotis and Fiorillo, 1997); D, biting midge (ceratopogonid) feeding on hadrosaur (?Corythosaurus) blood, based on mouthpart structure of fossils and extant descendants (Borkent, 1995); E, black fly (simuliid) feeding on probable ornithischian, based on mouthpart structure (Kalugina, 1992). See Figure 4 for additional documentation.

insect functional feeding groups in the fossil record are external foliage feeding, leaf mining, and galling—sporivory/pollinivory and piercing-and-sucking are much less encountered.

External Foliage Feeding

External foliage feeding is the consumption of live leaf tissue from without, and is typically indicated by dark, thickened callus tissue rimming the excised margin of a leaf. External foliage feeding is a broad category that includes margin feeding, or consumption along the margin of a leaf, regardless of the tortuosity of the feeding trace; hole feeding, consisting of tissue removal surrounded on all sides by callus tissue; skeletonization, or the consumption of softer interveinal tissue, leaving a meshwork of vascular tissue; surface abrasion, in which one or more layers of foliar tissue are removed, leaving at least one lamina intact; free feeding, characterized by consumption of almost the entire blade, with only primary venation and possibly a few flaps of mesophyll tissue remaining; and bud-feeding, a specialized type whereby an insect "tunnels" through a leaf bud,

leaving a stark and repetitive sequence of "shot-holes" in the furled, mature leaf or frond (Coulson and Witter, 1984). Frequently it is difficult to differentiate skeletonization from surface abrasion, and comparison to the surrounding sediment matrix may resolve the differences.

External foliage feeding extends minimally to the Late Carboniferous (Scott and Taylor, 1983; Chaloner et al., 1991; Labandeira, 1998b) and possibly to the Early Devonian (Kevan et al., 1975). All subtypes of external foliage feeding except for bud-feeding are documented from an Early Permian flora in north-central Texas (Beck and Labandeira, 1999). The foliage of early Mesozoic plants such as ferns, cycadophytes and seed-ferns were also attacked by external feeders (Grauvogel-Stamm and Kelber, 1996; Ash, 1997), although there has been no quantification of these data. Little is known of external foliage feeding for Late Jurassic or Early Cretaceous floras, but floras such as the Cenomanian Dakota flora of the central United States (Labandeira et al., 1994) (Fig. 3A–C) and the Turonian Beleutinskaya Formation of Kizyl-Djar, Kazakstan (Kozlov, 1988) were heavily attacked.
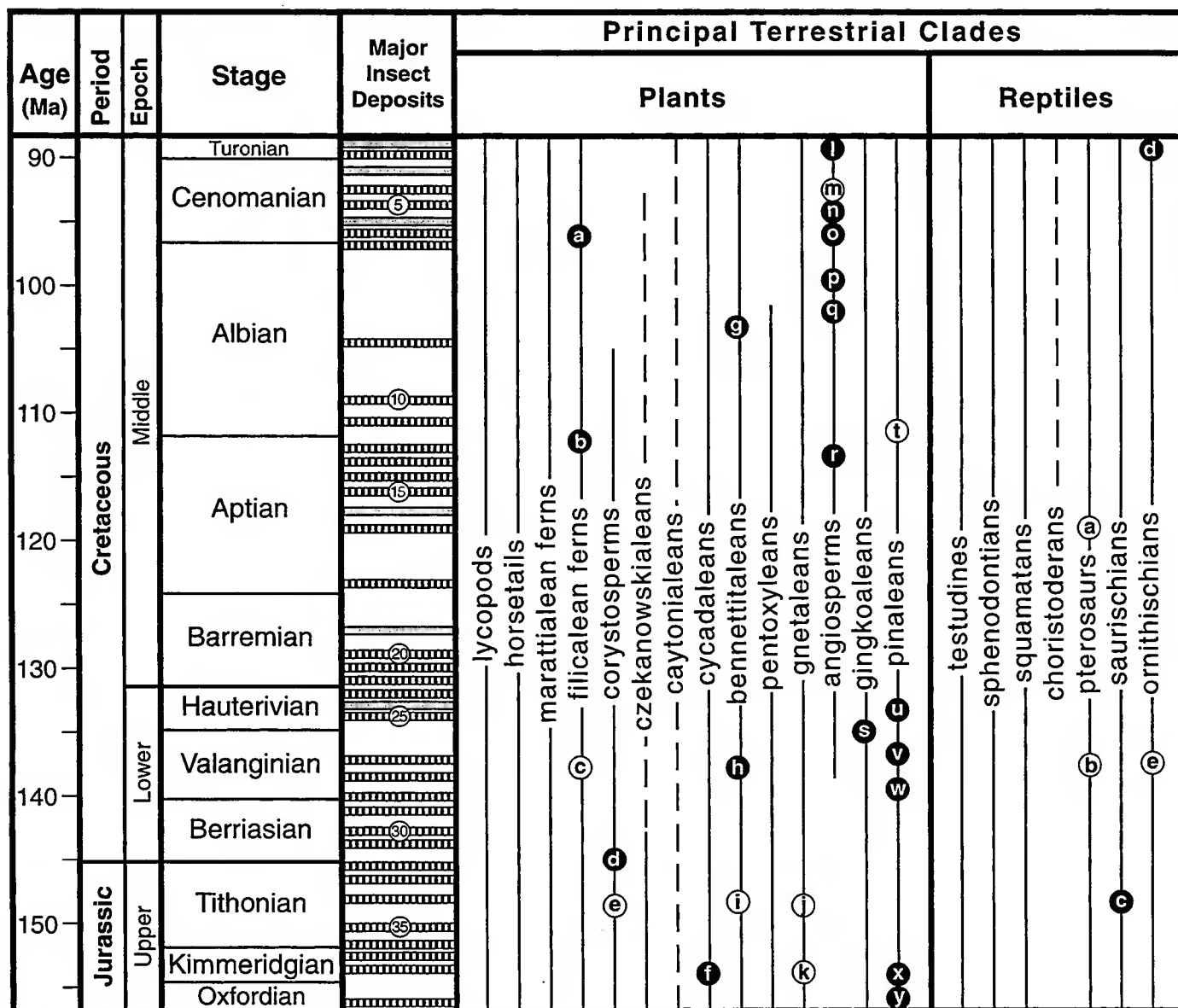
Leaf Mining

Leaf mining is the extraction of live, internal, foliar tissue by holometabolous larvae (Hering, 1951), or possibly certain mites (Fernandez and Athias-Binche, 1986). Leaf miners typically lack access to the external environment until emergence at the end of the larval or pupal stage. Patterns of tissue consumption by leaf miners are frequently highly stereotyped, especially in terms of oviposition site, mine width, two-dimensional trajectory of the mine, nature of the frass trail, and disposition of frass in the terminal chamber (Needham et al., 1928; Hering, 1951). Leaf mines of holometabolous insects are produced only by larvae of moths (Lepidoptera), flies (Diptera), sawflies (Hymenoptera) and beetles (Coleoptera), and either are linear and serpentine, frequently undulatory or irregular in progression, or they are ovate or multilobate blotches. All leaf mines evidently are constrained to some extent by primary and often secondary leaf venation. Because of the pronounced plant host specificity of modern leaf-mining taxa, knowledge of the host spectrum of modern leaf miners is helpful in the identification of Cenozoic leaf-mines, and can be of use in identifying basal leaf-mining taxa on basal angiosperm taxa for Middle and Late Cretaceous floras (Kozlov, 1988; Labandeira et al., 1994; Davis, 1994).

Leaf mining is the only major functional feeding group without convincing representation in the Paleozoic, although certain damage to Pennsylvanian and Early Permian *Macroneuropteris* seed-fern foliage is suggestive (Müller, 1982; Labandeira and Beall, 1990). The earliest documented evidence is on the Late Triassic broadleaved conifer *Hediphyllum* (Rozefelds and Sobbe, 1987), consisting of high-sinuosity, small-diameter traces that may have been produced by beetle larvae. Known preangiospermous leaf mines are very rare; in addition to the Triassic example, Skalski (1979) mentioned but did not illustrate mines on seed-fern foliage from the Late Jurassic Karatau flora of Kazakstan, and Rozefelds (1988) figured and described mines that he referred to the lower lepidopteran clade, Nepticuloidea, on the corystosperm seed fern *Pachypteris* (Fig. 2A), a conclusion bolstered by specialist opinion. Modern Nepticulidae mine primitive and advanced dicotyledonous angiosperms. If Rozefelds's identification is secure, and barring the occurrence of Late Jurassic angiosperms, these important specimens imply that the radiation of the Lepidoptera occurred endophytically on seed ferns, not on angiosperms. Accordingly, nepticuloids subsequently became miners on angiosperms either through a corystosperm to angiosperm line of descent, or by lateral host-switching later during the Early Cretaceous. Certainly by earliest Cenomanian times, several leaf-mine morphotypes were present, including the monotrysian Nepticulidae and the ditrysian Gracillariidae, established on multiple lineages of magnoliid, rosid and hamamelid dicots (Fig. 4D–E), exhibiting considerable host specificity (Labandeira et al., 1994). The expansion of leaf-mining taxa on a broad spectrum of host-plant taxa continued throughout the Cretaceous, and includes mines on additional hamamelids of the families Trochodendraceae, Cercidiphyllaceae (katsura tree) and Platanaceae (sycamores) as well as on rosid and dilleniid host taxa (Kozlov, 1988; Stephenson, 1992; Labandeira et al., 1995).

Galling

The formation of insect or mite galls starts with the invasion of plant tissue by either an egg inserted by an ovipositor or by subsequent burrowing into subdermal tissue by a newly emerged larva or nymph from a surface-deposited egg (Meyer, 1987). Once in contact with plant tissue, substances from the larva that mimic various plant-produced hormones locally induce anomalous tissue proliferation, resulting in formation of a gall. Gall formation typically includes an outer sclerenchymatous tissue to provide protection and support, and inner nutritive tissue as a source of rich food to the encapsulated, developing nymph or larva (Meyer, 1987). Galls thus are abnormal, three-dimensional expansions of proliferated plant tissue encapsulating one or more immature insects in a central chamber. They occur on particular organs and tissue types, and virtually all gallers possess high host specificity, many requiring a particular host species for successful development. Galls are classified according to their location on a plant, and include twig, petiole, leaf midrib, leaf lamina and floral types, although the most typically encountered as fossils are midrib and lamina galls of leaves. Three major terrestrial groups of arthropods are gallers on vascular plants: mites, which

FIGURE 2. Examples from the literature of insect associations with vascular plants from Late Jurassic to Middle Cretaceous ecosystems. A, Lepidopteran leaf mine (?Nepticulidae) on the corystosperm seed fern *Pachypteris*, from the Jurassic–Cretaceous boundary of Queensland, Australia (redrawn from Rozefelds, 1988). B, The surface-foraging termite *Meiatermes bertrani* (Lacasa and Martínez-Delclís, 1986) (Hodotermitidae), from the Berriasian of Spain (Martínez-Delclís and Martinell, 1995). C, Stylet or ovipositor marks on *Pseudofrenelopsis* cuticle and epidermis (Cheirolepidaceae), from the late Aptian to early Albian of Glen Rose, Texas (Watson, 1977). D, Borings, probably by beetles, in the stem of *Hermanophyton* (?Corystospermaceae), from the Tithonian of southwestern Colorado (Tidwell and Ash, 1990). E, The beetle ichnogenus *Paleoscolytus sussexensis* (Jarzembowski, 1990) within conifer cambium, from the Berriasian to Valanginian interval of England. F, Excavated galleries, undoubtedly by beetles, revealed in a longitudinal section of *Cycadeoidea* (Bennettitales), from Early Cretaceous of South Dakota (Delevoryas, 1968). White arrow indicates terminus of frass-containing tunnel. G, Probable beetle borings in the ovuliferous bracts of an *Araucaria* cone, from the Late Jurassic of Argentina (Stockey, 1978). White arrow at bottom indicates position of tunnels in bract tissue; black arrows at top indicate smaller and subdermally placed resin canals. H, Gallery with coprolites from oribatid mites in the stem of the fern *Tempskya*, from the Aptian to Albian transition of Montana (Seward, 1924). I, The hagloid orthopteran, *Aboilus*, with pollen-laden gut contents (indicated by arrow), from the Late Jurassic (Kimmeridgian) of Kazakhstan (Krassilov et al., 1997b). White arrow indicates position of food bolus that contains pollen. J, A *Classopollis* pollen grain, found in the gut of the orthopteran illustrated in (I) (Krassilov et al., 1997b). K, The xyelid sawfly *Ceroxyela*, with gut contents of gymnosperm pollen, from the Lower Cretaceous (?Valanginian) of Transbaikalia, Russia (Krassilov and Rasnitsyn, 1983). White arrow indicates position of pollen-containing food bolus. L, A conifer pollen grain of *Pinuspollenites*, from the intestine of an xyelid sawfly (Krassilov and Rasnitsyn, 1983). M, The eccoptarthrinid weevil *Jarzembowskia*—a probable feeder on gymnospermous reproductive structures, from the Berriasian of Spain (Zherikhin and Gratshev, 1997). N, A deep-throated, funneliform flower from the Cenomanian of Orapa, Botswana (Rayner, 1993). O, Elongate mouthparts of the cranefly, *Heleus*, a probable nectar-feeder, also from Orapa (Rayner, 1991). P, A pollinating nemestrinid fly, *Florinemestrinus* (Ren, 1998a, 1998b), from the probable Tithonian of China. Q, Detail of head and elongate mouthparts of *Florinemestrinus* shown in (P) (Ren, 1998a). Scale bars: solid = 1cm; striped = 0.1 cm; dotted = 0.01 cm; backslashed = 0.001 cm.
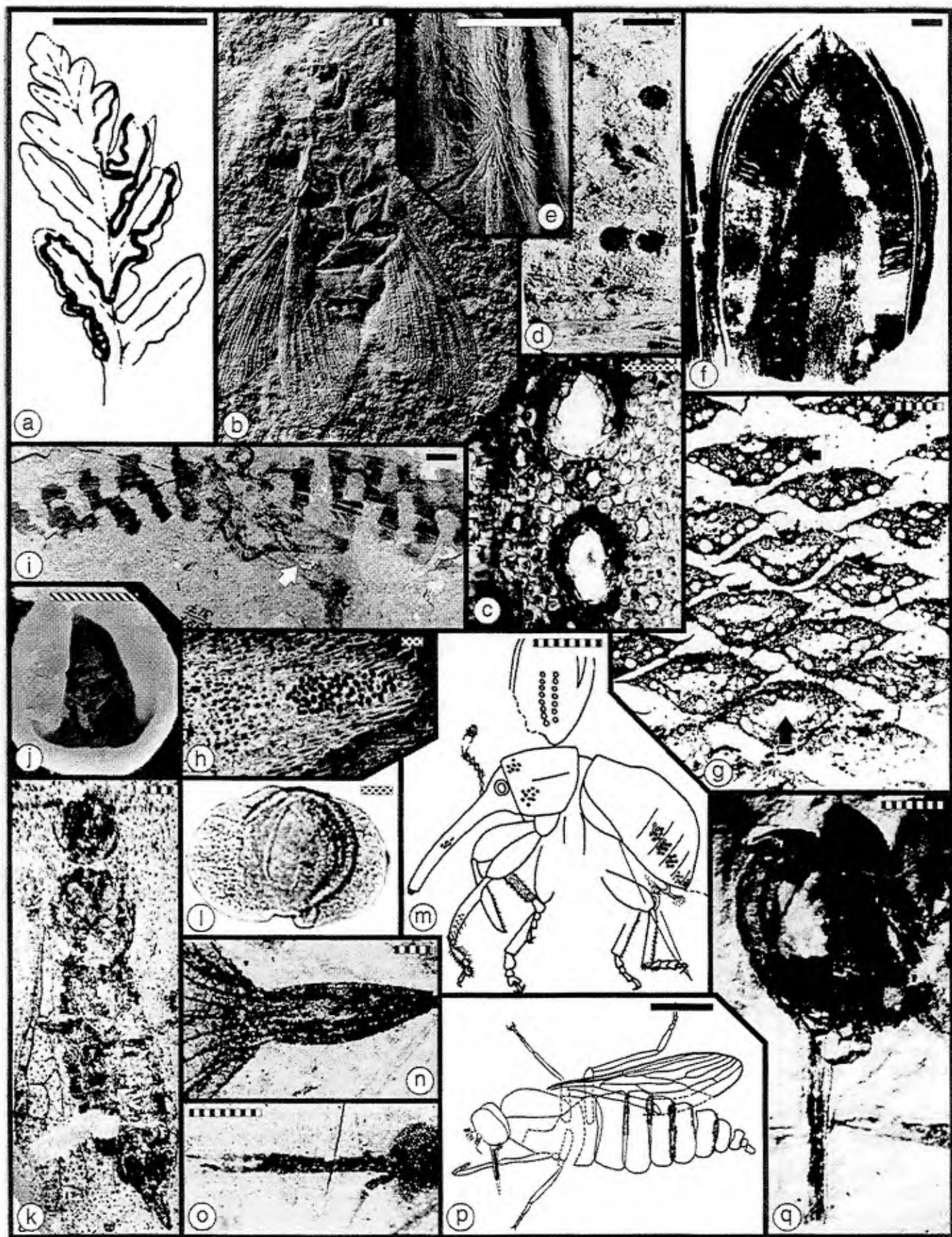
generally form smaller foliar galls (Jeppson et al., 1975); hemipteroid insects consisting of thrips (Ananthakrishnan, 1978) and certain hemipterans (Rohfritsch and Anthony, 1992); and holometabolous insects, of which the same four orders that mine leaves also gall vascular plants (Dreger-Jauffret and Shorthouse, 1992).

The earliest known certifiable galls of vascular plants are from permineralized tree-fern rhachises from the Upper Pennsylvanian of Illinois (Labandeira and Phillips, 1996b), although earlier unusual structures on sphenophyte compressions from Europe (Thomas, 1969) may also be galls (Van Amerom, 1973). Twig galls are well known on Late Triassic conifers from North America (Ash, 1997) and Europe (Grauvogel-Stamm and Kelber, 1996); leaf galls on the bennettitalean *Anomozamites* are known from the Bajocian Jurassic of Europe (Alvin et al., 1967). They are common on various angiosperms from the Cenomanian Dakota flora, especially platanoids (Fig. 4F–H) and lauraleans (Stephenson, 1992; Labandeira and Dilcher, 1993). Isolated foliar galls have also been illustrated for earlier Albian angiosperms (Hickey and Doyle, 1977; Upchurch et al., 1994) as well as post-Cenomanian Cretaceous floras (Fritsch, 1882; Fric, 1901; Stephenson, 1992; Larew, 1992; Scott et al., 1994). Both gall mites (Acari: Eriophyoidea) and gall midges (Diptera: Cecidomyiidae) are the probable causative agents of many of these galls; less clear is whether all gall-forming species, such as gall wasps (Hymenoptera: Cynipidae) or gallicolous weevils (Coleoptera: Curculionoidea) were responsible for these galls.

Wood Boring

Tunneling by arthropods into indurated tissues is one of the oldest feeding methods on land, with examples extending to the Early Pennsylvanian (Labandeira et al., 1997) for vascular plants, and to the Early Devonian for fungi (Arnold, 1952; Hotton et al., 1996). Boring into wood or other hardened tissues, such as seed sclerotesta, can be done while the host is alive (Solomon, 1995) or dead (Hickin, 1975). Typically, borings consist of an entry hole at the surface that connects with an internal network of tunnels and possibly galleries whose structure and three-dimensional geometry is more or less stereotyped. Depending on the taxon, certain tissues are targeted for consumption, such as cambium for bark beetles or secondary wood for horntails, often with the assistance of intestinal symbionts for degradation of lignin and cellulose. In fossils, damage to tissues is initially recognized by circular entry or exit holes; for gallery systems paralleling wood . grain, exposure of borings can be made by delamination of the bark, exposing the targetted cambial tissue. Most two-dimensional cambial borings are made by bark beetles (Scolytidae), bark weevils (Curculionidae) and agromyzid miners (Diptera: Agromyzidae). Three-dimensional borings into other tissues are produced by diverse taxa, including xyelid, siricid and tenthredinoid sawflies, anobiid, buprestid and cerambycid beetles, sesiid and cossid moths, agromyzid flies, as well as much smaller oribatid mites (Hickin, 1975; Solomon, 1995; Labandeira et al., 1997). Many of these tunnel systems are intricate and extensive, requiring creative use of a rock saw for exposure and reconstruction.

Although boring by oribatid mites on decomposing woods is an ancient habit, it has been documented principally for the Paleozoic and Recent (Labandeira et al., 1997); very little is known about this functional feeding group for Mesozoic and Cenozoic plants. An exception was illustrated by Seward (1924), although

he did not attribute the gallery system to any particular arthropod clade (Fig. 3H). Other borers of dead woody tissues are principally insects (Hickin, 1975). However, it is difficult to determine if the boring occurred while the plant host was alive or dead; occasionally evidence indicating that the plant host was alive is the presence of products of plant response to endophagy, including scar tissue and plugs in tunnels composed of resins, mucilage or other extracellular plant substances (e.g., Zhiyan and Bole, 1989). Alternatively, assignment of a stereotyped fossil tunnel-and-gallery system can be made to a modern taxon possessing high host specificity, although this method generally is not available to mid-Mesozoic borings. Published examples of fossil wood borings include Permian to Triassic glossopterid woods from South Africa and Germany (Linck, 1949; Zavada and Mentis, 1989; Goth and Wilde, 1992), several beetle taxa on Late Triassic araucarian wood (Walker, 1938; Hasiotis and Dubiel, 1993), possible deathwatch beetle galleries in unknown Early Jurassic wood from Germany (Jurasky, 1932), beetle borings in Middle Jurassic cupressaceous or taxodiaceous wood from China (Zhiyan and Bole, 1989), and cambium borings attributable to a scolytid (Jarzembowski, 1990) or curculionid (Stephenson, 1992) beetle in conifer wood from England (Fig. 2E). Other plant hosts with stem borings are a dipteridaceous fern from the Middle Jurassic of Antarctica (Yao et al., 1991) and borings on Late Jurassic *Hermanophyton* from Colorado (Fig. 2D), an enigmatic gymnospermous wood, perhaps similar to corystosperm seed ferns (Tidwell and Ash, 1990).

Piercing-and-Sucking

Piercing-and-sucking is a distinctive type of mite- or insect-mediated damage whereby stylets pierce host tissue either intra- or intercellularly to take up fluid food ranging in accessibility from subdermal mesophyll to deep-seated vascular tissue. The host plant responds to trauma resulting from endophytic consumption (although the consumer is located external to the plant) by producing callus or other reactive tissue which frequently is expressed on the affected surface by characteristic spotting, wilting or curling of leaves or by gnarling of adjacent tissue on twigs and stems. Detection of piercing-and-sucking damage in the fossil record requires either well-preserved, three-dimensionally permineralized material with resulting histological and cellular detail (Banks and Colthart, 1993; Labandeira and Phillips, 1996a) or two-dimensional preservation of cuticular surfaces, often as processed macerals, with retention of puncture holes and surrounding reaction rims (Watson, 1977; Fig. 2C). Surface puncture holes in even well-preserved compression material lacking cuticle are undetectable. However, it can be inferred by large-scale teratologies such as spotting and leaf curl, known to be induced by piercing-and sucking insects such as thrips (Fennah, 1962; Bournier, 1970), whiteflies (Latta, 1937) and lace bugs (Crosby and Hadley, 1915). In rare instances, there is retention of the attachment scars on leaf surfaces by piercing-and-sucking scale insects.

Of approximately equal antiquity to boring on plant and fungal substrates is piercing-and-sucking, which probably was present during the Early Devonian (Kevan et al., 1975; Labandeira and Phillips, 1996a) and is well documented on tree-fern petioles, seed-fern pollen organs, and platyspermic cordaite seeds from the Upper Pennsylvanian and Lower Permian (Sharov, 1973; Labandeira and Phillips, 1996a; Labandeira, 1998b). The culprits of this Paleozoic damage were paleodictyopterid insects, in

contrast to the few instances of post-Paleozoic damage attributable principally to hemipteroid insects (Fig. 2C). The lack of significant documented evidence of piercing-and-sucking is partly attributable to confusion with fungal attack. In fact, open dermal wounds left by insects with stylate mouthparts are point sources often targeted by invading fungi, that subsequently expand after colonization to form a similar pattern of leaf spotting.

Sporivory and Pollinivory

Evidence for consumption of spores and pollen is qualitatively different than the five preceding functional-feeding-groups. Sporivory and pollinivory are not detectable as plant damage; consequently, a parallel ichnofossil record of coprolites and gut contents has been exploited to reveal the taxonomic identities of both the insect culprits and their interacting plants. When

evaluated throughout the Phanerozoic, four assemblages of pollinating insects and their source plants have been characterized (Labandeira, 1998a), commencing during the latest Silurian to Early Devonian, with coprolites consisting entirely or partially of spores from primitive vascular plants, produced by unknown terrestrial arthropods (Edwards, 1996). The second assemblage is composed of both Late Carboniferous dispersed coprolites from coal-swamp deposits and Early Permian insect gut contents in drier, upland habitats. Collectively, this assemblage documents consumption of cordaite, conifer and seed-fern pollen as well as marattialean tree-fern spores during the late Paleozoic (Rasnitsyn and Krassilov, 1996a, 1996b; Labandeira, 1998a, 1998b). The ichnofossil record for spore and pollen consumption fades after the Permian and does not resume until the mid-Jurassic, when dispersed coprolites consisting of *Caytonia* pollen from the Yorkshire Flora (Harris, 1957) enter the

FIGURE 3. A sample of varied insect damage on dicotyledonous foliage from the Dakota Formation, an early angiosperm-dominated flora located at Braun's Ranch, near Delphos, Cloud Co., Kansas (see also Labandeira et al., 1994). A, Two galls (white arrows), margin feeding (top) and hole feeding (between midrib and right margin) on the lauralean *Crassidenticulum* (UF11867). B, Hole feeding reminiscent of modern weevil (Coleoptera: Curculionidae) damage on the lauralean *Crassidenticulum* (UF12660'). C, Hole feeding reminiscent of modern leaf beetle (Coleoptera: Chrysomelidae) damage on the lauralean *Pandemophyllum* (UF7250). D, Serpentine leaf mine (Lepidoptera: Nepticulidae) possibly on the lauralean *Pabiana* (UF16173). E, Serpentine leaf mine (Lepidoptera: Nepticulidae) on an unidentified angiosperm fragment (UF7252). F, Midrib galls (?Diptera: Cecidomyiidae) on a platanoid leaf (UF12730). G, Detail of gall structure outlined at top in (F). H, Detail of gall structure outlined at bottom in (F). Abbreviation: UF = paleobotanical collections at the University of Florida Museum of Natural History in Gainesville. Scale bars: solid = 1cm; striped = 0.1 cm.

record.

It is this third assemblage of consumed gymnospermous pollen, the subsequent fourth assemblage of angiosperm pollinivory, and their probable overlap, that is of interest for the Late Jurassic to Middle Cretaceous interval (Labandeira, 1998a; Ren, 1998a). From the Kimmeridgian Karatau biota of Kazakstan, aboilid orthopterans (grasshoppers) have yielded gut contents (Fig. 2I) consisting of a distinctive type of *Classipollis* pollen (Fig. 2J) assignable either to the Coniferales or Gnetales (Krassilov et al., 1997a, 1997b). Evidence for consumption of exquisitely-preserved gymnospermous pollen also was found in the Lower Cretaceous Baisa biota of Russia, where isolated conifer pollen of *Alisporites, Pinuspollenites and Vitimipollis* (Fig. 2L) were lodged in the guts of three genera of xyelid sawflies (Fig. 2K) (Krassilov and Rasnitsyn, 1983). Pollen also has been found in the guts of xyelid sawflies from the Aptian Santana Formation of northeastern Brazil (Caldas et al., 1989); except that the consumed pollen is *Afropollis*, a form-genus assigned to winteraceous angiosperms (Doyle et al., 1990) and the earliest example of insect-consumed angiosperm pollen in the fossil record (see also Lloyd and Wells, 1992). Kampmann (1983) has described spore-bearing coprolites from the Lower Cretaceous of Germany, also attributable to hymenopterans. Lastly, from the Turonian locality at Orapa, Botswana, Rayner and Waters (1991) have described staphylinid beetles with extensive pollen attached to their vestiture, suggestive of pollinivory. Evidently consumption of pollen from clades as diverse as conifers, cycads, gnetaleans, and bennettitaleans was occurring during the Late Jurassic to Middle Cretaceous, indicating as well that the origin of modern-style pollination was among seed plants prior to the ecological expansion of angiosperms (Dilcher, 1995; Labandeira, 1998a). At present, it is impossible to determine whether gymnospermous and angiospermous pollen during the Early Cretaceous were being trophically partitioned by different taxa of insect pollinivores.

Nectarivory

Because of the presence of both pollen- and nutrient-rich surface secretions in most seed plants, there is a tight association between pollinivory and nectarivory. Even if nectar consumption is the sole insect reward, the transfer of pollen to conspecific plant hosts is an indirect but beneficial effect resulting in a mutualism that can be maintained for extended intervals of geological time. Nectarivory is the imbibation of secretions rich in carbohydrates, lipids or amino acids (Baker and Baker, 1975), which are secreted by specialized epidermal glands (nectaries) that are associated with reproductive or vegetative structures (Durkee, 1983) in a variety of ferns and seed plants, especially angiosperms (Bonnier, 1879; Mamay, 1976; Fahn, 1979; Proctor et al., 1976). Fossil evidence for nectarivory is relatively indirect, and typically is of two types: insect mouthpart structures consistent with biomechanical, functional or morphological analogy to modern nectarivores, or as floral structures modified for the reception of insect mouthparts, such as placement of floral nectaries at the bottom of a deep, tubular corolla (Crepet, 1996). Additionally, there is evidence from modern nonangiospermous seed plants indicating that insect nectaring occurs in gnetaleans (Van der Pijl, 1953; Meeuse et al., 1990; Kato and Inoue, 1994) and cycads (Brekton and Ortiz, 1983; Tang, 1987).

Appropriate insect mouthparts are known from the fossil record, such as the very elongate proboscis of a scorpionfly from
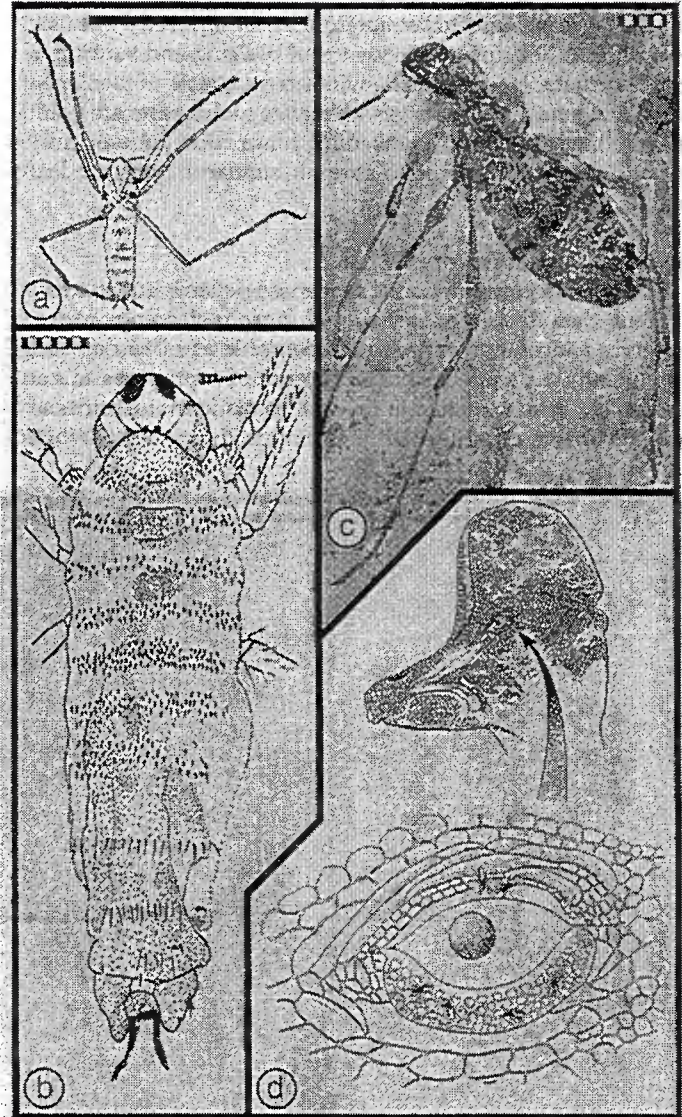

FIGURE 4. Examples from the literature of insect associations with reptile-grade vertebrates during Late Jurassic to Middle Cretaceous. A, Ventral view of the enigmatic insect *Saurophthirus*, a possible pterosaur ectoparasite, from the Lower Cretaceous of Transbaikalia, Russia (Ponomarenko, 1976). B, Detail of dorsal body surface structures, including vestiture, genitalia and setation of leg bases (Ponomarenko, 1976). C, The presumed flea, *Tarwinia*, from the Aptian of Victoria, Australia (Riek, 1970; Jell and Duncan, 1986; also see Poinar, 1995). D, Interpretive rendering of life habits of *Culicoides canadensis* (Boesel) (Diptera: Ceratopogonidae) as a blood-feeder on exposed eye membranes of *Corythosaurus*, from the Upper Cretaceous of Alberta, Canada (Borkent, 1995). Scale bars: solid = 1cm; striped = 0.1 cm.

the Kimmeridgian-age Karatau biota of Kazakstan (Novokshonov, 1997). The most spectacular examples from this deposit are the suite of brachyceran fly species, especially members of the family Nemestrinidae, with elongate proboscides or investitures of dense hair (Rohdendorf, 1968b; see also Nartshuk, 1996). The younger Tithonian Yixian Formation of China also contains a relatively diverse suite of brachyceran fly species, including Nemestrinidae, Tabanidae and Apioceridae (Ren 1998a, 1998b), which strongly indicate that nutrient rich

fluids secreted by seed plants normally inaccessible to insects with short mouthparts, were being accessed by nectarivorous flies with elongate and specialized fluid-feeding proboscides (Fig. 2P–Q). Also of Tithonian age, the Solnhofen Formation in Germany has revealed a nemestrinid fly, although it is poorly preserved (Bernardi, 1973). In addition to the evidence from Mecoptera and especially Diptera above, is Kozlov's (1989) description of an Upper Jurassic siphonate lepidopteran from Karatau.

In contrast to the Late Jurassic compression deposits, relevant deposits of Early Cretaceous age contribute relatively little insight into the existence of nectarivory, and the evidence for this functional feeding group does not reappear until the Middle Cretaceous. During the Turonian this evidence consists of various floral structures (Crepet, 1996; Crepet and Nixon, 1996) and the presence of a bee (Michener and Grimaldi, 1988) in New Jersey amber, and crane fly mouthparts (Fig. 2O) and floral structures (Fig. 2N) from Botswanan compressions (Rayner and Waters, 1991; Rayner, 1993). To date there is no known physical evidence for Cretaceous angiosperm floral damage that would be expected from mess-and-soil pollinators such as beetles (Thien, 1974; Grinfel'd, 1975; Gottsberger, 1988). The closest evidence for a precursor to this pollination type is found in female reproductive strobili of Early Cretaceous bennettitalean *Cycadeoidea* (Delevoryas, 1968; Crepet, 1974) (Fig. 2F), though the culprits for this damage suggest pollination syndromes of modern cycads rather than modern angiosperms (Crowson, 1991; Labandeira, 1997). Moreover, nemonychid, curculionid and other weevils are known with long, decurved rostra, and probably were consuming conifers or cycads either as larvae (Fig. 2G) or as adults (Fig. 2M), thus representing additional evidence for the antiquity of beetle-mediated pollination (Zherikhin and Gratshev, 1997).

Other Interactions

Plant, fungal and animal structures undoubtedly provided insects with protection and shelter, as they do in extant ecosystems (Scott et al., 1992). However, fossil documentation of such interactions is sparse because insect domiciles other than the ones mentioned above are rarely preserved in the fossil record. Leaf-rolling and leaf-tieing are obvious candidates (Johnson and Lyon, 1991) but are limited to a Cenozoic record of rare occurrences. Another suspect is mite domatia, but presently domatia are not known from the Mesozoic, and their earliest occurrence is Eocene (O'Dowd et al., 1991). The best example is caddisfly cases, which have a pervasive record throughout the later Mesozoic and Cenozoic (Sukacheva, 1982), characterized by selective use of plant and animal materials for case construction by these aquatic larvae. In fact, an informal ichnotaxonomy has been developed to refer to these compositionally and structurally distinct domiciles (Sukacheva, 1982). A notable example is a type of caddisfly case fabricated from seeds of the extinct gingkoalean, *Karkenia* (Krassilov and Sukacheva, 1979), from the Lower Cretaceous Mongolian locality of Shin-Khuduk.

Insect–Fungus Associations

The fossil record of insect–fungal associations reveals two, documentable modes of occurrence. The first mode is as microscopic gut endosymbionts that provide compounds for the digestion of such refractory foods as lignin and cellulose, typically by wood-boring insects such as termites (Darlington, 1994), bark beetles (Norris, 1979; Beaver, 1989), and sawflies (Madden and Coutts, 1979). Although gut endosymbiont microfossils from Late Jurassic to Middle Cretaceous insects have not been found, such associations may be found in Cretaceous amber (see documentation of microfossils in Miocene amber [Grimaldi et al., 1994]). Nevertheless, these associations can be inferred from the presence of late Mesozoic wood-boring insects whose modern descendants obligately require intestinal endosymbionts for survival (Batra, 1979; Wheeler and Blackwell, 1984; Wilding et al., 1989). These type of associations are documented through the Cenozoic and into the Lower Cretaceous (Labandeira, 1999b), and include a Lower Cretaceous scolytid or curculionid boring in conifer wood (Jarzembowski, 1990) and the earliest credible trace-fossil of an insect boring with fungi from the Early Jurassic of Germany (Müller-Stoll, 1936), consisting of wood borings with cell walls degraded by fungi and lined with hyphal masses along their inner wall. Presumed anobiid, buprestid and scolytid beetle borings in *Araucarioxylon* wood of the Late Triassic Chinle Formation (Walker, 1938) are questionably assigned (Crowson, 1981) and lack evidence of fungi.

The second preservable mode of association between fungi and insects is the cultivation of megascopic fungi, typically in underground cavities, by certain clades of termites (Wilson, 1971; Batra and Batra, 1979; Wood and Thomas, 1989) and ants (Weber, 1979; Cherrett et al., 1989; Hölldobler and Wilson, 1990). While termites and ants have a good Cenozoic record, the body fossils of these social insects extend only to the Lower Cretaceous (Grimaldi, 1997, Grimaldi et al., 1997, respectively) (Fig. 2B), although reports of older ichnofossils for both groups extend to the Late Triassic Chinle Formation (Hasiotis and Dubiel, 1993, 1995) but await confirmation. Several Cretaceous termite body fossils have been assigned to the families Hodotermitidae and Mastotermitidae (Grimaldi, 1997); the oldest is *Meiatermes bertrani* from the Valanginian of Montsec, Spain (Lacasa and Martínez-Delclís, 1986). Trace-fossil evidence for the presence of Isoptera is confined to the Upper and Middle Cretaceous, consisting of fecal pellets with distinctive hexagonal cross-sections within characteristic galleries of wood from the Maastrichtian of Texas (Rohr et al., 1986), an unspecified interval from the Upper Cretaceous of Argentina (Genise, 1995) and the Cenomanian of British Columbia (Ludvigsen, 1993).

Known fossil representatives of ants and their immediate ancestors extend to the Aptian Santana Formation of Brazil (Brandão et al., 1990), although true ants (Formicidae) have a Turonian earliest documented occurrence from New Jersey amber (Wilson et al., 1967; Grimaldi et al., 1997). Evidently the caste system that characterizes ants was well-established during Turonian time, but its presence during the earlier Cretaceous presently has not been demonstrated because of difficulty in evaluating appropriate structural features of individuals preserved as compressions. The only extant clade with Mesozoic fossils is the Ponerinae, represented in New Jersey amber, which implies that most of the higher-level cladogenesis had transpired during the Lower Cretaceous and Cenomanian, and that an earlier radiation of ants (Crozier et al., 1997) also cannot be ruled out. Because of this sparse Early to Middle Cretaceous record, and the absence of Cretaceous body-fossils of mound-building and fungus-culturing clades (albeit cladistic relationships indicate their presence), it becomes important to verify recent claims of Late Jurassic ant nests from the Morrison Formation (Hasiotis and Demko, 1996) and even the Late Triassic Chinle Formation (Dubiel and Hasiotis, 1995).

Insect–Vertebrate Associations

The extent and quality of evidence indicating insect–vertebrate associations is substantially less than those for plants and insects. The evidence comes in two principal forms. The first are external features that are consistent with an ectoparasitic or free-living bloodfeeding way of life and occur on insect fossils present in the deposits that also yield appropriate tetrapod hosts (Fig. 4). The second is postmortem damage to bones, such as borings by carrion insects on dinosaur skeletons. A third type of evidence, so far limited to the Late Cretaceous, involves unique structures in dinosaur coprolites and associated sediment that suggest use of dung as a food substrate and nesting site by scarab beetles. Most of these data are indirect, particularly the circumstantial evidence of trophically linked, co-occurring insects and tetrapods, and associations should be inferred with caution.

Blood Feeding

Within the lower Diptera, or Nematocera, there is evidence indicating that bloodsucking is the primitive feeding habit for the Culicidae (mosquitoes), Simuliidae (black flies), Chaoboridae (phantom midges), Ceratopogonidae (biting midges), and probably Chironomidae (aquatic midges), based on morphologic examination, phylogenetic analyses and study of Mesozoic fossils (Downes, 1971; Borkent et al., 1987; Grogan and Szadziewski, 1988; Kalugina, 1992). With the exception of the Culicidae, whose earliest known representative is from the Late Cretaceous (Friedrich and Tautz, 1997), the other four families have Jurassic and Early Cretaceous first occurrences (Craig, 1977; Kalugina and Kovalev, 1985; Crosskey, 1991; Kalugina, 1992; Szadziewski, 1996; Johnston and Borkent, 1998), indicating that blood-feeding on terrestrial tetrapods occurred during the mid-Mesozoic (see also Hennig, 1972). Additionally, several taxa occurring in Jurassic and Early Cretaceous deposits have relict descendants that do not suck blood, but probably were blood-sucking based on fossil mouthpart structure (Kalugina and Kovalev, 1985; Kalugina, 1992).

The more difficult issue is what were the identities of their hosts? In a recent exhaustive examination of a diverse suite of ceratopogonid taxa from Upper Cretaceous (Campanian) amber from Alberta, Canada, Borkent (1995) deduced that two and possibly three species of the biting midge *Culicoides* were feeding on the blood of large vertebrates that produced sufficient amounts of carbon dioxide for downwind detection. This inference was based on robust associations between feeding on large vertebrates and mouthpart stylet dentition and palpal sensilla location and number for species of modern *Culicoides* (Rowley and Cornford, 1972; McKeever et al., 1988). Borkent proposed that the females of these species attacked exposed and vascularized membranes, especially eyelids, or interscutal integument of large hadrosaurs (Fig. 4D). In older Turonian amber from New Jersey, Borkent (1997b) interpreted *Culicoides grandibocus* as a feeder on dinosaur blood. The other nine *Culicoides* species of this fauna were probably insect feeders.

In addition to dipteran lineages, presumptive taxa of siphonapterans (fleas) or taxa closely related to Siphonaptera, are present in the Aptian Koonwarra locality of Australia (Jell and Duncan, 1986). These fossils long have been contentious (Riek, 1970; Willmann, in Hennig, 1981; Poinar, 1995) and exhibit a general siphonapteran body facies (Fig. 4C), including distinctive pronotal and tergal combs, but their large size, presence of prominent, elongate antennae and lack of leg jumping specializations disallows placement in the Siphonaptera as presently defined. Nevertheless, the three taxa described at Koonwarra clearly display features consistent with an ectoparasitic life-habit, including laterally compressed bodies, long legs, dorsal setal combs, and elongate, probably stylate, mouthparts.

Parasitism

Two intriguing Lower Cretaceous discoveries from Eurasia suggest that insects were living ectoparasitically on a hair- or possibly feather-bearing vertebrate, perhaps a pterosaur. The first discovery was made by Ponomarenko (1976), who described the well-preserved compression fossil *Saurophthirus longipes* from the Baisa locality of Transbaikalian Russia (Fig. 4A–B). This dorsoventrally flattened, nonwinged insect bears an elongate head with stylate mouthparts, and free but modified antennae; the thorax and abdomen are scarcely differentiable from each other but contain setae and hairs occurring as similar segmental patterns. The legs are very long and have tarsal claws designed for firm attachment to hair or possibly feathers. This enigmatic insect was probably holometabolous, related possibly to the Mecoptera or Siphonaptera, and sharing an overall resemblance to nycteribiid flies and polyctenid bugs, both which are bat parasites. A similar, more poorly preserved insect has been recorded from the younger Gurvan locality in western Mongolia (Ponomarenko, 1986). This taxon, *Saurophthiroides mongolicus*, has greater differentiation of the thorax and abdomen than *Saurophthirus* but curiously resembles a peculiar group of winged, aquatic Mesozoic orthopteroids known as chresmodeans.

Carrion Feeding

Several occurrences of damage to bones, mostly in the form of small borings into bone tissue, are known from the Late Jurassic and Late Cretaceous tetrapod record. This damage consists of borings that are circular to elliptical in cross-section, and occurs in theropod and sauropod dinosaur bones. They have been attributed to pupae of carrion beetles (Coleoptera: Dermestidae). Examples are known from the Tithonian Morrison Formation of northeastern Utah (Hasiotis and Fiorillo, 1997) and Wyoming (Laws et al., 1996) and from the Campanian Two Medicine Formation of northwestern Montana (Rogers, 1992). Near identical dermestid borings occur in modern decomposing carcasses (Martin and West, 1995) and have been documented more extensively in Late Cenozoic bone assemblages. It is noteworthy that calliphorid pupae have been reported from the Campanian Edmonton Formation of Alberta, Canada (McAlpine, 1970), indicating that blow flies, which feed on rotting flesh, were part of a carrion community during the Late Cretaceous, and possibly earlier.

Coprophagy

The degradation and recycling of large amounts of tetrapod fecal material by dung beetles (Scarabaeidae) is a pervasive life-habit in many modern temperate and tropical regions. While scarabaeid body fossils occur throughout the Cenozoic and Mesozoic (Crowson, 1981), until recently ichnofossils were only known from the Cenozoic. Several have previously suspected that Mesozoic tetrapod communities supported dung beetles (e.g., Halffter and Matthews, 1966). Recently, Chin and Gill (1996) have established unequivocal fossil evidence for backfilled burrows and other distinctive modification by dung beetles of conifer-rich

dinosaur dung from the Campanian Two Medicine Formation of Montana. Supportive evidence may be gleaned from the body-fossil record of scarab beetles, which extends to the Lower Jurassic (Arnol'di et al., 1977; Rohdendorf and Rasnitsyn, 1980; Crowson, 1981), but it is not clear which of these specimens, if any, are true dung-beetle taxa in the subfamilies Scarabaeninae and Geotrupinae. Additional examples of associations between vascular plants, dung beetles and herbivorous dinosaurs probably occur in earlier strata, but await discovery.

LATE MESOZOIC ECOSYSTEM CHANGE AND THE PRESENT

Other than obvious microorganisms, the four taxonomic cornerstones of terrestrial ecosystems are vascular plants, fungi, arthropods (dominantly insects), and vertebrates. These dominant groups have provided the overwhelming bulk of taxa by which terrestrial communities are structured and, through additions and subtractions, have determined the course of ecosystem change during the past few hundred million years. When viewed through a Late Jurassic to Middle Cretaceous prism, it is clear that the greatest changes have been with the plants and vertebrates, considerably less so with insects. The role of the fungi is still speculative, based on their very poor fossil record. During this 70 million year period of Mesozoic time, plants experienced a virtual complete overturn at the highest taxonomic levels—a shift from a typical "mesophytic" flora of ferns, seed ferns, bennettitaleans, conifers, cycads, gingkoaleans and ephedraleans, to a "cenophytic" flora of dominantly angiosperms and subdominantly conifers. During this interval, tetrapod assemblages also changed, perhaps in ways not as dramatic as the angiosperm revolution. Insects apparently underwent a different pattern, wherein virtually all orders originated during the early Mesozoic or earlier, and most suborders and superfamilies, and many families were in existence by the Late Jurassic (Labandeira and Sepkoski, 1993). This was paralleled by a similar modern ecological breadth by Late Jurassic times, as measured by the number of occupied mouthpart classes, functional feeding groups and dietary guilds (Labandeira, 1997, 1999b). Perhaps insects were buffered from the vicissitudes experienced by plants and vertebrates by their elevated diversities, high abundance, and widespread ecological ubiquity. However, insects undoubtedly also experienced extinctions when their plant and vertebrate hosts succumbed to major environmental challenges.

A reasonable expectation of these data is whether there is any evidence in the modern world for this Late Jurassic to Middle Cretaceous world? The obvious, perhaps trivial, candidates are *Gingko*, araucarian and podocarp conifers and cycads for plants, *Sphenodon*, crocodiles and turtles for tetrapods, and much of the present-day insect fauna. A more revealing answer, however, would address the associations between two or more interactive organisms. The most frequent examples are insect herbivores and their plant hosts, for which some modern studies provide an inkling that the earlier Mesozoic world has not been entirely swamped out by the subsequent advance of more modern angiosperms and mammals. For example, a few studies have documented the persistence, to the modern day, of taxa and associations datable to approximately 95 Ma. One is the prolonged genus-level stasis of the cranefly Helius (Rayner and Waters, 1990) and another is the association between genera of leaf-mining moths and their platanaceous (sycamore) host plants (Labandeira et al., 1994), although there are contrary views

(Kuschel et al., 1994). More to the point is a cladistic study of the Curculionoidea and Chrysomeloidea—two clades of beetles that are almost entirely phytophagous on live plants—wherein hostplant taxa were mapped onto a well-corroborated and fossil-calibrated cladogram of the insect herbivore phylogeny (Farrell, 1998). The results strongly indicate that primitive insect lineages have been tracking primitive plant lineages—in this case, conifers and cycads—since the Late Jurassic and Early Cretaceous. Similar relationships probably exist for other lineages of cycad beetles (Endrödy-Younga and Crowson, 1986; Crowson, 1990), and the dominantly phytophagous symphytan *Hymenoptera* and their fern and conifer host plants (Vilhelmsen, 1997), although any signal in basal lepidopteran phylogeny and their host plants probably has been masked by the angiosperm radiation (see Thien et al., 1985). Supportive of this view are data indicating that the earliest lepidopteran leaf mines are on latest Jurassic or earliest Cretaceous seed ferns (Rozefelds, 1988); nectaring Late Jurassic brachyceran flies were more likely to probe nonangiospermous seed plants than angiosperms (Labandeira, 1998a; but see Ren, 1998a); and Late Jurassic to Early Cretaceous grasshoppers and sawflies consumed a variety of gymnospermous pollen types (Krassilov and Rasnitsyn, 1983; Krassilov et al., 1997b), followed by the earliest insects with gut contents of angiosperm pollen occurring later during the Albian (Caldas et al., 1989). Although some of these associations have not persisted to the present, there are extant cycads with phylogenetically primitive weevil pollinators (Chadwick, 1993; Forster et al., 1994; Norstog et al., 1995; Farrell, 1998), and some associations of basal angiosperm lineages and their insect herbivores from the Middle Cretaceous have continued to the present day (Labandeira et al., 1994). A tad of these dynamic Late Jurassic to Middle Cretaceous asociations are still with us, albeit in unanticipated contexts.

CONCLUSIONS

1. There is an under-appreciated fossil record of Late Jurassic to Middle Cretaceous associations between insects and other organisms. This record of vascular plant and insect associations is far richer than the record of insect and tetrapod associations, but both can be improved significantly by documenting subtle details of fossils that reveal interorganismic activity.

2. The Late Jurassic to Middle Cretaceous was an interval of profound change for vascular plants and tetrapods, much less so for insects, and unknown for fungi.

3. At the beginning of this interval, the major associations between insects and vascular plants are with herbivorous insects and seed plants. By the end of this interval, associations with vascular plants shifted overwhelmingly toward angiosperms.

4. The mid-Cretaceous angiosperm revolution swamped out earlier seed plant and insect associations so that they exist today as rare occurrences in descendant taxa. These extant taxa are frequently basal members of their respective lineages.

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