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A large, detailed fossil of an insect, possibly a dragonfly or damselfly, is embedded in a light-colored, textured rock surface. The insect's body is dark and segmented, with long, thin legs and large, veined wings. The rock surface is uneven, with various small pits and inclusions. The word "INSECTS" is printed in large, bold, black capital letters across the center of the image, partially overlapping the fossil.

INSECTS

Recent and Exciting Developments in Understanding Fossil Insects and their Terrestrial Relatives.

By Conrad C. Labandiera

During the past decade considerable advances have been made in the study of fossil insects and their broader environmental context. When compared to a review I prepared for this magazine 12 years ago, it is clear from worldwide output from all aspects of paleoentomology in all types of publications—primary reports, monographs, reviews, articles for the popular press and papers in related fields—that the proliferation of fossil insect data has been steady and sustained. That output has now increased to more than an article per day. Much of this productivity represents a shift from an almost entirely descriptive science, which still constitutes the bread-and-butter of the discipline, toward testing a variety of ecologically-, biomechanically- and behaviorally based hypotheses. This emphasis has reinvigorated the field and has brought it into greater contact with evolutionary biologists who also have interest in the insect fossil record.

New groups, earliest and latest occurrences, and reinterpretations

The discovery of a major group of terrestrial arthropods is not a common occurrence. For hexapods (insects plus their closest six-legged relatives), the last time this happened was the decade between 1904 and 1914 in which five orders of poorly known forms were described. Thus it comes as a surprise that a new order of insects, the Mantrophasmatodea, was erected by Klass and colleagues in 2002; more surprising is that this order had a long-known but previously unplaced representative from 45-million-year-old Baltic amber.

Other recently described marvels include a new order of arthropleurid millipeds from the Middle Devonian Gilboa site in New York State by Heather Wilson and William Shear in 2000, specimens of which are less than 5 mm long, a far cry from the approximately 2 m long species of *Arthropleura* from the more recent Paleozoic. At the other end of the terrestrial arthropod timescale was the discovery by Michael Engle of ten new genera of bees that belong to a derived group within the Family Apidae (orchid bees, bumble bees, stingless bees and honey bees), but possess tibial pollen baskets, in contrast to the 98 percent of all other bees that lack such structures. Almost all of these newly described bee taxa are from Middle Eocene Baltic amber and apparently did not survive the epoch. This proliferation of bee species represents a major expansion of the social habit, or “eusociality” during the early Cenozoic. As shown by Engle, however, it did not result in increased diversity among subsequent evolutionary lineages.

Another eusocial group, ants, has representatives of two extant subfamilies throughout the Late Cretaceous indicating that they initially radiated during the Albion of the Early Cretaceous. This pattern is similar to other groups of social

insects during the Early Cretaceous, including termites and vespid wasps.

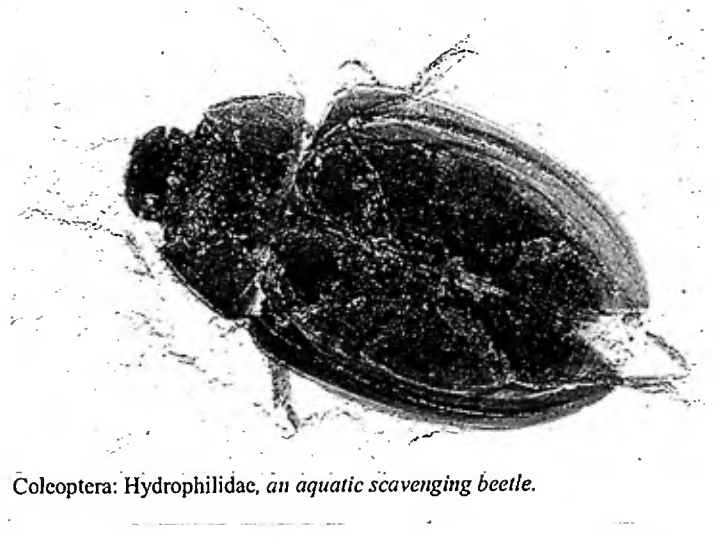
Regarding the earliest occurrence of any terrestrial arthropod group, nothing could be more interesting than the earliest known insect, a status which now has been extended to Rhyniognatha from the Early Devonian Rhynie Chert of Scotland. This fossil, consisting only of a pair of enigmatic mandibles and associated structures, was first figured about 80 years ago, and if the interpretation of its authors, Michael Engel and David Grimaldi, is correct, then these parts are assignable to winged insects, and thus imply indirectly the presence of winged insects very early in the terrestrial record, about 95 million years before the first actual fossils of wings at the Mississippian-Pennsylvanian boundary.

Later, during the late Paleozoic, other crucially important groups were originating, one of which currently constitutes about 90 % of all insects: the Holometabola (a.k.a. Endopterygota). This group is characterized by an egg->larva->pupa->adult sequence of postembryonic development. Although the earliest body-fossil record of the Holometabola is Early Permian, 28 amazingly well-preserved galls from the Late Pennsylvanian of the Illinois Basin have been assigned to the Holometabola. My colleague Tom Phillips and I described these earliest insect galls on the petioles of a primitive tree fern in 2002. The other major feeding guild on the internal tissues of plants, leaf mining, now has an earliest occurrence from the Late Triassic of South Africa, on the broad leaves of a conifer, thanks to work by Andrew Scott and colleagues last year. Other than assignment to an unknown holometabolous lineage, more data is needed regarding a more precise identity of the group that was responsible for these mines.

In addition to the earliest insect occurrences, latest occurrences sometimes have interesting consequences. For example the thrips group Lophioneuridae, known exclusively as compressions mostly from the Late Permian and Triassic, now is known from two amber deposits from the Late Cretaceous based on work by the late Vladimir Zherikhin. One of these, Burmese amber, preserves details of mouthpart and internal abdominal structure and a unique pattern of wing venation, providing a previously unavailable window into the detailed structure of a relict group whose heyday was considerably earlier. Similarly, last year André Nel and colleagues announced a new last known occurrence of the even more enigmatic family Chresmodidae (which is so strange we don't even know what order to place them in) from the Late Cretaceous of Lebanon. This find reveals unexpected details of a female egg-laying device, the ovipositor, that is elongate and serrated, evidently used for insertion of eggs into aquatic plants.



Hemiptera: Cicadelloidea (*leafhopper*). Note cibarial pump at top and associated beak along the midline of the sternal region.



Coloptera: Hydrophilidae, an aquatic scavenging beetle.

Revealing more natural history: appearances, locomotion and feeding

Of all the external attributes of modern insects, the one that is most elusive in fossils is color. Under exceptional conditions, color can be preserved in deposits such as the Lower Eocene oil shales at Messel in Germany, as demonstrated in 1994 by Sonja Wedmann and Thomas Hörnschmeyer. Until recently, the processes of fossilization (or taphonomy) by which color is preserved have been unclear. Andrew Parker and David McKenzie recently demonstrated that in a Messel beetle, original organic material on the wing covers contained layered materials of differing refractive indices and thicknesses, resulting in iridescence, typically brilliant blues and greens. Modeling the thicknesses of these finely laminated structures could yield original surface colors, even with mineralogical replacement.

Behavioral features of fossil insects are frequently preserved, as in the case of Dominican amber leaf beetles, of probable Early Miocene age. As shown by George Poinar, these structures include conspicuous eye spots on the hard wing covers or elytra, thought to be important in predator avoidance, and the presence of protective larval cases constructed of fecal pellets, important in defensive behavior.

Appearances can be deceiving, but the mechanisms proposed by evolutionary biologists to explain the origin of insect flight historically have been downright confusing. Periodically a hypothesis is presented that explains a unique collection of behavioral, biomechanical and ecological data from both modern and fossil insects. Such was the case of the 1994 surface skimming hypothesis for the origin of insect flight by James Marden and Melissa Kramer, inspired by observations of modern stonefly locomotion on pond surfaces. The authors described a type of nonflying aerodynamic locomotion transi-

tional between running on water surfaces and active, aerial flying, in which wing flapping is used for propulsion and limited lift while the insect's legs remain in contact with the water surface to minimize weight. Such a method of propulsion, in conjunction with small protowings, could have been a prelude to sustained aerial flight. Additionally, others have examined the wings of Pennsylvanian and Permian insects, and have discovered a variety of flight mechanisms. Robin Wootton and colleagues have reported the very early acquisition among the earliest dragonflies of a wing structure and associated biomechanical features that enabled them to be agile and efficient aerial predators. Wootton and Jarmila Kukalová-Peck have shown that there is an astounding array of wing shape, size, and flight styles among the four orders of Late Paleozoic paleodictyopteroid insects, an extinct clade externally similar to dragonflies but with distinctive heads that house elongate piercing-and-sucking mouthparts.

Like wings, mouthparts provide considerable ecological data for the life-habits of present and past insects. Two recent studies, by Art Borkent and Dong Ren, present intriguing implications for the relationships of insects with large vertebrates and seed plants, respectively. In a study of the piercing-and-slicing, bladelike mouthparts of biting midges (Family Ceratopogonidae) from Lower Cretaceous Lebanese amber, Borkent concluded that there was blood feeding on large, probably dinosaurian, vertebrates. This is based on the presence of finely serrate dentition on the mandibular blades, retorse teeth on the maxillary blades, and capitate sensilla on the third maxillary palp segment, indicating feeding on large vertebrate hosts. In similarly aged Lower Cretaceous Chinese deposits, Ren noted that three other groups of dipterans, especially tanglevein flies (Family Nemestrinidae), possess very long pro-

boscides. They are similar to extant descendants that feed in deep-throated angiosperm flowers with basal nectaries in a hovering manner similar to modern sphinx moths. Although Ren attributed these specialized, elongate mouthparts to evidence for early angiosperms, in my view they more reasonably are attributable to another advanced seed-plant group, particularly as angiosperm with presumably deep, tubular flowers did not evolve until much later.

Fossil gut contents can also tell us about ancient associations between insects and plants. Several recent studies by Valentin Krassilov and colleagues have documented instances in which both the consumer and consumed are known, in the Early Permian of Russia, and the Late Jurassic of Kazakhstan. These gut contents are frequently accompanied by a high degree of pollen host specificity. Amazingly, dispersed coprolites (fossil feces) that bear spores and vegetative tissues of some of the most primitive land plants known, are now documented from terrestrial ecosystems of the Late Silurian and Early Devonian. Diane Edwards and colleagues demonstrated in 1995 that these coprolites can be attributed to small, litter-dwelling arthropods.

Charting Diversification of Insects and their Host Plants

Patterns of insect feeding in the fossil record also can be investigated by determining the evolutionary family trees, or phylogenies, of insects and their host plants. This can be approached using fossils, modern forms, or both. An ideal group of insects for which this can be done is the overwhelmingly plant-feeding and very diverse Phytophaga, consisting of longhorn and leaf beetles as well as weevils. In a comprehensive study of this group in 1998, Brian Farrell examined the molecular phylogeny of major subgroups within the Phytophaga, concluding that five early lineages, some represented by Jurassic fossils, were associated with conifers and cycads; by contrast, lineages feeding on monocot and dicot angiosperms repeatedly originated during the later Cretaceous and Paleogene, and were associated with greater rates of diversification and an increased number of episodes of evolutionary radiation. When Phytophaga subgroups were examined in 2000 by Peter Wilf and colleagues, it was found that their highly distinctive leaf damage on fossil ginger hosts indicated an association by the latest Cretaceous. Documentation of this specialized and conservative relationship, together with knowledge of the phylogenies of leaf-beetle groups and their associated monocot plant hosts, indicate that the adaptive radiation of hispine beetles occurred contemporaneously with the diversification of monocots during the Late Cretaceous.

Future Directions

Given the direction of paleoentomological research during the past 12 years, I expect several trends in the near future. There will be continued discovery of new fossil insect, myriapod, and arachnid taxa and their placement within more precise phylogenies. This trend will occupy the majority of practitioners in the field, but it will also be supplemented by

new interests. There will be a shift to overt studies of paleoecological investigations of interspecific interactions, such as discussed above, but also community-based examinations such as food web structure and analyses of insect herbivore diversity from well-preserved fossil plant assemblages. Additionally, there will be a greater focus on extinction and origination in the insect fossil record, particularly as it applies to victims and survivors at key events. Another trend will be use of geochronological dates from earliest fossil insect occurrences for the calibration of divergence times in molecular phylogenies. And last, there will be an expansion of interest in the role of insects in taphonomy. During the next decade the study of fossil insects will become even more exciting as we continue to probe the history of the most speciose group of all time. **[P]**

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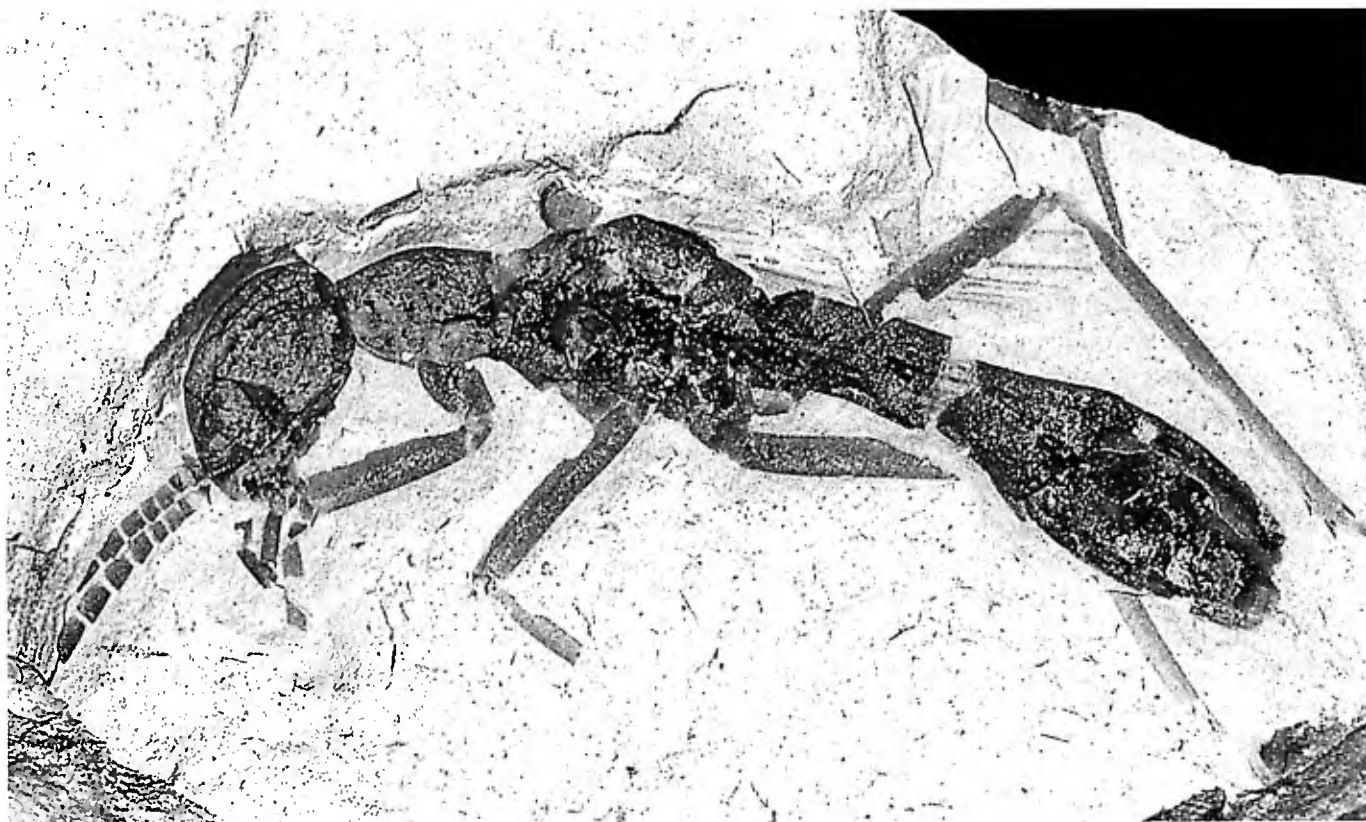
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Hymenoptera: Formicidae (ant)