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Pollination drops, pollen, and insect pollination of Mesozoic gymnosperms

Conrad C. Labandeira^{1,2}, Jiří Kvaček³ & Mikhail B. Mostovski^{4,5,6}

¹ Department of Paleobiology, P.O. Box 37012 (MRC-121), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013-7012, U.S.A. labandec@si.edu (author for correspondence)

² Department of Entomology, University of Maryland, College Park, Maryland 20742, U.S.A.

³ Department of Palaeontology, National Museum, Václavské nám. 68, Prague 1, Czech Republic

⁴ Natal Museum, Private Bag 9070, Pietermaritzburg 3200, South Africa

⁵ School of Biological and Conservation Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, 3209 South Africa

⁶ Paleontological Institute, Russian Academy of Sciences, 123 Profsoyuznaya Str., Moscow, 117997 Russia

Recent focus on plant-insect associations during the angiosperm radiation from the last 30 million years of the Early Cretaceous has inadvertently de-emphasized a similar but earlier diversification that occurred among gymnosperms. The existence of gymnosperm-insect associations during the preangiospermous Mesozoic is evidenced by mouthparts capable of reaching and imbibing pollination drops or similar fluids, availability of pollen types consistent with entomophily, and opportunities for related consumption of pollen, seeds, and reproductively associated tissues in major seed-plant groups, namely seed ferns, conifers, cycads, bennettitaleans, and gnetaleans. Based on stereotypical plant damage, head-adherent pollen, gut contents, wing structure, mouthpart morphology and insect damage to plant reproductive organs, the likely nectarivores, pollinivores and pollinators were orthopterans, phasmatodeans, web-spinners, sawflies and wasps, moths, beetles, mecopteroids, and true flies. These associations are ranked from possible to probable although the last three insect clades provide the strongest evidence for pollinator activity. We document two mid Cretaceous examples of these associations—cycadeoideaceous bennettitaleans and beetles and a cheirolepidiacean conifer and flies—for which there are multiple lines of evidence for insect consumption of plant reproductive tissues but also pollination mutualisms. These data highlight the independent origin of a major phase of plant-insect pollinator-related associations during the mid Mesozoic that served as a prelude for the separate, iterative and later colonization of angiosperms.

KEYWORDS: *Alvinia*, Bennettitales, Cheirolepidiaceae, Coleoptera, Diptera, insects, Mesozoic, plant-insect associations, pollination drop, seed plants

INTRODUCTION

Considerable attention has been devoted to the angiosperm radiation and their co-radiating insect herbivores and pollinators during the mid-Cretaceous from 135 to 90 million years ago (Ma) (Crepet, 1996; Grimaldi, 1999). However, a more prolonged, extensive, and evolutionarily important colonization of gymnospermous seed plants, especially by basal clades of holometabolous insects, transpired during the mid-Triassic from about 245 to 220 Ma, continued throughout the Jurassic and into the earlier Cretaceous at around 100 Ma (Labandeira, 2006). The worldwide expression of this process consisted of major assemblages of plant hosts harboring damage attributable to diverse types of external feeding, galling, leaf mining, piercing-and-sucking, seed predation, wood boring and oviposition. Instances of this damage occur in stereotypical and intricate patterns that are confined to particular plant-host species but also blanket regional floras (Krassilov & Rasnitsyn, 1983; Jarzembowski, 1990; Reymanówna, 1991; Grauvogel-Stamm & Kelber, 1996;

Ash, 1997; Scott & al., 2004). One neglected aspect of this insect herbivore radiation on gymnosperm hosts is evidence for nectarivory, pollinivory, and varied damage on ovuliferous or microsporangiate strobili, some of which are interpretable as pollination mutualisms. These associations represent specialized relationships that were analogous to those occurring later on angiosperms. Thus, these gymnosperm-based associations constituted the third evolutionary phase of the plant-insect associational fossil record that commenced during the Early Triassic (252 Ma), after the end-Permian extinction, and continued throughout the Mesozoic, albeit at significantly decreased diversity as angiosperms assumed ecological dominance (Labandeira, 2000, 2006). The mid-Triassic to mid-Cretaceous co-radiations of insects and gymnosperms are contrasted with the fourth phase of the radiation of angiosperms and their insect associates that commenced during the Early Cretaceous (115 Ma), an expansion that has been increasing in dramatic ecological ways to the present.

In this contribution, the inferred pollination-related associations of Mesozoic gymnospermous seed plants

(Fig. 1A) and their insect participants (Fig. 1B) will be documented and new data and interpretations will be presented. Previously, a near exclusive focus on angiosperms has been predominant in the fossil insect literature, characterized by skepticism with regard to evidence for pollination or autecologically coupled types of feeding such as nectarivory, pollinivory or seed predation during the preangiospermous Mesozoic (Grimaldi & Engel, 2005). This view persists despite considerable evidence for and common recognition of these earlier associations (Crepet, 1974; Gottsberger, 1988; Crowson, 1991; Krassilov & Rasnitsyn, 1999; Labandeira, 2000; Gorelick, 2001; Klavins & al., 2005). For example, some authors (Oberprieler, 2004) have asserted a parallel delay in pollination and related associations of cycads to the angiosperm dominated part of the fossil record, even though extant major lineages of obligately insect-pollinated cycads extend back in time from the Early Cretaceous to Middle Triassic or possibly earlier (Gao & Thomas, 1989; Klavins & al., 2003; Anderson & al., 2007). Significantly, a predilection for understanding angiosperms and their pollinators forms an important backdrop for the increased number of associations seen during the Late Cretaceous and Cenozoic (Crepet, 1979; 1996; Crepet & Nixon, 1998; Grimaldi & Engel, 2005), and especially the modern world (Grant & Grant, 1965; Faegri & Pijl, 1981; Proctor & al., 1996).

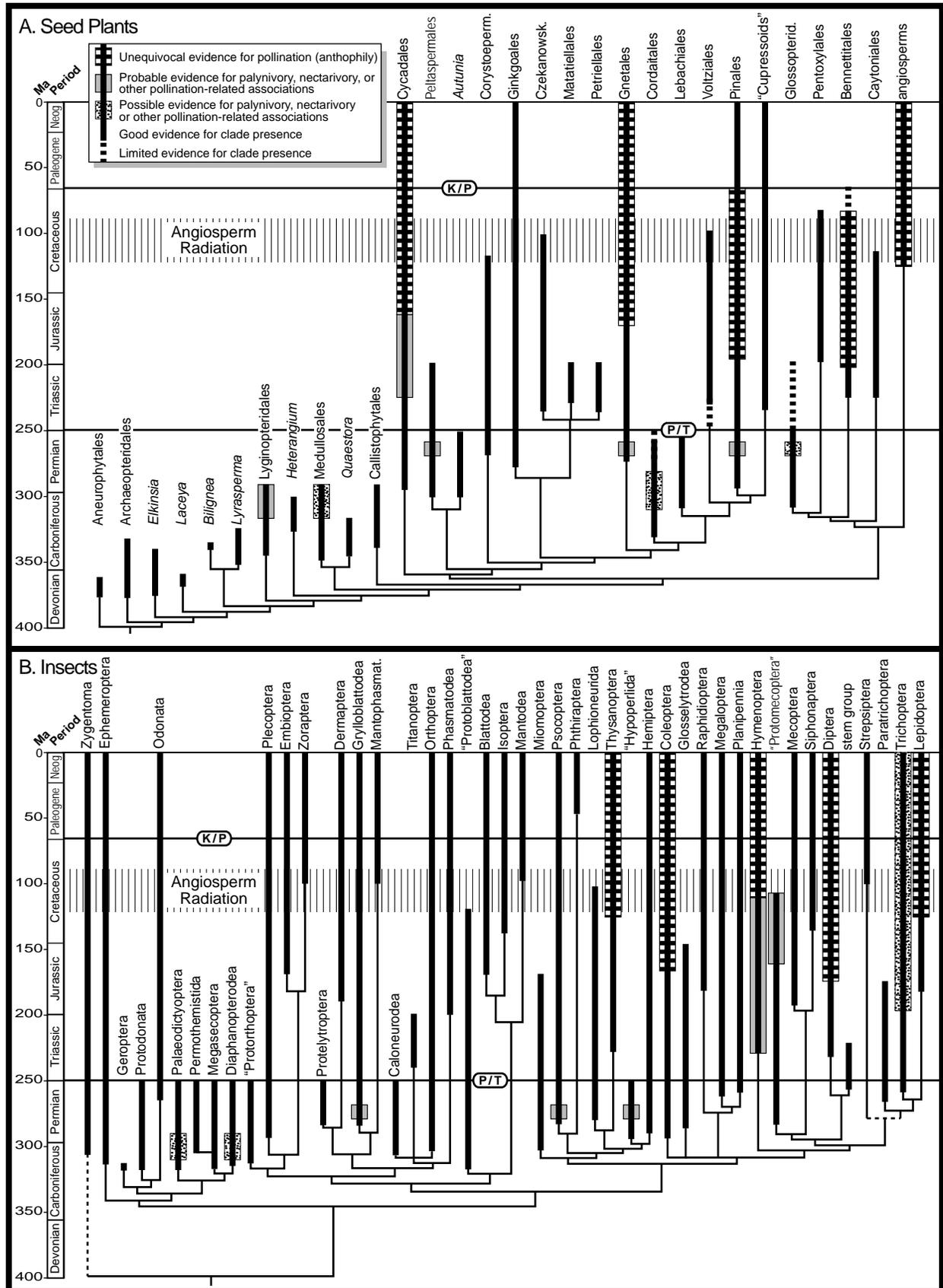
An underappreciated fact is that the ensemble of Mesozoic gymnospermous lineages were the physiognomic equals of angiosperms. Mesozoic gymnosperms included forms with herbaceous growth, lianas, shrubs, pachycauls, mangroves, stem succulents, monocot-like pteridospermous trees, and trees with true secondary xylem deployed as polyaxial, branched dicot-like forms or as monaxial conifers (Upchurch & Doyle, 1981; Retallack & Dilcher, 1988; Tidwell & Ash, 1990; Niklas, 1997; Rothwell & al., 2000; Dilcher & al., 2004). Similarly, studies indicate that more basal Mesozoic lineages of extant anthophilous insect lineages were interacting with seed-plant clades in ecologically modern and specialized ways (Pellmyr, 1992; Krassilov & Rasnitsyn, 1999; Norstog & Nicholls, 1997; Labandeira, 2000, 2005; Gorelick, 2001). For example, the obligate associations between extant cycads and their pollinators (Schneider & al., 2002) are at least as ancient and

specialized as analogous associations between figs and fig wasps (Machado & al., 2001), and undoubtedly are older (Farrell, 1998; Klavins & al., 2005). This increase in specialized associations between Mesozoic plant hosts and their herbivore- and pollinator associates forms the ecological backdrop for the spectacular success of one terminal, initially inconspicuous clade that displaced the dominant, earlier Mesozoic gymnospermous clades—the angiosperms. Given this context and evidence presented below, it is appropriate to restate a hypothesis regarding the origin of angiosperm pollination, namely that it was the gymnospermous pollination drop mechanism and its varied modifications (Baker & Hurd, 1968; Norstog 1987; Lloyd & Wells, 1992; Kato & Inoue, 1994; but see Frame, 2003a), that served as a functional, anatomical, and ecological prelude to early angiosperm pollination.

GYMNOSPERMOUS POLLINATION DROP MECHANISM, ZOOIDOGAMY, AND SIPHONOGAMY

Seed plants originated during the Late Devonian, at which time there was among progymnosperms a mechanism for the reception of motile antherozoids (Rothwell & Serbet, 1992) that evolved into an ovular pollination-drop mechanism. The pollination drop mechanism ancestrally was used for prepollen or pollen capture (Fig. 2A), followed by various developmental events that ended in fertilization. The earliest fossil evidence for the pollination drop mechanism is the callistophytacean seed fern *Callospermarion pusillum* Eggert & Delevoryas from the Middle Pennsylvanian of the Illinois Basin, U.S.A. (Figs. 2B, C; Rothwell, 1977; but also see Retallack & Dilcher, 1988). Although this type of pollen capture presumably occurred in several extinct seed plant lineages throughout the Late Paleozoic and Mesozoic, it currently is exclusively confined to the four remaining gymnospermous taxa: Pinopsida (Figs. 2D, E, G), Ginkgoopsida (Fig. 2F), Cycadopsida (Fig. 2I), and Gnetopsida (Figs. 2H, J). There are modifications of this mechanism in a minority of extant conifer taxa for which pollination drops are absent, as in the case of Araucariaceae, *Saxegothaea*, and some species of

Fig. 1. Phylogenetic relationships and stratigraphic ranges of gymnospermous seed-plant (A) and insect (B) clades, highlighting those lineages possessing significant examples of taxa engaged in pollinivory, nectarivory and pollination. Degrees of confidence for assignment of clades are provided in the box at upper-left in (A), and based on a variety of data, principally plant reproductive features, stereotypical plant damage, dispersed insect coprolite contents, insect gut contents, insect mouthparts, and dietary assignments consistent with life-habit attributes of extant descendants. Data for seed plants principally are from Hilton & Bateman (2006) and Anderson & al. (2007); data for insects originate from Labandeira (1994), Rasnitsyn & Quicke (2002), and Grimaldi & Engel (2005); time scale is that of Gradstein & al. (2004). The striped horizontal bar during the Cretaceous represents the turnover interval from a gymnosperm- to angiosperm-dominated flora. Abbreviations: Ma, millions of years ago; Neog., Neogene; P/T, Permian-Triassic boundary; K/P, Cretaceous-Paleogene boundary; Corystosperm., Corystospermales; Czekanowsk., Czekanowskiales; Glossopterid., Glossopteridales; Mantophasmat., Mantophasmatodea.



Abies and *Tsuga*. In a few other taxa, such as *Larix* and *Pseudotsuga* (Doyle & O'Leary, 1935; Tomlinson & al., 1991; Owens & al., 1998), the production of pollination drops is delayed until after pollen lands on a dry micropylar surface but occurs prior to fertilization. In extant gymnosperms, pollination drops are timed for maximum reception of saccate or non-saccate pollen by variously oriented ovules (Gelbart & Aderkas, 2002).

Pollination drops are produced by nucellar and/or adjacent secretory tissues within a chamber located at the archegonial pole, which typically is the exposed end of the ovule. This ovular region bears enveloping tissues that are formed into a thickened and tubular beak, the micropyle (Fig. 2A). The terminal end of the micropyle traps pollen by secreting an often sugary fluid that forms an extruded film or drop at its aperturate terminus. Soon after pollen capture, the pollination film or drop recedes back into the micropylar tube through evaporation or tissue resorption until the male gametes and nuclei reach the ovular archegonium that typically forms the bottom surface of a pollen chamber (Moussel, 1980). The fluid consists principally of carbohydrates, amino acids and lipids dissolved in a dilute to rather concentrated solution. Among extant gymnosperms, pollination drops typically contain dilute to concentrated carbohydrates with ancillary amino-acid components (Table 1; Ziegler, 1959; Chesnoy, 1993; Gelbart & Aderkas, 2002). The composition of sugars and amino acids in pollination drops has been reported for several species of conifers such as *Cephalotaxus*, *Pinus*, and *Thuja* (Ziegler, 1959; Nygaard, 1977; Serdi-Benkaddour & Chesnoy, 1985; Chesnoy, 1993); *Ginkgo* (Dogra, 1964); cycadopsids (Ziegler, 1959; Baker & Baker, 1983; Tang, 1993; 1995); and gnetopsids (Ziegler, 1959; Carafa & al., 1992). Although the presented values for gymnosperms exhibit highly variable concentrations of sugars and amino acids (Table 1), they encompass the range found among angiosperms. It is likely that there is an imbalance of both nutritional components given the wide range of sugar and amino acid concentration values reported (Table 1) and a lack of correlation between concentration levels for both nutritional classes, at least among angiosperms (Gottsberger & al., 1984).

It is possible to reconstruct a three-step evolutionary process by which gametes became transported to the ovular archegonial surface by means of pollination-drop or related processes. The first developmental type, zooidogamy, was characterized by the release from prepollen of motile antherozoids through the proximal aperture, the antherozoids then swam to an archegonium for fertilization (Poort & al., 1996). An important feature of this mechanism was that a prepollen grain lacked a pollen tube for providing nutrition or as a device for transporting gamete cells or nuclei to the archegonium. This condition, found particularly in lyginopteridalean and medullosean pteridosperms but also some cordaites, lasted until the late Paleozoic. It was replaced by an intermediate developmental type in which there was continued release of motile antherozoids proximally (zooidogamy), but with the additional distal outgrowth of a haustorial, often branched, pollen tube exclusively for absorbing nutrients or water (Poort & al., 1996). This early pollen type typified late Paleozoic conifers and seed ferns such as the callistophytacean *Callospermarion undulatum* (Neely) (Rothwell, 1972), continued in some pteridosperm lineages into the early Mesozoic, and is present in modern cycads and *Ginkgo*. The third developmental type is siphonogamy, in which the pollen grain abandoned motile antherozoids and instead transported gametes and nuclei solely by means of a pollen tube. Siphonogamy is found in all modern conifers, gnetopsids, and angiosperms, although there are significant modifications of the process, and it probably was present in some Mesozoic gymnosperm lineages such as bennettitaleans.

It was the pollination drop mechanism or its modification, in conjunction with true siphonogamy, which characterized most mid-Mesozoic ovuliferous structures attractive to insects. Although overwhelmingly a key part of extant gymnosperm pollination, the pollination-drop mechanism should not be construed as the only mode of producing ovular fluids in Mesozoic gymnosperms. Like stigmatic exudates and other reproductively associated surface secretions present in gymnosperms and basal angiosperms (Gelbart & Aderkas, 2002; Frame, 2003a), the typical pollination drop mechanism with a tubular micro-

Fig. 2. Micropyle secreted pollination drops from a Late Carboniferous seed fern (B, C) and the four major clades of extant gymnospermous seed plants (D–I). The generalized mechanism for production of pollination drops in gymnosperms is provided in (A), whereby an integumented unfertilized ovule bears a pollen chamber apically and is surmounted by a tubular micropyle filled with a nectar-like fluid for capture of pollen (from Gifford & Foster, 1989). This mechanism occurred in Late Pennsylvanian seed ferns such as *Callospermarion pusillum* (Rothwell, 1977), found as a permineralized substance containing pollen grains within a micropyle in (B) (abbreviations: n, nucellus; s, sclerotesta; p, pollination drop), magnified in (C). Pollination drops are illustrated for *Sequoiadendron giganteum* (Pinopsida: Cupressaceae) in (D) (abbreviation: mp, micropyle) (Takaso & Owens, 1996); *Phyllocladus glaucus* (Pinopsida: Podocarpaceae) in (E) (abbreviation: c, ovulate cone) (Tomlinson & al., 1997); *Ginkgo biloba* (Ginkgoopsida: Ginkgoaceae) in (F); *Taxus baccata* (Pinopsida: Taxaceae) in (G) (Proctor & al., 1996); an unidentified species of *Ephedra* (Gnetopsida: Ephedraceae) in (H) (Gifford & Foster, 1989); *Zamia pumila* (Cycadopsida: Zamiaceae) in (I) (Tang, 1995); and *Welwitschia mirabilis* (Gnetopsida: Welwitschiaceae) in (J) (Gifford & Foster, 1989).

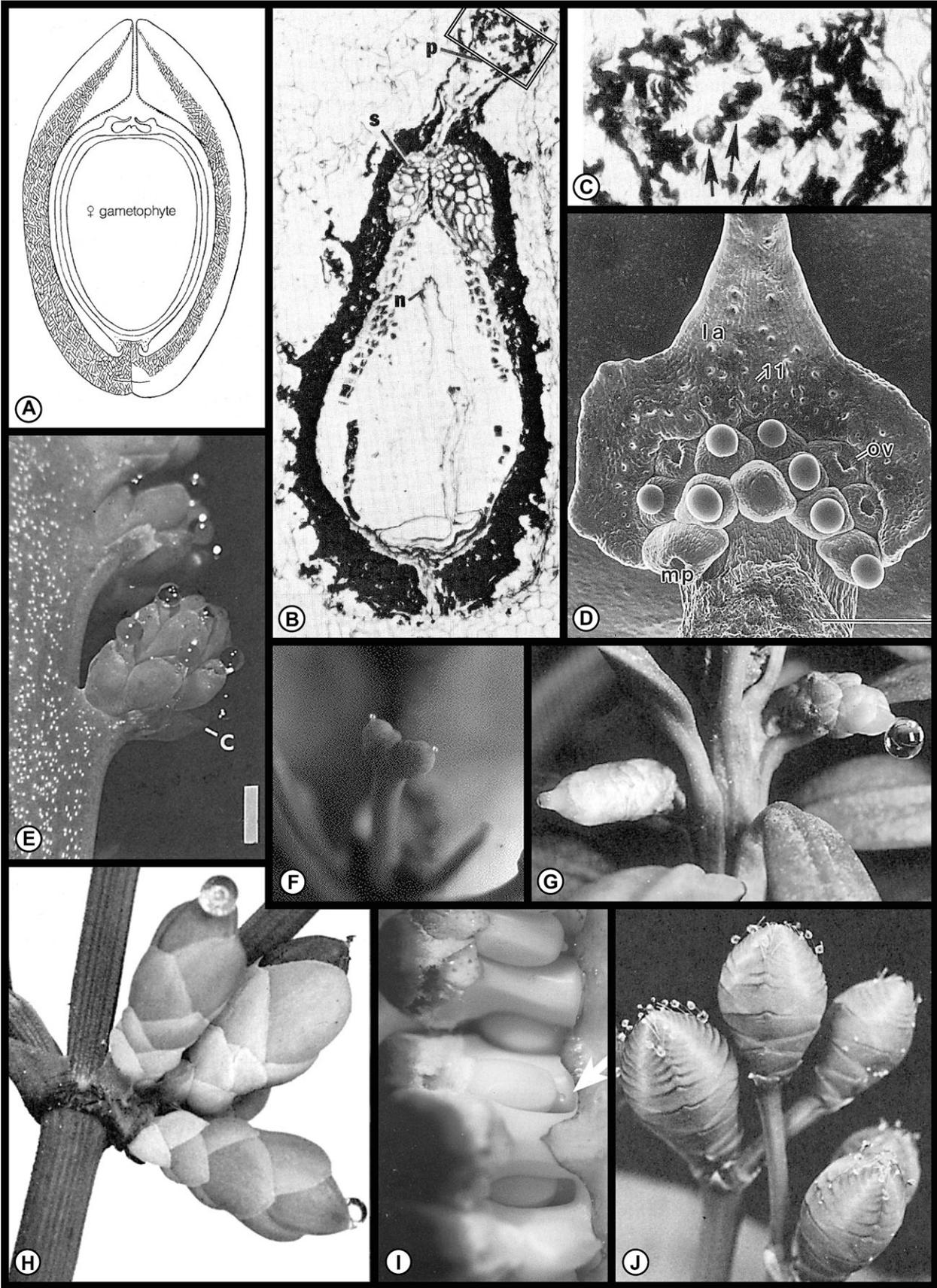


Table 1. Extraneuphial nectary, pollination drop and nectar concentration values of sugars and amino acids in major groups of vascular plants.

Taxon	Insect pollinated?	Sugar concentration (%) ^a	Amino acid concentration (μmol/ml) ^b	Angiosperm nectar site	References	Overall comparative characterization
Extraneuphial nectary (ferns)						
Aspleniaceae	N/A	46	98		Koptur & al., 1982	Sugars: Clustered, intermediate values differing by a factor of 2. Amino acids: Moderately clustered, differing by ~ a factor of 4.
Polypodiaceae	N/A	30	391		Koptur & al., 1982	
Polypodiaceae	N/A	54	195		Koptur & al., 1982	
Polypodiaceae	N/A	63	98		Koptur & al., 1982	
Pollination drops (gymnosperms)						
Cupressaceae	N	—	9180		Chesnoy, 1993	Sugars: Highly variable values differing by ~ 1 order of magnitude.
Cycadaceae	?	5–14	—		Tang, 1995	
Ephedraceae	Y	81.3	406–606		Bino & al., 1984a	Amino acids: Extremely variable values, differing by almost 2 orders of magnitude.
Ephedraceae	Y	79.8	379–496		Bino & al., 1984a	
Gnetaceae	Y	14–16	—		Kato & al., 1995	
Welwitschiaceae	Y	85	—		Carafa & al., 1992	
Zamiaceae	Y	5–14	1200		Tang, 1993	
Zamiaceae	Y	9–12	200–1,600		Tang, 1987	
Nectar (basal angiosperms)^b						
Magnoliaceae	Y	69.8	—	petal	Dieringer & al., 1999	Sugars: Low to intermediate values differing between 1 and 2 orders of magnitude.
Nymphaeaceae	Y	3–4 ^b	2,420	stigma	Capperino & Schneider, 1985	
Winteraceae	Y	20.3	—	stigma	Frame, 2003a	Amino acids: Highly variable values differing ~ by 1 orders of magnitude, but few studies.
Winteraceae	Y	13	—	stigma	Frame, 2003a	
Proteaceae	Y	23.7	284	floral nectary	Gottsberger & al. 1984	

^aSome taxa expressed as range values, others as averages; dashes indicate lack of known studies; some amino acid molar values converted from Baker scores.
^bSimilar small percentages of sugars have been recorded for other congeneric species, such as 3 % for *Nymphaea odorata* (Meeuse & Schneider, 1980).

pyle and subsurface chamber containing secretory tissues may have been more relevant as an adaptation to long-proboscid nectarivores. By contrast, other types of surface-accessible secretions produced by gymnosperm ovules would have been available to insects with shorter, non-intrusive mouthparts. Besides insect food sources such as ovular fluids and pollen, other (unfossilizable) reproductive associated attractants and rewards are likely to have been present such as color, heat and fragrance, features often found in extant cycadopsids, gnetopsids, and angiosperms (Pellmyr & Thien, 1986; Gottsberger, 1988; Kato & al., 1995; Stevenson & al., 1998; Wetschnig & Depisch, 1999).

Considerable evidence exists for extant associations between surface fluid-feeding insects and gymnosperms that produce pollination drops. All of the four existent gymnospermous clades—pinopsids, the ginkgoopsid *Ginkgo*, cycadopsids, and gnetopsids—produce pollination drops (Dogra, 1964; Kato & al., 1995; Norstog & Nicholls, 1997); and gnetopsids and cycadopsids, like angiosperms, have extensive associations with insects and overwhelmingly are insect pollinated. By contrast, pinopsids and *Ginkgo* are fundamentally wind-pollinated (Ackerman, 2000), although insects do occasionally feed on their pollen and probably pollination drops.

The dioecious Gnetopsida consists of three, distantly related, monogeneric families that possess a suite of characters involved in insect pollination. These entomophilous features are boat-shaped saccate pollen that is sticky and forms clusters, strong scents, frequent extrafloral nectaries, and showy or otherwise colorful bracts (van der Pijl, 1953; Lloyd & Wells, 1992). Most importantly, these taxa produce pollination drops on both microsporangiate and ovuliferous cones, and include sterile ovules positioned peripheral to the

fertile regions of microsporangiate cones (Haycraft & Carmichael, 1992). All three modern genera have insect visitors feeding on the pollination drops of both ovuliferous and microsporangiate cones, and wind pollination (anemophily) is insignificant, although certain species of *Ephedra* may have an important aerial component in the transport of pollen to receptive ovules (Hesse, 1984; Buchmann & al., 1989).

In monotypic *Welwitschia mirabilis* Hooker of southwestern Africa, conspicuous pollination drops are produced in ovuliferous and microsporangiate cones when ovules are mature and receptive (Marsh 1982; Wetschnig & Depisch, 1999). Pollinators are insects, consisting mostly of a broad spectrum of cyclorrhaphan flies possessing a short but broad labella, which are addressed to plant surfaces for sponging fluids (Graham-Smith, 1930). Brachyceran flies with broad labella also are pollinators, some lineages of which extend deep into the Mesozoic. However, the most efficient spongers are cyclorrhaphan flies that have an origin during the Late Cretaceous (Grimaldi & Cumming, 1999).

The genus, *Gnetum*, is represented by about 40 species of lianas, shrubs and trees in tropical to subtropical southeastern Asia, especially Indonesia (Price, 1996). *Gnetum* also secretes pollination drops but is pollinated by a wider variety of small insects, particularly small flies and subordinately small moths (Pijl, 1953; Kato & al., 1995). Pollen is sticky and aggregates in linear clusters that are released synchronously with distinctive microsporangiate cone odors.

The third genus, *Ephedra*, is represented by about 50 species throughout xeric habitats in Eurasia, northern Africa and the Americas, and consists of scale-leaved, woody, small, sometimes climbing, shrubs or small trees (Price, 1996). *Ephedra* produces pollination drops with levels of sugar concentration significantly higher than that of wind-pollinated taxa of other seed plants (Porsch, 1916; Kato & Inoue, 1994). The pollen of *Ephedra* is clustered and sticky because of elevated sugar concentrations and not because of pollenkitt, an angiosperm feature (Hesse, 1984). The micropyle for a typical species (*E. distachya* L.) is 1 mm in inner minimum diameter and produces multiple pollination drops, each following a previous pollination episode (Moussel, 1980). Curiously, such a micropylar diameter is narrower than the outer proboscis diameters of many larger, actively flying insects. Pollinators typically are small insects, particularly flies (Bino & al., 1984a; Meeuse, 1990), but also hymenopteran parasitoid wasps such as chalcidoids (Moussel, 1980) and small bees that produce honey from the drops (Ordetx, 1952). A general pattern emerges that extant gnetaleans are pollinated by small, actively flying insects which use their proboscides to consume surface fluids, such as small- to medium bodied flies and moths having modestly prolonged mouthparts. Such a pattern would be expected for fossil members of

the gnetopsids whose interval of greatest diversity is the Early Cretaceous (Crane & Upchurch, 1987; Sun & al., 2001), but also were present earlier during the Jurassic (Krassilov, 1997).

The insect visitors and associates of the Cycadopsida overwhelmingly have targeted pollen and other tissues such as endosperm, leaf epidermis and receptacular parenchyma as the principal plant rewards. As would be expected, secreted liquids in Cycadopsida have low sugar and amino acid content (Table 1) in contrast to the surface fluids of Gnetopsida (Donaldson, 1997). These insects—mostly beetles but also some thrips—enter the environs of the pollination drop with their whole body rather than a manipulated proboscis (Norstog & Nicholls, 1997; Terry, 2001). Thus, the associates of cycads are comparatively small mandibulate beetles and to a lesser degree thrips, which have “punch-and-suck” mouthparts; both groups preferentially consume pollen (Crowson, 1991; Kirk, 1984; Mound & Terry, 2001; Schneider & al. 2002). Limited evidence indicates that strong musty scents and pollination drops lure pollinivorous beetles to ovules (Pearson 1906; Pellmyr & Thien, 1986; Tang 1987) even though the latter fluids are infrequently consumed by beetles. Rather, the dilute pollination drops likely make the micropyle terminus sticky for adherent pollen as weevils brush across ovuliferous structures. In addition to pollen and pollination drops, cone thermogenesis and a brood site for oviposited eggs in the case of two *Zamia* species also are major rewards (Pellmyr & Thien, 1986; Stevenson & al., 1998; Dobson & Bergström, 2000). Major pollinators of cycads are a broad array of polyphagan beetles, including members of the Erotylidae, Boganiidae, and especially taxa from the diverse clade Polyphaga, namely the Belidae, Curculionidae, Brentidae, and Anthribidae (Crowson, 1991; Schneider & al., 2002). An exception to the dominance of beetles is the aeolothripid thrips genus *Cycadothrips* that obligately pollinates the cycad *Macrozamia* in Australia, an association considered to antedate cycad-beetle associations, and possibly goes back as early as the Middle Jurassic (Mound & Terry, 2001; Terry & al., 2005; but see Oberprieler, 2004). Additionally, mycetophilid midges and bees feed on pollination drops of *Zamia pumila* and may play a role in pollination (Breckon & Ortíz, 1983; Ornduff, 1991).

There is no evidence for insects playing any role in the pollination of extant pinopsids and *Ginkgo biloba* L. Typically, wind-pollinated gymnosperms are characterized by round to lenticular, 20 to 50 µm in diameter, smooth pollen grains, which lack sticky substances and are unclumped (Wodehouse, 1935; Whitehead, 1969), and produced in prolific amounts (Ackerman 2000; Gorelick 2001)—features typical of modern pinopsids and *Ginkgo*. By contrast, the size range of entomophilous pollen (including functional units such as tetrads and pollinia) is

much wider, varying from 10 to 150 μm or even greater. To our knowledge, there have been no published observations of insect feeding on conifer or *Ginkgo* pollination drops, although it seems likely that such surface fluids may be sources of nutrition for insects. More notable is the consumption of pollen on microsporangiate pinaceous cones by holometabolous insects such as mecopteroids and xyelid sawflies (Burdick 1961; Malyshev, 1968), which have lineages that extend to the Middle Triassic (Rasnitsyn, 1964; Grimaldi & Engel, 2005). Several other insect lineages, such as hover flies, also consume conifer pollen (Holloway, 1976; Stelleman, 1981; Leereveld, 1982), but are not implicated in pollination, supporting the view that extant pinopsids are universally anemophilous. The lack of entomophily in *Ginkgo* may be related to the fact that it was only known from cultivation in eastern Asia and hence, may have lost its ancient complement of herbivores and pollinators.

PLANT PROVIDERS OF NECTAR, POLLEN AND ASSOCIATED REPRODUCTIVE TISSUES

During the Mesozoic there was more higher-ranked seed-plant lineages inferred to have been dominantly insect pollinated than there are today: 5 versus 3. For the Mesozoic interval, excluding the Pteridospermopsida whose insect-associated members arguably are confined to the Paleozoic, there are the Pinopsida, Cycadopsida, Bennettitopsida, Gnetopsida, and Angiospermopsida, compared only to the Cycadopsida, Gnetopsida, and Angiospermopsida of today. The pollination biology of these gymnospermous lineages will be briefly discussed with regard to pollination drop and similar mechanisms, as well as the role of pollen in facilitating possible entomophilous associations of pollinating insects.

Pteridospermopsida. — Pteridosperms (seed ferns) are a paraphyletic assemblage of mostly early seed plants that consist of several lineages basal to remaining seed plants (Hilton & Bateman, 2006). Their ovules were characterized by the pollination drop system and typically bore wind-dispersed prepollen. Evidence for insect pollination occurs among a few Late Carboniferous pteridosperm species, particularly the medullosacean *Pachytesta illinoensis*, of Late Pennsylvanian age from the Illinois Basin of north-central U.S.A. This plant geochronologically is the earliest plant with a well documented syndrome of anatomical and micromorphological features consistent with insect pollination. *Pachytesta illinoensis* had unusually large, heavy, and nonsaccate prepollen assigned to the form-genus *Schopfipollenites* (Taylor, 1978; Dilcher, 1979); enclosure of microsyrangia by glandular trichomes and distinctive fleshy tissue that may have

provided a nutritive reward; and presence of coprolites in the same deposit as *P. illinoensis* whose contents contain monospecific populations of *Schopfipollenites*, indicating pollinivore targeting of conspecific syngangiate prepollen organs (Retallack & Dilcher, 1988; Labandeira & Phillips, unpubl. data). Lastly, foliage of *P. illinoensis* had the most extensive herbivory of any co-occurring plant species within the surrounding peat swamp, suggesting an accommodationist antiherbivore strategy involving rapid rather than delayed pollination that is more consistent with entomophily (Eisikowitch, 1988; Labandeira & Phillips, unpubl. data).

The heyday of medullosacean associations and possible insect pollination can be contrasted to a respectable diversity of pteridosperm species during the Triassic and Jurassic that generally were wind-pollinated. Accordingly, entomophily has not adequately been demonstrated for any well-known, Mesozoic pteridosperm species (Retallack & Dilcher, 1988). However, taxa such as *Peltaspermum thomasi*, based on a peltasperm fructification (Anderson & Anderson, 2003), may be a candidate for insect pollination. The smooth, large (up to 40 μm) lenticular pollen was contained within pollen sacs which bore glandular excrescences on the surface (Retallack & Dilcher, 1988). The relatively large pollen argues against the plant being wind-pollinated. However, it is not clear if *P. thomasi* had a pollination drop mechanism and further study of the reproductive biology of this genus, which extends to the Late Triassic, is warranted. However, there are other taxa related to peltaspermalean seed ferns, such as the Ginkgoales (Hilton & Bateman, 2006), that may have been insect pollinated. For example, seed predation on the ginkgoalean seed, *Avatia bifurcata* (Anderson & Anderson, 2003), from the Molteno Formation of South Africa, could be related to a pollination syndrome in which immatures are seed predators and adults are pollinivores or nectarivores that pollinate the same host plant (also see Reymanówna, 1991). Similar associational combinations are found throughout modern cycads and angiosperms, except that immatures, in this case larvae, are often pollinivores (Johnson, 1970; Norstog & al., 1992; Pellmyr & Leebens-Mack, 1999).

Pinopsida. — Provided that the Pinopsida does not include the Gnetopsida as a subordinate clade or that the two are sister taxa, the Cheirolepidiaceae may be the only lineage of pinopsids that ever evolved insect pollination. It should be noted that the “gnetopsids as conifers” hypothesis (Chaw & al., 2000) conflicts with morphological and some molecular data consistent with the “anthophyte hypothesis” (Donoghue & Doyle, 2000; Rydin & al., 2002), an issue that apparently remains unresolved. Regardless, within the several families of extant conifers a variety of abiotic pollination mechanisms have evolved and involve features such as varied orientations

of the ovule during pollination, presence, modification or absence of the pollination drop mechanism, and whether the pollen is saccate (buoyant) or nonsaccate (sinking) (Owens & al., 1998). These varied mechanisms suggest that other abiotic and biotic pollination mechanisms may have been present during the earlier Mesozoic when there was considerable proliferation of family-level clades, and higher-rank conifer diversity was greater prior to when global “competition” from nectar-bearing angiosperms came into play during the Cretaceous (but see Owens & al., 1998 for an alternative view).

Given this context, the Cheirolepidiaceae are ecologically a very anomalous taxon that colonized mostly xeric, mesic and saline habitats (Srivastava, 1976; Upchurch & Doyle, 1981; Watson, 1988; Uličný & al, 1997) during the Middle Triassic to the Cretaceous-Paleocene boundary (Scheuring, 1976) and possibly into the Paleocene (Pocock & al., 1990; N.R. Cúneo, pers. comm.). The Cheirolepidiaceae represent a wide variety of growth forms ranging from herbs, mangroves, shrubs, arborescent pole-like trees, and succulent halophytes (Upchurch & Doyle, 1981; Alvin, 1982; Batten & MacLennan, 1984; Watson, 1988; Axsmith & Jacobs, 2005). They are morphologically united principally by the presence of a very distinctive pollen type that has several features consistent with insect pollination and to a lesser extent by highly variable but typical cone-like organization of separate microsporangiate and ovuliferous reproductive organs. The Cheirolepidiaceae also exhibit distinctive and unique specializations of the ovuliferous scale that strongly suggest insect pollination (Cerceanu & al., 1976; Clement-Westerhof & van Konijnenburg-van Cittert, 1991; Alvin & al., 1994; Kvaček, 2000; Axsmith & al., 2004).

Cycadopsida. — Modern cycads are descendants of an ancient lineage that have roots during the Permian (Mamay, 1976; Gao & Thomas, 1989). Modern genera and their pollinators are thought to have recently evolved during the Cenozoic to Late Cretaceous (Oberprieler, 2004), although there is significant evidence that some genera extend to the earliest Cretaceous and many into the Jurassic (Pant, 1987; Artabe & Stevenson, 2004; Anderson & al., 2007). Cycad associations with insects are old and thought by many to extend to the earlier Mesozoic (Crowson, 1991; Farrell, 1998; Labandeira 2000; Mound & Terry, 2001; Brenner & al., 2003). Evidence for some ancient associations comes principally from phylogenetic analyses of the insect herbivores of recent cycads, which indicate that allocorynine and antliarrhinine weevils, aulacoscelidine leaf beetles (Coleoptera) and cycadthripine aeolothripids (Thysanoptera) are modern representatives of clades that extend to the mid to latest Mesozoic (Farrell, 1998; Mound & Terry, 2001; Gratshev & Zherikhin, 2003). For example, there is strong biogeographic evidence of an ancient relationship between the two closely related

host plants *Encephalartos cycadifolius* of southern Africa and *Macrozamia riedlei* of western Australia (Zamiaceae, Tribe Encephalarteae) and their similarly closely related beetle pollinators, respectively *Metacucujus encephalarti* and *Paracucujus rostratus* (Boganiidae: Tribe Paracucujini). This distribution indicates a Gondwanan vicariant separation across the Indian Ocean which began during the Middle Jurassic for these poorly dispersing plant-host and insect-herbivore pairs (Endrödy-Younga & Crowson, 1986; Labandeira, 2000). In addition, several distinctive cycad genera have host-specific pollinating erotylid beetles that likely originated during the mid-Mesozoic, providing circumstantial evidence of ancient associations, at least for the more encompassing clades if not for lower-ranked taxa as well (Oberprieler, 1995; Schneider & al., 2002).

There is little evidence for pollinator-related cycad associations from the fossils themselves, with the exception of galleries and coprolites in cones of a Middle Triassic cycad from Antarctica (Klavins & al., 2005). This damage is similar in pattern and detail to some extant beetle-cycad associations, and attribution of the plant host to a modern taxon of cycads was described as “remarkably similar” (Klavins & al., 2005). Additionally, cycad foliage contains sporadic damage from external foliage feeders during the later Mesozoic that may be consistent with some modern erotylid and aulacosceline leaf beetle herbivory (Labandeira & al., 2002; pers. observ.). Leaves and pollen are the favored food of extant, cycad-associated adult beetles, and pollen and associated microsporangial tissues are typically consumed by their endophytic larvae.

Bennettitopsida. — The Bennettitopsida, consisting of the Bennettitales and tentatively, the Pentoxylales, comprised a group, perhaps a clade, readily differentiated from superficially similar cycads by possession in most species of bisexual strobili and a second ovular integument (Bose & al., 1985; Crane, 1988), features which they share with gnetopsids and angiosperms (Crepet & al., 1991). The Bennettitales are known for their flower-like strobili consisting of a robust, central, columnar- to dome-shaped receptacle bearing numerous pedunculate ovules interspersed among interseminal scales. The strobilar axis gave rise to a few long, pinnate microsporophylls and numerous ovules above. In those taxa that had closed strobili, the microsporophylls were recurved toward the receptacle, each of which housed several microsporangiate synangia on lateral pinnae. These microsporophylls, in turn, were subtended by a spiral series of enclosing and abutting bracts that insured tight closure of the strobilus, and effectively prevented wind-pollination because the apices of the enclosing sterile tissue barely protruded beyond the leaf bases of the plant trunk. In addition, sterile tissues separately enveloped the ovuliferous and microsporangiate reproductive structures early in

development, thus insuring their complete segregation (Crepet, 1974).

The Bennettitales comprised the Williamsoniaceae and Cycadeoidaceae. The former are known from the Late Triassic to Late Cretaceous and were characterized by dissected, open, unisporangiate or bisporangiate strobili on relatively delicately-branching plants (*Williamsonia*, *Weltrichia*, *Williamsoniella*) (Harris, 1969; Watson & Sincock, 1992); it is likely that this group were wind- or, more probably, insect-pollinated. By contrast, the Cycadeoidaceae, of Late Jurassic to Late Cretaceous age, featured closed, bisporangiate strobili the microsporangiate organs of which were buried among persistent, thickened leaf bases on pachycaulous plants (*Monanthesia*, *Cycadeoidea*) (Watson & Sincock, 1992). It has been proposed that this group was “highly” self-compatible but also experienced some insect-pollination possibly by beetles (Crepet, 1974). The shift from open, williamsoniaceae, to closed, cycadeoidaceae, strobili probably paralleled a broad, temporal change from wind- to insect-pollination within the Bennettitales clade. Entomophily in the Cycadeoidaceae may have originated from later Jurassic williamsoniaceae descendants. The probably related Pentoxylales, such as *Pentoxylon*, bore vegetative features, particularly trunk anatomy, that was significantly different than the Bennettitales, but the two taxa nevertheless shared reproductive features (Bose & al., 1985). The Bennettitales are better understood morphologically and ecologically than the Pentoxylales (Doyle & Donoghue, 1986; Watson, 1988); they reached their greatest species diversity during the Middle Jurassic to Early Cretaceous, and inhabited xeric to mesic habitats similar to that of the Cheirolepidiaceae and most gnetopsids.

Gnetopsida. — Although the Gnetopsida originated during the Triassic (Crane, 1996), the fossil pollen record of gnetopsids indicates a past diversity considerably greater and more recent than the described numbers of fossil whole-plant species would indicate. This is particularly true for the Early to mid-Cretaceous, during which the group had the highest diversity (Crane, 1996) and underwent a radiation that paralleled the diversifying angiosperms (Crane & Lidgard, 1990; Wing, 2000) and during which additional, high-ranked and extinct clades are known. The variety of basic gnetopsid pollen types during this interval significantly exceeded the current level of three, disparate, extant families (Doyle & al., 1982; Takahashi & al., 1995), and at least two, extinct, high-ranked clades were additionally present during the Early Cretaceous. In addition, there has been the discovery of novel growth forms such as herbaceous taxa that no longer are present within the extant clade (Crane & Upchurch, 1987). The ubiquity of pollination-drop formation and insect-pollination in extant taxa strongly suggests that fossil

Mesozoic gnetopsids also were insect-pollinated (Midgey & Bond, 1991; Lloyd & Wells, 1992). This inference is buttressed by forms with beaked micropyles resembling modern entomophilous *Ephedra* in the Lower Cretaceous of northwestern China (Sun & al., 2001) as well as pollen closely resembling extant insect-pollinated Welwitschiaceae (Rydin & al., 2003). Undescribed gnetopsid material from the Early Cretaceous of northeastern China (Guo & Wu, 2000) preserves ovular structures, which could have been pollinated by long-proboscate insects.

INSECTS AS CONSUMERS OF NECTAR, POLLEN AND ASSOCIATED REPRODUCTIVE TISSUES

From the previous overview of Mesozoic gymnosperms and from an insect morphological perspective, there are two basic ways to consume relatively inaccessible pollination-drop or related fluids and pollen that may be hidden in gymnosperm fructifications. The first are whole body encounters, as in thrips, small flies, and parasitoid wasps, and beetles with hardened elytra. The second type is mouthpart retrieval, exemplified by proboscate Diptera and Lepidoptera that have large bodies and robust wings. Small insects can crawl toward the fluid of dietary choice whereas in the second mode, considerably larger insects such as mid-Mesozoic mecopteroid lineages and brachyceran flies required use of elongate proboscides for food access, assisted by hovering flight in some species. Both types of pollinivory and nectarivory were present throughout the Triassic and Cretaceous interval, and variously occur in eight major orders in the Mesozoic fossil record—Orthoptera (katydid), Phasmatodea (stick insects), Embioptera (webspinners), Coleoptera (beetles), Mecopteroidea (“scorpionflies”), Diptera (true flies), Hymenoptera (sawflies and wasps), and Lepidoptera (moths), although weaker evidence also exists for the Thysanoptera (thrips).

The relevant time period for the first occurrence of these associations predates the accumulation of amber with insect inclusions in the geologic record, taken to be approximately 120 Ma. Thus, the relevant fossil record is almost exclusively dependent on compression material from the Middle Triassic to mid-Early Cretaceous. Compression fossils require exceptionally good preservational conditions of entire insect bodies, particularly heads and mouthparts, which require rapid sedimentation in lake and fluvial deposits.

Orthoptera. — Katydid, comprising the suborder Ensifera of the Order Orthoptera, have a fossil record extending to the Late Paleozoic (Sharov, 1971), and like their descendants, presumably were herbivorous. Mesozoic Ensifera were diverse, and include pollinivorous forms such as the Haglidae, for which some taxa of the Proplango-

psinae include species containing apparently fresh *Classopollis* pollen (the form produced by Cheirolepidiaceae) in their guts (Figs. 3S, T; Krassilov & al., 1997). Evidence from taxa such as *Aboilus amplus* Gorochov from the Late Jurassic of Karatau, Kazakhstan, indicate that the pollen organs of Cheirolepidiaceae were consumed by large, externally feeding insects, and thus were also available to other large-bodied pollinators such as sawflies and stick insects. Some taxa of extant Orthoptera are known to be nearly exclusively pollinivorous (Grinfel'd, 1962). In a few instances katydids and grasshoppers are implicated as pollinivores and nectarivores as well as pollinators in modern ecosystems, typically in understories of tropical or subtropical habitats (Schuster, 1974; Rentz & Clyne, 1983).

Phasmatodea. — As in the Orthoptera, the Order Phasmatodea, or stick and leaf insects, are obligately herbivorous, although no modern forms are known to consume pollen. A phasmatodean, *Phasmomimoides minutus* Gorochov, was reported also from the Late Jurassic deposits of Karatau, Kazakhstan (Krassilov & Rasnitsyn, 1999), with considerable, apparently freshly consumed *Classopollis* pollen in its gut (Figs. 3Q, R). The occurrence of pollen in the guts of phasmatodeans, orthopterans and embiopterans (see below) may indicate the presence of a speciose Mesozoic dietary guild of non-holometabolous palynivores which lack modern analogs.

Embioptera. — Embiids, or webspinners, constitute a small group of ground dwelling insects occurring in warm climates that construct silken galleries and typically consume a wide variety of foods, especially dead plant tissues, moss, and fungi. Webspinners are rare in the fossil record and are considered to be descendants of the Grylloblattida (Rasnitsyn & Quicke, 2002) that probably originated during the mid-Jurassic. The enigmatic, Late Jurassic Brachyphylophagidae are one of the earliest lineages of Embioptera, and share a few but important synapomorphies with extant webspinners (Rasnitsyn & Quicke, 2002). Within this family, the species *Brachyphylophagus phasma* Rasnitsyn and *B. phantasmus* Rasnitsyn from the early Late Jurassic of Karatau, Kazakhstan, notably had gut contents that contained cheirolepidiaceae foliar fragments accompanied by *Classopollis* pollen grains (Rasnitsyn & Krassilov, 2000; Krassilov & al., 2006).

Coleoptera. — Pollen has not been documented in the gut contents of any presumed pollenivorous or otherwise herbivorous beetle in a preangiospermous deposit. Some data for possible herbivorous roles of beetles on Mesozoic gymnosperms have been gleaned from mouthpart structure (Labandeira, 1997), and from the presence of ancestral characters of extant clades known to consume live tissues of gymnosperms (Farrell, 1998). Alternatively, distinctive and recurring insect damage, such as those on bennettitalean strobili, are a significant line of evidence for beetle-gymnosperm associations

involving reproductive organs. Modern beetles typically pollinate seed plants by mandibulate mouthparts rather than various types of haustellate, siphoning, sponging or other fluid-feeding (Labandeira, 1997), and thus often leave conspicuous damage patterns on fructifications, microsporangia, flowers, and other reproductive organs (Gottsberger, 1988; Proctor & al., 1996).

There is significant evidence for damage of bennettitalean strobili by beetles or by insects that cause beetle-like damage. Evidence for borings, microsporangial and seed predation and other endophytic damage by beetles on Mesozoic gymnospermous tissues is known from cycad pollen organs, bennettitalean strobili, pentoxylalean-like fructifications and pinalean cone axes (Figs. 4A–F; 5A–G; Crepet, 1974; Nishida & Hayashi, 1996; Falder & al., 1998; Klavins & al., 2005). Likely, culprits are polyphagan beetles, in many instances probably members of the subclade Phytophaga. Other than positing extinct clades, such as the rostrate and probable archostematan Obrieniidae which co-occur with bennettitaleans (Gratschev & Zherikhin, 2003), suspect members of the Phytophaga capable of producing bennettitalean damage include the Belidae, Nemonychidae, basal Curculionidae and Aulacoscleridae, all of which have extant members with non-angiospermous host associations (Zimmermann, 1994; Farrell, 1998; Santiago-Blay, 2004). The likelihood of these potential culprits is based on: (1) phylogenetic relationships of basal clades of polyphagan beetles with cycad and conifer hosts that extend to the Jurassic interval or earlier (Farrell, 1998; Zhang, 2005); (2) stereotyped, beetle-like patterns of damage on reproductive and adjacent vegetative tissues of gymnospermous clades as varied as cycads, conifers, and bennettitaleans (Crowson, 1981; Falder & al., 1998; Klavins & al., 2005); and (3) at least one case of an encapsulated polyphagan larva occurring in an extinct gymnosperm fructification (Nishida & Hayashi, 1996). Some of these published associations are provided in Figs. 4 (top) and 5 (A–G).

Mecopteroidea. — Modern Mecoptera (scorpionflies) are largely detritivorous (Palmer & Yeates, 2004), but infrequently have been implicated in consuming floral nectar and other surface plant secretions (Porsch, 1958). Feeding in extant taxa is accomplished by an extended hypognathous rostrum with moderately elongate mandibulate mouthparts that originate proximally near the base of the head but process and comminute solid food at the terminus, accompanied by a suction pump centered on the frontal region of the head (Heddergott, 1938; Hepburn, 1969). This highly stereotyped condition is found virtually in all extant taxa, although the basal family Nannochoristidae has a shortened rostrum and terminally expanded labial palps that are reminiscent of a dipteran labellum (Hoyt, 1952). In contrast to the basic mouthpart structure of extant species, there were three lineages of Middle Triassic to mid-Cretaceous taxa—the Pseudo-

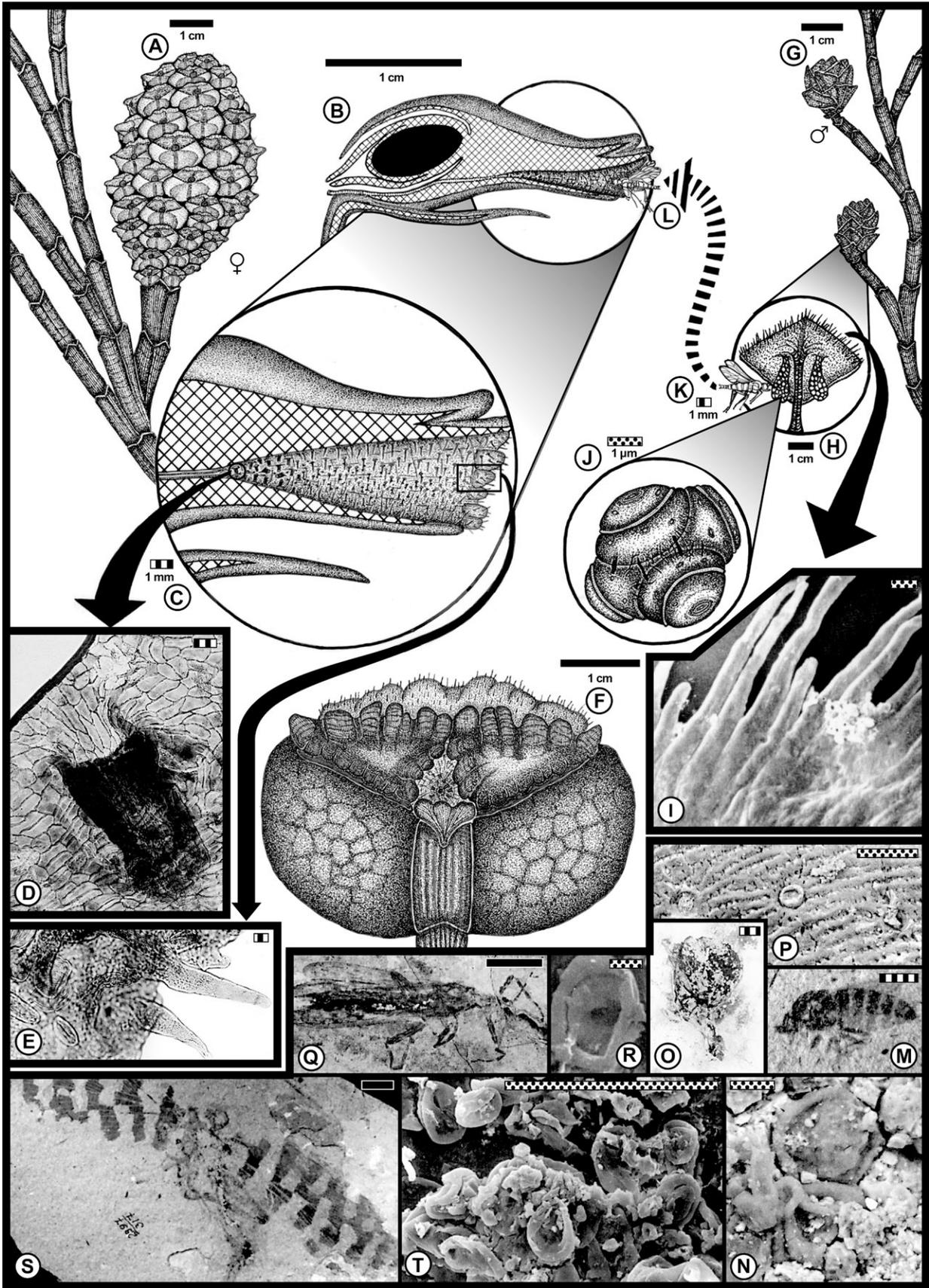
polycentropidae (Fig. 4I; Novokshonov, 1997; Grimaldi & al., 2005), Aneuretopsychidae (Figs. 4M, N; Rasnitsyn & Kozlov, 1991), and Mesopsychidae (Labandeira, pers. observ.)—that bore significantly different mouthpart apparatus than that of any modern species. Members of these three lineages, probably paraphyletic to extant Mecoptera, exhibited conjoined maxillary galeae that were prolonged into a tubular, uncoilable but somewhat flexible, siphonate proboscis. These proboscides were from 0.3 to 1.4 cm long and ventrally tipped with paired, either diminutive labelum-like pads or homologous larger lobes. Such mouthpart structures were convergent with certain elements of the brachyceran dipteran proboscis, but homologous to the glossae of lepidopterans (Eastham & Eassa, 1955) which evolved significantly later, during the mid-Cretaceous (Kristensen & Nielsen, 1981; Labandeira & al., 1994). The heads bearing proboscides in these taxa were relatively small but bore distinctive clypeal regions, suggesting a modest sucking pump for ingesting solutions that probably ranged from dilute to intermediate concentrations.

The siphonate condition that occurs among these mecopteroid lineages also is convergent with independent originations among several major clades of brachyceran dipterans (Nagatomi & Soroida, 1985) and in nemognathine

meloid beetles (Grinfel'd, 1975), among other extant clades. In almost all recent lineages such proboscides are used for uptake of nectar and other nutritious and carbohydrate rich surface fluids of angiosperms. For the fossil taxa, the most plausible food sources are relatively inaccessible pollination drops secreted by micropyles and hidden strobilar nectaries of various seed plants and possibly ferns, examples of which have been documented in modern, Mesozoic and Paleozoic plants (Bonnier, 1879; Koptur & al., 1982; Power & Skog, 1987; Krings & al., 2002). This basal, paraphyletic clade of “scorpionflies” evidently became extinct during the angiosperm radiation—an interval coincident with the diversification of glossate lepidopterans (Labandeira & al., 1994; Grimaldi & al., 2005).

Diptera. — Several major basal clades of brachyceran dipterans were present during the Early Jurassic to mid-Cretaceous, some of which bore long, tubular proboscides used for consuming fluid foods (Labandeira, 2005). Although it is possible that some of these lineages were hemataphagous (Grimaldi & Engel, 2005), multiple lines of evidence indicate that these taxa were minimally nectarivorous and probably engaged in pollination of various gymnosperm seed plants. The evidence includes: (1) the long, tubular and nonstyle structure of the proboscides;

Fig. 3. The inferred insect pollination mechanism for the mid Cretaceous whole-plant species consisting of *Frenelopsis alata* (Feistmantel) Knobloch for foliage and microsporangiate cones and *Alvinia bohémica* Kvaček for ovuliferous cones (Pinopsida: Cheirolepidiaceae), based on photodocumentation and reconstructions by Kvaček (2000) and additional data on cheirolepidiaceous reproductive and vegetative material (Hlušík & Konzalová, 1976a, 1976b; Watson, 1977, 1988; Alvin & Hlušík 1979; Pons, 1979; Alvin, 1982) (A–J). Inferred insect pollinators from earlier Cretaceous deposits are depicted in K–P, examples of Late Jurassic insect consumption of cheirolepidiaceous *Classopollis* pollen are provided in (Q–T). The ovuliferous cone, *A. bohémica* on *F. alata* foliage is shown in (A), an ovuliferous cone scale of which is enlarged in longitudinal section in (B), following the reconstruction in figure 5 of Kvaček (2000). Depicted in (B) is a paramedian, longitudinal section (cross-hatched pattern) with a distally directed and flaring funnel positioned between lateral adjacent lobes. The funnel is magnified in (C), where it is shown three dimensionally (stippled pattern). Above and below the funnel are the upper and lower appendages, respectively, and proximally positioned is an ovoidal anatropous ovule with an downwardly facing micropyle and associated chamber expanding toward the ovular surface, megaspore membrane, integumentary layer, and outer covering flap, all of which are subtended by a lower bract (B). Note a tubular structure originating from the telescoped base of the funnel, which traverses lower ovuliferous cone scale tissues and terminates at or near the micropyle (Kvaček, 2000). Epidermal features lining the inner surface of the funnel, illustrated in C, include cylindrical and apparently secretory protuberances positioned near the funnel mouth enlarged in (D), and distal from the mouth are structurally different, slender, and acuminate trichomes shown in (E). A distal surface view of a mature ovuliferous cone scale with the bract removed is depicted in (F). This view illustrates the position of the oblique ovular insertion ridge that separates the two lateral upper lobes (with incised margins) from the more robust, lateral lower lobes (termed an “ovuliferous scale” in Kvaček, 2000). Above the dwarf shoot is the central funnel orifice, as it may appear to an airborne insect. This reconstruction is based on specimen F2694 in Kvaček (2000). In (G) is a view of the smaller microsporangiate cone drawn with associated *F. alata* foliage (also see Hlušík & Konzalová, 1976a), of which a constituent scale is illustrated in (H), the margin of which is rimmed with elongate trichomes in (I). Microsporangiate cones bore two (perhaps more?) pollen sacs, each which bears numerous *Classopollis* pollen tetrads, one of which is enlarged in (J) (Srvistava, 1976; Courtinat, 1980; Taylor & Alvin, 1984; Pocock & al., 1990). A small, undescribed, therevid brachyceran fly (K–M), from the mid-Early Cretaceous of Russia, was found to have *Classopollis* pollen on its head surface adjacent to its proboscis, illustrated as an SEM micrograph in (N) (also see Labandeira, 2005). Miniscule flies are inferred to be one type of insect responsible for *A. bohémica* pollination via entire-body entry of the funnel, although much larger bodied, long proboscate brachyceran taxa alternatively could have thrust their proboscis deep into the funnel during hovering flight, such as *Protapiocera* sp. (Mydidae) (O), which also has *Classopollis* pollen—though not as tetrads—on its head, as illustrated in (P). Evidence of palynivory of *Classopollis* sp. pollen is found in the gut contents in Late Jurassic insects, such as the phasmatodean (stick insect) *Phasmomimoides minutus* Gorochov in (Q) and (R), and aboline haglid orthopteran (katydid) *Aboilus amplus* Gorochov in (S) and (T), both from the Karatau deposits of Kazakhstan (Krassilov & al., 1997; Krassilov & Rasnitsyn, 1999). Drawings made by the senior author. Scale bars: solid = 1cm; striped = 1 mm; stippled = 10 µm.

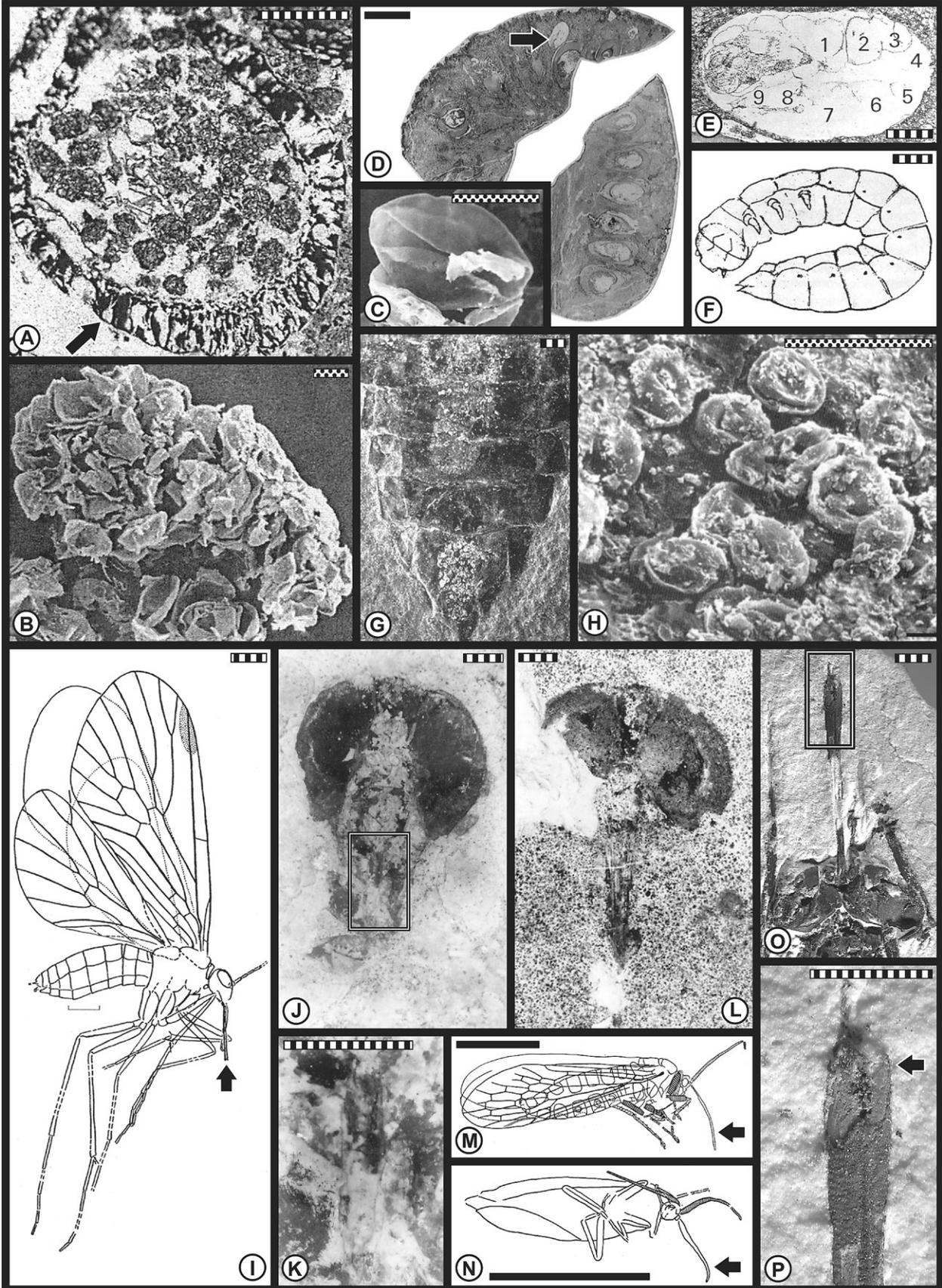


(2) wing shape and longitudinal veins that are upwardly recurved on the distal wing margin venation indicating hovering flight, especially in the Nemestrinidae; (3) prominent body pubescence; (4) holoptic and dorsomedially converging eyes; (5) presumed entomophilous pollen such as *Classopollis* present on the heads of several species; and (6) the entomophilous life-habits of their modern descendants (Kneipert, 1980; Mostovski, 1998; Zaitzev, 1998; Goldblatt & Manning, 2000; Labandeira, 2000, 2005; also see Downes & Dahlem, 1987). Numerous brachyceran taxa, representing multiple separate originations of the long proboscate condition for imbibing surface fluids, are present worldwide in Late Jurassic and Early Cretaceous deposits. The principal relevant deposits, from which most taxa are known, are the early Late Jurassic (Oxfordian or Kimmeridgian) Karatau lithographic limestones from the Karabastau Formation of eastern Kazakhstan (Doludenko & al., 1990); the Early Cretaceous (Hauterivian) shales from the Zaza Formation of Transbaikalia in Russia (Zherikhin & al., 1999); the Early Cretaceous (Barremian) lithographic limestones from the Yixian Formation, Liaoning, China (Ren & al., 1995); and the Early Cretaceous (Aptian) lithographic limestones from the Santana Formation, Ceará State, northeastern Brazil (Grimaldi, 1990). These and other occurrences represent five lineages of basal brachyceran Diptera that originated during the Jurassic and evolved long, tubular proboscides: Nemestrinidae (Rohdendorf, 1968; Mostovski, 1998); Mydidae (Figs. 3O, P; 4J–L); Tabanidae–Pangioninae (Ren, 1998; Labandeira, 1998a); undescribed Therevidae (Mostovski, unpublished; Figs. 3M, N); and the enigmatic Cratomyiidae represented

by a single occurrence (Mazzarolo & Amorim, 2000; Figs. 3O, P).

The Nemestrinidae (tanglevein flies) have a comparatively good fossil record during the Jurassic and Early Cretaceous compared to other long-proboscate dipterans, and probably were consumers of Mesozoic gymnospermous pollination drops and perhaps pollen. Forms exhibiting features consistent with nectarivory and pollination have been found at Karatau in Kazakhstan, Baissa in Russia, and Liaoning in China, spanning the early Late Jurassic to mid-Early Cretaceous (Labandeira, 2005). Their modern descendants are keystone species forming a nectarivore pollination guild, together with other members such as pangioniine tabanids (horse flies), acrocerids (small-headed flies) and vermilionids (wormlions), which pollinate deep-throated flowers of Iridaceae and Geraniaceae (Manning & Goldblatt, 1996). Morphologically similar ancestors mentioned by Rohdendorf (1968) possessed “head[s that are] slightly prolonged, with a prominent proboscis,” (in Nagatomi & Yang, 1998). Other features indicating a role in pollination include wing modifications for hovering flight, heads with holoptic eyes and extensive body pubescence. Their occurrences in preangiospermous deposits or in later deposits that contain flowers inappropriate for pollination by long-proboscid insects suggest that gymnosperms were hosts to nemestrinid and other long-proboscate flies. Reproductive structures reachable by air such as the unisexual cones of Cheirolepidiaceae or possibly ovuliferous structures of Caytoniaceae were probably targeted by nemestrinid and other flies, rather than the closed bisexual strobili of the Cycadeoideaceae

Fig. 4. Middle Triassic to Late Cretaceous plant-insect associations (A–H) representing cycadalean, gnetalean and probable pentoxylalean hosts, and Middle Jurassic to Early Cretaceous mecopteroids and dipterans with long-proboscate mouthparts (I–P), consistent with nectarivory and possibly pollinivory. In (A), a pollen sac of the Middle Triassic cycad *Delemaya spinulosa* Klavins & al. (2003) from the Central Transantarctic Mountains is laden with numerous coprolites, one of which is enlarged as an SEM micrograph in (B) (Klavins & al., 2005) and containing monocolpate pollen of the host plant, an undigested example of which is provided in (C) (Klavins & al., 2003). The black arrow in (A) indicates the distinctive pollen sac wall, which was avoided by palynivores. An undiagnosed gymnosperm fructification closely resembling a pentoxylalean cone, with radially juxtaposed seeds within parenchymal ground tissue, contains an encapsulated beetle larva (D, black arrow), enlarged in (E) and reconstructed in (F), assignable to the family Nitidulidae (Nishida & Hayashi, 1996). In (G) two food boluses are evident in the abdomen of the xyelid sawfly *Ceroxyela dolichocera* Rasnitsyn (Krassilov & al., 2003), the larger mass occurring in abdominal segments 1–3 and the smaller mass in segments 5–7, a SEM of this last (H), shows *Cryptosacciferites pabularis* Krassilov & Tekleva pollen of unknown gymnospermous affinities. The small, pseudopolycentropid mecopteroid, *Pseudopolycentropus latipennis* Novokshonov, from the Late Jurassic (Oxfordian) Karabastau Formation of Karatau, in southern Kazakhstan, has a 2 mm long tubular proboscis (I) (black arrow). Undetermined lower brachyceran fly *Protapiocera* sp. (Mydidae), from the Early Cretaceous (Hauterivian) of Zaza Formation in Transbaikalia of Russia (J), possesses an elongate, tubular and distally labellate proboscis, the prelabellar 2.5 mm of which is enclosed by the vertical rectangle and shown in (K). Another species of *Protapiocera* from the same Transbaikalian locality, is shown in (L), exhibiting a more gracile, long proboscis that terminates in a heart-shaped labellum, of which one lobe is evident. Two species of aneuretopsychid mecopteroids, from the same Jurassic locality of Karatau (Kazakhstan) as in (I), are illustrated in (M) and (N), with arrows indicating their proboscides (Rasnitsyn & Kozlov, 1991). *Aneuretopsyche rostrata* Rasnitsyn & Kozlov is depicted in (m), and in (N) is a smaller specimen, ?*A. minima* Rasnitsyn & Kozlov. The enigmatic brachyceran fly, *Cratomyia macrorrhyncha* Mazzarollo and Amorim (2000), from the Lower Cretaceous (Aptian) Santana Formation of northwestern Brazil, has an 8 mm long proboscis (O), the labellate terminus, indicated by the vertical rectangle, is enlarged in (P). The black arrow points to a terminal labellum. Scale bars: solid = 1 cm; striped = 1 mm; stippled = 10 µm.



(Mostovski, 1998; Ansoerge & Mostovski 2000; Mostovski & Martínez-Delclòs, 2000). It is of note that deep-throated angiosperm flowers evolved much later during the Cretaceous (Crepet & Friis, 1987; Rayner & Waters, 1991). One question that remains to be resolved for some Mesozoic long-proboscate flies is whether pollination drops or similar gymnospermous ovular fluids were sufficient for nutritional balance, or if hematophagous feeding, especially by females supplemented such a diet with protein and lipids. Diverse fluid diets incorporating carbohydrate, protein and lipids are important nutritional requirements of some descendant taxa (Wilson & Lieux, 1972; Watanbe & Kamimura, 1975; Kneipert, 1980). If so, mouthpart differences between conspecific male taxa would be expected. Gender-based mouthpart and behavioral dimorphisms also have been documented for modern tabanids (Mitter, 1918; McKeever & French, 1999). However, for lineages having larvae that were parasitoids on other arthropods, such as Nemestrinidae and Acroceridae, sufficient protein and lipid reserves were likely accumulated from their larval hosts so that gender-based nutritional and morphological dimorphisms would be absent (Labandeira, 2002b).

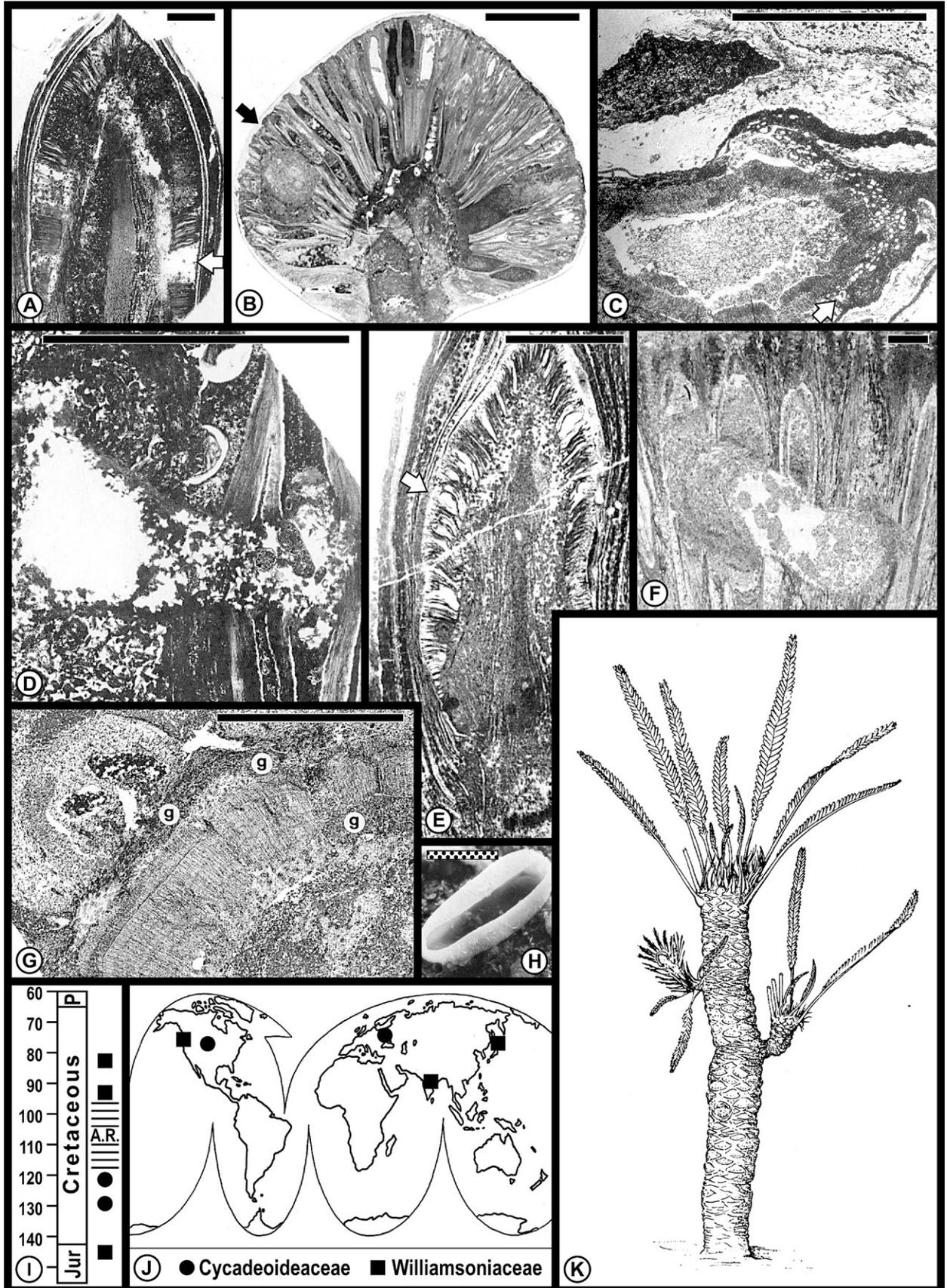
Hymenoptera. — The Xyelidae (sawflies) are Hymenoptera that are major consumers of pinaceous pollen in modern ecosystems (Burdick, 1961). The occurrence of xyelids during the Middle Triassic (Rasnitsyn, 1964) is highly consistent with their phylogenetic position as the earliest, basalmost clade of Hymenoptera (Rasnitsyn, 1980) and their characterization as modern phylogenetic relicts. Although xyelids, and presumably other pollinivorous symphytan taxa, are not implicated in the pollination of Mesozoic conifers, it is reasonable to assume that such a diet could have been co-opted by gymnospermous plant hosts as a pollination mutualism. Such an interpretation is buttressed by several studies which have found gymnospermous pollen types in the guts of Mesozoic xyelids,

including pollen from cheirolepidiaceans, bennettitaleans, gnetaleans, and angiosperms (Krassilov & Rasnitsyn, 1983; Caldas & al., 1989; Krassilov & al., 1997, 2003). These ingested pollen collectively lack large sacci, are relatively large, and possess other features typical of insect dispersal.

After the mid-Triassic appearance of sawflies, an extensive radiation of parasitoid wasps occurred throughout the Jurassic and into the Cretaceous (Rasnitsyn, 1980; Labandeira 2002b). Most of these wasps were small bodied and could have played a major role in consuming gymnosperm pollination drops from the Cheirolepidiaceae, Cycadales, Gnetales, or even Pentoxylaceae and Caytoniaceae, much in the way modern taxa currently do on *Gnetum* (Kato & al., 1995), *Ephedra* (Bino & al., 1984a, b), and especially on angiosperms (Jervis & al., 1993). Alternatively, parasitoid wasps could have been involved in more specialized pollination systems, such as the case of the cheirolepidiaceous *Frenelopsis alata/Alvinia bohemica* plant discussed further on. Dietary evidence from fossils is lacking, and inferences come from the autecology of descendant taxa. The most recent round of hymenopteran pollinators are bees and their immediate sister taxa, albeit evidence for their earliest occurrence resides in the late Early Cretaceous (Elliott & Nations, 1998; Poinar & Danforth, 2006), a colonization confined to angiosperm hosts.

Lepidoptera. — Basal lepidopteran clades during the Jurassic and Early Cretaceous may have been involved in palynivory, nectarivory or seed predation, but fossil mouthpart data are extremely sparse, and evidence from modern taxa is indirect. Early lepidopteran lineages were almost exclusively phytophagous and consist of small moths whose modern descendants are known to feed on nectar, including taxa with relatively short siphonate proboscides (Downes, 1968; Brantjes & Leemans, 1976; Kawakita & Kato, 2004). Significantly, one of the most primitive clades of Lepidoptera, the Agathiphagidae, are

Fig. 5. Bennettitalean plant-insect associations emphasizing borings and their coprolite and other frass accumulations. Specimens (A), (C), (D), and (E) are *Cycadeoidea* (Cycadeoideaceae); specimens (B) and (F) are *Williamsonia* and (G) is a *Bucklandia* axis (both Williamsoiaceae). A *Cycadeoidea dacotensis* Wieland specimen in (A) shows the destruction of an entire segment of ovular and adjacent interseminal scales to form a gallery (white arrow) that is connected with a much narrower tunnel system (Delevoryas, 1968; Crowson, 1981). This specimen is from the Lower Cretaceous Blackhawk locality of South Dakota, U.S.A. In (B), a *Williamsonia harrisiana* Bose specimen from the Upper Jurassic Rajmahal Basin of India bears a circular gallery of frass which has replaced ovules and interseminal scales (Bose, 1968). From the Lower Cretaceous of Poland are xylary, parenchymatic and other trunk tissues of *Cycadeoidea* sp. (Reymanówna, 1960) (C), which contain a curvilinear tunnel filled with small ellipsoidal fecal pellets, probably made by a small larva. A larger gallery in (D) cross-cuts receptacular, microsporophyll and possibly microsporangial tissues of a *Cycadeoidea* sp. specimen from the Blackhawk locality (Crepet, 1972). In (E), an extensive larval tunnel occurs at the interface between ovules and interseminal scales, and microsporophylls and associated microsporangial tissues in *Cycadeoidea* sp., also from the Blackhawk locality (Crepet, 1974). A similar gallery occurs in a *W. bockii* Stockey & Rothwell specimen from the Upper Cretaceous of British Columbia of Canada (F) (Stockey & Rothwell, 2003). A gallery traverses several ovules and their associated interseminal scales. In *Bucklandia kerae* Saiki & Yoshida from the Upper Cretaceous of Japan (G), are tunnels within trunk cortical tissues, representing early-instar larval or less plausibly oribatid mite activity (Saiki & Yoshida, 1999). A *Monosulcites* pollen grain, typical of bennettitalean microsporangia, is illustrated in (H) (Taylor, 1973). The spatio-temporal distribution of insect-damaged taxa illustrated in (A–G) is detailed in (I) and (J); horizontal lines represent the angiosperm radiation. The habitus of *W. sewardiana* Sahnii is illustrated in (K) (Taylor & Taylor, 1993). Scales: solid = 1 cm; stippled = 10 µm.



seed predators on the araucarian genus *Agathis* (Kristensen, 1999)—an association that may extend to the Jurassic (Powell & al., 1999). Other more derived lineages are the Nepticulidae and Gracillariidae, which were well established by the latest Early Cretaceous (Lopez-Vaamonde & al., 2006). Unfortunately lepidopteran siphons are rarely preserved in the fossil record even though their mouthpart structure in modern forms is well documented (Szucsich & Krenn, 2000).

TWO PROBABLE MESOZOIC POLLINATION SYNDROMES ON GYMNOSPERMS

We present here two examples of host plants, *Frenelopsis alata* and *Cycadeoidea dactotensis*, for which paleobotanical and paleontomological evidence support the existence of insect feeding on pollen, pollination drops or other secretory fluids, or some combination thereof, as well as the presence of pollination mutualisms. Our reconstruction of these associations is based on from multiple lines of evidence: the reproductive morphology of plants, plant damage, insect gut contents and mouthpart structure (Labandeira, 2002a).

Ovuliferous and microsporangiate cones of *Frenelopsis alata* (Cheirolepidiaceae). — Historically, the pollen of Cheirolepidiaceae, *Classopollis*, has presented some of the most compelling evidence for entomophily in Mesozoic gymnosperms. *Classopollis* pollen is characterized by comparatively large, smooth, disk-shaped to flattened spheroidal grains resting in tetrads by adherent exinal threads (Scheuring, 1976; Courtinat, 1980). It has been postulated that plants bearing such pollen were self-incompatible (Zavada & Taylor, 1986). The *Classopollis* character complex was especially prevalent among taxa occurring prior to, and during, the ecological expansion of angiosperms; however, Late Cretaceous cheirolepidiaceae taxa were anemophilous (Pocock & al., 1990). The presence of a typical gymnospermous pollination drop mechanism was probably lacking or modified because the pollen chamber in these plants is atypical. Nonetheless, for most species fluid films probably assisted pollen landing on ovuliferous cones to germinate and directed the pollen tube toward the ovule for a considerable distance (Taylor & Taylor, 1993). Pollen transport to the ovuliferous cones could have been made by taxa such as haglid orthopterans (Krassilov & al., 1997), phasmatodeans (Krassilov & Rasnitsyn, 1999), xyelid hymenopterans (Krassilov & Rasnitsyn, 1983), mecopteroids (Rasnitsyn & Kozlov, 1991; Novokshonov, 1997), and brachyceran dipterans (Ren, 1998; Mostovski & Martínez-Delclòs, 2000; Labandeira, 2005), as evidenced by gut contents containing abundant *Classopollis* in the first three examples, and siphonate mouthparts and clusters

of *Classopollis* pollen grains on the heads of other taxa. These five, phylogenetically distant insect groups variously present during the Late Triassic to Early Cretaceous, demonstrate generalized pollinivory, and suggest pollination types in which both pollen and fluid plant secretions were important rewards. Of the five, the mecopteroids and dipterans may have been the only pollinators.

The relatively simple system of pollination typical of gymnosperms (Figs. 1, 2) was present in some Mesozoic cheirolepidiaceae taxa, whose reproductive biology recently has become better known (Pocock & al., 1990; Clement-Westerhof & van Konijnenburg-van Cittert, 1991; Axsmith & al., 2004). The best example is based on the morphology and associated pollination biology of the ovuliferous cone of *Alvinia bohemica* and its corresponding microsporangiate cone and foliage, *Frenelopsis alata*; the whole plant of which grew in saline habitats and relatively dry climates during the earliest Late Cretaceous in what is now the Czech Republic (Kvaček, 2000). Ovuliferous cones were broadly ovoid, surmounted on a robust axis about 1.0 cm in width, approximately 5.0 cm long and somewhat shorter in width, and consisted of at least 30 helically arranged imbricate, rhomboid scales (Fig. 3A). Ovuliferous cone scales (Fig. 3B) were subtended from the axil of a wide bract, were fleshy rather than woody, and bore sterile basal and apical scales. The structure of mature ovuliferous cone scales was complex and consisted of two ovules laterally positioned next (proximal) to the cone axis at maturity, or alternatively there was a single functioning ovule adjacent a considerably smaller aborted ovule. Each ovule had a 1.8 mm long micropyle projecting proximally, and a chamber which narrowed toward the distal ovular apex; a single strongly ribbed integument about 1 cm in diameter surrounded the ovule (Fig. 3B).

The position, structure, and surface features of ovuliferous cone-scale appendages are important for understanding the pollination biology of *Alvinia bohemica*. On the upper margin of the cone scale, proximal to its subtending axis, was a single covering flap which overlaid and protected each ovular region up to the level where the micropyle and tubular “pipe-like structure” protruded (Fig. 3B; also see below). Distal from the axis, at the upper margin of the ovuliferous cone scale there was a medially inserted, single appendage that was the continuation of the covering flap and formed another upper, but outwardly directed lobe of the ovuliferous scale. Also distally positioned, but located centrally below the uppermost appendage were two lateral distally directed appendages, the upper lobate margins of which were trichome-lined and the lobes overlapped medially. Each of these lateral lobes was attached to the ovuliferous scale by an oblique ridge that also was associated with ovular insertion (Fig. 3F). These conspicuous and flattened appendages, together with the uppermost appendage, outwardly and distally surrounded the deep, cone-shaped fun-

nel that narrowed proximally into a small aperture (Fig. 3C), the continuation of which was a “pipe.” This pipe apparently traversed lower ovuliferous scale tissues below the ovular integument and emerged proximally adjacent to the micropyle. Presumably this tube aided pollen tube growth toward the micropyle by providing transmission tissue or perhaps fluids, which nourished and/or directed the pollen tube (see Frame 2003a). As a channel for directing pollen toward the pipe, the funnel functioned as an “inverted stigma” and was lined throughout by prominent multiseriate trichomes (Fig. 3E), laden mostly with *Classopollis* but also other types of pollen. In the deeper recesses of the funnel occurred large, cylindrical, multicellular protuberances, or papillae, that were significantly larger than adjacent trichomes (Fig. 3D). These cellular papillae contained secretory fluids whereas trichomes likely were responsible for pollen entrapment. Below the funnel and oblique ridge was the main body of the ovuliferous scale, in whose axil was attached a single, large, transversely elongate ellipsoidal bract (removed in Fig. 3F), which extended as far up as the lower periphery of the funnel orifice.

The pollen cone, *Frenelopsis alata* (Fig. 3G), was the source of *Classopollis* pollen which pollinated *A. bohemica* ovules. Male (*Frenelopsis alata*) cones were considerably smaller than female (*A. bohemica*) ones; they were slightly greater than 1.0 cm long and had a more conifer-like appearance than the fleshy ovuliferous cones. Each diamond-shaped microsporangiate cone scale was fringed with prominent trichomes along the margin (Fig. 3I) that were a likely source of food for fluid-feeding insects. The microsporophylls each bore two (perhaps more?) pollen sacs (Fig. 3H), one on each side of its base. When cones were mature, pollen sacs released numerous pollen tetrads (Fig. 3J), either by sac wall degradation, insect disturbance during trichome manipulation or direct consumption by insects, or a combination of these. Inferred insect vectors include basal clades of long-proboscate mecopteroids, small therevid flies (Figs. 3K–N) and much larger long-proboscate mydid flies (Figs. 3O, P); much larger pollinivorous phasmatodeans (Figs. 3Q, R) and orthopterans (Figs. 3S, T) are more remote possibilities. A small-bodied (3.5 mm) therevid fly is depicted in Fig. 3 (K, L) as the pollinator of *A. bohemica*, although long-proboscate flies also are candidates.

Pollination of *Alvinia bohemica* ovules could have been achieved either by wind currents (anemophily), transport by insect vectors (entomophily), or both strategies (ambophily). Evidence for wind pollination principally is provided by the elevated abundance of *Classopollis* pollen in many Mesozoic environments occupied by cheirolepidiaceae plants—both in palynologically macerated sedimentary matrices (Vakhrameev, 1991; Upchurch & Doyle, 1981) and in the receptive tissues of ovuliferous cones (Kvaček, 2000). Such abundance, typical for anemophilous plants,

however, is known to occur in some insect-pollinated angiosperms, such as *Papaver rhoeas* L. (McNaughton & Harper, 1960). By contrast, a diverse suite of evidence from both plant and insect structures indicate entomophilous pollination. First are atypical anatomical features of several cheirolepidiaceae taxa which are understandable in the context of insect-pollination, such as the aforementioned stigma-like structures of *A. bohemica* (Figs. 3A–J; Kvaček, 2000). Second are features of individual *Classopollis* grains, including their comparatively large size (Figs. 3J, N, P, R, T), thick exine, and grains occurring as tetrads held together by sticky exinal threads (Taylor & Alvin, 1984; Clement-Westerhof & van Konijnenburg-van Cittert, 1991). Third is the presence of pollen tetrads and single pollen grains of *Classopollis* on the heads of likely Late Jurassic and Early Cretaceous pollinating insects. Fourth is the presence of insects with elongate siphonate proboscides, or alternatively very small-bodied insects, particularly dipterans (Fig. 3M), that were present in Middle Jurassic to mid-Cretaceous floras either prior to the earliest fossil occurrence of angiosperms or in floras contemporaneous with the initial appearance of angiosperms but prior to the advent of angiosperms having tubular flowers. Fifth is the occurrence of near-monospecific *Classopollis* food boluses in the guts of members of Phasmatodea, Orthoptera, and Hymenoptera, indicating the frequent use of cheirolepidiaceae pollen as food. Collectively these data indicate that entomophily was widespread among cheirolepidiaceae plants and that pollination was carried out by several distantly related insect groups.

Bisexual strobilus of *Cycadeoidea dacotensis* (Cycadeoidaceae). — Bennettitalean strobili of the Cycadeoideaceae were closed, bisporangiate (hermaphroditic) structures not open to the dissemination of pollen by wind, thus requiring in situ mechanisms of pollen transfer (Crepet, 1974). Several important studies have documented damage to receptacles, ovules, microsporophylls and other strobilar tissues (Reymanówna, 1960; Delevoryas, 1968; Bose, 1968; Crepet, 1972, 1974; Crowson, 1981; Saiki & Yoshida, 1999; Stockey & Rothwell, 2003). This damage is analogous to known beetle damage in extant cycads (Crowson, 1981; Norstog & Nicholls, 1997; Labandeira, 1998b). Insect-mediated bennettitalean damage, found on taxa such as *Cycadeoidea dacotensis* from the Upper Lower Cretaceous of South Dakota (Fig. 6A), but also on several other taxa belonging to the Cycadeoideaceae and Williamsoniaceae, provide rare autecological snapshots of the life-history of insect larvae as they proceeded from egg hatching, to early larval penetration of external strobilar tissues, to consumption of various internal bennettitalean vegetative and reproductive tissues, to eventual emergence from the host plant and subsequent transformation to the adult phase. In addition to the best documented species, *C. dacotensis*, our reconstructed life-history is gleaned

from data of several other plant-host taxa (Figs. 5A–G), each of which document one or more phases of tissue consumption and formation of a tunnel or gallery systems. These fossil data collectively are integrated to a generalized account of insect consumption of live tissues within *Cycadeoidea strobili* and their associated pollination (Fig. 6), using the reconstruction by Crepet (1974) as a basis for charting larval life-history. However, the insect damage patterns do not represent any single host-plant species. Rather, a general pattern of herbivory, ovule predation and pollination is established that undoubtedly was common to multiple beetle taxa engaged in similar associations among multiple bennettitalean host plants (Reymanówna, 1991; Labandeira, 1998b).

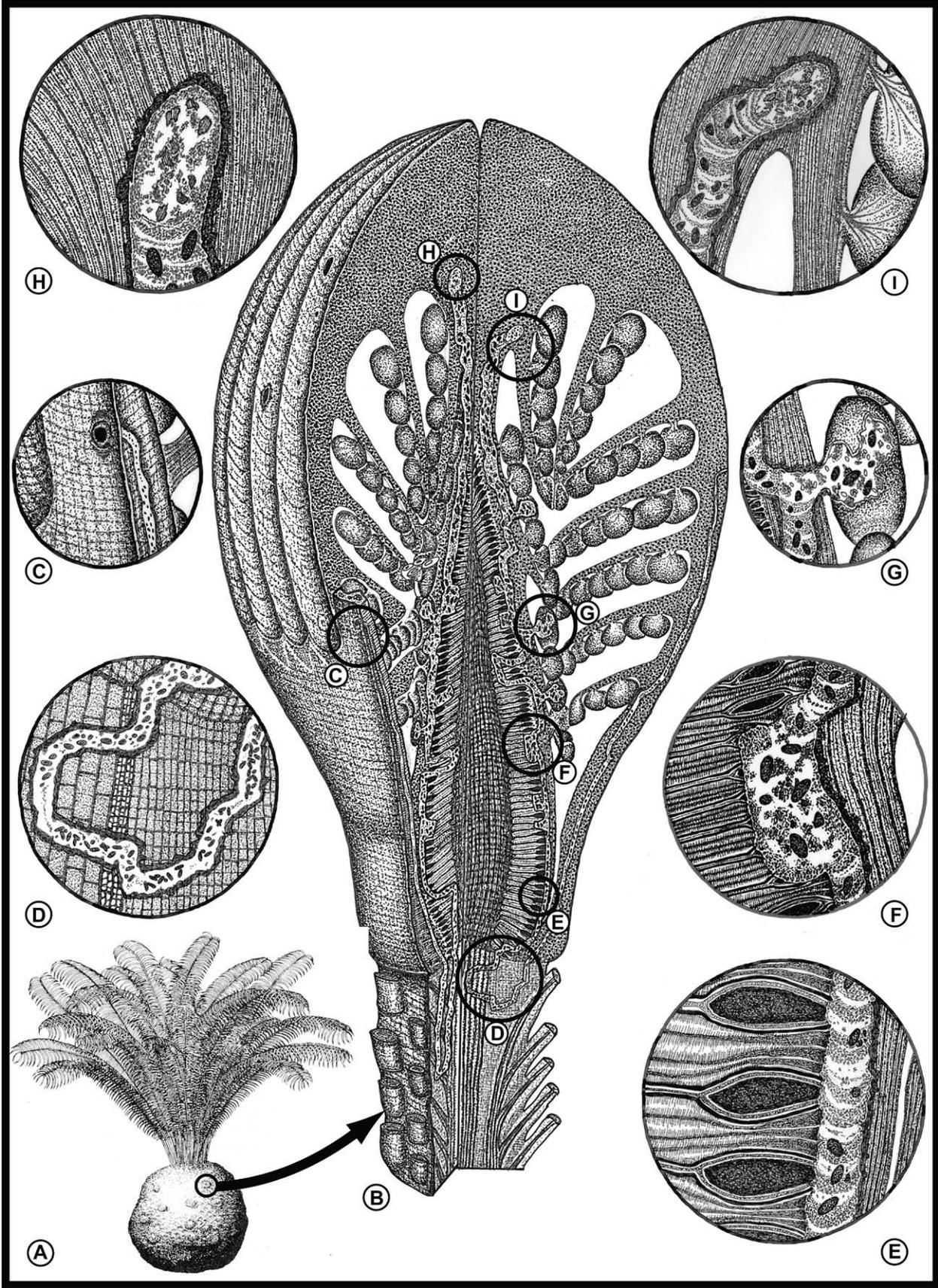
From these data the associational pattern of insect larvae and bennettitopsisid plant hosts in general and *C. dacotensis* in particular can be divided into five, more or less characterizable larval phases. The first phase was oviposition and initial larval entry into accessible or otherwise exposed strobilar tissues, most likely the tops of microsporophylls, bracts, or possibly adjacent tissues such as the rametum that forms the ground tissue from which the apices of strobili project beyond the general *Cycadeoidea* trunk surface (Fig. 6A, B). Insects likely oviposited in or on the surface of these structures, the stimulus for which may have involved a period of ovular receptivity, analogous to that of extant cycads (Stevenson & al., 1998). The second stage was penetration and consumption by early larval instars of vegetative tissues initially microsporophylls and bracts, and subsequently, trunk tissues through the creation of small-diameter tunnels (Figs. 5C, G; 6C). As subsequent larval instars underwent size increases, the third phase was initiated by the establishment of a tunnel system that occurred in the stem (Fig. 6D) and thence into the zone between the inner ovule-bearing and interseminal scales originating from the receptacular axis and the outer, more peripheral pollen-bearing microsporophylls (Figs. 5E; 6E). The nutritional lure for these larvae could have been nutritive fluids secreted by the micropylar surfaces, nearby pollen sacs, or perhaps the fleshy, club-shaped ends of the interseminal scales, or any combination of these and adjacent tissues

(Haslett, 1989). The fourth phase was occasional excursions of the tunnel system from this zone, principally consisting of consumption of pollen sacs and their contents as well as inner ovules and their adjacent interseminal scales. In these gamete-associated tissues spacious galleries were formed and filled by unconsumed plant fragments, fecal pellets, and other frass (Figs. 5A, B, D, F; 6F, G). Larger instars targeted the reproductive tissues, likely resulting in pollen transfer from pollen sacs to the micropyles of unconsumed ovules. The fifth and final phase of larval development was when the final instar constructed a comparatively large tunnel that was established toward the outer, exposed tissues and where emergence occurred (Fig. 6H, I). This phase was terminated by pupation into the adult instar occurring either within a terminal chamber or alternatively by the larva dropping to the leaf litter below. Adult beetles continued the life cycle, copulating outside the plant then ovipositing on conspecific hosts.

Overall, the type of damage found in bennettitalean strobili is most consistent with relatively small, compact, robust beetles (Crepet, 1974), most likely members of the suborder Polyphaga or its subclade, the Phytophaga, which includes cerambycids (longhorned beetles), chrysomelids (leaf beetles), and curculionoids (weevils) (Farrell, 1998). The Phytophaga antedate considerably the origin of angiosperms (Arnol'di & al., 1977; Zhang, 2005). In particular, the plesiomorphic curculionoid families, Belidae and Nemonychidae (Zimmermann, 1994), may be the closest extant lineages exhibiting similar life-history attributes to that inferred for mid-Mesozoic bennettitalean damage. Insect damage on bennettitalean strobili is consistent with extant coleopteran pollinators of cycads, which have life cycles featuring adults as pollinivores or folivores and larvae as consumers of pollen, adjacent microsporangiate tissues, and receptacular pith tissues (Crowson, 1991; Norstog & al., 1992; Oberprieler, 1995).

There is limited paleobiological data on the insect associates of bennettitaleans. One interaction is the presence of the bennettitalean pollen, *Vitimipollis*, in the gut of a xyelid sawfly from the Early Cretaceous of Russia (Krassilov & Rasnitsyn, 1983). However, the gut

Fig. 6. The inferred insect pollination mechanism for *Cycadeoidea dacotensis* Wieland (Bennettitopsida: Cycadeoidaceae). The plant-host anatomy is based on reconstructions by Crepet (1974). For the purposes of simplicity, larval borings and galleries are illustrated in 2-dimensions. Patterns of plant-insect damage are from sources illustrated in Fig. 5. A whole-plant reconstruction is provided in (A) (Delevoryas, 1971), bisporangiate cones are embedded in a thick rametum of bracts and other tissues. A three-dimensional cut-away view of *C. dacotensis* is provided in (B), illustrating important tissues for insect borers involved in pollination. The initial oviposition site is given in (C), with eggs deposited on or in surface tissues. In (D) is depicted the initial larval boring through vegetative tissues such as microsporophyll parenchyma and receptacle (and possibly trunk?) tissues (Reymanówna, 1960). Tunnels formed at the intersection of the ovular/interseminal scale layer and the microsporophyll layer are provided in (E), with micropylar secretions and pollen probably being the principal rewards. Gallery formation occurs within the zone containing receptacle-borne ovules and adjacent interseminal scales, replete with coprolites and other types of frass deposition as a consequence of extensive consumption (F) (Delevoryas, 1968; Crowson, 1981). The final phase of larval borings are provided in (H) and (I), resulting in an exit hole associated with pupation that may occur in a terminal chamber within the host plant or on the subjacent ground as in some extant cycad pollinating beetles (Oberprieler, 2004). Drawings made by the senior author.



contents of this specimen also contained conifer pollen of *Alisporites* and *Pinuspollenites*, indicating a polylectic adult feeding strategy. Also, there are three clades of basal weevils—Belidae, Nemonychidae, and Eccoptarthridae as well as the enigmatic Obrieniidae—that infrequently co-occur with bennettitaleans in certain Late Jurassic and Early Cretaceous deposits (Doludenko & Orlovskaya, 1976; Arnol'di & al., 1977; Zherikhin & Gratshev, 1997; Sun & al., 2001; Gratshev & Zherikhin, 2003). Extant descendants of these first two weevil clades currently are found on cycad and conifer plant hosts (Zimmermann, 1994; Farrell, 1998). Additional features indicating insect pollination are: (1) the relatively large size and psilate exine sculpture of bennettitalean pollen, characters associated with animal pollination; (2) the presence of extranuptial nectaries in microsporangiate cones of one species (Harris, 1973), possibly a nutritional lure for pollinators; and (3) decurved, rostrate mouthparts with robust terminal mandibles characteristic of many curculionoid taxa from Late Jurassic and Early Cretaceous deposits indicative of ovipositing into plant tissues (Zimmerman, 1994; Anderson, 1995; Labandeira 1997).

Endophytic insect damage on bennettitalean strobili has been found in five geographically disjunct localities from the Late Jurassic to early Late Cretaceous (Figs. 5I, J). The most extensive documentation of tunnel and gallery formation is known from South Dakota, U.S.A. (Figs. 5A, D, E; Delevoryas, 1968; Crepet, 1974), but other similar examples have been described from British Columbia, Canada (Fig. 5F; Stockey & Rothwell, 2003), Japan (Fig. 5G; Saiki & Yoshida, 1999), Poland (Fig. 5C; Reymanówna, 1960), and India (Fig. 5B; Bose, 1968). The widespread geographic distribution, targeting of a particular plant-host clade and highly stereotyped damage of this association collectively suggest a distinctive pollination strategy by beetles similar to that of extant cycads (Stevenson & al., 1998). It is possible that there was a transfer of the bennettitalean insect pollination syndrome, though not necessarily by the same taxa, to that of cycads during the Jurassic, long before the ecological expansion of angiosperm pollination mechanisms. This co-optation may have been likely since the three extant families of cycadopsids (Cycadaceae, Stangeriaceae, Zamiaceae) geochronologically overlap with the bennettitalean Williamsoniaceae (including the “Wielandiaceae” of some

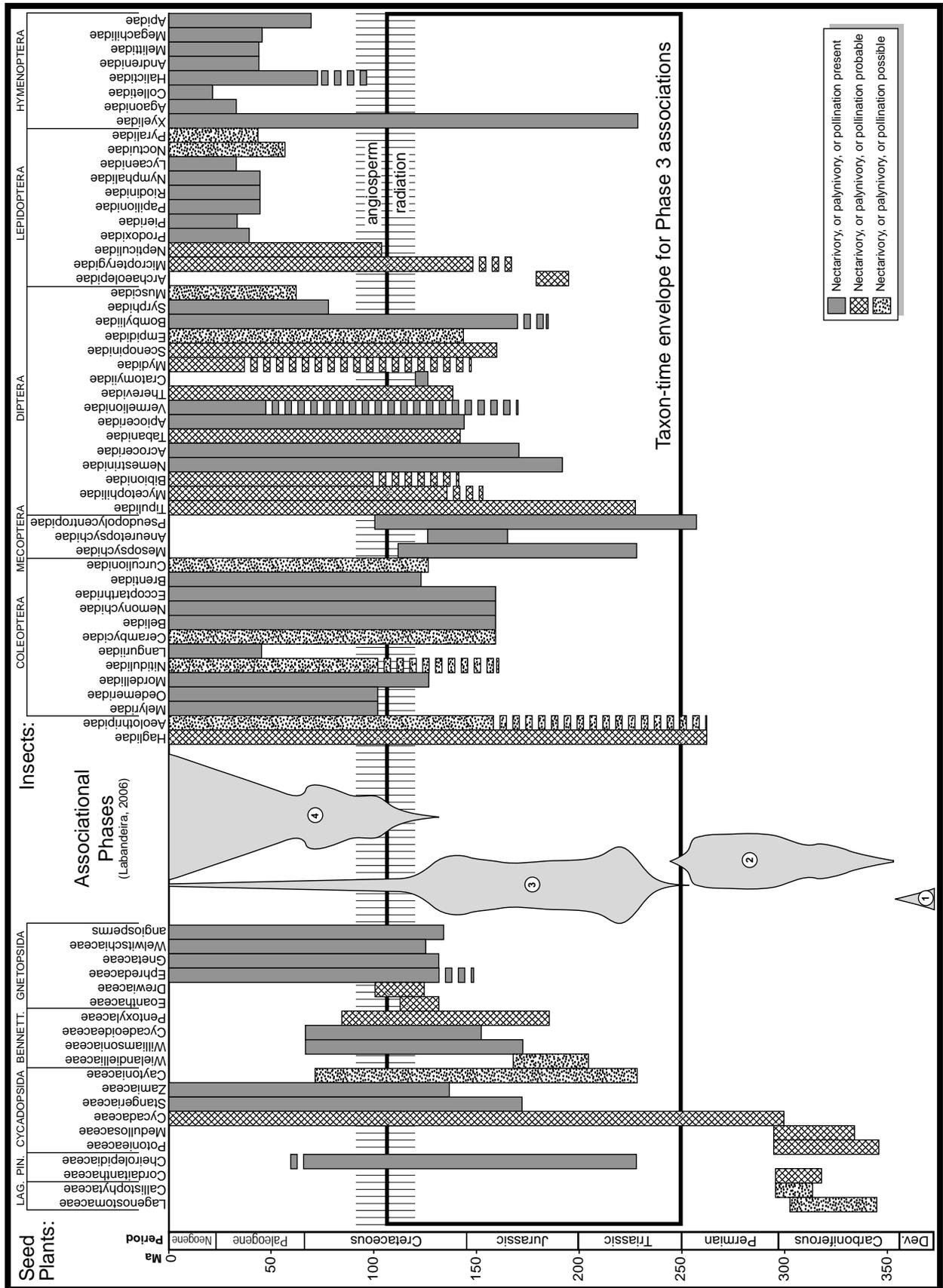
and early Cycadeoideaceae (Artabe & Stevenson, 1999, 2004; Anderson & al., 2007). It also is possible that this syndrome of beetle pollination of relatively closed reproductive structures was common during the Mesozoic, early evidence for which is provided by Middle Triassic insect consumption of pollen in cycad reproductive organs (Figs. 4A–C; Klavins & al., 2005), and evidence provided by a Late Cretaceous permineralized fructification, probably referable to the closely related Pentoxylales, which harbored a completely preserved larva within a chamber adjacent to seeds within the ground tissue (Fig. 4D–F; Nishida & Hayashi, 1996). This larva was assigned to the beetle family Nitidulidae, for which adults of modern representatives are frequent pollen feeders (Gazit & al., 1982; Ekblom & Borg, 1996).

THE BROADER PALEOBIOLOGICAL CONTEXT

Two issues are evident from this examination of the Mesozoic seed-plant record of insect associations involving pollination and consumption of reproductive associated structures. First, how do Mesozoic preangiospermous pollination mechanisms fit into a larger perspective of insect consumption of reproductively associated structures through time? Second, what can be inferred in the switch from gymnosperm- to angiosperm dominated modes of insect pollination.

Insect consumption of reproductively-associated plant tissues in deep time. — The fossil record has revealed that palynivory (consumption of spores, prepollen and pollen) is one of the most ancient feeding strategies of terrestrial arthropods in general and hexapods in particular (Labandeira, 2000, 2006). Coprolite assemblages laden with spores, many plant-host specific, are known from the latest Silurian and Early Devonian of the United Kingdom (Edwards & al., 1995). These and other associations (Labandeira, 2000, 2006) constitute Phase 1 of the development of palynivory, nectarivory and associated diets, though only spore consumption occurred (Fig. 7, middle). The subsequent, Carboniferous coprolite record shows the consumption of fern spores and sporangia, particularly those of marattialean tree ferns, and towards

Fig. 7. Summary of seed-plant and insect families for which there is some to considerable evidence for nectarivory, palynivory or pollination. The emphasis is on Phase 3 associations from the Middle Triassic to the mid-Cretaceous angiosperm radiation, as detailed in Labandeira (2000, 2006). Levels of confidence are assigned to possible (stippled), probable (cross-hatched) and unequivocal (dark grey) associations based on available features such as plant reproductive biology, plant damage, dispersed insect coprolites, insect gut contents, insect mouthparts, and to a lesser extent taxonomic uniformitarianism (see Labandeira 2002a). Note for insects, Haglidae (here the Aboilinae) are a family of Orthoptera and Aeoiothripidae (Cycadothripinae) a family of Thysanoptera. Geochronologic abbreviation: Dev., Devonian Period. Higher-level plant-group abbreviations: LAG., Lagenostomopsida; PIN., Pinopsida, and BENNETT., Bennettitopsida. Geochronological range data are from a variety of sources, including Taylor & Taylor (1993), Labandeira (1994), Grimaldi & Engel (2005), and Anderson & al. (2007), based on the time scale of Gradstein & al. (2004).



the end of the period, specialist feeding on cordaite and pteridosperm prepollen (Labandeira, 1998a; 2002a). The deposit at Chekarda, from the Lower Permian of the Russian central Ural Mountains, bear several species of diverse insect lineages that have gut contents of pollen that are affiliated with equally diverse plant hosts (Krassilov & Rasnitsyn, 1999; Afonin, 2000). These palynivores include early insect taxa which were consuming pollen from peltasperm and glossopterid seed ferns, cordaites, conifers, and gnetopsids (Rasnitsyn & Krassilov, 1996; Krassilov & Rasnitsyn, 1999; Krassilov & al., 2006). The prepollen and pollen form taxa occurred as both mixed and non-specific gut accumulations, supporting earlier, well-preserved coprolite data from coal-swamp forests from the Late Carboniferous in which there was intense targeting of particular host plants for consumption (Labandeira, pers. observ.). Also at Chekarda are body fossils of insects that display prominent, prognathous mandibulate mouthparts, interpreted as adaptations to pollinivory (Rasnitsyn, 1977; Novokshonov, 1997). Unlike pollinivory, Paleozoic evidence for feeding on plant secretions is considerably less and indirect, such as the existence of the pollination drop mechanism (Rothwell, 1972, 1977) and the presence of epidermal secretory glands adjacent to reproductive structures (Mamay, 1976; Krings & al., 2002). By the end of the Paleozoic, insect targeting of fern spores and seed plant pollen was well-established and were common occurrences in at least some terrestrial habitats. The Carboniferous and Permian interval represents Phase 2 of palynivore, nectarivore and related associations (Fig. 7, middle) and provides a prelude to Mesozoic modes of insect consumption of gymnospermous reproductive tissues.

During the Triassic there is minimal evidence for consumption of pollen or nectar, except for pollen-laden coprolites within pollen organs from a taxon that is “remarkably similar” to that of extant cycads (Figs. 4A–C; Klavins & al., 2005). Other evidence is more indirect, such as the earliest appearance of pollinivorous xyelid sawflies (Rasnitsyn, 1964; Krassilov & Rasnitsyn, 1983), and early mecopteroid lineages that are known to have had long-proboscate, apparently nectar-feeding, mouthparts that date from the Middle Jurassic (Fig. 4I, M, N; Rasnitsyn & Kozlov, 1991; Novokshonov, 1997). During the Late Jurassic and Early Cretaceous, there is significant documentation of gymnosperm pollinivory from Eurasia (Figs. 3Q–T; 4G, H; Rasnitsyn & Krassilov, 1996; Krassilov & al., 1997). Concomitant with this, and continuing into the mid-Cretaceous, was the appearance of several other major insect mouthpart types which were designed for feeding on nectar or pollen, or for boring into ovular or seed tissues. These forms are found among several major lineages of brachyceran flies (Figs. 4J–L, N, P; Rohdendorf, 1968; Mostovski, 1998; Ren, 1998; Mazzarollo & Amorim, 2000) as well as phytophagous curculionoid weevils (Arnol’di & al., 1977).

Thus, Phase 3 (Figs. 3–5) is marked by palynivory, nectarivory and related associations during the Early Triassic to mid-Cretaceous (Fig. 7, middle). By contrast, Phase 4 of these associations is the most recent expansion of plant-palynivore and related associations, which began during the mid-Early Cretaceous expansion of angiosperms and has continued to recent times. This co-radiation eclipsed, but also highlighted, an earlier interval whereby currently extinct gymnosperm host plants and their insect pollinators contributed major pollination strategies.

The Mesozoic shift from gymnosperm to angiosperm entomophily. — The disappearance of at least some of the older, Mesozoic lineages of gymnosperms and their insect pollinators probably was attributable to the appearance of angiosperms during the Early Cretaceous. Angiosperms provided a more nutritionally efficient system for consumption of surface fluid and transfer of pollen rewards among conspecific hosts when compared to older entomophilous gymnosperm lineages, an idea compatible with Frame’s (2003b) hypothesis of the overall greater edibility of angiosperms. Entomophilous cheirolepidiaceae taxa became extinct during the Late Cretaceous, perhaps because they were at a disadvantage in the context of more efficient angiosperm insect pollination systems. For example, the presence of an intricate, inverted stigma-like structure at considerable distance from the micropyle but connected to it by a tubular structure that resulted in eventual pollination, may have been inefficient when compared to early angiosperm structures, such as simple stigmatic exudates secreted prior to anthesis (Frame, 2003a), small and perfect flowers with nectaries (Gottsberger, 1988; Thien & al., 2000), or even more complex floral mechanisms involving pollinator entrapment (Thien & al., 2003; Gandolfo & al., 2004). Similarly, but representing a different pollination pattern, entomophilous bennettitalean taxa were supplanted by more highly refined and host specific beetle (and thrips?) pollination systems of extant cycad lineages (Norstog & Nicholls, 1997; Terry, 2001). Notably, insect exploitation of the pollination-drop was not completely transferred to or terminated with angiosperm ecological expansion during the Late Cretaceous. It currently survives or has re-evolved in the form of diverse small insects, especially flies, moths, and parasitoid wasps having abbreviated labellate and sponging proboscides, on gnetopsid and, to a lesser extent, cycadopsid plants providing micropylar secretions (Kato & al., 1995; Tang, 1995).

SUMMARY AND CONCLUSIONS

Seven summary statements and concluding inferences can be made from this examination of pollination and related associations from the preangiospermous Mesozoic.

There is emerging evidence for a largely extinct phase of preangiospermous pollination syndromes involving several major clades of seed plants and insect pollinators. New fossil data suggest that we have only a glimpse of these extinct pollination biologies.

(1) Extant gymnospermous seed plants provide a source of liquid nutrition, typically in the form of micropylar pollination drops, used by a variety of insects, especially small flies. Such associations undoubtedly were present among gymnospermous seed plants during the preangiospermous Mesozoic.

(2) Major Mesozoic plant-host clades or groups which have suspected to well-documented palynivore, nectarivore and pollination associations include the Pteridospermopsida, Pinopsida, Cycadopsida, Bennettitopsida, and Gnetopsida. These taxa have family-level lineages that were largely extinguished during the later Mesozoic.

(3) Major Mesozoic insect nectarivores, pollinivores or pollinators for which there is circumstantial to well corroborated evidence are the Orthoptera, Phasmatodea, Embioptera, Coleoptera, Mecopteroidea, Diptera, Hymenoptera, and Lepidoptera. The Coleoptera, Mecopteroidea and Diptera present the most convincing evidence for an early pollinator role, with either nectar or pollen being the primary rewards.

(4) Many of the gymnosperm plant-host clades and their insect nectarivore, pollinivore or pollinator clades became extinct during the mid to Late Cretaceous for a variety of reasons, but probably involving the more efficient stigma-based angiosperm pollination system. One reason for this replacement was that some gymnosperm taxa possessed structurally and functionally complex pollination systems that were superseded by more efficient angiosperm systems.

(5) Two gymnosperm seed-plant clades had probable pollination associations with insects. The first is the outcrossing coniferalean *Frenelopsis alata/Alvinia bohémica* whole-plant species (Cheirolepidiaceae), which bore accessible ovuliferous scales with stigma analogs. The second is a bennettitalean species of *Cycadeoidea* (Cycadeoideaceae) possessing closed strobili. These two plants had very different types of pollination mutualisms. For the Cheirolepidiaceae, small-bodied or alternatively large-bodied, long proboscis flies aerially carried pollen from other plants, presaging the evolution of pollination mechanisms in angiosperms. For the Cycadeoideaceae, in situ beetle larvae consumed internal vegetative and reproductive tissues and in the process transported pollen within the closed strobilus, analogous to pollination mechanisms in cycads.

(6) Mesozoic plant-insect associations involving gymnosperms and their nectarivores, pollinivores and pollinators described herein (as well as other feeding guilds of herbivores), represent the third of four distinctive

phases of plant-insect associations which characterize the fossil record. This long-ranging third phase involved a distinctive colonization of gymnosperm plant hosts by insects followed by extensive diminution and replacement by mid Cretaceous angiosperms.

(7) Anatomically and structurally well-preserved compression and permineralized fossils provide significant evidence addressing major issues in the pollination history of insects and seed-plants. Such fossil evidence can supply information and insights which are otherwise difficult (or impossible) to gain by means of phylogenetical and ecological approaches. The modern perspective is based on a highly culled, small sample of recent gymnospermous seed plants and their insect associates.

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