

AN EXTENSION OF THE SMRS CONCEPT INTO A
PHYLOGENETIC CONTEXT

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ABSTRACT: This paper examines the difference between hierarchically related organisms and groups standing alone by studying the concept of the specific mate recognition system (SMRS). The notion that SMRS systems qualify as group-level features is introduced. A distinction is made between SMRS systems as group-level features and organismal characters of the SMRS. The notion that the ability to interbreed is a primitive feature of a clade is refuted.

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One of the fundamental tenets of evolutionary theory is that homologies provide evidence for a historical pattern produced by common descent (Darwin 1859). Some authors have proposed that the ability to interbreed with different organisms be viewed the same way other characters are, in terms of descent. For example, both Rosen (1979) and Nelson (1989) hold that the ability to interbreed is a primitive feature of a clade.

Most characters, including reproductive traits, can be polarized into primitive and derived states, and in a phylogenetic context this allows organisms to be arrayed hierarchically according to differing degrees of relatedness. The same may not be true of the features of interbreeding systems belonging to groups of sexually reproducing organisms. Such features have been dubbed the specific mate recognition system (SMRS) by Paterson (1980). The SMRS is a fertilization system which allows the initiation of reproductive interactions by signalling between mating partners or their cells (Paterson 1985). The SMRS is thus both a group-level feature which requires a male and a female in order to operate, and an organism-level character of those males and females. Paterson's SMRS-based view of species (his 'recognition concept') sees the limits of interbreeding as defining the species' boundary.

When we consider SMRS systems as group-level features, organisms are either included in, or excluded from, an SMRS-based species. There is no spectrum of degree of difference and no nested pattern of resemblance among specific mate recognition systems. Conspecifics will not interbreed with their sister-species nor with a species in a different phylum. Thus, there is no way to use different SMRS systems to relate organisms phylogenetically.

While the SMRS systems of species are essentially non-comparable, male or female reproductive traits, when considered separately, clearly can be homologized and used, like any other character in conventional phylogenetic analysis. For example, many characters are relevant for assessing the phylogenetic relationships of the three taxa *Homo sapiens*, *Felis leo*, and *Crocodilus niloticus*. If we were to confine our analysis to the SMRS of the three species, however, we would have no way of determining the relationships of these three

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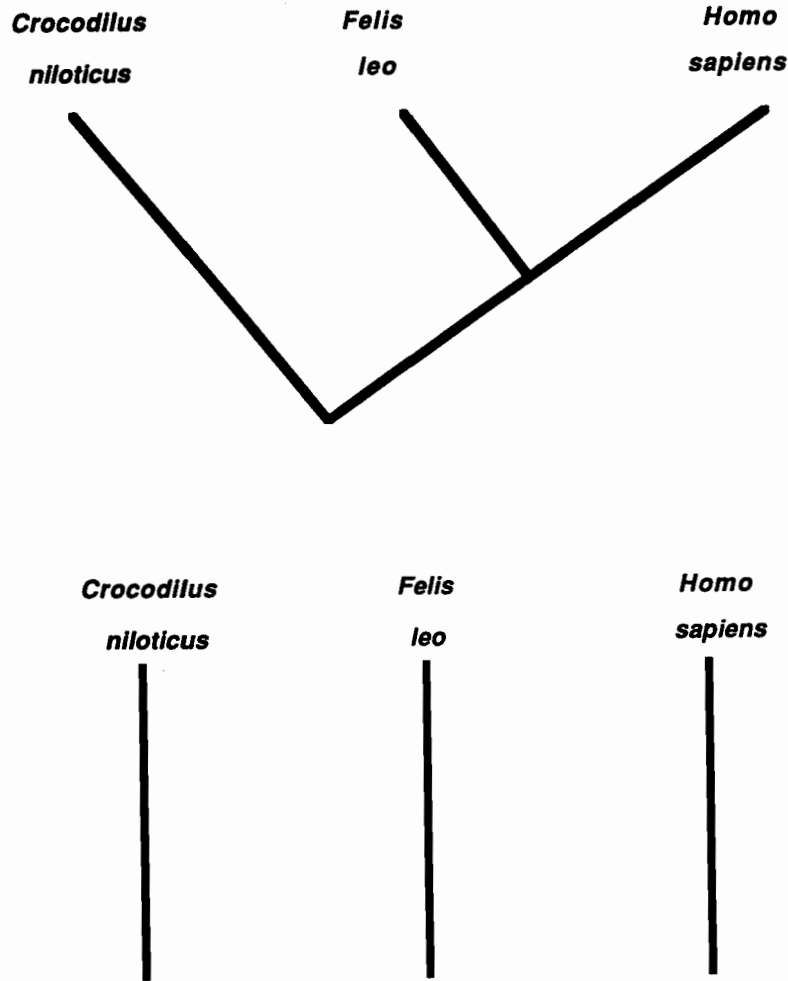


FIGURE 1-- This figure illustrates the difference between a potential phylogeny depicting the relationships of three taxa deduced from character analysis, and the same three taxa that could be separated, but not related, by the existence of their specific mate recognition systems (SMRSystems).

 taxa. They would simply be separated (See Figure 1).¹ Other anatomical characters may potentially be homologized and could demonstrate affinity. These characters may include components used in the SMRSystems of males and females - for example, the uterus. The uterus is a component of the reproductive anatomy of females of mammalian species, and it is also a synapomorphy of mammals. Other examples include horns, which are an important component of the SMRS of bovids (Vrba 1980, 1984). Vrba's (1979) phylogenetic analysis of the alcelaphine antelopes uses certain characters of their horns as

¹ However, in plants there may be differing degrees of reproductive compatibility between different 'species' which could conceivably be related as a transformation series (Mishler pers. comm.).

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characters. However, as components of an SMRS both of these characters only exist as part of a joint male-female package. The SMRS is an overarching group-level property because the SMRS cannot be ascribed to a single organism. Both a male and female are required for the SMRS to exist. This implies that species are biological entities that have real properties. These group-level properties are to be construed as features that lack phylogenetic information, but which can be used to separate species. Organisms have characters, and these can be used to establish phylogenetic relationships.

These differing conceptions of the SMRS correspond to de Queiroz and Donoghue's (1988, 1990) important analysis of species and taxa that emphasizes the difference between descent criteria and exclusivity of relationship (reproduction). The analysis herein views these two qualities of life as corresponding to the difference between organismal characters and group features of the SMRS, respectively, and this has relevance for Rosen's (1979) and Nelson's (1989) claim that the ability to interbreed is primitive.

Because evolution is a dynamic process, we should expect to see patterns in SMRS systems that are analogous to continuous or intergrading morphological features.

"If we look at a large number of such arrays (that is species), it is only natural that we should find a few that are just going through the process of breaking up. This does not invalidate the reality of these arrays; just as the Paramecium 'individual' is a perfectly real and objective concept, we find in most cultures some individuals that are either conjugating or dividing (Mayr 1942, p.152)."

Such intermediates typically manifest themselves as patterns of mating asymmetry in which females of a derived group accept males from an ancestral group whereas females of an ancestral group will typically not mate with derived males (Kaneshiro and Kurihara 1981). Such cases, documented for drosophilid flies in Kaneshiro and Giddings (1987) and Kaneshiro and Boake (1987), represent cases of incipient speciation in which full-fledged SMRS systems have not yet developed. Asymmetric patterns of mating during incipient speciation clearly exist in flies, and the direction of female choice may be phylogenetically informative. That is to say, there can be phylogenetic differentiation within a single SMRS. However, if at a later time mating experiments unambiguously show that these groups do not interbreed, then these groups can merely be separated and not related by their SMRS systems. Phylogenetic patterns may exist within a single SMRS. However, once SMRS systems have become distinct, they can no longer be used to elucidate phylogenetic relationships.

CONCLUSIONS

In the past systematists have encountered difficulties when they attempted to apply the biological species concept to their taxonomic system (see Mishler and Donoghue 1982; Donoghue 1985). This is because differentiated historical entities (taxa), such as kin-groups, 'sub-species', and the like, exist within larger groups of potentially interbreeding organisms (de Queiroz and Donoghue 1988). This has led to assertions that inclusive reproductive criteria are inadequate for

the recognition of species. However, because SMRSystems cannot be compared they are different from other characters; they do not necessarily make sense if used to reconstruct history. SMRSystems as group-level features cannot be polarized into primitive and derived states like attributes of single organisms. Thus, SMRSystems can never be primitive [contra Rosen (1979) and Nelson (1989)]. They only exist as unique features of species. These SMRSystems can only be related after the history of a group has been elucidated by other characters. Such characters may be parts of males and/or females that are used in specific mate recognition.

In addition, because of the principle of common descent, evolution is an historical process, and components of the SMRS in closely related species will be similar. The study of the features of interbreeding groups and the characteristics of organisms in those groups may prove very important, for their interaction occupies the nexus between pattern/process and macro/micro-evolutionary approaches.

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