GULLAN, P.J.

Division of Botany and Zoology, The Australian National University, Canberra, ACT 0200, Australia

WHY THE TAXON HOMOPTERA DOES NOT EXIST.

ABSTRACT

Why the taxon Homoptera does not exist.

Many researchers still use the name Homoptera for the higher taxon of any member of the Sternorrhyncha (Aleyrodoidea, Aphidoidea, Coccoidea and Psylloidea) or Auchenorrhyncha (Cercopoidea, Cicadoidea, Cicadelloidea and Fulgoroidea), or to refer collectively to the Sternorrhyncha plus Auchenorrhyncha. Recent work based on morphological and molecular studies provide phylogenetic evidence that the Homoptera is paraphyletic and therefore its use should be abandoned.

Key words: honeydew, ant-attended, sap-sucking, carnivory.

Traditionally the Homoptera has been regarded either as a distinct order or as a suborder of the order Hemiptera. In either classification, the Homoptera consists of the Auchenorrhyncha (Cercopoidea, Cicadoidea, Cicadelloidea and Fulgoroidea) plus the Sternorrhyncha (Coccoidea, Aphidoidea, Psylloidea and Aleyrodoidea) and usually also the Coleorrhyncha (Peloridoidea: Peloridiidae or moss bugs). Hennig (1981) recognised that the Homoptera might not be monophyletic (in the sense of not containing all descendants of the common ancestor) because the diagnostic features used to separate it from the Heteroptera are all plesiomorphies that must have been present in the common ancestors of both groups. In homopterans, the labium is inserted close to the prosternum (without the intervening gula area seen in Heteroptera), and the fore-wings, if developed, are in the form of tegmina of approximately uniform texture, i.e. without differentiation into corium and membrane (as in Heteroptera), and often are held roofwise over the abdomen (Woodward et al., 1970). The insects traditionally recognised as homopterans all feed on plant saps (mostly from phloem or xylem) (Goodchild, 1966; McGavin, 1993) and a number of families, especially among the Sternorrhyncha, possess the obvious biological traits of eliminating honeydew from the anus and being ant-attended (e.g., Buckley, 1987; Bourgoin, 1997). In contrast, the Heteroptera have more diverse food habits, including plant sap-sucking and carnivory on invertebrate prey or, more rarely, vertebrate blood (Goodchild, 1966; McGavin, 1993; Schuh & Slater, 1995), and, with a few rare exceptions (e.g., Maschwitz et al., 1987), the Heteroptera do not produce honeydew and are not ant-attended.

Ideally, all higher taxa should be monophyletic because natural groups provide an unambiguous representation of relationships, can be efficiently diagnosed (by one or more shared derived features), are stable to the addition of new taxa, and have maximal value in application to other studies (e.g., behavioural, biogeographic or evolutionary investigations). Polyphyletic groups, based on the misinterpretation of convergence as evidence for genealogy, are unnatural and always are rejected when detected. Paraphyletic groups also are unnatural as they do not contain all of the descendents of their ancestor, generally due to the removal of a divergent monophyletic group from the clade (e.g., the class Reptilia is rendered paraphyletic by recognition of the class Aves for the morphologically-derived reptiles that we call birds), and are difficult or impossible to uniquely diagnose due to the lack of shared derived features. Such groups appear to be common at all taxonomic levels in our existing classifications of insects and yet, in the interests of nomenclatural stability, we should not reject them without good evidence from thorough character evaluation and rigorous phylogenetic analysis. The testing of phylogenetic hypotheses, and thus classifications, using data sets that are independent of morphology (e.g., nucleotide sequence data from mitochondrial or nuclear genes) is desirable given that our existing classifications are based almost exclusively on morphology.

The phylogenetic relationships of the various higher groups of Hemiptera have been much disputed (e.g., see chapters in Schaeffer (1993) or the review in von Dohlen & Moran (1995)). Recent cladistic re-interpretations of morphological data (reviewed in Campbell et al., 1995b) and particularly phylogenetic analyses of 18S rDNA nucleotide sequence data (von Dohlen & Moran, 1995; Campbell et al., 1995b) do not support the monophyly of the Homoptera. Available evidence suggests that the Auchenorrhyncha are more closely related to the Heteroptera (including the Coleorrhyncha) than to the Sternorrhyncha (Wheeler et al., 1993; von Dohlen & Moran, 1995). Furthermore, the Auchenorrhyncha also may be paraphyletic because the Fulgoroidea may be more closely related to the Heteroptera than to the other auchenorrhynchan groups (Campbell et al., 1995a,b; Sorensen et al., 1995). The molecular data, however, strongly support the monophyly of the Sternorrhyncha (Campbell et al., 1994, 1995a,b; von Dohlen & Moran, 1995) and thus validate the previous morphological evidence for the naturalness of this group (Schlee, 1969).

Despite this recent evidence for the non-monophyly of the Homoptera, the concept has been used so widely and for so long that many researchers appear loathe to discard it. However, if entomologists wish to use a phylogenetically-based higher classification, then they should abandon the use of the name Homoptera and instead refer to their favourite bug group as part of the relevant superfamily of the order Hemiptera. Several books (e.g., Carver *et al.*, 1991; McGavin, 1993; Gillott, 1995) now use a classification with three, or more rarely four, suborders, namely the Auchenorrhyncha, Sternorrhyncha, Heteroptera and sometimes with a separate Coleorrhyncha for the Peloridiidae. Using such schemes, the scale insects, for example, could be referred to as "Hemiptera: Coccoidea" or "Hemiptera: Sternorrhyncha: Coccoidea". Sorensen *et al.* (1995) have taken the radical step of discarding the names Auchenorrhyncha, Coleorrhyncha and Heteroptera, and erecting three new hemipteran suborder names, based on relationships suggested by their 18S rDNA gene trees. This action may be premature; major nomenclatural changes should await confirmation of the postulated relationships from additional genes or other new data sources.

ACKNOWLEDGEMENTS

I thank Lyn Cook and Peter Cranston for comments on a draft of the manuscript and Chris Hodgson for hosting the VIIIth International Symposium of Scale Insect Studies at which the topic of this paper was discussed by participants.

REFERENCES

- BUCKLEY, R.C., 1987 Interactions involving plants, Homoptera, and ants. Annual Review of Ecology and Systematics, 18: 111-135.
- BOURGOIN, T., 1997 Habitat and ant-attendance in Hemiptera: a phylogenetic test with emphasis on trophobiosis in Fulgoromorpha. In: Grandcolas, P. (ed.), The Origins of Biodiversity in Insects: Phylogenetic Tests of Evolutionary Scenarios. *Mémoires du Muséum national d'Histoire naturelle*, 173: 109-124.
- CAMPBELL, B.C., STEFFEN-CAMPBELL, J.D., GILL, R.J., 1994 Evolutionary origin of whiteflies (Hemiptera: Sternorrhyncha: Aleyrodidae) inferred from 18S rDNA sequences. *Insect Molecular Biology*, 3: 73-88.
- CAMPBELL, B.C., STEFFEN-CAMPBELL, J.D., GILL, R.J., 1995a Origin and radiation of whiteflies: an initial molecular phylogenetic assessment. Pp 29-51, *in* Gerlang, D. and Mayer, R.T. (eds), *Bemisia* 1995: Taxonomy, Biology, Damage Control and Management. Intercept Ltd, Andover.
- CAMPBELL, B.C., STEFFEN-CAMPBELL, J.D., SORENSEN, J.T., GILL, R.J., 1995b Paraphyly of Homoptera and Auchenorrhyncha inferred from 18S rDNA sequences. *Systematic Entomology*, 20: 175-194.
- CARVER, M., GROSS, G.F., WOODWARD, T.E, 1991 HEMIPTERA. Pp 429-509, in CSIRO, The Insects of Australia. A Textbook for Students and Research Workers, Vol. I, 2nd ed. Melbourne University Press, Carlton. 1137pp.
- GILLOTT, C., 1995 Entomology, 2nd ed. Plenum Press, New York and London. 798pp.
- GOODCHILD, A.J.P., 1966 Evolution of the alimentary canal in the Hemiptera. *Biological Reviews*, 41: 97-140.

- HENNIG, W., 1981 Insect Phylogeny (English edition translated and edited by A.C. Pont), John Wiley & Sons, Chichester, New York, Brisbane, Toronto.
- McGAVIN, G.C., 1993 Bugs of the World. Blandford, London.
- MASCHWITZ, U., Fiala, B., Dolling, W.R., 1987 New trophobiotic symbioses of ants with South East Asian bugs. *Journal of Natural History*, 21: 1097-1107.
- SCHAEFER, C.W. (ed.), 1996 Studies on Hemipteran Phylogeny. Entomological Society of America, Maryland.
- SCHLEE, D., 1969 Die Verwandtschaftsbeziehungen innerhalb der Sternorrhyncha aufgrund synapomorpher Merkmale. Phylogenetische Studien an Hemiptera II: Aphidiformes (Aphidina + Coccinea) als monophyletische Gruppe. *Stuttgarter Beiträge zur Naturkunde*, 199: 1-19.
- SCHUH, R.T., SLATER, J.A., 1995 True Bugs of the World (Hemiptera: Heteroptera): Classification and Natural History. Cornell University Press, Ithaca and London. 336pp.
- SORENSEN, J.T., CAMPBELL, B.C., GILL, R.J., STEFFEN-CAMPBELL, J.D., 1995 Non-monophyly of Auchenorrhyncha ("Homoptera"), based upon 18S rDNA phylogeny: ecoevolutionary and cladistic implications within pre-Heteropterodea Hemiptera (s.l.) and a proposal for new monophyletic suborders. *Pan-Pacific Entomologist*, 71: 31-60.
- VON DOHLEN, C.D., MORAN, N.A., 1995 Molecular phylogeny of the Homoptera: a paraphyletic taxon. *Journal of Molecular Evolution*, 41: 211-223.
- WHEELER, W.C., SCHUH, R.T., BANG, R., 1993 Cladistic relationships among higher groups of Heteroptera: congruence between morphological and molecular data sets. *Entomologica Scandinavica*, 24: 121-137.
- WOODWARD, T.E., EVANS, J.W., EASTOP, V.F., 1970 Hemiptera. Pp 387-457, in CSIRO, The Insects of Australia. A Textbook for Students and Research Workers. Melbourne University Press, Carlton. 1029pp.