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WHAT'S NEW WITH FOSSIL INSECTS?

by Conrad C. Labandeira

During the past fifteen years the study of fossil insects has experienced an intellectual renaissance. From what was a near exclusive (but important!) task of inventorying and describing new fossil forms, paleoentomologists currently are describing specimens as well as assessing derivative patterns that contribute to a holistic understanding of the paleoecological and macroevolutionary history of the most species-rich group of organisms ever to inhabit the planet.

Prominent examples of this rebirth in paleoentomology include: (1) in conjunction with phylogenetic exploration of major groups of extinct and extant insects, closely examining often generalized Paleozoic insects for features that can illuminate their systematic positions; (2) the use of body- and trace-fossil evidence to establish the earliest evidence for the existence of holometabolous (that is, completely metamorphosing) insects during the Paleozoic; (3) describing and assessing the importance of ecological associations between fossil insects and their plant or animal hosts; (4) documenting insect diversity patterns from the fossil record for determining the quality of the record, dynamics of origination versus extinction in generating insect diversity, and whether there is any coupling of insect diversity to particular major biotic events; and (5) using biomolecules to assess rates of evolution in insect lineages with representatives preserved in amber.

Fate of the Uniramia and the Protorthoptera

In 1972 Manton presented the term "Uniramia", to refer to the ancestrally primitive single limb condition that is found in hexapods (predominately insects), myriapods (centipedes, millipeds and their relatives) and onychophorans

(*Peripatus* and kin). However, there have been subsequent difficulties in circumscribing Manton's Uniramia. Recently, Kukalova-Peck has described several Paleozoic insects that bear exites at the intersegmental membranes of their walking limbs, concluding that Paleozoic insects were polyramous and that the term Uniramia, should be dropped from usage. Reasons for this abandonment not only include fundamental problems in the misattribution of a biological condition, but also that the

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component Onychophora of Manton's Uniramia is probably not even closely related to the Hexapoda, as Ballard et al. (1992) have demonstrated (see *American Paleontologist*, v.1, n.2). Consequently, if onychophorans are not "uniramians" then the residual group, Myriapoda+Hexapoda can be better referred to by the terms Atelocerata (Heymons 1901) or even Tracheata (Lankester 1904), which have priority. Thus there is strong evidence indicating that the taxa included in Manton's Uniramia constitute an unnatural, polyphyletic group.

In addition to the phasing out the Uniramia, there also is the ongoing disassembly of the Paleozoic order, "Protorthoptera." While many historically have acknowledged that the "Protorthoptera" was a wastebasket taxon, only recently have there been explicit recognition that many of the approximately 65 families of the order can be defined by unique characters, or possibly allocated to other orders. The most significant of these "protorthopteran" taxa are ancestral hemipteroid families that apparently have modifications of the head, mouthparts and wings, and which Rasnitsyn (1980) and Kukalova-Peck (1993) placed in a new order. In fact, a very few of these "protorthopterans" may even be primitive holometabolous insects (see below).

New Evidence for Late Carboniferous Holometabolous Insects

Although many entomologists have asserted that holometabolous insects must have existed during the Pennsylvanian, until recently there has been no direct evidence for such an early occurrence. This claim has been motivated primarily because of the occurrence of several distinct, modern-aspect holometabolous clades during the Early Permian, necessitating rapid evolution in the Late

Pennsylvanian. Recent evidence from two disparate sources may provide credence to this notion. They include: a figured but undescribed caterpillar-like larva in a Middle Pennsylvanian ironstone from Mazon Creek, Illinois (Shear and Kukalova-Peck 1990), and eight specimens of permineralized petiole galls from the Upper Pennsylvanian Calhoun Coal of Illinois and Indiana (Labandeira 1991). Each petiole gall occurs within the basal frond rhachis of a Psaronius tree fern and consists of a frass-containing axial lumen with surrounding parenchymatic reaction tissue. Thus there is evidence for plant-consuming holometabolous larvae during the later Pennsylvanian, with both endophagous (petiole-mining) and apparently ectophagous (external foliage feeding) trophic modes. This indicates that the great radiation of the most diverse clade of all time was well underway in both peat- and clastic-dominated swamp ecosystems of equatorial Euramerica. (The Holometabola currently consists of 88 percent of all insects, and includes beetles, flies, moths and butterflies, and wasps and bees).

Contributions of Plant/Insect Interactions to Ecosystem Evolution

While the exquisite permineralization of a plant/insect interaction on a petiole gall can suggest the ecology and the taxonomic relationship of its maker, other kinds of insect/plant interactions can reveal details of ecosystem structure that are frequently not available in terrestrial deposits. For example, evidence from Early and Middle Pennsylvanian coal-ball deposits indicate ecosystems dominated by arthropod detritivores. By contrast, latest Middle and Late Pennsylvanian coal-ball floras provide clear indications of a significant shift toward herbivory. This evidence originates from coprolite-bearing litter layers indicating the heightened consumption of frond pinnules, and other tissues such as sporangia and spores.

From these early forays into Paleozoic herbivory, a fast-forwarding of the geochronological tape to the mid-Cretaceous Dakota Formation, indicates that herbivore strategies were highly diversified, well-entrenched on early flowering plant hosts, and modern in character. Preliminary evidence from Dakota leaf-compressions indicates a variety of leaf miners, several types of leaf galls, (continued on following page)

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and external foliage feeding in the form of leaf-margin and leaf-center consumption, and even skeletonization. Between these two time slices, there is a 200 million year data gap that ranges from diffuse herbivorous patterns during the later Pennsylvanian, to the modern, highly stereotyped spectrum of interactions found on early flowering plants. However, several recent discoveries from this interval are noteworthy: lepidopteran leaf mines occur in a leaf from the Late Jurassic/Early Cretaceous of Australia (Rozeffelds 1988); galleried wood borings with reaction tissue produced by a beetle are found in wood of Middle Jurassic age from China (Zhiyan and Bole 1989); and a stem gall resulting from an unknown insect have been described in a conifer from the Early Triassic of France (Grauvogel-Stamm 1978). Additionally, Rasnitsyn and Kozlov (1991) have tentatively identified from the Late Jurassic to Early Cretaceous of Russia a mecopteran-like insect with a butterfly-like siphon for a proboscis, suggesting surface fluid-feeding preceding the earliest known angiosperms. These and other data indicate an underappreciated but existent record of plant/insect interactions during the preangiosperm Mesozoic. Filling the details of the ecological evolution of varied insect herbivory on the gymnosperm-dominated flora of this interval will be a fascinating undertaking.

Assessing the Macroevolutionary Pattern of Phanerozoic Insect Diversity

Although there are studies of the macroevolutionary diversity patterns for virtually every major group with a significant fossil record, insects have been conspicuously ignored. Recently, Labandeira and Sepkoski (1993) have analyzed family-level diversity patterns of insects from the fossil record and have arrived at several intriguing conclusions. These data supersede Carpenter's recent compendium (1992), which unfortunately was a decade out of date when it appeared. (In fact, significant advances in our knowledge of fossil insects postdates Carpenter's 1982 cutoff date. These advances include the backward geochronological extension of numerous families found in Cretaceous and Tertiary amber and compression Lagerstätten, and thus provide a significantly updated version of

many family durations).

These results indicate that, after the Early Carboniferous, insect families were more diverse than any other known terrestrial group, and this diversity was achieved by low rates of extinction rather than high rates of origination. Additionally, with the exception of the Permo-Triassic extinction, when the archaic orders of Paleozoic insects became extinct, there has been no demonstrable effect of extinction on insect diversity, including the effect of the terminal Cretaceous event. In terms of studies on coevolution, which historically derived much of their theoretical underpinning from associational studies of holometabolous insects and their angiosperm hosts, it is noteworthy that insect family-level diversity actually drops during the radiation of flowering plants of the mid Cretaceous. This conclusion is bolstered by a study of insect mouthparts (Labandeira 1990), which indicates that of the 30 mouthpart classes for which there is significant fossil evidence, all originate prior to the dominance of angiosperms in terrestrial ecosystems. These data indicate, therefore, that the angiosperm radiation had no demonstrable effect on increasing the ecological amplitude of insects, as indicated by familial taxonomic diversity or mouthpart morphological disparity.

Insect DNA from Amber and Phylogeny Reconstruction

The early claim by Brues (1951) that insect fossils in Baltic amber lack preserved soft tissue, and thus represent voids surrounded by husks of exoskeleton, has been solidly refuted by Poinar and Hess (1982) and Henwood (1992). These authors have documented ultrastructural preservation of organelles such as endoplasmic reticulum, nuclei and mitochondria in insect tissue from Baltic amber. However, the information content of amber fossils does not end with organelle-bearing tissue, but includes biomolecules such as DNA. Insect DNA extractions from a Paleogene Dominican amber termite were made by DeSalle et al. (1992), who characterized and compared the DNA sequence to a modern descendent of the same termite lineage. Similar extractions and characterizations for phylogenetic analysis are being conducted for a bee from the same deposit (Cano et al. 1992). These

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initial probes into fossil insect DNA provide tremendous potential for phylogeny reconstruction, establishing minimum species durations, and estimating rates of evolutionary change for Cretaceous and Tertiary ambers that span an interval of 135 million years. Nevertheless, the scenario envisaged by "Jurassic Park", is still, at least for now, science fiction.

New Vistas

All five of the developments mentioned above demand continued research, as well as cooperation among paleobiologists (particularly fossil insect workers and paleobotanists) and cooperation between paleobiologists and evolutionary biologists (especially molecular systematists). However, there are additional frontiers that have considerable potential for increasing our understanding of the insect fossil record.

There needs to be continuation of basic fossil descriptions and adding new discoveries of terrestrial arthropod faunas from pre-Pennsylvanian deposits. Successes include the Early Devonian Rhynie Chert in Scotland and the Middle Devonian Gilboa deposits in New York (Selden and Edwards 1989). Additional promising localities include Gaspé in Quebec (Labandeira et al. 1988) and East Kirkton in Scotland (Rolfe et al. 1991).

There undoubtedly is considerable promise in the use of Cretaceous and Tertiary insects as paleoclimate indicators. Modern insect species and bulk insect faunas possess relatively narrow climate tolerances, and their presence as fossils can provide singular or corroborative evidence with other fossil groups for important climatological parameters. Fossil termite distributions are a case in point. Establishing population-based criteria for assessing the range of variation in wing venation for modern insects should be an important goal for inferring the wing-based systematics of fossil insects. Studies on recent cockroaches indicate that structural variation in wing venation is broad (Schneider 1977, 1978). Such studies need to be extended to other modern groups for which there is an abundant, wing-dominated fossil record.

In summary, the study of fossil insects is currently one an exciting field of diverse research

activity. It no longer a field characterized only by the amassing of new insect descriptions.

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