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The genome challenge: *why study morphology?*

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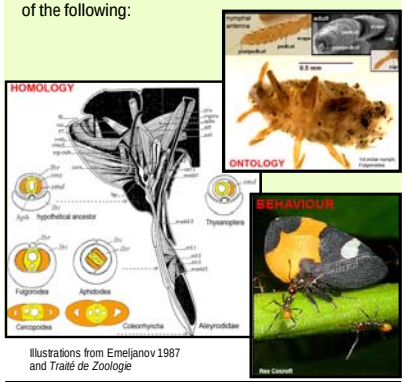
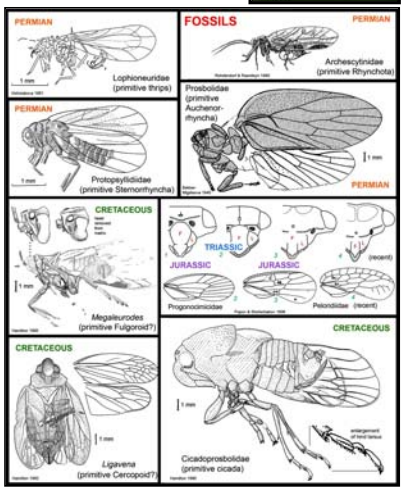
Introduction

Classifications of insects are increasingly becoming dependent upon genetic research.

- Morphology is widely interpreted using Hennigian methodology to determine close relationships and genetic divergence, but seldom generates strong discriminations at the suprageneric level.
- Genetic analysis agrees with morphological evidence at the species level, but challenges our assumptions about higher taxa.
- Despite the advantages of genetic data, it cannot contribute directly to understanding any of the following:



Illustrations from Emeljanov 1987 and *Traité de Zoologie*



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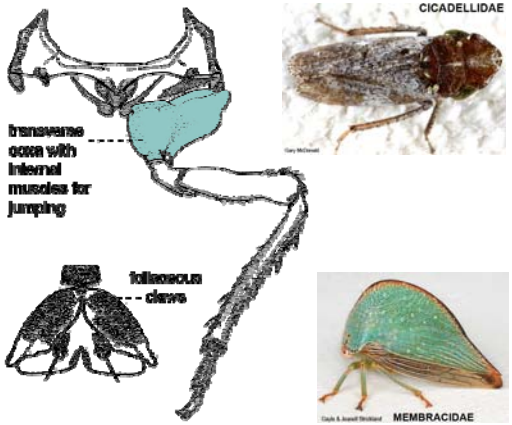
Objectives

This study analyses morphological criteria to find ones that correlate well with genetic and palaeontological evidence above the genus level, thus providing a sounder basis for insect classifications.

Methods

Analyses of vertebrate fossils rely largely upon morphology of bone structures that appear distinctive, and therefore provide convincing evidence of relationships. Such characters are invaluable in palaeontological studies, but are little used in phylogeny of *invertebrates* as the numbers of whole-bodied fossils and reliable characters are much fewer. In insects, these are largely confined to wing venation; and wing venation is particularly labile and unreliable in Hemiptera.

This study utilizes a similar methodology advanced by Hansen (1890) who recommended basing relationships of insects only upon "unique" (i.e., non-homoplastic) characters. His observations were based on the work of Stål (1868) who analysed leg structure and concluded that very dissimilar Hemiptera (Cicadellidae and Membracidae) are in fact related. This methodology predates that of Hennig but is little known in entomology.

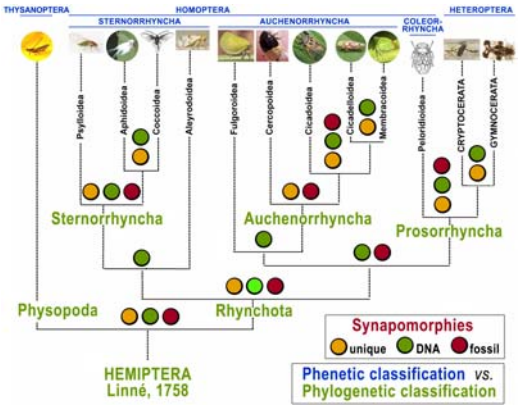


Results of such analyses were compared to various genetic data sets (Dietrich *et al.* 2001, van Dohlen and Moran 1995) to find how much congruence exists between morphological and genetic evidence. In addition, 600 species of leafhoppers and treehoppers were "bar-coded" using a simple genetic test, and the results were compared to phylogenies based on "unique" morphological characters.

Results & discussion

"Bar-coding" data correlates well with morphology, but is useful only at the generic level. Other genetic analyses correlate well with morphology only above 95% bootstrap values, which are rare, thus requiring large data sets from 30 or more genes to show strong evidence of all clades (Zwick 2010). Hansenian analysis is easier to use than Hennigian methodology, and avoids the pitfalls of common homoplasies (convergences).

Correlation of morphological and genetic data confirms that treehoppers are modified leafhoppers, and (together with fossil evidence) may also be used to clarify the basal lineages of the order as a whole.



Conclusions

Unique morphology is most helpful in understanding evolutionary processes, but these characters are seldom encountered and must be supplemented by evidence from genetic analyses and fossils.

When all such data is in accordance, classifications should be emended to reflect the best-supported aspects of phylogenies (e.g., thrips should no longer be excluded from Hemiptera; they were originally included by Linnaeus and no refutation of this relationship has been attested).

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Acknowledgements

Photographs as credited, except for those of 1st instar nymph of Fulgoroidea, provided courtesy of Mike Ferro, LA State University.

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