BOOK REVIEWS

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Studies on Hemipteran Phylogeny.—C. W. Schaefer (ed.). 1996. Proceedings, Thomas Say Publications in Entomology. 244 pp. Entomological Society of America, Lanham, Maryland.

The editor introduces this volume with the hope that included papers will stimulate further discussion of hemipteran phylogeny. I offer in the following paragraphs comments on some of the issues raised by the contributors.

The 11 included papers were presented in a symposium at the 18th International Congress of Entomology held in Vancouver, British Columbia, Canada, in 1988. As is typical of symposia at such congresses, the list of contributors is international. Hemiptera, as used in the title, is in the broad sense. There is broad general agreement concerning the monophyly of the Hemiptera and of the Heteroptera. My comments will concentrate to a great degree on the recognition of groups and interrelationships among the classic Homoptera.

If this book is about Hemiptera, there is also one thing that it is not about—cladistics. Don't get me wrong, there are branching diagrams, some called cladograms, and lists of characters, some called apomorphies, but the sum of the discussion is not cladistic. Although the term cladistics is used many times, there is little coherence of method, and certainly much doubt expressed concerning the usefulness of cladistic methods. Although this may seem odd for a group of papers on phylogeny prepared in the late 1980s by which time the current methods were well tested and entrenched, it may seem less surprising when one considers that many of the arguments and much of the data come from paleontology. Because of the varied approaches of the contributors, I found interpretation and comparison of approaches and results difficult.

Within the Hemiptera, fossil representation of groups not known in the Recent fauna appears to be greatest in the classic Homoptera. K.G.A. Hamilton (Ottawa) attempts to resolve some descrepancies in the classification of the Auchenorrhyncha through the use of Cretaceous fossils from the Santana formation of the Northeast of Brazil; many of these represent the oldest known fossils which possess bodies and appendages in addition to wings. Hamilton begins by saying, "One of the most widely used techniques for elucidating [evolutionary] relationships is cladistics, the deducing of sister groups and their common ancestors by the distribution of derived characters in modern taxa. This still remains a controversial technique." He then proceeds to give a brief summary of the superfamilies in which Mesozoic fossil "Homoptera," represented primarily by wings, might be placed.

Hamilton draws several conclusions, primarily from study of the Santana fossils. The most general is that "Fossils frequently exhibit character states that cannot be predicted by cladistic analysis of recent forms." The states which seem most problematic, in his mind, are those that are suppressed altogether or totally transformed in modern lineages. No wonder that cladistics could not predict them.

Hamilton concludes that four monophyletic "suborders" can be recognized within

the Hemiptera: Psyllomorpha (=Sternorrhyncha), Cicadomorpha (Auchenorrhyncha less Fulgoroidea and possibly including Aleyrodoidea), Fulgoroidea, and Heteropteroidea (or Heteropterodea). Hamilton presents branching diagrams to portray the composition and relationships of these groups. Unfortunately, he fails to include the Heteropteroidea in these diagrams, and therefore leaves unclear the position of that group within the Hemiptera.

In a similar vein, D. E. Shcherbakov (Moscow) offers a paleontological view of auchenorrhynchan evolution. His fossil-based presentation has higher groups evolving from other higher groups, as for example, "Bugs (Heteroptera) arose from some scytinopteroids, possibly from Paraknightiidae. . . ." His discussion is so replete with such characterizations that nearly every group mentioned must be considered paraphyletic. His most compelling conclusion may be that although in the Triassic now extinct groups of Auchenorrhyncha still dominated, in the Cretaceous the fauna looked like the modern one.

J. Koteja (Krakow) reviews the morphology of the scale insects, offering a list of characters that he hopes will be of value in phylogenetic work. Neither he, nor any other author, argues that the Coccoidea (or Coccinea) are not a monophyletic group. Koteja devotes most of his effort to determining what the ground plan of the scale insects should be, but little space is given to placing the scale insects in a broader phylogenetic perspective, which made it difficult for me to judge many of his arguments about the polarity of characters. This paper will be particularly interesting to coccidologists.

H. Derreck Blocker (Manhattan, Kansas) reviews the largely pre-cladistic literature dealing with auchenorrhynchan relationships. Blocker's review makes it clear that there are virtually as many published schemes of higher group relationships within the "Homoptera" as their are possible topologies for those groups.

Y. A. Popov and D. E. Shcherbakov (Moscow) portray evolution in the Coleorrhyncha as evidenced by the fossil record. This paper has the trappings of being cladistic, offering a list of characters and a cladogram. Yet, all other aspects of the paper suggest classic paleontological reasoning. Some quotes may serve to make the point. First, "Coleorrhyncha, regarded as a suborder of Hemiptera (sensu lato), forms a phyletic lineage somewhat parallel to but nevertheless distinct from Heteroptera, both descending independently from primitive Auchenorrhyncha Cicadomorpha." Second, "Paleontological data confirm the auchenorrhynchous affinities of the Peloridiidae [=Coleorrhyncha in part] beyond doubt, so the suggested synapomorphies of the family and Heteroptera should be reconsidered." And, "Except for their flattened habitus, bugs [=Heteroptera] and Coleorrhyncha disagree in fundamental apomorphies. . . . The evidence discussed above forces us to reject Schlee's Heteropteroidea [Coleorrhyncha + Heteroptera] and treat both Heteroptera and Coleorrhyncha as suborders of Hemiptera along with Auchenorrhyncha and Sternorrhyncha." There may be merit in the conclusion of Popov and Shcherbakov that the Peloridiidae are relict in the far Southern Hemisphere. Their remaining conclusions are far less persuasive.

M. H. Sweet (College Station, Texas) offers one of the most character-rich contributions in his paper on the pregenital abdomen. Most of his treatment is devoted to homologizing sclerites, the first such effort, according to him, since 1893. He proposes the pleural origin of the connexival sclerites, adopting the terms "hypo-

pleurite" and "epipleurite" for the dorsal and ventral (or inner and outer) laterotergites, respectively. The value of such an undertaking would be to understand morphological change in the pregenital abdomen irrespective of the notoriously inconstant spiracle positions, if such were actually possible.

In my view Sweet's contribution has some obvious merits and some equally obvious drawbacks. On the positive side, he recognizes four apparently monophyletic suborders within the Hemiptera (Sternorrhyncha, Auchennorhyncha, Coleorrhyncha, Heteroptera) on the basis of long appreciated and apparently apomorphic characters, rather than agonizing over variability in group–defining characters, especially for the Auchenorrhyncha. The drawbacks may be of two types. First, the characters he discusses are nearly all in the pregenital abdomen, hardly a complete sampling of morphological diversity in any of the groups. Second, many of his arguments for the apomorphous nature of characters are functional, and almost nowhere does he attempt to bring his concept of apomorphy into agreement with optimization of characters on a cladogram.

Some of Sweet's arguments are patently unconvincing. He notes, for example, that the pregenital abdomen in the Cicadellidae is relatively uniform in structure. In contrast, he finds the pregenital abdomen in the Cercopidae to be morphologically much more diverse, and concludes that there is merit in raising the latter group to superfamily rank, especially if the Cicadellidae are raised to superfamily through elevation of some subfamilies to family rank.

Sweet observes that at least some Fulgoroidea have fields of trichobothria on certain abdominal sterna and hypopleurites, as earlier pointed out by Ossiannilsson (1978). China (1962) and Carver, Gross, and Woodward (1991) observed similar setae in the Peloridiidae. Sweet conjectures that the "trichobothria" in these two groups may be homologous with the abdominal trichobothria in pentatomomorphan Heteroptera. I would observe that trichobothria exist on many parts of the heteropteran body, including the head, antennae, scutellum, femora, and in apparently nonhomologous forms on the abdomen in several families. These well-documented observations would seem to weaken Sweet's tentative theory of abdominal trichobothrial homology for the Fulgoroidea, Peloridiidae, and Trichophora.

Sweet argues that the ground plan of the Heteroptera has ventral spiracle bearing hypopleurites. He proposes a new infraordinal name—Aradomorpha—for the Aradoidea (Aradidae + Termitaphididae). He justifies this on the basis of abdominal structure, saying that the "turned over" connexivum of the Leptopodomorpha and Pentatomomorpha sensu Sweet [=Trichophora] in which the hypopleurites are dorsalized and the epipleurites are infolded is "strictly homologous and constitute[s] a synapomorphy relating these infraorders. . . ," presumably more closely than either is related to the Aradoidea.

The similarity of abdominal structure noted by Sweet in the Leptopodomorpha and Trichophora is not unique. Examination of abdominal structure in the Cimicomorpha, for example, reveals great variation, including ventral "hypopleurites" and dorsal "epipleurites" with spiracles 2–8 ventral on the hypopleurites in many Reduviidae and Nabidae, for example, and a completely dorsalized connexivum with spiracles 2–8 ventral on the mediosternite in the Miridae and Tingidae. He does not resolve the incongruence of spiracle position in the trichophorous Pentatomomorpha

(ventral on the mediosternite, except in some Lygaeoidea) and Leptopodoidea (dorsal on the "hypopleurite," except in *Leotichius*).

Furthermore, Sweet disregards several other attributes which argue for the monophyly of the Pentatomomorpha sensu lato. Possibly most obvious among these is the remarkably similar structure of the pretarsus—unqique among the Heteroptera—in all recognized families in the group, the claws being large and curved with a proximally attached pulvillus extending nearly the length of the claw (see scanning micrographs in Schuh and Slater, 1995:figs. 10.5 G–I); the parempodia always exist as a single, symmetrical, setiform pair; and median dorsal and ventral arolia are absent in all life stages as far as is known. Also, uniquely among Heteroptera, the eggs of all Pentatomomorpha, including Aradoidea, have distinctive micropylar processes. By way of contrast, the pretarsus is Leptopodomorpha is unlike that of Pentatomomorpha, most notably possessing arolia in some life stage as do all "lower" Heteroptera and lacking pulvilli; the eggs of Leptopodomorpha do not possess micropylar processes. Finally, the modest amount of available DNA sequence data groups Aradidae (not the Leptopodomorpha) with the Trichophora (Wheeler et al., 1993).

In sum, Sweet's arguments for the Aradomorpha are constructed in a phylogenetic vacuum and on the basis of a single character system which shows little consistency with other characters which show great constancy of form and which consistently argue for the monophyly of the Pentatomomorpha sensu lato.

D. B. Thomas (Weslaco, Texas) reviews chromosome numbers in the Heteroptera, attempting to determine whether polyploidy has played a role in the evolution of the group. His survey of the literature makes it clear that the story told by existing knowledge is far from clear. The reasons can be stated as follows: 1) the sample of taxa is small, with little accounting for within-group variation; 2) the phylogenetic relationships he postulates to explain chromosome data are often questionable; and 3) his assumptions about the plesiomorphic condition in many groups are at most a guess. These are the obvious limitations of his analysis.

Perhaps much more important is the problem of homology. Does simple counting of similar-appearing chromosomes actually represent a valid comparison? Thomas presents the results of some studies of chromosome volume that indicate otherwise. Furthermore, no banding patterns are known, thus, we might conclude that all theories of chromosome homology are outright suspect. Possibly symptomatic of the larger question is the so-called "m" chromosome, or micro-chromosome. This karyotypic feature has been used in establishing schemes of relationships within the Pentatomomorpha, yet it also occurs in such distantly related groups as the Nepomorpha. I can only conclude from Thomas' survey that karyology has a long way to go before it is capable of making a useful contribution to understanding mechanisms of diversification or establishing schemes of phylogenetic relationships within the Heteroptera.

Four additional papers offer further observations, primarily on the Heteroptera, but provide little in the way of phylogenetic context. These are: P. Stys (Prague) on some groundplan characters in the Heteroptera; R. J. Wootton (Exeter, England) on the functional aspects of hemipteran wings; J. R. Aldrich (Beltsville, Maryland) on the status of knowledge of pheromones; and H. Mori (Tokyo) on coalescence of ventral nerve ganglia from an embryological perspective.

Summarizing my impressions of the papers of this volume, I would say the following.

The application of the paleontological methods flaws the conclusions of all papers dealing with fossils. There seems great reluctance on the part of the paleontologists to view classifications as being based on characters, rather than some abstract concept of taxa which allows one group to be descended from another. Because the Paleozoic and early Mesozoic Hemiptera are largely represented by wings, there may be little hope that the taxa can be precisely characterized. This hardly seems a justification for continuing to treat these extinct groups as ancestral (and paraphyletic) simply because they appear early and disappear early.

Two works widely cited are those of Carver et al. (1991) and Sorensen et al. (1995). The former is cited as a justification for rejecting the Homoptera as a natural group. The latter is cited as a source of evidence for that conclusion. All contributors in this volume echo the view that the classic Homoptera must be abandoned as a group, yet draw little in the way of coherent conclusions as to what the new scheme should be.

Nonetheless, the desire to create a new subordinal nomenclature, even with little evidence to support it, seems to be great. This drive may be most conspicuous in the work of Sorenson et al. (1995) who coined several new names in a study using 18s rDNA data. In the present volume K.G.A. Hamilton is of a like mind, noting that the suborders should be designated with equivalent names. One might conclude from reading these papers that scientific problems can be solved simply by proposing new higher-group names. I fail to see what those problems are.

Clearly, the most pressing grand scale problem in hemipteran phylogenetics is to refine the diagnoses of higher groups within the Homoptera and to form a stable scheme of interrelationships within those groups. The consistent application of the core principles of cladistics—the use of character congruence to test theories of homology and the use of outgroups to determine character polarity—would go a long way toward achieving that objective.—*Randall T. Schuh, Department of Entomology, American Museum of Natural History, New York, New York 10024.*

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