

INSECT EVOLUTIONARY HISTORY FROM HANDLIRSCH TO HENNIG, AND BEYOND

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ABSTRACT—Significant investigators and aspects in the past century of insect paleontology are briefly reviewed. Despite the pervasive influence of the paleontologist Willi Hennig in systematic biology, the study of fossil insects remains more descriptive than most other paleontological areas. Hypotheses are reviewed on relationships and chronologies of early divergences in insects (Paleozoic, Lower Mesozoic), particularly living and extinct orders of the lower pterygotes and putative monophyly of the Paleoptera (Odonata + Ephemeroptera). The Dictyoptera (Mantodea, Isoptera, Blattaria) illustrate relationships and discrepancies between stratigraphic record and phylogenetic relationships. Future directions in the field are suggested.

INTRODUCTION

HEXAPODAN ARTHROPODS (including insects and the much smaller groups Collembola, Protura, and Diplura) have an ancient history whose known fossil record extends to approximately 400 Ma. Indeed, they are among the earliest, diverse terrestrial animals, and probably the first terrestrial animals to have formed intimate relationships with plants. These modest beginnings were the basis for the most diverse radiation known in the 4-billion-year history of life on earth, with approximately one million described species of insects and perhaps 5–10 million total (Wilson, 1992). While fossils of insects are considered to be sporadically concentrated, they are no more so than many other terrestrial taxa and even better than some. An extensive literature on fossil insects was produced during the 20th century, but interpretation of this vast, extinct diversity has been compromised by only occasional use of phylogenetic methods.

The founding of paleoentomology, at least in the 20th century, arguably begins with the publication of Anton Handlirsch's treatise, "Die fossilen Insekten und die Phylogenie der rezenten Formen," published in parts between 1906 and 1908. Known to Handlirsch and his contemporaries were a small number of Cenozoic and Mesozoic deposits containing fossil insects, among the most significant being the following: Florissant, Colorado (Eocene-Oligocene); Bavaria, Dobbertin, and Solnhofen, Germany (Jurassic); Oeningen, Switzerland (Miocene); Weald, England (Cretaceous); Baltic amber (Eocene); and the Carboniferous deposits of Commentry, France first studied by Brongniart (1878, 1893). Slightly later contemporaries of Handlirsch were prolific describers of hundreds of species, such as C. T. Brues (publishing 1906–1950) and F. M. Meunier (publ. 1893–1925) working extensively on Baltic amber; S. H. Scudder (publ. 1862–1900) on the Florissant fauna; and the prolific T. D. A. Cockerell (publ. 1899–1943), who published hundreds of papers on various deposits, including Baltic amber and the Florissant shales. R. J. Tillyard (publ. 1917–1937) was the first to seriously address Permian insects, from deposits of Australia and Elmo, Kansas. The work of A. V. Martynov (publ. 1923–1940) revealed extensive diversity of insects from the Jurassic and Permian of Eurasia, and he published several seminal papers on the evolution of wing venation in insects (Martynov, 1925) and evolution of lower pterygotes (Martynov, 1938). In the latter work he proposed such taxa as Paleoptera, Neoptera, and Polyneoptera. Moreover, he was the founder of a dynasty of Russian paleoentomologists.

The mid 20th century witnessed an explosion in studies of fossil insects, partly due to Martynov's disciples who formed the Arthropoda Laboratory in the Paleontological Institute of the Russian Academy of Sciences, Moscow ("PIN"). These scientists (and some of their most significant works) included O. M. Martynova (publ. 1939–1962), A. G. Sharov [publ. 1948–1977 (especially Sharov, 1966)], G. M. Zalesky (publ. 1931–1956), and

of particular importance, B. B. Rohdendorf (publ. 1938–1977). Rohdendorf, who became head of PIN, published important syntheses on fossil insects (Rohdendorf, 1962; Rohdendorf and Rasnitsyn, 1980), the fabulously diverse Jurassic deposit from Karatau, Kazakhstan (which is still being studied) and the fossil record of the Diptera (Rohdendorf, 1971). A. G. Ponomarenko (publ. 1961–1990), A. P. Rasnitsyn (publ. 1963–2000), and V. V. Zherikhin (publ. 1971–2000) are among the current authorities from PIN, specializing primarily on fossil Coleoptera and Hymenoptera. An enduring result of such an extensive paleontological pedigree at PIN is the largest collection of fossil insects in the world.

The most significant accomplishments among western paleoentomologists during this time were studies of the Permian and Carboniferous, which are very important periods in the origin and early diversification of insect orders. These included studies by J. W. Evans (publ. 1943–1972) and E. F. Riek (publ. 1950–1985) on the Permian of Australia and South Africa; P. Guthörl (1930–1965) and D. Laurentiaux (1949–1981) on the Paleozoic of Europe; and F. M. Carpenter (publ. 1928–1992) on the Carboniferous of France and the Carboniferous and Permian of the U.S.A. Carpenter, a professor at Harvard's Museum of Comparative Zoology, produced an important series of careful studies on the famous Carboniferous insects from Commentry, France; Mazon Creek, Illinois; and what are probably the largest, most diverse Permian deposits, from Elmo, Kansas and Midco, Oklahoma. He was conservative in his technique and interpretation of fossils. His criteria for recognition of insect orders were based minimally on preservation of wings (i.e., venation) as well as the mouthparts. As a result, he recognized nine Paleozoic orders of insects, versus the 55 that had been proposed over the years (many by Handlirsch and Tillyard). Some of these 55 orders Carpenter considered *incertae sedis*, but many were synonymized under the nine he recognized. While this created a more manageable taxonomy, it also resulted in several large, extensively paraphyletic "orders," some of them discussed below. Besides his original studies on Paleozoic insects, his most important contribution was the hexapod portion of the *Treatise on Invertebrate Paleontology* (Carpenter, 1992). It is a very thorough, illustrated catalogue covering the large, arcane literature on fossil insects up to 1984—an essential reference.

The architect of phylogenetic systematics, Willi Hennig, was an entomologist who was also active during this mid-century Renaissance of paleoentomology (publishing ca. 1932–1972). He studied living as well as fossil insects, primarily Diptera preserved in Cretaceous and Baltic ambers (e.g., Hennig, 1965). His 1969 book, "Die Stammesgeschichte der Insekten," was translated into English and annotated with 455 footnotes by 11 authorities (Hennig, 1981). The book was an attempt to synthesize what was

known at the time of the phylogenetic relationships and chronology of major groups of living and extinct insects. In part, it succeeded. Soon after his death, several seminal papers were published (Kristensen, 1975; Boudreaux, 1979), which considered more extensive morphological evidence for insect phylogeny. Although these works did not discuss fossils, they expanded on Hennig's phylogenetic approach towards understanding the phylogeny of insect orders, and they refined his hypotheses. Hennig (1981), Kristensen (1975, 1991, 1999), and Boudreaux (1979) have had major impact on present-day phylogenetic studies of extant insects. *Ironically, with a few exceptions* (e.g., Willmann, 1999; Engel, 2001), *Hennigian (phylogenetic) systematics has had little impact on paleoentomology*. In the study of vertebrates and plants, for example, higher-level relationships have been considered primarily by paleontologists (Crane, 1986, 1995; Gauthier, 1986; McKenna and Bell, 1997; Padian and Chiappe, 1998; Sereno, 1997; Simpson, 1945). Despite Hennig's influence and background, paleoentomology remains largely descriptive and taxonomic.

The collective past diversity of insects was probably at least an order of magnitude greater than it is now, so descriptions will continue to be absolutely necessary, particularly accurate ones and as new deposits are found. But without a synthetic context of phylogenetics, descriptions of numerous new taxa that are plugged into existing classifications simply magnify old, artificial schemes. These classifications then become used, for example, for inferring historical patterns of diversity (Labandeira and Sepkoski, 1993; Jarzembowski and Ross, 1996). The taxic approach unfortunately confounds effects of artificial classifications and can lead to erroneous conclusions of extinctions and other patterns of diversification (Smith, 1994).

This essay is not an appropriate space for a review of the insect fossil record, which has been summarized elsewhere (Carpenter and Burnham, 1985; Wootton, 1981; Kukalová-Peck, 1991; Grimaldi, in press). I prefer to briefly discuss what I consider to be one of the most significant problems in paleoentomology: interpretation of the Paleozoic orders. Wings with powered flight are one of the most profound modifications in insects, the other is complete metamorphosis. These two features are directly related to the greatest species diversity among insects.

Because of their influence, the views of Rohdendorf (1961) and Hennig (1981) provide important bases for discussion (Fig. 1). Rohdendorf's scheme contains paraphyletic elements ("Apterygota," "Palaeoptera"), although Hennig too maintained a close relationship between Ephemeroptera and Odonata (Paleoptera), but on the basis of derived features, not the symplesiomorphic condition of the resting wing positions. Significant differences between the two workers concern the position of the Embioptera [a basal neopteran group to Hennig, near the Plecoptera (stoneflies) to Rohdendorf], and of the Plecoptera (of uncertain affinities to Hennig). Rohdendorf and Hennig both hypothesized a relationship of the Dermaptera (earwigs) to the Dictyoptera (cockroaches, mantises, and termites). Despite the recited virtue of the cladistic method as being explicit (and therefore, testable or falsifiable), Hennig was surprisingly vague in the phylogenetic placement of Lower Mesozoic and Paleozoic insect fossils (Fig. 1). As a highly skilled morphologist, he was in a position to assess the evidence. Most interesting was that both Hennig and Rohdendorf hypothesized divergences that are much older than currently believed or indicated by present definitive evidence. For example:

1) Pterygota appeared in the Devonian (the Silurian even, according to Rohdendorf).

2) Basal Neoptera originated in the Devonian.

3) Embioptera (present-day web-spinners) originated in the Carboniferous. Kukalová-Peck (1991) figured and mentioned a Permian embiopteran, but the features are vague and its assignment not definitive (Engel and Grimaldi, 2001).

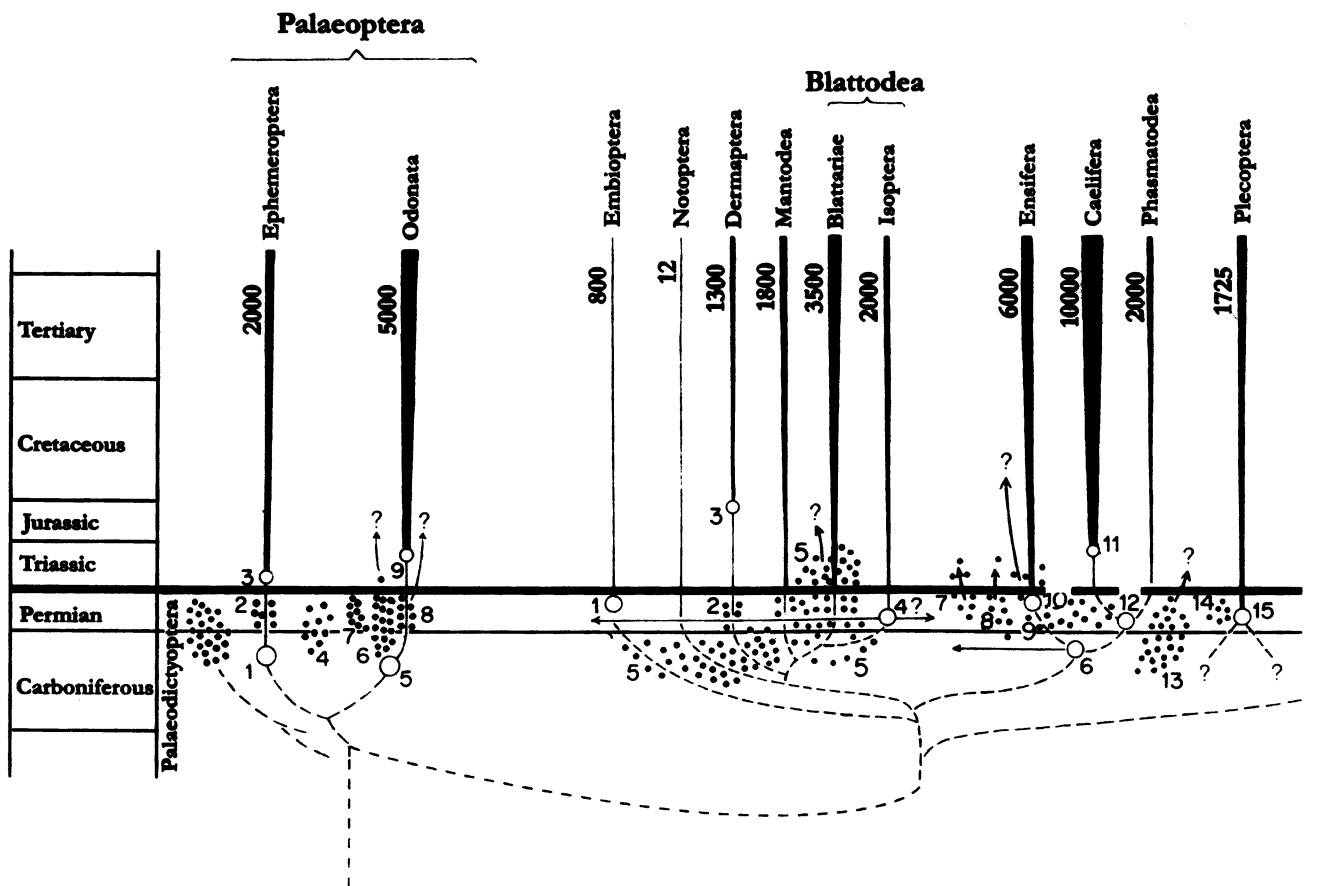
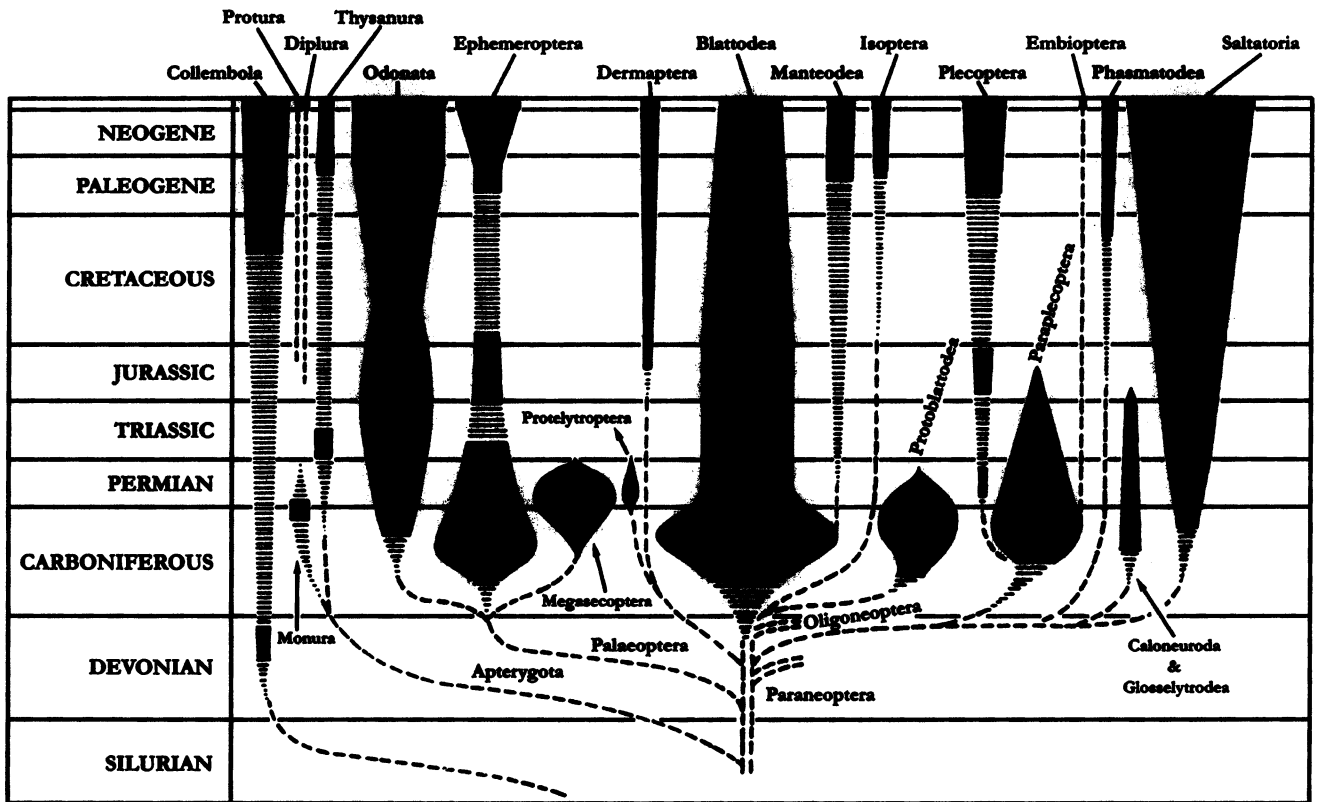
4) Dermaptera originated in the Carboniferous (their stem group in the Devonian even, according to Rohdendorf).

5) Isoptera and Mantodea originated in the Permian, or even the Carboniferous in Rohdendorf's view (see below for more discussion of the history of this group).

While the estimated divergence time in 1 is a possibility, those in 2–5 are highly improbable to completely implausible.

Kukalová-Peck (1991) provided the most recent synopsis of her extensive work on Paleozoic insects. Her phylogeny (1991, fig. 6.7) is classically paraphyletic, with one branch for most dichotomous branches being paraphyletic (e.g., Entognatha-Ectognatha, Monocondylia-Dicondylia, Apterygota-Pterygota, etc.). Her hypotheses on morphological groundplans have more significant implications for insect phylogeny. Kukalová-Peck (1987, 1991, 1992) described in some Carboniferous and Permian fossils intricate details of leg segmentation, coxal styli (small lobes at the base of the leg), and paired appendages of the male genitalia. Her elaborate hypotheses of groundplans are inconsistent with evidence from extant insects [e.g., the wing articulation groundplan of pterygote insects (Hörschemeyer, 1998)]. Moreover, they depend entirely on accurate interpretation of obscure fossilized features, such as of small basal wing veins, prothoracic structure, and pteralia (minute sclerites at the base of the wings, which are difficult to discern even in living species). Carpenter (1987) and Willmann (1999), for example, independently re-examined the Carboniferous "mayfly" *Lithoneura lameerei* Carpenter, which Kukalová-Peck had described as having long antennae. This is significant because all extant Ephemeroptera have short, aristate antennae, like modern Odonata—a feature often considered synapomorphic for these two orders. If Carboniferous ephemeropterans had long antennae, this would indicate convergence (homoplasy) of the antennal structure among extant paleopterans. Carpenter and Willmann independently recognized the "long antennae" of *Lithoneura lameerei* as plant fragments. Additionally, important details of the wing base reported by Kukalová-Peck (1985) in the holotype of *L. lameerei* were not observed in that specimen (Willmann, 1999). Likewise, Rasnitsyn (1999, p. 152) re-examined the holotype of *Dasyleptus lucasi* Brongniart, from the Upper Carboniferous of France, and was unable to observe "exceptional structures illustrated by Kukalová-Peck (1998, fig. 19.5c,d) (supernumerary ocelli, dorsal section of the maxillary tergum, multiple subdivision of the frontoclypeus and labrum)." Rasnitsyn concluded that instead of representing the separate order Monura (Sharov, 1966; Kukalová-Peck, 1987), *Dasyleptus* is a large juvenile form of the extant order Archaeognatha, with which I concur (Fig. 2). Before incorporating into current phylogenetic hypotheses putatively unique, fossilized features of insect ground plans, it is most appropriate to re-examine the original fossils.

Paleopterous orders.—Figure 2 is a preliminary attempt at a scheme of phylogenetic relationships among basal orders of hexapods. It is based on 75 characters, nine of which are highly unlikely to be preserved in fossils. This is not an exhaustive list, but employs characters of minimal homoplasy that could also be observed in fossils. Numerical cladistic analyses of total evidence could be applied in any situation, including this one, but I suspect that the effects of so many missing characters in the fossils (like sperm ultrastructure, DNA sequences, etc.) would result in a profoundly polytomous hypothesis for pterygote orders. The effects of missing characters can be circumvented in situations of exceptional preservation of arthropod fossils, such as three-dimensional, microscopic preservation by silification, phosphatization, or in amber (Grimaldi et al., 1995). In a study of the basal phylogeny of living and fossil ants (Grimaldi et al., 1997; Grimaldi and Agosti, 2000), cyclorrhaphan flies (Grimaldi and Cumming, 1999), and bees (Engel, 2001), trees were robust and nearly fully



resolved because the amber fossils possessed 90 percent or more of the total characters used. But, these are restricted situations since the oldest amber with arthropods is from the Lower Cretaceous. Most Paleozoic insects are known only by their wing venation since wings are the least degradable parts of insects, so phylogenetic schemes will rely on venational characters. Thirty percent of the characters used in Figure 2 pertain to wings or venation; another 50 percent of the characters are from other appendages (legs, mouthparts, antennae), where they have been preserved. Unfortunately, the reliability of characters in early fossils, like venation of Paleozoic pterygotes, can rarely be weighed against the plethora of characters found in extant species, because Paleozoic taxa are so divergent from extant groups and many structures have no modern homologs.

An interesting example of testing the “reliability” of preserved characters regards several features relating to the monophyly of the Paleoptera. According to some recent molecular studies (e.g., Carpenter and Wheeler, 1999; Wheeler et al., 2001), the Odonata are the sister group to the Neoptera. This implies that the loss of an imaginal molt in Odonata and Neoptera are homologous (which I espouse), and that the aristate antenna in Odonata and Ephemeroptera are convergent. Obviously the DNA and molting characters are highly unlikely to be preserved in fossils, but the modern evidence indicates that a putative synapomorphy of the Paleoptera, the arista (a fossilizable character), should be scrutinized. My quick survey of the antennal structure of extant odonates and mayflies indicates that the flagellum, though aristate in both groups, is structurally different (Fig. 3). In Ephemeroptera, the flagellum (arista) is virtually unsegmented; where it is segmented the segments are short and barely distinguishable annuli. In Odonata, the flagellum is divided into two to four distinct, long flagellomeres, with the basal one being stouter (sometimes considerably so), and a distinct articulation between all flagellomeres. Such differences strongly suggest convergent reduction in the antennal flagella of odonates and mayflies. Bechly (1998) concluded this convergence occurs, but on the basis of a long flagellum in the stem-group mayfly, †*Protoreisma*, and in †*Namurotypus*. †*Namurotypus* is one of many lineages within a Paleozoic grade of stem group Odonatoptera, of which Odonata (dragonflies and damselflies) is a recent crown group. Odonatoidea is another name used for the living Odonata and their extinct stem group relatives (Kukalová-Peck, 1991).

Other fossil evidence, though, supports Paleoptera monophyly, particularly of “Eupalaeoptera” (sensu Bechly [1998] = Odonatoptera + Ephemeroptera). He provides 10 features of the wings that indicate “strikingly similar” venation between stem-group mayflies (“ephemeroids”) like †*Protoreisma*, †*Bojophlebiidae*, and †*Syntonopteridae* (the latter placed in Paleodictyoptera by Carpenter [1992] but in the Ephemeroptera by most other authors), and stem-group Odonatoptera like †*Eugeropteridae* and †*Erasipteridae*. Indeed, the venation is compellingly similar, but to some extent this is expected among some of the earliest known, generalized pterygotes from the Carboniferous. Is it a sympleomorphic resemblance? Bechly (1998, elsewhere) indicates that the possession of a median terminal filament (character 33 in Fig. 2) in some stem-group odonatopterans indicates that they cannot be the sister group to the Neoptera (which lost this structure).

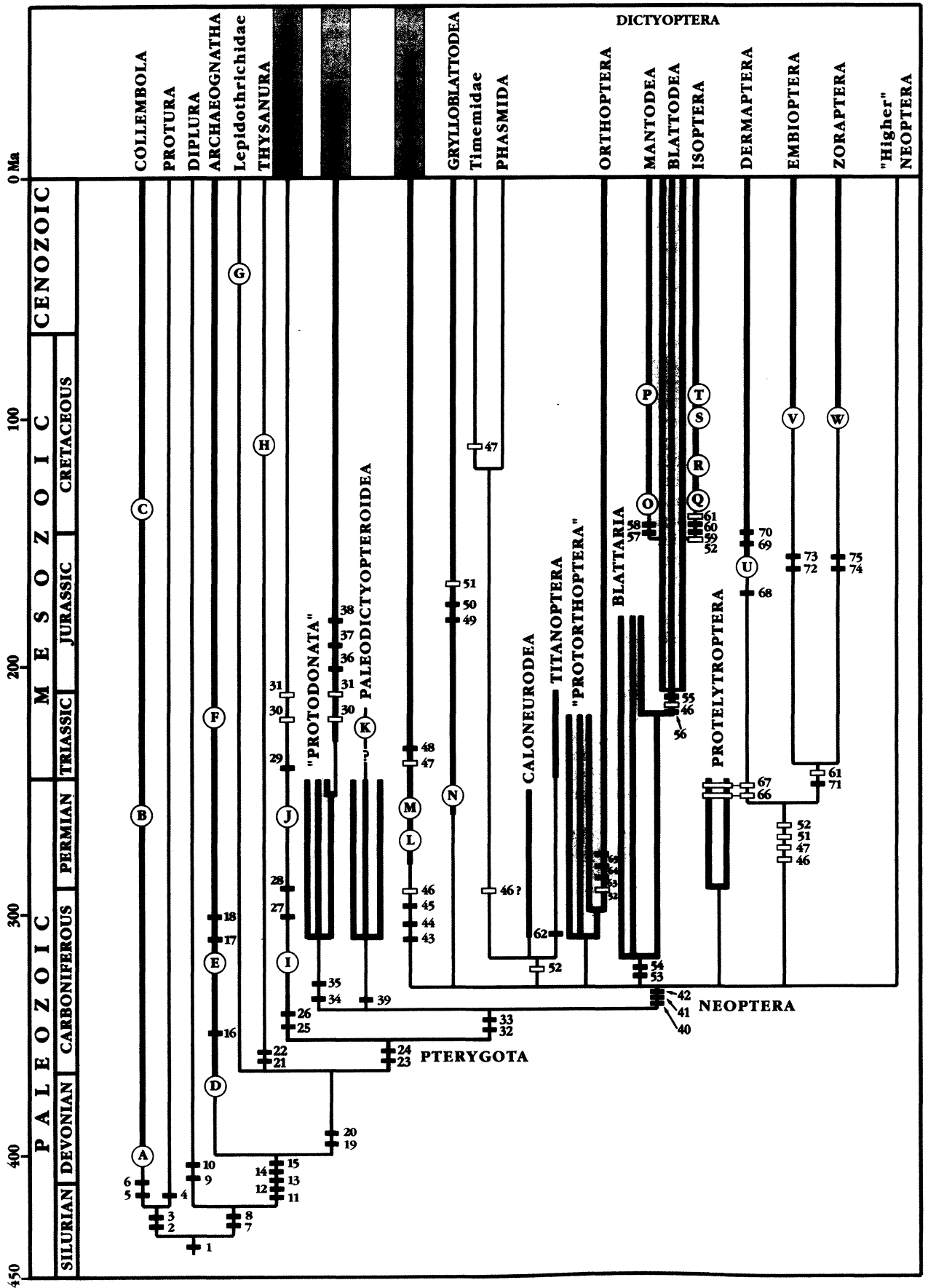
Indeed, the prevailing view among those concerned with Paleozoic insects is that Paleoptera is monophyletic (Bechly, 1998; Kukalová-Peck, 1991; Willmann, 1999).

But, can the loss of an imaginal molt in modern odonates and Neoptera (among other features) be simply attributed to convergence? I feel it cannot. Molting is a complex suite of features involving the interplay of secretions of juvenile hormone, prothoracicotropic hormone, ecdysone, bursicon, and susceptibility of target tissues (Sehnal et al., 1996). It would seem highly improbable for this kind of development to simply “pop up” twice. Although there are serious flaws in the coding of some morphological characters in the DNA-total evidence study of hexapod orders (Carpenter and Wheeler, 1999; Wheeler et al., 2001), results from that study indicate consistent grouping of Odonata + Neoptera. I believe the morphological and developmental evidence best supports this hypothesis of relationships, but admit the relationships are still ambiguous.

Along with stem group Ephemeroptera (ephemeroids) and Odonatoptera (odonatoids), the †Paleodictyopteroidea are certainly among the most intriguing Paleozoic insects. Some were huge (up to 55 cm wing span); some had colorful, patterned wings. Their monophyly is undisputed, given the five elongate, stiff mouthpart elements forming a distinctive beak, and an enlarged clypeus. Relationships among the orders of this group have been poorly investigated. Venation of †*Diaphanopteroidea*, †*Megasecoptera*, and †*Permothemistida* (originally in the Odonatoptera) is distinctive, so each of these are probably monophyletic. The order †Paleodictyoptera, though, is almost certainly paraphyletic with respect to the other orders in the superorder. Bechly (1998) indicates the loss of the terminal filament (character 33) in Paleodictyopteroidea is convergent with the Neoptera and some derived Odonatoptera (†*Tarsophlebiidae* + Odonata), although I have indicated this feature possibly had a single origin for Odonatoptera, †Paleodictyopteroidea, and Neoptera. It is commonly thought that the paleodictyopteroideans may be the most primitive pterygotes, which is intriguing given the striking paraprnotal lobes that often have venation on them. These have been interpreted as serially homologous with wings, and even may have served in providing lift during gliding flight, though basal articulations have never been found that would indicate they were movable. The †Paleodictyopteroidea are thought to have become extinct at the end of the Permian (Labandeira and Sepkoski, 1993), but a Triassic species, †*Thuringopteryx gimmi* has recently been assigned to the order †Paleodictyoptera, “most likely related to †*Spilapteridae*” (Bechly, 1997). Since this species is known only from wings, and there are no venational synapomorphies for the superorder or order, the reliability of the venational features that allow assignment to †*Spilapteridae* would be essential to know. Stratigraphy of the middle “Bundsandstein” of Thuringia, Germany is almost without question Triassic in age, so if the attribution of †*Thuringopteryx* from this deposit is correct, it would be a unique record of the †Paleodictyopteroidea persisting through the cataclysmic P/Tr extinction.

Based on the scheme in Figure 2 it is plausible that hexapods, but primitively wingless ones, appeared in the Silurian, even though there is present evidence only for Collembola and Archaeognatha in the Devonian. There are huge gaps in the early

FIGURE 1—Earlier hypotheses on relationships and chronology of major lineages of paleopterous and lower Neoptera insects. Above: “spindle” phylogeny from Rohdendorf (1962), which also includes the primitively wingless hexapods; below, from Hennig (1981) (both redrawn from original figures). Dashed lines indicate relationships, solid lines/black areas indicate known ages. Black dots in Hennig’s diagram indicate approximate positions of Paleozoic and early Mesozoic fossils (some of the most significant numbered 1–15); numbers near the names refer to approximate numbers of species described at that time.



fossil record, since several basal hexapod groups have not been found at all in the Paleozoic: Protura, Diplura, and Thysanura. It is possible that Pterygota occurred as early as the Upper Devonian, but, again, there is no evidence for this. Another major gap in the fossil record is from the Lower Carboniferous, when we would expect early, stem-group pterygotes, perhaps forms that would help resolve relationships among Odonoptera, Ephemeroptera, and †Paleodictyopteroidea. Despite the existence of some Neoptera in the Carboniferous (Blattaria, Orthoptera), it is highly unlikely that Dermaptera, Embioptera, Zoraptera, and “higher” orders in the Neoptera would be any older than Upper Permian. The Dictyoptera is actually a relatively recent group, far younger than Rohdendorf and Hennig imagined.

The Dictyoptera.—It is often surprising to biologists how insects in three ecologically disparate orders can be classified into the Dictyoptera: the predatory mantises, detritivorous roaches, and highly social, cellulose-consuming termites. But, morphological and molecular evidence indicates that monophyly of the Dictyoptera is well defined. Relationships among the three orders are controversial, with hypotheses having been proposed for each one of the four possible sets of relationships. Resolution of the problem is largely attributable to consideration of the taxonomic scale. Without doubt, Mantodea and Isoptera are monophyletic, but with a few exceptions (Klass, 1997) there has been widespread assumption that Blattaria (roaches) are also monophyletic (i.e., Thorne and Carpenter, 1992). I suggested (Grimaldi, 1997) on the basis of the fossil record that Blattaria must be paraphyletic, although living Blattaria could be a monophyletic group. Living roaches are derived from a paraphyletic assemblage of Paleozoic–Early Mesozoic Blattodea (“Blattoptera”) that possess, like modern roaches, a large discoid pronotum and tegminous forewings with a distinctive venation. The early blattodeans also possessed, symplesiomorphically, a long ovipositor. All living roaches have a highly vestigial, internal ovipositor, as in Isoptera (slightly less vestigial in Mantodea). Since the only Isoptera and Mantodea that occur in the Cretaceous are primitive (Thorne et al., 2000; Grimaldi, 1997), there is reliable evidence that these two orders have a much more recent history than the Blattaria.

A recent molecular study has confirmed paraphyly of the living roaches, or Blattaria (Lo et al., 2000). In this study, the sister group to termites is *Cryptocercus*, a small, relict Laurasian genus of colonial, wood-eating roaches, which had been suggested since 1934 to be a close relative of termites. In many other respects, though, *Cryptocercus* is highly modified, and the most primitive extinct and living termites are more generalized. Phylogenetic position of *Cryptocercus* itself is highly debated, the genus either representing a monogeneric family of several possible relationships (McKittrick, 1964; Kamhampati, 1995, 1996), or it is within the diverse family Polyphagidae (Grandcolas, 1994, 1996; Grandcolas and D’Haese, 2001). The hypotheses by Grandcolas and Kamhampati consistently place Isoptera as the sister group to the Blattaria, which is a result entirely biased by their use of Isoptera as an outgroup taxon for polarization of roach characters. It is likely that termites are derived from a lineage of polyphagid roaches, including *Cryptocercus*, but one which is now largely extinct. This is an example how the morphological, molecular,

paleontological, and even behavioral and microbiological, evidence finally revealed an interesting set of relationships. Termites are highly modified, social, myopic, wood-eating roaches. Are mantids, likewise, just predatory roaches? The fossil record suggests so, but the molecular analyses suggest that their relationships extend deeper, as sister group to all Blattaria + Isoptera.

FUTURE WORK

1. The case for using phylogenetic methodology in the study of insect fossils has been abundantly made. The techniques are not without problems, such as dealing with large amounts of missing characters in an analysis that incorporates living taxa. Nonetheless, phylogenetic analysis holds promise for resolving relationships of extensively paraphyletic assemblages of stem-group taxa, such as the “†Protorthoptera”/“Grylloblattida,” which is what I consider to be among the most important problem in paleoentomology. Kukulová-Peck and Brauckmann (1992) hypothesized that most “†Protorthoptera” are stem-group hemipteroids (Psocodea + Thysanoptera + Hemiptera), but this problem requires further attention. Full resolution of this assemblage into monophyletic groups is probably intractable, but portions can no doubt be resolved, as in stem-group ephemeropterans and odonopterans. Phylogenetic analysis of the Paleodictyopteroidea would likewise be very promising.

2. Improved morphological studies. The study of fossil insects will always be a morphological pursuit, since the preservation of DNA in fossils is implausible, and even putative DNA from amber is seriously questioned. The most fundamental step includes restudy of type and other important specimens described by Handlirsch, Rohdendorf, and others, whose descriptions we now know to be commonly inaccurate. Similarly, fossils reported as having dramatically unique structures for insects should be re-examined. It would be very useful to convene a dozen or so of the most accomplished paleoentomologists to examine together the most controversial specimens.

Some would argue that it is essential to weigh the morphological evidence of fossil and extant taxa against the larger arsenal of molecular characters. This has been applied, for example, to the putative synapomorphy of the paleopteran arista; but, then, study of the detailed structure of the arista itself strongly suggests convergence. There will always be many fossil features that cannot be incorporated into a “total evidence parsimony” analysis of DNA and morphology. Particularly for early fossils, they are just too different. Also, it is well known that a molecular tree just reflects the history of that gene or the several genes used in the study (Brower et al., 1996; Caterino et al., 2000). Any one morphological structure in insects is usually highly polygenic, but still no morphological systematist today would think of proposing a phylogeny solely on the basis of a wing vein or an antennal segment. A *balanced* use of morphological, molecular, and paleontological evidence is most appropriate.

3. Increased prospecting. There are gaping holes in our knowledge of hexapod history, such as:

- The Devonian, known thus far for terrestrial arthropods only from three significant localities.

FIGURE 2—Preliminary hypothesis of phylogenetic relationships among major and interesting groups of living and extinct hexapods and basal pterygote Insecta. Numbers refer to synapomorphies (see Table 1); empty boxes are homoplasious synapomorphies. Some significant fossils are denoted by circled letters (see Table 2), but many fossils are not listed for most groups. Thick lines indicate the approximate chronology of lineages. The number of lineages depicted for paraphyletic lineages (“Protodonata,” “Protorthoptera,” Blattaria [Blattoptera]) are arbitrary, and simply indicate multiple, unresolved lineages. The names of orders with freshwater aquatic larvae are shaded (a presumed ancestral habit). Relationships are based on Kristensen (1975, 1991, 1999), Willmann (1997, 1999), Grimaldi (1997, for Dictyoptera), Engel and Grimaldi (2000, Zoraptera and related orders), and others.

TABLE 1—Characters used in Phylogenetic Hypothesis of Basal Hexapod Orders (Fig. 2).

1. 3 pairs of walking legs.
2. Well developed entognathy (more pronounced than in Diplura).
3. Antennae reduced (number of flagellomeres <6), or lost
4. Antennae and eyes lost; forelegs used as sensory structures.
5. Ventral tube present.
6. Fusion of tibia and tarsi into a tibiotarsus.
7. Cerci present (pair of multiarticulate sensory appendages on segments XI or X).
8. Pair tarsal claws.
9. Loss of eyes, ocelli.
10. Gonopore preapical; between segments VIII and IX*.
11. Antennal flagellum multiarticulated.
12. Antennal flagellum without intrinsic musculature*.
13. No ventral articulation of coxae.
14. Ovipositor well developed, composed of gonapophyses on VIII+IX
15. Terminal filament on segment XI.
16. Single, long median caudal filament (in nymphs only?).
17. Large, dorsally contiguous compound eyes.
18. Jumping mechanism*
19. Coxal styli lost.
20. Dicondylic mandibles
21. Compound eyes reduced, ocelli lost
22. 3–4 tarsomeres (vs. 5).
23. Abdominal eversible vesicles lost.
24. Flight and associated apparatus: wings, pteralia, thoracic musculature.
25. Vein CuP simple.
26. Veins Rs, M, Cu forming “triad.”
27. Forewing with costal brace.
28. Hindwing with anal fan small.
29. Hind wing small, angulate (sometimes lost/highly reduced)
30. Galea and lacinia fused*.
31. Antennal flagellum reduced, aristate.
32. Loss of adult ecdysis.
33. Loss of terminal (median) abdominal filament (–15).
34. Vein MA fused with R basally, forming “incipient arculus,” MP + CuA absent.
35. Legs spinous, apparently predacious.
36. Forewing with a nodus.
37. Forewing with an arculus.
38. Male with accessory copulatory organs on sternites II–III.
39. Haustellate beak.
40. Wings folded via Ax₃ muscle attachments.*
41. Ovipositor present: 3 pairs of gonapophyses, sheathed by 3rd pair.
42. Vein R never with a forked base.
43. Nymphs with 3–4 tarsomeres.
44. Nymphs with pair of gills on each abdominal segment.
45. CuA branched, M3-branched.
46. Ovipositor highly reduced to lost.
47. Adults with 3 tarsomeres (vs. 4–5).
48. Segmented abdominal gills.
49. Apterous.
50. Eyes reduced or absent.
51. Ocelli lost.
52. Cerci reduced (1–2 segmented).
53. Large, discoid pronotum, usually concealing head dorsally (reduced in Isoptera, Mantodea, some Blattodea).
54. Forewing coriaceous, with distinct arched groove formed by CuP.
55. Eggs laid in ootheca (some modern roaches ovo- and viviparous).
56. Proventricular structure.*
57. Prothorax elongate.
58. Predatory, with raptorial forelegs.
59. Eusocial, with castes.
60. Cellulose digestion via symbiotic, intestinal microbes.*
61. Wings dehiscent.
62. Forewings with large, stridulatory “window” or drum (usually).
63. Forewings tegminous.
64. Hindlegs saltatorial.
65. Pronotum expanded ventrolaterally.
66. Shortened, coriaceous forewings with reduced venation.
67. Anal lobe of hind wing expanded into a large fan.
68. Forewings hemelytrous, devoid of venation.
69. Hind wing with anal lobe having radiating fan of anal branches.
70. Cerci modified into heavily sclerotized forceps (secondarily annulate in some ectoparasites).
71. Enlarged metafemur with depressor muscle.*
72. Spin webs with glands from an enlarged fore tarsus.
73. Wing veins developed as blood sinuses, allows deflation of wings in galleries.*
74. Venation highly reduced.
75. Tarsi 2-segmented.

* Characters that are highly unlikely to be preserved in fossils.

TABLE 2—Significant Fossils Indicated in Figure 2 (circled letters).

- A. *Rhyniella praecursor*, Devonian (Scotland).
- B. *Permobrya mirabilis*, Permian (South Africa).
- C. Various living families, Lower Cretaceous amber (Lebanon, elsewhere).
- D. Undescribed archaeognathan, Devonian (eastern Canada).
- E. *Monura (Dasyleptus)*, Carboniferous (Europe).
- F. *Triassomachilis*, Triassic (Europe).
- G. *Lepidotrix*, Eocene amber (Baltic).
- H. Unnamed Lepismatidae, Lower Cretaceous (Brazil).
- I. *Lithoneura*, Upper Carboniferous (Illinois).
- J. *Protoreisma*, Permian (Kansas, Oklahoma).
- K. *Thuringopteryx* (?Paleodictyopteroidea), Triassic (Germany)
- L. Lemmatophoridae, permian (USA, Europe).
- M. Paleoperlidae, Permian (Eurasia).
- N. Various Grylloblattida
- O. Various mantodeans, Lower Cretaceous (Eurasia)
- P. *Jersimantis* and undescribed mantodean, mid Cretaceous amber (New Jersey).
- Q. *Meiatermes*, *Valditermes*, Lower Cretaceous (Spain, England).
- R. Undescribed Hodotermitidae, Lower Cretaceous amber (Lebanon).
- S. *Cretatermes carpenteri*, Lower Cretaceous (Canada), and others.
- T. *Carinatermes*, mid Cretaceous amber (New Jersey).
- U. Protodiplatyidae, Jurassic (Kazakhstan).
- V. *Burmitembia*, undescribed forms, Cretaceous amber (Burma).
- W. Undescribed, Cretaceous amber (Burma).

- The Lower Carboniferous, which will surely reveal the earliest pterygotes and unique information on the origin of wings.
- The Lower Triassic. Most Triassic insects are known from the uppermost Triassic (Carnian), but to address how insects were affected by the P/Tr extinctions (if at all) requires better sampling in the earliest Mesozoic.
- The Jurassic, presently represented best only in Europe and central Asia, and very poorly known in the Western Hemisphere, Australia, and Africa.
- The Paleocene. While the Cretaceous and later parts of the Cenozoic have become perhaps the best sampled Periods in insect geological history, the Paleocene is virtually unknown. New deposits from this period are likely to be extremely important for

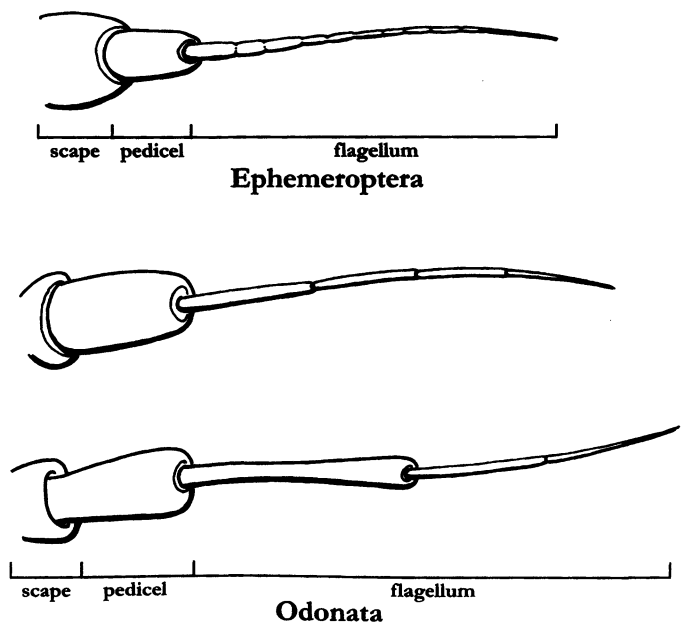


FIGURE 3—Basic structure of the antennae of living Ephemeroptera and Odonata (for the latter, several forms). Though the flagellum in both orders is highly modified into an arista, the modification is dissimilar and consistent with the hypothesis that the antennal arista is convergent.

understanding early diversification of large, recent radiations like higher termites; schizophoran flies; ditrysian Lepidoptera; and ants, bees, and other aculeate Hymenoptera (Grimaldi, 2000).

Prospecting involves not just the discovery of new outcrops and deposits, but discovery of productive new excavation methods. Fossils preserved with life-like fidelity have profound effects for systematics, such as how the cuticular remains of Devonian terrestrial arthropods affected our views of earliest terrestrialization (Shear, 1991). Paleobotany was revolutionized by the discovery of diverse, exquisitely preserved charcoalfied flowers from Cretaceous clays (Friis and Skarby, 1981, and numerous subsequent papers.). The paleoentomological equivalents to these charcoalfied flowers are the many diverse deposits of fossiliferous Cretaceous ambers (Alonso et al., 2000; Azar, 2000; Grimaldi, 2000; McAlpine and Martin, 1969), although it is unclear why productive amber deposits from the Cretaceous are virtually restricted to the Northern Hemisphere. It is impossible to predict what new kind of spectacular fossil insect preservation may be discovered.

In the past century there has been a quantum leap in the discoveries of new deposits and taxa of fossil insects, which one would only hope for in a field that seeks the history of the most diverse group of organisms. But it is the refinement of phylogenetic hypotheses of major insect lineages, in conjunction with brilliant new field discoveries, that will provide paleoentomology with an insight far exceeding that which was known to Handlirsch and even Hennig.

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