

# The evolution of sexually selected traits in male swordtail fishes (*Xiphophorus*: Poeciliidae)

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Sexual rather than natural selection can account for the evolution of exaggerated male ornaments that appear to be detrimental to survival. Such a sexually selected trait is the sword-like caudal fin extension in males of species that belong to the genus *Xiphophorus*. Swordtail fishes feature prominently in empirical work and theories of sexual selection. Recently, the pre-existing bias hypothesis was offered as an explanation for the evolution of swords in these fishes. Under this hypothesis, the female preference was postulated to predate the origin of the male's sword and to have driven its evolution directly. A reconstruction of the evolution of this trait, using a traditional, largely morphology-based phylogeny of this genus, and recent behavioural experiments suggest that female preference for mating with sworded males arose in ancestrally swordless species. The applicability of the pre-existing bias hypothesis is questioned, however, by a molecular phylogeny of *Xiphophorus*, which differs from the traditional one. It demonstrates that some features (e.g. possibly coloration and black ventral margin) of the character complex 'sword' are likely to have been present in the common ancestor of all species of *Xiphophorus*. The propensity to develop ventral caudal fin extensions is intra-specifically variable in several *Xiphophorus* species; this variation may be phylogenetically widespread and plesiomorphic for poeciliid fishes. It is shown that many male secondary sexual characters are evolutionarily labile. They are probably more easily lost and regained than are female preferences for them, which might be phylogenetically more resilient to change. Differences in the rates of evolution of female preference and male traits might be caused by stronger natural selection pressures on males than on females.

**Keywords:** character coding, comparative method, pre-existing bias hypothesis, sexual selection.

## Introduction

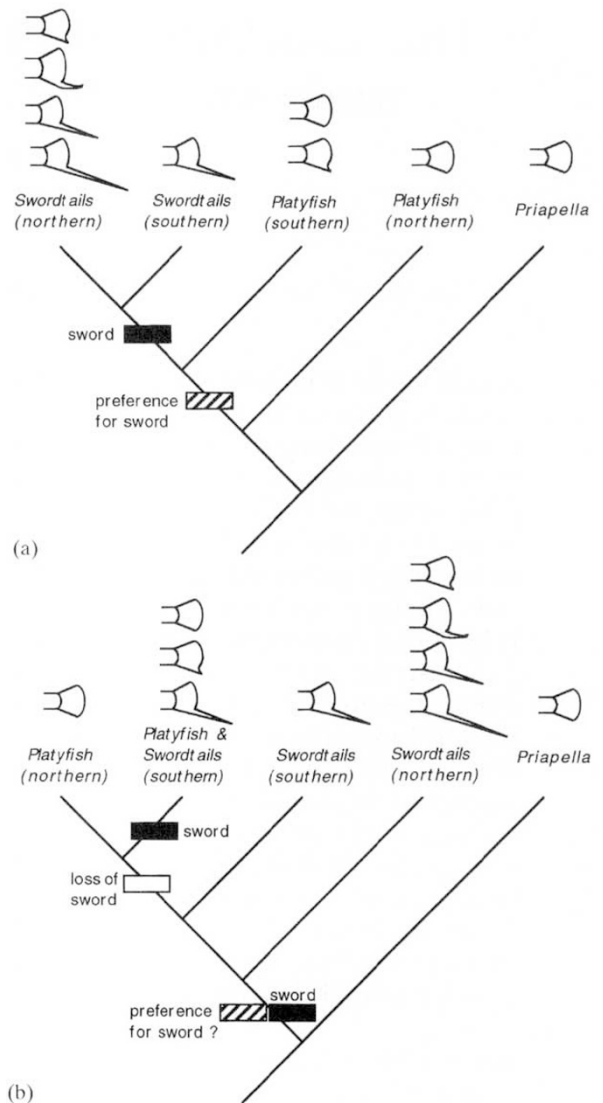
Several classic 'co-evolutionary' models of sexual selection (e.g. reviewed in Bradbury & Anderson, 1987; Maynard Smith, 1987, 1991; Partridge & Harvey, 1987; Pomiankowski, 1988; Schluter & Price, 1993; Iwasa & Pomiankowski, 1995) and, more recently, the 'sensory exploitation' hypothesis (e.g. reviewed in Ryan, 1990; Kirkpatrick & Ryan, 1991; Pomiankowski, 1994; Shaw, 1995) attempt to explain the exaggerating evolution of the male's secondary sexual traits. In the latter hypothesis, a presumed 'pre-existing bias' in the female's sensory system through any physiological, e.g. neurological, bias allowed males to 'exploit' the females' bias in

order to increase their mating advantage (Basolo, 1990a, 1991; Ryan, 1990; Ryan *et al.*, 1990; Kirkpatrick & Ryan, 1991; Ryan & Rand, 1993). Males accomplish this by evolving and exaggerating the structure to which the females respond favourably. Unlike other models of sexual selection, the sensory exploitation hypothesis attempts to explain not only the continued increase in secondary male structures but also their evolutionary origin. Through the comparative method (Felsenstein, 1985), phylogenies can serve to reconstruct the evolutionary history of male traits and female preferences when information about them is available. The validity of the pre-existing bias hypothesis can be tested in an explicitly phylogenetic context (Felsenstein, 1985), as the evolutionary origin of the male trait must occur later than the proposed origin of the females' bias.

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In only a few examples has the pre-existing bias hypothesis been implicated to account for the evolution of secondary male traits (recently reviewed by Shaw, 1995). One of the two prominent examples is the swordtails and platyfishes of the genus *Xiphophorus*. The pre-existing bias hypothesis was proposed to account for the origin and continued evolution of swords, ventral elongations of the caudal fin of males, in some species of this genus (Basolo, 1990a, 1991). This suggestion is based on a set of choice experiments (Basolo, 1990a,b, 1995a), in which females from swordless southern platy species (*Xiphophorus maculatus* and *X. variatus*) were observed to spend more time on the side of a choice chamber where males with artificial swords were visible than on the side with swordless, or colourless sworded, specimens. The traditional phylogeny of fishes of the genus *Xiphophorus* (Rosen, 1979; Rauchenberger *et al.*, 1990) suggested that the generally swordless platy fishes (Fig. 1a) are basal in the genus *Xiphophorus*, and the typically sworded swordtails are derived (Fig. 1a). Hence, the behavioural experiments were interpreted as showing that females of the common ancestor of the unsworded *X. maculatus* (a southern platyfish) and the sworded *X. helleri* (a southern swordtail) possessed a preference for a sword-like structure. The (traditional) phylogenetic hypothesis also implied that males of this common ancestral species were unsworded. Hence, the pre-existing bias appears to have evolved before the sword itself, and the sword may thus subsequently have arisen in the swordtail clade (Basolo, 1990) (Fig. 1a).

In the light of the traditional hypothesis, these interpretations of the behavioural observations seem perfectly reasonable. However, a new DNA-based phylogeny based on almost 1300 nucleotides from two mitochondrial and one nuclear gene from all 22 species of the genus *Xiphophorus* (Meyer *et al.*, 1994; Lockhart *et al.*, 1995) (Figs 1b and 2) calls this interpretation into question (see also Pomiankowski 1994; Shaw, 1995). It suggests that the northern swordtail clade is the sister group of the southern swordtail plus platyfish clade (compare Figs 1a, b and 2). The molecular phylogeny (see original papers for details on the estimations of the phylogenetic hypotheses based on these DNA sequences) suggests that the evolution of ventral caudal fin extensions (see discussion about the definition of this trait below) coincides with or possibly predates the evolution of the females' preference for males with swords (Fig. 1b). The sword is likely to have evolved in the common ancestor of the genus, been lost and then re-evolved (Fig. 3). Thus, the



**Fig. 1** (a) Simplified traditional morphology-based phylogenetic hypothesis for the four species groups of fishes of the genus *Xiphophorus* (Rosen & Bailey, 1963; Rosen & Kallman, 1969; Rosen, 1979; Rauchenberger *et al.*, 1990). *X. andersi* and *X. xiphidium* are two species of southern platyfish with a small sword. Based on current phylogenetic knowledge, it appears that *Priapella* is the sister group (its males do not have elongated coloured swords) to *Xiphophorus* (Rosen & Bailey, 1963; Rosen & Kallman, 1969; Rosen, 1979; Meyer *et al.*, 1994). This phylogeny might suggest that the swordless condition is ancestral, and the sworded condition is derived. (b) Simplified phylogeny of the major groups of *Xiphophorus* fishes, based on Meyer *et al.* (1994), suggests that the sworded condition might be ancestral for the genus and that preference for swords might therefore have coevolved with swords or occurred later than the evolution of swords; swords might also have been lost and regained. Caudal fin shapes are shown to indicate the predominant lengths of caudal fin extensions in species found in each of these clades.

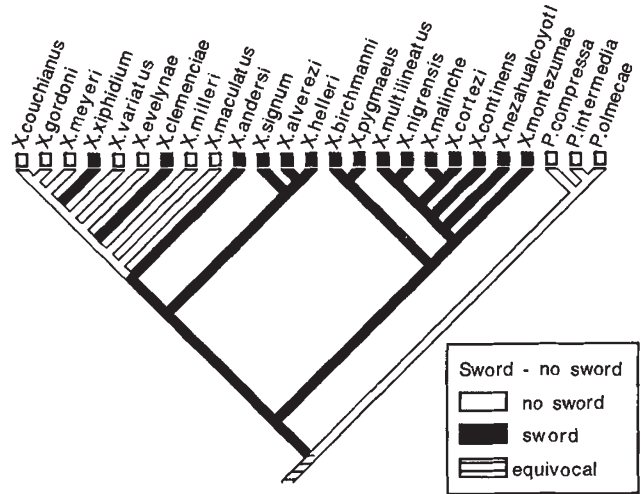
pre-existing bias hypothesis might not account for the evolution of swords in swordtails.

Female preference has been tested in only three of the 22 species of swordtail fishes and recently also in a closely related species, *Priapella olmecae* (Basolo, 1995b). By revisiting this issue here, difficulties in the reconstruction of the evolution of female preferences and male traits, and hence their interpretation in the light of sexual selection theory, are highlighted. The analysis is complicated not only because of the lamentable lack of data on female preference but also because of the widespread phylogenetic distribution of some male traits, population variation and definitional issues about some male secondary sexual traits.

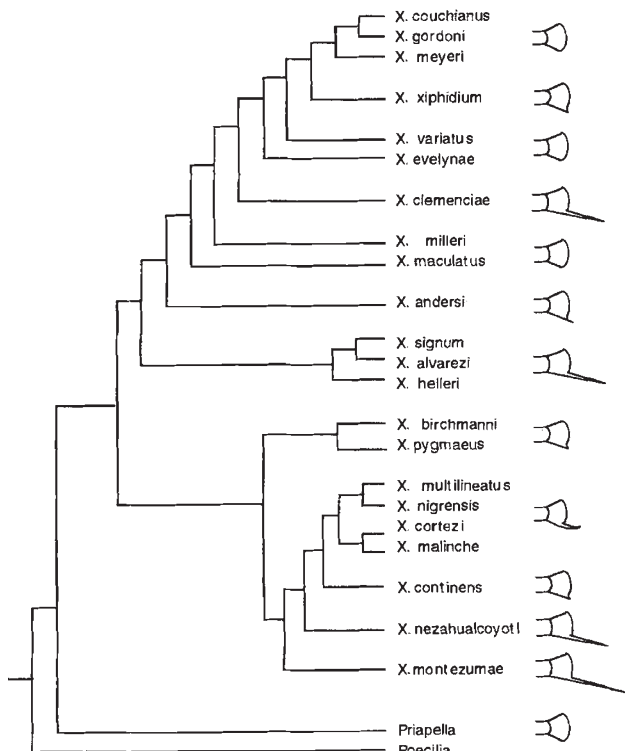
**Results**

*Coding swords as two- or three-character state traits and as ordered or unordered*

Mapping (MacClade Version 3.01; Maddison & Maddison, 1992) sword character state evolution on the molecular phylogeny was carried out using the



**Fig. 3** Most parsimonious reconstruction (MacClade 3.01; Maddison & Maddison, 1992) of the evolution of the sword in *Xiphophorus* (treated as a two-state character: sword – no sword), based on the molecular phylogeny (Fig. 2), would suggest that the common ancestor most likely possessed a sword (four steps) (see also fig. 4 in Meyer *et al.*, 1994 and fig. 1a in Wiens & Morris, 1996). Forcing the ancestor of the genus to be swordless adds one more step.



**Fig. 2** Simplified DNA-based maximum parsimony phylogeny (see Meyer *et al.*, 1994 and Lockhart *et al.*, 1995 for details) showing the typical tail lengths for all 22 described species of *Xiphophorus*.

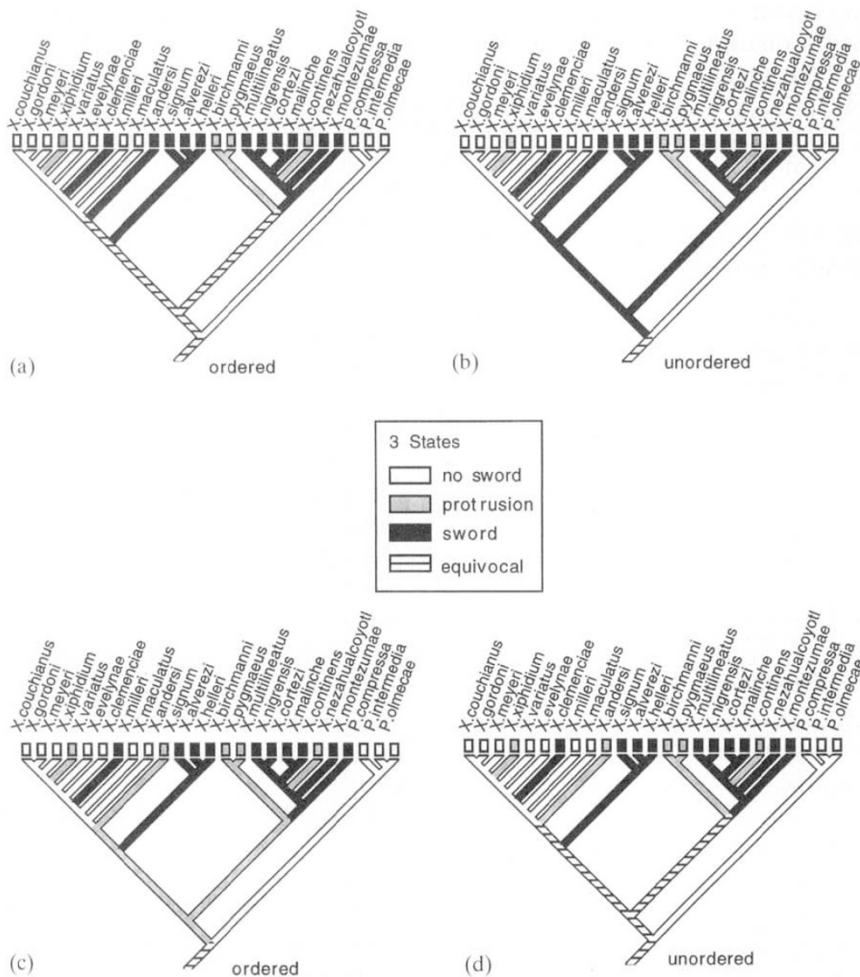
comparative method of Felsenstein (1985) in two different ways. First, a two-state character definition (sword/no sword) was adopted that ignored the size of the sword. Under this hypothesis, the common ancestor of the genus was inferred to have been sworded (four steps); forcing the ancestor to be swordless required an extra step (Fig. 3). This implies that swords might have been present in the common ancestor of all swordtail fishes (Meyer *et al.*, 1994).

Secondly, a three-character state definition was adopted that took three length classes into consideration (no sword, protrusion and sword) (Fig. 4a, b). If the character states are coded in this manner, then *X. birchmanni*, *X. pygmaeus*, *X. continens* and *X. xiphidium* have a ‘protrusion’, whereas *X. andersi* has a longer ventral extension that is considered a sword (Meyer & Schartl, 1980) (Fig. 2). If it is further assumed that the trait evolved in an ordered fashion [i.e. protrusion (P) is an intermediate step in the evolution of swords (S) from no swords (NS), NS–P–S], then the common ancestor of all species of *Xiphophorus* most likely had a protrusion or a sword (both nine steps) (Fig. 4a). Under these conditions of reconstruction, 10 steps would be required if the ancestor was swordless. If NS–P–S character state transitions are treated as unordered, the common ancestor is likely to have been sworded

(six steps) (Fig. 4b) rather than unsworded or possessing a protrusion (both seven steps).

A further complication is that *X. andersi*'s ventral elongation could be considered a protrusion rather than a sword. Under this hypothesis, if the character state changes are treated as ordered, then the

common ancestor of all species of *Xiphophorus* was more likely to have had a protrusion (eight steps) (Fig. 4c) rather than no sword or a sword (both nine steps). If the character evolution is assumed to be unordered, the common ancestor is equally likely to have had a protrusion as not (all three require seven



**Fig. 4** Mapping of the traits 'no sword', 'protrusion' and 'sword', following Basolo's (1991) definition (except coloration and black ventral margin; see Fig. 5), on the phylogeny. Here, the character 'sword' is treated as a three-state character (no sword–protrusion–sword). If the characters are coded in this manner, then *Xiphophorus birchmanni*, *X. pygmaeus*, *X. continens* and *X. xiphidium* have a protrusion and *X. andersi* possesses a sword [(a) and (b)]. The other species are classified as sworded and unsworded based on typical sword lengths in Fig. 2. In (a) and (c) the transition is treated as 'ordered' [i.e. protrusion is an intermediate step in the evolution of swords from no swords, NS–P–S: (a) and (c)]. (a) Nine steps required, common ancestor equally likely to have had a sword or a protrusion, 10 steps required for a swordless ancestor. (b) Same treatment as in (a), but character state transition is unordered, six steps required and the ancestor is likely to have been sworded; protrusion or swordless ancestral condition would require seven steps. The effect of reclassifying *X. andersi* as having a protrusion rather than a sword is shown in (c) and (d). (c) Eight steps required, the common ancestor is more likely to have had a protrusion than no sword or a sword both of which require nine steps. (d) Same treatment as in (c), but character state transition is unordered. Seven steps are required for all three possible ancestral states for the common ancestor of the genus.

steps) (Fig. 4d). It should be mentioned that there is extensive population variation in terms of the length of the caudal fin in most sworded *Xiphophorus* and that both age and social rank also influences the length of the sword in males (Zander, 1969; Zander & Dzwillo, 1969; M. Schartl, personal communication).

#### The trait 'sword' as a character complex including coloration and black ventral margin

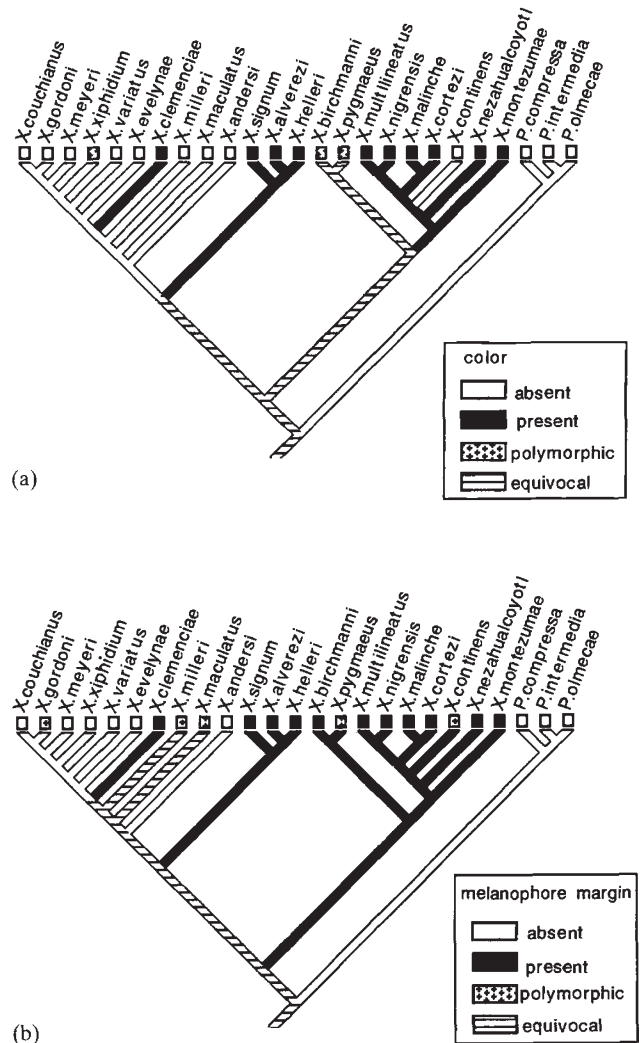
These above-mentioned reconstructions of ancestral states of the sword only consider its length. They ignore coloration and black margins in the sword. Most researchers on swordtails regard extensions on the ventral end of the caudal fin alone as swords (e.g. Rosen & Kallman, 1969; Meyer & Schartl, 1980; Rauchenberger *et al.*, 1990, p. 20). However, Basolo (1991) applies a more restrictive definition to the character complex 'sword', which not only includes length (a sword as a ventral extension is  $0.7\text{--}6.0 \times$  the length of the caudal fin, and a 'protrusion' as a ventral extension is  $0.1\text{--}0.3 \times$  the length of the caudal fin), but also includes coloration of the sword and the presence of a black ventral margin. Three traits of the composite character complex 'sword', (i) its length, (ii) its coloration and (iii) the presence of a black ventral margin, vary between, and in some cases within, species (see below) (e.g. Fig. 2 and discussions in Rauchenberger *et al.*, 1990). The evolution of these three features are all parts of Basolo's (1990) definition of 'coloured swords', and their evolution can be reconstructed using the DNA-based molecular phylogenetic hypothesis.

Adoption of Basolo's (1991) definition of swords results in the reclassification of five species (*X. birchmanni*, *X. pygmaeus*, *X. continens*, *X. xiphidium* and *X. andersi*) from being sworded (Fig. 2) or having a protrusion (Figs 2 and 4c, d) to having a colourless no-sworded condition. Hence, if coloration as well as length of the ventral extension of the caudal fin is considered, then the composite trait 'coloured swords' would have evolved independently at least three times in the genus and the common ancestor will have lacked colour (Wiens & Morris, 1996; but see Fig. 5a) but have had a ventral caudal fin extension of some kind (Figs 3 and 4).

#### Sword characteristics other than length

The reconstruction of coloration at the ventral margin of the caudal fin is somewhat complicated because there is intraspecific (and ontogenetic) vari-

ation in terms of the degree of coloration in some species of northern swordtails (e.g. *X. birchmanni* and *X. pygmaeus*; Rauchenberger *et al.*, 1990; Wiens & Morris, 1996; M. Schartl, personal communication) and southern platyfish (*X. xiphidium*; M. Schartl, personal communication) (Fig. 5a). Considering this intraspecific polymorphism in the character state reconstructions makes it equally



**Fig. 5** (a) Reconstruction of coloration of the caudal ventral extension (irrespective of length). Males in several species (e.g. *X. birchmanni*) are polymorphic for the presence or absence of coloration and black ventral margin of their caudal fin extensions. The ancestor is as likely to have had a coloured as a colourless ventral caudal fin extension. (b) Reconstruction of the presence of melanophores at the ventral edge of the caudal fin. Again, several species are polymorphic for the presence of the trait (see text). The *Xiphophorus* ancestor is as likely to have had a black margin at its caudal fin as not.

parsimonious that the common ancestor of the genus *Xiphophorus* did or did not have colour in its ventral caudal fin margin (Fig. 5a).

It has recently been shown that females of the southern platy species *X. variatus* prefer to spend time with males with a ventral black margin in their caudal fin rather than with males that do not possess this trait, although males of this species do not have this trait (Basolo, 1995a). The reconstruction of the presence of melanophores at the ventral edge of the caudal fin showed that the *Xiphophorus* ancestor is as likely to have had a black margin as not (Fig. 5b). Interestingly, variable presence of black ventral margins is known in some *Xiphophorus* species (e.g. *X. maculatus* and *X. gordonii*; Basolo, 1995a; *X. milleri* and *X. pygmaeus*; M. Scharl, personal communication). Moreover, intraspecific variability occurs in most populations of *X. birchmanni* (Rauchenberger *et al.*, 1990), and this trait is also found in poeciliids outside of this genus (e.g. always in *Poecilia petenensis*, and in some populations of *P. reticulata* and *P. latipinna*). Also, the dorsal black margin of the sword is sometimes not fully developed (e.g. in *X. multilineatus*) or is lacking entirely in some populations that otherwise typically have a complete 'coloured sword' (e.g. *X. nigrensis*; Rauchenberger *et al.*, 1990). In *X. maculatus*, the presence of a black ventral margin of the caudal fin is coupled with the presence of melanophores in the gonopodium, a modified anal fin that serves in internal fertilization (M. Scharl, personal communication). The presence of melanin in the gonopodium is a polymorphic trait in both *X. variatus* and *X. milleri* (M. Scharl, personal communication). Black gonopodia are found in males of the genus *Brachyrhaphis*, in which the gonopodium is also emphasized with yellow or orange coloration. Males of several other species of poeciliid fishes highlight the ventral and dorsal margins of their caudal fins with light rather than with black margins (e.g. *Priapella compressa* and *P. intermedia*).

## Discussion

Recent developments in sexual selection theory (Schluter & Price, 1993) have predicted that differences in male traits will be larger than variation in female preferences, as male traits will be more susceptible to variation in environmental conditions and natural selection than are female preferences. However, knowledge about preferences is slight and the degree of intra- and interspecific variation in

female preferences is largely unknown. Iwasa & Pomiankowski (1995) recently showed that Fisher's runaway process is intrinsically unstable and would promote the continuous change in a sexually selected trait through a cyclic change in female preference and the male's response to it. Based on current phylogenetic knowledge, it is apparent that male traits in the genus *Xiphophorus* are remarkably labile (within and between species), because length, coloration and melanophores in the ventral margin of the sword seem to be lost and/or regained many times and evolve relatively quickly and independently, despite the fact that females presumably prefer to mate with males that have all of these characteristics strongly developed. There is also sometimes considerable variation for some of the characteristics of the sword among populations — e.g. for *X. maculatus* and *X. gordonii* (in the black ventral margin, see Fig. 5b), *X. birchmanni* and *X. pygmaeus* (black ventral margin and coloration of the sword), *X. xiphidium* and *X. pygmaeus* (in coloration; M. Scharl, personal communication), *X. montezumae* and many others (extensive variation in the length of the sword).

### *The homology of ventral caudal fin extensions in poeciliid fishes*

The issue of homology as it pertains to the sword and the applicability of the pre-existing bias hypothesis needs to be touched on briefly. Protrusions and swords are likely to be homologous structures. Developmental and genetic evidence exists that has some bearing on this issue (Gordon *et al.*, 1943; Dzwillo, 1963, 1964; Zander, 1967, 1969; Zander & Dzwillo, 1969). Both structures share positional homology and are made up of the same structures morphologically (e.g. Dzwillo, 1963, 1964; Rosen & Bailey, 1963; Rosen & Kallman, 1969; Zander & Dzwillo, 1969; Rosen, 1979; Meyer & Scharl, 1980; see Rauchenberger *et al.*, 1990 for discussion). Moreover, hormonal treatment of typically swordless species will lead to the expression of protrusions or elongations of already existing swords in four of the eight species tested (e.g. in *X. maculatus*, *X. milleri*, *X. pygmaeus* and *X. helleri*; Dzwillo, 1963, 1964; Dzwillo & Zander, 1966; Winkvist *et al.*, 1991). These hormone experiments support the suggestion that 'sword genes' are present even in typically swordless species and that the expression of protrusions and swords is under similar genetic control (Zander & Dzwillo, 1969; Meyer *et al.*, 1994).

Furthermore, as ventral caudal fin extensions can be artificially selected for in *Poecilia reticulata* (e.g.

Schröder, 1974) (Fig. 2) and coloured protrusions are present in all males of *Poecilia petenensis*, this trait may be evolutionarily older and phylogenetically much more widespread in poeciliid fishes than only in the genus *Xiphophorus*, and might even be a widespread characteristic of the whole family of Poeciliidae (Meyer *et al.*, 1994).

#### *The relevance of protrusions for the pre-existing bias hypothesis*

It has recently been suggested (Wiens & Morris, 1996) that the presence of protrusions (Figs 4 and 5) or uncoloured swords in the common ancestor of *Xiphophorus* fishes are of no importance in assessing the pre-existing bias hypothesis because females (at least in the species tested so far) do not respond to these structures. However, the reconstructed presence of a protrusion (which may or may not have been coloured and with a black margin; see Fig. 5) or sword in the common ancestor of all swordtail fishes, whether or not it was coloured or had a black ventral margin, is of importance for this discussion. The initial function of protrusions and swords and whether females respond to them is not relevant for the reconstruction of ventral caudal fin extensions. It matters whether these traits were already present when female preference for those modified fin extensions evolved. It would be interesting to investigate the causes and circumstances of the evolutionary origin of ventral caudal fin extensions and if they were later co-opted into their current function through sexual selection by female preference. However, as long as the origin of the male's structure predates the females' bias for it, the female bias cannot have driven its evolutionary origin, and the pre-existing bias hypothesis is unlikely to apply.

#### *Possible selective forces against 'swords'*

Opposing costs in terms of natural selection might counteract mating benefits derived from sexual selection and may be responsible for population variation and the repeated loss of swords in *Xiphophorus* fishes because swords are highly visible and inefficient for swimming (Haines & Gould, 1994; Meyer *et al.*, 1994;). Coloured swords would tend to make sworded males more visible to predators and less able to escape attacks (irrespective of coloration) (Haines & Gould, 1994). It has not been pointed out before that many of the species that lost long coloured swords are also typically smaller in body length than their sworded relatives (e.g. *X.*

*pygmaeus*, *X. continens* and most of the platy species). This might be an indication of natural selection pressures through predation on highly visible larger prey or strong natural selection against large body size through food limitations or through highly variable and unpredictable environments selecting for smaller males.

#### *Need for more behavioural work on female preferences*

Unfortunately, female preference (in general, but in particular for swords) has not been characterized in a sufficiently large number of poeciliid species (only in *X. maculatus*, *X. variatus*, *X. helleri* and *Priapella olmecae*; Basolo, 1990a,b, 1995a,b) to be mapped extensively for the genus and the family Poeciliidae (Meyer & Lydeard, 1993). The molecular phylogeny shows that it would be worth investigating female preferences from several other species of *Xiphophorus* and other genera (e.g. the highly polymorphic *X. birchmanni*). The relative strengths of preferences for length, coloration and melanophore stripe of the caudal fin extension should also be quantified. More experiments on the exact physiology of the preference, its phylogenetic distribution, the criteria of choice and the underlying behavioural mechanisms would be worthwhile (e.g. Haines & Gould, 1994). Further behavioural work on the applicability of the pre-existing bias hypothesis to the evolution of swords in the genus *Xiphophorus* and other poeciliid species is needed (some is ongoing, e.g. T. Zbaka and J. Gould, Princeton University, personal communication). Females might not simply prefer tail size but also certain attributes of the male's behaviour as, for example, tail size seems to be linked to display rate in guppies (*Poecilia reticulata*) (Bischoff *et al.*, 1985).

Behavioural work on female preferences for swords was recently extended to include work on *Priapella*, a genus related to *Xiphophorus* (Basolo, 1995b) (Figs 1 and 2). In this interesting experiment, it was shown that females of *P. olmecae* prefer to spend time with males of their species with artificial swords. Because species of this genus do not have swords, it would suggest that the common ancestor of *Xiphophorus* and *Priapella* was swordless, yet its females might have already preferred males with swords in support of the pre-existing bias hypothesis. This would constitute evidence to suggest that a bias existed in the common ancestor of this genus. In the light of the above-mentioned issues on the possibly phylogenetically widespread distribution of 'sword genes', the variable nature of sword characteristics

and the evolutionary resilience and retention of female preferences, it would be interesting to ask whether *Priapella* males or other poeciliid species respond to hormone treatment by developing swords. Finally, a complete molecular phylogeny of fishes of the family Poeciliidae (and behavioural data on female preferences) might reveal whether the suggested sister group relationship of *Xiphophorus* and *Priapella* is supported and whether this female preference is likely to have evolved only once or repeatedly in this family (Meyer *et al.*, in preparation).

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**Note added in proof**

After the submission of the final version of this manuscript an article with relevance to this issue was published: Basolo, A. L. 1996. The phylogenetic distribution of a female preference. *Syst. Biol.*, **45**, 290–307.