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.

General rights
It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: https://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.
Summary
This paper is the result of an invited talk, given at the 2nd International Symposium on Livebearing Fishes, Querétaro, Querétaro, Mexico, March 19 – 23, 2002. The origin of the genus *Poecilia* is estimated. The Gondwanian origin of the Poeciliidae and the occurrence of *Poecilia* on Hispaniola suggest that it arose at a time before the Tertiary.

A biogeographical account of the Central American species is given and a species account, based on meristic data, is given.

Introduction
The purpose of this paper is threefold. First, although the origin of *Poecilia* Bloch and Schneider, 1801 as a separate genus in the Poeciliini is hard to date, I will try to give an estimate in this paper. The developments thereafter are outlined based on a phylogeny (Chapter 9), combined with the geological history of the Caribbean Region. Coincidentally, theories on Dinosaur extinction provides information on the early history of *Poecilia*.

Second, the taxonomic history of subgeneric separations of the Central America mollies is examined, with nomenclatural consequences as exemplified in the taxonomic histories of *Poecilia petenensis* Günther, 1866 and *Mollienesia petenensis* Günther, 1866.

Third, the biogeographic scenario that I present for the Central American mollies is a new approach based on consideration of i) hybridization events, ii) endemism, and iii) character displacement (cf. Poeser, 1998). This approach provides information on all Central American mollies presently known. A species list is included (see Appendix).

I. Phylogeographical analysis of the Poeciliini, or where did it all begin?
Parenti (1981) concluded that the live-bearing tooth carps originated on Gondwana, i.e., in the Southern Hemisphere. *Poecilia* is a monophyletic group, related to three other genera, viz., *Limia* Poey, 1854, *Pamphorichthys* Regan, 1913, and an as yet unrecognized genus (Costa, 1991) presently known as "*Poecilia*" *heterandria* (Poeser, submitted¹). The latter taxon, a monotypic genus, is considered a relict population surviving in a limited coastal area in Venezuela. *Pamphorichthys* Regan, 1913 is also a South American genus ranging into the inland areas of Bolivia and Brazil. *Limia* has a more or less Hispaniolan range, whereas *Poecilia* is booming and blooming in Central America, with a peripheral range in South America and present with three species on Hispaniola (Fig. 1). Therefore, the Poeciliini are scattered widely over the Neotropics. How and when did they disperse over such a large area?

¹ Subsequently published as *Pseudolimia* Poeser, 2002
Figure 1. Geological developments in the Caribbean region from the Cretaceous until present (see next page for explanation)
Figure 1A. 160 Mya. The America’s and Africa formed an interconnected landmass. This is a possible period for the origin of the Poeciliidae sensu Parenti (1981), presently occurring in the Neotropics as well as in Africa. Note that Hispaniola is connected to the western part of South America.

Figure 1B. 120 Mya. North America rifted from the Southern continents, South America and Africa started to break up. Note that also Hispaniola and Cuba, originating at the Pacific side of South America, lost their connection to the continent.

Figure 1C. 80 Mya. All continents, as well as the Proto-Antilles, are separated. The different genera of the Poeciliini have their independent developments.

Figure 1D. 60 Mya. Geologically like in C, with a rapid dispersal of Poecilia to Central America, possibly aided by the impact of the Alvarez meteorite near Yucatan.

Figure 1E. 40. Mya. Geologically like in C, with subsequent development of Poecilia in Central America.

Figure 1F. Present. Subsequent to the formation of the Panama connection between Central America and South America at the end of the Miocene, Poecilia re-entered South America.

Geological evidence (Pitman et al., 1990) suggests that Hispaniola, i.e., present-day Haïti and Dominican Republic and presently located in the Caribbean Sea, had a Pacific origin (Fig. 1A). Moreover, if the Poeciliini originally came from Gondwana, the most likely center of origin would be South America. Therefore, in order for Poecilia and Limia to disperse onto Hispaniola, as well as to Central America, the (Proto-) island of Hispaniola must have been located at one time between the two continents (Figs. 1B&C). This suggests an origin of Poecilia prior to the end of the Cretaceous, i.e., prior to 65 Mya! During the Cretaceous, a large inland sea was located east of the Andes, making a coastwise dispersal for Pamphorichthys to “inland localities” (= east of the Andes) possible (Harrington, 1962).

How did the poeciliid fishes become so dominant in the Caribbean region? The Hispaniolan Island connection was broken again between the Late Cretaceous (80-70 Mya.) and the Chicxulub impact, at the K/T boundary (Fig. 1D). As a direct result of the asteroid impact the complete freshwater fauna present in the Caribbean region was probably terminated. Opportunists as they are, the poeciliids could then have occupied all free niches in Central America and on the proto-Antilles. From the Late Cretaceous (say 80 Mya.) until the formation of the Panamanian Landbridge (Figs. 1D-F, say 5 Mya.) the species of Poecilia have developed in Central America (and Hispaniola) without any competition arriving from South America. Their occurrence in South America is explained by a new re-dispersal to South America.

II. Taxonomy of Central American species of Poecilia

To identify the separate species in Central America, I broke down the question from top to bottom. The first question was to investigate an old controversy: What makes a molly different from other species of Poecilia?

LeSueur (1821) distinguished between his Mollienesia and Poecilia mainly by the position of the anal fin, which is modified and positioned more anteriorly in males (see: Introduction of this thesis). When the position of the anal fin was no longer considered a generic distinction (after Heckel’s [1848] findings in swordtails, and Steindachner’s [1863] findings in mollies), the number of dorsal fin rays became the diagnostic character. Günther (1866)
even included the green swordtail, *Xiphophorus helleri* Heckel, 1848 in *Molliesenia* based on this character. However, Regan (1913) found intermediates in dorsal fin ray numbers, viz., in *Limia formosa* Girard, 1859 and *Poecilia petenensis* Günther, 1866, and directed the attention to gonopodial differences. Whereas the gonopodia of *Poecilia* had a smooth tip, the gonopodia of *Molliesenia* had well-defined hooks extruding from the tip. In the upper row (Introduction to this thesis, Fig. 6A-C), the “*Poecilia*” gonopodia are shown, followed by the guppy (Introduction to this thesis, Fig. 6D, only one drawn with palp, although this palp is present in all gonopodia in this figure), a member of *Limia* (Introduction to this thesis, Fig. 6E) and a as last the gonopodium of a member of Regan’s “*Molliesenia*” (Introduction to this thesis, Fig. 6F). Thereafter, Hubbs (1926) found intermediate gonopodia, linking *P. sphenops* and *P. latipinna* to *P. vivipara*, but he retained *Molliesenia* separated from *Poecilia*. After the merging of *Molliesenia* and *Poecilia* by Rosen and Bailey (1963), Miller (1975) separated them at subgeneric level, based on a single gonopodial detail, viz., serrae present on the gonopodial ray 4a in *P. vivipara*. This resulted in about 28 Hispianolans, Central and South American mollies more related to each other than either of them to *P. vivipara*, despite of a smooth transitory range of characters, linking *P. latipinna* to *P. sphenops*, to *P. gillii*, to *P. vandepolli*, to *P. vivipara* (Poeser, in press). This appears very unlikely.

So what does make the differences among mollies? Dorsal fin ray numbers are the first, easily discovered characters separating one group of mollies from another. However, as we saw above, there are exceptions to this rule. *Poecilia formosa* was already considered an intermediate by Regan (1913), together with his *Molliesenia gracilis*, a replacement name for *Poecilia petenensis* Günther, 1866. Günther (1866) described two species, a short-finned molly, i) *Poecilia petenensis* and ii) a sailfin molly, *Molliesenia petenensis*. Regan (1913) reassigned *P. petenensis* to *Molliesenia gracilis*, which was thereafter submerged in the synonymy of *P. sphenops* by Rosen and Bailey (1963). These authors reassigned *Molliesenia petenensis* to *Poecilia petenensis*, notwithstanding the occupation of this name by Günther’s short-finned Péten molly. In a paper on this subject, I renamed the sailfin to *P. kykesis*, after resurrecting *P. petenensis* from the synonymy of *P. sphenops* (cf. Poeser, 2002). Like *P. formosa*, it is not unthinkable that *P. petenensis* (= the short-finned molly) also originated after hybridization of a sailfin molly and a short-finned molly. As in *P. formosa*, the diagnostic characters are intermediate in *P. petenensis*.

A molecular study on the origin of *P. formosa* yielded a surprising result. Schartl et al. (1995) determined that the short-finned *P. latipunctata* is genetically more like *P. latipinna*. Is *P. latipunctata* also the product of a hybridization? While its range lies in the middle of shared sailfins/short-fins territory, I will not discern this possibility immediately. (Note: the molecular phylogeny presented by Dr Ptacek [submitted for this volume] confirms that *P. latipunctata* is included in the sailfin clade. These sailfins are shown to be the sister group of the remaining Central American mollies, i.e., separated from the ancestral short-fins prior to “shortfin speciation”)

Now, two clusters of species have been identified: three sailfins (Fig. 6), viz., *Poecilia latipinna*, *Poecilia kykesis*, *Poecilia velifera*, and three “hybrid” species, viz., *Poecilia formosa*, *Poecilia petenensis*, and *Poecilia latipunctata*.
III. biogeography of the species of Poecilia in Central America

Within the remaining species of shortfin mollies, viz., the Poecilia sphenops species group (Appendix 2), six “endemic” species are found, all in Mexico. Poecilia thermalis is a species that was described from a sulphurous well, misidentified as an El Salvadorian species and ignored ever since, but never disproved in any serious study. Poecilia sulphuraria is like P. thermalis an endemic sulphurophile species. Poecilia pallida from the Rio Balsas system was formerly known as P. maylandi. Poecilia catemaconis is endemic in Lake Catemaconis. Poecilia chica is found in the Rio Purificacion system. Poecilia teresae is an endemic species in the base region of the Yucatan Peninsula.

Finally, the P. sphenops complex consists of six wider ranging species, which are identified with somewhat more difficulty (Garman, 1895; Regan, 1913; Hubbs, 1926; Rosen and Bailey, 1963; Schultz & Miller, 1971; Menzel & Darnell, 1973; Miller, 1983). The two best known species are P. sphenops and P. mexicana (Appendix 2). Poecilia mexicana differs from P. sphenops merely in tooth shape: unicuspid inner teeth versus tricuspid inner teeth. However, in sympatric populations, more differences are found (Menzel & Darnell, 1973). Conditions like this are defined as character displacement, i.e., when the areas of distribution of two species of animals overlap geographically, the differences between them are accentuated in the zone of sympatry and weakened or lost entirely in the parts of their ranges outside this zone (Brown & Wilson, 1956).

Poecilia gillii ranges from Guatemala to South America, differing in several characteristics, like body size, body shape, dorsal fin coloration, body spots, even in gonopodial features (Poeser, in Press). However, intraspecific populations of P. gillii show very little meristic differentiation. Poecilia marcellinoi has the exact same differentiation, and differs from P. gillii only in dental characters: unicuspid versus tricuspid inner jaw dentition (Poeser, 1995). Like P. mexicana and P. sphenops, they form a species pair, showing character displacement when they occur sympatrically (Poeser, 1995, 1998). Poecilia gillii strictly has ten dorsal fin rays in the presence of P. marcellinoi, which only has nine dorsal fin rays when co-occurring with P. gillii.

Poecilia gillii differs from Poecilia mexicana merely in the number of scales around the caudal peduncle: 16 versus 18 scales. Poecilia marcellinoi differs from Poecilia sphenops merely in the number of scales around the caudal peduncle: 16 versus 18 scales. From the Isthmus of Tehuantepec to (say) Nicaragua P. sphenops co-occurs in disperse populations with populations of both P. gillii and P. marcellinoi.

The Pacific coast of Mexico

The species of the P. sphenops complex occur in pairs: A unicuspid/tricuspid species pair on the Atlantic coast of Mexico, both with 18 scales around the caudal peduncle, and a unicuspid/tricuspid species pair on the Pacific coast south of Mexico, both with 16 scales around the caudal peduncle. Both species pairs are explained by assuming a single species that differentiated in food choice, and subsequently in tooth shape (Poeser, 1998). In addition, Schultz and Miller (1971) found several populations of mollies with 16 or 18 scales around
the caudal peduncle, with unicuspid and tricuspid teeth, and eight anal fin rays. Based on these characters, a complex of several species can be distinguished: *P. butleri* on the Pacific coast north of Cabo Corrientes, unicuspid inner teeth, 8 anal fin rays and with 18 scales around the caudal peduncle, and a complex combination of unicuspid/tricuspid species on the Central Pacific coast between Cabo Corrientes and the Isthmus of Tehuantepec. *Poecilia nelsoni* (unicuspid, 16 scales around the caudal peduncle, 8 anal fin rays) seems to co-exist *P. marcellinoi* (tricuspid, 16 scales around the caudal peduncle, 9 anal fin rays), and the tricuspid endemics *P. chica* and *P. pallida*.

In conclusion, based on differences in tooth shape (unicuspid vs. tricuspid), caudal peduncle scales (16 vs. 18), and anal fin rays (8 vs. 9), I recognize *P. sphenops*, *P. mexicana*, *P. gillii*, *P. butleri*, *P. nelsoni*, and *P. marcellinoi* as the Central American species of the *P. sphenops* complex.

**Acknowledgements**

I want to thank the organizing committee for their invitation and the opportunity to contribute to the understanding of the biogeography of the genus *Poecilia* in Central America. I cannot think of a better way to show my appreciation by underlining the merits of the symposium (see also above). During the symposium, a number of data came available to me, confirming the distributional patterns and accompanying mechanisms I proposed for the *P. sphenops* species group (Poeser, 1998). Within the sailfin mollies, the data presented by Dr Ptacek indicated extensive intraspecific differentiation in behavior. When this trait is combined with intraspecific selection, e.g., for food, character displacement will occur to diminish intraspecific competition and unwanted “hybridization” of specialized characteristics. Populations will diverge, possibly resulting in speciation. These data were also confirmed in the oral presentation of Dr Macías Garcia on reproductive behavior, again presenting possibilities for intraspecific selection.

Furthermore, on a poster presented by M. Mateo and R.C. Vrijenhoek, the phylogeography in the genus *Poeciliopsis* was examined. Species differentiation within this Pacific genus showed remarkable similar distribution patterns with the patterns proposed for *Poecilia*, conforming my resurrection of *P. nelsoni* as a valid species from the synonymy of *P. butleri*.

Moreover, I am greatly indebted to Mrs. Mateo, who correctly interpreted the data presented in Schultz and Miller (1973) on the distributional ranges of the Pacific mollies. Based on her comments, I have been able to correct the data presented in this paper.

**References**


From the Amazon river to the Amazon molly and back again: Chapter 10


Poeser, F. N. (in prep.) From the Amazon-river to the Amazon-Molly and back again: The evolution and systematics of the genus Poecilia Bloch and Schneider, 1801.- Ph. D. Thesis, University of Amsterdam.


