The Pollination of Mid Mesozoic Seed Plants and the Early History of Long-proboscid Insects

THE POLLINATION OF MID MESOZOIC SEED PLANTS AND THE EARLY HISTORY OF LONG-PROBOSCID INSECTS[1,2,3]

Conrad C. Labandeira[4,5]

ABSTRACT

A defining event for Mesozoic plant-pollinator interactions is the angiosperm radiation, which extended the reach of pollinating insects during the Early Cretaceous in a brief interval of geologic time. Recent evidence indicates that events beginning in the Early Permian and increasing during the Middle Jurassic provided repeated opportunities for insect feeding on pollen, pollination drops, and reproductive tissues of extinct gymnosperm lineages. Pollination was an associated development. Studies on the detailed mouthpart structure of several fluid-feeding insect lineages indicate targeting of certain tubular features of gymnosperm ovulate organs that previously were considered anomalous and difficult to interpret. One mouthpart type, the long-proboscid condition, consists of elongate, tubular (siphonate) proboscises that accessed surface fluids powered by a cibarial pump, often assisted with a distal proboscis sponging organ. These proboscises were received in ovulate organs through often intricate cupulate integumental tubes, interovular channels, salpinx tubuli, pappus tubules, prolonged micropyles, and a catchment funnel-pipe-micropyle device. These ovulate structures also are consistent with insect access to nutritive rewards, including pollination drops, nectarial secretions, and pollen. Other evidence for pollination includes the entomophilous structure and size of pollen found on insect and plant contact surfaces and in insect guts, nutritional levels of modern pollination drop fluids similar to angiosperm nectar for supporting metabolically high activity levels of aerially active insects, and plant-host outcrossing. While the long-proboscid pollination mode of fluid feeding targeted gymnosperm hosts that

deployed unisexual reproductive organs at some distance from each other, either on the same or on different plants, another mode of pollination, that of mandibulate insects, consumed typically solid tissues in compact bisexual strobili, targeting pollen and perhaps pollination drops (adults), and associated sterile tissues (larvae). These two groups of pollinator associations were irretrievably altered as angiosperms diversified during a 35-million-year interval of the Early Cretaceous, evident in three patterns. First was the demise of most pollinator associations that evolved during the preceding 65 million years; second was the lateral transfer of some of these associations onto angiosperms that continue today as relicts; and third was emergence of new pollinator associations with angiosperms.

A transformation that provided much of the structure to the modern terrestrial world was the initial diversification of flowering plants, commencing during the mid Early Cretaceous and continuing into the early Late Cretaceous, from 125 million years ago (Ma) to ca. 90 Ma. During this 35-million-year interval there were significant shifts in the major ecological associations among plants, fungi, insects, vertebrates, and other organismic groups dominant on land. This ecological change resulted in structural transformation of terrestrial communities such that, by the end of the Cretaceous, there were few remaining taxonomic, ecological, or biogeographic biotal elements that were present at the beginning of the period (Friis et al., 1987; Lucas et al., 1998). These ecosystem-wide changes are often heralded as a profound development for life on land, of which the early co-radiation of insects on flowering plants is a textbook example of the beginning of a world that is familiar to us today.

Discussions of the magnitude and consequences of the event associated with the diversification of angiosperms historically can be contrasted with what is known of the immediate, preangiospermous world of the earlier Mesozoic flora dominated by extinct gymnospermous seed plants of seed ferns, cycads, conifers, bennettitaleans, and gnetophytes, as well as ferns, sphenopsids, and bryophytes (Willis & Mc-Elwain, 2002; Taylor et al., 2009). Similarly, speciose insect clades that interacted with these plants included lineages that either became extinct or were represented by closely related, but early groups of extant lineages (Grimaldi & Engel, 2005). These major insect clades include mid Mesozoic representatives of the four major groups that have complete metamorphosis, the Coleoptera (beetles), Hymenoptera (wasps, ants, and bees), Diptera (true flies, such as mosquitoes, midges, and horseflies), and Lepidoptera (moths and butterflies). Also included were representatives of currently less diverse clades that played more prominent roles during the earlier Mesozoic, such as the Mecoptera (scorpionflies), Neuroptera (lacewings, owlflies, mantispids, and antlions), and Trichoptera (caddisflies), and among clades with incomplete metamorphosis, the Hemiptera (aphids, whiteflies, scale insects, and bugs), Blattodea (cockroaches), and Orthoptera (katydids, grasshoppers, and crickets). Interestingly, the pattern for insects does

not hold for the dominant megafaunal elements of the Mesozoic; dinosaurs and other lesser well-known lineages became extinct at the end of the Cretaceous.

Recent evidence provides a broad understanding of how some gymnosperms were used in different ways by phytophagous insects. The expansion of earlier Mesozoic insect phytophagy was a worldwide event that began during the Middle and Late Triassic (Labandeira, 2006a, b) and perhaps provided the origin for later Jurassic pollinator associations. In addition, recent data have documented the reproductive biology of pollinator relationships between preangiospermous plants and their insect associates.

Approach

In this paper, fossil occurrence data of pollen and nectar feeding, as well as known pollination modes between modern plants and insects, are mapped onto recent phylogenetic syntheses of major clades of extinct and extant seed plants and insects (Figs. 1, 2). A variety of evidence is used to establish nectar and pollen feeding in the Mesozoic fossil record, but of special interest is the distribution of inferred associations between gymnosperm hosts with deep tubular structures and their matching long-proboscid pollinators (Figs. 1, 2). Establishment of the long-proboscid pollination mode is supported by recent and ongoing examination of the reproductive anatomy of gymnosperm ovulate organs and especially of co-occurring long-proboscid insect mouthparts. These are known from late Middle Jurassic and mid Early Cretaceous examples from China and temporally intervening deposits from elsewhere, especially Eurasia (Engel, 2005b; Labandeira, 2005a; Labandeira et al., 2007a; Ren et al., 2009). Other types of inferred mid Mesozoic pollination modes also are discussed. Lastly, I discuss the evolutionary and ecological patterns resulting from the gymnosperm to angiosperm transition in pollination style and its implications for angiosperm and insect history.

Types of Evidence

Detection of pollen and nectar consumption as well as pollination mutualisms in the fossil record requires

multiple types of evidence. The most important aspect of this evidence is consilience, particularly the interplay between insect mouthpart morphology and relevant plant features such as ovulate organ architecture and pollen type (for a modern example, see Patt et al., 1997). The evidence needed for recognition of a particular pollination mode originates both from candidate insect and plant taxa as well as the environmental context of the possible association. Decipherment of such data requires several techniques; specifically, anatomical or morphological reconstruction, use of various exploratory and confirmatory instrumentation, and the application of functional morphology. Establishing types of direct and indirect paleoecological evidence is important for revealing feeding types and pollination modes that may be extinct or have survived to the present (Ren et al., 2009).

Seven types of evidence are used to infer the presence of palynophagy (pollen consumption), nectarivory (nectar consumption), and pollination in the fossil record (Labandeira, 1998, 2002a). First are insect mouthpart structure and its functional interpretation, including details of surface setation, cuticular ornamentation, specializations of the proboscis tip, and adjacent structures such as palps, sucking pumps, and antennae (Rasnitsyn, 1977; Rayner & Waters, 1991; Novokshonov, 1998; Ren, 1998; Szucsich & Krenn, 2000; Borrell & Krenn, 2005; Krenn et al., 2005). Second, and equally significant, are plant structures receiving the mouthparts. For gymnosperms, such features would include catchment funnels, integumental tubes, pappus tubules, and micropylar extensions in ovulate organs consistent with insect pollination (Harris, 1933, 1940, 1951b; Kvaček, 2000; Sun et al., 2001; Santiago-Blay et al., 2005; Anderson et al., 2007; Krassilov, 2009). Third, pollen size, shape, ornamentation, clumping, presumed stickiness, and abundance level indicate entomophily (Courtinat, 1980; Haslett, 1989b; Alvin et al., 1994; Zetter & Hesse, 1996; Axsmith et al., 2004; Hu et al., 2008). Fourth is the occurrence of pollen on insect contact surfaces such as the head capsule or mouthparts (Gilbert, 1972; Jervis et al., 1993; Nicholson, 1994; Labandeira, 2005a). Also, its preservation as intestinal contents directly links the consumer and consumed (Holloway, 1976; Krassilov & Rasnitsyn, 1983, 1996; Haslett, 1989b; Krassilov et al., 1997b, 2003, 2007; Afonin, 2000) and provides insight into the possible presence of pollination (Jervis et al., 1993; Labandeira, 2005a). Fifth, although a weaker source of evidence, dispersed coprolites often contain identifiable pollen grains but rarely indicate the responsible palynophage (Harris, 1945; Crepet, 1974; Pant et al., 1981; Labandeira, 2002a; Lupia et al., 2002; Hu et al., 2008). Sixth, related plant damage can document herbivory or seed predation on host

plants, suggesting a reward structure for a broader plant-pollinator association (Crepet, 1974; Norstog et al., 1995; Nishida & Hayashi, 1996; Klavins et al., 2005). Last, involving more modern fossils, the known biologies of particular plant and insect clades can be used to infer the associational dynamics of recent fossil ancestors (Labandeira, 2002a).

THE INSECTS

The most obvious feature of an insect that reveals consumption of nectar or pollen, or the existence of a pollinator association, is the mouthparts and head structure (Smith, 1985; Chaudonneret, 1990). Mouthparts of insects can be categorized into three major types based on diet: (1) consumers of solid food, typically entire tissues; (2) fluid feeders, such as invasive feeders that may imbibe xylem or phloem sap or cellular protoplasts, or alternatively surface fluid feeders that imbibe nectar; and (3) particle consumers that mostly access spores and pollen (Labandeira, 1997; Krenn et al., 2005). When considering mouthpart structure, there are three groups of pollinators: (1) biting and chewing mandibulate mouthparts involved in palynophagy; and two modified, haustellate mouthparts involved in fluid feeding, namely (2) siphonate, sponging, and lapping mouthparts involved in nectarivory, and (3) piercing and sucking mouthparts, particularly stylate ensembles that puncture plant tissues and pollen grains for their contents, and effect pollination in the process.

MANDIBULATE MOUTHPARTS

Mandibulate mouthparts are the first distinctive group of insect mouthparts used in nectarivory and palynophagy for effecting pollination. Characterized by biting and chewing, the mandibulate condition possesses many structural modifications used for the collection, processing, and consumption of pollen (Schicha, 1967; Fuchs, 1974; Kevan & Baker, 1983), although specializations for nectarivory are known for some taxa (Handschin, 1929; Schremmer, 1961). The ancestral condition in insects is mandibulate mouthparts, which extends to the Early Devonian in primitively flightless insects, such as bristletails (Labandeira et al., 1988), occurring as relatively weak, milling mouthparts that were housed in an internal pouch of the head capsule. The more powerfully musculated mouthparts of major detritivorous and herbivorous lineages of Orthopteroidea (grasshoppers and early relatives), Blattodea, Psocoptera (booklice), and Coleoptera (beetles) were present in the Pennsylvanian and Early Permian (Labandeira, 1997). During the Permian, several insect lineages bore mouthparts forwardly directed on the head capsule that had palynophagous adaptations (Rasnitsyn, 1977;
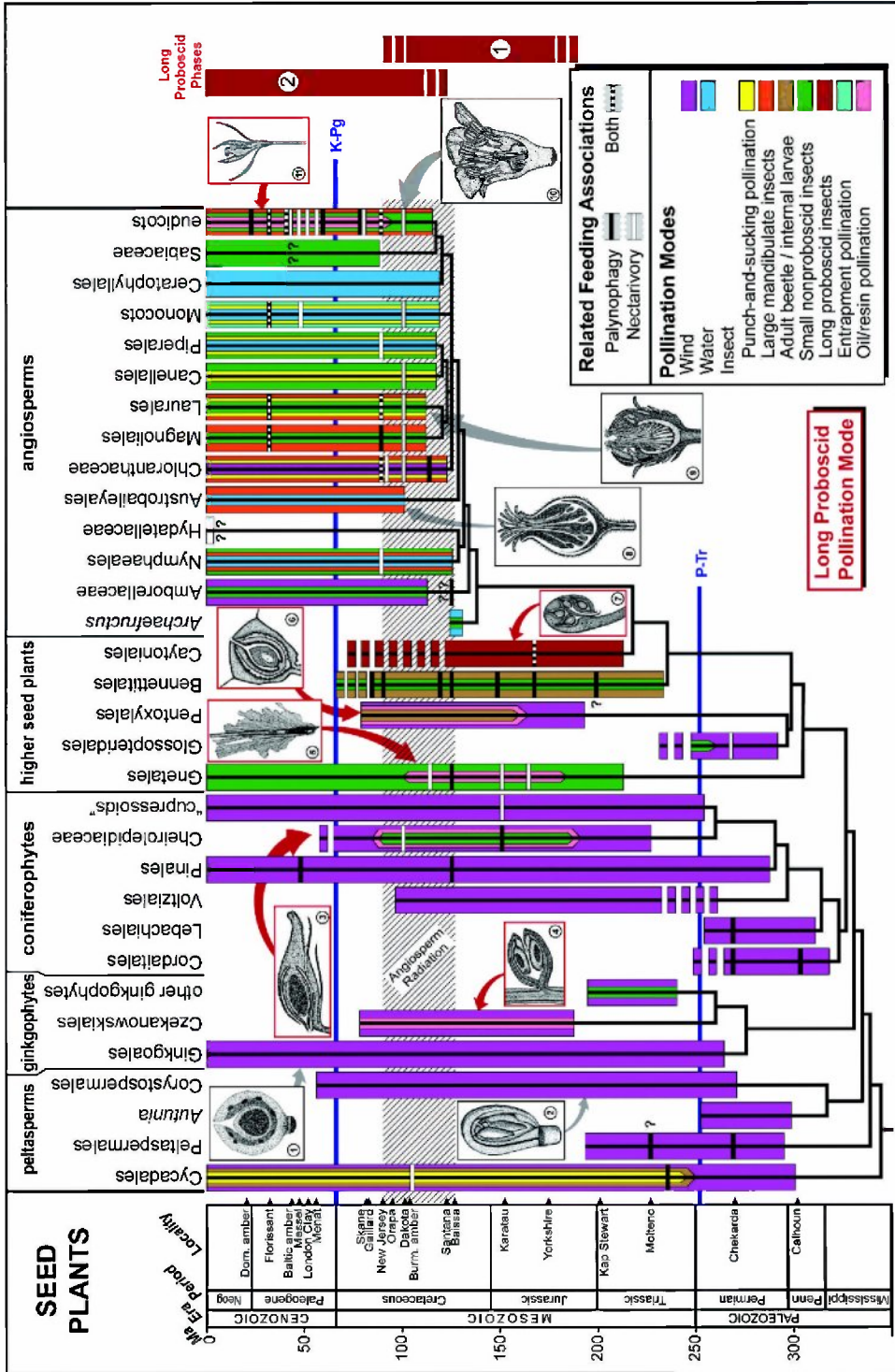
Novokshonov, 1998; Novokshonov & Rasnitsyn, 2000), often with robust, asymmetric mandibles reminiscent of a mortar-and-pestle mechanism for crushing pollen (Schicha, 1967). In some instances, these lineages preserved gut contents enriched in fossil pollen (Krassilov et al., 2007). Early clades of major holometabolous insects often bore adult specializations for pollen feeding during the early Mesozoic, such as Xyelidae (Hymenoptera: Jervis & Vilhelmsen, 2000), Micropterygidae and Agathiphagidae (Lepidoptera: Kristensen, 1997), and Cupedidae (Coleoptera: Hörnschemeyer et al., 2002). Although palynophagy is an ancient feeding style for holometabolous insects that extends to the Paleozoic, Coleoptera currently includes the greatest diversity of palynophagous taxa (Samuelson, 1989), an expansion commencing during the Middle and Late Jurassic (Arnol'di et al., 1977; Hunt et al., 2007).

Mandibulate, palynophagous insects process pollen in many ways. They may collect pollen and swallow the grains whole, as in anthophilous sawflies (Burdick, 1961), beetles (Kirejtshuk, 1997), bees (Klungness & Peng, 1984), and spoonwing lacewings (Picker, 1987; Popov, 2002). Intact fossil pollen may be found in gut contents and in dispersed coprolites (Willemstein, 1980; Caldas et al., 1989; Labandeira, 2006b). A variety of unique mouthpart modifications may accomplish the consumption of entire pollen grains, best documented in beetles (Barth, 1985; Krenn et al., 2005). Such modifications include jutting, prognathous mouthparts, laciniae and galeae with several types of hairs that entrap pollen with spoonlike or other catchment structures (Fuchs, 1974), or modifications of bristles that cause pollen to adhere to trumpet-shaped concavities (Schicha, 1967). Hairs occasionally coalesce to form brushes or combs that sweep and deliver pollen to the mouth (Nel & Scholtz, 1990). Mandibles are often extensively modified into laminar flaps that assist the collection and kneading of pollen into a consumable mass. Once in the intestinal tract, recent studies indicate that processes such as osmotic shock (Dobson & Peng, 1997) and chemical degradation by co-consumed plant cells (Rickson et al., 1990) can rupture intact pollen grains through their pores or other structural weaknesses—releasing nutritionally rewarding protoplast contents, yet leaving grains that appear intact (Barker & Lehner, 1972; Baker & Baker, 1979). Similarly, ingestion of whole pollen grains through siphonate mouthparts has parallels in some fluid-feeding Diptera, such as Syrphidae (hover flies) and Bombyliidae (bee flies), and in Nymphalidae (nymphalid butterflies) of the Lepidoptera (Holloway, 1976; Erhardt & Baker, 1990; Szucsich & Krenn, 2000). These entire pollen grains are ingested either as a primary diet source or secondarily in a nectar diet. Nectar and pollen may be consumed by anthophilous insects more commonly than strict diets of either, as the two food sources are complimentary and are required for insect nutritional balance (Gilbert, 1985; Haslett, 1989a; Roulston & Cane, 2000).

The second mechanism is to use specialized mandibles to crush pollen grains as a mortar and pestle or similar device. As we have seen, this type of palynovory is evident in the phylogenetically basalmost lineage of the Hymenoptera, xyelid sawflies, with a fossil record extending to the Middle Triassic (Rasnitsyn, 2002). Modern Xyelidae feed mostly on gymnospermous, especially pinaceous pollen (Burdick, 1961), and their mandibles are highly asymmetrical and

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Figure 1.   The distribution of pollination modes in seed plants, emphasizing Mesozoic lineages, shown as thick, vertical, colored bars linked to pollination modes at lower right. Seed plant lineages document 51 feeding association occurrences documented by smaller horizontal bars, defined in the center-right legend and keyed to the 20 (and other) fossil localities at left. Assignment of pollination modes is based on evidence from fossil fructification structure, pollen size and surface features, and modern determinations from surviving lineages, including pollination drop nutritional status and especially numerous studies of the pollinators of basal angiosperm lineages (also see Fig. 2). Each lineage column provides the dominant pollination mode, up to the three most common modes. Lineages with dashed segments indicate inferred presence, often occurring around major extinction events. Small horizontal bars within the lineage columns indicate fossil evidence for pollen, nectar, or both, presented for insect consumption. Note the presence of the early phase of the angiosperm radiation, indicated by a horizontal band from 130 to 90 Ma. These data are not exhaustive and spotlight Mesozoic associations, defined by the lower P-Tr and upper K-Pg extinction events; the Late Paleozoic and Cenozoic are de-emphasized. Seed plant phylogeny follows Hilton and Bateman (2006), with minor modifications; basal angiosperm phylogeny is provided by several sources (Sun et al., 2002; Soltis & Soltis, 2004; Anderson et al., 2005; Burleigh et al., 2009; also see Soltis et al., 2009). Geochronology at left is based on Ogg et al. (2008). Ovulate structures of seed plants indicating insect associations are shown in insets, with red arrows pointing to affiliated lineage, but not necessarily pointing to their geochronologic occurrence within the specified lineage. Examples are (1) *Allicospermum xystum* Harris (Harris, 1935) (Yimiaceae); (2) *Petriella triangulata* Taylor (Taylor et al., 1994) (Petriellaceae); (3) *Alvinia bohemica* Kvaček (Kvaček, 2000) (Coniferales: Cheirolepidiaceae) (Labandeira et al., 2007a); (4) *Leptostrobus caacer* Harris (Harris, 1951b) (Czekanowskiaceae); (5) *Problematospermum ovale* Turutanova-Ketova (?Gnetales) (Wang, pers. comm., 2009; Wang et al., 2009); (6) *Carnoconites compactus* Srivastava (Pentoxylaceae) (Bose et al., 1985); (7) *Caytonia sewardi* Harris (Harris, 1933) (Caytoniaceae); (8) *Monimia rotundifolia* Thouars (Monimiaceae) (Heywood, 1993); (9) *Jerseyanthus calycanthoides* Crepet (Crepet et al., 2005) (Calycanthaceae); (10) *Paleorosa similkameensis* (Rosaceae) (Stewart & Rothwell, 1993); and (11) *Vanilla planifolia* Andrews (Orchidaceae).
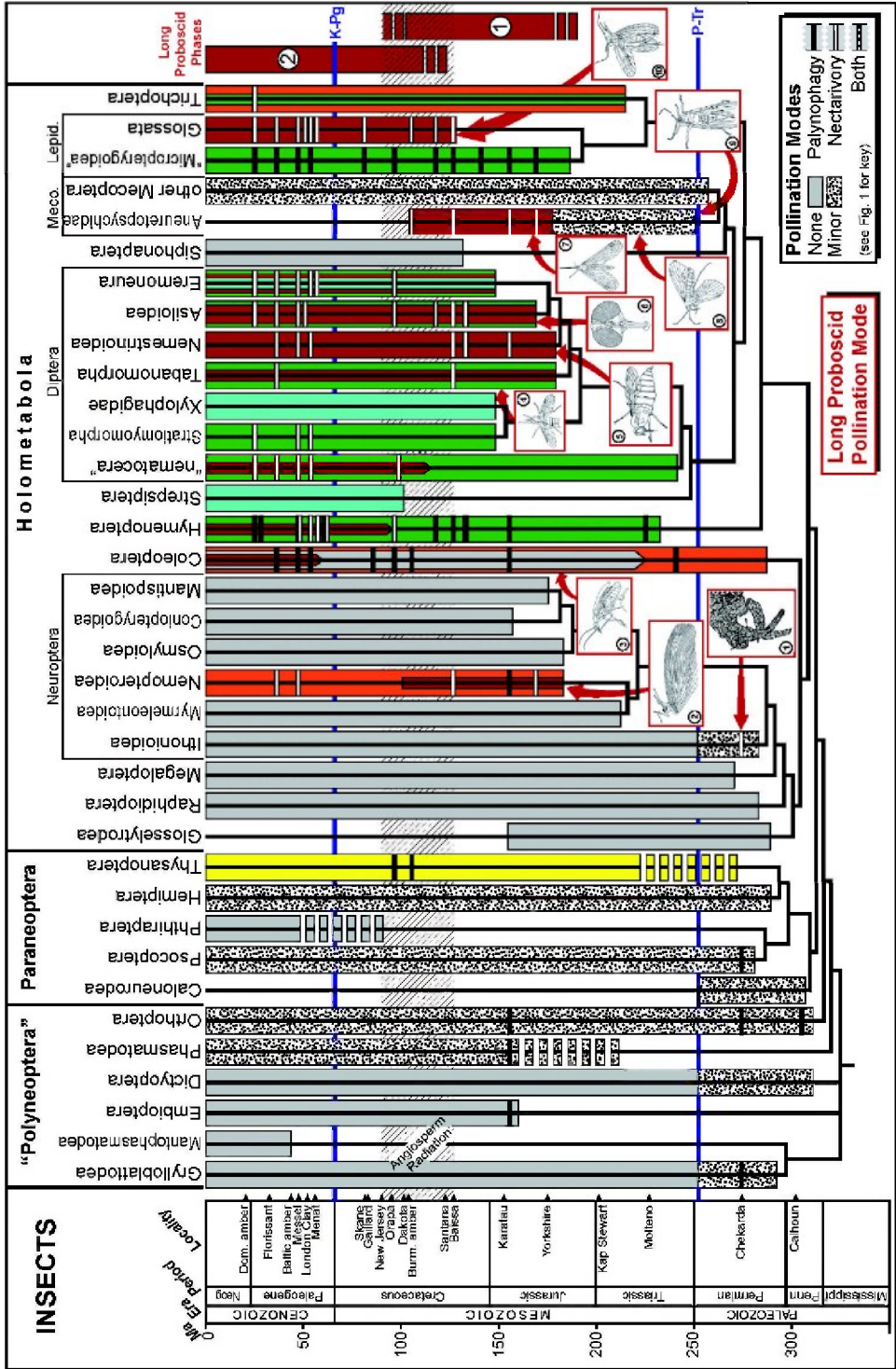
designed to crush pollen (Jervis & Vilhelmsen, 2000). The crushed pollen is further processed in a capacious oral cavity that is lined with modified teeth (Vilhelmsen, 1996). There are Triassic insect coprolites containing fragmented pollen within Triassic cycad cones (Klavins et al., 2005). Late Paleozoic evidence for this feeding mechanism also includes dispersed coprolites with fragmented palynomorphs (Labandeira, 2006b) and some extinct lineages of Permian insects with adult prognathous mouthparts bearing asymmetric mandibles (Rasnitsyn, 1977) may have fed in this way (Schicha, 1967). Another holometabolous clade, the Lepidoptera, also has early diverging lineages—the Micropterygidae, Agathiphagidae, Heterobathmiidae, and presumably the Early Jurassic–Early Cretaceous Eolepidopterygidae—with pollen-grinding mouthparts (Hannemann, 1956; Kristensen, 1984, 1997; Labandeira, 2009, pers. obs.). The basalmost extant lineage of Coleoptera, the archostematan Cupedidae (Hunt et al., 2007), processes pollen with similarly comminuting mouthparts (Hörnschemeyer et al., 2002). Other groups of insects, such as the Psocoptera (Chaudonneret, 1990), have mortar-and-pestle mouthparts but may not be highly palynophagous, while groups such as the Blattodea (Vlasáková et al., 2008) are commonly palynophagous but do not use pollen-crushing mouthparts.

HAUSTELLATE MOUTHPARTS

A second, distinctive, and more recently evolved group of mouthparts involves the modification of ancestral mandibulate mouthparts into the derived haustellate condition (Chaudonneret, 1990). This modification has occurred numerous times in insects and involved piercing-and-sucking behavior common in the Hemiptera and Diptera, as well as surface fluid feeding in the major holometabolous lineages of Diptera, Lepidoptera, and Hymenoptera, and less commonly in Coleoptera and Trichoptera (Labandeira, 1997). The focus here is on external surface feeders, which are the pre-eminent haustellate clades. Various permutations of the labial, maxillary, and often adjacent regions became modified into an elongated structure, such as a tubular proboscis or a labellum, for nonpenetrative probing and imbibing of fluids (Ulmer, 1905; Handschin, 1929; Takeuchi & Tokunaga, 1941; Eastham & Eassa, 1955; Holloway, 1976; Houston, 1983; Szucsich & Krenn, 2000; Krenn et al., 2002, 2005; Borrell & Krenn, 2005). Piercer-and-suckers play a minor role; examples are some dipterans where female individuals have a dual role of puncturing integument for blood and surface feeding on nectar (Kneipert, 1980).

In some haustellate mouthparts, the labral, maxillary, and labial structures variously combine to produce a siphon. The siphon may be composed of conjoined maxillary galeae, as in the glossate Lepidoptera and nemognathine Coleoptera, or sutured labial palps, without or with additional elements, as in the Diptera. In addition, the terminus of the siphon may bear cuticular structures such as ridged crests or undulatory ribbing, dense patches of hairs, specialized setae, sponging pads, or even several slits adjacent to scooplike structures for efficient capillary

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Figure 2. Pollination modes of mid Mesozoic insect lineages, showing the distribution of major insect pollinator types as thick, vertical bars linked to legend at lower right. Insect lineages contain 86 documented feeding associations as smaller horizontal bars, defined in the center-bottom legend and keyed mostly to the 20 fossil localities at left. Assignment of pollination modes is based on evidence inferred from mouthpart structure, gut contents, adpressed pollen clumps on insect bodies, and matching structure of nectared ovulate fructifications from contemporaneous seed plants (also see Fig. 1). Each lineage column bears the dominant pollination mode or modes, up to the three most dominant (see key in Fig. 1); alternatively, insect pollination may be absent or minor. Dashed segments within the lineage columns indicate probable presence of the lineage. Small horizontal bars within the lineages indicate consumption of pollen, nectar, or both; polyneopteran clades at left indicate occurrences where taxa consume pollen with considerable foliage; some hymenopteran occurrences indicate evidence for resin- or oil-collecting bees. Note the presence of the early phase of the angiosperm radiation, indicated by a vertically dashed, horizontal band from 130 to 90 Ma. The data are not exhaustive; the focus is on the Mesozoic, defined by the P-Tr and K-Pg extinction events; less specificity is provided for the Late Paleozoic and Cenozoic. Insect phylogeny is principally from Grimaldi and Engel (2005), supplemented by various sources in Labandeira (2005a) for Diptera subclades, and Labandeira et al. (in prep.) for Neuroptera subclades. Geochronology at left is from Ogg et al. (2008). Special emphasis is placed on the siphonate long-proboscid pollination mode, illustrated in red motif from camera lucida or overlay drawings of fossil specimens except (3), which is modern. Examples of long-proboscid siphonate insects from holometabolous insect lineages (indicated at top and arrow at bottom) consist of nine lineages that overwhelmingly acquired the condition independently. They include (1) *Tschekardithonopsis ?oblivius* Vilesov (Neuroptera: Permithonidae, a basal neuropteran); (2) *Heterokallihemerobius myrioneurus* (Neuroptera: Kalligrammatidae, a lacewing); (3) *Nemognatha* sp. (Coleoptera: Meloidae, a modern blister beetle); (4) *Palaeopangonius eupterus* Ren (Diptera: Tabanidae, a horsefly); (5) *Florinemestrius pulcherrimus* Ren (Diptera: Nemestrinidae, a tanglevein fly); (6) *Protapiocera* sp. (Diptera: Apioceridae, a flower-loving fly); (7) *Lichnomesopsyche gloriae* Ren, Labandeira & Shih (Mecoptera: Mesopsychidae, a scorpionfly); (8) *Pseudopolycentropus janeanae* Ren, Shih & Labandeira (Mecoptera: Pseudopolycentropodidae, a scorpionfly); (9) *Jeholopsyche liaoningensis* Ren, Shih & Labandeira (Mecoptera: Aneuretopsychidae, a scorpionfly); and (10) *Oegoconites borisjaki* Kusnezov (Lepidoptera: Gelechiidae, a twirler moth). See also Figures 3–10; sources for long-proboscid data are Kusnezov (1941), Ren (1998b), Labandeira (2005a, pers. obs.), and Ren et al. (2009).

uptake of fluids and particulate pollen (Schremmer, 1961; Elzinga & Broce, 1986; Jervis et al., 1993; Faucheux, 1999; Krenn & Kristensen, 2000). Siphonate mouthparts are powered by a suction pump of a series of compressor muscles attached to chamber walls in the front of the head, often adjacent to the antennal bases (Eastham & Eassa, 1955; Ren et al., 2009). There may be a second salivary pump formed of the pre-esophageal region (Gouin, 1949; Zaka-ur-Rab, 1978; Eberhard & Krenn, 2003). Consequently, most siphonate mouthparts operate by a single or a double pump combination that works in tandem with capillary or other means of fluid absorption at the proboscis terminus. Long-proboscid mouthparts occur in true flies, moths and butterflies, three extinct scorpionfly lineages, two extinct lacewing lineages, wasps and bees, beetles, and caddisflies. A modification occurs in two modern lepidopteran lineages where the siphon cradles clustered masses of pollen that are extraorally treated by digestive enzymes for subsequent intake and digestion (Boggs et al., 1981; Eberhard et al., 2009).

Alternatively, pollen may be acquired in behaviorally stereotyped wiping movements by palps or other cleaning appendages that collect pollen for delivery to the esophagus (Schicha, 1967). Assisting these movements is hydraulic protrusability of mouthparts and their retractability, powered by intrinsic musculature within a particular element and extrinsic muscle bundles originating from the head capsule. Elongate head shapes further add to the reach of the mouthparts. A prominent example of such a mouthpart mechanism is the labial-maxillary complex of small parasitoid wasps and larger bees (Jervis & Vilhelmsen, 2000), which has been transformed into a distinctively concealed, nectar extraction apparatus that can be folded and collapsed when not in use by lever-based muscles (Gilbert & Jervis, 1998; Jervis, 1998). This tubular proboscis has originated many times among wasps and other hymenopteran taxa (Krenn et al., 2002), but the wealth of mouthpart diversity in these forms is beyond the scope of this contribution (see Jervis [1998] and Krenn et al. [2005] for brief reviews).

Another mechanism for surface fluid feeding is the modification of the proboscis terminus into a prominent, expansive, terminal region, e.g., the distinctive, fleshy labellum of flies (Peterson, 1916; Elzinga & Broce, 1986) and the haustorium of caddisflies (Crichton, 1957). The labellum consists of expansions of the labial palps that form a single, conjoined, sponging organ that is adpressed to surfaces for imbibing fluids; solid substances may be liquefied by salivary enzymes (Graham-Smith, 1930; Szucsich & Krenn, 2000). The fly labellum consists of pseudotracheae, or small, linear channels that ramify into larger collecting tubules that move fluid to the proboscis food canal and ultimately to the esophagus (Bonhag, 1951; Elzinga & Broce, 1986; Szucsich & Krenn, 2000). Flies with labella are often nectarivorous (Kevan & Baker, 1983; Larson et al., 2001; Labandeira, 2005a). Structural analogs to the labellum occur among the pseudolabellae of extinct scorpionflies (Ren et al., 2009) and the haustorium of extant caddisflies (Crichton, 1957), which are used to imbibe surface fluids, presumably pollination drops and nectar, respectively. Sponging structures in these two groups lack true dipteran pseudotracheae, although linear creases or setae probably serve the same function.

PIERCING AND SUCKING

The Hemiptera, Thysanoptera (thrips), and many Diptera have invasive stylate mouthparts. These mouthparts penetrate plant and animal tissue. They generally consist of elements housed as two pairs of short to very long stylets, one mandibular pair and an opposing maxillary pair to penetrate tissue. There is considerable modification of the number and arrangement of stylets. The Hemiptera bear two stylet pairs that are collectively ensheathed, whereas the Diptera frequently have an additional, fifth needlelike stylet. By contrast, the asymmetrical mouthcone of the Thysanoptera contains three stylets and lacks the right mandibular stylet. Some piercer-and-suckers are blood feeders that target the capillary blood or subdermal lymph in vertebrates or consume the fluidized contents of small arthropod prey (Lehane, 1991). Alternatively, other piercer-and-suckers are phytophagous and consume mesophyll and cambial tissue protoplasts, sap from phloem and xylem, petal or secretory tissues of flowers, or contents of individual pollen grains (Grinfel'd, 1959; Weber, 1968; Lewis, 1974). Some are mycophagous and feed on fungal tissues or individual spores (Lewis, 1974; Ananthakrishnan & James, 1983). A few Hemiptera, principally phytophagous bugs, are pollinators (Ishida et al., 2008). Thrips commonly are associated with flowers (Pellmyr et al., 1990; Totland, 1993; Momose et al., 1998; Jürgens et al., 2000) and use the punch-and-suck feeding for extracting individual protoplasts from pollen grains (Grinfel'd, 1959; Kirk, 1984). This technique apparently was used by thysanopteran ancestors on Permian noeggerathialean spores (Wang et al., 2009) and evolved separately in some modern ceratopogonid midges of the Diptera (Billes, 1941; Downes, 1955). With the exception of thrips, piercing-and-sucking mouthparts are minimally important to pollination.

THE PLANTS

Several major seed plant clades with gymnospermous reproduction were probable sources of nutrition for diverse guilds of mid Mesozoic insects feeding on

reproductive tissues. Mandibulate, biting-and-chewing insects, such as beetles, probably consumed internal and perhaps exposed tissues of large bisexual (hermaphroditic) strobili and cones, typical of cycads, bennettitaleans, and probably pentoxylaleans. Internal, mostly parenchymatic, tissues were consumed by larvae, whereas external tissues, such as micropylar secretions of pollen drops and prepollen and pollen, provided fluid food for conspecific adults while incurring the incidental benefit of pollination for the host plant.

PLANT FEATURES ASSOCIATED WITH MANDIBULATE INSECT POLLINATORS

Mid Mesozoic plants, including cycads, bennettitaleans, and pentoxylaleans, have been suggested as being largely pollinated by mandibulate insects (Crepet, 1972, 1974; Klavins et al., 2005; Labandeira et al., 2007a). During the Early Cretaceous, a few lineages of basal angiosperms with large, showy flowers undoubtedly were similarly pollinated (Gottsberger, 1988; Bernhardt, 2000). Early angiosperms, such as the Nymphaeaceae, Schisandraceae, and Magnoliaceae, had floral structures that mimicked unrelated gymnosperms, being similar in gross morphology and thermogenic behavior (Dieringer et al., 1999; Bernhardt, 2000; Seymour & Matthews, 2006; Thien et al., 2009). The mandibulate insects implicated in these convergent associations were dominantly Coleoptera that ranged an order of magnitude in size (cf. Thien et al., 2009). The larvae consumed internal tissues while the adults ate accessible pollen and probably associated strobilar and vegetative tissues. Other mandibulate taxa, such as anthophilous Neuroptera, based on modern nemopterid pollinator biology (Popov, 2002), may have played a role as fluid or pollen feeders. Other vectors probably included Blattodea, Orthoptera, and Trichoptera (Porsch, 1958).

Four major modifications of gymnospermous seed plants are associated with pollination predominantly by mandibulate insects. First is the evolutionary developmental compaction of unisexual ovulate and pollen organs into a compound, bisexual (hermaphroditic) strobilus (Rudall et al., 2009; see Specht & Bartlett, 2009, for reviews). In a bisexual strobilus, short-distance pollination by relatively nonvagile, sedentary insects, such as beetles, is easy. However, there is a potential genetic cost of inbreeding depression, and mechanisms to enhance outcrossing might be selected for.

A second modification is establishment of a reward structure centered on the compact bisexual strobilus and the coexisting, sedentary to moderately mobile insect pollinators. The predominant insect reward for cycads, bennettitaleans, and presumably pentoxylaleans overwhelmingly emphasized pollen, but only subordinately pollination drops (Tang, 1987a). This is inferred from studies of extinct and extant insect taxa responsible for damage of fertile strobilar tissues as well as the adult insect mouthpart structure of likely descendant or analog pollinators (Crepet, 1983; Crowson, 1991; Watson & Sincock, 1992; Norstog et al., 1995; Schneider et al., 2002; Labandeira et al., 2007a). However, there are some beetle pollinators that do not directly feed on pollen but instead cover their bodies with unconsumed grains, some of which result in pollination (Donaldson, 1997). The dominance of a pollen-based reward in these gymnosperms contrasts with the dominance of fluid-based rewards that provide highly mobile, occasionally hovering insects with carbohydrate rewards to provide calories required for longer distances and powered flight (Haslett, 1989a; Wäckers, 2002; Nepi et al., 2009).

Third is protection of the ovulate part of the strobilus from the potentially destructive feeding damage by mess-and-soil pollinators such as beetles. The closest gymnospermous analog to the bitegmic ovule of angiosperms is the cupule of †*Caytonia* (Specht & Bartlett, 2009), if reduced to a single ovuled structure. The inner wall of ovulate tissues is developmentally separate from an outer wall formed by the enveloping cupule (Doyle, 2008). In the case of bennettitaleans, protection from insects would be afforded to ovules by extraovular structures, including encompassing bracts, thickened microsporophyll tissue, interseminal scales, and/or timing changes such as the retardation or acceleration of pollen maturation and ovular receptivity (Crane & Herendeen, 2009).

Distinct from the primary pollinator rewards (pollen, pollination drops, nectar) is a fourth type of plant-host specialization for mandibulate insects, specifically the production of decoy tissue. Decoy tissues deflect or deter pollinators from consumption of essential reproductive tissue such as ovules and pollen. Bennettitalean receptacular tissue and interseminal scales may be decoy tissue based on evidence from insect tunneling damage in several bennettitalean strobili (Crepet, 1972, 1974; Labandeira et al., 2007a) and pentoxylalean fructifications (Nishida & Hayashi, 1996). Abundant receptacular tissue could have protected the reproductive organs at the expense of vegetative tissue in Late Jurassic and Cretaceous bennettitalean strobili, many of which have borings overwhelmingly in reproductively inessential tissues (Labandeira et al., 2007a). Some early angiosperm lineages with large flowers (Dieringer et al., 1999; Seymour & Matthews, 2006) favor use of vegetative tissues ostensibly to reduce the extent of damage to reproductive organs. Another decoy example is strobilar thermogenesis in cycads, attracting insects for mating and brood sites (Tang, 1987b; Roemer et al., 2005). Decoys were variably and independently elaborated in early angiosperms, culminating in modern

insect-mimicking pseudocopulation in orchids (Paulus & Gack, 1990), members of a lineage that originated by the latest Cretaceous (Ramírez et al., 2007).

CYCADALES

Cycads probably had an origin during the Pennsylvanian, based on several late Paleozoic taxa with cycad features (Mamay, 1976; Anderson et al., 2007; Taylor et al., 2009). They evidently were pollinated by insects, based on circumstantial evidence from Permian cone structure, surrounding vegetative glands, and other possible insect-reward tissues (Mamay, 1976; Taylor et al., 2009). More convincing documentation of palynophagy on a male cone comes from the Middle Triassic of Antarctica (Klavins et al., 2005), and reproductive features for the similarly aged †*Anarcticycas*, a member of the Cycadaceae, that indicate insect pollination (Hermsen et al., 2009). Insects are involved in the pollination of the most plesiomorphic, extant cycad taxon, *Cycas* L. of the Cycadaceae (Ornduff, 1991; Yang et al., 1999; Kono & Tobe, 2007). Extant Zamiaceae and Stangeriaceae, whose earliest occurrences are Jurassic, are obligately insect pollinated by a spectrum of beetle pollinators, such as Boganiidae, Erotylidae, Belidae, and Curculionidae (Norstog, 1987; Norstog & Fawcett, 1989; Crowson, 1991; Donaldson, 1992; Forster et al., 1994; Norstog et al., 1995; Tang, 1997; Wilson, 2002; Hall et al., 2004; Oberprieler, 2004), and also by the aeolothripid thrips *Cycadothrips* (Okajima, 2000; Mound & Terry, 2001; Terry et al., 2005). It has been suggested that most of these associations are ancient and mid Mesozoic in origin. This inference is probably correct, as several beetle and thrips lineages have mid Mesozoic body-fossil records (Arnol'di et al., 1977; Farrell, 1998; Gratschev & Zherikhin, 2003; Grimaldi et al., 2004) and all extant cycads are dioecious (Norstog, 1987).

BENNETTITALES

The Bennettitales are a moderately diverse group of arborescent, Laurasian seed plants with cycadlike foliage and pachycaulous or perhaps woody stems, but with characteristic unisexual or bisexual strobili. The group consists of two morphologically distinctive and temporally disjunct clusters of taxa. An earlier assemblage contains several poorly known lineages occurring during the Middle and Late Triassic (Anisian–Rhaetian) that bear unisexual strobili but with the ovulate strobilus not typically differentiated into ovulate and interseminal scales (Pedersen et al., 1989; Anderson et al., 2007). Minimally overlapping with this assemblage are three, better known, family-level lineages ranging from the Late Triassic to Late

Cretaceous (Carnian–Campanian), comprising the Williamsoniellaceae, Williamsoniaceae, and Cycadeoideaceae (Watson & Sincock, 1992). These taxa frequently possessed bisexual strobili with female portions differentiated into ovulate and interseminal scales (Crane & Herendeen, 2009). This later Mesozoic assemblage is especially prominent in Late Jurassic and Early Cretaceous floras, often co-existing with gnetaleans and later with angiosperms, and shows evidence for insect pollination, inferred to be mandibulate insect associates, particularly beetles.

Networks of galleries traverse receptacular, microsporophyll, megasporophyll, and reproductive tissues, with interseminal scales often consumed at the contact between ovulate and pollinate organs (Crepet, 1974; Labandeira et al., 2007a). Based on the structure, geometry, and presence of coprolites in these borings, the culprits probably were larval beetles feeding on solid tissues. Also, this type of insect interaction is similar to that of extant cycads, where weevils consume strobilar tissues and effect pollination (Norstog et al., 1992, 1995). Presumably, there was enough migration of adult beetles among conspecific bennettitalean individuals to prevent inbreeding depression.

PENTOXYLALES

The Pentoxylales, by some accounts, are closely related to bennettitaleans (Anderson et al., 2007) and also harbored insect larvae that bored into fructifications. A three-dimensionally preserved, silicified fructification bearing an arc of ca. 12 seeds embedded in fleshy tissue was described by Nishida and Hayashi (1996), which was assigned to the Pentoxylales, most likely a new lineage similar to †*Pentoxylon* (Bose et al., 1985). In this specimen was an excellently preserved, reflexed larva enclosed in a lined ellipsoidal chamber amid interseminal fleshy tissue, adjacent to seeds (Nishida & Hayashi, 1996). The larva was assigned to the Nitidulidae (sap beetles), a clade presently associated with angiosperms, whose adults typically feed on sap flows or are pollinators (Gazit et al., 1982; Kirejtshuk, 1997).

PLANT FEATURES ASSOCIATED WITH HAUSTELLATE INSECT POLLINATORS

In contrast to mid Mesozoic seed plant clades that bore compact strobili pollinated predominantly by mandibulate insects, other gymnosperm clades possessed dioecious ovulate and pollen organs loosely arranged on branches. The ovulate organs of these plants provided nutrient-rich fluids as a reward for aerially mobile fluid-feeding insects, such as various long-proboscid taxa. These gymnosperms had in common insect-related modifications of the basic

pollination drop system used extensively for wind pollination that currently is best demonstrated in conifers. The ancestral pollination mode in seed plants is wind pollination, wherein the distal part of an ovule bore a short, tubular micropyle that became filled with secretory fluids originating from vacuole-laden, secretory tissue adjacent to the nucellus. Secreted pollination fluid fills the micropylar tube, forming a bubble, or drop, at the terminus to trap ambient pollen (Chesnoy, 1993; Takaso & Owens, 1996). This is followed by fluid resorption or evaporation and withdrawal of the drop with trapped pollen to the nucellus where fertilization occurs through a pollen tube (Gelbart & von Aderkas, 2002). This condition has been demonstrated for late Paleozoic medullosan seed ferns (Rothwell, 1977) and a variety of fossil fructifications that have been described with ovules bearing relatively short, basally flaring micropyles consistent with wind pollination.

Modifications consistent with insect pollination are known for the Early Jurassic in several lineages of seed plants, based on ovulate organ structure and pollen types (Harris, 1932; Delevoryas & Gould, 1973; Pocock et al., 1990). This shift in pollination mode required five significant changes in plant morphology as well as mouthpart and presumably behavioral changes in co-occurring, haustellate insects.

1. For Jurassic gymnosperm lineages, the micropyle became significantly lengthened and its inner diameter became wider to accommodate narrow-diametered and prolonged insect proboscises in the range of 0.1–0.7 mm diam. to ca. 5–11 mm in length (Ren et al., 2009). During the Early Cretaceous, proboscis lengths extended to 15 mm or longer, approximately matched by micropylar lengths in certain species of the gnetalean †*Problematosper-mum* and some bennettitalean ovulate organs.

2. Related to this was the formation of various cupulate structures that connected deeply hidden micropyles to surface orifices by tubular structures that ranged in length from ca. 3 to 15 mm. These tubes were surrounded often by fleshy tissues, occasionally with an outer sclerified layer (Ren et al., 2009). These tubular structures bore surface entry points—salpinx tubules, integumental tubes, catchment funnels, tubuli, elongate micropyles—that are not homologous but represented convergent solutions for accessing deep-seated secretory fluids by long-proboscid insects (Labandeira et al., 2007a; Ren et al., 2009). Shorter tubular structures would afford access to short-proboscid and other insects, similar to the pollinators and fluid feeders on modern gnetaleans (Church, 1914; van der Pijl, 1953; Bino et al., 1984a, b; Marsh, 1987; Carafa et al., 1992; Kato et al., 1995; Wetsching & Depisch, 1999).

3. Studies of the nutritional value of insect-consumed secretions occurring in present-day plants, including extranuptial nectary secretions in ferns, pollination drops in gymnosperms, and nectar and nectarlike secretions in basal angiosperms, suggest a third modification (Pacini et al., 2003; Nepi et al., 2009). Fern nectaries produce watery, nutritionally poor secretions, whereas carbohydrate and amino acid concentrations of pollen drops from the four major lineages of gymnosperms—conifers, *Ginkgo* L., cycads, and gnetaleans—showed significantly more elevated nutritional levels, particularly in the two latter insect-pollinated clades (Labandeira et al., 2007a). Nutritional levels in pollination drops of the four gymnosperm clades are similar to those of nectar from basal angiosperm lineages (Labandeira et al., 2007a; Wagner et al., 2007; Nepi et al., 2009). Lipid levels were not measured. Pollen drops associated with wind pollination may be an exaptation (Gould & Vrba, 1982), being co-opted by insects that used the resource for an alternative feeding function, as high levels of carbohydrates and amino acids are important for sustaining the high levels of metabolic activity for highly mobile, winged insects (Baker & Baker, 1983; Gottsberger et al., 1984; Erhardt & Baker, 1990; Tang, 1997; Wäckers, 2002).

4. Studies of modern pollen indicate that characters consistent with entomophily are recognized throughout the palynological fossil record. Most obvious is size. Pollen larger than ca. 25 µm in maximum diameter tend to be insect vectored, and almost obligately so for larger-diametered taxa (Whitehead, 1969). Pollen shape also is significant; insect-pollinated grains typically lack bladders or sacci and frequently are spheroidal to ellipsoidal in shape (Ackerman, 2000). Related is the functional unit of transmission, in which the individual grain often is not the transported unit, but rather a larger pollen aggregate. Pollen of the cheirolepidiaceous conifer †*Classopollis* consists of four attached grains at the tetrad stage of development (Courtinat, 1980); this increases effective diameter during transportation, as do various types of clumping caused by sticky substances on pollen surfaces, such as viscin threads or pollenkitt (Nixon & Crepet, 1993; Zetter & Hesse, 1996; Hu et al., 2008). A pollinium is another way of bundling or packaging grains to achieve an efficient transportable size. Pollinia are known in several angiosperm lineages, such as orchids (Micheneau et al., 2009), but do not occur in gymnosperms. Similarly, certain surface ornamentation and exine ultrastructure indicate entomophily in modern angiosperms (Osborn et al.,

1991a; Hesse, 2000) and in fossil gnetophytes where taeniate pollen preferentially occur in Permian insect guts (Krassilov et al., 2007).

5. The breeding system of most Mesozoic nonangiospermous seed plants tends to emphasize outcrossing. Male and female organs are either on the same plant, typically on separate axes or on different individuals, or are alternatively hermaphroditic, with male and female monaxial organs compressed into a single, compact strobilus, as in some bennettitalean strobili or analogous angiosperm flowers.

CORYSTOSPERMALES

The corystosperms were a prominent seed-fern group during the Late Triassic and Jurassic, but continued to the Paleogene in Australia. Corystosperms are best represented by the Umkomasiaceae, ranging throughout the Triassic, a diverse Gondwanan assemblage of arborescent, wind-pollinated plants bearing †*Umkomasia* ovulate organs, †*Pteruchus* pollen organs, †*Rheoxylon* trunks and branches, and †*Dicroidium* foliage (Retallack & Dilcher, 1988; Anderson et al., 2007). However, two types of undescribed, rare, probable corystosperm seeds from the Late Triassic Molteno Formation contain considerably elongated micropylar extensions that suggest insect pollination (Labandeira, 2008, pers. obs.). Depending on the species, *Pteruchus* pollen organs produce †*Alisporites*-type, †*Pteruchipollenites*, or †*Falcisporites* pollen. These grains can be large, some ranging from 88 to 115 μm in maximum length (Taylor & Taylor, 2009) or measuring 46–93 μm (Cantrill et al., 1995), which indicates a dispersal mechanism other than wind. Nevertheless, significantly smaller pollen sizes were documented for bisaccate †*Alisporites australis* de Jersey, affiliated with †*Umkomasia granulata* Thomas (Retallack & Dilcher, 1988), supporting wind pollination, undoubtedly the norm for the group.

PENTOXYLALES

Pentoxylales were first described from India (Sahni, 1948), based on *Pentoxylon*, an anatomically distinctive trunk form-genus that ranged from late Early Jurassic to late Early Cretaceous and with mostly a Gondwanan distribution. The best-known, whole-plant pentoxylalean is a shrub, with affiliated *Pentoxylon* stems, †*Nipaniophyllum* foliage, †*Carnoconites* ovulate organs, †*Sahnia* pollen organs, and monocolpate pollen often affiliated with some †*Cycadopites* species, which were 17–22 μm long (Bose et al., 1985; Osborn et al., 1991b). Micropyles of ovules breaching the surface of conelike organs are very short, from 1 to 3 μm deep, presumably requiring the smallest of long-proboscid or small nonproboscid insects for pollina-

tion. Pollen drops would have been a reward in lieu of pollen, which could have been wind dispersed, suggesting ambiphilous pollination.

CZEKANOWSKIALES

As members of a broad ginkgoopsid alliance, Czekanowskiales, of which Leptostrobaceae is one of the better known families, ranged from the Late Triassic Rhaetian to the earliest Late Cretaceous Cenomanian of Eurasia and North America. The form genus †*Leptostrobus*, of unknown growth habit, consists of †*Czekanowskia* foliage, †*Ixostrobus* pollen organs, and *Leptostrobus* ovulate organs whose pollen is referred to certain *Cycadopites* species (Harris, 1951b; Anderson et al., 2007). The ovules are bivalved and apparently had a hard exterior, with ovules anatropously positioned such that ovule micropyles were directed adaxially (Harris, 1951b; Ollerton & Coulthard, 2009). The distance of the salpinx channel, between the *Leptostrobus* backwardly directed ovular micropyles that bore pollen drops and the terminal slit or aperture, was ca. 4–7 mm, depending on the species. The presence of pollen drops is inferred from micropylar structure and presence in *Ginkgo* (Dogra, 1964). This short channel probably represents an independent, seemingly unique, innovation for accessing plant pollen drops by fluid-feeding, long-proboscid insects.

CHEIROLEPIDIACEAE

Cheirolepidiaceous conifers were a dominant seed plant clade during the Late Jurassic and Early Cretaceous, although they have their origin probably during the Late Triassic. The lineage may have become extinct during the Campanian of the Late Cretaceous, although there is evidence that they survived into the Paleogene of Patagonian South America (N. R. Cúneo, pers. comm., April 2007). A well known, Early Cretaceous, European member of Cheirolepidiaceae is the arborescent whole-plant †*Alvinia bohemica* Kvaček, whose namesake is based on the ovulate cone. *Alvinia bohemica* is affiliated with the conspecific, smaller pollen cone, †*Frenelopsis alata* (Feistmantel) Knobloch, which produced distinctive *Classopollis* pollen, both of which are associated with foliage that is also known as *A. bohemica* (Kvaček, 2000). The ovulate scales on the cone of *A. bohemica* are one of the most complicated female reproductive structures known in seed plants (Labandeira et al., 2007a). Each scale has ca. 10 abaxial lobes, some of which would be conspicuous on the outside of the cone, while on the adaxial side are two ovules, one of which is usually aborted, whose micropyles are oriented adaxially. Opening on the abaxial aspect of the ovulate scale,

surrounded by conspicuous lobate processes, is a funnel-shaped structure oriented lengthwise within the scale. The aperture of the funnel is surrounded by long, unicellular trichomes that decrease in abundance as the gullet of the funnel narrows. Lining the narrowed funnel base are thickened, squat, multicellular, nectary-like glands that probably were secretory in nature. At the very base of the funnel, where the nectary-like structures end, there is an opening where the funnel merges into a linear, tubular extension or a pipe (Kvaček, 2000). This pipe traverses the rest of the inner tissue of the ovulate scale to end at the adaxial aspect of the scale, immediately adjacent and almost touching the micropyle of the remaining, viable ovule. The funnel portion of this conduit is minimally 6–8 mm long, somewhat longer than the 6-mm-long pipe.

The simplest interpretation of this tubular, abaxial to adaxial catchment funnel-pipe-micropyle complex is a device for insect pollination. Two types of pollinator activity are suggested by co-occurring insect taxa: long-proboscid, winged, perhaps hovering insects able to insert a long tubular siphon and imbibe a nectarlike secretory reward, or considerably more diminutive insects that could have walked into the funnel and directly probe the trichome- and nectary-lined wall for rewards (Labandeira et al., 2007a). In either case, *Classopollis* pollen would have been deposited at the base of the funnel, near the entrance to the pipe, which would have served as a conduit for the pollen tubes to the short micropyle. Given this hypothesis, the funnel, perhaps visually enhanced by colorful external lobes, can be considered an inverted stigma with nectarial secretory rewards (Kvaček, 2000). The *Classopollis*-bearing pollen organ would have provided a reward as well, perhaps the pollen itself, or alternatively a secretory fluid produced by unknown structures similar to those of the ovulate organ.

GNETALES

Gnetales were a diverse group that originated in the mid Triassic, were present in many Jurassic floras, and experienced a radiation during the Early Cretaceous, largely synchronous with that of angiosperms. Modern gnetaleans consist of three disparate lineages that represent a reduction of major morphologies compared to the diversity found during the Early Cretaceous (Crane, 1996). With possible exceptions in Ephedraceae, Gnetales are insect pollinated (Bino et al., 1984a, b; Kato et al., 1995; Wetsching & Depisch, 1999). Modern insects that pollinate the extant taxa—*Ephedra* L. (Ephedraceae), *Welwitschia* Hook. f. (Welwitschiaceae), and *Gnetum* L. (Gnetaceae)—are a broad array of small, short-proboscid or nonproboscid insects, predominantly flies, moths, and wasps, but also incon-

spicuous beetles with mandibulate mouthparts, as well as thrips with modified punch-and-suck mouthparts. Modern insect pollinators feed on nutritionally rewarding gnetalean pollination drops (Porsch, 1910; Meeuse, 1978; Carafa et al., 1992; Kato & Inoue, 1994) and often possess short proboscises that take up surface fluids from both male and female plant organs. Many of the extinct gnetalean taxa with ovulate organ morphology similar to the three extant lineages are inferred to have been similarly pollinated by small-winged insects (Lloyd & Wells, 1992). However, a few ovules, such as *Problematospermum* (Sun et al., 2001), bore exceptionally long micropyles (pappus tubes) extending from an achene base surrounded by a tuft of bracteate papery scales or tufts of feathery hairs (Krassilov, 2009), analogous to that of modern Asteraceae (Taylor et al., 2009), and appear to be an adaptation to insect pollinators with long, narrow proboscises. The encircling appendages may have served as a pollinator lure.

CAYTONIALES

Caytoniales comprise a few genera of which *Caytonia*, originally described from the early Middle Jurassic of Yorkshire, United Kingdom (Harris, 1933, 1940, 1957; Anderson et al., 2007), is best known. The Caytoniaceae are Eurasian in distribution and range from the Late Triassic (Carnian) to the lowermost Cretaceous (Berriasian). They are presumed to be woody shrubs or trees. The lineage may be closely related or is the sister group to angiosperms (Crane, 1985; Doyle, 2008). The most notable specimens of *Caytonia* are ovulate organs from the Bajocian to Bathonian in the Middle Jurassic of Yorkshire and are affiliated with distinctive †*Sagenopteris* Presl foliage, †*Caytonianthus* pollen organs, †*Amphorispermum* dispersed seeds, and †*Vitreisporites* pollen (Harris, 1951a, 1957; Zavada & Crepet, 1986; Retallack & Dilcher, 1988; Ren et al., 2009). The *Caytonia* plant bore an erect, thick, and probably fleshy recurved cupule that had several downwardly oriented seeds attached to placentation along the upper cupulate region. Each short micropyle ended in a tubule within the cupulate tissue that terminated in a surface opening under a distinctive lip adjacent to the subtending peduncle. The most intriguing anatomical feature of *Caytonia* are these tubular connections between the micropylar pollination drops and the lower lip, which are diachronously deployed, one at a time as each ovule reached maturation within the infructescence. The length of these integumental tubules ranges approximately from 2 to 6 mm and is consistent with similar measurements for the siphonal lengths of co-occurring long-proboscid insects (Ren et al., 2009).

Modes versus Syndromes

The notion of pollination syndromes was established early in pollination ecology, but recently has been challenged (Ollerton, 1996; Waser et al., 1996; Fenster et al., 2004). As originally defined, with subsequent modification, a pollination syndrome consists of a group of functionally related floral characters and behaviors that collectively are consistent with pollination by a similarly distinctive functional taxonomic group of animals that have convergent feeding strategies, functionally similar mouthpart types or foraging behaviors that access floral rewards in the same way. Floral rewards typically are nectar and pollen, but also include oils, resins, mating sites, warm resting places, and other less obvious attributes (Baker & Baker, 1979; Pellmyr & Thien, 1986; Haslett, 1989a; Thien et al., 1990; Bergström et al., 1991; Donaldson, 1992; Lopes & Machado, 1998; Azuma et al., 1999; Jürgens et al., 2000; Frame, 2003; Seymour & Matthews, 2006). Recently, the traditional notion of pollination syndromes, e.g., beetle-pollinated flowers (cantharophily), small fly-pollinated flowers (myiophily), and bee-pollinated flowers (melittophily), has been shown to be inconsistent with the realized spectrum of visiting animals. They also were inconsistent with the features of the pollinated flowers themselves when attributes of the animal pollinators were taken as predictable variables (see Ollerton et al., 2009, for an example). Such examinations frequently indicated that the suite of characters predicated by a type of animal pollinator was not borne out by post hoc confirmatory tests. Because the idea of a pollination syndrome has not been supported, and there is considerable evidence for overwhelming generalization over specialization in modern pollination systems (Ollerton, 1996; Waser, 1998), the more epistemologically neutral term "mode" is used herein, without attribution to a particular pollinator or pollinated clade.

A Brief History of Earlier Pollination-related Feeding

An early precursor to insect pollination during the mid Mesozoic involved the consumption of pollen, prepollen, and spores (palynophagy) and the imbibation of surface fluids such as extrafloral nectarial secretions, pollination drops, honeydew, and similar secretions (nectarivory). Fossil evidence indicates that palynophagy occurs significantly earlier than nectarivory (Labandeira, 1998, 2002a). Both major diet types contain various combinations of sugars, lipids, proteins, and other substances sufficient for nutritional sustenance (Labandeira, 2000).

Palynophagy

The earliest palynophagy occurred during the latest Silurian and Early Devonian Periods and is represented by coprolites containing either a single kind of plant spore or compositionally heterogeneous types of sporangial and vegetative tissues (Edwards et al., 1996). These coprolite assemblages indicate the targeting of early land-plant hosts by microarthropods, occasionally suggesting specialization on a single host (Edwards et al., 1996; Labandeira, 1998). The culprits were microarthropods, particularly wingless, phylogenetically basal, hexapod clades. Isolated reports of spore-bearing coprolites continue through the later Devonian and into the Mississippian, but palynophagy dramatically increased during the Pennsylvanian of Euramerica. Two lineages of insects, in particular the major extinct clade Palaeodictyopteroidea, included taxa that used modified piercing-and-sucking beaks for consumption of spores (Labandeira, 2006b). Also, distant mandibulate ancestors of Orthoptera (grasshoppers and crickets) consumed spores and sporangial tissues. Evidence for palynophagy from both insect groups is based on mouthpart structure, gut contents, permineralized coprolites, and feeding damage to spore-bearing plants in coal balls and compression deposits (Labandeira, 1998, 2006b).

The spectrum of palynivores increased significantly during the Permian. The evidence is mostly based on insect mouthpart morphology consistent with pollen feeding (Rasnitsyn, 1977; Novokshonov, 1998), but also from fossil macerations of insect gut contents from Chekarda, Russia, that reveal an eclectic breadth of consumed pollen types (Krassilov et al., 2007). A broad representation of Permian insect lineages—the Grylloblattodea (rock crawlers), Psocoptera (booklice), extinct Miomoptera, stem Hemipteroidea, and probably early thrips—were feeding on a diverse assortment of prepollen and pollen from host plants such as noeggerathialeans (†*Discinispora*), cordaites (†*Florinites*), glossopterids (†*Protohaploxypinus*), medullosans (†*Potoniesporites*), early conifers (†*Lunatisporites*), and gnetophytes (†*Vittatina*) (Rasnitsyn & Krassilov, 1996; Krassilov et al., 2007; Wang et al., 2009).

After the end-Permian extinction interval, the record of palynophagy resumes and expands toward the end of the Triassic and the Early Jurassic. During this interval, the emergence of modern lineages with known feeding habits occurs in both larvae and adults. During the Triassic and into the Jurassic, early mandibulate lineages of the Hymenoptera, Coleoptera, Lepidoptera, and perhaps other holometabolous orders were likely palynophagous, colonizing cycadalean, bennettitalean, pentoxylalean, and undoubtedly other plant hosts.

NECTARIVORY

The early fossil record of feeding on the external surface fluids of plants is tenuous and appears much later than palynophagy, probably beginning during the Late Pennsylvanian. Because fluid food, in contrast to pollen, is not preserved as insect gut contents, evidence for fluid feeding is more indirect and relies on reproductive morphologies of potential host plants and on the distinctive mouthparts of insects associated with nonpenetrative fluid feeding. The Pennsylvanian to Permian record for nectarivory suggests that the Palaeodictyopteroidea may have extended its sap-feeding mode of puncturing tissues to probing fructifications for access to fluids secreted in deep but accessible anatomical structures (Zherikhin, 2002). Additional evidence is provided by insects with specialized mandibulate mouthparts that could access surface fluids produced by secretory trichomes and other plant glands on exposed surfaces of fructifications and vegetative organs (Mamay, 1976; Taylor & Millay, 1979; Krings & Kerp, 1999; Labandeira, 2000). However, such secretory products might be antiherbivore deterrents to aid pollination, or alternatively might be seen as simply plant metabolic byproducts. There is evidence for siphonate mouthparts borne by small insects during the Permian. One late Early Permian neuropteran insect, from the Ural Mountains of Chekarda, Russia (Vilesov, 1995), had a distinctively extended siphonate proboscis consistent with fluid feeding, but only had a reach of approximately 2 mm.

From the Early Triassic to Early Jurassic, there is limited evidence for insect fluid feeding involving pollination. This comes mostly from seed plant reproductive structures rather than insect mouthparts (Labandeira, pers. obs.). Seed-fern taxa of this interval typically had a pollination-drop system for capture of wind-dispersed pollen, but this could have been modified, such as lengthening and widening of the internal diameters of micropyles to attract long-proboscid insects as more efficient vectors. The only compelling evidence for surface fluid feeding originates from distinctive, long-proboscid insect mouthparts preserved in compression deposits from the Eurasian Middle Jurassic, continuing into the Late Jurassic and into the late Early Cretaceous (Ren et al., 2009).

POLLINATION MODES DURING THE MIDDLE JURASSIC TO MID CRETACEOUS

Figures 1 and 2 depict the global Mesozoic distribution of nine pollination modes and the related feeding associations of palynophagy and nectarivory. Both plant-host (Fig. 1) and insect-pollinator (Fig. 2) perspectives are provided, with vertical patterns indicating the temporal duration of major pollination modes and horizontal bars providing the occurrences of related feeding associations from major compression and amber localities. An emphasis is placed on the long-proboscid pollination mode and convergences in ovulate anatomy and coordinate mouthpart structure, unlike the predominant evidence of mandibulate insects that heretofore has characterized the fossil record. Seven major pollination modes are discussed.

PUNCH-AND-SUCKING POLLINATION

Recent discovery of the significant role that thrips play in certain cycad genera of Australia (Terry et al., 2004, 2005; also see Okajima, 2000) has spurred interest in finding related, cycad-specific taxa in the fossil record. The finding of †*Cycadothrips chadwicki* Mound (Aeolothripidae: Cycadothripinae), and other related new species on modern cycads and in late Early Cretaceous Burmese amber (Mound, 1991; Grimaldi et al., 2004), indicates that this distinctive association extends to the mid Mesozoic. For some Australian cycads, thrips pollination may be the second most important pollinator, surpassed only by beetles (Terry et al., 2005). Thrips also are common pollinators on basal angiosperms, attributable to their small size and penchant for accessing petal tissues and individual pollen grains by their distinctive punch-and-suck feeding technique in extracting protoplasts (Grinfel'd, 1959; Kirk, 1984). In modern floras, thrips rarely exceed 4 mm in length and are frequently abundant in a wide variety of flowers (Momose et al., 1998; Williams et al., 2001).

LARGE MANDIBULATE INSECTS

The fossil history of large, externally feeding, mandibulate insects that are inferred as pollinators consists of insect lineages that have gut contents of pollen or certain pollen types on their head and mouthpart surfaces. These indicators of palynovory or pollination often provide evidence for identifying both the insect consumer and the consumed host plant. Nevertheless, demonstration of palynovory is insufficient for identifying a pollination mutualism. With the exception of the Coleoptera, large mandibulate insects currently are minor pollinators, and consist of the Blattodea (cockroaches), Orthoptera (katydids and crickets), Phasmatodea (stick and leaf insects), and Trichoptera (caddisflies) (Porsch, 1958; Proctor et al., 1996). Mandibulate insects disproportionately characterize the fossil record of pollination when compared to evidence for haustellate forms, such as long-proboscid insects. Even so, they probably had greater participation in past palynovory and nectarivory than their current descendant lineages would indicate.

Modern Blattodea have been implicated in generalist pollination of angiosperms in the tropics (Billes, 1941; Proctor et al., 1996), although there are few specific cases of pollinator function. Examples include an undescribed species of *Hemithyrsocera*, an undetermined genus (both Blatellidae) on *Uvaria elmeri* Merr. (Annonaceae) from Sarawak, Malaysia (Nagamitsu & Inoue, 1997), *Paratropes bilunata* Saussure & Zehntner (Blattidae) on *Dendropanax arboreus* L. (Araliaceae) from Costa Rica (Perry, 1978), and *Amazonina platystylata* Hebard (Blatellidae) on *Clusia* L. sp. indet. aff. *sellowiana* (Clusiaceae) from French Guiana (Vlasáková et al., 2008). Blattodea would be prime candidates for large-mandibulate insect pollinators for the mid Mesozoic.

Unlike the Blattodea, there is a fossil record of palynophagy that indicates katydids (Orthoptera) as pollinators during the Late Jurassic. Several species of the Haglidae, such as †*Aboilus amplus* Gorochov, from the Karatau shales in Kazakhstan (Doludenko & Orlovskaya, 1976; Krassilov et al., 1997a), were documented as having *Classopollis* and other pollen types in their guts. Modern Haglidae apparently are not pollinators; however, other extant orthopterans are implicated in recent pollination (Grinfel'd, 1957; Schuster, 1974), including the related katydid lineage Tettigoniidae. The tettigoniid *Anthophiloptera dryas* Rentz & Clyne is a pollen and nectar feeder on *Angophora floribunda* (Sm.) Sweet (Myrtaceae) in eastern Australia (Rentz & Clyne, 1983). A more spectacular example is the Madagascan orchid *Angraecum cadetii* Bosser, which is pollinated by an unidentified, spinose cricket of the Gryllacrididae (Micheneau et al., 2009).

There are no records of modern walkingsticks or leaf insects (Phasmatodea) consuming pollen or acting as pollinators. However, there is a fossil phasmatodean, †*Phasmomimoides minutus* Gorochov (Susmaniidae), from the Late Jurassic of Karatau that may have been palynophagous. Its diet contained principally *Classopollis* pollen, but also a significant amount of foliar material from the same host plant (Krassilov & Rasnitsyn, 1998). It is unclear if the species was a generalist feeder on varied tissues of a cheirolepidiaceous host, or whether it was incidentally including conspecific pollen as a specialist folivore.

The Trichoptera have long been known to be occasional nectarivores (Porsch, 1958; Nozaki & Shimada, 1997), with fluid being taken up by sponging mouthparts that are convergent with the fleshy labellae of the Diptera (Crichton, 1957). Nevertheless, their importance in pollination is limited, consisting of rare occurrences, although *Stenophylax permistus* MacLachlan (Rhyacophilidae) can be a common visitor on the herb *Adoxa moschatellina* L. (Adoxaceae) in the

United Kingdom (Holmes, 2005). *Tinodes waeneri* L. (Psychomyiidae) nectars various apiaceous plants in the United Kingdom (Petersson & Hasselrot, 1994), and *Nothopsyche ruficollis* Ulmer (Limnephilidae) is rewarded on a variety of herbaceous hosts in Japan (Nozaki & Shimada, 1997). These occurrences indicate opportunistic pollination.

Overwhelmingly, the most diverse group of large mandibulate pollinators is Coleoptera. Pollen and nectar consumption, as well as pollination mutualisms, have originated numerous times within the order (Crowson, 1981), particularly within lineages of the Polyphaga, such as the Elateridae (click beetles), Buprestidae (metallic wood-boring beetles), Cleridae (checkered beetles), Nitidulidae (sap beetles), Mordellidae (tumbling flower beetles), Oedemeridae (false blister beetles), Meloidae (blister beetles), Scarabaeidae (scarabs), Cerambycidae (longhorn beetles), and Chrysomelidae (leaf beetles). Some of these are known from fossils, and cladistic evidence suggests that they extend to the Middle and Late Jurassic, or earlier (Arnol'di et al., 1977; Farrell, 1998; Zhang, 2005; Hunt et al., 2007). This assemblage of palynivores, and subordinately nectarivores, that currently pollinate large, showy flowers once was considered the ancestral syndrome for angiosperm pollination (Diels, 1916), later elaborated by Grinfel'd (1975) and Gottsberger (1989). Studies of the pollination biology within the Nymphaeaceae (Capperino & Schneider, 1985; Williamson & Schneider, 1994; Hirthe & Porembski, 2003; Seymour & Matthews, 2006), Calycanthaceae (Crepet et al., 2005), Magnoliaceae (Azuma et al., 1999; Dieringer et al., 1999), and Annonaceae (Gottsberger, 1989) all implicate these taxa and others with similar floral features in the attraction of larger-sized beetle pollinators—the cantharophily syndrome (Proctor et al., 1996). Specializations for this type of pollen feeding include maxillary pollen brushes (Fuchs, 1974) and modified mandibular teeth (Grinfel'd, 1975), which should be retrievable from fossils, or perhaps digestive enzymes (Johnson & Nicholson, 2001).

ADULT BEETLES WITH LARVAE IN INTERNAL PLANT TISSUES

In some Mesozoic fossils, the internal tissues of large ovulate or bisexual organs occasionally contain borings or interconnected galleries and tunnels evidently made by beetle larvae. Modern cycad analogs of these tunnel networks are associated with conspecific adult beetles that are pollinators of the same host plants (Norstog et al., 1992, 1995). As fossils, these networks most commonly occur in bennettitaleans (Crepet, 1974; Labandeira et al., 2007a). Limited destruction of ovulate and pollen

organs is indicated by tunneling in bisexual bennetti-talean strobili and in modern cycads, whereby vegetative and some seed megagametophytic tissues are sacrificed as a reward to larvae of the adult pollinators. Beetles responsible for these tunneling networks in modern unisexual cycad cones typically are Curculionidae (common weevils), although other related beetle pollinator taxa such as the Belidae (cycad weevils), Nemonychidae (pine flower snout weevils), and, more distantly, the Aulacoscledidae and Erotylidae (pleasing fungus beetles), could have assumed a similar role in mid Mesozoic bennettitalean strobili. Similar evidence for an endophytic, paly-nophagous beetle association occurs in a Middle Triassic cycad, †*Delmaya spinulosa*, described by Klavins and colleagues (2005), containing conspecific pollen packed into ellipsoidal coprolites amid tissue fragments within a pollen sac. A probable pentoxylalean fructification contained a nitidulid larva in the inter-seminal parenchyma of a fleshy fructification (Nishida & Hayashi, 1996), indicating a conspecific adult pollinator. Endophytic beetle borings are common throughout the Late Triassic to Early Cretaceous, involving vegetative and frequently woody tissues of conifers and extinct seed-ferns (Labandeira, 2006a), suggesting pollination by medium-sized adult beetles.

SMALL NONPROBOSCID INSECTS

Small nonproboscid insects of approximately 3–8 mm in total body length, minus appendages, have frequently been cited as the type of insect associated with the earliest flowering plant lineages. Most early angiosperm flowers were comparatively small in size (Dilcher, 1995; Crepet, 2008; Taylor et al., 2009; Thien et al., 2009) and may have developed from a preangiospermous ancestor possessing an ovulate longitudinal slit with access to pseudostigmatic secretions (Dilcher, 2010). This model is consistent with small, nonproboscid, fluid-feeding insects as the earliest pollinators of small-flowered, dull-colored, unscented angiosperms. This hypothesis contrasts strongly with the idea that large mandib-ulate insects (discussed above) were the insect pollinators of large, conspicuous flowers of the earliest angiosperms. However, these are not alter-native options, as both floral types probably reflect early angiosperm history. Nevertheless, small, non-proboscid insects apparently were more abundant and diverse in the initial pollinator colonization of angiosperms than the less diverse, large mandibulate beetles (Thien, 1980; Thien et al., 2009).

The major players of the small nonproboscid insect assemblage were flies (Diptera), representatives of which spanned the entire order during the Early Cretaceous, excluding derived cyclorrhaphous lineag-es that evolved later (Grimaldi & Cumming, 1999). An additional group was diverse, small, parasitoid wasps, which underwent a radiation during the Jurassic (Labandeira, 2002b; Rasnitsyn, 2002) and may have fed on gymnosperm pollination drops and subsequent-ly shifted to angiosperm nectar. Monotrysian and early ditrysian moths evolved during the Early Cretaceous (Labandeira et al., 1994; Grimaldi & Engel, 2005) and had relatively short proboscises compared to those of later lepidopterans; extant members are pollinators on a variety of angiosperms (e.g., Kawakita & Kato, 2004). Another nonproboscid element was small beetles; several lineages were considerably smaller than large mandibulate insects or medium-sized weevils discussed above. Amid this diverse assortment of nectar-feeding, small nonproboscid insects were perhaps pollinators of extinct seed plants such as *Pentoxylon* and *Caytonia*, with access to pollen drops through short distances of a few millimeters, similar to extant Gnetales that are pollinated by similarly small insects.

ENTRAPMENT POLLINATION

Originating several times within angiosperms and possibly other seed plants is the entrapment of insects for a crucial period of time while the plant host is receptive to pollination, followed by their release (Proctor et al., 1996). Lures and rewards enticing insect visitation include heat from host thermogenesis (Roemer et al., 2005), provision of mating sites (Petersson & Hasselrot, 1994), aroma produced by volatile compounds (Bergström et al., 1991), as well as the typical rewards of pollen and nectar. Entrapment is accomplished by a fascinating array of recurved trichomes at entry sites, initially allowing one-way access and subsequent release, stiff tissues that provide unidirectional entry that later deliquesces and provides for an exit, or closure devices such as flexibly hinged lids. These modifications to floral structure occur in several basal angiosperm lineages, notably the Nymphaeales and Magnoliales. Entrap-ment pollination represented in both lineages has been present at least since the latest Early Cretaceous (Ervik & Knudsen, 2003; Gandolfo et al., 2004).

OIL AND RESIN POLLINATION

The use of plant oils and resins as a reward extends to the Turonian of the early Late Cretaceous (Crepet & Nixon, 1998). This is based on specialized floral features of clusiaceous plant fossils from New Jersey, consistent with known floral biology of extant Brazilian Clusiaceae pollinated by euglossine bees (Lopes & Machado, 1998). This association may have

occurred earlier, as there is now evidence that bees extend to the latest Early Cretaceous (ca. 105 Ma) based on †*Melittosphex burmensis* Poinar & Danforth (2006), a small but non-oil-collecting specimen.

MID MESOZOIC LONG-PROBOSCID INSECTS AND THEIR SEED PLANT HOSTS

The oldest studies of the pollination of modern deep-throated flowers by long-proboscid insects involved morphological descriptions of pollinator mouthpart and head structure, and of receptive floral morphologies in pollinated plants (Heddergott, 1938; Takeuchi & Tokunaga, 1941; Schneider & Jeter, 1982; Zetter & Keri, 1987). Such studies historically have been done separately by entomologists and botanists and involved characterizations of insect mouthpart and plant floral structure without inference of function. More recently, there have been investigations of how insect feeding mechanisms work. Examples include capillary fluid uptake at the terminal proboscis, fluid food transport through the proboscis and the effects of possible pollen inclusion, the musculature and valvular control of single or double suction-pump system in the head frontal region or proboscis base, and ancillary structures that aid in the detection, uptake, and subsequent processing of food, such as palps, setae, and mechanosensillae and chemosensillae (Graham-Smith, 1930; Barth, 1985; Proctor et al., 1996; Faucheux, 1999; Szucsich & Krenn, 2000; Borrell & Krenn, 2005). Similar analyses were made for floral structure and function, including receptivity to and physiological responses from insect pollination (Szucsich & Krenn, 2000; Ollerton & Liede, 2003). Also addressed has been the allocation of insect pollinator and plant host resources so as to maximize joint and individual reproductive fitness. This includes study of the timing and duration of pollinator feeding and host-plant receptivity, pollination efficiency indices, detection of host-plant specificities, and ecological and morphological correlates of proboscis length and floral tube depth (e.g., Whittall & Hodges, 2007; Pauw et al., 2008). One question that has been posed involves the coevolutionary consequences of variously loose to iconically tight plant-pollinator relationships in time and space; for example, the study of how coevolutionary relationships are established, are maintained, or are eventually extirpated at the population (Thompson, 2005) or species (Armbruster & Baldwin, 1998) levels. Finally, there is the detection of insect pollination in the insect and seed plant fossil record and establishing macroevolutionary correlates. Although evidence for insect pollination has been long known in prominent Cenozoic deposits (Cockerell,

1913; Bequaert & Carpenter, 1936), an understanding of Mesozoic insect pollination in seed plants has been developed only recently and remains poorly known. It is this last aspect—the early evolution of the pollination of plants, particularly by long-proboscid insects with siphonate mouthparts—that I will dwell on for the rest of this section.

These recent investigations involve modern clades of adult holometabolous insects and their angiosperm hosts (but see Terry, 2001), both of which experienced major turnover events during the mid Cretaceous to Paleogene. For seed plants, many clades originated during or soon after a mid Cretaceous evolutionary turnover (Fig. 1; Niklas et al., 1985; Wing & Boucher, 1998). In insects, there was a major, earlier turnover in insect clades with the Permian-Triassic extinction, resulting in the origin of early, plesiomorphic representatives of modern clades during the earlier Mesozoic, in turn succeeded by more derived lineages that appeared later in the mid Cretaceous (Fig. 2; Grimaldi & Engel, 2005). This latter event is partly identified by a slackening of family-level insect diversification (Labandeira & Sepkoski, 1993) that corresponded temporally to the shift in potential host plants from gymnosperms to angiosperms. Evidence for this global turnover is reflected by increased insect origination rates and, to a lesser extent, increased extinction rates demonstrated in family-level diversity studies (Labandeira & Sepkoski, 1993; Jarzembowski & Ross, 1996; Dmitriev & Ponomarenko, 2002; Labandeira, 2005b), as well as saturation of mouthpart disparity (Labandeira, 1997). In this context, Sepkoski and Kendrick (1993) have used model-based analyses to validate the use of taxic diversity data and methodology for understanding major macroevolutionary patterns (e.g., Crepet & Niklas, 2009).

There is an approximate 20-million-year overlap between these two intervals approximately spanning the early Aptian to latest Albian of the mid Cretaceous (120–100 Ma). Consequently, fossil occurrences of the long-proboscid condition are divided into two overlapping intervals: the Middle Jurassic to late Early Cretaceous (phase 1), lasting ca. 65 million years from 165 to 100 Ma, and the mid Early Cretaceous to Recent (phase 2), commencing at 120 Ma and lasting ca. 120 million years to the Recent (Figs. 1, 2, right margins).

The long-proboscid condition did not originate in clades outside the Holometabola or in subadult developmental stages, past or present (Table 1). Most likely this is attributable to the embryologic genetics of adult mouthpart formation (Jürgens & Hartenstein, 1993). Mouthpart elements from the maxillary and labial regions are developmentally available for co-optation and modification into compound tubular structures, such as the siphon (Handschin, 1929; Eastham & Eassa,

1955; Nagatomi & Soroida, 1985), often with anatomical contribution from adjacent mouthpart regions (Krenn et al., 2005). Siphonate proboscis formation undoubtedly is a recurring process and occurs, perhaps in a genetically and developmentally homologous way, in the conversion of mandibulate mouthparts into piercing-and-sucking haustellate mouthparts in nonholometabolous Hemiptera (Rogers & Kaufman, 1997).

Examples of functionally convergent siphonate mouthpart structures have been found in seven of the 13 holometabolous clades, including representatives of the Lepidoptera, Diptera, Coleoptera, and Hymenoptera, and the less diverse Mecoptera, Neuroptera, and Trichoptera (Table 1). The occurrence of siphonate mouthparts within these lineages ranges from more than 99% of the species in the huge lepidopteran clade Glossata (Kristensen, 1997), to a few, major clades in the brachycerous Diptera (Labandeira, 2005a), where the condition may be plesiomorphically primitive, to a major extinct clade of the Mecoptera (Ren et al., 2009), two extinct lineages in the Neuroptera (Labandeira, pers. obs.), two minor, probably related clades within the Coleoptera (Rivnay, 1929; Bologna & Pinto, 2001), a few sporadic species in the Trichoptera (Ulmer, 1905; Cummings, 1913, 1914), and many originations across the Hymenoptera (Takeuchi & Tokunaga, 1941; Schedl, 1991; Krenn et al., 2005). These functional convergences have originated minimally 25 to 120 times in holometabolan history, most in the Hymenoptera; major occurrences are provided in Table 1. Other fossil and modern examples undoubtedly await discovery. With the exception of a small, siphonate insect from the Early Permian by way of introduction, the long-proboscid clades of phases 1 and 2 are discussed below.

A LATE PALEOZOIC PRECURSOR TO THE MID MESOZOIC LONG-PROBOSCID CONDITION

The permithonid †*Tschekardithonopsis* ?*oblivius* Vilesov (Vilesov, 1995) from the diverse Early Permian (Kungurian) fauna of Chekarda, in the central Ural Mountains of Russia, exhibits a prominent, ca. 1.7-mm-long proboscis (Fig. 3). The preserved proboscis of this specimen apparently consists of conjoined maxillary palpal elements that still retain segmental divisions, including a thickened terminal region bearing fine setae. A comparatively narrow food tube is present, indicating a use for feeding on fluids, possibly secretions accessible from small, concealed, reproductive organs (Mamay, 1976).

MECOPTERA (PHASE 1 OCCUPANT)

Extant adult Mecoptera (scorpionflies) are detritivores or scavengers, occasionally predators, but rarely

are associated with flowers (Piggott, 1958; Porsch, 1958). Modern scorpionfly mouthparts are fundamentally mandibulate, located terminally at the end of a long, downward, projecting extension of the head capsule (Heddergott, 1938). The labium, while elongate, consists of a medial structure basally attached to the head capsule, but bears free processes, the medial glossae and laterally positioned paraglossae typical of the mandibulate condition. Mandibles are prolonged-triangular and functional, and are used in biting for feeding on solid, often dead, food.

By contrast, the proboscis of the early derived Aneuretopsychina (Rasnitsyn & Kozlov, 1991), a clade consisting of the three Mesozoic families, Mesopsychidae (Figs. 4, 5), Aneuretopsychidae (Fig. 6), and Pseudopolycentropodidae (Fig. 7), is considerably different, consisting of siphonate mouthparts (Novokshonov, 1997; Grimaldi et al., 2005; Ren et al., 2009). The proboscis structure of the Aneuretopsychina is better known than any other clade of long-proboscid insects in the Mesozoic fossil record, a consequence of superb preservation in the Middle Jurassic Jiulongshan (165 Ma) and the mid Early Cretaceous Yixian (125 Ma) Formations of China. The length of these proboscises varies considerably, from ca. 2 to ca. 11 mm; widths vary from ca. 0.2 to 0.6 mm, with proportional variation in their food canal widths (Figs. 4–7). The proboscises are generally long and gracile, and not thick and short. Among these three modestly diverse families, the proboscid surface can be smooth or ribbed, occasionally ornamented with transverse ridges, or clothed in fine or coarse setae of various densities. The tip of the proboscis may lack capillary uptake organs, or more commonly may be surmounted by three types of pseudolabellae, depending on the species. The proboscis is connected to a cibarial pump underlying the clypeus, providing a suction to assist the capillary-based uptake of fluids by pseudolabellae. There is some evidence for a second suction pump at the proboscis base in the Mesopsychidae (Ren et al., 2009). Three-segmented, setose labial palps are present only in the Mesopsychidae; taxa of the other families are palpless.

Relevant to the origin of the long-proboscid clade is the Nannochoristidae, a plesiomorphic extant lineage whose fossil record extends to the early Mesozoic. Its distribution was once worldwide, though the clade now is confined to the western Gondwanan region of eastern Australia, New Zealand, and southern South America. The phylogenetic position of the Nannochoristidae has been highly debated, variously considered as the basalmost extant scorpionfly clade, a separate order, a sister-group to the Diptera, or even a clade within the Siphonaptera (fleas), due to its atypical mouthparts for extant mecopteran taxa (Ren

Table 1. Representative mid Mesozoic extinct and extant long-proboscid insects with siphonate mouthparts.[1]

Focal taxon and insect order	Stage-level geochronology	Best example and figure references herein	Biogeography and locality[2]	Major proboscis elements	Inferred plant hosts	References[3]
		Permian precursors				
Permithonidae (Neuroptera)	Kungurian	*Tschekardithonopsis ?oblivius* Vilesov (Fig. 3)	Eurasia: Chekarda, Russia	maxillary (palps)	seed ferns	Vilesov, 1995
		Phase 1: Middle Jurassic (Bathonian) to Early Cretaceous (late Albian)				
Aneuretopsychidae (Mecoptera)	Bathonian to Barremian	*Jeholopsyche liaoningensis* Ren, Shih & Labandeira (Fig. 6A–C)	Eurasia: Daohugou, China	labial	seed ferns	Rasnitsyn & Kozlov, 1991; Labandeira et al., 2007a; Ren et al., 2009
Pseudopolycentropodidae (Mecoptera)	Bathonian to Cenomanian	*Pseudopolycentropus janeannae* Ren, Shih & Labandeira (Fig. 7A–D)	Eurasia: Daohugou, Karatau, Yixian, and Burmese amber	labial	seed ferns	Novokshonov, 1997; Grimaldi et al., 2005; Labandeira et al., 2007a; Ren et al., 2009
Mesopsychidae (Mecoptera)	Bathonian to Barremian	*Lichnomesopsyche gloriae* Ren, Labandeira & Shih (Figs. 4, 5)	Eurasia: Daohugou and Yixian, China	labial	seed ferns, cheirolepidiaceous conifers	Grimaldi et al., 2005; Labandeira et al., 2007a; Ren et al., 2009
Kalligrammatidae (Neuroptera)	Bathonian to Barremian	undescribed genus and species 1 (Fig. 8)	Eurasia: Daohugou, Karatau, Yixian	maxillary (?galeal)	seed ferns, cheirolepidiaceous conifers	Engel, 2005a; Grimaldi & Engel, 2005; Labandeira, pers. obs.
Nemestrinidae (Diptera)	Kimmeridgian to Barremian	*Florinemestrius pulcherrimus* Ren (Fig. 9C, D)	Eurasia: Karatau, Yixian	labial	seed ferns	Mostovski, 1998; Ren, 1998b; Labandeira, 1998, 2000, 2005a; Ren et al., 2009
Apioceridae (Diptera)	Hauterivian to Barremian	*Protapiocera* sp.	Eurasia: Karatau, Baissa, Yixian	labial	seed ferns	Labandeira, 2005a; Labandeira et al., 2007a
Tabanidae–Pangoniinae (Diptera)	Kimmeridgian to Barremian	*Palaepangionius eupterus* Ren	Eurasia: Yixian	labial	seed ferns	Ren, 1998b; Labandeira et al., 2007a
Cratomyiidae (Diptera)	Aptian	*Cratomyia macrorrhyncha* Mazzarolo & Amorim (Fig. 9E–G)	South America: Santana	labial	seed ferns	Mazzarolo & Amorim, 2000; Labandeira et al., 2007a
Therevidae (Diptera)	Hauterivian	undescribed material	Eurasia: Baissa	labial	seed ferns, cheirolepidiaceous conifers	Mostovski, pers. comm., June 2006; Labandeira, 2005a; Labandeira et al., 2007a

Table 1. Continued.

Focal taxon and insect order	Stage-level geochronology	Best example and figure references herein	Biogeography and locality[2]	Major proboscis elements	Inferred plant hosts	References[3]
Phase 2: Early Cretaceous (early Aptian) to Recent						
Glossata (Lepidoptera)	Aptian to Recent	Oegoconites borisjaki Kusnezov (also Fig. 10A)	Eurasia: Baltic amber	maxillary	angiosperms	Kusnezov, 1941; Labandeira et al., 1994
Nemestrinidae (Diptera)	Eocene to Recent	Prosoeca (Palembolus) florigera (Scudder)	North America: (Florissant)	labial	angiosperms	Bequaert & Carpenter, 1936
Tabanidae–Pangoniinae (Diptera)	?Aptian[4] to Recent	currently no siphonate fossil record from the phase 2 interval[5]				Labandeira, pers. obs.
Mydidae (Diptera)	?Aptian[4] to Recent	Mydas miocenicus Cockerell	North America (Florissant)	labial	angiosperms	Cockerell, 1913; Meyer, 2003
Apioceridae (Diptera)	?Aptian[4] to Recent	undescribed taxon	North America: Green River	labial	angiosperms[6]	Labandeira, pers. obs.
Bombyliidae (Diptera)	Kimmeridgian[6] to Recent	currently no siphonate fossil record from the phase 2 interval				Grimaldi & Cumming, 1999; Labandeira, 2005a
Syrphidae (Diptera)	Early Eocene to Recent	Platycheirus lethaeus Hull	North America (Florissant)	labial	angiosperms	Melander, 1949; Meyer, 2003; Grimaldi & Engel, 2005
Nemognathinae (Coleoptera: Meloidae)	Middle Eocene to Recent	Nemognatha nemorensis Hentz (Fig. 10B)	North America, Europe (modern)	maxillary (galeal)	angiosperms	Schremmer, 1961; Barth, 1985; Bologna & Pinto, 2001; Kaupp et al., 2001; Engel, 2005b
Nemognathinae (Coleoptera: Meloidae)	Middle Eocene to Recent	Leptopalpus rostratus Fabricius	Europe (modern)	maxillary (palpal)	angiosperms	Handschin, 1929; Schremmer, 1961; Kasab, 1962; Bologna & Pinto, 2001
Macrosiagonini (Coleoptera: Ripiphoridae)	Cenomanian to Recent	Macrosiagon sp.	North America, Europe	maxillary	angiosperms	Rivnay, 1929; Perrichot et al., 2004; Batelka et al., 2006
Dipseudopsis (Trichoptera: Dipseudopsidae)	Recent	Dipseudopsis africana Ulmer	sub-Saharan Africa	maxillary (galeal)	angiosperms	Ulmer, 1905; Cummings, 1913; Crichton, 1957; Weitschat & Wichard, 2002
Plectrotarsus (Trichoptera: Plectrotarsidae)	Recent	Plectrotarsus gravenhorstii Kolenati	Australia	maxillary (galeal)[7]	angiosperms	Ulmer, 1905; Cummings, 1914; Crichton, 1957

Table 1. Continued.

Focal taxon and insect order	Stage-level geochronology	Best example and figure references herein	Biogeography and locality[2]	Major proboscis elements	Inferred plant hosts	References[3]
Nipponorhynchus (Hymenoptera: Tenthredinidae: Adelestini)	Recent	*Nipponorhynchus mirabilis* Takeuchi	Japan	maxillary and labial	angiosperms	Takeuchi & Tokunaga, 1941; Naito, 1975; Jervis & Vilhelmsen, 2000
Eurys (Hymenoptera: Pergidae: Euryinae)	Recent	*Eurys nitidus* Kirby	Australia	labial	angiosperms	Schedl, 1991; Jervis & Vilhelmsen, 2000; Krenn et al., 2005
Euhesma tubulifera (Hymenoptera: Colletidae: Euryglossinae)	Recent	*Euhesma tubulifera* Houston	Australia	maxillary (palpal)	angiosperms	Houston, 1983; Michener, 2000

[1] This is far from an exhaustive list; only prominent and detailed studies of higher-ranked insects with siphonate, long-proboscid mouthparts are reported.

[2] Common, recognized names of localities are provided.

[3] References include all literature sources, including species descriptions, phylogenetic analyses, mouthpart morphology studies, and other relevant citations.

[4] The lower boundary of phase 1 is poorly constrained by appropriate fossil deposits, occurring sometime within the early angiosperm radiation.

[5] A possibly proboscate species, *Cratotabanus stenomyomorphus* Martins-Neto & Santos (1994), from the Crato Formation of Brazil (ca. 120 Ma), may be placed here.

[6] It is unclear whether basal taxa of Bombyliidae, from Late Jurassic to Early Cretaceous, bore long proboscides; they are assigned to phase 2.

[7] The siphonate "haustellum" is traversed apparently by two tubes, one presumably a food canal and ingestive, and the other a salivary canal and secretory.

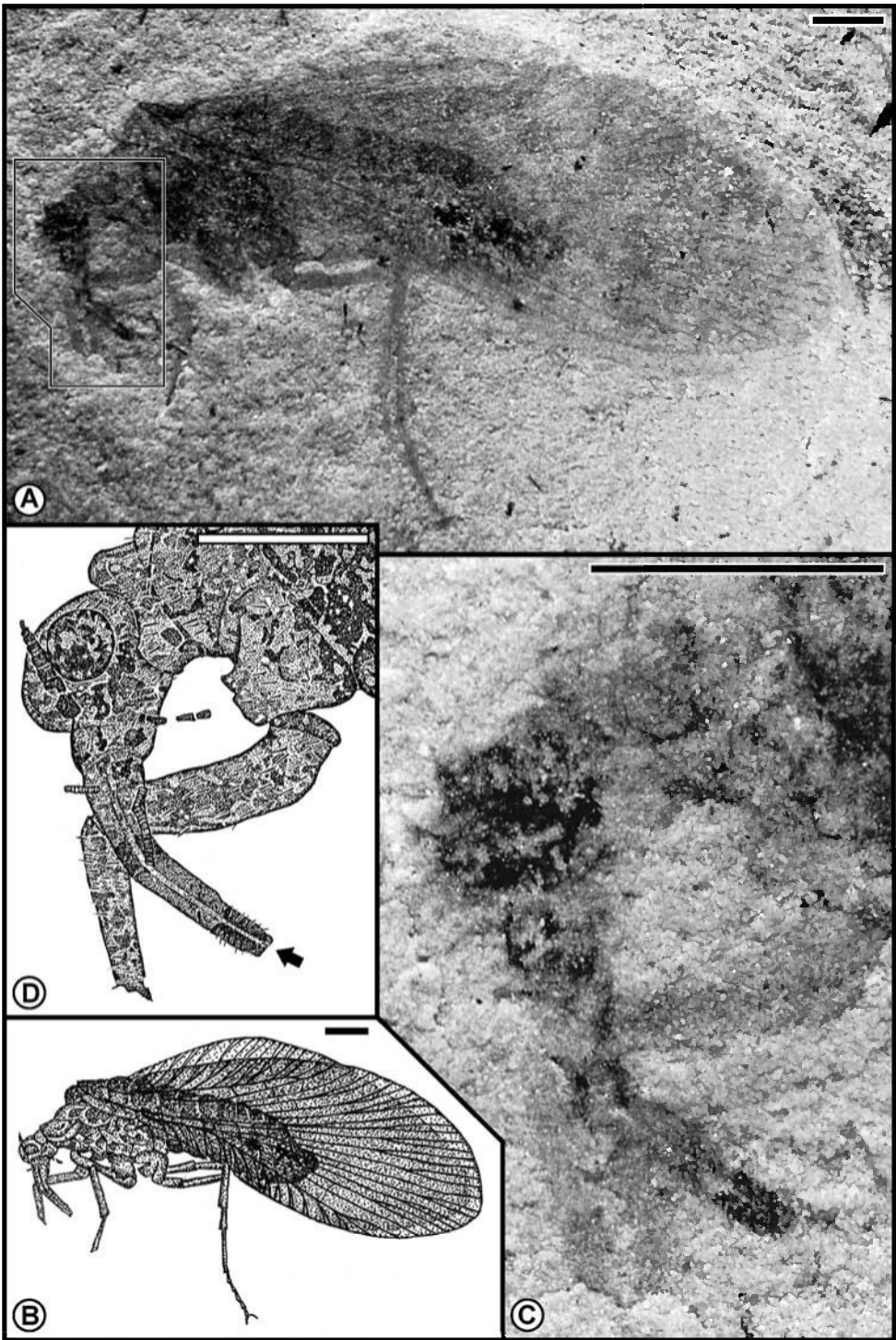Figure 3. The earliest known long-proboscid siphonate insect, *Tschekardithonopsis ?oblivius* Vilesov (Vilesov, 1995), from the Koshelvka Formation of Chekarda, central Ural Mountains, Russia, of Lower Permian (Kungurian) age. —A. Photograph of entire specimen. —B. Overlay drawing of A. —C. Photograph of outlined area in A. —D. Overlay drawing of head, mouthparts, and thorax in C. Scale bars = 1 mm.
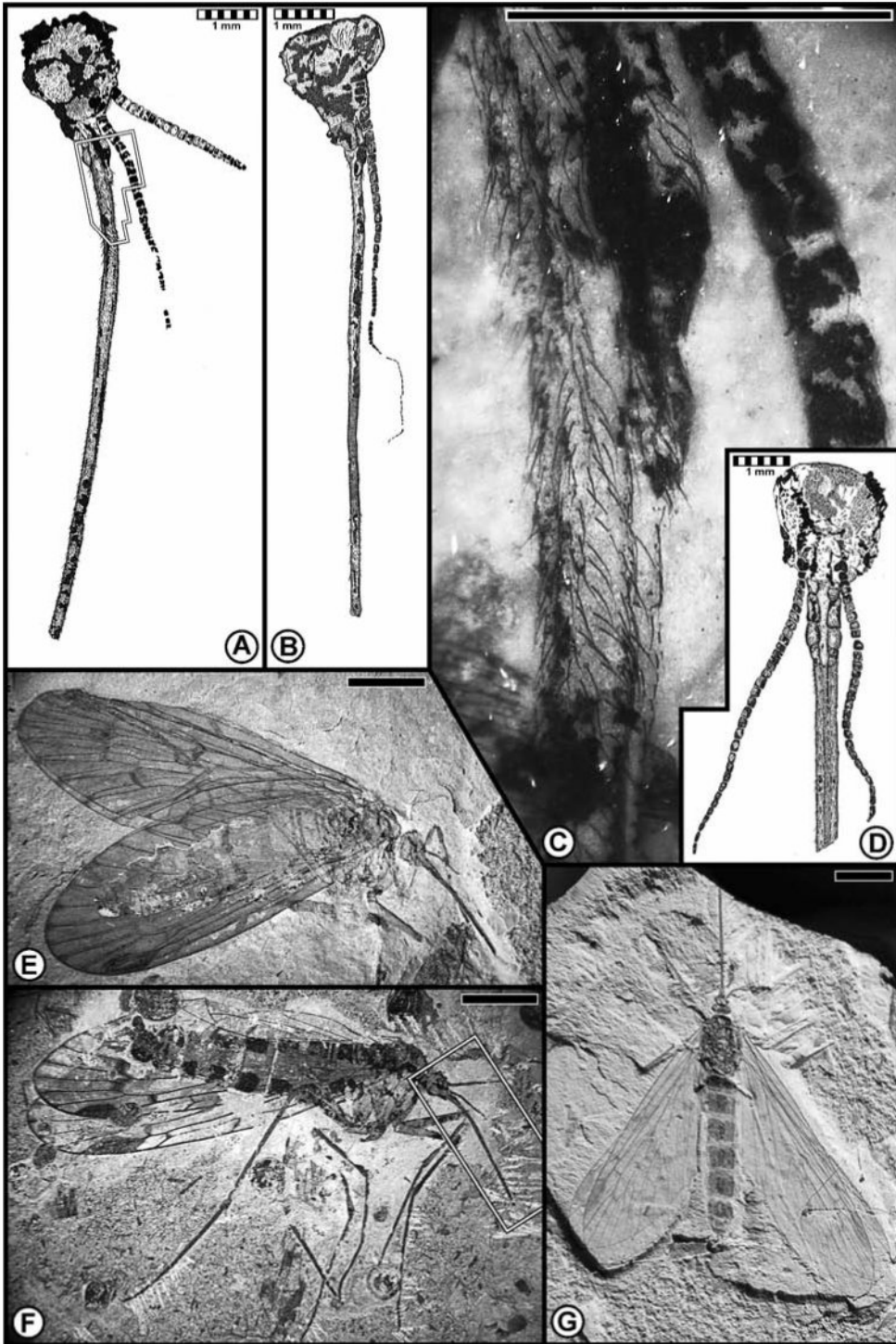
Figure 4. The long-proboscid siphonate condition in mid Mesozoic Mecoptera: Family Mesopsychidae. —A. Overlay drawing of *Lichnomesopsyche gloriae* Ren, Labandeira & Shih, showing head, proboscis, labial palps, and antennae, enlarged from F below (Ren et al., 2009); specimen CNU-M-NN2005-021-1; scale bar = 1 mm. Proboscis length is ca. 9 mm. —B. Overlay drawing of a second specimen modified slightly from Ren et al. (2009); CNU-M-NN2005-024; scale bar = 1 mm. Proboscis length is ca. 9 mm. —C. Photographic detail of siphon with setae (center), 3-segmented labial palp (center right),
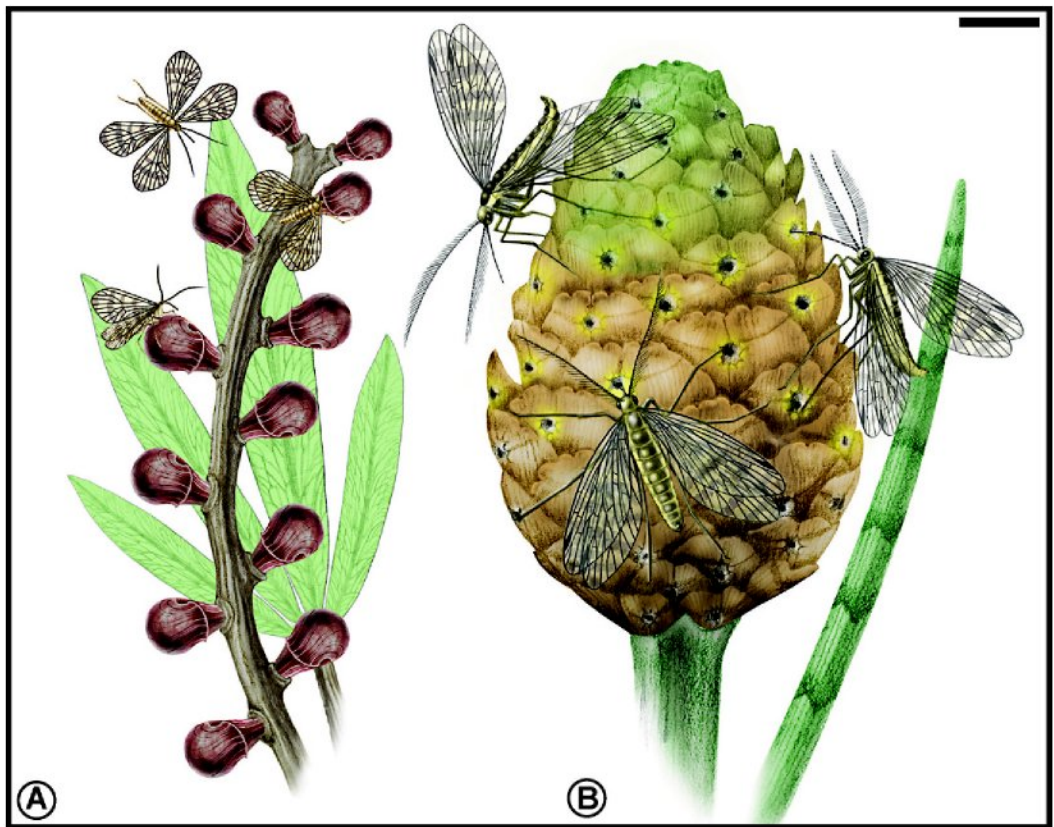
Figure 5.   Reconstruction of two mid Mesozoic associations between mesopsychid scorpionflies and their inferred host plants. Courtesy of Smithsonian Institution. Painting by M. Parrish. —A. *Lichnomesopsyche gloriae* feeding on the pollen drops of *Caytonia sewardi* Harris through an integumental tube under the cupule's lower lip. Associated pollen, *Vitreisporites* sp., would have been obtained from conspecific *Caytonianthus arberi* (Thomas) Harris pollen organs nearby. The affiliated foliage of *Sagenopteris colpodes* Harris is shown for this Eurasian, Middle Jurassic whole-plant assemblage (Ren et al., 2009). —B. The mesopsychid *Vitimopsyche kozlovi* Ren, Labandeira & Shih feeding on catchment funnel nectaries of the cheirolepidiaceous ovulate cone *Alvinia bohemica* Kvaček. *Classopollis* sp. pollen would have been vectored by this scorpionfly from conspecific *Frenelopsis alata* (Feistmantel) Knobloch pollen cones on the same or different plants. Affiliated foliage, also termed *F. alata*, is also shown for constituting this Eurasian, mid-Lower Cretaceous assemblage (Ren et al., 2009).

et al., 2009). The Nannochoristidae is characterized by a modified, projecting but short, tubular labium inferred to take up fluid food (Beutel & Baum, 2008), an early mecopteran mouthpart type that likely was a precursor to the long-proboscid condition of the Aneuretopsychina (Ren et al., 2009).

NEUROPTERA (PHASE 1 OCCUPANT)

Adult and larval neuropterans are overwhelmingly insectivorous. With the minor exceptions of the proboscis borne by one species of Early Permian Permithonidae (Fig. 3) and some modern Nemopter-

←

and filiform antenna (right) of same specimen in A (Ren et al., 2009); scale bar = 1 mm. Preserved proboscis length is 4.5 mm, but probably extended to ca. 9 mm. —D. Overlay drawing of a third specimen of *L. gloriae* showing head, mouthparts, palps, and antennae (proboscis truncated); CNU-M-NN2005-023; scale bar = 1 mm. —E. Photo image of dorsal oblique view of a fourth specimen (Ren et al., 2009); CNU-M-027-2; scale bar = 5 mm. Proboscis length is ca. 9 mm but incomplete. —F. Photo of a complete specimen whose mouthparts are detailed in A above; head and proboscis at lower right; scale bar = 5 mm. —G. Photo of a fifth specimen, with proboscis at top center (Ren et al., 2009); CNU-M-NN2005-020-1; scale bar = 1 mm. Proboscis length is ca. 10 mm. Note: in Figures 4 and 6–9, all head sizes are standardized to a scale bar that represents 1 mm to establish a comparison of the relative sizes, shapes, aspect ratios, and other features of the long-proboscid specimens. All specimens on this figure are *L. gloriae* from the Middle Jurassic Jiulongshan Formation, Inner Mongolia, northeastern China. Parts A–C, E, and G reprinted with permission from Ren et al. (2009).
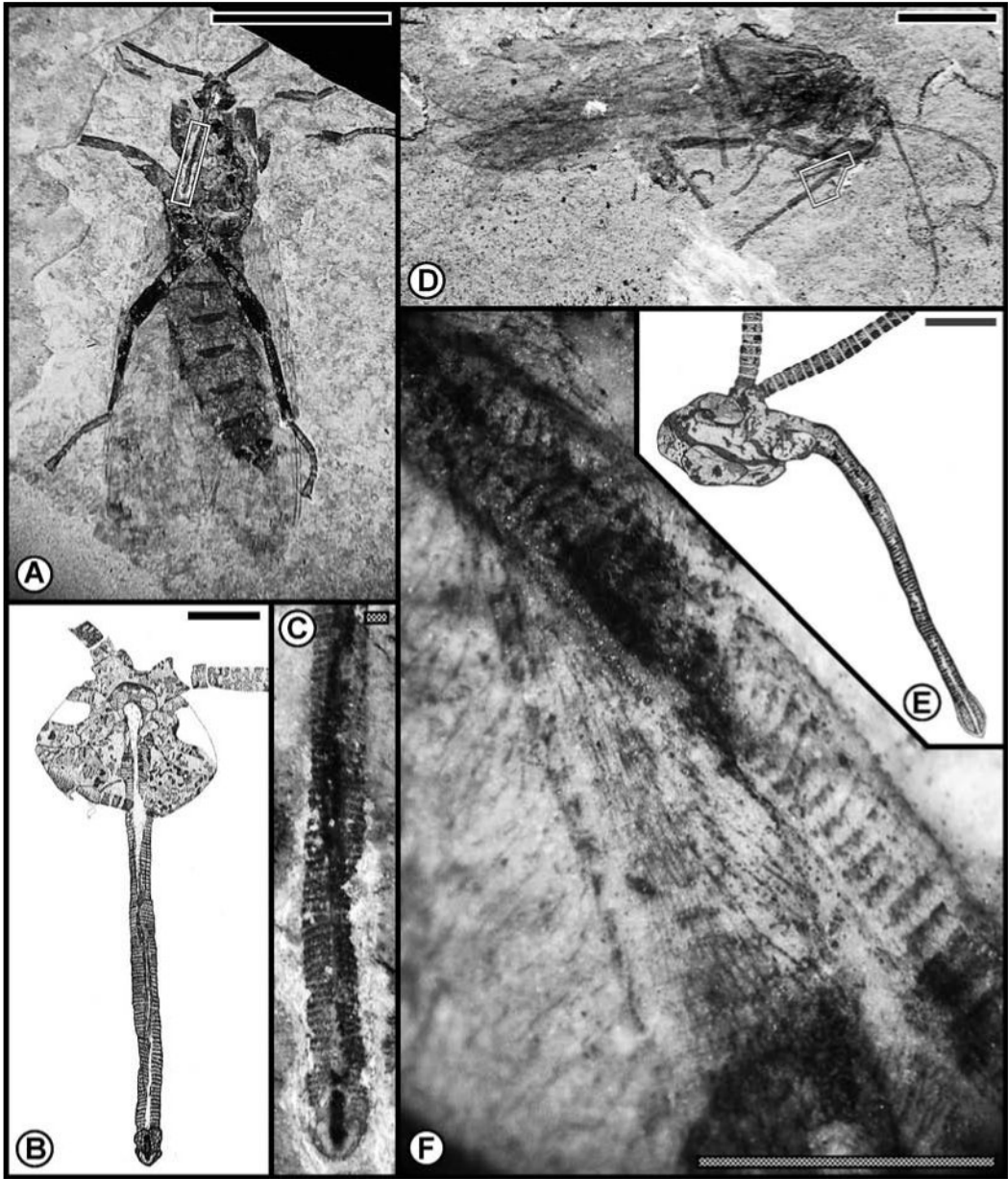
Figure 6.   The long-proboscid siphonate condition in mid Mesozoic Mecoptera: Family Aneuretopsychidae. —A. Photo of *Jeholopsyche liaoningensis* Ren, Shih & Labandeira, showing head and proboscis at top center; CNU-M-NN2005-002-1; scale bar = 10 mm. Proboscis length is ca. 7 mm. This specimen is from the Yixian Formation of Liaoning, northeastern China (Ren et al., 2009). —B. Overlay drawing of an enlargement of the head in A above, with compound eyes, antennal bases, and proboscis; scale bar = 1 mm. —C. Detail of proboscis in A and B, showing transverse ribbing and a terminal pseudolabellum surrounding an ellipsoidal mouth. —D. Photo of an undetermined species of *Jeholopsyche* with head, antennae, and proboscis at right, enlarged and rotated in E below; CNU-M-NN2005-001; scale bar = 5 mm. Proboscis length is ca. 6 mm. —E. Overlay drawing of an enlargement of head and proboscis in D above; compare to the head of a congeneric species in B; scale bar = 1 mm. —F. Photo indicating detail of ribbing, setae, and other ornamentation on proboscis and leg in D and E above; scale bar = 0.1 mm. Note: in Figures 4 and 6–9, all head sizes are standardized to a scale bar that represents 1 mm to establish a comparison of the relative sizes, shapes, aspect ratios, and other features of the long-proboscid specimens. Parts A, B, D, and E reprinted with permission from Ren et al. (2009).
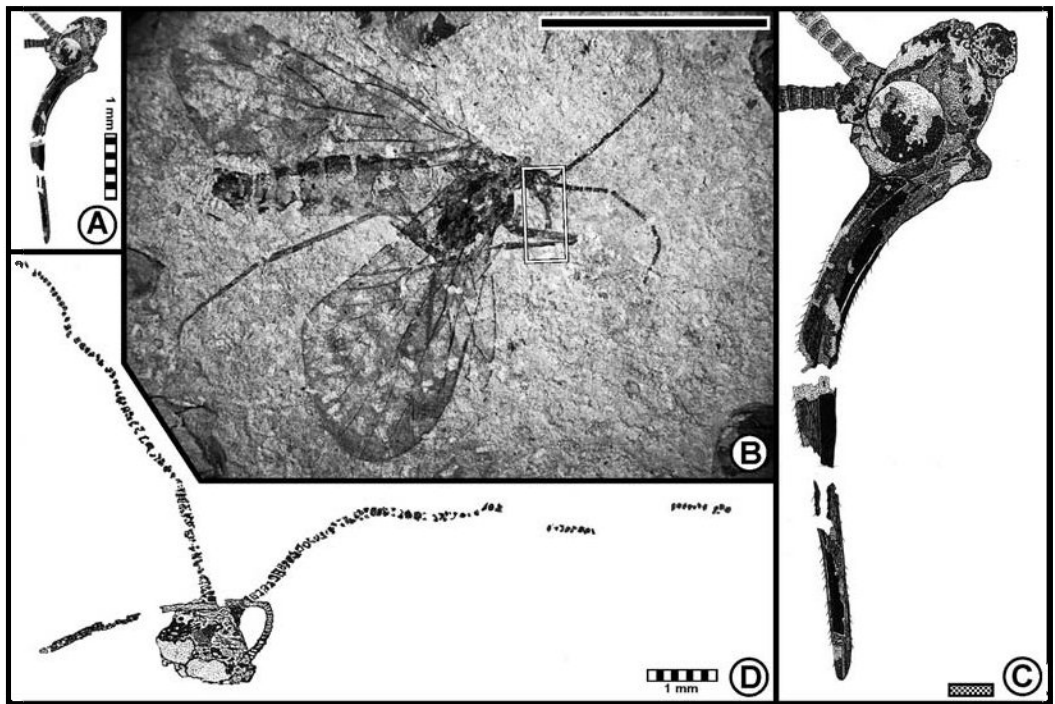
Figure 7. The long-proboscid siphonate condition in mid Mesozoic Mecoptera: family Pseudopolycentropodidae. —A. Overlay drawing of head, antennal bases, and proboscis of *Pseudopolycentropus janeanne* Ren, Shih & Labandeira, from B at right; CNU-M-NN2005-004; scale bar = 1 mm. Proboscis length is ca. 2 mm. Both specimens of this figure are from the Middle Jurassic Jiulongshan Formation of Inner Mongolia, northeastern China (Ren et al., 2009). —B. Photo of entire specimen of *P. janeanne* whose head and proboscis at center are enlarged in A at left; scale bar = 5 mm. —C. Enlargement of specimen in A to show detail; scale bar = 0.1 mm. —D. Overlay drawing of a second specimen of *P. janeanne*, showing proboscis curvature indicating flexibility; CNU-M-NN2005-003; scale bar = 5 mm. Proboscis length is ca. 2 mm. Note: in Figures 4 and 6–9, all head sizes are standardized to a scale bar that represents 1 mm, to establish a comparison of the relative sizes, shapes, aspect ratios, and other features of the long-proboscid specimens. Parts A, B, and D reprinted with permission from Ren et al. (2009).

idae (Tjeder, 1967; Krenn et al., 2008), there has been very little in Neuroptera phylogeny or mouthpart morphology to indicate that the group was ever involved in palynophagy, nectarivory, or pollination. However, one extinct lineage, the butterfly-like, mid Mesozoic Kalligrammatidae, may have been a major exception, assumed to have had unspecified associations with plants (Zherikhin, 2002; Engel, 2005b; Grimaldi & Engel, 2005). The Kalligrammatidae have been considered as fundamentally mandibulate (Grimaldi & Engel, 2005), like the mouthpart morphological spectrum of modern neuropteran lineages (e.g., Tjeder, 1967). Recent specimens from the same two mid Mesozoic deposits in China that produced siphonate mecopterans also have yielded impressively large kalligrammatid neuropterans exhibiting siphonate mouthparts as well (Fig. 8). Their known proboscises range in length from a slender 11 mm to a robust 20–25 mm. Interestingly, the extant related lineage Nemopteridae (spoonwing lacewings) displays active

nectaring of herbaceous plants (Krenn et al., 2008), though it possesses elongate and modified, but basically mandibulate, mouthparts (Tjeder, 1967). Unlike the fundamentally labial proboscis structure in the Mecoptera and Diptera, the kalligrammatid proboscis consists of conjoined maxillary galeae to form a tubular siphon that is anatomically similar to that of the lepidopteran Glossata (Labandeira, pers. obs.).

DIPTERA (PHASE 1 AND PHASE 2 OCCUPANTS)

Diptera exhibit various modifications of the labium and supporting structures, with palps and labellae functionally transformed into ensembles for nectaring and occasional pollen ingestion. Several major clades of nematocerous and especially lower brachycerous flies have convergently evolved long proboscises (Nagatomi & Soroida, 1985; Borrell & Krenn, 2005), often involved in pollination mutualisms. Proboscid lengths in Mesozoic taxa ranged from 4 to 9 mm, and
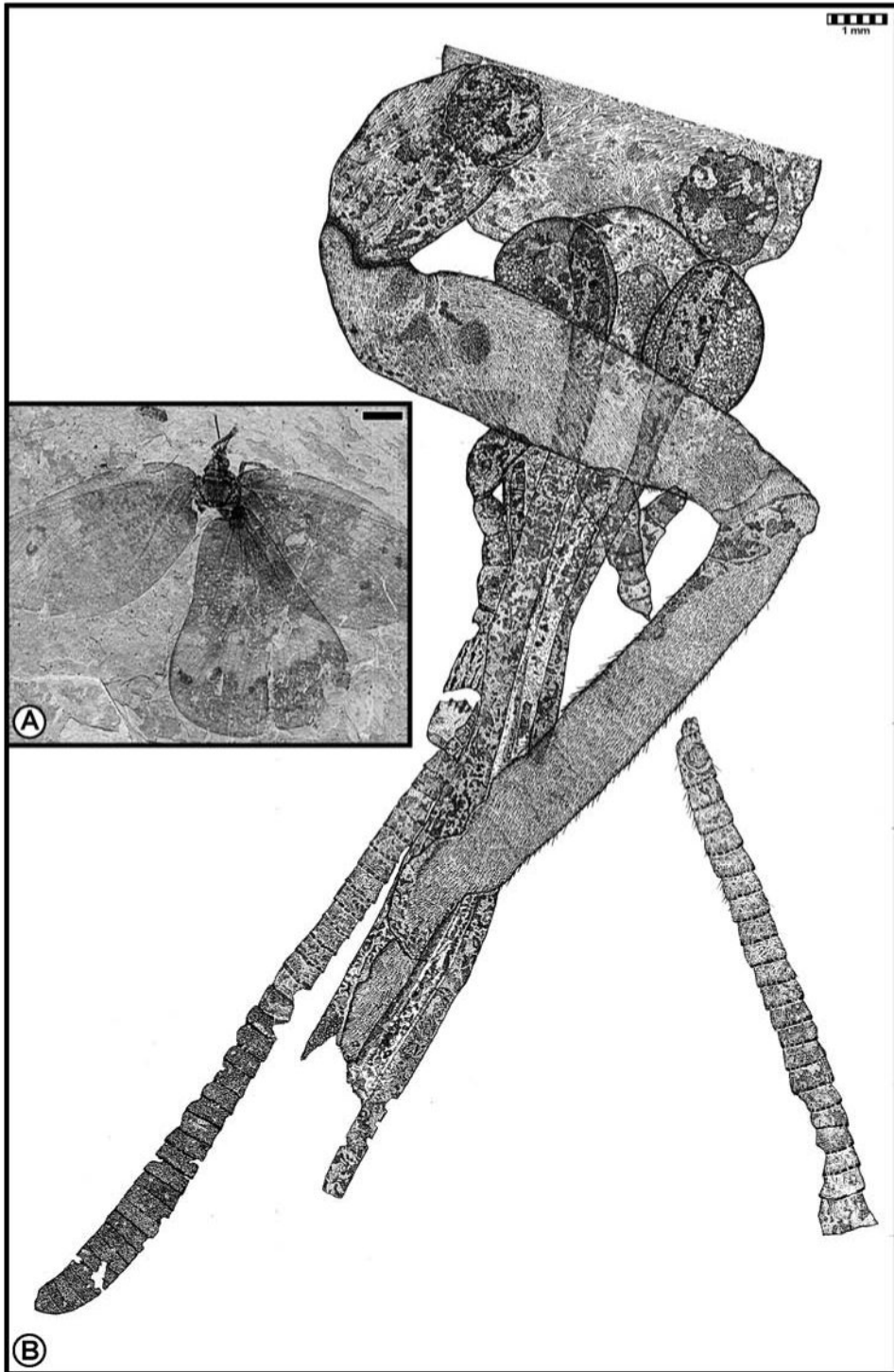
Figure 8. The long-proboscid siphonate condition in mid Mesozoic Neuroptera: family Kalligrammatidae. —A. Photo of undescribed genus and species, showing wing eyespots; CNU-NEU-NN2009-032-2; scale bar = 5 mm. —B. Overlay drawing of enlargement of the ventral aspect of the head and mouthparts from top center in A, showing antennae, compound eyes, maxillary palps, and right prothoracic leg; bold, dashed scale bar = 1 mm. The preserved proboscis length is 14 mm, but probably extended to ca. 24 mm, inferred from other, more complete proboscises and their aspect ratios. Note: in Figures 4 and 6–9, all head sizes are standardized to a scale bar that represents 1 mm to establish a comparison of the relative sizes, shapes, aspect ratios, and other features of the long-proboscid specimens.

aspect ratios varied from gracile to robust, as in Early Cretaceous Nemestrinidae (tanglevein flies; Fig. 9). Brachyceran taxa of Tabanidae, Nemestrinidae, Apioceridae, and others (Figs. 2, 9) are first known from Middle Jurassic Eurasian deposits that reveal siphonate proboscises either for nectaring, as in the case of the Nemestrinidae, or conceivably involved in bifunctional siphonate-stylate proboscises that would involve nectaring in males and joint nectaring and blood feeding in conspecific females, as in the pangioniine horseflies of the Tabanidae (Mostovski, 1998; Ren, 1998a; Mazzarolo & Amorim, 2000; Labandeira, 2005a). However, these mid Mesozoic clades are implicated in feeding only on surface fluids based on distinctive siphonate proboscises and associated mouthpart features (Mostovski, 1998; Ren, 1998b; Labandeira, 2005a), clumps of gymnospermous *Classopollis* pollen on their heads (Labandeira, 2005a; also see Nicholson, 1994), and high pollination-drop nutritive values from extant insect-pollinated gymnosperms (Labandeira et al., 2007a; Nepi et al., 2009). Accordingly, these nectarivorous and palynophagous brachyceran flies initially targeted gymnospermous seed plants during the Middle Jurassic and evidently transferred their diets to angiosperms during their initial radiation of the Early Cretaceous. Insect clades such as the Nemestrinidae, Apioceridae, and Tabanidae continued through this transitional interval and persist to the present day on angiosperm nectar (Manning & Goldblatt, 1996; Morita, 2008), but with decreased diversity and relict distributions.

TRICHOPTERA (PHASE 1? AND PHASE 2 OCCUPANTS)

In adult Trichoptera the principal feeding organ consists of conjoined and expanded maxillary palps whose distal segment is expanded into a labellum-like sponging organ, the haustorium, for uptake of surface fluids (Crichton, 1957). At least two modern taxa have diverged independently from this condition and evolved an analog to the lepidopteran siphon. The closely adpressed galeae from the maxillary region form a tubular structure that joins in a relatively loose arrangement, resulting in a tubular or near-tubular proboscis for imbibation of nectar and other fluids. The galeal origin of this siphon is similar in arrangement to that of the kalligrammatid Neuroptera, glossate Lepidoptera, and ripiphorid and nemognathine Coleoptera. This distinctive proboscis is associated with flower-feeding and occurs in the unrelated *Dipseudopsis africana* Ulmer (Dipseudopsidae) from southern Africa and *Plectrotarsus gravenhorstii* Kolenati (Plectrotarsidae) from eastern Australia (Ulmer, 1905; Cummings, 1913, 1914).

LEPIDOPTERA (PHASE 2 OCCUPANT)

Constituting almost all of the lepidopteran taxa, the diverse clade Glossata is exemplified by a proboscis consisting of maxillary, paired galeal elements uniquely joined into a figure-8 configuration in transverse section and sutured by a zipperlike arrangement of modified setae (Kristensen, 1984; Fig. 10A). The lepidopteran proboscis is almost always distinctively coiled due to angled, intrinsic galeal musculature, and has a characteristic knee bend ca. one third of the length from the base (Kristensen, 1984, 1997). The lepidopteran proboscis is derived from the same mouthparts region as the proboscis of kalligrammatids and meloid beetles. The origin of the lepidopteran proboscis occurred once during the mid Early Cretaceous, contemporaneous with the angiosperm radiation, based on the earliest documented moths with siphonate mouthparts and the presence of latest Early Cretaceous leaf-mining plant damage attributable to larvae of the Glossata (Labandeira et al., 1994; Grimaldi & Engel, 2005). However, there is a distinct possibility that the Glossata, partly defined by the synapomorphy of a siphonate proboscis, may have originated earlier, in association with gymnospermous seed plants, and they moved to early angiosperm hosts whose diminutive flowers accommodated probes by short-siphoned moths (but see Powell et al., 1999).

COLEOPTERA (PHASE 2 OCCUPANT)

Coleoptera are the most speciose order of insects and exhibit dietary diversity and mouthpart variation that rival those of the Diptera and Hymenoptera (Crowson, 1981; Godfray et al., 1999; Skevington & Dang, 2002; Grimaldi & Engel, 2005). Although most Coleoptera possess mandibulate mouthparts and biting-and-chewing feeding habits, the clade is rife with mouthpart modifications. In phytophagous lineages, there are several major mouthpart types, some of which center on pollen feeding and others that involve diverse ways of nectar consumption (Crowson, 1981). A siphon formed from conjoined galeae is found among the Macrosiagonini of the Ripiphoridae (ripiphorid beetles), and particularly the Meloidae (blister beetles), the latter in the subfamily Nemognathinae (Rivnay, 1929; Barth, 1985; Fig. 10B). The Nemognathinae are illustrated by the nectar-feeding *Leptopalpus rostratus* Fab. and *Nemognatha punctulata* Fab., which have conjoined maxillary galeae, although in some species the galeal halves are incompletely connected, suggesting a channel rather than an enclosed tube (Handschin, 1929; Barth, 1985; Borrell & Krenn, 2005). A larval meloid fossil has been found from the middle Eocene (Engel, 2005a)
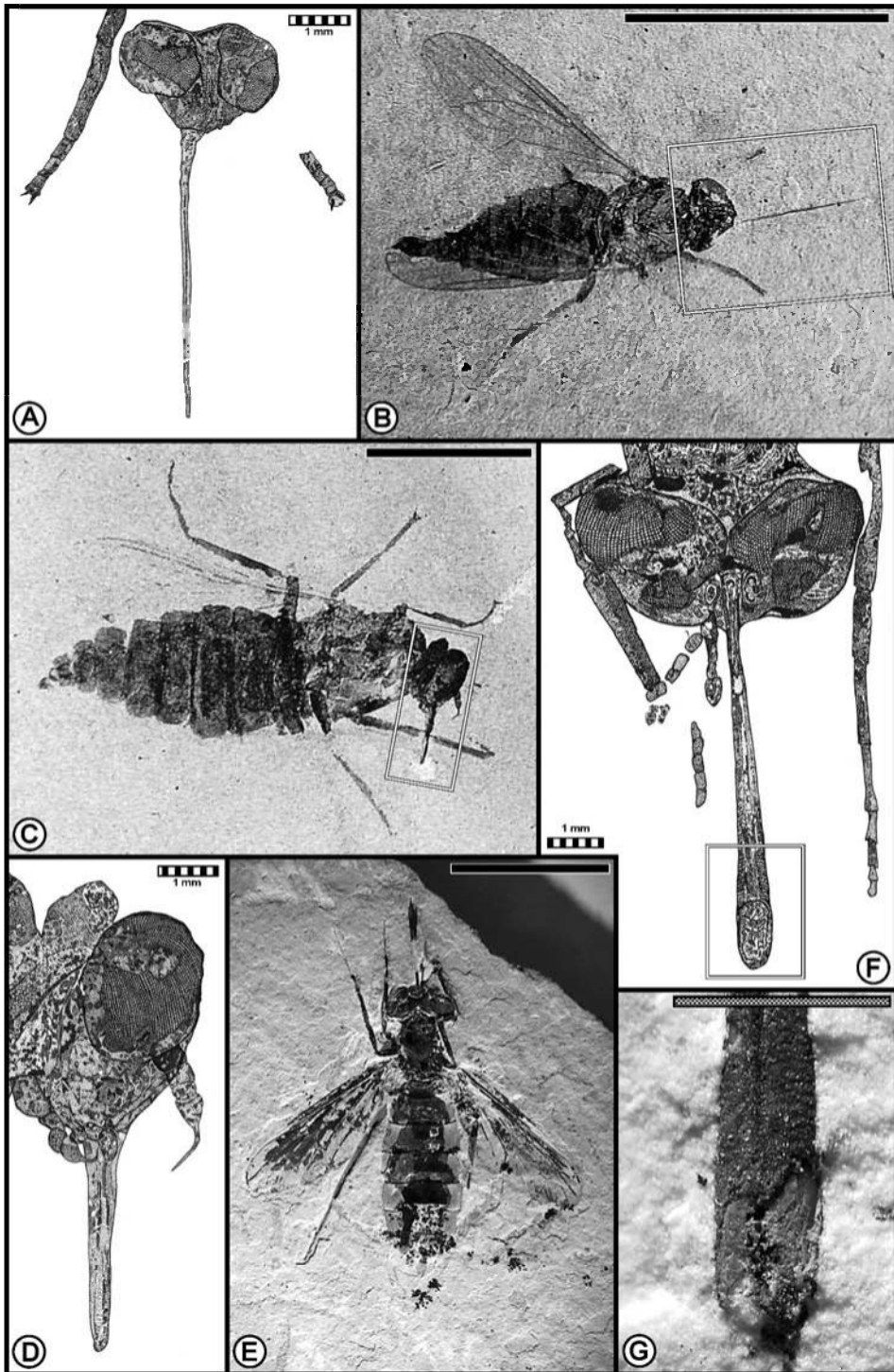
Figure 9. The long-proboscid siphonate condition in mid Mesozoic Diptera: families Nemestrinidae and Cratomyiidae. —A. Overlay drawing of dorsal aspect of head, proboscis, and prothoracic legs of *Protonemestrius jurassicus* Ren (Ren, 1998a) (Nemestrinidae), from the mid Early Cretaceous of northeastern China, enlarged from B at right; CNU-LB1997-005; scale bar = 1 mm. The comparatively thin and gracile proboscis length is ca. 5 mm. —B. Photo of entire (female) specimen with head and proboscis shown in A at left. Scale bar = 5 mm. —C. Photo of *Florinemestrius pulcherrimus* Ren (Ren, 1998a)

and poorly known adult ripiphorids extend earlier to the latest Early Cretaceous (Perrichot et al., 2004), though it is unclear whether these taxa are associated with siphonate mouthparts.

HYMENOPTERA (PHASE 2 OCCUPANT)

The central mouthpart feature of Hymenoptera that projects into flowers for nectaring is the concealed nectar extraction apparatus (CNEA). As an integration of maxillary and labial elements, the CNEA can be deployed in leverlike fashion for projecting into flowers or similar structures for extraction of nectar (Jervis et al., 1993; Jervis, 1998). The CNEA is used typically by small parasitoid wasps and probably originated during the parasitoid revolution of the Early Jurassic (Labandeira, 2002b), although it has been transformed into multielement siphonate mouthparts of independent origin approximately 100 times, particularly in more recent lineages that have larger body size, such as vespid wasps, ants, and especially bees (Krenn et al., 2005). The CNEA represents a distinctive mouthpart complex when compared to the comparatively simpler, long-proboscid mouthparts occurring in other major holometabolous lineages. There are a few taxa from earlier, basal groups of Hymenoptera—the Symphyta (sawflies)—which are convergent with the long-proboscid condition (Table 1). Some symphytans that have tubular or channelized proboscides are the sawfly *Eurys* of the Pergidae (Schedl, 1991), which includes only proboscis labial components, and the common sawfly *Nipponorhynchus* of the Tenthredinidae (Takeuchi & Tokunaga, 1941), which includes both maxillary and labial elements. At the opposite end of the hymenopteran phylogenetic spectrum is the plasterer bee *Euhesma* (Colletidae), which has a tubular proboscis formed solely of maxillary palpal structures (Houston, 1983).

DISCUSSION

Several persistent themes characterize the evolution of pollination modes between seed plants and insects during the mid Mesozoic. The first theme is

the phenomenon of separate structural and functional convergence in insect mouthparts and in the receiving structures of seed plants. One remarkable aspect is the variety of ways that insects have convergently produced similar mouthparts that have been fashioned from different appendicular structures of the major segmental regions of the insect head, especially the elaboration of maxillary and labial appendages. The same can be said for the various structural accommodations that have been used by gymnospermous seed plants, especially to facilitate pollination-drop probing and pollination by diverse, long-proboscid insects. A second theme is plant host and insect pollinator turnover, reflecting three evolutionary patterns as various gymnosperm lineages were extirpated while angiosperms underwent a major radiation. A third theme addresses how the data in this contribution provide for an explanation in long-recognized Mesozoic trends in the diversity records of fossil insects, fossil plants, and their associations.

FUNCTIONAL CONVERGENCE IN HOST AND POLLINATOR ATTRIBUTES BEFORE ANGIOSPERMS

Similar genetic and developmental programs account for the parallelisms between gymnosperms and angiosperms as well as between quite different holometabolous insects in achieving similar pollination mechanisms. The efficiency of these mechanisms was presumably modulated by architectural and phylogenetic constraints that resulted initially in suboptimal solutions, undoubtedly reflected by temporal lags between the initiation of the association and its subsequent fine tuning. Nonetheless, there was generational continuity of both the pollinated plant and insect pollinator.

Plant ovulate structure

If the hypothesis that certain mid Mesozoic gymnospermous plants provided pollen and nectar rewards to insects in return for more efficient pollination is correct, then an expected outcome would be multiple, independent, and varied solutions

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(Nemestrinidae), from the mid Early Cretaceous of China; head at right enlarged in D below; CNU-LB1997-008; scale bar = 5 mm. —D. Overlay drawing of right lateral view of head, proboscis, antennae, and compound eyes of nemestrinid specimen in C; scale bar = 1 mm. The comparatively thick and robust proboscis length is ca. 4 mm. —E. Photo of *Cratomyia macrorrhyncha* Mazzarolo & Amorim (Mazzarolo & Amorim, 2000) (Cratomyiidae), from the mid Albian of northeastern Brazil; DBRP-0050; scale bar = 1 mm. —F. Overlay drawing of the ventral aspect of *C. macrorrhyncha* head in E, showing convergent compound eyes, proboscis, antenna, and prothoracic legs; scale bar = 1 mm. The distally thickening proboscis is ca. 7.5 mm long. —G. Photo of proboscis tip detail in F showing labellar lobes; scale bar = 0.1 mm. Note: in Figures 4 and 6–9, all head sizes are standardized to a scale bar that represents 1 mm, to establish a comparison of the relative sizes, shapes, aspect ratios, and other features of the long-proboscid specimens.
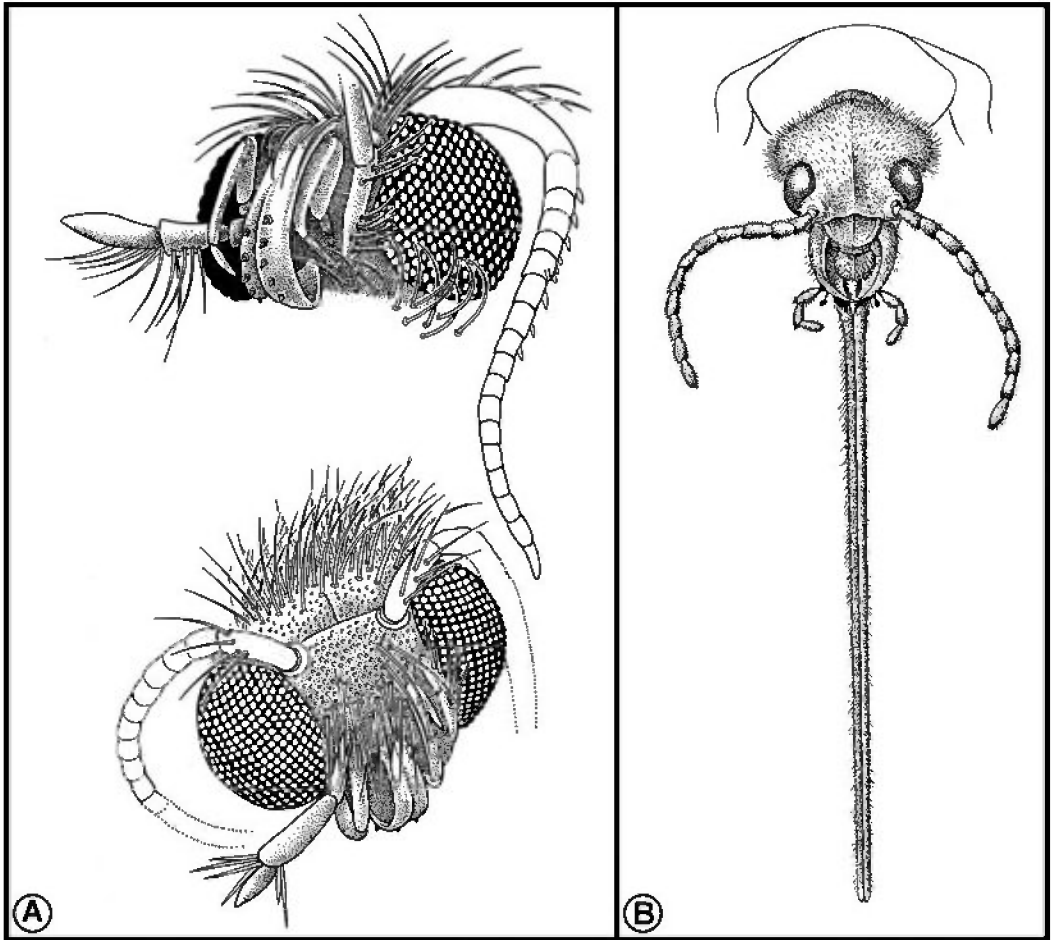
Figure 10.   The long-proboscid siphonate condition in Early Cretaceous Lepidoptera and modern Coleoptera. —A. Frontal and occipital views of the head and separated maxillary galeae of an undescribed glossate moth (Lepidoptera: Glossata), from the early Late Cretaceous (Turonian) of New Jersey (Grimaldi & Engel, 2005: fig. 13.22). Reprinted with permission from Grimaldi, D. A. & M. Engel. 2005. Evolution of the Insects. Cambridge University Press, Cambridge. —B. Head and mouthparts, including a proboscis of conjoined galeae, of the recent nemognathine blister beetle *Nemognatha* sp. (Coleoptera: Meloidae) from central Europe (Barth, 1985: fig. 31). The proboscis length in A is estimated as 4 mm and in B it is approximately 10 mm. Reprinted with permission from Barth, F. G. 1985. Insects and Flowers: The Biology of a Partnership, 1st ed. Princeton University Press, Princeton, New Jersey.

to insect pollination mechanisms, some of which were less reliable than those of today (Campbell, 2008). The diverse structures and inferred mechanisms seen in seed plant ovulate organs to facilitate pollination are instructive. For example, in candidate insect-pollinated lineages of gymnosperms, a wide variety of ovule-associated, elongate tubular structures received proboscises of various lengths, widths, and aspect ratios (Labandeira et al., 2007a; Ren et al., 2009).

These tubular structures originate from various ovulate and adjacent plant tissues, but share the function of accepting a proboscis for a reward of pollination drop fluids in return for depositing pollen. In *Caytonia*, an inserted proboscis was likely received by an integumental tube surrounded by cupulate tissue connecting each micropyle to a surface aperture (Harris, 1933, 1940). For the bivalved *Leptostrobus*, pollination was accomplished by anatropous ovules oriented adaxially, but with an abaxial entry point at the exposed, opposite end of the ovulate organ, through which a 4- to 7-mm-long interovular channel was available to access deeply sequestered pollination drops. For ovules reported in *Pentoxylon* and *Umkomasia*, structures consistent with wind pollination, an additional mode could have been insertion of a short insect proboscis into the micropyle, providing a simple reward of pollination fluid with minimal modification of surrounding extraovular tissue. Gne-

taleans such as *Problematospermum* were achenelike
ovules that bore broad micropylar pappus tubes
extending at least to 14 mm, at whose base originated
enveloping, bracteate, papery structures and setose
plumes (Krassilov, 2009; Taylor et al., 2009), possibly
attracting mobile, winged pollinators.

Undoubtedly, the most complex construction for
insect pollination in any seed plant is reported from
arborescent cheirolepidiaceous conifers (Alvin et al.,
1994; Axsmith et al., 2004; Labandeira et al., 2007a),
whose ovulate organs apparently were more compli-
cated than that of any other Mesozoic gymnosperm or
angiosperm. The morphology of *Alvinia bohemica*
ovulate scales is consistent with entomophily through
the provisioning of lures, such as the prominent
abaxial lobes perhaps directed to indicate the funnel
opening, and rewards such as secretions from deeper
nectary-like structures at the funnel base and perhaps
glandular trichomes near its opening. Smaller con-
specific pollen cones accordingly supplied *Classopol-
lis* pollen that would have been transported by long-
proboscid or small nonproboscid insects. In addition,
Classopollis pollen has been identified as intestinal
boluses and smeared on the head capsules of several
coeval mid Mesozoic insects (Krassilov et al., 1997a;
Labandeira, 2005a).

Insect mouthparts

With the exception of siphonate mouthpart exper-
imentation during the Early Permian, Mesozoic
mandibulate and stylate mouthparts were transformed
to long-proboscid siphonate mouthparts up to 12
separate times in four to perhaps as many as seven
orders of insects, based on occurrence data from
phase 1 and the earlier part of phase 2 (Table 1).
These changes parallel the convergence mentioned
above in seed plant ovules. Major, mid Mesozoic
insect clades with this mouthpart morphology are:
(1) Mecoptera (Mesopsychidae, Aneuretopsychidae,
Pseudopolycentropodidae); (2) Diptera (Nemestrinidae,
Apioceridae, Mydidae, Thereviidae, pangioniine Ta-
banidae, Vermileonidae); (3) Lepidoptera (Glos-
sata); (4) Neuroptera (Kalligrammatidae); and pos-
sibly (5) Trichoptera (descendants of Permian or
ancestors of modern siphonate taxa); (6) Hymenoptera
(parasitoid wasps or apoid bees and their wasp
relatives); and conceivably (7) Coleoptera (macro-
siagonine Ripiphoridae and nemognathine Meloidae)
(Table 1; Borrell & Krenn, 2005; Krenn et al., 2005;
Labandeira, 2005a; Labandeira et al., 2007a; Ren et al.,
2009). It is instructive that two species of extant
Trichoptera and a token three species of Hymenop-
tera with long-proboscid taxa lack a fossil record
(Table 1). Extant and fossil long-proboscid mouthparts

typically have a rich vestiture of setae, particularly on
the palps, regions of the head surrounding the eyes, and
frequently the proboscis itself. Other features related to
pollen, nectar consumption, and pollination include a
ridged or ribbed proboscis in Aneuretopsychidae and
some recent butterflies (Ren et al., 2009), and structures
at the proboscis tip for capillary uptake of fluids,
including the dipteran labellae, mecopteran pseudola-
bellae, trichopteran haustorium, and flattened plates at
the siphon tips of some glossate lepidopterans (Barth,
1985; Chaudonneret, 1990; Krenn et al., 2005) and
perhaps kalligrammatids. Often, such proboscises are
accompanied by palps that are absent or significantly
reduced (Chaudonneret, 1990; Ren et al., 2009).

There also are convergent parallels between long-
proboscid mouthpart features and gymnosperm ovulate
features mentioned above, suggesting close associa-
tions or even mutualisms, however imperfect. If these
ovulate and insect mouthpart features evolved in
tandem, a true coevolutionary relationship may have
existed, although coevolution is demonstrated from
genetic reciprocal feedback in modern organisms
(Janzen, 1980) and is difficult to test in the fossil
record. However, the congruence between ovulate
organs and co-occurring insect mouthparts is more
than fortuitous (Ren et al., 2009). First, both plants and
insects with apparently linked structures co-occur in
space and time. Second, the morphological repertoire of
tubelike features in ovulate organs tightly matches the
coeval spectrum of insect mouthpart sizes and shapes
that would fit into these tubes. Third, the pollen
morphology is more consistent with insect than wind
dispersal. Fourth, pollen grains from candidate ovulate
organs presumed to be insect pollinated are the same
grains found on mouthpart contact surfaces and in the
guts of the suspect insect pollinators. Finally, the
pollinated plants were bisexual and presumed to
outcross with conspecific pollen organs.

PATTERNS IN THE EVOLUTIONARY SHIFT FROM GYMNOSPERMOUS TO ANGIOSPERMOUS POLLINATION

Not counting an Early Permian occurrence, the
assemblage of gymnosperm–insect pollinator associa-
tions (phase 1) lasted ca. 65 million years, from the
Middle Jurassic (165 Ma) to approximately the late
Early Cretaceous (100 Ma), well into the angiosperm
radiation. The overlap of phase 1 with phase 2
occurred at a time when many earlier gymnosperm-
insect associations were rare, uncommon, or extirpat-
ed (Figs. 1, 2). During the 20-million-year co-
occurrence of phase 1 and phase 2 associations, and
continuing into the Turonian Stage of the early Late
Cretaceous, angiosperms expanded their initial evo-
lutionary and ecological scope, accompanied by

geographical shifting, decline, and demise of gymno-spermous groups. During the mid Cretaceous interval of mounting angiosperm dominance, there were three macroevolutionary patterns of plant hosts and insect pollinators. First was the extinction of many gymno-sperms and their insect pollinators. Second was the survival of other, older, mid Mesozoic insect-pollinating lineages that transferred their host preferences from gymnosperms to angiosperms. Third was the origination of new angiosperm taxa and their new insect pollinators; this latter pattern has been dominant since the mid Cretaceous.

Pattern 1: Extinction

Several major seed plant lineages with pollinator associations either became extinct or were significantly diminished in diversity during or soon after the angiosperm radiation. Czekanowskiales, Voltziales, Pentoxylales, and Caytoniales became extinct around this interval, whereas Corystospermales, Cheirolepidiaceae, and Bennettitales survived in decreased diversity until the Cretaceous-Paleogene (K-Pg) boundary or shortly thereafter (Fig. 1). Insect pollinator lineages that underwent a similar extinction during the angiosperm radiation were Mesopsychidae, Aneuretopsychidae, and Pseudopolycentropodidae (Mecoptera), Kalligrammatidae (Neuroptera), and Cratomyiidae (Diptera). Many other nonpollinating but nonetheless plant-associated insect lineages also became extinct at this time, such as the Palaeotinidae (Hemiptera), Lophioneuridae (Thysanoptera), and Eolepidopterygidae (Lepidoptera).

Pattern 2: Lateral transfer

One particular insect clade, Diptera, experienced limited pollinator extinction during the interval when angiosperms became ecologically dominant. Modern, floricolous, long-proboscid dipteran lineages, such as Nemestrinidae, pangioniine Tabanidae, Apioceridae, Thereviidae, and Mydidae, had their origins in the Jurassic as associates of gymnosperms. This continuity indicates a shift from earlier fluid feeding on pollination drops of gymnosperms to subsequent nectaring on angiosperms. These transfers probably represent opportunistic cladogenetic events in the plant and fly lineages, with an effect at higher taxonomic ranks, seen in family-level diversity data (Labandeira & Sepkoski, 1993; Jarzembowski & Ross, 1996). It is unknown why, for pollinators, only the Diptera escaped the extinction blitz. Further insights may be gained in establishing which biological properties protected numerous other, nonpollinating, phytophagous insects from extinction, allowing their host shifts from gymnosperms onto angiosperms.

Pattern 3: Origination

Major clades of insects had their origins as pollinators and phytophages on angiosperms during their initial radiation, traceable through fossil occurrences and phylogenetic data (Dilcher, 1979; Crepet & Friis, 1987; Gottsberger, 1988; Labandeira et al., 1994; Farrell, 1998; Grimaldi, 1999; Bernhardt, 2000; Thien et al., 2003, 2009; Danforth et al., 2006; Moreau et al., 2006; Hu et al., 2008). In particular, numerous pollinating clades of Hymenoptera, Coleoptera, Diptera, and Lepidoptera had their origins during the early, formative period of angiosperm evolution, representing the 25-million-year interval from the late Barremian (125 Ma) to the end of the Early Cretaceous (100 Ma), and probably continuing to the mid Turonian (90 Ma). Much of what has been documented for this crucial longer interval involves the radiation of angiosperms and their associated, especially pollinating, insect clades and consequently focuses on the origins of much of the current land biota (Crepet, 1983, 2008; Crepet & Friis, 1987; Grimaldi, 1999; Grimaldi & Engel, 2005; Crepet & Niklas, 2009). The remarkable co-radiation of insects and angiosperms is better documented than earlier associations between plants and insects, such as the Late Triassic event in Gondwana (Labandeira, 2006a, b) or the Middle Jurassic origin of gymnosperm pollinating clades discussed here. Whether earlier, mostly Jurassic, associations, including pollinator associations between insects and gymnosperms, have a role in explaining the success and launching of angiosperms remains an unexplored question.

MACROEVOLUTIONARY AND MACROECOLOGICAL INTEGRATION

One perspective for understanding the major pattern of insect pollination during early angiosperm diversification was provided by Grimaldi (1999), later updated in Grimaldi and Engel (2005). This has been supplemented by the accumulation of new data and a more comprehensive understanding of plant-insect associations long before, during, and soon after the diversification of basal angiosperm lineages (Gorelick, 2001; Labandeira, 2005a, b; Labandeira et al., 2007a; Crepet, 2008; Nepi et al., 2009; Ollerton & Coulthard, 2009; Ren et al., 2009). Recent associational data build on the systematic placement of pollinating insect clades and their synchronicity or asynchronicity with emerging and radiating angiosperm lineages, and also contributes to a broader integration of more spatiotemporally diverse ecological data. Any enlarged synthesis regarding pollination dynamics during the mid Mesozoic should (1) incorporate important information from older, Juras-

sic and Early Cretaceous compression deposits; (2) encompass data from additional insect taxa that also emphasize mandibulate insects; (3) include knowledge of mouthpart structural details and feeding modes that reveal convergences; (4) add crucial plant associational evidence such as the reproductive structure of plant ovulate organs and pollen types consistent with entomophily; (5) assess the habits of endophytic larvae, perhaps immatures of conspecific pollinating adults in their consumption patterns of plant reproductive tissues; and (6) provide additional data of the later Mesozoic record of insect diversity for a broader synthesis of extinction and origination patterns. Although this list requires considerable interdisciplinary and atypical integration of paleobotanists, paleoentomologists, and ecologists, there have been three areas of improvement in understanding the Mesozoic history of insect pollination.

Two basic types of mid Mesozoic pollination

The record of mid Mesozoic pollination is divided into two fundamental types of pollination and related associations. (1) Mandibulate palynophagous insects that interact with plant hosts bearing bisexual reproductive organs with rewards typically being pollen and expendable reproductive tissues. Larvae often are endophytic consumers of reproductive tissues from the same host plant used by conspecific adult pollinators. Inferred associations are predominantly those between beetles and plants with large, often bisexual strobili, such as Bennettitales, but also including the physiognomically similar cycads and probably pentoxylaleans. (2) Fluid-feeding insects with siphonate proboscises that interact with a different and broader range of seed plant hosts. A wide variety of insect clades access this type of pollination reward; they have long-proboscid mouthparts with features consistent with penetration of various tubular devices in gymnospermous ovules and associated tissues. A detailed contrast of these two different types of pollination is provided by Labandeira et al. (2007a).

The existence of a distinctive type of long-proboscid pollination on gymnosperms during the mid Mesozoic

The mid Mesozoic long-proboscid insect pollination mode discussed in this and two other recent reports (Labandeira et al., 2007a; Ren et al., 2009) was predicted earlier by pollination biologists working on modern seed plants (Meeuse, 1978; Lloyd & Wells, 1992). However, earlier discussions did not propose any credible, co-occurring insect pollinators, and no

functional interpretation was given for the various tubular structures in reproductively anomalous seed plants such as the Cheirolepidiaceae (Axsmith et al., 2004; Axsmith & Jacobs, 2005) and Caytoniaceae (Harris, 1957; Dilcher, 2000; Ren et al., 2009). Recent skepticism for the existence of a preangiospermous pollination mode on gymnosperms by fluid-feeding insects has been superseded by additional structural evidence for insect-mouthpart and plant-ovulate features indicating diverse pollination modes that preceded angiosperms. Whether these novel data impact theoretically or mechanistically on the origin of the angiosperm flower remains to be seen. But it would appear that criteria based on more efficient angiosperm pollination, particularly given the wide variety of disparate receptive structures found in gymnosperms, may provide a way forward.

The impact of mid Mesozoic pollination data on understanding plant and insect diversity in the fossil record

There is a significant drop-off in gymnosperm-pollinating clades during the Early Cretaceous (Niklas et al., 1985; Ren et al., 2009), and many more nonpollinating, phytophagous lineages, such as piercer-and-suckers and external foliage feeders, similarly became extinct. One hypothesis for this interval of insect extinction, supported by their preangiospermous occurrences and occasional knowledge of their biologies, is that their life cycles were closely connected to gymnosperm hosts that similarly became extinct or significantly reduced in diversity (Gottsberger, 1988; Gorelick, 2001; Labandeira et al., 2007a; Ren et al., 2009). Angiosperms and their newfound insect associates diversified considerably after an approximate 25-million-year lag after their origin (Grimaldi, 1999; Crepet, 2008), initially with a comparatively small number of clades but subsequently increasing to the elevated levels during the Eocene, recorded in the Green River and Florissant formations, Baltic amber, and Messel Lake (Bequaert & Carpenter, 1936; Kusnezov, 1941; Melander, 1949; Lutz, 1993; Wilf et al., 2000; Weitschat & Wichard, 2002; Meyer, 2003; Engel, 2005a; Labandeira et al., 2007b; Michez et al., 2007; Wedmann et al., 2009).

Although the family-level analyses of fossil insect diversity by Labandeira and Sepkoski (1993) need to be updated, these and other analyses (Jarzembowski & Ross, 1996; Dmitriev & Ponomarenko, 2002) indicate that the plateau in the earlier semilogarithmic rise of family-level insect diversity may be real, attributable to a biological event that transformed plant species dominance from gymnosperm to angiosperm. An alternative explanation is that this plateau represents

a lull in the recovery of insect taxa from earlier deposits with high numbers of insect species. Consequently, taxic data analyses can capture fossil insect diversity data (Sepkoski & Kendrick, 1993), indicating that global biotic changes resulted in major decreases in insect diversity. This diversity decrease is wedged between an earlier extinction episode and a subsequent diversification event in seed plants.

From the plant fossil record we know that deep-throated flowers did not originate among the earliest lineages of angiosperms, which tend to be bowl-shaped, open, and accessible to a variety of small nonproboscid insects (Friis et al., 1987). The earliest angiosperm flowers indicate pollination predominantly by small nonproboscid, large mandibulate, and punch-and-sucking insects (Dilcher, 2000; Labandeira, 2005a). The earliest deep-throated flowers specialized for long-proboscid insect pollination are of Turonian age (Crepet, 2008), occurring ca. 45 million years after the earliest angiosperm fossils. If angiosperms are older, as some molecular phylogenies indicate (Magallón, 2010), it is highly unlikely that they presaged the apomorphies found in deep-throated flowers, particularly given recent work in the developmental genetics of angiosperm origins (Rudall et al., 2009; Specht & Bartlett, 2009). A significantly different pattern would have occurred if early angiosperms originated from a *Caytonia*-like ancestor (Doyle, 2008), in which a Jurassic origin involved long-proboscid pollination.

SUMMARY AND CONCLUSIONS

This study, partly informed by two related contributions that precede it (Labandeira et al., 2007a; Ren et al., 2009), provides the following seven conclusions.

1. Evidence for pollinator mutualisms. Six lines of evidence are used for establishment of pollinator mutualisms in the fossil record. They are: (1) the structure of insect mouthparts and related head features; (2) the structure of ovulate organs and especially features for provisioning rewards for insects; (3) the structure of pollen and its placement on plant and insect contact surfaces; (4) palynivore gut contents and dispersed coprolites; (5) the host occurrence, geometry, and feeding patterns of insect plant damage on reproductive structures; and (6) knowledge of the present-day life histories of the nearest, closest relatives of both fossil plant hosts and their insect pollinators. These features, often in combination, provide a mosaic of evidence that can identify the nature of a particular relationship between an insect pollinator and a host plant.

2. The past versus recent spectrum of insect and plant associates. There now is more knowledge of the spectrum of fossil insect and plant clades involved in pollination and associated feeding patterns during the mid Mesozoic. Pollinating insects that bore mandibulate mouthparts principally consisted of beetles, as today, but in the past may have included other large mandibulate insects. Principal host plants of mandibulate pollinators were cycads, bennettitaleans, and pentoxylaleans. By contrast, for insects with haustellate mouthparts, in particular diverse long-proboscid pollinators, the principal insects were aneuretopsychine scorpionflies, ca. five major lineages of brachyceran flies, kalligrammatid neuropterans, and perhaps glossate lepidopterans and caddisflies. Their inferred host plants were corystosperms, pentoxylaleans, czekanowskialeans, cheirolepidiaceous conifers, gnetaleans, and caytonialeans. The two major trajectories of pollination and related feeding associations—mandibulate versus haustellate insects—define gymnosperm hosts of the mid Mesozoic as well as angiosperm hosts of the mid Cretaceous to the present.

3. Opportunism as a key principle in the evolution of pollination and related associations. Recent tests of the pollination syndrome hypothesis have failed, rendering use of the concept an uncertain enterprise. Instead, the term "pollination mode" is introduced, where the referent is to a common mechanism rather than to a particular insect clade as the essential identifier. This suggests an opportunistic pattern of pollination associations for the Mesozoic fossil record.

4. The long-proboscid, siphonate condition originated during the Early Permian. The plesiomorphic, perhaps basalmost, neuropteran clade, Permithonidae, included a small, fluid-feeding species that bore siphonate mouthparts. The primitive, elongate proboscis of this taxon consisted of conjoined maxillary palpi that retained segmental divisions and encompassed a comparatively narrow food canal.

5. Documentation for major, mid Mesozoic pollination modes. Based on the fossil record, seven distinct pollination modes define the mid Mesozoic, although other, unknown modes undoubtedly were present. The modes are: (1) punch-and-sucking, (2) large mandibulate insects, (3) medium-sized beetle pollinators with larvae in internal tissues, (4) small, nonproboscid insects, (5) entrapment pollination, (6) oil and resin pollination, and the focus of this report, (7) long-proboscid insects.

6. The demise of the long-proboscid pollination mode on gymnosperms and its partial continuation on newly emerging angiosperms. A diverse group of long-proboscid insects became a distinctive pollinator

mode from the Middle Jurassic to the Early Creta-
ceous on a variety of gymnosperm hosts. Most clades
of long-proboscid insects became extinct during the
Early Cretaceous, whereas some lineages survived and
underwent a host-plant shift onto angiosperms ap-
proximately at this time. A third group of long-
proboscid insects originated on emerging angiosperms
during their evolutionary radiation.

7. *The importance of the long-proboscid pollination
mode for understanding mid Mesozoic fossil plant and
insect diversity.*   First, there has been an expansion of
knowledge about the biology of mid Mesozoic insect
pollination. In particular, there is greater understand-
ing of palynophagy and nectarivory for mandibulate
insects and their inferred host plants that bear large
unisexual or bisexual strobili. Also, long-proboscid,
siphonate insects likely occurred on a variety of
gymnospermous hosts with receiving tubular struc-
tures. Second, the replacement of the long-proboscid
pollination mode, in existence for ca. 65 million years
on gymnosperms, by a similar but simpler pollination
mode on angiosperms may be related to the origin of
the flower and its greater pollinator efficiency. Third,
new Mesozoic pollinator data support previous studies
on fossil insect diversity during this interval. These
pollinator data represent a sample of mid Mesozoic
standing insect diversity, indicating that the global
biotic turnover from gymnosperm to angiosperm floras
also reflects initial decline and extinction of varied
gymnosperm hosts and pollinators. This was followed
by a 20-million-year plateau of lowered diversity
levels that was replaced by subsequent angiosperm
diversification and their new pollinator lineages.

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