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Splitting or widening: remarks on the taxonomic treatment of paraphyletic taxa

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A paraphyletic entity may be split into its monophyletic constituents, or it may be rendered monophyletic by being widened to include additional taxa. In a given case only one of these treatments may be appropriate. The significance of the flea/fly example used by Michener (1978), Syst. Zool. 22:344) to illustrate a criticism of phylogenetic systematics is disputed.

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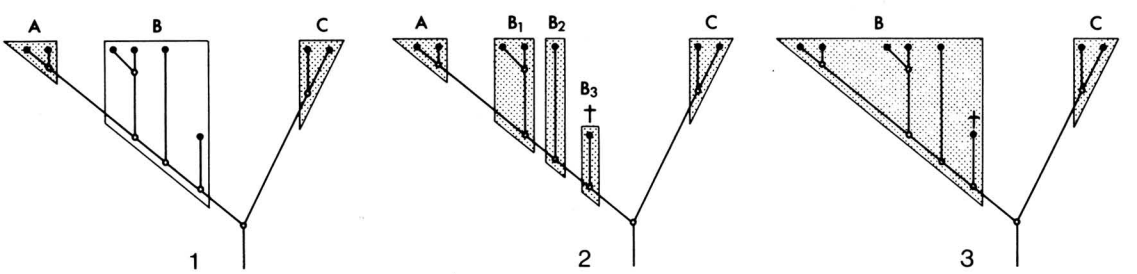
A paraphyletic entity (Fig. 1, B) is an assemblage of taxa which includes the last common ancestor (stem species) of its constituent members, but not all known descendants of this ancestor. A paraphyletic entity does not have an evolutionary history of its own and is not admissible in a strictly phylogenetic (cladistic) classification. Paraphyletic taxa of pre-existing classifications may be treated in two ways within the framework of phylogenetic systematics: either they can be split into a number of smaller entities (Fig. 2: B_1, B_2, B_3) which are all truly monophyletic (i.e., each of which includes all known descendants of the stem species), or they can be rendered monophyletic by being widened (Fig. 3, B) to include those descendants of their stem species which were previously excluded for reasons of phenetic distinctness.

Many major taxa in conventional animal systematics are paraphyletic entities which were once established through an 'A/not-A' division of the nearest more inclusive categories in question. Such entities have to be split into their monophyletic constituents, since widening would be meaningless. If, for example, the entity 'Exopterygota' among winged insects were to be widened sufficiently to become monophyletic, it would, of course, be rendered equivalent with the taxon Pterygota itself. Establishment of new categories and taxa by the splitting procedure may become excessive if subordination schemes of classification are employed, but can be rendered more manageable by application of the sequencing principle of classification and the 'plesion' concept (Nelson 1973, Patterson & Rosen 1977; see also Wiley 1979, Eldredge & Cracraft 1980). It is suggested that when possible under the Code of nomenclature (i.e., in the case



Figs. 1—3. The paraphyletic entity (1: B) is split into its monophyletic constituents (2: B_1, B_2, B_3), or rendered monophyletic (3:B) by being widened to include taxon A). Monophyletic taxa are shaded. Solid circles represent known taxa, open circles hypothesized ancestors.

of taxa above the rank of family group), the name of a split paraphyletic entity should be abandoned altogether (rather than be retained to denote one of the division products) when the splitting is at all extensive. In the case of paraphyletic entities which have not originally been established in the aforementioned manner, widening will often yield the most informative result and it is particularly appropriate, where the ground plan of the paraphyletic entity (and hence of the widened monophyletic taxon) is truly distinct from neighbouring monophyletic taxa.

Michener's recent (1978) criticism of phylogenetic systematics is, in my opinion, largely based on a misunderstanding of the treatment of paraphyletic entities by proponents of this school of systematics. Michener illustrates his point by outlining one consequence for Diptera systematics if it were true that the fleas (Siphonaptera) have their closest relatives among nematoceran flies of a pre-mycetophilid lineage (as suggested by Rohdendorf; Michener himself makes express reservations about the actual relationships in this example). Michener states, that "Because of their phenetic distinctiveness, virtually everyone regards fleas as a separate order and, so far as I know, *wishes to continue to do so instead of making them a family of the Nematocera*" (italics mine). He then expounds how cladists with this view would be forced to subdivide the Diptera so that "all the dipteran families or superfamilies that diverged below the mycetophilid line... would have to become separate orders". Certainly, such splitting of the Diptera at the ordinal level would be unwieldy. But I think Michener is mistaken in the belief that cladists generally would wish to retain the fleas as a separate order if the relationships of the group were as outlined. Certainly most cladists would have no hesitation in making fleas a subordinate taxon within the Diptera if it were known for certain that their closest relatives were a group of flies (the Diptera, incidentally, already contain a number of smaller apterous groups which phenetically are extremely aberrant). The downgrading of an overall specialized animal group A as an entity subordinate in another group B need not impede the recognition of (and, for instance, teaching about) the specializations of A; moreover, this arrangement provides some information (viz. the evolutionary background of these specializations) which would not be inherent in the classification if A were retained as a separate high-rank taxon. The reason why fleas are not now placed within the Diptera (or the Mecoptera) in the phylogenetic insect system is simply that their ground plan includes some plesiomorphic traits which, according to our present interpretations, appear to forbid such placement. It is for the same reasons that the lice are currently excluded from the Pscocopetera and the Strepsiptera from the Coleoptera (Kristensen 1981), and whether the exclusions shall continue to be upheld is dependent only upon future assessments of the validity of these interpretations.

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