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A review of cladistic classification as applied to Lepidoptera.*)

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Throughout the last years the cladistic — phylogenetic methodology as originally formulated by the late Dr. W. Hennig (1950, 1965, 1966) has gained much acceptance among biosystematists. As Hennig himself was a dipterist, his ideas first strongly influenced systematic work on Diptera, while only during the most recent years have awareness and use of cladistic-phylogenetic theory and methods been seen among lepidopterists. This paper gives a brief outline of the basic ideas together with a few examples on the use of cladistics in Lepidoptera.

The only type of group accepted in phylogenetic systematics is the strictly monophyletic group (the clade): *the biological species or a group of all and only the descendents of one ancestral species*. The species in a monophyletic group are more closely (phylogenetically) related to each other than to any other species outside the group.

Two species created by a (dichotomus) speciation process are called sister-species. Two monophyletic groups that are the closest relatives of each other are called sister-groups. Sister-species are considered the closest relatives of each other, having a more recent ancestor in common with each other than they have with any other species. Sister-groups, likewise, are more closely related to each other than they are to any other group.

The degree of phylogenetic relationship is therefore measured by *recency of common ancestry*. In Fig. 1 the species D and E are more closely related to each other than to the species C, as D and E have a common (hypothetical) ancestor, IV, which ist not ancestral to C.

Hennig (*op. cit.*) applied the terms apomorphic and plesiomorphic to a homologous character in the relatively primitive (or original) and the relatively advanced (or derived) states, respectively. In a character transformation series (or anagenetic series) of a homologous character, an earlier state of a feature is relatively plesiomorphic compared to any later change of the feature, which is relatively apomorphic. The features of a common ancestor of a group of species are by definition plesiomorphic for that group — the ground plan of the group (characters of hypothetical ancestor I in Fig. 1).

In phylogenetic systematics similarity of features can be of three different types: 1. The plesiomorphic feature is present unchanged in the descendants — *symplesiomorphy*. 2. A unique change of a feature can be transferred to two or more descendants — *synapomorphy*. 3. A particular change in a feature might originate twice or more independently —

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convergence. Phylogenetic relationship is only indicated by shared derived
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features, synapomorphies, not by symplesiomorphies or convergences. A unique change of a feature transferred to only one descendant is an *autamorphy* of that clade, and does not indicate phylogenetic relationship.

Species grouped exclusively based on shared plesiomorphic characters (symplesiomorphis) are paraphyletic, and groups based on convergences are polyphyletic, i.e., groups that do not possess the historical integrity of the monophyletic group and are not natural.

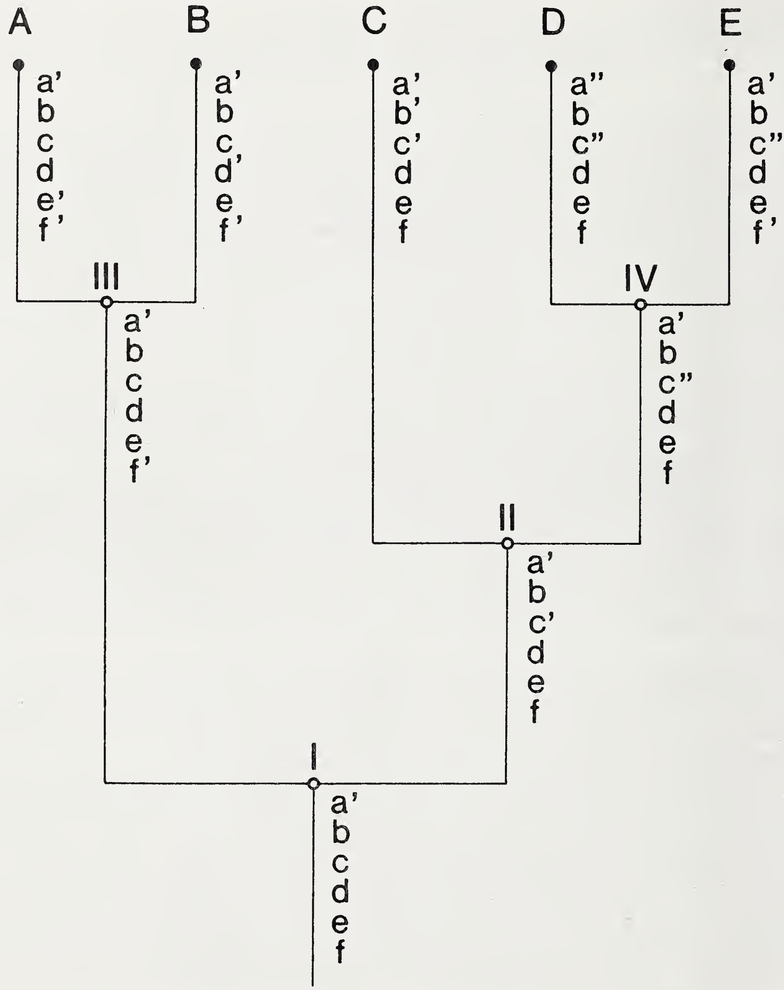

Fig. 1. Assumed true phylogeny of five species or monophyletic groups, A-E. Hypothetical ancestral species: I—IV. Plesiomorphic features a—f, corresponding apomorphic features a'—f'; c, c', c" from transformation series. A+B, C+(D+E), and (A+B)+(C+(D+E)) are monophyletic groups, possessing the synapomorphies f', c' and a' respectively. B+C+D+E is a paraphyletic group based on the symplesiomorphy e. A+B+E is a polyphyletic group based on f', a convergent.

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As the monophyletic group is an integrated evolutionary unit, and as the phylogenetic relationships amongst such groups are an expression of the factual historical processes, and as there ist only one such evolutionary history, the hierarchical system which reflects this unique phylogeny is our best choice of a single general references system.

The phylogenetic relationships can be expressed precisely in a cladogram (Fig. 1) or in a hierarchical classification where sister-groups are given the same rank.

Biologically the phylogenetic system is very important in that very significant comparisons can be made between sister-groups, as they are the two possibilities realized during evolution of a single gene-pool. Likewise, properly reconstructed cladograms become a very important tool in the study of biogeography (Brundin, 1972).

For a comprehensive review on cladistic-phylogenetic systematics, including many references, see Bonde (1977).

Examples of the usages of cladistic-phylogenetic analysis in Lepidoptera:

1. On the ordinal level in insects, one of the best documented sisterorder relationships is that of Trichoptera + Lepidoptera (constituting the Amphismenoptera), as the orders have been demonstrated to share a considerable number of synapomorphies (Hennig, 1969; Kristensen, 1973). This is of special interest in discussions of the basic evolutionary pattern in Lepidoptera, making „out-group" comparisons very reliable.

2. The exact position of Zeugloptera has long remained uncertain. Some authors recognize three orders in Amphismenoptera: Zeugloptera, Trichoptera and Lepidoptera. However, as pointed out by Kristensen (1971), the Zeugloptera-Trichoptera similarities are symplesiomorphies, while a considerable number of Zeugloptera-Glossata similarities are synapomorphies. Zeugloptera are therefore included in the order Lepidoptera, and regarded as the most primitive grade, and given suborder status (Hennig, 1953).

3. On the family level Kristensen (1975) presented a phylogenetic classification of the butterfly families, mainly based on Ehrlich (1958) and co-workers' observations. Hesperioidea and Papilionoidea were shown to constitute a monophyletic group sharing four probable synapomorphies.

4. Recent examples of cladistic analysis on the generic level are the classification of the Holarctic Sesiidae by Naumann (1971), and that of the north European genera of Elachistidae (Traugott-Olsen & Nielsen, 1977).

5. The generic position of *Elachista abbreviatella* Stainton, 1851 (syn.: *Scirtopoda myosotivora* Müller-Rutz, 1837), and *Perittia cedronellae* Walsingham, 1908 (Elachistidae), have long remained uncertain. However, these species have been shown to share a distinctive synapomorphy with the species in *Stephensia* Stainton, 1858, wherefore they could be allocated unambiguously to that genus (Nielsen & Traugott-Olsen, 1978). The genus most likely has an Old World origin, as only a single subordinate species is so far known from the New World.

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