



## Character Definitions, Sexual Selection, and the Evolution of Swordtails

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## NOTES AND COMMENTS

CHARACTER DEFINITIONS, SEXUAL SELECTION,  
AND THE EVOLUTION OF SWORDTAILS

Recent years have seen increasing awareness of the utility of comparative studies using phylogenies to test hypotheses of evolutionary process (e.g., Felsenstein 1985; Donoghue 1989; Brooks and McLennan 1991). The importance of accurate estimates of phylogeny in such research programs has been emphasized repeatedly. Yet, the conclusions of these studies can also depend critically on how traits are defined and interpreted in the light of the phylogeny. This point is well illustrated in a recent article by Meyer et al. (1994).

Meyer et al. (1994) call into question the preexisting bias hypothesis of sexual selection as an explanation for the evolution of the elongate caudal fin (the "sword") in the fish genus *Xiphophorus*. The preexisting bias hypothesis predicts that sexually selected male traits (such as the sword) arise after the evolution of female preference for these traits (Basolo 1990a). Based on their phylogeny derived from DNA sequence data, Meyer et al. (1994) suggest that the sword's appearance is not subsequent to the evolution of female preference, in contrast to conclusions drawn from a morphology-based phylogeny (Basolo 1990a).

Yet, the conclusions of Meyer et al. (1994) depend on what they considered to be a sword. Their preferred interpretation of the evolution of the sword is that a short caudal fin extension (0.1–0.3 times the length of the caudal fin) is equivalent to a full sword (0.7–6.0 times the length of the caudal fin) and that the ancestor of the genus therefore had a sword (their fig. 4, our fig. 1A). Meyer et al. (1994) do not consider the coloration of the caudal fin in their definition of the trait.

Although Meyer et al. (1994) believe they refute Basolo's (1990a) hypothesis, their claim is based on a different definition of sword. Basolo (1990a) considers a sword to be a colored extension of the caudal fin and one that is 0.7–6.0 times the length of the caudal fin (Basolo 1991). This definition clearly has some biological justification. Female preference for males with short caudal protrusions has not been demonstrated, and in those species in which there is only a short caudal protrusion (*X. andersi*, *X. birchmanni*, *X. continens*, *X. pygmaeus*, *X. xiphidium*), the protrusion is colorless (except in some individuals of *X. birchmanni*; Rauchenberger et al. 1990). Basolo (1990a) found that females respond to males with colorless swords the same as to males with no caudal protrusion whatsoever. This observation strongly suggests that the presence of a short, colorless caudal fin protrusion and the swordless condition are the same in the eyes of the female.

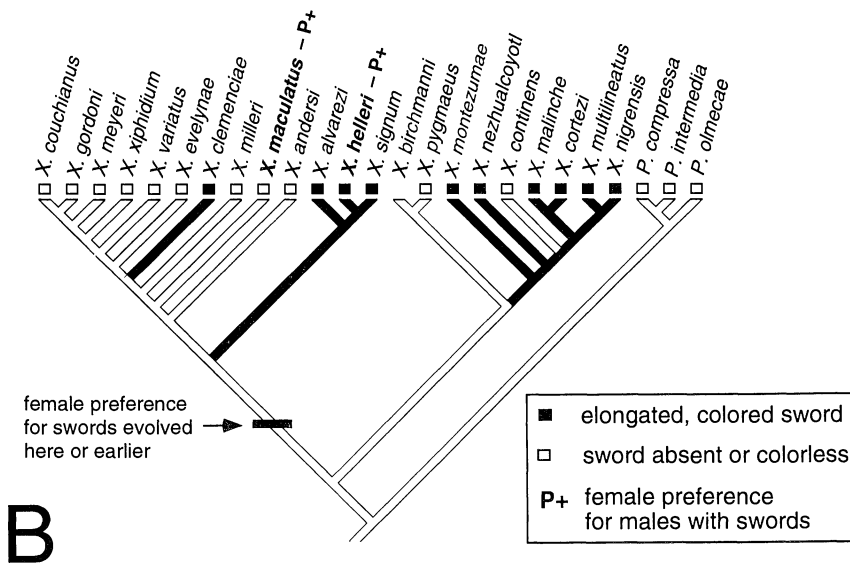
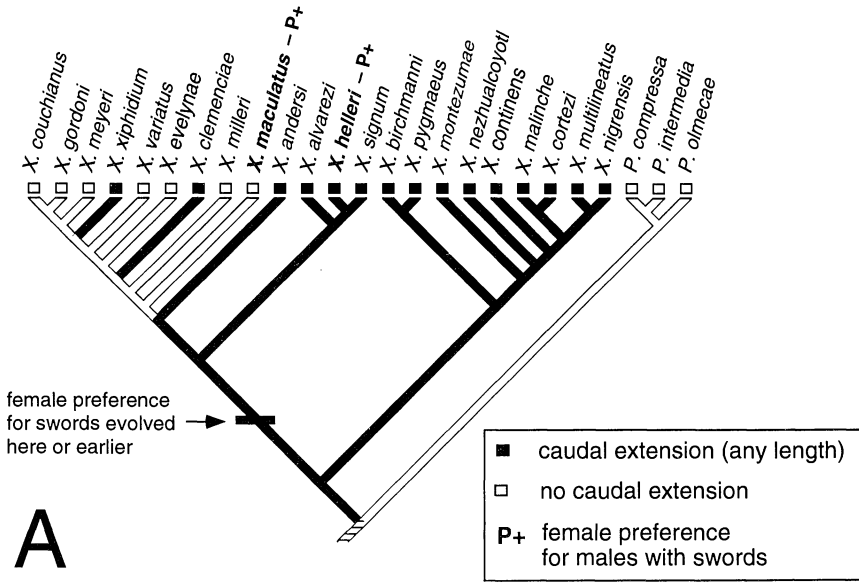


FIG. 1.—Evolution of the sword mapped onto the preferred molecular phylogeny of Meyer et al. (1994; their fig. 4) for species of *Xiphophorus* (swordtails and platyfishes) and *Priapella*, using MacClade 3.01 (Maddison and Maddison 1992). *A*, When the sword is defined as an extension of the caudal fin of any length, the sword may appear before evolution of female preference for the sword (consistent with the interpretation of Meyer et al. 1994). *B*, When the sword is defined as an elongated, colored extension of the caudal fin (taking into consideration the demonstrated preference of females for colored caudal extensions; Basolo 1990a), female preference for colored swords evolves before the sword, and the Meyer et al. (1994) phylogeny does not reject but instead supports the preexisting bias hypothesis in *Xiphophorus*. Because of intraspecific variability in the presence and absence of the caudal fin extension and its coloration, *X. birchmanni* was treated as unknown (“?”).

Using Basolo's (1990a) definition of the sword, one finds that the implication of the Meyer et al. (1994) tree for the preexisting bias hypothesis of sexual selection is reversed. When the presence or absence of the elongated, colored protrusion (referred to hereafter as the sword) is mapped onto the tree used by Meyer et al. (1994) using MacClade 3.01 (Maddison and Maddison 1992), the most parsimonious interpretation is that the sword was absent in the ancestor of *Xiphophorus* and evolved independently three times within the genus (fig. 1B). The two species in which female preference for swords had been tested (*X. helleri* [Basolo 1990b] and *X. maculatus* [Basolo 1990a]) are nested within a clade in which the absence of the sword is primitive. Within that clade, the most parsimonious interpretation is that the female preference for the sword evolved before the sword itself. Thus, the tree of Meyer et al. (1994) supports rather than rejects the preexisting bias hypothesis of sexual selection in *Xiphophorus*.

Clearly, the available data on female preference in *Xiphophorus* are very limited and must be expanded considerably before a strong conclusion can be reached. Furthermore, different interpretations of the evolution of the sword do not differ greatly using a simple parsimony criterion, even when using the same tree and the same definition of the sword (e.g., four versus five steps for the ancestor to be reconstructed as "sworded" versus "swordless"; Meyer et al. 1994). Future studies should include greater sampling of species for female preference, phylogenies based on diverse types of data, and careful coding, mapping, and testing of the evolution of the morphological and behavioral traits in question. The present studies of *Xiphophorus* (Basolo 1990a; Meyer et al. 1994) have provided a real example in which using different definitions of a character can be as influential as using different phylogenies in testing evolutionary hypotheses.

*Note:* The recent observation that females of *X. variatus* (in which the males lack swords) prefer male models with elongate, colored swords (Haines and Gould 1994) was unknown to Basolo (1990a) and Meyer et al. (1994), but it is consistent with both of their interpretations.

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