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## MATTERS OF THE RECORD

### Forging a future for fossil insects: thoughts on the First International Congress of Paleoentomology

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Insects are the most diverse macroorganismic group to ever inhabit the planet, constituting a major share of the animal biomass in terrestrial and freshwater ecosystems. Since their first appearance in the fossil record some 400 million years ago, they have expanded ecologically into almost every niche except the ocean below the photic zone. When fossilized, their chitinous exoskeletons typically are well preserved, as evidenced by a respectable fossil record. They are found notably in lacustrine shales and amber but also occur in siderite nodules, lithographic limestone, sinter deposits, asphalt, and various glacial deposits. Insect fossils are major subjects in phylogenetic studies but are used to a lesser extent in understanding past ecological associations and reconstruction of ancient environments.

So, why has paleoentomology never become an integral component of paleobiology in North America? Notably, paleoentomology does not have the rich historical legacy it does in Europe and especially in Russia. Its North American heyday occurred earlier this century, coincident with the extensive exploration of the western United States by Scudder during the late 1800s, the prolific output of Cockerell until the mid 1930s, and more recently the careers of Jarmila Kukalová-Peck and Frank Carpenter, the latter summarized in his herculean *Hexapoda* volume (1992) for the *Treatise of Invertebrate Paleontology*. Despite this extensive early work in the field, North American paleoentomology has contributed little to

the development of theory in paleobiology. This default is all the more glaring since a major chunk of biodiversity preserved in the macrofossil record has been bypassed and its potential can be compared to the vital role that modern insects have played in virtually all fields of biology, including plant-animal associations, coevolutionary theory, and developmental genetics.

Although paleoentomology is a mainstream discipline in Europe and northern Asia that has traditionally been rooted in systematic analysis of taxonomic groups from dozens of rich fossil deposits in Europe and northern Asia, change is now afoot. Recent efforts have been made by several research groups to understand insect systematics, the detailed taphonomy of insect deposits, the ecological roles of fossil insect taxa, and their use in biostratigraphic zonation. All of these themes were discussed in oral and poster presentations at the First International Congress of Paleoentomology, which was held in Moscow from August 30 through September 4, 1998. Representatives came from 12 countries, including a large number of attendees from the host country, Brazil, Germany, Poland, and the United States. Five days of presentations and animated discourse characterized the sessions, but always there was a spirit of inquiry, exchange, and mutual understanding.

#### Systematics

One of the most-discussed issues at the conference was the recognition of major problems resulting from the use of current orthodox cla-

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distic methods in the phylogenetic analysis of modern *and* fossil insect taxa. One widespread criticism was the use of modern taxa, sometimes with the inclusion of fossils, as data for the phylogenetic reconstruction of lineages. Such techniques frequently render fossil taxa paraphyletic simply because descendants of older lineages tend to be absent as modern exemplars (Zherikhin 1997). An effect of this technique is to relegate fossils to poorly defined stem-groups, plesions held in limbo, unresolved polytomies, and other noncircumscribed entities. Because of extinction, lack of knowledge of modern descendants (probably less than 10 percent of the modern insect fauna is known or described [Erwin 1991]) and other confounding variables, paleoentomology is in the ironic position that as more and more insect fossils are found, particularly in the older part of the record, the less robust phylogenies become. A more robust method, pioneered by Krzeminski (1992) for early Mesozoic flies, is to produce phylogenies of only those taxa occurring at particular slices of time, ignoring all subsequent and thus temporally irrelevant cladogenetic and anagenetic events and processes. Thus, phylogenies are constructed from the bottom to the top, as time's arrow would indicate, rather than inferring what may have happened from a top-to-bottom approach. The consensus of the meeting was that sequential isochronologic analyses of insect clades is the best approach for reconstructing the true phylogeny of a clade, rather than deconstruction after the fact from a highly culled sample of modern terminal taxa.

### Taphonomy

A second theme which was addressed at the conference was the very important role that taphonomy plays in explaining the fossil insect record and verifying the claims of paleoentomologists. Of great interest was the disproportionately large number of lacustrine deposits preserving insects when compared with other depositional settings. Lake deposits are probably the most important sources of fossil insect information and span the greatest breadth of environmental settings in time and space, ranging from shallow playas to deeper

graben-formed basins. Lacustrine ecosystems have been around since the late Paleozoic and have resulted in a distinctive and continuous taphonomic mode for the past 300 million years. However, lacustrine insect assemblages may be complex to interpret. Actualistic studies have demonstrated patterns of bias in the lacustrine fossil insect record and illustrated the necessity of conducting similar studies in a variety of modern preservational environments (Smith unpublished data). Amber deposits, by comparison, represent a more limited subset of environments and are confined to certain forest communities during the last 120 million years.

There was a stark contrast in the time intervals that various countries emphasized, reflecting the available records in each region. For example, our Russian colleagues concentrated on Mesozoic ecosystems whereas Europeans and Americans addressed Cenozoic ecosystems. In Germany, for example, there has been a trend toward the study of several notable Cenozoic deposits in stratigraphic, geochemical, sedimentologic, and palynologic context, while still focusing on very precise descriptions of insect taxa. As a result, localities such as Messel, Randecker Maar, and Enspel are probably the best-documented in the world in terms of both their paleoenvironmental context and their insect inhabitants (Ansorge and Kohring 1995; Lutz 1990, 1997; also see Rust 1998).

### Ecological Associations

The broad field of insect paleoecology encompassed many subthemes during the conference, including the structure and evolution of aquatic insect communities, insect diversity patterns through time, and the association of insects with plants. Evidence for paleoenvironmental fluctuation—including climatic oscillation, changes in diversity of insect taxa, and shifts in food-web flow—was presented during the meeting for several lake deposits of sufficient temporal duration to reveal a several-million-year record. Such studies have only begun in North America, and the Eocene Green River lake complex was deemed a prime candidate for such an analysis.

Evidence for a wide spectrum of associa-

tions between insect herbivores and their plant hosts rekindled interest in several approaches for assessing the coupling of plant hosts and their insect herbivores. The two major tracks in this topic were (1) presentation of general yet diverse plant/insect associations such as plant-tissue consumption patterns in equatorial Euramerican coal-swamp forests (Labandeira 1998) and (2) discussion of more faithful types of interactions, such as the evolution of pollen-consumption and pollination syndromes among multiple lineages of insects (Krassilov and Rasnitsyn 1997). In particular, considerable evidence was marshaled to document the patterns of insect consumption of vascular plant spores and pollen in space and through time, indicating the multiple re-evolution of this feeding pattern. Insects may have had a direct effect on the selection of plant reproductive structures and this process may have guided plant evolution, perhaps exemplified by the recurrent appearance of structurally convergent pollen types. Our Russian colleagues expanded previous documentation (Krassilov et al. 1997) of both non-angiospermous and angiospermous pollen associated with fossil insects from Upper Jurassic to Lower Cretaceous strata.

### Biostratigraphy

The use of insects for biostratigraphic zonation of terrestrial deposits was an early goal of both Russian and American paleoentomologists, although this approach has been characterized by only modest successes thus far. It has been limited principally by the paucity of continuous successions of appropriate deposits, many of which are not linked to magnetostratigraphic, palynologic, or other zonation schemes to ensure internal accuracy and thus universal applicability to other regions. However, several papers at the conference have reinvigorated insect biostratigraphy, providing considerable promise for Late Carboniferous and Early Permian zonation in Europe and mid-Mesozoic zonation in Central Asia (Sukacheva 1982; Schneider and Werneberg 1993). Although insect biostratigraphy historically has been the purview of only a few practitioners, as more taxa become described and recognized as identical in time and space, addi-

tional biostratigraphically useful and temporally bounded insect chronofaunas may be enumerated in the near future. One example is the evolution of complexity in the construction of caddisfly cases, the phases of which are temporally constrained.

### Summary

Many other issues were presented at the meetings. A limited sample includes the origin of insects and their flight apparatus, morphological reinterpretations of controversial Paleozoic insects, the Mesozoic origin of modern lineages of cockroaches and early lineages of flies, and the presence of Late Jurassic, albeit taxonomically unassignable, moths. One poignant example of how much is still unknown, but serendipitous, regards the enigmatic taxon *Umenocoleus*, from the Lower Cretaceous Baisa locality in Transbaikalia, Russia. This taxon has been variously considered an extinct protelytropteran, a beetle, and a higher-level taxon in its own right. Evidence presented at the conference, however, shows that it is a derived, albeit aberrant, cockroach that has equally bizarre relatives occurring in other Cretaceous deposits as well as undescribed relatives occurring in Vietnam today.

These, and other presentations during the conference, indicate that paleoentomological research is still in an expansion phase, even in Europe. In North America, paleoentomology is still in its infancy. An important realization is that fossil insects are not absent from the North American record but in fact are resources that have been underutilized far too long. With growing interest in paleoentomology worldwide, we can look forward to the wide range of stimulating topics that will be discussed at the Second International Paleontological Congress, scheduled to be held in 2001, in Krakow, Poland.

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