From the Amazonriver to the Amazon molly and back again

Poeser, F.N.

Citation for published version (APA):
Poeser, F. N. (2003). From the Amazonriver to the Amazon molly and back again. Amsterdam: IBED, Universiteit van Amsterdam.
The role of character displacement in the speciation of Central American members of the genus *Poecilia* (Poeciliidae).

FRED. N. POESER

*Department of Ichthyology. University of Amsterdam,*

*P.O. box 94766, 1090 GT Amsterdam (The Netherlands)*

**ABSTRACT**

Fishes of the genus *Poecilia* are predominant inhabitants of the Central American mainland and of the Greater Antilles. The genus also occupies specific habitats on the South American continent and adjacent islands. In Central America, there is a confusing array of species, in which morphological and meristic characters show more variation within species than between species. By applying the principle of character displacement to the genus, several regularities emerge. Three species pairs (of which one has unicusp inner jaw teeth, the other has tricuspid inner teeth for each species pair) are present, amongst which six widely dispersed species may be discriminated. A species concept based on phylogenetic and taxonomic methods is defined for the genus *Poecilia*. The application of a peculiar mode of character displacement to two species of fish from El Salvador suggests a general mechanism that explains much of the morphological variation within the Central American members of *Poecilia*. This method also defines species boundaries and patterns of speciation based on ecologically derived mechanisms.

**KEY WORDS:** *Poecilia* - Character displacement - Species pairs - Speciation.

**INTRODUCTION**

Character displacement is a controversial subject in evolutionary studies. In its preliminary form it is a fruitful mechanism, explaining many observed distribution patterns in fish communities. Originally, character displacement was observed (and subsequently defined) as variation of morphological features within species, or obtain a larger difference between species when two species encounter each other in sympatry. The observed interspecific differences were subscribed to ecological interactions and/or to reproductive isolation mechanisms. Character displacement always act on intraspecific character shifts (Brown & Wilson, 1956, in: Loftus-Hills & Littlejohn, 1992). It might act in a single species, or work on a species pair.

Usually, populations of related species show character divergence (are less like each other in sympatry), sometimes only one species shows character shifts and becomes different, sometimes both species have character shifts. Sometimes, differences convergence (and species are more like each other) when a character is beneficial for both species. Both species might grow larger, in order to obtain a more favourable ecological position. Character displacement is divided in the following categories: character release, ecological character displacement, and reproductive character displacement (Loftus-Hills & Littlejohn, 1992).
CHARACTER DISPLACEMENT IN FISH

In a study of literature on this subject, Robinson & Wilson (1994) found numerous examples in which fish communities shared the same general features. They concluded: "First, competition is a diversifying force that creates differences between species (character displacement) and within species (character release, when other closely related species are absent). Second, differentiation in lakes occurs along predictable pathways and almost always includes pelagic and benthic forms."

Habitat preference was related to morphological features: in species pairs, both species were adapted to its own microhabitat, the single species was not specialised to a single microhabitat.

Character release in guppies in a study on morphological adaptation in guppies (Poecilia reticulata Peters, 1859)

Robinson & Wilson (1995) showed that morphological differentiation can be generated under laboratory conditions. Modifications of morphological and behavioural traits were produced within one generation: fish that grew up under certain conditions adapted their bodies and subsequent behaviour.

Character displacement in two species of Poecilia from El Salvador

In my own studies, on P. cf. salvatoris Regan, 1907 and P. marcellinoi Poeser, 1995, I encountered an intriguing example of character displacement. Initially, I did not look for character displacement: I set out to investigate ecomorphological differentiation in Poecilia populations.

ECOMORPHOLOGICAL DIFFERENTIATION

Earlier, Poeser (1992) investigated ecomorphological differentiation for a 'one-species-in-a two-environments' study. Originally defined by Hubbs (1926), this is a mechanism causing differences within a species, based on the interaction of fish populations with salinity or temperature. Fish developing in saline or cold environments have less meristic development and more somatic development (= larger size). This mechanism was tested on P. cf. salvatoris and P. marcellinoi.

Both species are variable in size: P. cf. salvatoris ranges from 44.4 mm (brackish water) to 51.0 mm (fresh water), P. marcellinoi ranges from 37.9 mm (brackish water) to 47.2 mm (fresh water). Both species have 9 to 10 dorsal fin rays. Both species always have 9 anal fin rays and 16 scales around the caudal peduncle. P. cf. salvatoris (always) has unicuspid inner teeth and (in general) a blotch in the dorsal fin. P. marcellinoi (always) has tricuspid inner teeth and (in general) a caudal blotch.

The ecomorphological prediction would be that both species were larger in the coastal population. However, coastal populations of both species are smaller than the inland
population. In coastal areas, *P. cf. salvatoris* is larger than *P. marcellinoi*. In stable freshwater populations, no size difference is encountered.

The ecomorphological prediction would be that both species have less dorsal fin rays in coastal populations. However, in coastal populations, *P. cf. salvatoris* has 9 to 10 dorsal fin rays (9.5 average) and strictly 10 dorsal fin rays in stable fresh water populations. In coastal populations, *P. marcellinoi* also has 9 to 10 dorsal fin rays (9.5 average) and strictly 9 dorsal fin rays in inland populations.

This prompted me to consider character displacement as a possible explanation for the variations in *Poecilia*. Instead of a 'one-species-in-two-environments' mechanism, character displacement is a 'two-species-in-one-environment' mechanism (the fifth criterium *sensu* Schluter & McPhail, 1992). But neither mechanism explained the observed character divergence and character convergence encountered in *P. cf. salvatoris* and *P. marcellinoi*.

In El Salvador, ecological character displacement causes size convergence and reproductive character displacement causes both species to differ in an obvious character: the presence of a blotch in the red dorsal fin is amplified by the broader dorsal fin in *P. cf. salvatoris* versus the presence of a caudal blotch in *P. marcellinoi*, which lacks black pigment in its yellow dorsal fin.

This is only true in freshwater conditions; in brackish environments character displacement is absent. Therefore, I demonstrated a mode of character divergence in a 'two-species-in-two-environments' situation. This new mechanism is based on the predictions whether differentiation (i.e., character displacement) is possible or restricted (dictated by environmental conditions). It is shown that in suitable environments ecological and reproductive character displacement is evident, whereas unsuitable environments counteracts character displacement.

In accordance with the ecomorphological hypothesis, freshwater populations have more possibilities to modify their characters. In other words, character displacement is more likely to occur in freshwater populations.

If character displacement is a mechanism causing character divergence, it is a useful tool to recognise different species. When the species themselves are determining species boundaries, ichthyologists should be able to detect these boundaries. If it works for fish, it should for humans too.

Concluding: two populations of different species will exhibit character displacement, so if two populations do not exhibit character displacement, they do not belong to two different species.

**MORE EXAMPLES IN POECILIA AND A POSSIBLE EVOLUTION**

Character displacement caused the occurrence of species pairs in stickleback (Schluter & McPhail, 1992) based on trophic, i.e., benthic and limnetic, differentiation. Laboratory induced differentiation is demonstrated in *P. reticulata* (cf. Robinson & Wilson, 1995). In
From the Amazon molly to the Amazon molly and back again: Chapter 3

Poecilia, three widely distributed species pairs exist, differing in the shape of their inner jaw dentition:

i) *P. mexicana* (unicuspid) and *P. sphenops* (tricuspid) in Mexico (Atlantic coast),
ii) *P. butleri* (unicuspid) and *P. cf. sphenops* (tricuspid) in Mexico (Pacific coast),
iii) *P. cf. salvatoris* (unicuspid) and *P. marcellinoi* (tricuspid) in El Salvador.

Because most species in *Poecilia* are unicuspid, this character is here considered primitive and the tricuspid state as derived. When the ancestral stock of (unicuspid) *Poecilia* immigrated into Central America 60 million to 20 million years B.P. (Rosen, 1975; Bussing, 1985), three species originated from vicariance events. Subsequent character release caused intraspecific differentiation, from which two morphs were derived. When these populations became more specialised, both morphs of these species have attained maximum trophic efficiency. Now, character displacement will prevent hybridisation, i.e., reduce gene flow and effectuate reinforcement (ecological character displacement). In this hypothetical case, three unicuspid/tricuspid species pairs are formed.

OTHER OBSERVATIONS IN *POECILIA* INDICATING CHARACTER DISPLACEMENT

In Mexico, *P. mexicana* has 26 to 28 scales in a lateral series, as does the Central American *P. gillii*. In sympatric populations in Nicaragua and Costa Rica, *P. mexicana* has 28 to 30 scale in a lateral series (Villa, 1982; Bussing, 1987).

On the Pacific side of Mexico, northern populations of *P. cf. sphenops* have 16 scales around the caudal peduncle, where *P. butleri* has 18 scales around the caudal peduncle. In southern populations, *P. butleri* has 16 scales around the caudal peduncle, where *P. cf. sphenops* has 18 scales around the caudal peduncle (Schultz & Miller, 1971. Note: there is considerable overlap between the Isthmus of Tehuantepec and Cabo Corrientes, where both species have 16 scales around the caudal peduncle. This may be caused by the presence of other congeneric species).

Without specifying the characters, Menzel & Darnell (1973) reported: "in populations [of *P. mexicana*], sympatric to *P. sphenops*, character divergence is pronounced". Rivas (1982) studied character displacement in *P. dominicensis* and *P. hispaniolana*.

IMPLICATIONS FOR PHYLOGENETIC THEORY

These observations have profound influence on the phylogenetic studies in this group. Preliminary data concerning the systematic relations in *Poecilia* (Poerse & Isbrucker, in prep.) suggest that the cladistic interrelations are represented by an unresolved bush. Although this finding supports the stated evolution, it also has an unwanted effect an phylogenetic analyses. When three species pairs are analysed, all three unicuspid species, as well as all three tricuspid species, are grouped together, suggesting that, for instance, *P. sphenops* is more related to *P. marcellinoi* than to *P. mexicana*. In the scheme proposed in this paper, this would be erratic.
REFERENCES


