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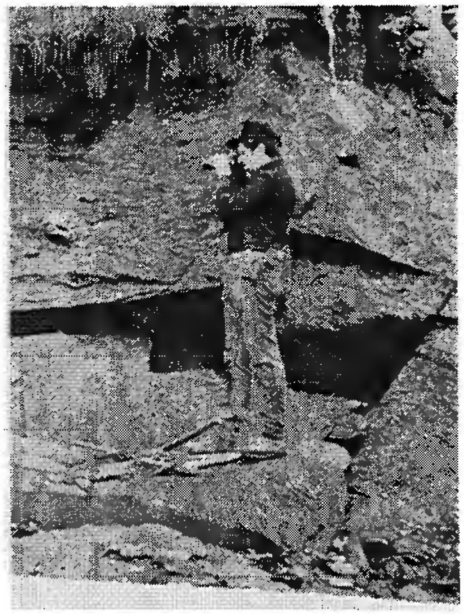
ONLINE

The Real Meaning of Insect Fossils

A few years ago, if asked, "What is the state of insect paleobiology?", one could only point to Anton Handlirsch's magnum, 1430-page, opus *Die Fossilien Insekten*, published during the first decade of this century, and more recently, to Willi Hennig's 1969 seminal *Die Stammegeschichte der Insekten*, translated and extensively annotated in 1981 to become *Insect Phylogeny*. While Hennig's work provided a stimulating contraposition between emerging cladistic methodology and a historical backdrop of evolutionary systematics and typological approaches, it explicitly discussed insect fossils and reinvigorated the factual base of insect systematics, spawning considerable research into the evolutionary relationships of past and present insect clades. Although Handlirsch's tome is still referenced today, it has been superseded by Frank Carpenter's recent *Hexapoda* volume of the *Treatise on Invertebrate Paleontology*. Consequently, it is no surprise that much of modern insect paleobiology is purely systematics. Nevertheless we should also ask the question, "What else does insect paleobiology have to offer?"

The answer is a lot, and much of it novel and innovative. As I see it, there



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are five major intellectual vistas that study of fossil insects currently has to offer. All of these unconventional paths have much to do with the origin and evolution of terrestrial ecosystems. Ultimately, they address ecosystem evolution and current issues of biodiversity.

The Earliest History of Insects and Their Relatives. Still obscured by an unyielding Devonian and Mississippian fossil record is the origin and early cladogenesis of insects and their close relatives. Currently, all that is known is a modicum of scraps and some semicomplete specimens from the Early and Middle Devonian. This earlier Devonian material is consistent with what has been previously predicted. Nevertheless, nothing is known from a 55 million-year period spanning the Late Devonian and all the Mississippian, immediately after which at least a dozen major insect clades appear worldwide and geologically instantaneously. Because of this depauperate record, the pre-Pennsylvanian terrestrial insect record resembles paleoanthropology: the numbers of (admittedly few) researchers is approaching the number of specimens available for study! However, there is opportunity in this poverty: even additional scraps from existing localities, or additional, insect-producing localities can provide significant evidence for substantively altering existing theories of early insect evolution, including the timing and sequence of trophic groups in the arthropod invasion of land.

New Understandings of Early Insect Structure. It is difficult to define a subgroup of a phylum as diverse and complex as the Arthropoda, in terms of a single, morphological descriptor. But Sidney Manton did just that in the 1970's by providing the term, Uniramia, to define a phylum of arthropodan-grade invertebrates possessing, for each body segment, a single lateral, multisegmented appendage that generally constitutes the walking leg. She included in this group myriapods (millipeds, centipeds and relatives), hexapods (insects and relatives) and onychophorans, and stated that this group has no clear relationship to any other arthropod group. Recent paleobiological and neobiological evidence indicates otherwise. Interesting work by Jarmila Kukalová-Peck has documented several Paleozoic insects that were polyramous for each body segment, and an intriguing cladistic analysis by Bill Ballard and colleagues has indicated that while onychophorans may be closely related to myriapods, both groups are phylogenetically distant from hexapods. Ballard's study also concluded that the arthropoda are monophyletic. Given these recent discoveries, the Uniramia of Manton is being disassembled, and ultimately the term should be dropped from usage.

A similar situation exists for a Paleozoic order of insects, the Protorthoptera. Jarmila Kukalová-Peck has recognized head and wing autapomorphies that define subclades that are now either being reallocated to existing orders, or are constituting a new order. It long has been recognized that the Protorthoptera was the most unnatural of higher insect taxa, and its disassembly into groups with definable characters is a major step in making sense of a clearly polyphyletic taxon.

Plant-Insect Interactions in Terrestrial Ecosystems. The third major impact that fossil insects have to offer is not so much as body fossils, but rather their impact upon plants. This effect, mostly evidenced directly as plant damage or indirectly as insect coprolites, is best demonstrated in permineralized deposits of some of the earliest known, well-preserved, and extensive terrestrial ecosystems—the Pennsylvanian coal swamp deposits of Euramerica. In these deposits there now is good evidence for an intriguing array of plant-insect interactions that previously were not suspected to occur in the Paleozoic. Anatomical evidence is now available for stem galls, probably by grub-like larvae, stylet tracks in plant tissues that indicate sap-sucking by insects with piercing-and-sucking beaks, and wholesale consumption of sporangia by unknown mandibulate insects. Evidence for leaf mining and spore dispersal syndromes is more equivocal. However it has become clear that insects and plants were interacting in misty Pennsylvanian coal swamps in ways that were hardly conceivable a decade ago.

During the Mesozoic, as appreciation for the fossil records of insects and plants improve, there is increasing realization that insect pollination syndromes were already coevolved with the earliest flowering plants during the lower Cretaceous. Moreover, recent investigations have established the role of insects in the pollination of cycads and gnetaleans, and there is circumstantial fossil evidence for beetle-like consumption of bennettitalean ovulate cones. These data indicate that insect pollination was present during the earlier Mesozoic, long before flowering plants were ecologically dominant. Thus a more comprehensive understanding of the evolution of diversity in land ecosystems can be furthered by continued examination of insect-plant interactions, particularly during the Late Carboniferous to the Cretaceous.

Extraction of Insect Proteins and DNA from Amber. It long has been known that amber fossils contain a wealth of insect exoskeletal detail, comparable to modern insect material. However, only recently has there been an appreciation that insect cuticle does not surround empty space, but often encases exquisitely preserved tissue. This tissue, particularly flight muscle, can contain extractable and characterizable proteins and DNA. Importantly, insect DNA in amber is providing a spectacular opportunity for estimating rates of extinction and evolutionary change, establishing topologies of those modern clades with amber-entombed members, determining symbiotic relationships between insects and their parasites and mutualists, and assessing the taphonomy of amber preservation.

Fossil Insect Diversity. The entire span of the fossil insect record—from unclear Devonian origins, to the first extensive, diverse forest ecosystems of the Pennsylvanian, to the entrapment by amber during the post-Jurassic—can be characterized by a generally plentiful and taxonomically diverse record. The received wisdom about insects having a poor fossil record is outright wrong; at least 63 percent of modern insect families have a fossil record, a pretty respectable capture rate when compared to other major terrestrial taxa. More importantly, this diversity can be used to test fundamental evolutionary hypotheses, such as whether the origin of modern insect diversity was coupled to the angiosperm radiation or whether it had its origins earlier during the Mesozoic. It turns out that the standard maxim is not supported, and that the diversification of modern insect clades precedes the first known angiosperm by 100 million years. In the context of these conclusions, there is a larger message. While we should always countenance criticisms from our neobiological colleagues, we should still (albeit cautiously) trust our primary data. Fossils are the primary historical documents of life, and when abundant, they certainly are as relevant in assessing patterns of evolutionary or ecological change as modern data.

To return to the theme that initiated this essay, insect paleobiology has much to offer. The necessary and vital job of describing additional insect fossils is essential to increase the representation of insect fossils in our collective awareness, and the mainstream of fossil insect research probably always will be descriptive taxonomy and phylogenetic inference. However, certainly there are new and exciting avenues of current research, much of it involving the use of insects in paleoecologic inference. These include the role of insects in the origin of terrestrial ecosystems, deciphering the original body plan of insects, using plant-insect interactions for evaluating hypotheses of ecosystem evolution (such as Vermeij's escalation hypothesis on land), extracting insect DNA from Cretaceous and Tertiary ambers for establishing clade topologies and estimating rates of evolutionary change, and using the diversity record of insects themselves as a test of macroevolutionary hypotheses (such as parallelism in the angiosperm and insect radiations). Indeed, the state of insect paleobiology is one of revitalization, regardless of whether *Jurassic Park* ever becomes realized.

—CONRAD C. LABANDEIRA