# THE CO-RADIATIONS OF POLLINATING INSECTS AND ANGIOSPERMS IN THE CRETACEOUS[1]

*David Grimaldi*[2]

## ABSTRACT

The origins of many groups of flower-visiting insects are generally believed to have been in the Cretaceous. However, a recent hypothesis has concluded that many modern families of insects originated in the Jurassic, and that the Cretaceous radiation of angiosperms had little positive effect on the diversity of insect families. It is shown here, based on critical and phylogenetic interpretation of Mesozoic fossils, that radiations of major anthophilic groups of insects took place in the late part of the Lower Cretaceous to Upper Cretaceous: the bees (Apoidea/Apidae sensu lato), pollen wasps (Vespidae: Masarinae), various families of brachyceran flies (Acroceridae, Apioceridae, Bombyliidae, Empididae, Nemestrinidae, Stratiomyidae, and Syrphidae), and the Lepidoptera. The pattern of diversification of these insects, centered in the mid-Cretaceous, is consistent with the chronology of appearance of entomophilous syndromes in Cretaceous flowers, and not with a model of late Jurassic or earliest Cretaceous diversification of pollinating insects. Despite a more refined understanding of the timing of Cretaceous insect-angiosperm co-radiations, cause and effect relationships remain obscure.

Working on a group of organisms with perhaps 5 million species, entomologists are not easily impressed by groups other than insects. Nonetheless, even they admit to the central role that the angiosperms have in terrestrial communities. Based simply on the dazzling array of colors, patterns, and morphologies of flowers specialized for attracting insects, it is reasonable to estimate that at least two-thirds of the 250,000–300,000 living angiosperm species are insect pollinated. On this basis alone insects would be the most ecologically important group of terrestrial animals, without even taking into consideration their other ecological roles. The intimate and obligate associations that have evolved between thousands of species of angiosperms and insects are among the most significant mutualistic relationships to occur among all organisms. Understanding the origins of this relationship is, thus, hardly a trivial consideration.

Insects feeding on, or from, the reproductive structures of plants is an ancient habit, probably beginning in the Carboniferous with the Paleodictyopteroidea (Taylor & Scott, 1983; Labandeira, 1998). This assemblage of extinct insect orders had sucking mouthparts, presumably used for obtaining plant fluids or reaching into small spaces, such as the sporangia of Carboniferous medullosan pteridosperms. Indeed, the very large pollen (to 600 μm diam.) of some of these plants is thought to have precluded wind pollination, and they may have been pollinated by paleodictyopterans. It was the Coleoptera, though, that clearly set the stage for pollination of the early seed plants, probably beginning as early as the debut of beetles in the Permian (reviewed in Carpenter, 1992). Evidence that Mesozoic beetles were significant pollinators is largely circumstantial, and is based on the fact that various kinds of beetles today are facultative, and some even obligate, visitors to flowers of generalized morphology and exposed floral rewards (Armstrong & Irvine, 1990; Dafni et al., 1990; Gazit et al., 1982; Proctor et al., 1996). For example, En-

[2] Department of Entomology, American Museum of Natural History, New York, New York 10024-5192, U.S.A. grimaldi@amnh.org

dress (1987a, b) reported bisexual members of the primitive family Chloranthaceae to be pollinated by beetles and short-tongued flies, whereas unisexual species were wind pollinated. Also, certain weevils have been found to be essential to the pollination of some cycads (Norstog, 1987; Ornduff, 1997). Because beetles have chewing (mandibulate) mouthparts, they are not restricted to feeding on exposed pollen or nectar, but can also consume the ovules. It has been hypothesized that the fundamental angiosperm structure of closed carpels evolved as a mechanism to protect the ovules from visitors like beetles. The common occurrence of inferior ovaries may also have afforded a protective function. Despite their presumed early dominance of the anthophilous niche, Coleoptera were eclipsed as pollinators by Lepidoptera, aculeate wasps (including bees), and various brachyceran flies. The hardened forewings, or elytra, enable beetles to exploit tight spaces in which the wings of other insects would be damaged; as a result, however, beetles fly poorly compared to most other insects, which makes them less efficient at visiting many flowers.

## EVIDENCE FOR INTERPRETING ANCIENT INSECT POLLINATION

### DIRECT EVIDENCE

Direct evidence of insect-pollen interactions is provided by fossil insects with pollen preserved on or in them. Impressive examples are provided by the insects *Idelopsocus diradiatus* Rasnitsyn (Hypoperlida), *Tshekardaenigma pollinivorum* Rasnitsyn (Grylloblattida?), and *Sojanidelia florea* Rasnitsyn (Grylloblattida), from the Lower Permian (Kungurian) of the Urals (Rasnitsyn & Krassilov, 1996a, b), all found with masses of pollen in their guts. The pollen varied in preservation and was referred to the genera *Lunatisporites*, *Protohaploxypinus*, and *Vittatina* (Gymnospermae, Peltaspermales). The amount of pollen in the gut, and the fact that each gut was filled with only one pollen type, indicates that the insects were selectively feeding on pollen, and thus perhaps transporting it from plant to plant.

Several similar examples are known from the Cretaceous. Three species of sawflies in the primitive, living family Xyelidae (Hymenoptera), from the Lower Cretaceous (?Neocomian) of Baissa, Transbaykalia, are known to have fed as adults on the pollen of *Alisporites* (a pollen form-genus probably produced by the macrofossil conifer *Wilsiostrobus*), *Pinuspollenites* (?Pinaceae), and *Vitimipollis* (taxon unknown) (Krassilov & Rasnitsyn, 1982). Another xyelid with *Afropollis* pollen (possibly an-

giospermous) is briefly reported from the Santana Formation limestone of Brazil (Aptian: Lower Cretaceous) (Caldas et al., 1989).

In the Tertiary, apine bees in the Eocene shales of Germany (Lutz, 1990, 1993) have corbicula filled with angiosperm pollen. Stingless bees, *Proplebeia dominicana* (Wille), which are quite common in the Miocene amber from the Dominican Republic, can be found with masses of pollen in their abdomen preserved with perfect fidelity (Grimaldi et al., 1994; Grimaldi, 1996), although the pollen has not been identified.

The preservation of pollen in the guts of fossil insects appears to be more widespread than previously believed, and investigations on specimens from diverse Mesozoic deposits with exceptional preservation are likely to reveal fascinating data. Of particular interest would be the examination of the gut contents of beetles from the Lower Cretaceous and Upper Jurassic, and sphecid wasps from the Lower and mid-Cretaceous, since these groups are implicated as faithful visitors to early angiosperms. Nonetheless, pollen in the gut of fossil insects will probably always be a sporadic occurrence and not very illuminating for elucidating major patterns of insect-angiosperm diversification.

### INDIRECT EVIDENCE

#### 1. Pollinators of Extant, Primitive Angiosperms and Close Relatives.

Documenting the pollinators of primitive angiosperms and close relatives has been an active field of inquiry: for *Magnolia* (Thien, 1974), Chloranthaceae (Endress, 1987a, b), Winteraceae (Thien et al., 1985), *Illicium* (Thien et al., 1983), *Ephedra*, and *Gnetum* (Kato & Inoue, 1994). Gottsberger (1988) and Endress (1990) provided useful reviews and new information on several additional systems. In general, pollination of these gnetaleans and basal angiosperms is done by insects with a relatively generalized morphology, like beetles, short-tongued flies, and primitive Lepidoptera. Primitive insects can be engaged in some very specialized pollination relationships (e.g., *Tegiticula* moths and *Yucca*), but this is rare. Basal angiosperms visited by generalized insects is a rather consistent pattern, but it is difficult to tease out the extent to which this is due to a persistent symbiotic relationship or to the generalized, non-exclusionary morphology of these flowers. Also, it is not intuitively obvious as to why an ecological relationship that originated perhaps 100 Ma should persist to modern descendants virtually unmodified, in the face of dramatically changing ecological conditions as well as op-

portunities to develop new ecological interactions. Bees are the most dedicated and significant group of anthophilous insects; but even some species of the recently derived meliponines (stingless honeybees) have reverted to gathering spores of cycads (Ornduff, 1997) and even to feeding on carrion (Roubik, 1989).

## 2. Fossil Record of Angiosperms and Pollination Syndromes.

It has been well established that angiosperms are closely related to the relict and largely extinct Gnetales, as well as extinct Bennettitales, all three taxa comprising the Anthophyta (Doyle & Donoghue, 1986; Crane et al., 1995). The non-angiospermous anthophytes originated in the Triassic and reached a peak of diversification in the mid Cretaceous (Crane & Lidgard, 1990). Angiosperms, on the other hand, have their earliest palynological and macrofossil geological records in the Lower Cretaceous (Crane et al., 1995). Crane and Lidgard (1990) and Lidgard and Crane (1988) surveyed the generic and species diversity of angiosperms in the fossil record and found that generic diversity dramatically rises in the Albian to the Turonian (115–90 Ma), with a slightly less dramatic trend when species are surveyed. Thus, the explosive diversification of the angiosperms is well documented to be in a rather narrow window of time in the mid-Cretaceous.

Crepet (1985, 1996) and Crepet and Friis (1987) focused on the chronology of first appearance in the fossil record of morphological features associated specifically with insect pollination. Flowers often have suites of such features ("syndromes") that not only reflect whether the flowers are pollinated by insects, but may also indicate the order(s) of insects that visit the flowers. Data summarized by Crepet (1996) have considerably narrowed the time frame for radiations of pollinating insects, and the timing is consistent with the pattern of overall diversification (e.g., Lidgard & Crane, 1988). Crepet (1996) surveyed the earliest appearances of 36 reproductive features of angiosperms, many of them associated with insect pollination; the earliest of these appear in the Aptian (2), in the Albian (10), in the Cenomanian (20), and by the Turonian all 36 features had appeared. Based on these data, insect anthophily was well established by the Cenomanian (100 Ma), and virtually fully intact by the Turonian (90 Ma). Some highlights of this chronology are: sepals, petals, and long, filamentous stamens in the Cenomanian; and bilateral symmetry, corolla tubes, clawed petals, polyads and viscin threads on pol-

len, resin rewards, floral nectaries, and various modified anthers in the Turonian.

These data provide an essential basis of comparison with the insect fossil record. If the diversifications of angiosperms and anthophilous insects were coupled, we would expect major radiations of these insects between the Albian and Turonian/ Campanian.

## 3. Insect Fossil Record.

Labandeira and Sepkoski (1993) statistically analyzed insect families in the fossil record and reported that the number of insect families decreased since the mid Cretaceous radiation of the angiosperms. They concluded (Labandeira & Sepkoski, 1993: 313): "The more startling interpretation that can be drawn from the data . . . is that the appearance and expansion of angiosperms had no influence on insect *familial* diversification" (italics mine). According to their data, it does indeed appear true that many insect families appeared before the angiosperm radiation; but as will be shown and discussed later, it would be very misleading to extrapolate from this data that the angiosperm radiations had no effect on diversification of insects in general, such as species, genera, and other subfamilial taxa (see also Crepet, 1996). Also, insect families and orders are dramatically uneven in their species diversity, their relationship to plants, and in their significance as pollinators.

The oldest fossils of various insect families or orders are usually cited as evidence for the earliest records of pollinators or potential pollinators, but this can be very misleading. For example, some empidid flies today are facultative visitors to flowers, but this does not mean that early empidids in the Mesozoic were as well (in fact, they were probably predaceous). Ideally, there should be some morphological indicator in the fossil that reflects a feeding specialization for pollination. Compared to entomophilous angiosperms, insects have very few overt morphological specializations for anthophily. In part this may reflect the variety of behavioral rather than structural adaptations that pollinating insects employ, such as bee "buzzing," nectar robbing and theft, grooming pollen from the body, and learning differential rewards. Bees (Sphecoidea: Apidae s.l.) have the greatest number of anthophilic specializations: scopae and corbiculae, or brushes and baskets of hairs in which pollen is carried; plumose body hairs, to which pollen adheres particularly well; various combs and scrapers, for grooming pollen from the body hair; and, in many bees there is a long, maneuverable, retractile glossa

(tongue) (Thorp, 1979). Unless preserved in amber, only some of these minute features are likely to be observed in a fossil.

Other major groups of anthophilous insects have few morphological specializations, but the most obvious and repeatedly derived feature is a proboscis. In most Lepidoptera, some Diptera, and Hymenoptera (and even an instance in the Coleoptera [*Nemognatha*]), the mouthparts are elongate, which allows the extraction of nectar and pollen from deep and narrow flowers. An elongate proboscis has evolved numerous times in association with other lifestyles, such as in eight families of Diptera where females suck blood of vertebrates or prey on other insects. (One cannot always determine from structure alone if proboscides function primarily for anthophily or hematophagy. The females of many ceratopogonids and mosquitoes supplement their diet with nectar, or at least the male feeds on nectar. In some cases hematophagous midges are primary pollinators, such as ceratopogonids visiting *Theobromia cacao* [Young et al., 1984] and mosquitoes visiting the small North American orchid *Habenaria obtusata* [Dexter, 1913; Thien, 1969a, b]).

The ground plan for insects is to have mouthparts with three paired structures (maxillae, labial appendages, and mandibles) and three main central structures (the labium, labrum, and hypopharynx). In the many convergent cases where a proboscis has evolved, the constituent parts of the mouthparts are modified in different ways. Unfortunately, while an elongate proboscis may be preserved even as a compression fossil, the component parts are usually not distinguishable, and this can lead to ambiguity about the function of long proboscides in some fossil insects. *Pseudopolycentropus latipennis* Martynov (Paratrichoptera: Mecoptera), from the Upper Jurassic of Karatau, Kazakhstan, has a long, slender proboscis nearly twice the length of the head, which is much longer and more slender than any living mecopteran (Novokshonov, 1996). Since some mecopterans, the Bittacidae, have predatory adults, it is possible that this species had similar habits. If the detailed morphology of the proboscis components were preserved well enough, one could probably resolve whether *Pseudopolycentropus* used the proboscis for impaling prey or probing flowers.

Tracking the appearance of an elongate proboscis in the fossil record as an index to insect anthophily is a conservative approach. Without documentation of ingested fossil pollen, insects with a generalized morphology that visited flowers are easily overlooked. Most insects visiting flowers, in fact, have a generalized morphology. A four-year study of the insects visiting flowers of wild carrot (*Daucus carota*) in Logan, Utah, revealed 334 species in 37 families (Hawthorne et al., 1956). In a similar study of the insects on ragwort flowers (*Senecio jacobaea*), 178 species were found (Harper & Wood, 1957). In one area of Nova Scotia, 93 species of insects in 15 families were found visiting blueberries, *Vaccinium angustifolium* Aiton and *V. myrtilloides* Michaux (Finnamore & Neary, 1978). A total of 192 species of insects are known to visit blueberry flowers in eastern North America. Many of these species are itinerant, casual visitors without specialized structures for feeding from flowers. However, also included are some obligate anthophiles, like *Apis* (honeybees), halictids (sweat bees), and syrphids (flower flies), which are morphologically specialized and also the most persistent insect visitors. On the whole, obligate anthophiles are the most efficient pollinators, the most morphologically specialized, and ecologically most important for pollination; their history should better reflect angiosperm history than other groups of insects.

4. Phylogeny and Fossils of Obligate Anthophiles.

The approach taken here was to examine the phylogeny, fossil record, and biogeography (where applicable) of those insect lineages that predominantly comprise obligate visitors of flowers: Lepidoptera, Apidae sensu lato (bees), masarine wasps, and various families of lower Brachycera flies. The fossil record of each of these groups is spotty—typical for most insects—such that a generic or species-level diversity analysis will add little further resolution. Rather, a chronology is more accurately inferred by understanding the phylogenetic position of those few, critical fossils. I have attempted to superimpose cladistic relationships on a geological chronology by assessing the phylogenetic positions of fossils. This approach relies on phylogenetic studies for the various groups and scrutinizing the fossil for evidence of salient, diagnostic features (for the latter I often had to rely on accuracy of the published descriptions). Ages of clades, then, are strictly based on minimum estimates. However, I have also tried to estimate absolute ages based on correlations between phylogenetic position and fossil age.

HYMENOPTERA

BEES: SPHECOIDEA: APIDAE SENSU LATO

Bees are, by far, the most important group of insect pollinators. Many bees are foraging specialists, thus making them efficient pollen vectors. According to a study by Moldenke (1976), about 2000

species of bees occur in the Great Basin, Sonoran Desert, and xeric regions of the western U.S., 60% of which are specialists on a genus or family of flowering plants. The social bees, in particular, are spectacularly efficient at foraging, because the division of labor allows specialization of tasks and rapid recruitment to new resources. This is why colonies of *Apis* can harvest honey in such surplus that it is productive for agriculture, and why they can outcompete wild bee species wherever they colonize.

Traditionally, the bees are put into the superfamily Apoidea, with varying numbers of families, although it has been known for a long time that the bees were closely related to and perhaps derived from within the Sphecidae. Alexander's (1992) exploratory cladistic study of the tribes of Sphecoidea is the most comprehensive analysis of the group thus far. Instability in the sphecoid cladogram varies with the use of characters having problematic polarity, inclusion of enigmatic taxa, and methods of analysis. Some regions of the most parsimonious cladograms, however, are quite stable. In particular, the Apidae appear closest to a clade that consistently groups together the sphecid tribes Philanthini + Aphilanthopini + Cercini + Pseudoscolini + Psenini + Xenosphecini. Relationships among these tribes were highly unstable in Alexander's analysis, but as expected, the bees are a monophyletic group. All bees should best be phylogenetically categorized as a family in the Sphecoidea. In the cladogram of bee families and significant genera, though (Fig. 1), I have retained the traditional bee taxonomy simply for ease of recognition.

The fossil record of bees needs to be considered in the context of the fossil record of all aculeates (the stinging wasps, including ants and bees), but particularly the Sphecidae. The earliest fossil aculeates are the extinct family Bethylonymidae, from the Upper Jurassic of Kazakhastan, which is also the only family of aculeates known from the Jurassic. Modern families of aculeates appear first in the Cretaceous, most of them in the mid- to Upper Cretaceous (e.g., Grimaldi et al., 1997, for ants; review of aculeate families up to 1984 in Carpenter, 1992). The Sphecidae are no exception, with 11 records from the Cretaceous, 6 of them in various ambers: *Archisphex* Evans (Santonian, Siberia; Hauterivian, Weald Clay, England), *Angarosphex* Rasnitsyn (Lower Cretaceous, Baissa; Weald Clay), *Cretosphex* Rasnitsyn (Aptian, Brazil; and others), *Eopinoecus* Budrys (Santonian, Siberia), *Gallosphex* Schlüter (Cenomanian, France), *Lisponema* Evans (Santonian, Siberia), *Pittoecus* Evans (Campanian, Canada),

an undescribed genus from the Turonian of New Jersey, and several very primitive, undescribed forms from the Lebanese Neocomian amber. The genera from Brazilian limestone (Darling & Sharkey, 1990), and from Canadian, Siberian, and New Jersey amber are pemphredonines, and Jarzembowski (1991) considered *Archisphex* and *Angarosphex* to possibly be pemphredonines. According to Alexander's (1992) analysis, the Pemphredoninae are of intermediate phylogenetic position in the Sphecidae. It is virtually certain that sphecoids originated in the Lower Cretaceous, perhaps in the uppermost Jurassic, which helps explain the chronology of bees.

Bee phylogeny was most recently and comprehensively treated by Alexander and Michener (1995) and Roig-Alsina and Michener (1993). The cladograms in both studies were highly unstable, so the topology on which fossils are superimposed in Figure 1 is one of several of the most parsimonious schemes. This should not affect basic conclusions on bee origins. With the exception of stingless honeybees (Meliponini) in some Cenozoic ambers, bees are not common fossils. In fact, until the last decade, the fossil record of bees was almost entirely reflected by fossils from particularly rich Lagerstätten, especially the vast deposits of Eocene-Oligocene Baltic amber, and the Oligocene shales of Florissant, Colorado. Evaluating the systematic position of most fossil bees, particularly those preserved as compressions, is complicated by the lack of crucial, minute details, such as of the mouthparts.

A report of bees from the Triassic is easily dismissed, particularly since it antedates by 50 Ma the earliest appearance of the most primitive aculeate wasps, the Bethylonymidae. In the Chinle Formation (Upper Triassic, Arizona) are nest cells preserved in araucarioid wood (Wilford, 1995), but critical features of wood-nesting bee cells are not preserved, such as pollen clumps and special linings. It is most likely that these "cells" are gallery chambers of wood-boring beetles, such as cupedoids.

The oldest definitive fossil bee is *Trigona prisca* (Michener & Grimaldi, 1988a, b), in Cretaceous amber from New Jersey (Fig. 2). (A fossil wasp, *Paleapis beiboziensis* Hong, 1983, from the lower Cretaceous of China, can be dismissed as clearly not a bee; C. D. Michener, pers. comm. 1997). *Trigona prisca* is a controversial fossil for various reasons, several of which are discussed in Rasnitsyn and Michener (1991). Firstly, it belongs to one of the most highly derived groups of bees, the Meliponini, which to some experts is implausibly of

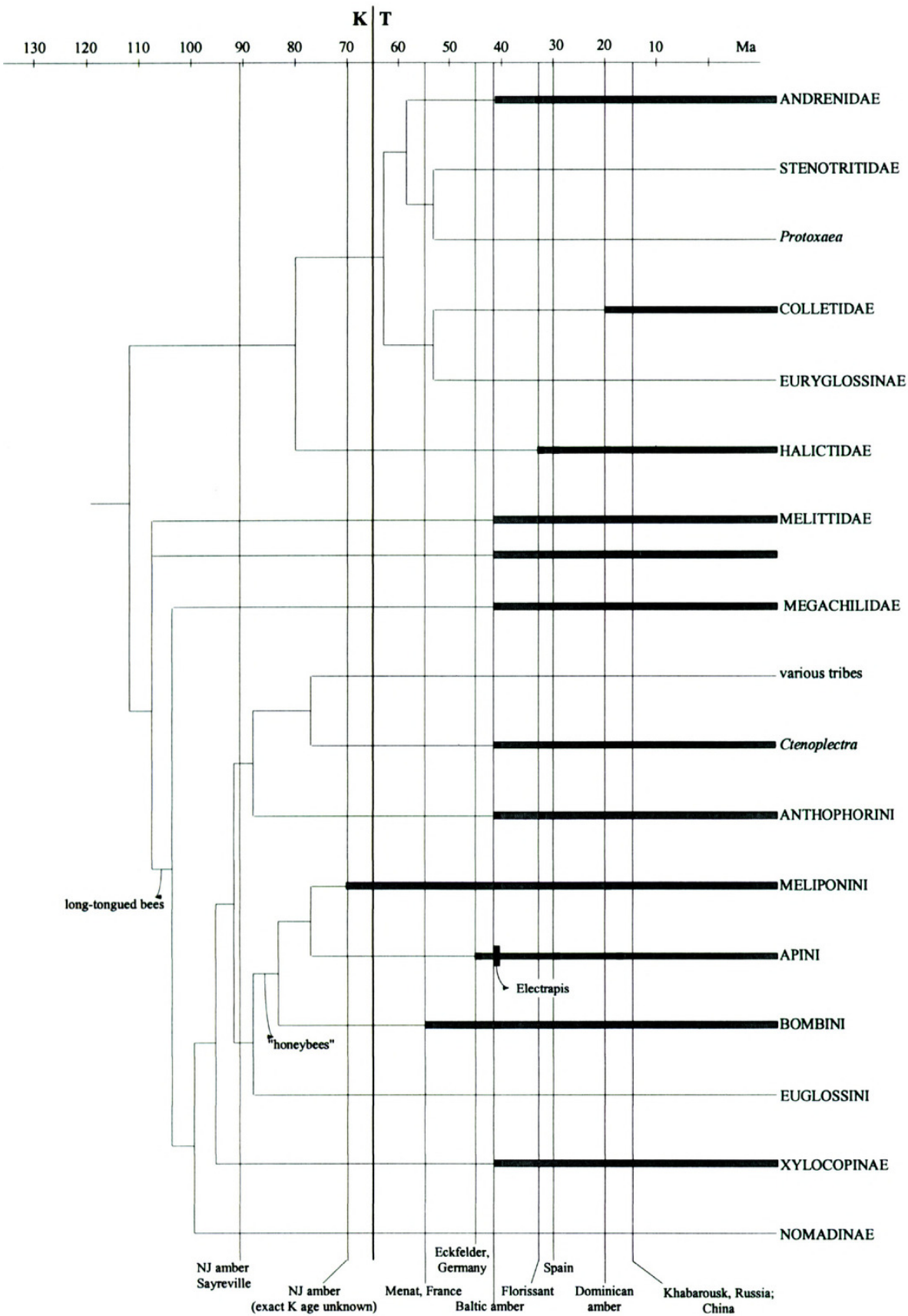Figure 1. One of several most parsimonious cladograms of families, subfamilies, and some genera of bees, taken from Alexander and Michener (1995) and Roig-Alsina and Michener (1993), with dates of representative fossils included. The basal diversification of bees in the Cretaceous is constrained by the fossil record of the Sphecidae, from which bees are derived. The earliest sphecid is from the Barremian.
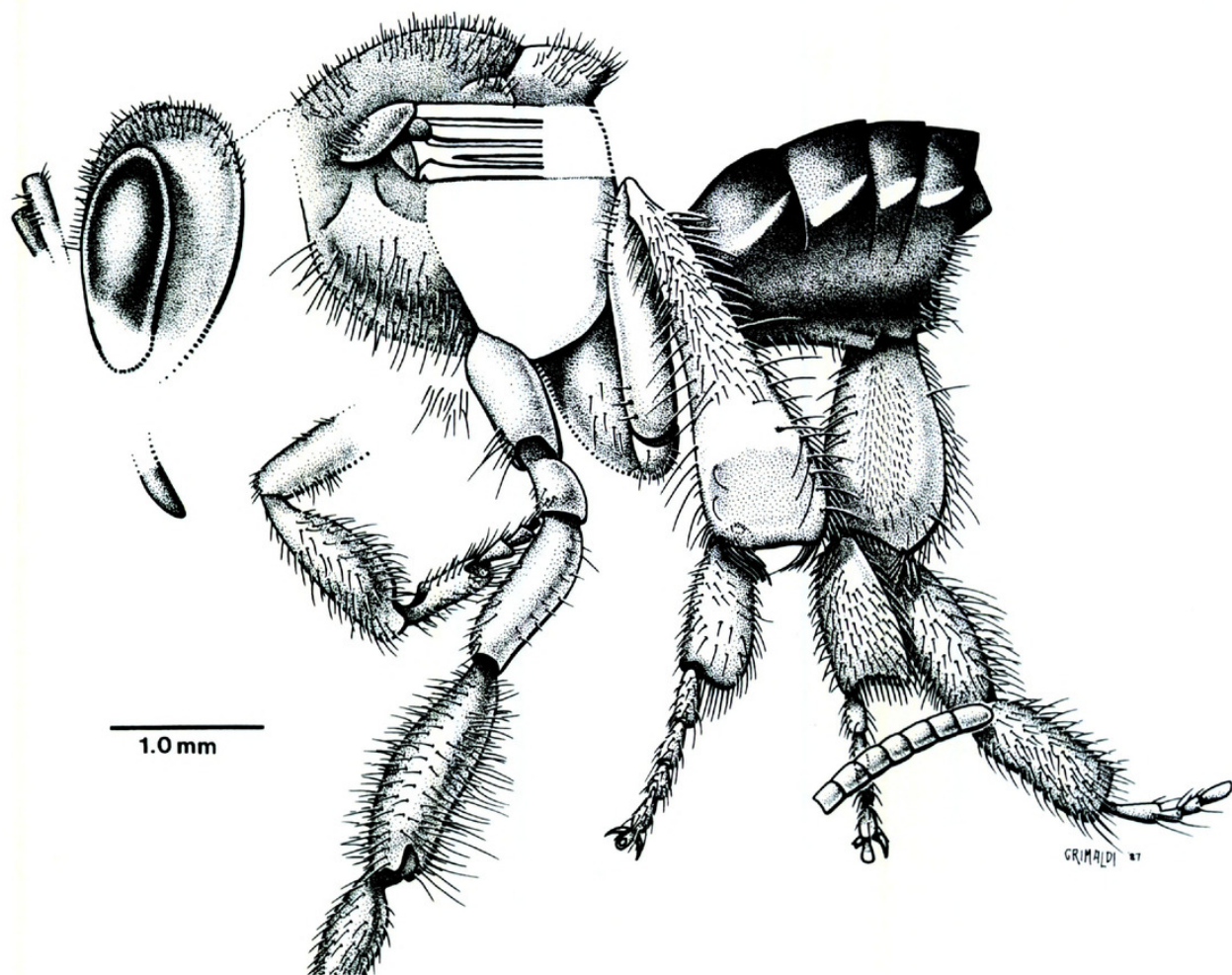
Figure 2. The oldest known bee, *Trigona prisca* (Apidae: Meliponini), in amber from the (presumably uppermost) Cretaceous of New Jersey.

Cretaceous age (Alexandr Rasnitsyn, pers. comm. 1990). Secondly, it was discovered in an old collection of amber fossils, labeled with the collector and town of origin (Kinkora, New Jersey), but stratigraphy is unknown, leading some to believe it is not even Cretaceous. Lastly, there are various other insects preserved in the same piece of amber as *Trigona prisca*, such as a wing of a termitid or rhinotermitid termite, a milichiid fly, and an emesine reduviid. All are fossils of rather derived insect groups that are regarded by some as improbably of Cretaceous age.

Evidence consistent with the Cretaceous origin of the *Trigona prisca* amber piece is the following: (1) Infrared spectroscopy and pyrolysis gas chromatography of barren fragments taken from the piece compares closely with amber samples collected in New Jersey by myself, which have well-documented stratigraphy (Grimaldi et al., 1989). (Since these samples have been taken, the fragile piece has been embedded in synthetic casting resin to protect it from accidental damage and oxidative degradation). (2) Based on some mayflies, staphy-

linids, neuropterans, dipterans, and other groups in amber from New Jersey that is accurately dated to Turonian, it is not at all unusual for there to be from this time period extinct species belonging to extant genera, or genera very closely related to modern ones. Also, since rampant morphological convergence in meliponines obscures tribal relationships, it is not even entirely clear that *T. prisca* is a *Trigona* (Michener, 1990). (3) The mid-Cenozoic diversity of bees is probably biased by the vast deposits of Baltic amber; excellent preservation of a sphecoid in such amber allows unequivocal determination of whether it is a bee or not. If, for example, a fossil bee that did not possess an obvious derived feature, like corbiculae, were preserved as a compression, it is doubtful it would be recognized as a bee at all. In contrast, some Cretaceous compression fossil sphecids are plausibly bees, but the exact relationships of the fossils are obscured because critical characters like branched hairs are not preserved. For example, some species of the Cretaceous genus *Cretosphex* are plausibly bees (see Darling & Sharkey, 1990). It is only in

the Cenozoic that we find compression fossilized bees with unequivocal identity, because many other, derived characters like enlarged corbiculae are preserved (e.g., *Eckfeldapis*, which actually appears to be synonymous with *Electrapis* in Baltic amber; M. Engel, pers. comm. 1997). Also, Cretaceous nests of aculeates may be halictid bees but lack definitive, diagnostic features. Nests of cells from the Upper Cretaceous of Uruguay were considered to be halictids (Zeuner & Manning, 1976), while nests of similar morphology, age, and location, tentatively identified as *Sceliphron* (Sphecidae) or Eumeninae (Vespidae) (Schlüter, 1984) have cells with one convex and one concave wall, as in the nests of bees and particularly similar to ground-nesting halictids (J. Wenzel, pers. comm. 1997). (4) The existence of undisputed, mid- (Turonian) and Lower (Aptian) Cretaceous pemphredonine sphecids is consistent with the presence of bees during the Cretaceous. (5) The existence of some bees in the Apinae from the lower Cenozoic is also consistent with Upper Cretaceous meliponines. These include extinct species from the Oligocene of Germany belonging to the living genus of honeybees, *Apis* (Engel, 1998a); a bombine (bumblebee) from the Paleocene of France; and eusocial bees in the extinct sister genus to *Apis*, *Electrapis*, from Eocene Baltic amber (e.g., Engel, 1998b). (6) True, resinous amber from New Jersey is known only from the Upper Cretaceous, but varies in age from Cenomanian to latest Maastrichtian (the latter being at the K/T boundary) (Grimaldi et al., 1989). Thus, it is quite possible, even likely, that *T. prisca* comes from the uppermost Cretaceous, ca. 65 Ma. *Trigona prisca* minimally indicates that the history of bees reaches into the Cretaceous. In Figure 1 I have concentrated the basal divergences of bees near the Cenomanian and Aptian based on indications from the much better fossil record of the sphecids. This scenario hypothesizes a very explosive radiation of bees in the mid-Cretaceous, with the origins of many bee subfamilies, tribes, and other such taxa somewhat later.

VESPIDAE: MASARINAE (POLLEN WASPS)

The Masarinae are a relatively small group (ca. 300 species worldwide) of solitary vespid wasps, one of six extant subfamilies of Vespidae. The eumenines, by contrast, have approximately 3000 species. The masarines are the only wasps besides bees that provision nests with nectar and pollen. Most species are found in South Africa (155 species), the Mediterranean region (90 spp.), Australia (32), and then southern South America (16) and

western North America (14). Carpenter (1993) provided a general area cladogram of world genera, with relationships being: Australia (South America (south Africa (Palearctic + Nearctic)))—a classic Gondwanan distribution. Gess (1996) reviewed the natural history, distributions, behavior, and ecology of the masarines, and Carpenter (1989, 1997) examined phylogenetic relationships of masarine genera. The wasps are small, 4–20 mm in length, with proboscides 0.14–1.3 times the length of the body, depending on the species (Fig. 3). The records of flower associations indicate a high degree of oligolecty in these wasps and their importance as pollinators (Gess, 1996).

There are no fossil masarines, but fossil vespids in other subfamilies (Carpenter & Rasnitsyn, 1990; Wenzel, 1990), some patterns of biogeographic distributions (Carpenter, 1993), and the phylogeny of vespid subfamilies (Carpenter, 1981, 1990) allow a fairly good estimate of masarine age. The oldest vespids are *Priorvespa*, in the extinct subfamily Priorvespinae; and *Curiosivespa* in the most primitive, living subfamily (Euparagiinae). Both of the fossil genera are known from the Lower Cretaceous (Barremian/Aptian) of Baissa, with *Curiosivespa* also known from the mid-Cretaceous (Turonian) of Kzyl-zhar. An undescribed, primitive eumenine is known from Turonian amber from New Jersey (Carpenter, in litt.); and the oldest fossil of social vespids (Polistinae + Vespinae) is *Celliforma* Brown, a fossil nest comb from Upper Cretaceous deposits of undetermined age from Utah (Wenzel, 1990). Another ichnogenus, *Desertina* Nessov, from the Upper Cretaceous of the Kyzylkum desert in Kazakhstan, appears very similar to *Celliforma* (J. Wenzel, pers. comm. 1997). Because *Celliforma* and *Desertina* are form genera, it is impossible to determine their phylogenetic position among the social vespids.

Excellent correspondence is found among the phylogenetic position of the Mesozoic fossil vespids and their ages (Fig. 4): the most primitive ones are Lower Cretaceous and mid-Cretaceous (Turonian); another Turonian fossil is of intermediate phylogenetic position; and a social vespid nest, the most derived of all vespids, is found in the Upper Cretaceous. The Vespidae probably originated in the lowermost Cretaceous, and most of the living subfamilies appear to have originated in the mid Cretaceous, which is consistent with the disjunct Gondwanan distribution of the masarines. Since genera and generic groups of masarines are highly endemic to continental areas (e.g., within southern Africa), most of the diversification of masarines has taken place since the mid-Cretaceous.
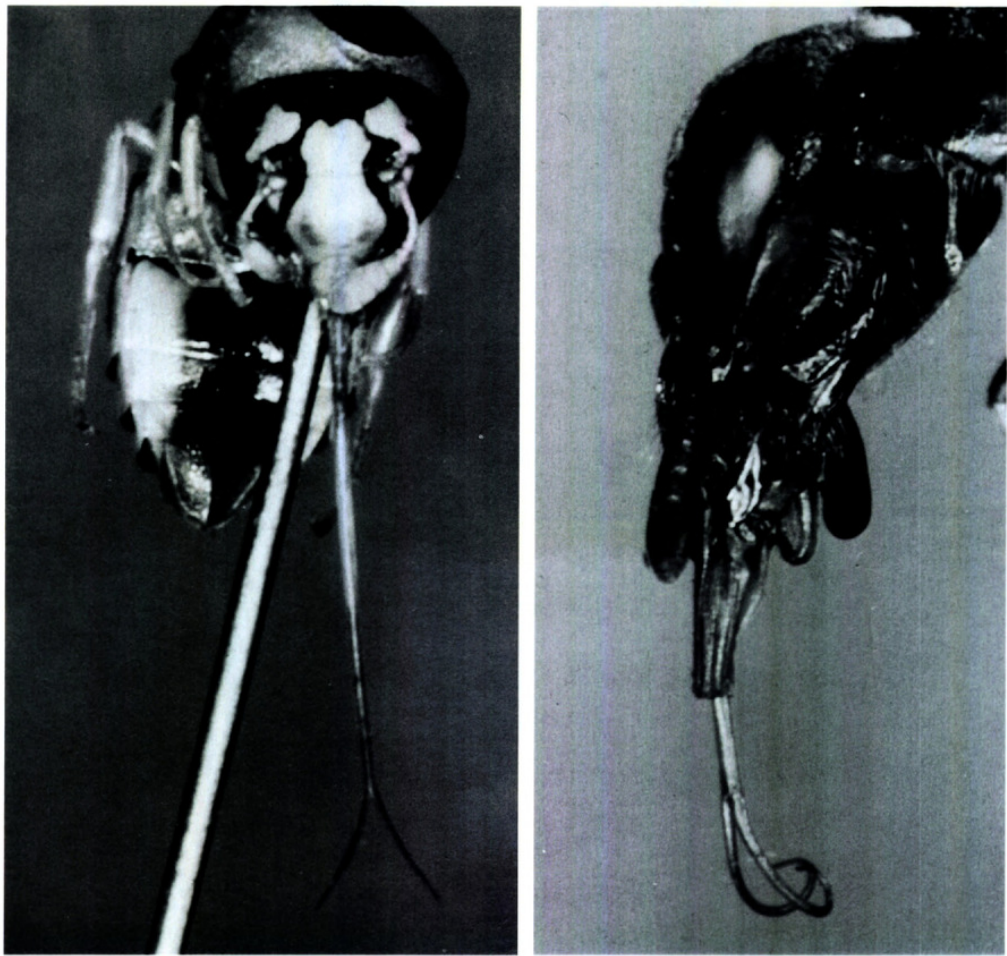
Figure 3. Extant species of masarine wasps, *Celonites varipennis* (left) and *Trimeria americana* (right). The glossa of *Celonites* is fully distended. Photos by J. M. Carpenter.

## DIPTERA

The ecological significance of the Diptera, or true flies, is often overlooked, especially with regard to pollination. Judging from morphology, obligate anthophiles are probably more widespread in the Diptera than are presently recognized. Long proboscides that are clearly not used for sucking blood, but are probably used for feeding from flowers, are scattered throughout the nematocerous Diptera, despite the characterization by Proctor et al. (1996) that nematocerous Diptera have generalized, short proboscides. In North America alone, genera of nematocerous Diptera with elongate probsocides are *Elephantomyia, Ornithodes, Toxorhina,* and *Limonia* (Geronomyia) (Tipulidae: craneflies); *Lygistorrhina* and *Gnoriste* (Mycetophilidae: fungus gnats); and *Eugnoriste* (Sciaridae). In addition, elongate proboscides occur in various phorids (scuttleflies); and in empidids, or dance flies (*Iteaphila, Toreus, Anthepiscopus,* and some *Empis*), which employ them for predation and/or flower feeding. In regions where bees are scarce, Diptera are often the dominant pollinating group. For example, McAlpine

(1965) found at least 18 species of flies feeding on flowers on Ellesmere Island in the Canadian Arctic, making this order the primary pollinator group in that region.

The recent reports by Ren (1998a, b) have emphasized the importance of Diptera as earliest pollinators. He reported three families of flies in Upper Jurassic rocks from Lianoning, China, which belong to the lower Brachycera. Representatives of two of these families, the Tabanidae and Nemestrinidae, had long proboscides equal to or longer than the head length. The third family, the extinct Protapioceridae, is dismissed as anthophilous by lack of evidence (see below under Apioceridae). The conclusion that the fossil Nemestrinidae were anthophilous is compelling (see below), but the evidence that the Jurassic tabanids were anthophilous is unconvincing.

Ren (1998a, b) described three Upper Jurassic tabanids from the Yixian Formation, which he placed in the family on the basis of pulvilliform empodia (on the feet) and the apices of wing veins $R_4$ and $R_5$ encompassing the wing tip; he placed
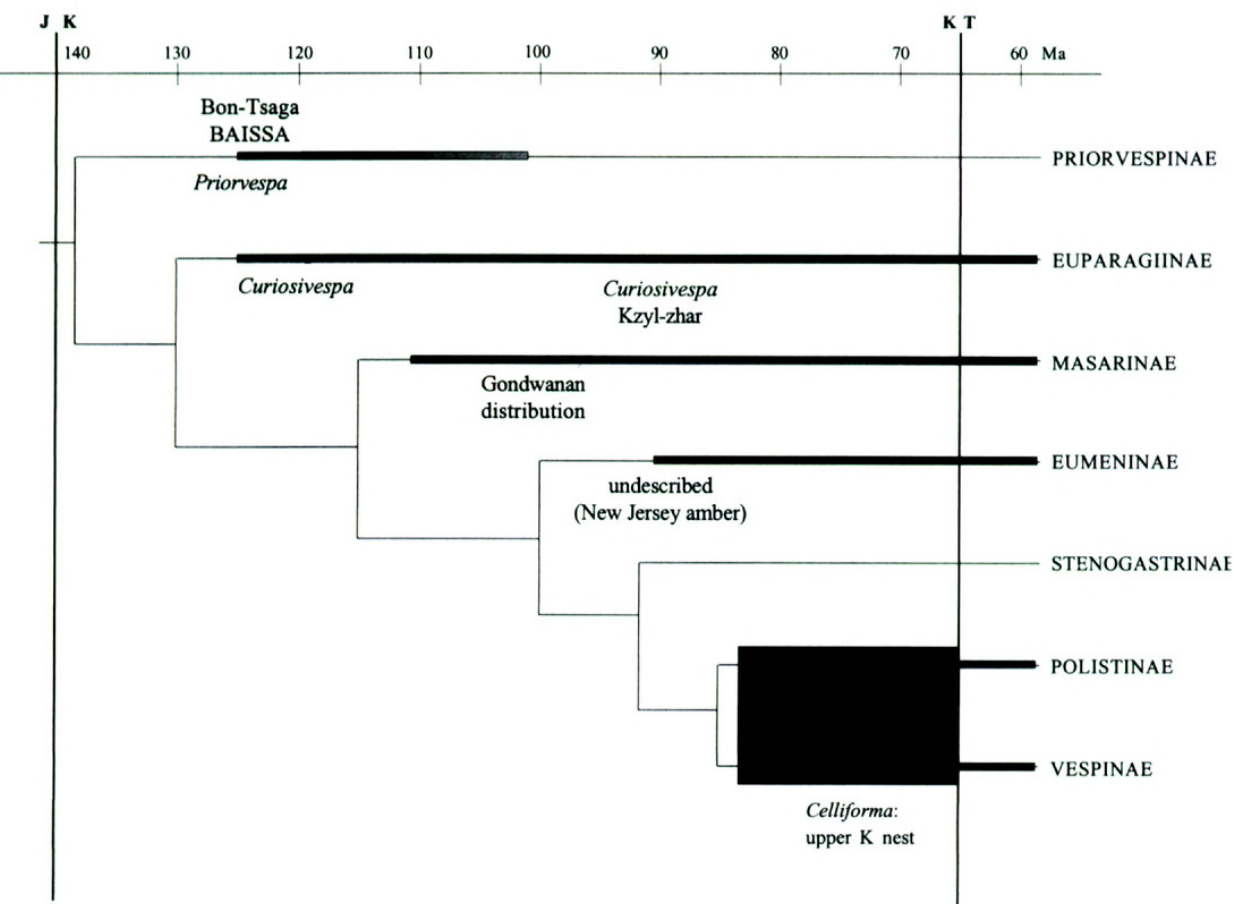
Figure 4.   Cladogram of subfamilies of Vespidae, from Carpenter (1981, 1990; Carpenter & Rasnitsyn, 1990), with positions of all known Mesozoic fossils included. Age of the Masarinae, or pollen wasps, is inferred on the basis of a Gondwanan distribution.

the flies specifically in the subfamily Pangoniinae on the basis of a long proboscis. Further, he cited Colless and McAlpine (1991), that "most extant pangoniines are exclusively flower feeders" (Ren, 1998b: 85). Colless and McAlpine (1991: 755) actually said: "Most of the Australian [pangoniine] species suck blood, but some species of *Scaptia* appear to be exclusively flower-feeders . . . ."

Identification of the Chinese Jurassic fossils as tabanids is uncertain, since a pulvilliform empodium is plesiomorphic for this family (and found throughout the lower Brachycera). In addition, the structure of radial wing vein apices seen in the fossils is also found in other families, like Pelecorhynchidae and *Pseudoerrina*, and even in the fossils they are less divergent than in living tabanids; veins $R_{4-5}$ in the fossils diverge near the posterior m crossvein, unlike modern tabanids and more like Rhagionidae; and the large lower calypter typical of tabanids is not preserved or is absent in the fossils. Ren's "tabanids" are therefore most likely to be rhagionid ("snipe") flies, a primitive family (suspected to be paraphyletic) that is well represented in Mesozoic deposits. Modern rhagionids are pred-

atory and some even hematophagous. Some Mesozoic rhagionids had projecting, but not particularly long, proboscides (Grimaldi & Cumming, 1999).

The main groups of pollinators in the Diptera are large-bodied species in various families of lower Brachycera: Acroceridae, Conopidae, Mydidae, Scenopinidae, Stratiomyidae, Nemestrinidae, Apioceridae, Bombyliidae, and Syrphidae, with the last four being the most ecologically significant pollinators. Most of these flies are fast fliers and excellent hoverers, making them very efficient for foraging from flowers. A convergent feature among the hovering, anthophilous Diptera is a concentration of the apical wing veins, which are also upturned (Fig. 5). These modified wing veins strengthen the apex of the wing blade from the intense forces generated at very high wing-beat frequencies. The only other kinds of flies with this apical wing vein scaffold are a few blood-sucking, parasitic, and insectivorous flies, like some tabanids (horseflies/deerflies) and asilids (robberflies), the tsetse flies (Glossinidae), and botflies (Oestridae); rarely, though, are the veins in these flies as distorted as in the hovering anthophiles. Nagatomi and Soroida
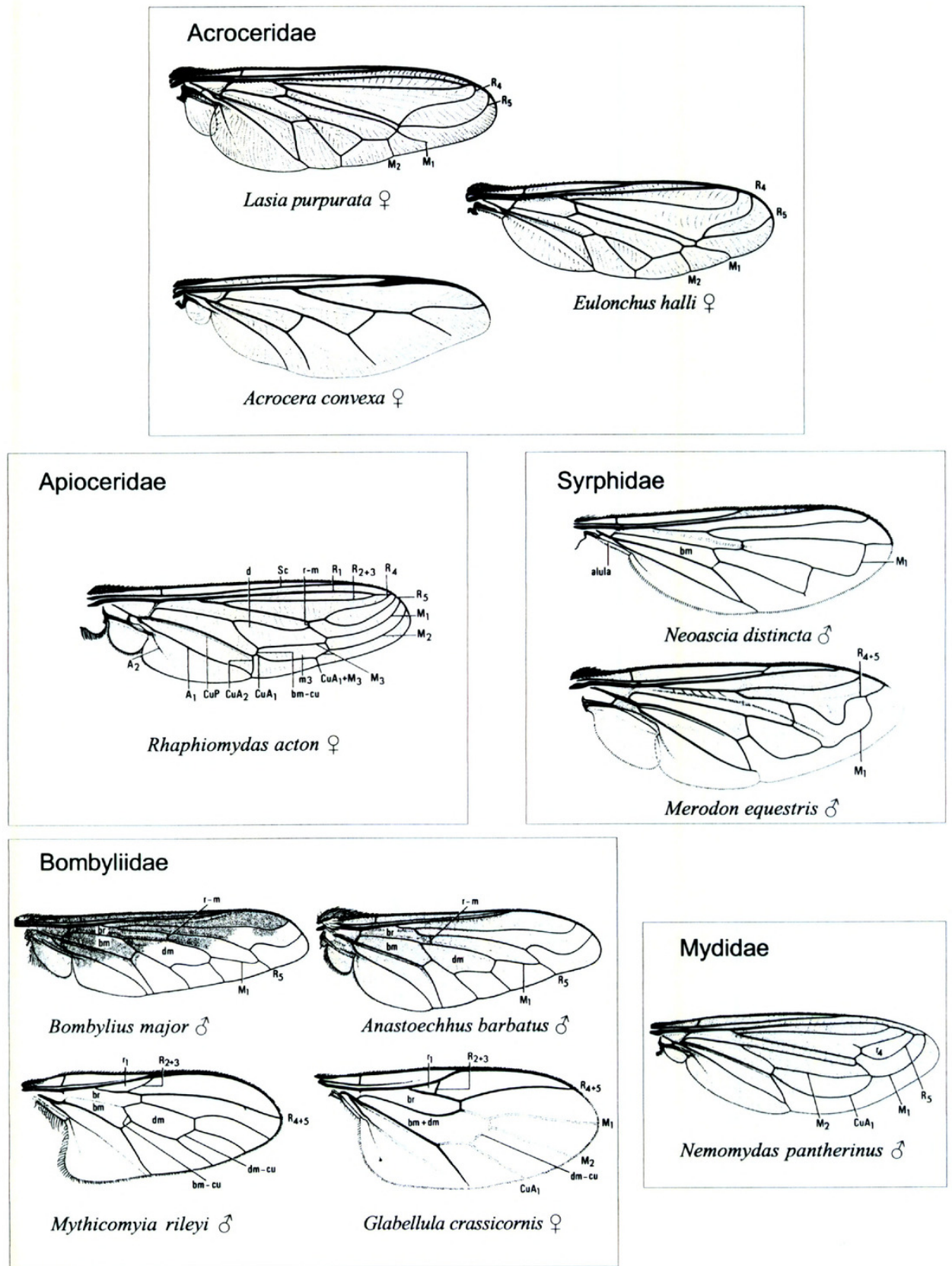
Figure 5. Wings of representative, extant anthophilic Diptera. Note the coalescence and curvature of the apices of the veins in some species. Development of this feature is strongly correlated with development of an elongate proboscis (see Fig. 6). Modified from McAlpine (1981).
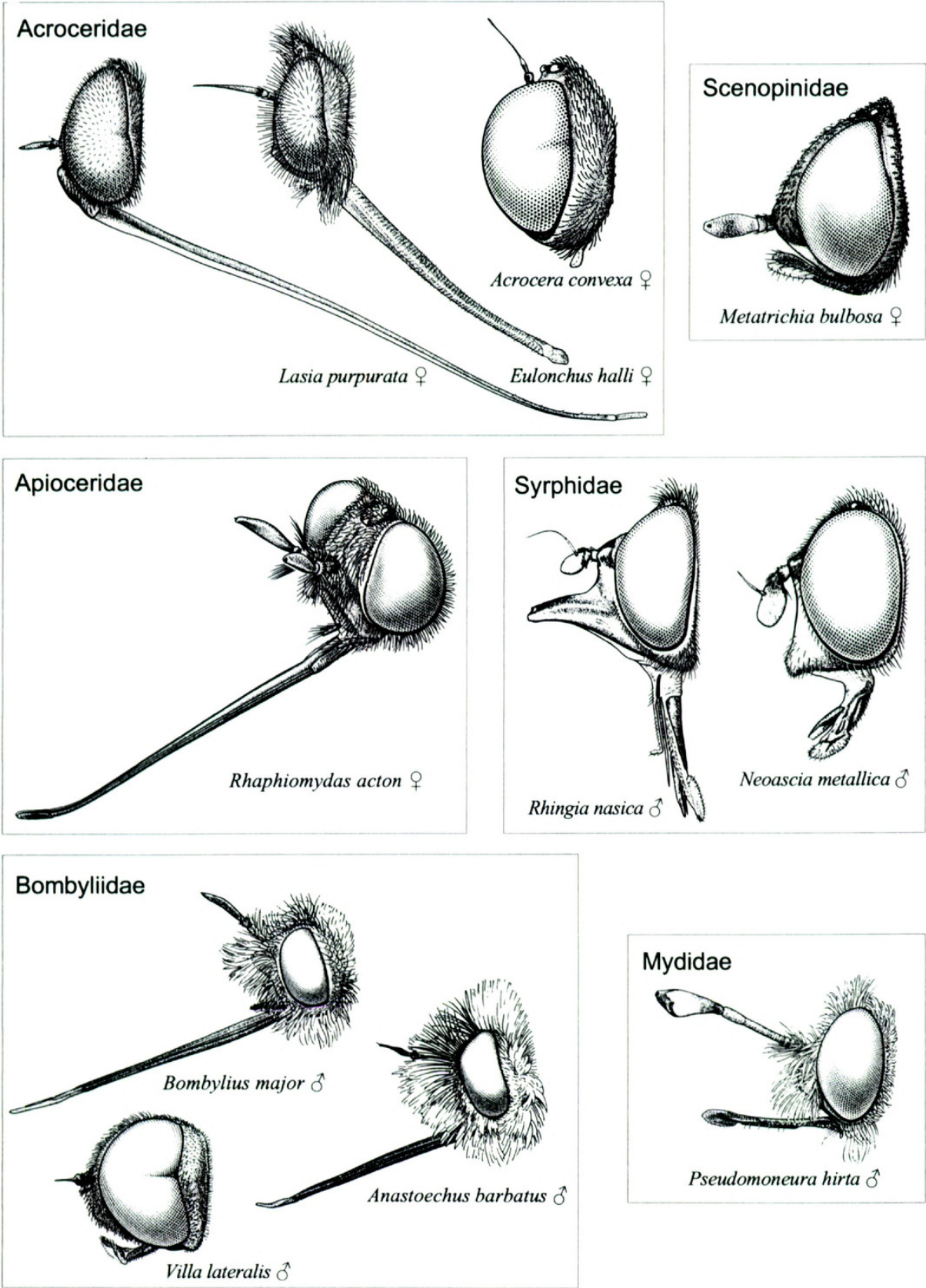
Figure 6.   Heads and proboscides of representative species of Diptera belonging to anthophilic families.

(1985) presented a comparative morphological study of the mouthparts of "orthorrhaphous" flies, illustrating various ways in which mouthparts are elongated into a proboscis.

Mesozoic fossils of "lower" Diptera are relatively abundant compared to the other orders, and the phylogenetic relationships within the order have been intensively investigated (Fig. 7). Nematocerous Diptera first appear in the Triassic (Shcherbakov et al., 1995; Fraser et al., 1996), and the Brachycera appear in the Lower Jurassic. Understanding of the biogeography of Diptera has also progressed, with development of phylogenetic systematics in the group and studies like those of Hennig (1960) and Brundin (1966) on austral Diptera. The south temperate Diptera, in fact, roughly reflect what is known about relationships and fossils. The Cyclorrhapha (= Muscomorpha), a monophyletic group and the most derived infraorder, shows barely any austral distributions. The suggestion is that this assemblage of about 70 families and some 60,000 described species is a post-Gondwanan radiation; that is, one that post-dated the separation of Australia, South America, and Africa some 100 Ma. The Conopidae are one family for which there are just several Cenozoic records and the phylogenetic relationships of genera have not been at all explored, so little can be said about the origin of this family.

## ACROCERIDAE

Acroceridae, or "small-headed flies," have very uniform life histories as internal, larval parasitoids of spiders, but their adult morphology is extremely varied. Some genera, like *Acrocera*, *Ocnaea*, and *Ogcodes*, have vestigial mouthparts and probably do not feed as adults. Other genera, like *Eulonchus*, *Lasia*, and *Philopota*, have among the longest proboscides in the Diptera, equal in length to the body. It is interesting to note that the long-proboscis genera also have wing venation that is complete and with apical veins that are crowded and upturned, typical of excellent hoverers (other genera have a venation that is so reduced that they probably cannot hover). Indeed, these genera are excellent hoverers, and even though acrocerids in general are rarely seen, the long-proboscis genera are usually encountered visiting flowers. For example, Schlinger (1960) and Grant and Grant (1965) reported *Eulonchus* to be faithful visitors to species of *Gilia* and *Linanthus* (Polemoniaceae), the flowers of which have long, slender corolla tubes.

Fossils of acrocerids are exceptionally rare; also, despite the fact that the family is small (50 genera

with 500 described species), the phylogenetic relationships of acrocerid genera have not been examined. The oldest fossils of the family are *Archocyrtus gibbosus* Ussatchov and *Juracyrtus kovalevi* (Nartshuk, 1996), from the Upper Jurassic (Kimmeridgian) of Karatau, Kazakhstan. *Archocyrtus* does not possess a long proboscis; the wing venation is simplified as in many acrocerid genera, and lacks the apical vein buttress. This fly certainly did not hover and probably did not feed on pollen. *Juracyrtus*, however, has similar, simplified venation but is reported as having a proboscis considerably longer than the length of the body. The rendering of the fossil (Fig. 8a) indicates that the interpretation of the long, thin structure as a proboscis is ambiguous: connection to the base of the head is not definite, nor is there any fine structure confirming it as a proboscis (or possibly a stray object). Most importantly, the wing venation is definitely not of the hovering type, which all living acrocerids have that also have proboscides of this length. Unfortunately, there are no Cretaceous acrocerid fossils, and the only other fossils are in Cenozoic amber. In Baltic amber (Eocene/Oligocene) there are *Glaesoncodes* Hennig (1968), *Prophilopota* and *Villalites* Hennig (1966a), all of which are closely related to extant genera. In Miocene Dominican amber, *Ogcodes exotica* is closely related to several African and Asian species (Grimaldi, 1995). The age and plesiomorphic nature of *Archocyrtus* and *Juracyrtus*, combined with two Tertiary amber records, are consistent with a late Mesozoic origin and Cretaceous diversification of the family.

## MYDIDAE AND APIOCERIDAE

These families, although not particularly closely related, are discussed together because several genera in both families have had a confused taxonomy. Fortunately, the phylogenetic work of Yeates and Irwin (1996) has rectified the taxonomic problems and even reported an illuminating biogeographic pattern. The fossil record of the two families is scant. An Oligocene fossil mydid is placed in the living genus *Mydas*, as *M. miocenicus* Cockerell. Two Mesozoic species exist, of the extinct genus *Protapiocera*, from the Upper Jurassic of China (Ren, 1998a, b). Ren placed *Protapiocera* in a separate family from the living Apioceridae, and the coalescence and near-coalescence of the apical parts of the radial wing veins definitely indicate a close relationship of the two taxa.

Mydids and apiocerids are mostly large flies of xeric habitats. They are excellent fliers, and particularly the Apioceridae are renowned for their hov-
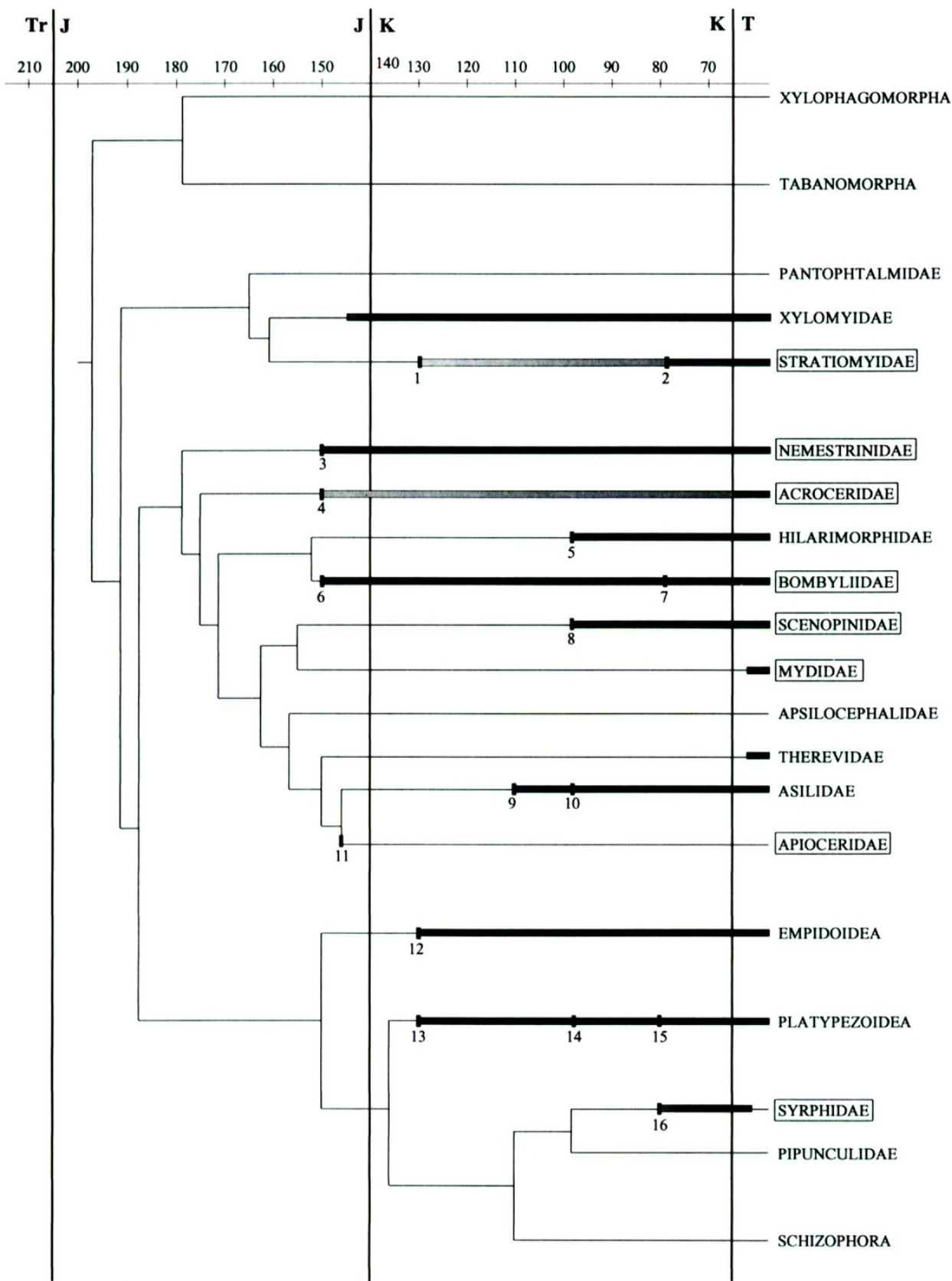
Figure 7. Relationships of families of lower Brachycera flies, derived from Woodley (1986), Yeates (1994), and Cumming et al. (1995). Total lengths of lines indicating clades provide a broad estimate of ages of various clades. Records of undescribed specimens from New Jersey and Lebanon are based on Grimaldi and Cumming (1999). Families in boxes are major anthophilic groups.

Numbers on cladogram: 1, undescribed stratiomyid, lower Cretaceous of Montsec, Spain; 2, *Cretaceogaster*, Canadian amber; 3, various described nemestrinids, Karatau, Kazakhstan; 4, *Archocyrtus* (placement is questionable); 5, undescribed hilarimorphid, Turonian amber, New Jersey; 6, *Paleoplatypygus*, Karatau; 7, *Procyrtosia, Proplatypygus*, in San-

ering ability. Some genera have short or vestigial mouthparts, while others have long proboscides (subgenus *Apiocera*, and in the Mydidae: *Rhaphiomidas* and *Neorhaphiomidas*). Species with medium to long proboscides are typically found feeding from flowers. According to the cladistic results of Yeates and Irwin (1996), the genus *Rhaphiomidas*, traditionally placed in the Apioceridae, is actually the sister group to the Mydidae, including the plesiomorphic subfamily Megascelinae of the Mydidae; the Megascelinae have an austral distribution. There is, in fact, perfect correspondence in the cladistic biogeography between the subgenera of *Apiocera* (the sole genus of the Apioceridae) and the plesiomorphic mydids. The biogeographic relationships are (western) North America (Africa (Australia + South America)). One must conclude that the ancestral clades of Apioceridae and Mydidae existed in the late Mesozoic, prior to the major Albian rifting ca. 110 Ma (Barron, 1987). An Upper Jurassic origin of these families suggested by Yeates and Irwin (1996) is supported by the recent discovery of the Chinese Jurassic *Protapiocera*.

Since *Rhaphiomidas* has a long proboscis and is the most primitive clade of the mydids, this might be suggestive of an Upper Jurassic-Lower Cretaceous origin of a long proboscis. Actually, this inference could only be made if all/most other primitive clades in *Apiocera* and Megascelinae also had a long proboscis, but in fact a long proboscis evolved three times in both groups. Thus, the long proboscis could have evolved at any time between the earliest Cretaceous and throughout the Cenozoic, and it is also significant that *Protapiocera* fossils, from the Upper Jurassic of China, do not have the mouthparts preserved. Ren (1998b), however, still concluded that these fossil flies were anthophilous, because of the hirsute body—a feature possessed by many anthophilous insects. This is entirely speculative, since species with hirsute bodies are scattered throughout non-anthophilous Diptera: many Asilidae, Therevidae, and some Empididae (predatory); some Tabanidae (hematophagous); and the Heleomyzidae, Psychodidae, and Scathophagidae (saprophagous and coprophagous). Conversely, many anthophilous Diptera are not particularly hir-

sute, such as the proratine scenopinids, Stratiomyidae, and many Syrphidae. A reasonable estimate is that a long proboscis and pollen feeding in apiocerids and mydids appeared in the Upper Cretaceous.

NEMESTRINIDAE

These are relatively large and hirsute flies that are superb fliers and that have the apical venation of the wing buttressed by extreme coalescence (hence their common name, "tangle-veined flies"). Among the 300 species and 20 living genera, all but a few genera (e.g., *Trichopsidea*) have a slender proboscis that is as long as the head or longer (the trichopsideines have a very reduced, vestigial, or even non-existent proboscis). The South African *Moegistorhynchus longirostris* has the longest proboscis of all insects relative to the body size, nearly four times the body length. Nemestrinids with the longest proboscides have extreme buttressing of the apical wing veins, to the point of the veins becoming reticulate. The apical veins in the wing of *Moegistorrhynchus*, for example, form a lacey network. Understanding the evolution of this group is greatly facilitated by the fact that it is probably the best represented family of Brachycera in the fossil record.

The oldest Nemestrinidae are from the very rich Upper Jurassic (Kimmeridgian) beds of Karatau, Kazakhstan (*Archinemestrius* Rohdendorf, *Protonemestrius* Rohdendorf, and *Eohirmoneura* Rohdendorf), and from the Yixian Formation, Upper Jurassic, of Liaoning, China (*Protonemestrius jurassicus* Ren, *P. beipaiaoensis*, and *Florinemestrius pulcherrimus* Ren [Ren, 1998a, b]). Fortunately, the venation of nemestrinids is so distinctive that there is little ambiguity about placing fossils of these flies: they possess a "diagonal vein" composed of several other veins and running obliquely through the middle of the wing. Bernardi (1973b) placed *Archinemestrius* and *Protonemestrius* in the most primitive subfamily, the Archinemestriinae Rohd.; and *Eohirmoneura* was placed close to the living genus *Hirmoneura*, also a basal lineage. Bernardi (1973b: 285) qualified this placement by indicating (285) that *Hirmoneura* is possibly a polyphyletic group.

←

tonian amber from Taymyr, Siberia; 8, undescribed scenopinid, Turonian amber, New Jersey; 9, *Araripogon*, Aptian, Brazil; 10, undescribed asilid, Turonian amber, New Jersey; 11, biogeographic dating (see text, based on Yeates & Irwin, 1996); 12, various taxa, oldest definitive Empididae in Neocomian amber, Lebanon; 13, undescribed, Neocomian amber, Lebanon; 14, undescribed Platypezidae, Phoridae in New Jersey amber; 15, *Prioriphora*, *Sciadophora* (Phoridae), and *Ironomyia* (Ironomyiidae) in Canadian amber; 16, undescribed, Santonian amber, Taymyr, Siberia.

**a.** *Juracyrtus kovalevi*

**b.** *Protonemestrius jurassicus*

**c.** Proratinae, indet., New Jersey amber

**d.** *Cretaceogaster pygmaeus*
Canadian amber

**e.** *Proplatypygus rohdendorfi*

**f.** *Procyrtosia sukatshevae*

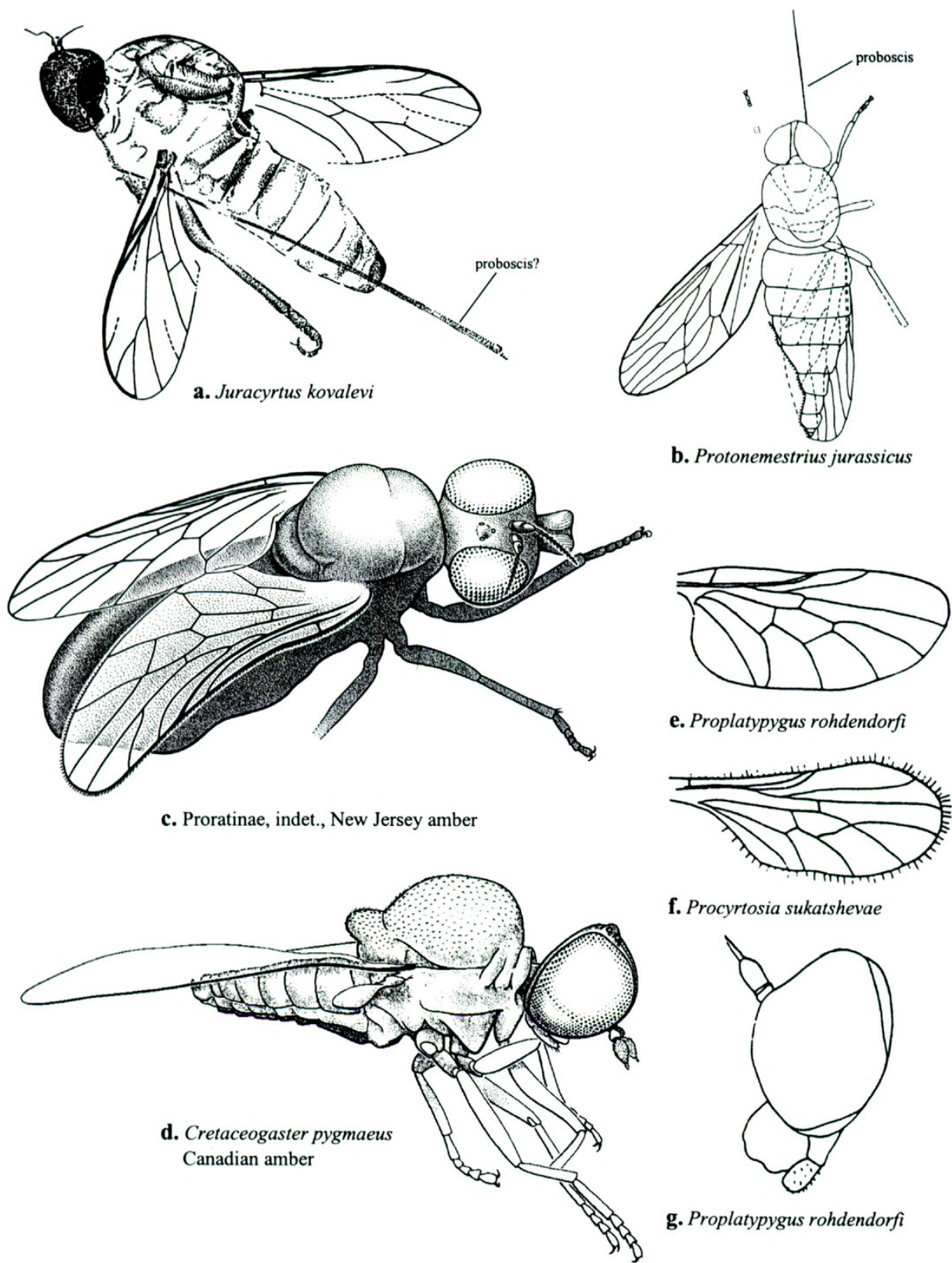**g.** *Proplatypygus rohdendorfi*

Figure 8.    Fossil Diptera belonging to anthophilic families. —a. *Juracyrtus kovalevi* (Acroceridae) (from Nartshuk, 1996). Note that the apical wing veins are not coalesced or upturned in *Juracyrtus, Proplatypygus,* or *Procyrtosia.* — b. *Protonemestrius jurassicus* (Nemestrinidae), from Jurassic of China (from Ren, 1998a). —c. Undescribed scenopinid in New Jersey amber (original). —d. *Cretaceogaster pygmaeus* (Stratiomyidae) in Canadian amber (original). e–g: Bombyliidae. —e. *Proplatypygus rohdendorfi* (Siberian amber). —f. *Procyrtosia sukatshevae* (wing) (Siberian amber: upper Cretaceous). —g. *Proplatypygus rohdendorfi* (head) (Siberian amber). f and g from Zaitsev (1987).

Not including the enigmatic genus *Rhagionemestrius* Ussatchev from Karatau, which is of questionable family placement (Bernardi, 1973a), two other Jurassic genera are described, from the Tithonian (uppermost Jurassic): *Sinonemestrius* Hong & Wang, from China, and *Prohirmoneura* Handlirsch, from the Solnhofen beds of Bavaria. Wing venation of *Prohirmoneura* is distinctly nemestrinid, but not well enough preserved to make a more accurate placement (unfortunately, the type and only known specimen cannot be located, so the accuracy of the original description cannot be checked). The taxa from Karatau have consolidated apical veins on the wing, but are not strongly curved upward nor are as consolidated as in many modern species. Thus, they probably did not hover at all, or at least not as well as the Cenozoic forms. Most fascinating is that some species of *Protonemestrius* are reported to have a proboscis (Rohdendorf, 1964; M. Mostovsky, pers. comm. 1997). Bernardi (1973b: 285) mentioned the proboscis in Archinemestriinae being ". . . short . . . rarely equal to the length of the head . . . ." If this is the case, *Protonemestrius* appears to be the earliest appearance of a proboscis in the fossil record that was almost certainly used for feeding on pollen or some other anthophyte reproductive reward, but interpretation of the proboscis may be as ambiguous as that of *Juracyrtus* (Acroceridae), discussed above. New hirmoneurine nemestrinids from Montsec, Spain (Aptian), lack a proboscis, but a new nemestrinine genus from Baissa, Siberia (Albian), possesses a *short* proboscis. In *Eohirmoneura*, the oral region is not well preserved, making preservation of a proboscis uncertain.

Most recently, several new taxa of fossil nemestrinids from the Upper Jurassic of China have reinforced the view that the nemestrinids were probably among the earliest obligate pollinators (Ren, 1998b). Of the three taxa described by Ren, two have anthophilic-type proboscides: *Protonemestrius jurassicus* and *Florinemestrius pulcherrimus* (proboscis of the latter is of moderate length, 1.2 times depth of head). Even though Ren (1998a) mentioned that many Late Jurassic examples were collected, only the holotype specimen of *P. jurassicus* was figured and discussed (Ren, 1998a, b). The one specimen makes it difficult to evaluate the structure of the proboscis, which is peculiar in being much finer than in any living species.

It is important to note that the Nemestrinidae are the most plesiomorphic family in the Asiloidea (Fig. 7), an assemblage of 10 families, half of which are important pollinators. This antiquity can account for the impressive late Jurassic diversification of this brachyceran family. Moreover, the distributions

of the subfamilies Nemestrininae and Cyclopsideinae are austral (Bernardi, 1973b), which is again suggestive of a Gondwanan pattern.

The main Cenozoic record of nemestrinid flies is in the Oligocene shales of Florissant, Colorado, with five species belonging to three extant genera (Bequaert & Carpenter, 1936), although Bernardi (1973b) indicated that the fossil genus *Palembolus* Scudder should be maintained for one of these species. *Neorhynchocephalus occultator* Cockerell, in fact, was indistiguishable from the living species *N. volaticus* largely on the basis of wing venation. At least one species, *Prosoeca florigera* (Scudder) (the genus is presently South African), had an elongate proboscis. Given the remarkable diversification of the nemestrinids by the Upper Jurassic (some 6 genera from Eurasia), one can conclude that somewhere between the Upper Jurassic and the Lower Cenozoic the radiations of modern nemestrinid genera took place. This family is at present the best candidate for the earliest obligate pollinator of angiosperms, and certainly the earliest record of a morphological structure specialized for feeding from flowers.

SCENOPINIDAE

Scenopinidae, or "window flies" (ca. 700 species described), are rarely encountered, with the exception of a few common species. Most genera have a short, jutting proboscis (Fig. 6), but some have a slender probscis that is equal to the length of the head or slightly longer. The higher-level relationships of the family were studied (Yeates, 1992), but there are only two fossils: *Metatrichia pria*, in Miocene amber from the Dominican Republic (Yeates & Grimaldi, 1993), which belongs to a rare extant genus; and an undescribed species from mid Cretaceous (Turonian) amber from New Jersey (Grimaldi & Cumming, 1999) (Fig. 8c). Certain apomorphies diagnostic of the Scenopinidae are not visible in the Cretaceous fossil, such as the pair of sensory patches on abdominal tergite 2, but the wing venation is very similar to certain proratine scenopinids, notably the genera *Acaenotus*, *Jackhallia*, and *Prorates*. These genera and two others belong to the proratines, which used to be placed in the Bombyliidae (e.g., Hall, in McAlpine, 1981; Hull, 1973). The proratines were reviewed by Nagatomi et al. (1994), classifying them according to Yeates's (1992) work. Proratines with a proboscis have a similar habit to bombyliids in their feeding from flowers, but some species have vestigial mouthparts (Liu & Nagatomi, 1995). Figure 9 is a cladogram of the higher relationships of the prora-
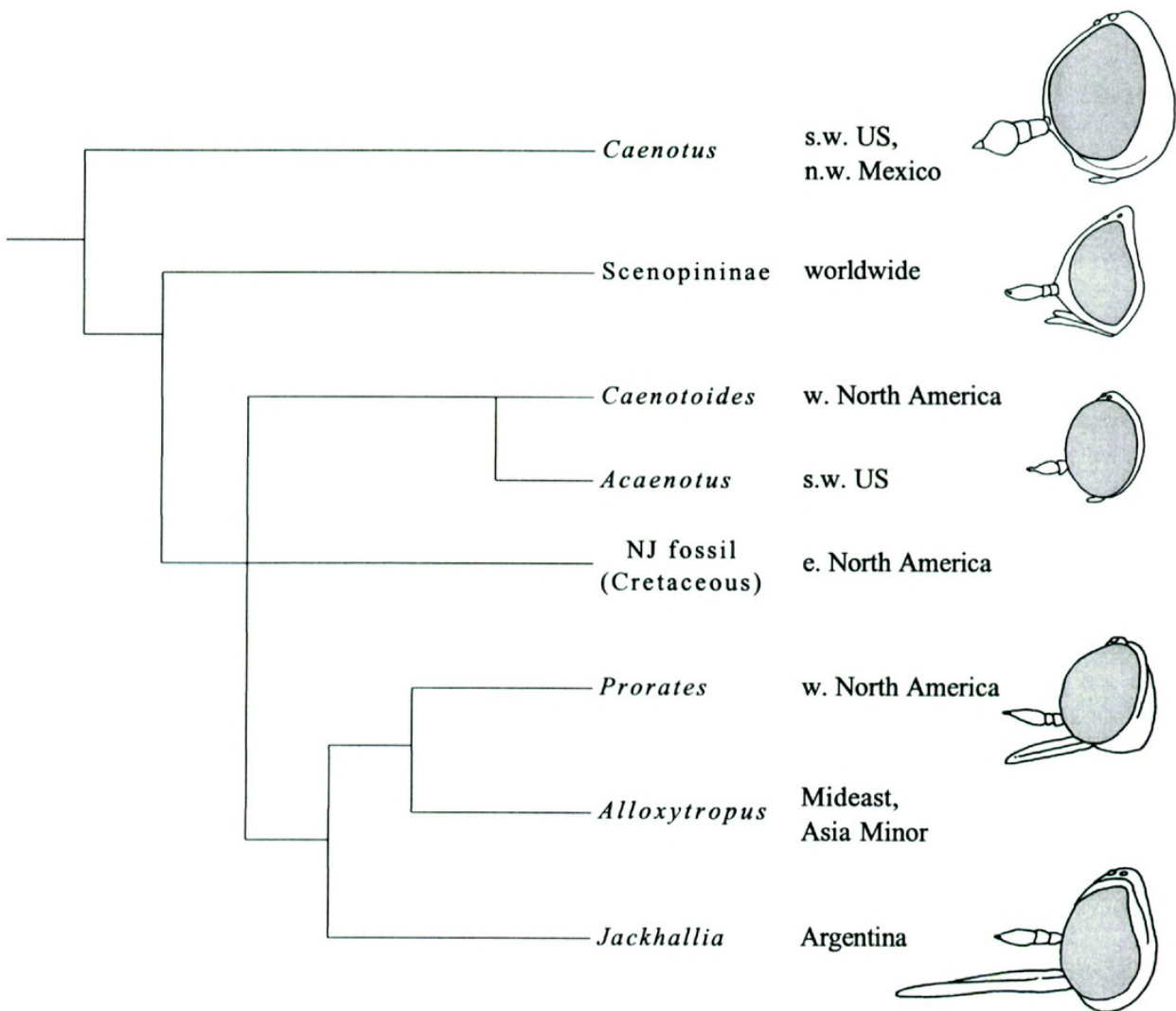
Figure 9. Cladogram of proratine scenopinids, showing diagram of heads and proboscides. Cladogram derived principally from Yeates (1992), with additional taxa from Nagatomi et al. (1994).

tines. The three most derived genera have the longest proboscides; the New Jersey amber fossil has a short proboscis that extends slightly beyond the oral margin. This is consistent with a Cretaceous origin of an anthophilic proboscis and of proratine scenopinid genera.

The distribution of proratines is centered in the arid regions of western North America, where most of the diversification appears to have occurred. There are some dramatic disjunctions, involving this area (four genera), the Mid East and central Asia (*Alloxytropus*), and Argentina (*Jackhallia*). Such disjunctions are suggestive of formerly widespread genera, which the Cretaceous fossil corroborates, but they must be interpreted very cautiously for such notoriously poorly collected and rare flies.

STRATIOMYIDAE

Stratiomyidae, or "soldier flies," superficially resemble syrphids in their bold yellow and black col-

or patterns. There are approximately 2000 described, extant species. Among the groups of flies discussed here, they are the least specialized for anthophily. Wing venation is not particularly modified for hovering, and their flight is not as maneuverable as in the other groups; with a few exceptions, the proboscis has a generalized structure. Of the described fossils, there are 16 Cenozoic genera (catalogued in Evenhuis, 1994, with several additional genera in Dominican amber), all of them extant or very close to extant genera. Only three Cretaceous fossils are known: *Cretaceogaster pygmaeus* Teskey, in Santonian amber from Canada (Fig. 8d); an undetermined beridine-like specimen in Turonian amber from New Jersey (Grimaldi & Cumming, 1999); and undetermined larvae from Lower Cretaceous limestone of Montsec, Spain (Gomez Pallerola, 1986).

The relationships of *Cretaceogaster* were discussed by Woodley (1986). The genus is most

closely related to *Parhadrestia* from south temperate South America. Together, they are the sister group to the Chiromyzinae + all other stratiomyids. Interestingly, the Chiromyzinae have an austral distribution that also includes Andean South America and southern Central America. Without knowledge of *Cretaceogaster* from the Northern Hemisphere, one might conclude that the basal clades of the Stratiomyidae had a Gondwanan distribution, whereas it had a much wider distribution in the Upper Cretaceous. The basal position of *Cretaceogaster* is consistent with a Lower Cretaceous origin of the stratiomyids. The position of the Lower Cretaceous specimens from Spain will probably not be particularly revealing since they are larvae. Unlike *Cretaceogaster*, the specimen in New Jersey amber is too fragmentary for accurate systematic placement, but its features are consistent with the Beridinae, a primitive clade of stratiomyids. The little data on Cretaceous stratiomyids indicate they were plesiomorphic at this time period.

## EMPIDIDAE

These flies are often implicated as significant pollinators because some species have long, rigid proboscides, which are used for preying on other insects and probing narrow corollas for nectar and pollen. *Empis tessellata*, for example, is recorded visiting 20 species of flowers in Britain (Hobby & Smith, 1961). In actuality, there are only a handful of empidid genera that are obligate or even largely pollen feeders, namely *Anthalia* (Ocydromiinae), *Iteaphila* and *Anthopiscopus* (Oreogetoninae), some *Empis* species, and possibly *Philetas* and *Hesperempis* (Empidinae).

The relationships among empidid subfamilies are well investigated (Cumming et al., 1995), as are the relationships of genera of some subfamilies (Sinclair, 1995). The family is also one of the best known from the Cretaceous, with extensive representation in ambers from the Neocomian of Lebanon, Cenomanian of France, and various Upper Cretaceous ages of Manitoba and Alberta, (Canada) New Jersey (U.S.A.), and Taymyr (Siberia) (Hennig, 1970, 1971; Kovalev, 1974, 1978; Negrobov, 1978; Grimaldi & Cumming, 1999). The oldest empidoid is *Protempis*, from the Upper Jurassic of Karatau, which has very primitive wing venation and is considered to be the sister group to the empidids on this basis. None of the Mesozoic empidoids have a proboscis that is even as long as the head, and in most other respects they are quite plesiomorphic. The oldest records of the living subfamilies Empidinae, Atelestinae/*Nemedina*-genus group, and Tri-

chopezinae occur in Turonian amber from New Jersey, and of Tachydromiinae and Ocydromiinae in Campanian amber from Canada (Grimaldi & Cumming, 1999). Strangely, one of the most derived clades, the Microphorinae and Dolichopodidae, occurs in the oldest fossiliferous amber, from the Neocomian of Lebanon, as well as in younger ambers. The origin of empidid subfamilies is therefore definitely a Cretaceous event, and modern genera did not appear until the latest Cretaceous and early Cenozoic.

## SYRPHIDAE

Syrphidae, or "flower flies," are almost certainly the most ecologically important group of anthophilous Diptera (Proctor et al., 1996), not because of any particular specializations, but rather because of their ubiquity, with some 6000 species and 180 genera worldwide. Species in the Syrphinae and Eristalinae visit flowers; those in the smaller subfamily Microdontinae do not, with most having small and vestigial mouthparts. None of the syrphines and eristalines have particularly long mouthparts, and there seem to be various degrees of specialization of pollen and/or nectar feeding.

There is, unfortunately, only one Cretaceous fossil syrphid, preserved in Santonian amber (ca. 84 Ma) from Taymyr, Siberia. It is very incomplete and appears to belong to the modern subfamily Cheilosiinae (M. Mostovsky, pers. comm. 1997). Also, the phylogenetic relationships of tribes and genera have been explored only piecemeal. The fossil record of the Syrphidae is summarized best by Vockeroth and Thompson (1986: 52): "There are 32 species known from Baltic amber [Eocene] ...; the others are from [Oligocene and Eocene] sedimentary deposits from western North America and Europe. Forty-five species are assigned to recent genera; the others belong to extinct genera, *which do not differ markedly from living Syrphidae* [italics mine]. Because of many changes in classification and the use of many additional taxonomic characters since Hull's [1945, 1949] study, the available material should be critically studied."

Thus, by the Eocene-Oligocene, a basically modern diversity of hoverflies was intact. The basal diversification of this family was almost certainly Cretaceous, probably Upper Cretaceous, based on constraints of only primitive platypezoids found thus far in the Cretaceous (Grimaldi & Cumming, 1999). Vockeroth (1969), in discussing the biogeography of syrphids, concluded that syrphids are like other groups of the Schizophora in showing no apparent austral distributions. The indication is

that the origin of major syrphid lineages postdates the rifting of Gondwanaland between the Aptian and Turonian.

## BOMBYLIIDAE (BEE FLIES)

Besides the Syrphidae, this is the fly family of greatest significance for pollination. These flies are generally very hirsute and are most diverse in xeric environments around the world where they are found hovering close to the ground and on flowers. Some species have small or vestigial mouthparts, many have a proboscis that projects beyond the head, but the ones with the longest proboscides (3–4 times the length of the head) are in the Bombyliinae (Fig. 6). Most of the species for which behavior is known occur in temperate regions, generally in the spring. These studies have revealed a remarkable degree of flower-constant foraging among various long-proboscis species. With their superb hovering ability, and "trap-lining" behavior, they are no doubt efficient pollinators of various herbaceous plants, especially those with flowers having narrow corolla tubes (Scott-Elliot, 1896; Graenicher, 1910; Knoll, 1921; Straw, 1963; Grant & Grant, 1965; van Someren, 1978; Evenhuis, 1983; Daniels, 1983; Grimaldi, 1988; Proctor et al., 1996).

Mesozoic fossils of the family are sparse, but the phylogenetic relationships of bombyliid subfamilies have been studied in detail by Yeates (1994) (Fig. 10). The oldest fossil is *Paleoplatypygus zaitsevi* Kovalev, from the mid-Jurassic of Siberia. According to Evenhuis (1994), who has been monographing the mythicomyiines, the wing venation of *Paleoplatypygus* is similar to extant members of the *Psiloderoides* group of genera. The adults of these genera have small to vestigial mouthparts. [Evenhuis (e.g., 1994) placed the Mythicomyiinae, the most primitive clade of a monophyletic Bombyliidae, into a separate family. The cladistic results of Yeates (1994) indicate that such splitting into families is unwarranted.] The only other Mesozoic bombyliids are in Upper Cretaceous (Santonian) amber from Taymyr, Siberia: *Procyrtosia sukatshevae* Zaitsev, and *Proplatypygus rohdendorfi* Zaitsev (Figs. 8e, g). All are mythicomyiines and have small to rudimentary mouthparts, while the Eocene *Proplatypygus succineus* Hennig and some recent *Platypygus* have proboscides that protrude even to several times the length of the head. *Zarzia* Zaitsev, also in Siberian amber, was transferred from the Bombyliidae to the Rhagionidae by Evenhuis (1994). Lastly, Evenhuis (1994) commented that *Crosaphis*, from the Upper Triassic (Carnian) of

Australia and Virginia, may be a mythicomyiine; it is actually an anisopodoid nematoceran (Fraser et al., 1996).

The fossil record of the non-mythicomyiine, higher bombyliids is entirely in the Cenozoic and includes some 32 genera and 50 species, reviewed by Evenhuis (1994). Lack of non-mythicomyiine Cretaceous bee fly fossils is a concern, but probably accurately reflects their absence given that various Brachycera are abundant in vast compression deposits from Botswana, Brazil, China, England, Mongolia, Siberia, and Spain. Although modern study of Cenozoic bee fly fossils is necessary, they all appear either close to or equivalent to modern genera. The Mesozoic fossils are few but consistent with the cladistics of the family: primitive, mythicomyiine bombyliids appear in the Upper Jurassic and Lower Cretaceous, and more derived taxa in the Cenozoic. Major radiations of bombyliids probably occurred in the Upper Cretaceous and Lower Cenozoic, contrary to Zaitzev's (1987) hypothesis that basal radiations of non-mythicomyiines occurred in the Upper Jurassic. Unfortunately, no biogeographic synthesis of even part of the bombyliids has been done, and is made difficult by the current tradition of faunistic-style systematics of the genera.

## LEPIDOPTERA

In terms of the number of species (ca. 110,000 worldwide), and their biomass in vegetated habitats, this is certainly among the most successful of the insect orders. Many lepidopterans are tiny, with wing spans down to 3 mm. Others have wingspans of nearly 30 cm, more expansive than any other living insect.

Lepidopterans are intimately associated with flowers, feeding on the pollen and nectar with their proboscis, a structure that is found in all but the most primitive lepidopterans. There are some extremely specialized relationships with flowers among Lepidoptera (Proctor et al., 1996), but it must also be noted that many Lepidoptera do not feed exclusively on flowers. The diet of many species is supplemented with, and sometimes made up exclusively of, fluids from puddles, dung, rotting fruit, and even the eye secretions of large animals. Some species of noctuids from southeast Asia have evolved a proboscis capable of piercing the rind of fruits in order to feed (Bänziger, 1982). The ground-plan function of the lepidopteran proboscis is actually uncertain, and not necessarily used for probing flowers (Kristensen, 1997). Feeding habits of the primitive, mandibulate moths, the Agathiphag-
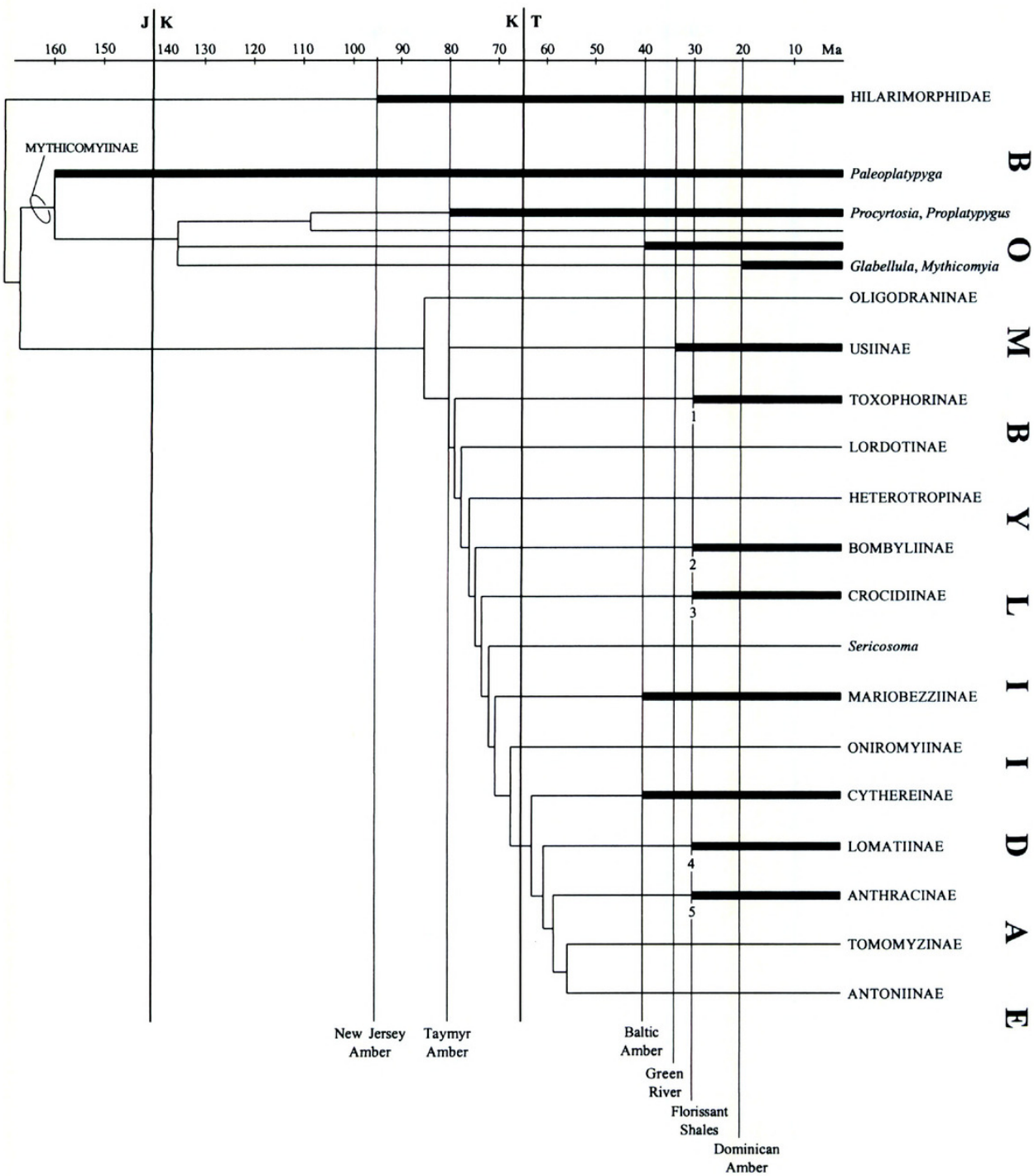
Figure 10.   Cladogram of bee fly (family Bombyliidae) subfamilies, from Yeates (1994), with geological ages and fossils overlaid. Lengths of branches grossly estimate ages of clades but will need refinement as fossils are more carefully re-studied and placed. Major radiation of "advanced," non-mythicomyiine bombyliids is hypothesized to be sudden and occurring in the late Cretaceous, in contrast to the hypothesis of Zaitzev (1991). Numbers on cladogram: 1, *Dolichomyia, Systropus*; 2, *Alepidophora, Bombylius*; 3, *Desmatomyia*; 4, *Alomatia*; 5, *Exoprosopa*.

idae, are unknown, but the other two mandibulate moth families (the Micropterigidae and Heterobathmiidae) feed on pollen and fern spores (Kristensen, 1997). With exception of the most primitive lepidopterans, the heteroneuran moths represent the largest clade of insects so wedded to vascular plants, and angiosperms in particular, as larval phytophages and adult anthophiles.

The Lepidoptera are highly modified, with 27 apomorphies proposed for the order (Kristensen, 1984). The most primitive lineages of lepidopterans, though, are only subtly different phenetically from the sister group, the order Trichoptera (caddisflies). The external apomorphies most easily observed are much more likely to be seen in amber fossils rather than compression fossils, and this

has complicated the interpretation of some Mesozoic fossils as discussed below. Critical lepidopteran apomorphies are: (1) vein $M_4$ lost (except in *Agathiphaga*); (2) presence of an epiphysis (a setulose spur) in the middle of the foretibia of most species; (3) scales on the fore *and* hind wing (where Trichoptera have scales, they are on the forewing only).

Excellent morphological work by Kristensen, Nielsen, and Davis has established a phylogenetic classification of basal Lepidoptera better than virtually any other major group of insects (Kristensen, 1984; Kristensen & Nielsen, 1979; Nielsen, 1987; Nielsen & Kristensen, 1996; Davis, 1986). DNA sequence data have been unable to revise or modify the morphologically based cladograms (Friedlander et al., 1996). The work of these morphologists has revealed and revised numerous apomorphies within the Lepidoptera, the most significant for present purposes being the proboscis, or tongue. This structure is an elongation of the paired galeae, which have also become fused. All but three of the most primitive families (Micropterygidae, Agathiphagidae, and Heterobathmiidae) possess a proboscis, and all but three of the most primitive glossatan families possess intrinsic musculature in the proboscis. Intrinsic musculature allows great elongation of the proboscis, by controlling the coiling and uncoiling of the structure and its probing movements. It must be stressed that the non-ditrysians represent only about 2% of all Lepidoptera, and that the relationships of ditrysian families as currently known are almost entirely polytomous (fig. 41.13 in Nielsen & Common, 1991). Understanding the basal, non-ditrysian relationships of the Lepidoptera, though, is essential to interpreting the Mesozoic lepidopteran fossils.

Table 1 summarizes the Mesozoic records of Lepidoptera. Figure 11 is an attempt to place these fossils into the currently recognized phylogeny of extant, basal Lepidoptera. Labandeira et al. (1994) also superimposed a phylogeny of lepidopterans on a geological time scale, but they placed all of the fossils into taxa where they were originally described. As Kristensen and Skalski (1997: 16) mentioned: "The bulk of the Mesozoic Lepidoptera so far described are believed to belong to the nonglossatan grade, but it is admittedly only in exceptional cases (*Parasabatinca*) that head structures are so well conserved that there is direct evidence for this assumption." Here, a critical view is also taken of the morphological evidence in the Mesozoic lepidopteran fossils (see Appendix); placement of the fossils seriously affects the hypothesized timing of lepidopteran radiations. The records of Me-

sozoic Lepidoptera were broken down into several categories, based on re-evaluation of the published evidence: Possible Lepidoptera; Lepidoptera incertae sedis; Lepidoptera Non-Glossata; Lepidoptera-Glossata; and Lepidoptera plausibly assigned to particular families/superfamilies. Justification for the placement of the fossils is discussed in detail in Appendix 1. This evaluation is hardly definitive since it is virtually essential to reexamine specimens of fossil insects, particularly compressions where venation and other critical but subtle details can be difficult to observe or appear ambiguous over the background texture of the matrix. Whalley (1986) and Skalski (1990) provided earlier, general reviews of Mesozoic Lepidoptera. I will not discuss Triassic records of putative lepidopterans, which were thoroughly discussed and mostly dismissed by Whalley (1986). However, my hypothesis differs from that of Whalley (1986) and Labandeira et al. (1994) in not postulating the existence of Lepidoptera in the Triassic, among other aspects.

Placement of the Mesozoic compression fossils is more conservative here than that in Labandeira et al. (1994), with our hypotheses on ages of various lineages differing dramatically. Labandeira et al. (1994) hypothesized the basal radiation of the order in the Lower Jurassic, the basal radiation of the Myoglossata in the mid Jurassic, and the basal radiation of the Ditrysia in the late Jurassic. This hypothesis critically depends on the placement of certain Jurassic and Lower Cretaceous fossils. One such fossil is a putative incurvarioid, which is a fragment of a wing in the Acra collection of Lebanese amber (Neocomian) and which is discussed in Appendix 1 as being Glossata incertae sedis.

The other old Mesozoic records concern mines, which have pivotal chronological effects on the dates hypothesized by Labandeira et al. (1994), so some discussion on the diagnostic characters of mines is germane. Mines are caused by a larva feeding in spaces it creates between the epidermal layers of a leaf. Leaf mines occur among the Hymenoptera (Pergidae, Argidae), Coleoptera (Chrysomelidae: Hispinae), Diptera (Agromyzidae, and a few others), and most commonly in primitive Lepidoptera. Among the 10 major families of "microlepidopteran" leaf miners, there is considerable variation in the morphology of the mine. Indeed, there are numerous features on which leaf mines can be recognized: geometry of mine (straight, serpentine, blotch, etc.), growth pattern of mine, pupation chambers, pattern of frass deposition, and taxon of host plant (although this is most useful for Cenozoic records and becomes problematic for mid- to Lower Cretaceous leaves, which are often

Table 1. Records of Mesozoic Lepidoptera. Placements are discussed in Appendix 1.

| Taxon/family | Age/locality | Reference |
|---|---|---|
| POSSIBLE LEPIDOPTERA | | |
| *Archaeolepis mane* | L. Lias/Dorset | Whalley, 1985 |
| *Auliepterix mirabilis* | U. Jurassic/Kazakhstan | Kozlov, 1989 |
| *Auliepterix minima* | UJ/LK/Mongolia | Kozlov, 1989 |
| *Daiopterix olgae* | LK/Chitinsk Oblast | Kozlov, 1989 |
| *Karataunia lapidaria* | U. Jurassic/Kazakhstan | Kozlov, 1989 |
| *Parasabatinca caldasae* | Aptian/Brazil | Martins-Neto & Vulcano, 1989 |
| *Undopterix carirensis* | Aptian/Brazil | Martins-Neto & Vulcano, 1989 |
| *Gracilepterix pulchra* | Aptian/Brazil | Martins-Neto & Vulcano, 1989 |
| LEPIDOPTERA, INCERTAE SEDIS | | |
| *Daiopterix rasnitsyni* | Aptian/Transbaykalia | Skalski, 1984 |
| *Eolepidopterix jurassica* | U. Jurassic | Rasnitsyn, 1983 |
| *Paleolepidopterix aurea* | U. Jurassic/Kazakhstan | Kozlov, 1989 |
| *Undopterix sukatshevae* | Aptian/Transbaykalia | Skalski, 1979a |
| *Micropteryx pervetus* | Cretaceous?/Myanmar | Cockerell, 1919 |
| MICROPTERYGIDAE | | |
| *Parasabatinca aftimacrai* | Neocomian/Lebanon | Whalley, 1977, 1978 |
| indet. (scales) | Cenomanian/France | Kühne et al., 1973 |
| GLOSSATA | | |
| *Protolepis cuprealata* | U. Jurassic/Kazakhstan | Kozlov, 1989 |
| undescribed (larva) | Neocomian/Lebanon | Grimaldi, 1996 |
| Incurvarioidea (scales) | Neocomian/Lebanon | Whalley, 1986 |
| Glossata indet. (adults) | Turonian/New Jersey | Grimaldi, unpubl. |
| indet. (larval head capsule) | Santonian/Canada | MacKay, 1970 |
| *Dyseriocrania perveta* | Cretaceous?/Myanmar | Cockerell, 1919 |
| ?Nepticulidae (mines) | U. Jurassic/Karatau | Skalski, 1979a |
| ?Nepticulidae (mines) | U. Jurassic/Karatau | Kozlov, 1989 |
| ?Nepticulidae (mine) | UJ/LK/Queensland | Rozefelds, 1988 |
| Nepticulidae (mines) | Cenomanian/Dakota Form. | Labandeira et al., 1994 |
| Gracillariidae (mines) | Cenomanian/Dakota Form. | Labandeira et al., 1994 |
| FAMILIES: GLOSSATA | | |
| Lophocoronidae? | Santonian/Siberia | Skalski, 1979b |
| Incurvariidae | Santonian/Siberia | Skalski, 1979b |

of uncertain relationships). As a result, some studies have attributed Miocene through Lower Eocene leaf mines as belonging to living genera of microlepidopterans (Opler, 1973, 1982), although one study of Paleocene leaves was more cautionary (Crane & Jarzembowski, 1980).

Mines of putative Nepticulidae, in the Monotrysia, are among the oldest records of all Lepidoptera (Kozlov, 1989; Labandeira et al., 1994; Rozefelds, 1988; Skalski, 1979a, b). If truly nepticulid, these mines would push the basal diversification of the Lepidoptera deep into the Jurassic. The leaves in which these mines occur are a non-angiosperm seed plant (Rozefelds, 1988: Upper Jurassic/Lower Cretaceous); Trochodendraceae (Kozlov, 1989: Turonian); and Platanaceae and Rosidae (Labandeira et al., 1994: Cenomanian) (Skalski, 1979b, did not indicate the kind of plant from which the Upper

Jurassic mines from Karatau, Kazakhastan, are recorded). Today, 70% of the known nepticulid mines are on Fagaceae and, to a lesser extent, Rosidae.

Based on hosts, the Cenomanian records would appear least problematic, but some of the characters used to make this identification are widespread among leafminers in general. These include gradual widening of the mine, culminating in a large blotch that obliterates some of the early mine, and a serpentine mine that has a central frass trail that is intermittently broken and culminates in "modestly expanded frass-free chamber"—a very generalized morphology of all sorts of mines, not just lepidopteran (Hering, 1951; Needham et al., 1928). That these Cenomanian mines were identified as the living genera *Stigmella* and *Ectoedemia*, in lieu of adult characters, is open to alternative interpretation. There are only about 600 species of extant
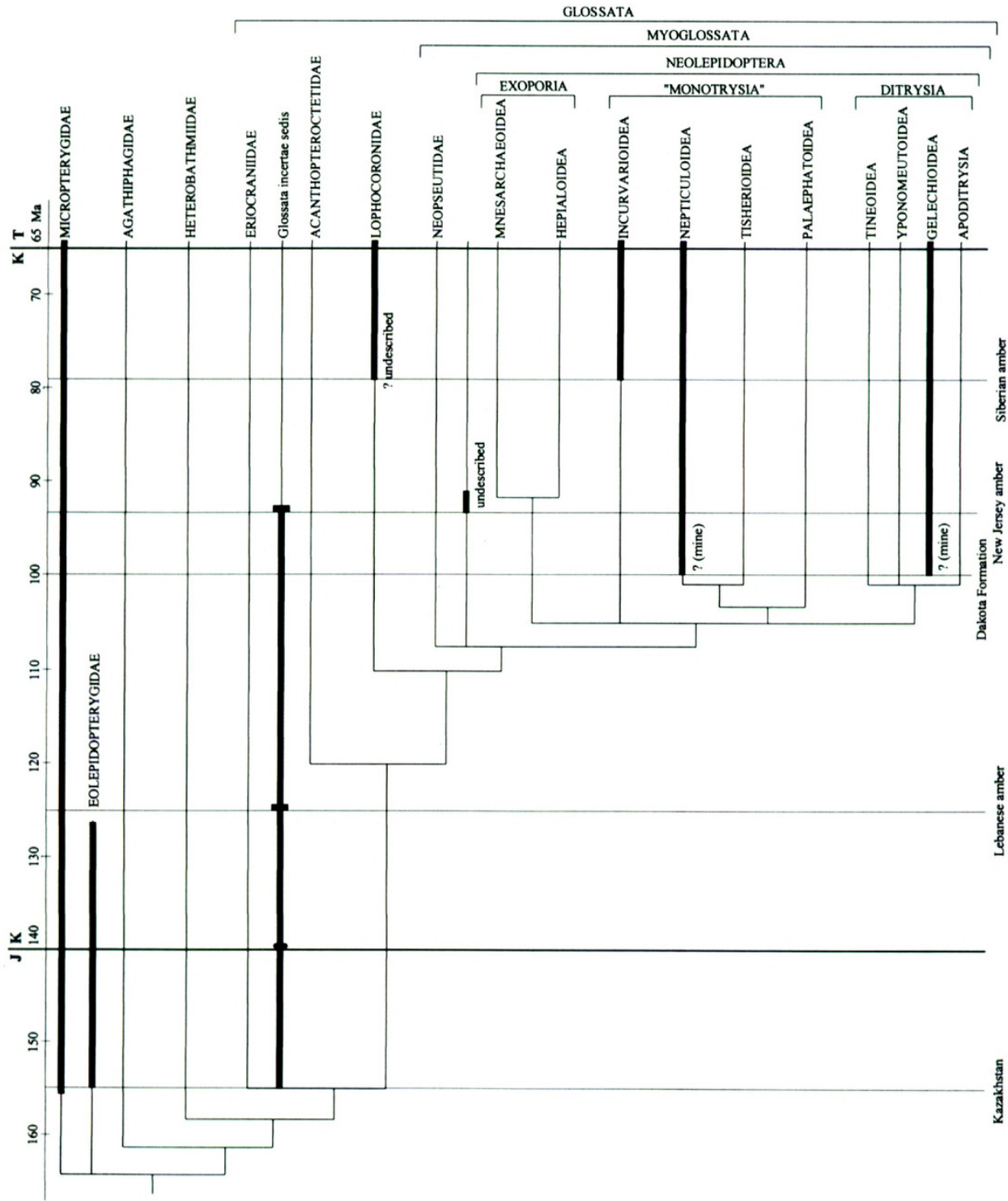
nepticulids described worldwide, and this is probably only a fraction of the entire fauna. Nepticulidae are generally poorly collected and studied, some genera in the family being the smallest lepidopterans. Judging from the proportions of described (16) and undescribed (estimated to be about 300) species of this family from Australia (Nielsen & Common, 1991), the actual world fauna is likely to be immense, particularly since the tropics have hardly been surveyed.

This point raises a serious concern about the identification of Mesozoic leaf mines in general. Powell (1980) estimated that 20–25% of the world's *described* species of microlepidopterans have hosts that are known (not just leafminers). These records are heavily biased toward the north temperate regions, and biased against tropical leafminers. Also, this does not include estimates of undescribed species. A reasonable approximation would be that 5% *of the mines of the total world species of lepidopteran leafminers is known.* For several presumed leafmining families, the Acanthopteroctectidae, Lophocoronidae, and Mnesarchaeoidae, the hosts and habits are entirely unknown. With that kind of sampling, what kind of confidence do we really have in the identification of leaf mines to family and especially to genus, particularly from the Mesozoic? In other words, how widespread or convergent are leaf-mine characters that are used to diagnose a certain genus, subfamily, or family? Modern leaf mines are never used to formally diagnose a genus or other taxon of microlepidopteran; adult morphology is considered the most reliable source of characters. In Figure 11 and Appendix 1 more conservative placements are made by assigning the Jurassic "nepticulid" mines as Lepidoptera-Glossata fossils incertae sedis; the Cenomanian mines from the Dakota Formation are included under the Nepticuloidea.

Also critical are mines from the Dakota Formation that have been assigned to living genera of the Gracillariidae, in the most derived subfamily Phyllocnistinae (Labandeira et al., 1994). The Gracillariidae are a large extant family with 1700 described species and 70 genera. The mines were found on leaves of Chloranthaceae and Lauraceae. If these are indeed gracillariid mines, they would be the oldest Ditrysia. Living species of gracillariids are most common on Fagaceae, then Fabaceae,

with Aceraceae, Betulaceae, Salicaceae, and Rosaceae also used. Magnoliidae are virtually unknown as hosts, although a genus from Chile mines leaves of *Drimys* (Winteraceae). The critical feature used to identify these mines as gracillariids is a central, zigzagging trail of frass. Although Kristensen and Skalski (1997) agreed with Labandeira et al. on the placement of the Dakota Formation leaf mines, the confidence in this identification depends on whether a zigzagging frass trail is eventually found to be entirely restricted to the gracillariids or not. The Gracillariidae are the largest family of leafminers and have the greatest host diversity, so the true diversity of mines in this group is very incompletely known.

Figure 11 hypothesizes the basal radiations of the Lepidoptera in the mid- to Upper Jurassic, the basal radiation of the Myoglossata in the mid-Cretaceous, and the basal radiation of the Ditrysia in the early Upper Cretaceous. Eventually, with the accrual of sufficient Mesozoic body fossils (especially from amber), we will be able to assess the evidence that the leaf mines from the Cenomanian Dakota Formation are indeed ditrysians.

It should be noted that Labandeira et al. (1994) postulated all basal radiations of Lepidoptera, even of basal Ditrysia, on Jurassic gymnosperms. This is contrary to evidence from the extant fauna (Powell, 1980). There are no radiations—significantly speciose, extant lineages—on pteridophytes or conifers, and angiosperms account for the vast majority of all phytophagous host records. In fact, no major living lineage subsists on a primitive subclass of angiosperms (e.g., Magnoliidae, Ranunculidae, and lower orders of Hamamelidae, with the exception of some Liliales in the monocots). Labandeira et al.'s (1994) hypothesis would assume the simultaneous shift of all basal lepidopteran lineages onto the more derived subclasses of angiosperms. Kristensen (1997) mentioned the "real possibility" that the ancestral heterobathmiid-glossatan moths were leafminers in the Fagaceae [sensu lato]. Primitive Fagaceae are documented from the Campanian of Georgia, U.S.A. (Herendeen et al., 1995), and Turonian of New Jersey (Nixon et al., in litt.). These are the oldest records thus far and are consistent with the diversification of "higher" Hamamelidae in the Turonian-Campanian (Herendeen et al., 1995). Since there is no evidence for gymnosperm-

Figure 11. Cladogram of basal families of the Lepidoptera, from Davis (1986), Kristensen (1984), Kristensen and Nielsen (1979), Nielsen (1987), and Nielsen and Kristensen (1996). Approximate positions of Mesozoic fossils are located on the cladogram, based on discussion provided in text and detailed discussion in Appendix.

based diversification in the Lepidoptera, a largely Cretaceous basal radiation of Lepidoptera is the most likely scenario. This timing is most consistent with a critical interpretation of the Mesozoic fossils.

## CONCLUSIONS

The earliest apparent adaptation to flower feeding is exhibited by several nemestrinid flies, from the Upper Jurassic of Karatau and China, which had proboscides several times the lengths of the heads. Other Jurassic flies reported to be long-tongued, like *Juracyrtus* (Acroceridae), have an elongate structure that is only questionably a proboscis; the report by Ren (1998b) that Jurassic tabanid-like and apiocerid-like flies were anthophilous is discussed above as not convincingly substantiated. It would be important that the fossil nemestrinids be critically re-studied to confirm the fine structure of the apparent long proboscis. Given that living nemestrinids today with long proboscides feed from flowers, it is difficult to say from what else the Jurassic forms could have been feeding. Ren (1998b) has forced the conclusion that these insects fed on flowers and used this as evidence to predict the existence of highly modified, entomophilous angiosperms in the Jurassic. However, it is possible that these ancient nemestrinids gleaned pollen from flower-like structures of Jurassic Bennettitales and gnetaleans. These non-angiospermous anthophytes originated in the Triassic and diversified until the late Cretaceous (Crane, 1996). The Bennettitales had flower-like reproductive structures composed of ovules/seeds and pollen-producing organs surrounded by perianth-like bracts (e.g., Pedersen et al., 1989). It is unclear how exposed the pollen would be for flies to harvest it. Judging from the living gnetaleans, reproductive structures of these plants certainly could have supported anthophilous insects. At least *Welwitschia* has exposed pollen and a decaying odor (Crane & Hult, 1988), which, in angiosperms, is known to be attractive to flies. Evenhuis (1994) even found mythicomyiine bombyliids feeding from flowers of *Welwitschia*. Thus, one need not infer the presence of angiosperms to account for the anthophilic specializations in Jurassic insects, like *Protonemestrius* (e.g., Ren, 1998b).

It is actually not until the late Early Cretaceous that there appear many of the first, definitive representatives of insects belonging to present-day anthophilic groups, and all these fossil forms are clearly generalized in morphology. Not until the Cenozoic do insects consistently appear with structures specialized for flower-feeding, most notably, the repeated appearance of elongate proboscides.

Despite the virtual absence of bee fossils in the Cretaceous, save for a single controversial specimen, the phylogenetic and stratigraphic constraints imposed by the much better record of the sphecid wasps indicate that bees could not have radiated prior to the mid Cretaceous. The historical record for vespid wasps is much better understood, based on thoroughly studied phylogenetic relationships and fossils for most of the subfamilies, save the one most germane to pollination, the Masarinae. But, again, constraints from phylogenetics and ages of other fossil vespids, as well as a compelling biogeographic pattern, indicate that the masarines did not arise and radiate until the post-Gondwanan Cretaceous, between the Aptian and Turonian.

Several families of Diptera were definitely in existence by the Upper Jurassic, notably the Acroceridae, Bombyliidae, and Nemestrinidae. But for the acrocerids and bombyliids, only primitive forms existed, and it is not until the Cenozoic that species with anthophilic adaptations are found. The families Apioceridae, Scenopinidae, and Stratiomyidae, paleontologically and biogeographically, appear not to have originated prior to the earliest Cretaceous, and to have their basal diversification in the Cretaceous. The flower flies, or Syrphidae, one of the most significant modern groups of anthophilic Diptera (with Bombyliidae) are clearly the youngest group. Although there is only one Cretaceous fossil syrphid, the occurrence of only primitive Cretaceous members of the closely related Platypezoidea indicates that syrphids probably did not diversify significantly until the Upper Cretaceous and especially Lower Cenozoic.

Phylogenetic relationships of the primitive Lepidoptera are exceptionally well known, which allows critical interpretation of fossilized adults (in rocks, amber, based just on scales, etc.), larvae, and even larval traces (e.g., leaf mines). Scrutiny of the evidence places the origins of the tongued Lepidoptera, the Glossata, possibly in the Upper Jurassic, with radiations of basal glossatan families in the Cretaceous. The Ditrysia, which comprise 98% of the current species diversity, probably did not radiate until the latest Cretaceous and certainly by the early Cenozoic.

All the available evidence is entirely consistent with the model proposed by Crepet (1996) based on a Cenomanian to Turonian diversification of entomophilous flowers. While many families of anthophilic insects existed prior to the Cenomanian, as Labandeira and Sepkoski (1993) concluded, there is little evidence for radiations of anthophilic

groups (e.g., clades of species) prior to the Cenomanian.

The only plausible scenario is that the original pollinators of the earliest angiosperms were generalized insects like beetles; primitive, short-tongued, and mandibulate moths; possibly sphecid wasps ancestral to bees; and various flies. The diversity of anthophilic Diptera indicates that this order was probably pivotal in early angiosperm pollination, including long- and short-tongued nemestrinids, short-tongued mythicomyiine bombyliids, proratine scenopinids, acrocerids, stratiomyids, empidids, as well as perhaps ceratopogonids and other nematocerans. The Masarinae, Syrphidae, Apidae, and Ditrysia almost certainly did not radiate until the major diversification of angiosperm families was intact. There is a consistent and rather perplexing pattern of very small flowers in the Cretaceous, perhaps due to preservational bias by charcoalification—the greatest source of angiosperm fossil flowers (e.g., Friis et al., 1994; Crane et al., 1994; Crepet & Nixon, 1994; and many other papers). If this pattern of diminutive Cretaceous flowers is real, it is also consistent with the early roles of flies and small, generalized aculeate wasps and lepidopterans as the earliest dedicated pollinators.

Such a scenario is based on various kinds of data, but as a whole the result is little different from the traditional view of Cretaceous co-radiations of insects and plants. It must be stressed that concomitant with the development of pollination symbioses is the development of various insect herbivore relationships, which spawned a dazzling array of angiosperm chemical defenses. The effects of pollination on breeding systems and genetic isolation in species of angiosperms is obvious, but the cladogenetic impact on plants of insect herbivory remains to be deciphered.

It may be significant to note that most of the pollinator groups that are discussed here have distributions concentrated in xeric regions, or areas of Mediterranean-type flora. As a result, many of these pollinators feed on flowers from shrubby and decumbent plants. This is particularly true of all the Diptera that were discussed, the vespids, and many of the bees (although there are significantly speciose groups of tropical bees, like the meliponines and euglossines). This pattern is consistent with Taylor and Hickey's (1992) hypothesis that the first angiosperms were decumbent herbaceous plants, and also with theories that the Cretaceous climate was globally drier than it is now (e.g., Wolfe & Upchurch, 1987; Spicer et al., 1993). Present-day distributions of greatest pollinator diversity may reflect Cretaceous "refugia."

Literature Cited

Alexander, B. A. 1992. An exploratory analysis of cladistic relationships within the superfamily Apoidea, with special reference to sphecid wasps (Hymenoptera). J. Hymenoptera Res. 1: 25–61.
——— & C. D. Michener. 1995. Phylogenetic studies of the families of short-tongued bees (Hymenoptera: Apoidea). Univ. Kansas Sci. Bull. 55: 377–424.
Armstrong, J. E. & A. K. Irvine. 1990. Functions of the staminodia in the beetle-pollinated flowers of Eupomatia laurina. Biotropica 22: 429–431.
Bänziger, H. 1982. Fruit-piercing moths (Lep., Noctuidae) in Thailand: A general survey and some new perspectives. Mitt. Schweiz. Entomol. Ges. 55: 213–240.
Barron, E. J. 1987. Cretaceous plate tectonic reconstructions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 59: 3–29.
Bernardi, N. 1973a. +Rhagionemestrius Ussatchov (Diptera: Brachycera), not a nemestrinid. Pap. Avulsos Zool., São Paulo 27: 111–113.
———. 1973b. The genera of the family Nemestrinidae (Diptera: Brachycera). Arch. Zool. Estado São Paulo 24: 211–318.
Bequaert, J. C. & F. M. Carpenter. 1936. The Nemestrinidae of the Miocene of Florissant, Colorado, and their relations to the recent fauna. J. Paleontol. 10: 395–409.
Brundin, L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. Kongl. Svenska Vetensk. Akad. Handl. Fjarde Sere. 11.
Caldas, E. B., R. G. Martins-Neto & F. P. Lima Filho. 1989. Afropollis sp. (pollen) no trato intestinal de Vespa (Hymenoptera: Apocrita: Xyelidae) no Cretaceo da Baccia do Araripe. Atas Simposio de Geologia do Nordeste, Fortalesa 13: 195.
Carpenter, F. M. 1992. Treatise on Invertebrate Paleontology (R), Arthropoda 4, Parts 3 and 4: Hexapoda. Geol. Soc. Amer., Univ. Kansas, Lawrence.
Carpenter, J. M. 1981. The phylogenetic relationships and natural classification of the Vespoidea (Hymenoptera). Syst. Entomol. 7: 11–38.
———. 1989. The phylogenetic system of the Gayellini (Hymenoptera: Vespidae; Masarinae). Psyche 95: 211–241.
———. 1990. Phylogenetic relationships and the origin of social behavior in the Vespidae. Pp. 56–67 in K. G. Ross & R. W. Matthews (editors), The Social Biology of Wasps. Cornell Univ. Press, New York.
———. 1993. Biogeographic patterns in the Vespidae (Hymenoptera): Two views of Africa and South America. Pp. 139–155 in P. Goldblatt (editor), Biological Relationships Between Africa and South America. Yale Univ. Press, New Haven.
———. 1997. Generic classification of the Australian pollen wasps (Hymenoptera: Vespidae; Masarinae). J. Kansas Entomol. Soc. (Suppl.) 69: 384–400.
——— & A. P. Rasnitsyn. 1990. Mesozoic Vespidae. Psyche 97: 1–20.
Cockerell, T. D. A. 1919. Two interesting insects in Burmese amber. The Entomologist 53: 169–170.
Colless, D. & D. K. McAlpine. 1991. Diptera. Pp. 717–786 in Insects of Australia, vol. 2. CSIRO, Canberra, and Cornell Univ. Press, Ithaca.
Crane, P. R. 1996. The fossil history of the Gnetales. Int. J. Pl. Sci. 157 (Suppl.): S50–S57.

——— & E. A. Jarzembowski. 1980. Insect leaf mines from the Palaeocene of southern England. J. Nat. Hist. 14: 629–636.

——— & C. D. Hult. 1988. *Welwitschia* the wonderful. Bull. Field Mus. Nat. Hist., Feb. 1988: 22–29.

——— & S. Lidgard. 1990. Angiosperm radiation and patterns of Cretaceous palynological diversity. Pp. 377–407 *in* P. D. Taylor & G. P. Larwood (editors), Major Evolutionary Radiations. Clarendon Press, Oxford.

———, E. M. Friis & K. Raunsgaard Pedersen. 1994. Palaeobotanical evidence on the early radiation of magnoliid angiosperms. Pl. Syst. Evol. (Suppl.) 8: 51–72.

———, ——— & ———. 1995. The origin and early diversification of angiosperms. Nature 374: 27–33.

Crepet, W. L. 1979. Insect pollination: A paleontological perspective. BioScience 29: 102–108.

———. 1985. Advanced (constant) insect pollination mechanisms: Pattern of evolution and implications vis-à-vis angiosperm diversity. Ann. Missouri Bot. Gard. 71: 607–630.

———. 1996. Timing in the evolution of derived floral characters: Upper Cretaceous (Turonian) taxa with tricolpate and tricolpate-derived pollen. Rev. Palaeobot. Palynol. [vol./pp.]

——— & E. M. Friis. 1987. The evolution of insect pollination in angiosperms. Pp. 181–201 *in* E. M. Friis, W. G. Chaloner & P. R.Crane (editors), The Origin of Angiosperms and Their Biological Consequences. Cambridge Univ. Press, Cambridge.

——— & K. C. Nixon. 1994. Flowers of Turonian Magnoliidae and their implications. Pl. Syst. Evol. (Suppl.) 8: 73–91.

Cumming, J. M., B. J. Sinclair & D. M. Wood. 1995. Homology and phylogenetic implications of male genitalia in Diptera-Eremoneura. Entomol. Scand. 26: 120–151.

Dafni, A., P. Bernhardt, A. Shmida, Y. Ivri, S. Greenbaum, C. O'Toole & L. Losita. 1990. Red bowl-shaped flowers: Convergence for beetle pollination in the Mediterranean Region. Israel J. Bot. 39: 81–92.

Daniels, T. H. 1983. *Carlowrightia*. *In*: Flora Neotropica 34: 1–116.

Darling, D. C. & M. J. Sharkey. 1990. Hymenoptera. Pp. 123–153 *in* D. Grimaldi (editor), Insects from the Santana Formation, Lower Cretaceous of Brazil. Bull. Amer. Mus. Nat. Hist. 195.

Davis, D. R. 1986. A new family of monotrysian moths from Austral South America (Lepidoptera: Palaephatidae), with a phylogenetic review of the *Monotrysia*. Smithsonian Contr. Zool. 434.

Dexter, J. S. 1913. Mosquitoes pollinating orchids. Science 37: 867.

Doyle, J. A. & M. J. Donoghue. 1986. Seed plant phylogeny and the origin of angiosperms: An experimental cladistic approach. Bot. Rev. 52: 321–431.

Durden, C. J. & H. Rose. 1978. Butterflies from the Middle Eocene: The earliest occurrence of fossil Papilionoidea (Lepidoptera). Texas Mem. Mus. Pearce-Sellards Ser. 29.

Endress, P. K. 1987a. The Chloranthaceae: Reproductive structures and phylogenetic position. Bot. Jahrb. Syst. 109: 153–226.

———. 1987b. The early evolution of the angiosperm flower. Trends Ecol. Evol. 2: 300–304.

———. 1990. Evolution of reproductive structures and functions in primitive angiosperms (Magnoliidae). Mem. New York Bot. Gard. 55: 5–34.

———. 1994. Diversity and Evolutionary Biology of Tropical Flowers. Cambridge Univ. Press, Cambridge and New York.

Engel, M. S. 1998a. Fossil honeybees and evolution in the genus *Apis* (Hymenoptera: Apidae). Apidologie 29: 265–281.

———. 1998b. A new species of the Baltic amber bee genus *Electrapis* (Hymenoptera: Apidae). J. Hymenoptera Res. 7: 94–101.

Evenhuis, N. L. 1983. Observations on territoriality of *Oligodranes mitis* Cresson (Diptera: Bombyliidae) on flowers of *Erigeron neomexicanus* (Asteraceae). Entomol. News 94: 25–28.

———. 1994. Catalogue of the Fossil Flies of the World (Insecta: Diptera). Backhuys, Leiden.

Finnamore, A. T. & M. E. Neary. 1978. Blueberry pollinators of Nova Scotia, with a checklist of the blueberry pollinators in eastern Canada and northeastern United States. Ann. Soc. Entomol. Québec 23: 168–181.

Fraser, N. C., D. A. Grimaldi, P. E. Olsen & B. Axsmith. 1996. A Triassic Lagerstatte from eastern North America. Nature 380: 615–619.

Friedlander, T. P., J. C. Regier, C. Mitter & D. L. Wagner. 1996. A nuclear gene for higher level phylogenetics: Phosphoenolpyruvate carboxykinase tracks Mesozoic-age divergences within Lepidoptera (Insecta). Molec. Biol. Evol. 13: 594–604.

Friis, E. M., K. Raunsgaard Pedersen & P. R. Crane. 1994. Angiosperm floral structures from the Early Cretaceous of Portugal. Pl. Syst. Evol. [Suppl.] 8: 31–49.

Gazit, S., I. Galon & H. Podoler. 1982. The role of nitidulid beetles in natural pollination of *Annona* in Israel. J. Amer. Soc. Hort. Sci. 107: 849–852.

Gess, S. K. 19 96. The Pollen Wasps. Ecology and Natural History of the Masarinae. Harvard Univ. Press, Cambridge.

Gomez Pallerolo, J. E. 1986. Nuevos insectos fósiles de las calizas litográficas del Cretácico Inferior del Montsec (Lérida). Bol. Geol. Mineral. 97: 27–46.

Gottsberger, G. 1988. The reproductive biology of primitive angiosperms. Taxon 37: 630–643.

Graenicher, S. 1910. The bee-flies (Bombyliidae) in their relations to flowers. Bull. Wisconsin Nat. Hist. Soc. 8: 91–101.

Grant, V. & K. Grant. 1965. Flower Pollination in the Phlox Family. Columbia Univ. Press, New York.

Grimaldi, D. 1988. Bee flies and bluets: *Bombylius* (Diptera: Bombyliidae) flower-constant on the distylous species, *Hedyotis caerulea* (Rubiaceae), and the manner of foraging. J. Nat. Hist. 22: 1–10.

———. 1995. A remarkable new species of *Ogcodes* (Diptera: Acroceridae) in Dominican amber. Amer. Mus. Novit. 3127: 1–8.

———. 1996. Amber: Window to the Past. Abrams/Amer. Mus. Nat. Hist., New York.

——— & J. Cumming. 1999. Brachyceran Diptera in Cretaceous ambers, and Mesozoic diversification of the Eremoneura. Bull. Amer. Mus. Nat. Hist. 239: 1–110.

———, C. W. Beck & J. J. Boon. 1989. Occurrence, chemical characteristics, and paleontology of the fossil resins from New Jersey. Amer. Mus. Novit. 2948: 1–28.

———, E. Bonwich, M. Delannoy & S. Doberstein. 1994. Electron microscopic studies of mummified tissues in amber fossils. Amer. Mus. Novit. 3097: 1–31.

———, D. Agosti & J. M. Carpenter. 1997. New and rediscovered primitive ants (Hymenoptera: Formicidae) in Cretaceous amber from New Jersey, and their phylogenetic relationships. Amer. Mus. Novit. 3208: 1–43.

Harper, J. L. & W. A. Wood. 1957. Biological flora of the British Isles. *Senecio jacobaea* L. J. Ecol. 45: 617–637.

Hawthorn, L. R., G. E. Bohart & E. H. Toole. 1956. Carrot seed yield and germination as affected by different levels of insect pollination. Proc. Amer. Soc. Hort. Sci. 67: 384–389.

Hennig, W. 1960. Die Dipteren-Fauna von Neuseeland als systematisches und tiergeographisches Problem. Beitr. Entomol. 10: 221–329 [English translation by P. Wygodzinsky in Pacific Inst. Monogr. 9: 1–81. 1966].

————. 1966a. Spinnenparasiten der Familie Acroceridae im baltischen Bernstein. Stuttgarter Beitr. Naturk. 165: 1–21.

————. 1966b. Bombyliidae im Kopal und im baltischen Bernstein (Diptera: Brachycera). Stuttgarter Beitr. Naturk. 166: 1–20.

————. 1968. Ein weiterer Vertreter der Familie Acroceridae im baltischen Bernstein (Diptera: Brachycera). Stuttgarter Beitr. Naturk. 185: 1–6.

————. 1969. Kritische Betrachtungen über die phylogenetische Bedeutung von Bernsteinfossilien: Die Gattungen *Proplatypygus* (Diptera, Bombyliidae) und *Palaeopsylla* (Siphonaptera). Mem. Soc. Entomol. Ital. 48: 57–67.

————. 1970. Insektenfossilien aus der unteren Kreide. II. Empididae (Diptera, Brachycera). Stuttgarter Beitr. Naturk. 214: 1–12.

————. 1971. Insektenfossilien aus der unteren Kreide. III. Empidiformia ("Microphorinae") aus der unteren Kreide und aus dem Baltischen Bernstein; ein vertreter der Cyclorrhaphaa aus der unteren Kreide. Stuttgarter Beitr. Naturk. 232: 1–28.

Herendeen, P. S., P. R. Crane & A. N. Drinnan. 1995. Fagaceous flowers, fruits, and cupules from the Campanian (Late Cretaceous) of central Georgia, U.S.A. Int. J. Pl. Sci. 156: 93–116.

Hering, E. M. 1951. Biology of the Leaf Miners. W. Junk, The Hague.

Hobby, B. M. & K. G. V. Smith. 1961. The bionomics of *Empis tessellata* F. (Dipt. Empididae). Entomol. Monthly Mag. 97: 2–10.

Hong, Y-C. 1983. Middle Jurassic Fossil Insects in North China, pp. 1–223. Geological Publishing House, Beijing.

Hull, F. M. 1945. A revisional study of the fossil Syrphidae. Bull. Mus. Comp. Zool. Harvard Univ. 95: 251–355.

————. 1949. The morphology and inter-relationship of the genera of syrphid flies, recent and fossil. Trans. Zool. Soc. London 26: 257–408.

————. 1973. Bee Flies of the World. The Genera of the Family Bombyliidae. Bull. U.S. Natl. Mus. 286.

Jarzembowski, E. A. 1991. The Weald Clay of the Weald: Report of 1988/89 field meetings. New insects from the Weald Clay of the Weald. Proc. Geol. Assoc. 102: 83–108.

Kato, M. & T. Inoue. 1994. Origin of insect pollination. Nature 368: 195.

Knoll, F. 1921. *Bombylius fuliginosus* und die Farbe der Blumen. (Insekten und Blumen I). Abh. K.K. Zool.-Bot. Ges. Wien 12: 17–119.

Kovalev, V. G. 1974. A new genus of the family Empididae (Diptera) and its phylogenetic relationships. Paleontol. J. 1974(2): 196–204.

————. 1978. A new fly genus (Empididae) from Late Cretaceous retinites of the Taymyr. Paleontol. J. 1978(3): 351–356.

Kozlov, M.V. 1989. New Upper Jurassic and Lower Cretaceous Lepidoptera (Papilionida). English translation in Paleontol. J. 23: 34–39 (1990).

Krassilov, V. A. & A. P. Rasnitsyn. 1982. A unique find: Pollen in the intestine of early Cretaceous sawflies. Paleontol. J. 16: 80–95.

Kristensen, N. P. 1984. Studies on the morphology and systematics of primitive Lepidoptera (Insecta). Steenstrupia 10: 141–191.

————. 1997. Early evolution of the Lepidoptera + Trichoptera lineage: Phylogeny and the ecological scenario. Pp. 253–271 *in* P. Grandcolas (editor), The Origin of Biodiversity in Insects: Phylogenetic Tests of Evolutionary Scenarios. Mém. Mus. Natl. Hist. Nat. 173.

———— & E. S. Nielsen. 1979. A new subfamily of micropterygid moths from South America. A contribution to the morphology and phylogeny of the Micropterygidae, with a generic catalogue of the family (Lepidoptera: Zeugloptera). Steenstrupia 5: 69–147.

———— & A. W. Skalski. 1997. Phylogeny and palaeontology. Pp. 7–25 *in* Handbuch der Zoologie: Lepidoptera (Insecta). W. Gruyter, Stuttgart.

Kühne, W. G., L. Kubig & T. Schlüter. 1973. Eine Micropterygide (Lepidoptera, Homoneura) aus mittelkretazischem Harz Westfrankreichs. Mitt. Deutsch. Entomol. Ges. 32: 61–65.

Labandeira, C. C. 1998. Early history of arthropod and vascular plant associations. Annual Rev. Earth Planet. Sci. 26: 329–377.

———— & J. J. Sepkoski. 1993. Insect diversity in the fossil record. Science 261: 265–396.

————, D. L. Dilcher, D. R. Davis & D. L. Wagner. 1994. Ninety-seven million years of angiosperm-insect association: Paleobiological insights into the meaning of co-evolution. Proc. Natl. Acad. Sci. 91: 12278–12282.

Lidgard, S. & P. R. Crane. 1988. Quantitative analyses of the early angiosperm radiation. Nature 331: 344–346.

Liu, N. & A. Nagatomi. 1995. The mouthpart structure of the Scenopinidae (Diptera). Jap. J. Entomol. 63: 181–202.

Lutz, H. 1990. Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt. Courier Forschungsinst. Senkenberg 124: 1–165.

————. 1993. *Eckfeldapis electrapoides* nov. gen. n. sp., eine "Honigbeine" aus dem Mittel-Eozän des "Eckfelder Maares" bei Manderscheid/Eifel, Deutschland (Hymenoptera: Apidae: Apinae). Mainzer Naturwiss. Archiv 31: 177–199.

Mackay, M. R. 1970. Lepidoptera in Cretaceous amber. Science 167: 379–380.

McAlpine, J. F. 1965. Observations on anthophilous Diptera at Lake Hazen, Ellesmere Island. Canad. Field-Naturalist 79: 247–252.

———— (editor). 1981. Manual of Nearctic Diptera, vol. 1. Agric. Canada Monogr. 27. Ottawa.

———— (editor). 1986. Manual of Nearctic Diptera, vol. 2. Agric. Canada Monogr. 28. Ottawa.

Martins-Neto, R. G. & M. A. Vulcano. 1989. Amphiesmenoptera (Trichoptera + Lepidoptera) na Formação Santana (Cretáceo Inferior) Bacia do Araripe, Nordeste do Brasil. I—Lepidoptera (Insecta). Anais Acad. Brasil. Ci. 61: 459–466.

Michener, C. D. 1990. Classification of the Apidae (Hymenoptera). Univ. Kansas Sci. Bull. 54: 75–164.

————. 1997. Genus-group names of bees and supple-

mental family-group names. Sci. Pap. Nat. Hist. Mus. Univ. Kansas 1: 1–81.

———— & D. Grimaldi. 1988a. A *Trigona* from Late Cretaceous amber of New Jersey (Hymenoptera: Apidae: Meliponinae). Amer. Mus. Novit. 2917: 1–10.

———— & ————. 1988b. The oldest fossil bee: apoid history, stasis, and the evolution of social behavior. Proc. Natl. Acad. Sci. 85: 6424–6426.

Moldenke, A. R. 1976. California pollination ecology and vegetation types. Phytologia 34: 305–361.

Nagatomi, A. & K. Soroida. 1985. The structure of the mouthparts of the orthorrhaphous Brachycera (Diptera), with special reference to blood-sucking. Beitr. Entomol., Berlin 35: 263–368.

————, N. Liu & K. Yanagida. 1994. Notes on the Proratinae (Diptera: Scenopinidae). S. Pacific Study 14: 137–222.

Nartshuk, E. P. 1996. A new fossil acrocerid fly from the Jurassic beds of Kazakhstan (Diptera: Acroceridae). Zoosyst. Rossica 4: 313–315.

Needham, J. G., S. W. Frost & B. H. Tothill. 1928. Leaf-Mining Insects. Williams & Wilkins, Baltimore.

Negrobov, O. P. 1978. Flies of the superfamily Empidoidea (Diptera) from Cretaceous retinite in northern Siberia. Paleontol. J. 1978(2): 221–228.

Nielsen, E. S. 1987. The recently discovered primitive (non-Ditrysia) family Palaephalidae (Lepidoptera) in Australia. Invert. Taxon. 1: 201–229.

———— & I. F. B. Common. 1991. Lepidoptera (moths and butterflies). Pp. 817–915 *in* CSIRO (editor), The Insects of Australia, 2nd ed. Cornell Univ. Press, Ithaca.

———— & N. P. Kristensen. 1996. The Australian moth family Lophocoronidae and the basal phylogeny of the Lepidoptera-Glossata. Invert. Taxon. 10: 1199–1302.

Norstog, K. 1987. Cycads and the origin of insect pollination. Amer. Sci. 75: 270–279.

Novokshonov, V. G. 1996. Some Mesozoic scorpionflies (Insecta: Panorpida = Mecoptea) of the families Mesopsychidae, Pseudopolycentropodidae, Bittacidae, and Permochoristidae. Paleontol. J. 31: 65–71.

Opler, P. A. 1973. Fossil lepidopterous leaf mines demonstrate the age of some insect-plant relationships. Science 179: 1321–1323.

————. 1982. Fossil leaf-mines of *Bucculatrix* (Lyonetiidae) on *Zelkova* (Ulmaceae) from Florissant, Colorado. J. Lepid. Soc. 36: 145–147.

Ornduff, R. 1997. Size classes, reproductive behavior, and insect associates of *Cycas media* (Cycadaceae) in Australia. Bot. Gaz. 152: 203–207.

Pedersen, K., P. R. Crane & E. M. Friis. 1989. The morphology and phylogenetic significance of *Vardekloeftia* Harris (Bennettitales). Rev. Palaeobot. Palynol. 60: 7–24.

Powell, J. A. 1980. Evolution of larval food preferences in microlepidoptera. Annual Rev. Entomol. 25: 133–159.

Proctor, M., P. Yeo & A. Lack. 1996. The Natural History of Pollination. Timber Press, Portland, Oregon.

Rasnitsyn, A. P. 1983. First find of a moth from the Jurassic. Dokl. Akad. Nauk SSSR 84: 53/ 269: 467–471.

———— & V. A. Krassilov. 1996a. First find of pollen grains in the gut of Permian insects. Paleontol. J. 30: 484–490.

————. 1996b. Pollen in the gut contents of fossil insects as evidence of coevolution. Paleontol. J. 30: 716–722.

———— & C. D. Michener. 1991. Miocene fossil bumble bee from the Soviet Far East with comments on the chronology and distribution of fossil bees (Hymenoptera: Apidae). Ann. Entomol. Soc. Amer. 84: 583–589.

Ren, D. 1998a. Late Jurassic Brachycera from northeastern China (Insecta: Diptera). Acta Zootax. Sin. 23: 65–81.

————. 1998b. Flower-associated Brachycera flies as fossil evidence for Jurassic angiosperm origins. Science 280: 85–87.

Rohdendorf, B. B. 1964. Historical Development of the Diptera. Trans. Paleontol. Inst. Akad. Nauk SSSR 100: 1–311.

Roig-Alsina, A. & C. D. Michener. 1993. No. 4. Studies of the phylogeny and classification of long-tongued bees (Hymenoptera: Apoidea). Univ. Kansas Sci. Bull. 55: 123–173.

Roubik, D. W. 1989. Ecology and Natural History of Tropical Bees. Cambridge Univ. Press, Cambridge and New York.

Rozefelds, A. C. 1988. Lepidoptera mines in *Pachypteris* leaves (Corystospermaceae: Pteridospermophyta) from the Upper Jurassic/Lower Cretaceous Battle Camp Formation, north Queensland. Proc. Roy. Soc. Queensland 99: 77–81.

Schlinger, E. I. 1960. A review of the genus *Eulonchus* Gerstaecker. Part I. The species of the *Smaragdinus* group (Diptera: Acroceridae). Ann. Entomol. Soc. Amer. 53: 416–422.

Schlüter, T. 1984. Kretazische Lebensspuren von solitären Hymenopteren und ihre Nomenklatur. Aufschluss 35: 423–430.

Scott-Elliot, G. F. 1896. Notes on flower-haunting Diptera. Trans. Entomol. Soc. London 1896: 117–128.

Shcherbakov, V., E. D. Lukashevich & V. A. Blagoderov. 1995. Triassic Diptera and initial radiation of the order. Dipterol. Res. 6: 75–115.

Sinclair, B. J. 1995. Generic revision of the Clinocerinae (Empididae), and description and phylogenetic relationships of the Trichopezinae, new status (Diptera: Empidoidea). Canad. Entomol. 127: 665–752.

Skalski, A. W. 1979a. A new member of the family Micropterygidae (Lepidoptera) fom the Lower Cretaceous of Transbaikalya. Paleontol. Zhurn. 1979(2): 90–97.

————. 1979b. Records of the oldest Lepidoptera. Nota Lepid. 2: 61–66.

————. 1984. A new Lower Cretaceous Lepidoptera (Homoneura). Bull. Polish Acad. Sci., Biol. 32: 389–392.

————. 1990. An annotated review of fossil records of Lower Lepidoptera. Bull. Sugadaira Montane Res. Cen. 11: 125–128.

Someren, G. R. C van. 1978. Observations on the behaviour and feeding of *Bombylius uniformis* Paramonov and *B. flammeus* Bowden (Dipt., Bombyliidae) in Kenya. Entomol. Monthly Mag. 114: 107–111.

Spicer, R. A., P. McArees & J. L. Chapman. 1993. Cretaceous phytogeography and climate signals. Philos. Trans., Ser. B 341: 277–286.

Straw, R. M. 1963. Bee fly pollination in *Penstemon ambiguus*. Ecology 44: 818–819.

Taylor, D. W. & L. J. Hickey. 1992. Phylogenetic evidence for the herbaceous origin of angiosperms. Pl. Syst. Evol. 180: 137–156.

Taylor, T. N & A. C. Scott. 1983. Interaction of plants and animals during the Carboniferous. BioScience 23: 488–493.

Thien, L. B. 1969a. Mosquito pollination of *Habenaria obstuata* (Orchidaceae). Amer. J. Bot. 56: 232–237.

———. 1969b. Mosquitoes can pollinate orchids. Morris Arbor. Bull. 20: 19–23.

———. 1974. Floral biology of *Magnolia*. Amer. J. Bot. 61: 1037–1045.

——— et al. 1983. The reproductive biology of a relict— *Illicium floridanum* Ellis. Amer. J. Bot. 70: 719–727.

——— et al. 1985. The pollination of *Zygogynum* (Winteraceae) by a moth, *Sabatinca*: An ancient association? Science 227: 540–542.

Thorp, R. W. 1979. Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. Ann. Missouri Bot. Gard. 66: 788–812.

Vockeroth, J. R. 1969. A revision of the genera of the Syrphini (Diptera: Syrphidae). Mem. Entomol. Soc. Canad. 62: 1–176.

——— & F. C. Thompson. 1986. Syrphidae. Pp. 713–743 in J. F. McAlpine (editor), Manual of Nearctic Diptera. Agric. Canada Monogr., Ottawa.

Wenzel, J. W. 1990. A social wasp's nest from the Cretaceous Period, Utah, USA, and its biogeographical significance. Psyche 97: 21–29.

Whalley, P. E. S. 1977. Lower Cretaceous Lepidoptera. Nature 266: 526.

———. 1978. New taxa of fossil and recent Micropterigidae with a discussion of their evolution and a comment on the evolution of Lepidoptera (Insecta). Ann. Transvaal Mus. 31: 65–81.

———. 1985. The systematics and paleogeography of the Lower Jurassic insects of Dorset, England. Bull. Br. Mus. (Nat. Hist.) Geol. Ser. 39: 107–189.

———. 1986. A review of the current fossil evidence of Lepidoptera in the Mesozoic. Biol. J. Linn. Soc. 28: 253–271.

Wilford, J. N. 1995. Which came first: bees or flowers? Find points to bees. New York Times, May 23: C1, C11.

Wolfe, J. A. & G. R. Upchurch. 1987. North American nonmarine climates and vegetation during the Late Cretaceous. Palaeogeogr. Palaeoclimatol. Palaeoecol. 61: 33–77.

Woodley, N. E. 1986. Parhadrestiinae, a new subfamily for Parhadrestia James and *Cretaceogaster* Teskey (Diptera: Stratiomyidae). Syst. Entomol. 11: 377–387.

Yeates, D. 1992. Towards a monophyletic Bombyliidae (Diptera): The removal of the Proratinae (Diptera: Scenopinidae). Amer. Mus. Novit. 3051: 1–30.

———. 1994. The cladistics and classification of the Bombyliidae (Diptera: Asiloidea). Bull. Amer. Mus. Nat. Hist. 219: 1–191.

——— & D. Grimaldi. 1993. A new *Metatrichia* window fly (Diptera: Scenopinidae) in Dominican amber, with a review of the systematics and biogeography of the genus. Amer. Mus. Novit. 3078: 1–8.

——— & M. E. Irwin. 1996. Apioceridae (Insecta: Diptera): Cladistic reappraisal and biogeography. Zool. J. Linn. Soc. 116: 247–301.

Young, A. M., M. Schaller & M. Strand. 1984. Floral nectaries and trichomes in relation to pollination in some species of *Theobromia* and *Herrania* (Sterculiaceae). Amer. J. Bot. 71: 466–480.

Zaitsev, V. F. 1987. New species of Cretaceous fossil bee flies and a review of paleontological data on the Bombyliidae (Diptera). Entomol. Rev. 66: 150–160.

———. 1991. The phylogeny and system of dipterous insects of the superfamily Bombylioidea (Diptera). Entomol. Rev. 71: 94–114.

Zeuner, F. E. & F. J. Manning. 1976. A monograph on fossil bees (Hymenoptera: Apoidea). Bull. Brit. Mus. (Nat. Hist.). Geol. 27: 149–268.

APPENDIX 1. Discussion of Mesozoic Lepidopteran Fossils. Most records listed in Table 1 are discussed below for diagnostic features. Qualifying remarks about the leaf mine fossils are presented in the main text of the paper; no remarks are made about the two taxa in amber from Myanmar, given the equivocal age of this amber (Grimaldi, 1996; Grimaldi et al., 1997).

POSSIBLE LEPIDOPTERA

*Archaeolepis mane* Whalley. A small (5 mm long) wing covered with scales from the Lower Lias of Britain (Whalley, 1985). Even though preservation of the wing is incomplete, such that no diagnostic venation shows, Whalley ruled out the possibility that the wing was not derived from other orders where scaled wings sporadically occur. He even concluded that the wing was a hind wing, which is very significant because those Trichoptera with scales have them on the forewings only. Unfortunately, Whalley's evidence that it is a hindwing is meager, based largely on the fact that the shape of the wing, according to Whalley, is most similar to the hind wings of Micropterygidae. All but the most distal tips of veins R and M are lost, and it is unclear how Whalley could have homologized these short segments in lieu of connections; yet he concluded that $M_4$ is lost—a lepidopteran apomorphy. He admitted to this uncertainty (Whalley, 1985: 180): "The exact number of median veins in *Archaeolepis* is difficult to determine but there are *probably* three branches..." (italics mine). Labandeira et al. (1994) assigned this fossil to the Zeugloptera (Micropterygidae) in their figure 2 cladogram. Kristensen and Skalski (1997) stated that this is the oldest fossil that can be referred to the Lepidoptera "with great certainty..." (p. 16) and "with reasonable certainty" (p. 17). The lack of critical features are only suggestive of its lepidopterous nature.

*Auliepterix mirabilis* Kozlov. Wing venation of this very small (3.4 mm wing length), Upper Jurassic fossil (Kimmeridgian/Oxfordian of Chayan, Kazakhastan) (Kozlov, 1989) is not completely preserved, but unusual for primitive Lepidoptera. The venation apomorphically possesses only $M_1$ and $M_2$, no $M_3$, and also a radial-cubital cell and reduced stem of the M vein. Kozlov attributed these features to miniaturization. A marginal fringe on the wing is mentioned, but wing scales are otherwise unknown. Neither mouthparts nor foreleg (e.g., ephysis) are preserved. Kozlov assigned the genus to the Micropterygidae on the basis of wing shape, shape of the pronotum, and lack of an ovipositor (a primitive feature)—all features of "gestalt."

*Auliepterix minima* Kozlov. From Ara-Khangayskiy, near Khotont Somon, Mongolia (Upper Jurassic/Lower Cretaceous) (Kozlov, 1989). This is an exceedingly small specimen (1.9 mm wing length), with a scaly wing covering. Only two wings are figured, and Kozlov did not mention if both were forewings (the right one certainly is, the left one appears too incomplete to be certain). Thus, it probably cannot be confirmed if the forewings and hindwings are scaled, nor if mouthparts and forelegs (e.g., ephysis) are preserved. Wing venation is incomplete, but Kozlov indicated that only three medial veins are present, which would be the best evidence for the fossil being lepidopteran. Labandeira et al. (1994) apparently assigned both *Auliepterix* species to the Micropterygidae on their cladogram (their fig. 2).

*Daiopterix olgae* Kozlov. This is another compression

fossil, from Shelopugino, Glushkovskaya series, Transbay-kal (Lower Cretaceous: exact age not provided) (Kozlov, 1989). Scales on the wing surface are either not present or not preserved, except for a fringe of "piliform" scales on the margin of the forewing, which was the evidence used to assign the fossil to the Lepidoptera by Kozlov. The mouthparts are apparently mandibulate; forelegs are not preserved; the wing venation is complete, including veins $M_1$–$M_3$, although Kozlov did not mention the absence of $M_4$ as evidence for its placement in the Lepidoptera. Beyond the absence of $M_4$ it would be useful to have other apomorphic features of the Lepidoptera preserved to confirm placement in the order.

*Karataunia lapidaria* Kozlov. A small specimen (fore-wing length 2.8 mm) from Chayan, Kazakhastan, Aulye locality, Upper Jurassic (Kozlov, 1989). Scales on the wings were not preserved or are absent. A foreleg or mouthparts are not preserved. At least the presence of a proboscis would need to be demonstrated before assigning this fossil (as Kozlov did) to possibly different families of Ditrysia, particularly on such tentative basis as incomplete wing venation.

*Parasabatinca caldasae, Undopterix carirensis, Gracilepterix pulchra.* From the Aptian limestone of Ceará, Brazil (Martins-Neto & Vulcano, 1989). None of the specimens have scales or mouthparts preserved. For most, the fragmentary remains of the legs are also insufficient to detect the presence of an epiphysis. In *Gracilipterix* and *U. carirensis* the wings apparently have vein $M_4$ lost, which would appear to be the only preserved evidence for placing them in the Lepidoptera. Labandeira et al. (1994) apparently put *Parasabatinca caldasae* on the Microptery-gidae clade in their cladogram figure 2.

## DEFINITIVE LEPIDOPTERA

### LEPIDOPTERA INCERTAE SEDIS

*Daiopterix rasnitsyni* Skalski (1984). Based on an almost complete specimen from the Aptian/Albian of Russia. The specimen has traces of scales on the fore and hind wings, veins Sc and $R_1$ are forked, and vein $M_4$ is lacking—indicating that this beautiful specimen is a lepidopteran. Forelegs and mouthparts are not preserved, but long apodemes connecting with the ovipositor are preserved.

Nepticulidae? Leaf mines, from the Battle Camp Formation (Early Cretaceous/Late Jurassic) of northern Queensland (Rozefelds, 1988). According to Rozefelds, the mines are poorly preserved, and although a noted lepidopterist (I. F. B. Common) examined the material and agrees the structure of the mines is similar to nepticulids, diagnostic features of the frass and the exit hole were not preserved. Kristensen and Skalski (1997) indicated that an assignment of this trace fossil to the Heteroneura "cannot be easily accepted on the basis of present knowledge" (p. 16), with which I concur. Skalski (1979b) reported leaf mines from the Upper Jurassic of Karatau, which he also assigned to the Nepticulidae on the basis of shape. Structure of the mines are highly suggestive of Lepidoptera.

### LEPIDOPTERA NON-GLOSSATA

*Eolepidopterix jurassica* Rasnitsyn (Fig. 12b). Found in the Upper Jurassic of Karatau (Kimmeridgian), Kazakhastan (Rasnitsyn, 1983). The specimen is small, ca. 7 mm. long, with a wing span approximately 12 mm (wings are incomplete), but with a virtually complete body. Since the foretibia has an epiphysis, examined by Skalski (cited in Whalley, 1986, and Kristensen, pers. comm. to DG), the fore *and* hind wings are scaled, and a pair of small brush-like structures flank the oral region (similar to lepidopteran pilifers), this is almost certainly a lepidopteran. The specimen has no proboscis, indicating that it is very primitive; but the presence of an apparent ovipositor with long internal apodemes is compatible with but not necessarily indicative of the Agathiphagidae, as was concluded by Skalski (1990). Long internal apodemes are even found in the Trichoptera and may be an amphiesmenopteran ground-plan feature.

*Paleolepidopterix aurea* Kozlov (Fig. 12c). A compression fossil with wings 5.2 mm long, from Chayan District, Kazakhastan, Upper Jurassic (Kimmeridgian/Oxfordian) (Kozlov, 1989). Kozlov mentioned scaled fore wings, but not the hind wings. Legs are not preserved, so the presence of a foretibial epiphysis cannot be determined. The wing venation is barely preserved, but the apparent presence of a well-developed jugum with a cluster of setae indicate it is a lepidopteran. Apophyses, again, indicate just a basal amphiesmenopteran. Kozlov placed the fossil in the Eolepidopterigidae with *Eolepidopteryx* Rasnitsyn. If this is the case, it would belong in the Agathiphagidae, but most of the mouthparts are not preserved.

*Parasabatinca aftimacrai* Whalley. A nearly complete, and well-preserved specimen in Lebanese amber, with venation, details of mouthparts, and fine structure of the scales preserved. Mouthparts and scales indicate the specimen is unequivocally a micropterigid.

?Micropterigidae (scales) (Kühne et al., 1973). These are loose scales in Cenomanian amber from Bezonnais, France. The fine structure of the scales indicates the plesiomorphic nature of the ribs and lacunae, similar to micropterigids.

### LEPIDOPTERA GLOSSATA

*Protolepis cuprealata* Kozlov (1989) (Fig. 12d). From the Upper Jurassic (Oxfordian/Kimmeridgian) of Kazakhastan. This may be the oldest glossatan. The presence of a short, curled proboscis would place this fossil in the Lepidoptera. Unfortunately, the wing venation is totally obscured by overlapping wings, and the presence of thickly scaled wing surface on both pairs of wings cannot be confirmed. Also, an epiphysis on the foretibia appears to be lacking. Presence of these features would be valuable independent confirmation that the short curled structure is indeed the proboscis. At a forewing length of 4.6 mm, the resolution of such minute structures like a proboscis is difficult against the background texture of the matrix. Also, the uncurled proboscis in lower Glossata is usually concealed between the larger labial and maxillary palps (the latter often extended in front of the head). Incredibly, Kozlov placed this species in the Ditrysia, probably near the Tineoidea (on the basis of overall similarity), because of ". . . short secondary ovipositor with distinctly pronounced anal papillae" (p. 38 of English translation). The concern about resolution of the proboscis pertains to the putative anal papillae. It would seem imperative that this specimen be re-examined using an SEM, so that presence and structure of the proboscis (is it the maxillary palp?), anal papillae, and wing scales (e.g., advanced/primitive) could be assessed.

The anal papillae are a pair of usually soft, fleshy lobes flanking the ovipore at the apex of the abdomen. There
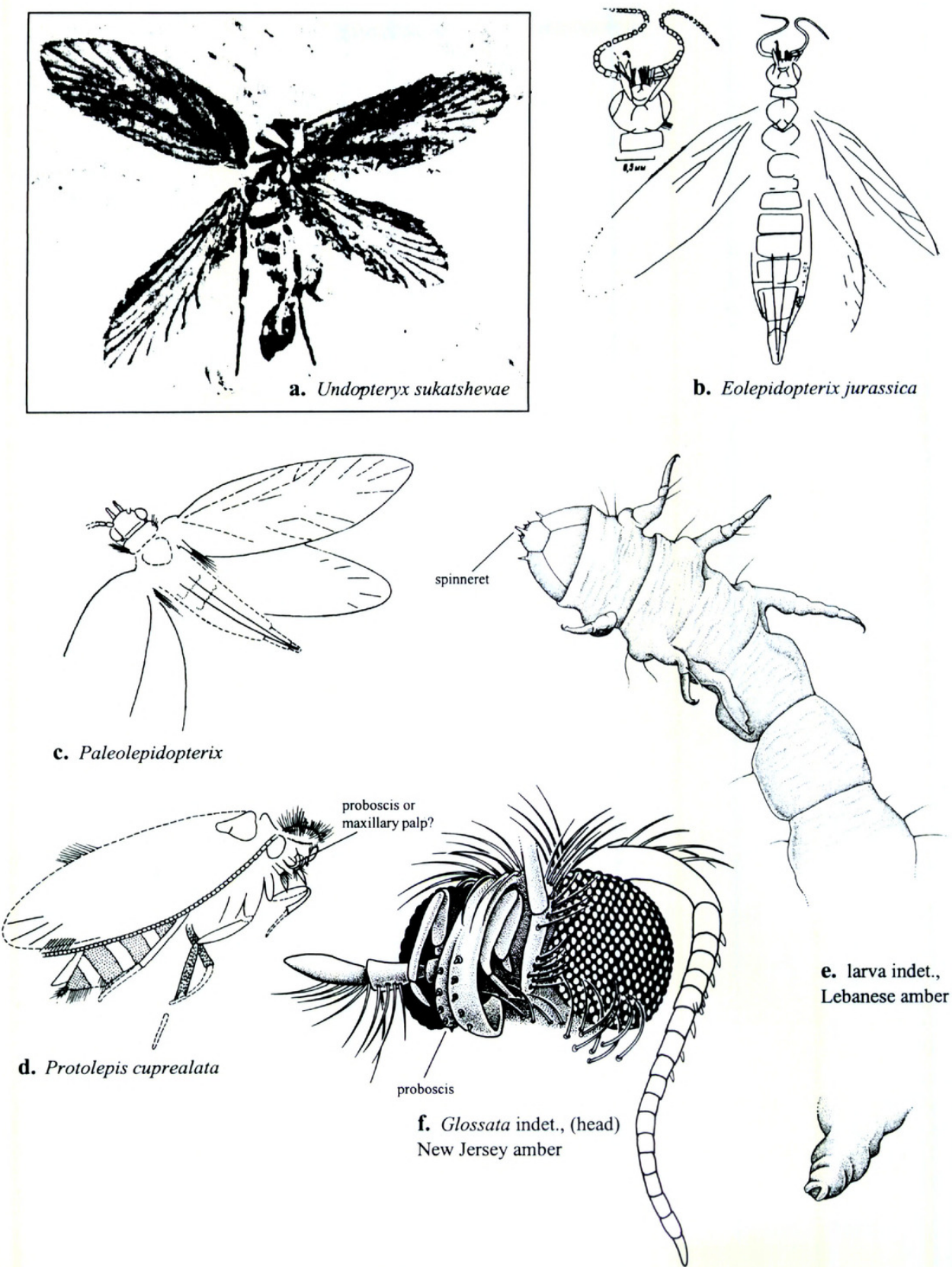
**a.** *Undopteryx sukatshevae*

**b.** *Eolepidopterix jurassica*

**c.** *Paleolepidopterix*

spinneret

**e.** larva indet.,
Lebanese amber

proboscis or
maxillary palp?

**d.** *Protolepis cuprealata*

proboscis

**f.** *Glossata* indet., (head)
New Jersey amber

Figure 12. Cretaceous Lepidoptera. —a. *Undopterix sukatshevae* (from Skalski, 1979a). —b. *Eolepidoteryx jurassica* (from Rasnitsyn, 1983). —c. *Paleolepidopterix aurea* (from Kozlov, 1989). —d. *Protolepis cuprealata* (from Kozlov, 1989). —e. Larva, in Lebanese amber (from Grimaldi, 1996). —f. Glossata indet. (head), in New Jersey amber (original).