Table IV. Characterisation of the subgenera in *Poecilia*.
Poecilia vivipara represents *Poecilia*; *P. sphenops* and *P. latipinna* represent *Mollienesia*; *P. dominicensis* represents *Psychtopoecilia*; *P. elegans* represents *Curtipenis*; *P. parae* represents *Micropoecilia*; *P. reticulata* represents *Acanthophacelus*; *P. caucana* represents *Allopoecilia*.

Species group	Serrae on ray 3	Hook on ray 3	Hook on ray 5p	Number of dorsal fin rays
Poecilia sphenops	+	+	+	8-11
Poecilia latipinna	+	+	+	12 or more[1]
Poecilia dominicensis	-	+	+	8-11
Poecilia elegans	+	-	+	8-11
Poecilia vivipara	+	-[2]	-[3]	7-11
Poecilia parae	+	-[4]	-[5]	8
Poecilia reticulata	+	-	+	6-7
Poecilia caucana	+	+/-[6]	+	8

[1] *Poecilia latipunctata* seems a noticable exception to this. Molecular data clearly indicate close relations with the *P. latipinna* species group (12-20 dorsal fin rays), although it does not have more than 11 dorsal fin rays (cf. Poeser, 2003).
[2] This character is "reduced to absent" in this species group (cf. Poeser, 2003).
[3] This character is "reduced to absent" in this species group (cf. Poeser, 2003).
[4] This character is "reduced to absent" in this species group (cf. Poeser, 2003).
[5] This character is "reduced to absent" in this species group (cf. Poeser, 2003).
[6] Frequently much reduced in this species group (cf. Poeser, 2003)

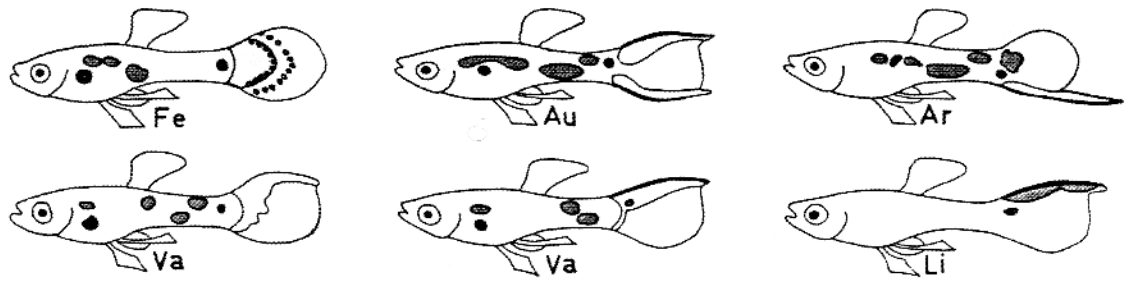

Fig. 7. Drawings of guppy phenotypes (after Westerhof, 1960) Ferriguneus, Auratus, Armatus and Variatus represent 'multi-spotted' males with different caudal fin patterns, Lineatus only indicate the caudal fin pattern.

There can be a bright area on the caudal peduncle, margined by heavily pigmented bars (Figs. 3-4), like in *P. parae* 'melanzona' (Fig. 8). Two explanations are possible. If these patterns occur sympatrically, it might be that these reflect better shoaling possibilities or adaptations to similar environmental demands. If these patterns do not co-occur, a special form of character displacement (cf. Poeser, 1995, 1998; present paper) might be present. Examination of these patterns, both genetically and bio-geographically, e.g., correlated to mimicry or character displacement, therefore, is a promising field of investigation, possibly explaining the occurrence of these patterns in wild guppies and in *Micropoecilia*.

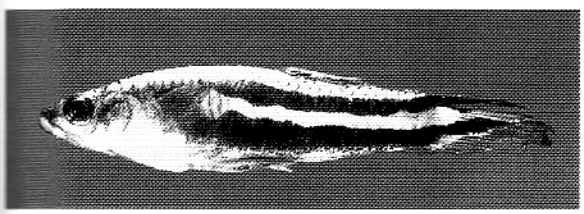

Fig. 8. Habitus of *Poecilia parae* 'melanzona'. The pigmented bars on the caudal peduncle resemble the phenotypes of guppies shown in Figures 3c and 4c.

Gonopodia. The gonopodium of both species of guppies (cf. Meyer, 1993; Fig. 6) has a retrorse hook on ray 5, but not on ray 3. The fleshy palp is much elongated, extending well beyond the tip. The ventral spines on the 3rd gonopodial ray are large, giving the gonopodium a bulb-like appearance. Both ray 4a and ray 4p have dorsal spines, the spines on 4a are much smaller than on 4p.

Habitat. Guppies are known to inhabit a wide vari-

ety of habitats with temperatures ranging from 18-30°C. They are not adapted to special biotopes but do not occur in purely marine environments.

Distribution area. The common guppy is presently circumtropical. However, it is believed to occur naturally only in the northeastern part of South America and on the Lesser Antilles (Fig. 9). We consider only the mainland areas of Venezuela, east of Lago de Maracaibo, further east to the Guiana's, the adjacent part of Brazil, Para district, and upstream the Amazon river (Rio Solimões) as its natural area of distribution. Based on data presented in the discussion section, the occurrence on Trinidad is undisputed. The island of Barbados (cf. Boulenger, 1912) is not considered part of its natural range (Poeser and Isbrücker, 2002).

Spatial distribution of the phenotypes of the freshly collected guppies

Life colours of the Orinoco variety of *P. reticulata* are characterised by one or two black spots, often enhanced by a metallic patch. This morph is named for the guppies from stations 8-10, which eventually are tributaries of the Río Orinoco. Guppies from stations 5 and 14 are similar to these phenotypes and are therefore also classified as Orinoco guppies. These specimens are like most guppies (*P. reticulata*) examined from the ZMA and UMMZ material.

Guppies caught below the El Cordon waterfall (El Cordon variety, station 6) differ from the Orinoco variety. Not only are they substantially bigger, body colorations are different too. Two specimens (of five collected males) had enormous 'peacock' caudal fins, i.e., a large black spot margined by a bright metallic, silvery blotch. One specimen was without any specific colours, except for exhibiting a metallic silver body. This latter specimen also had an enormous gonopodium, extending almost to the caudal base. The possible origin of the characteristics of this variation is discussed below.

In the areas of stations 11-13, 15 (Carúpano region), the guppies exhibited similar colour patterns as the Orinoco variety, with the addition of metallic polychromatic patterns. Where in the Orinoco guppies the metallic sheen is restricted to areas around the black spots, in *P. wingei* all colours are a brilliant array of metallic colours: red, blue and green to yellow (= gold). Dorsal fin is usually transparent, however, sometimes black or white markings are present. Caudal fin variegated, i.e., with red or black upper, lower or both margins, or a brownish blotch extending from the caudal base. Females are greyish, with a bright sheen over their bodies.

In the area around stations 1-4, 7 (Campoma region), guppies are found with colours like the Carúpano variety, with addition of a characteristic black midsection of the body. Individual specimens exhibit a black anterior part of the gonopodium, or a fine striped pattern on the anterior part of body, or a completely green body.

Evidence of character displacement

Character displacement is observed "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 and Wilson, 1956)". Summarising the spatial distribution of the phenotypes, the least variegated guppies (hereafter named type A) are the El Cordon variety, followed by the Orinoco variety that has black spots and some metallic fringes (type B). The Carúpano morph also has black spots, but is brilliantly metallic (type C), whereas the most extensive black and metallic colouring (type D) is found in the Campoma variety.

When plotted on a map (Fig. 10), the distribution of phenotypes shows coherence. The brilliant guppies occur exclusively in the Cariaco-Carúpano region, a valley of marshlands surrounded from south to east by the Cordilleras de la Costa. The northern parts of this region are enclosed by the dry Araya Peninsula and in the west it is bordered by the Golfo de Cariaco. It is from this latter area that *P. reticulata* can enter this territory. In the western part of this region, where *P. wingei* and *P. reticulata* may co-occur, both populations have their most extreme phenotypes, i.e., the Campoma variety of the Campoma guppy and the El Cordon variety of the Orinoco, or common, guppy. In the areas in which these two kinds of guppies do not co-occur the phenotypes are similar: the Carúpano variety of the Campoma guppy seems merely a brilliant version of the Orinoco guppy. Both phenotypes are here characterised by the typical black spots. So, while conspecific genetic variation supposedly would follow an A-B-C-D pattern in colour-type distribution, observed distribution is actually B-A-D-C. This

represents a clear example of character displacement, leaving little doubt that the Campoma guppy indeed represents a new species.

Character displacement as a pre-copulatory isolation mechanism has already been suggested to have mediated in the speciation of Hispaniolan short fin mollies (Rivas, 1982), short fin mollies from El Salvador (Poeser, 1995) and sailfin mollies (Gabor and Ryan, 2001). The example in guppies is new to science and its characteristics, i.e., easily accessible populations of a species already thoroughly studied and clearly limited geographical dimensions, makes it an almost perfect subject for further studies. The occurrence of this type of speciation was already predicted (Houde, 1997: 55): "... a distinctive guppy population from Venezuela that, at least in laboratory stocks, appears to be monomorphic, but is interfertile with Trinidad guppy populations ... A species-recognition function for colour patterns thus cannot be ruled out..."

The case study of Alexander and Breden (2004), examining this phenomenon, is fully discussed below.

While there is little doubt about the distribution of phenotypes of *P. wingei*, the origin of the El Cordon phenotype (= *P. reticulata*), based on only a small collection at one locality, remains the subject of further study. This phenotype can have arisen either by character displacement or by hybridisation.

Behavioural differences between *Poecilia reticulata* and *P. wingei*

Behaviour of the Common guppy

Guppies differ from all other species of *Poecilia* in their mating behaviour (Liley, 1966). Behavioural patterns herein described are personal observations, obtained from the field trip to Venezuela described herein, as well as from an earlier field trip (Kempkes, in 1993) and from aquarium observations. Our studies agree with the observations of other authors on *P. reticulata* (cf. Houde, 1997). Courtship behaviour in *P. reticulata* proceeds in strict sequential ordered elements (Table III). However, some variation in behaviour was observed when behavioural elements were occasionally skipped by courting males.

In the El Pilar river (Fig. 10) two isolated populations of *P. reticulata* were observed (15-07-2002, from 13.00 to 13.30 hr, and 18-07-2002 from 9.40 to 10.10 hr). Both populations occupied about a half square meter and the water was 10 - 20 cm deep, and both microhabitats were located near the riverbanks. No fish were observed to enter the fast flowing waters in the midsections of the river. Therefore, the population was found to be relatively constant, with no individuals leaving or entering the community. The action radius of males within the population appeared to be bigger than that of females. In these groups, being 'local populations', some territorial behaviour was observed in which the largest females maintained a bigger individual distance to other larger females. These females reacted to approaches of other females by biting them and chasing them away. Juvenile guppies predominantly inhabited the banks of the river, close to the main population. We think that in the shallow water, young guppies were relatively save from predators. Sexually mature males were continuously near the females of their group. The intra-sexual competition between the males was especially perceptible during the courtship: males constantly tried to disturb the courtship of other males, after which they attempted to court the same female. Female choice is apparent (cf. Houde, 1997), because of energy costs of internal maturation of eggs and the additional costs of swimming around highly pregnant. Furthermore, the supply insemination adds to what the males invest to the reproduction. In a laboratory test, Nicoletto (1993) described that female guppies favour large guppy males. The orange and iridescent colour areas at the bodies of the males are probably indications of the fitness of males. Female choice, combined with the establishment of local populations, should favour genetic drift. When populations remain at more or less the same geographical position, these populations will adapt to the specific requirements of these localities. It has been postulated that sneak copulation alone counteracts possible genetic drift (Magurran, 1998).

Behaviour of the Campoma guppy

The behaviour of *P. wingei* is new to science and is therefore extensively described. Observations were made on the 14th, 16th and 18th of July at Las Aguas de Moises, near the highway between Cariaco and Casanay. The Campoma guppies were observed in a

small stream of clear water. The river was about 150 cm deep with the bottom clearly visible, about 180 to 300 cm wide and no submerged vegetation was observed, the observation area was a stretch of about 40 meter. There were trees and some dense vegetation at several positions at the bank. The Campoma guppy was syntopic with the following species: *Catoprion* spec., *Crenicichla* spec., *Cichlasoma* spec., *Rivulus* spec., *Ampullaria* spec., and some unidentified crustaceans. The observed subpopulations, i.e., groups of about twenty adults of both sexes and about 20 subadult and juvenile fishes, occupied positions near the river banks. At different locations of this stream we observed other groups with approximately 60 adults, with about 50 subadults and juvenile fishes. The females were continuously grazing the loamy ground, swimming in groups of 6 to 10 fishes. In this stable environment, subgroups are formed consisting only of females. Stable all-female subgroups stay a relatively long time, about 20 to 30 minutes, at a certain locality within the territory, circa 100 square cm, where they seem to be constantly foraging. Strange females rarely enter this sub-community. Intra-sexual aggression, in which the largest females chase smaller females away, was also observed. When two females are equally big, they show a particular posture. These female opposed each other in a T-shaped position for half a second, spreading their fins. After this showing off they feed again. Only at one observation we saw two opponent females actually fight, one female was picking at the caudal peduncle of the other female. After about ten seconds they started feeding again. This behaviour had no apparent effect on the group structure. Two explanations for this behaviour are possible. Firstly, the females have some territorial behaviour related to foraging. Secondly, we suspect female-to-female competition related to sexual selection, i.e., male sexual selection not observed in *P. reticulata*. This latter conclusion is supported by further observations (see below).

During the observation period, males were continuously found in the proximity of the females. With every all-female subgroup, we observed how two or three males remained proximate, i.e., the males seemed less promiscuous compared to *P. reticulata*. In one case, such group was accompanied by a single male. In groups with more fishes, i.e., more than 40 adults, the males court more intensive. In relatively small groups, e.g., one to three males and one to seven females, the males show less intensive courtship behaviour compared to bigger groups. Males in smaller groups apparently need not show their fitness so often, because the females probably recognise individual males. When a male not already belonging to the subgroup started to show courtship behaviour to one of the females, the male already present showed the strange male his sigmoid display, after which the intruder stopped his courtship attempt. Males that initiate courtship approach the female from behind, preferably while she is busy searching food. As noted above, females are mostly stationary during foraging.

Observations indicated that the introduction phase in the Campoma guppy is relatively short compared to common guppies, whereas the last phase of their courtship behaviour, i.e., high courtship, is longer and more intensive. Correlated to the behavioural characteristics of *P. reticulata* (Table III), we recorded the following.

1a. A male attempts to position himself under the female, while his colour pattern darkens if he is successful.
2a. The male will attempt to become visible in the face-to-face position.
2b. He initiates the sigmoid-display. During the sigmoid-display the male turns both sides to the female, like the common guppy.
2c. Finally the male circles around the female and attempts to copulate with his forwardly turned gonopodium.

The significant differences between the courtship behaviour of the common guppy and the Campoma guppy, documented from about 35 observational moments, is summarised as follows.

- The Campoma guppy males court more from below during the first phase of the courtship behaviour. The males from the common guppy swim more from behind or from the side of the females.
- Because the female of the Campoma guppy did not flee, we did not observe any chasing from the males. The females float slowly in front of the males and show that they are co-operative. Females of the common guppy make clear, in a relatively early stage of courtship, whether they are inclined to copulate or not.
- The characteristic display jump of the common guppy during the courtship is only rarely observed in the Campoma guppy. We, therefore, assume that the display jump is not important for the courtship behaviour of the Campoma guppy.

- The females of the Campoma guppy swim away from the courting males when they attempt to copulate, i.e., they avoid courting males relatively late. The females from *P. reticulata* often flee at the beginning of the courtship. We never saw any aggression from the Campoma guppy females towards courting males. Under natural conditions, as well as in an aquarium, females of the common guppy attack obtrusive males. In general, the females of the Campoma guppy seem longer co-operative and receptive, rejecting males in a much later stage than do females of the common guppy.
- The courtship of the Campoma guppy male is relatively docile. Moreover, males attempt to court the same female longer and, after failure, often start to court the same female again.
- Although the competition is strong in big populations, we never saw a Campoma male attempting to court a female that is already courted by another male. The males in a big group show impressing behaviour only on occasion. We assume that inter-male aggression is not relevant for courtship in a big group.
- We observed sneak-copulation, i.e., copulation attempts without elaborate courtship, in the Campoma guppy too, but it is another kind of sneak-copulation, i.e., we never observed sneaky copulations without previous courtship. Common guppies will try to copulate without any prior courtship (cf. Houde, 1997).

Despite intensive observations no particular predator was found that directly attacked guppies. For example, in all locations, juvenile and subadult Campoma guppies were close to the *Rivulus*-like fish near the riverbanks. We did not find any *Rivulus* attacking any young guppies. At Las Aguas des Moises, adult guppies were found near a pair of *Crenicichla* with juveniles. No *Crenicichla* did pursue guppies, and in one occasion a subadult *Crenicichla* was seen to actually 'pass through' a shoal of guppies. No reason for this 'non-aggression pact' is apparent.

Remarks on population differentiation in Trinidadian guppies

In a paper on guppy population differentiation, Magurran (1998) posed an enigmatic dilemma: "Guppy populations evolve rapidly ... The rates of evolution involved can be up to seven orders of magnitude greater than those seen in the fossil record ... female choice appear to reinforce the divergence ...[however] perplexingly ... there is no reproductive isolation ... between populations ..." A substantial counteraction against speciation seemed to be 'sneaky mating', i.e., the mechanism enabling males to copulate without the consent of the females. Also different foraging niches for males and females is supposed to inhibit the development of feeding polymorphism, and therefore inhibit sympatric speciation (Magurran, 1998). This enigma was generated by the occurrence of genetic differentiation between guppies from the Quare-Orupuche drainage versus guppies from the Paría drainage on Trinidad (Fajen and Breden, 1992; Taylor and Breden, 2000). The guppies from the Trinidadian Paría drainage are closely related to Venezuelan and Guyanan mainland populations, whereas the Quare-Orupuche guppies form a separate monophyletic clade. Our discovery of the Campoma guppy gives the derivation of the Quare-Orupuche guppies a possibly different perspective.

Trinidadian guppies interbreed readily in laboratory circumstances with Campoma guppies (Houde, 1997; pers. obs.), although this seemed not to be the case in the late 1970's (see below in our discussion on the Endler's Live-bearer; Alexander and Breden, 2004). The geological environment, protecting the Campoma region from invasion of the Orinoco guppy, allows only a limited influx of foreign guppies into the region. Here, separation of the two guppy populations is secured by sexual selection, and subsequent character displacement reinforcing divergence (cf. Houde, 1997; Magurran, 1998). However, it is not unlikely that, while there might have been an initial separation on species level present on Trinidad, the geology of Trinidad did not allow for an enduring separation of these two species. While the dispersal from river to river in the Cumaná-Cariaco coastal strip limits the possibilities for guppies to enter the Campoma region, the Orinoco river probably provides a continuous 'bombardment' of heterospecific genetic material in the original Trinidadian guppies. These latter guppies might have been the same species as the Campoma guppies, or a closely related population. Ongoing introgression of Orinoco guppy genes has despeciated the original Trinidadian guppy, causing the genetic divergence observed today (Fajen and

Breden, 1992; Taylor and Breden, 2000). Therefore, the initial situation postulated by Magurran (1998) must be redefined. While she initially situated a single guppy species on Trinidad, diverging to the limit of speciation but, 'perplexingly', not going beyond that specific boundary, we postulate another scenario. The present day situation results from the introgression of genetic material of one species, viz., the Orinoco or common guppy, into a heterospecific population of 'original' Trinidadian guppies, actually converging genetic differences, i.e., despeciating the latter species. This despeciation in action was also already recorded, though not recognised as such. Magurran et. al. (1992) sampled molecular data from a guppy population that was supposed to be re-allocated by Haskins in 1957 from the Caroni drainage, i.e., part of the Paría drainage guppy populations, viz., Orinoco guppies, and removed them to the Orupuche drainage. There these Paría guppies replaced the residing guppies almost totally, a striking example of obvious higher fitness of the common guppy.

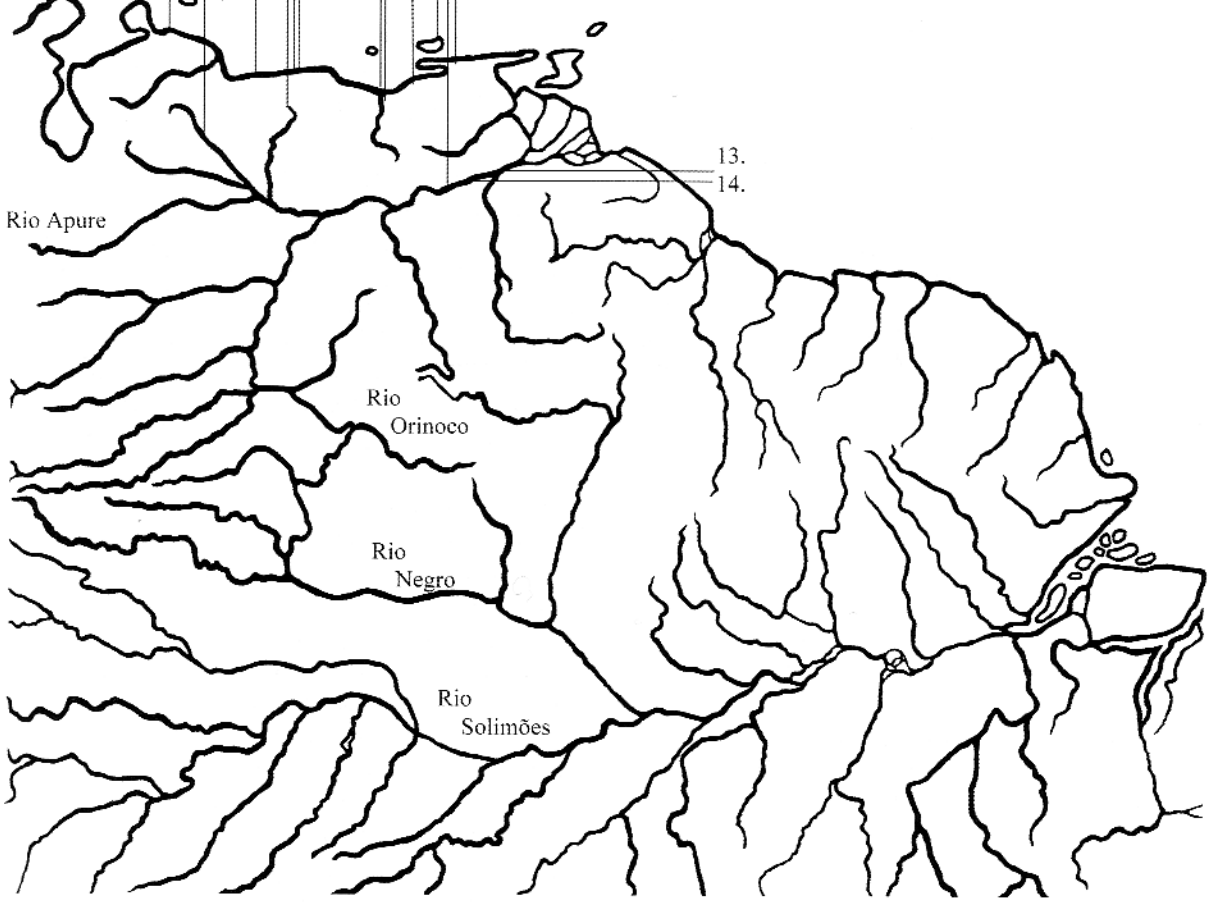

Fig. 9. Distribution area of the subgenus *Acanthophacelus*. The occurrence of Common guppies in the Río Santo Domingo, near Merida and the Río Apure, Llanos, Venezuela (both western rivers of the Rio Orinoco drainage) is confirmed by Kempkes (pers. obs.). Guppies claimed from the Rio Solimões are kept alive by Poeser. Occurrence of guppies upstream of the Río Orinoco and in the Rio Negro awaits confirmation. Numbered locations indicate examined museum material (bold numbers are figured): 1. ZMA 120.725; 2. UMMZ 158750; 3. UMMZ 158736; 4. UMMZ 158753; 5. UMMZ 158709; 6. UMMZ 158729; 7. UMMZ 158704; 8. UMMZ 158705; 9. UMMZ 158715; 10. UMMZ 158706; 11. UMMZ 158716; 12. UMMZ 158715; 13. UMMZ 158711; 14. UMMZ 158720.

Magurran (1998) dated the renewed contact of the common guppy with the original Trinidadian guppy very recent, i.e., 1,000-10,000 years ago, i.e., during the period that Venezuela was linked to Trinidad by the Cordilleras de la Costa. Molecular data (Fajen and Breden, 1992) date the break up between these two guppy populations long before this, i.e., 600,000 years ago. We, therefore, postulate that the Cordilleras were formed 600,000 years ago, blocking gene flow between the several populations of guppies. The Cordilleras also blocked the Río Orinoco from its northerly flow, redirecting its course just south of a rocky strip that is the present day northern range on Trinidad. Since about 10,000 years ago, this mountainous strip was severed from the Paría Peninsula and collected substantial strips of sand deposited by the Orinoco river, forming present-day Trinidad. The common guppy established itself firmly in the southeasterly drainages, whereas the Orupuche guppies retained some of their original genetic content. On the Paría Peninsula, the Campoma guppies have kept their specific identity since, whereas the Trinidadian guppies have lost this identity by the constant intrusion of Orinoco influences.

This hypothesis is testable. Obviously, when the molecular data of the Campoma guppy are compared with those of the two clades found on Trinidad (Taylor and Breden, 2000), we predict a closer relationship of the Campoma guppy with the guppies from the Orupuche drainage than to those from the Paría drainage.

Remarks on the 'Endler's Live-bearer'

The populations of Campoma-like guppies collected in a coastal area of Venezuela, in Cumaná, Laguna de los Patos (Endler, pers. comm.), might very well

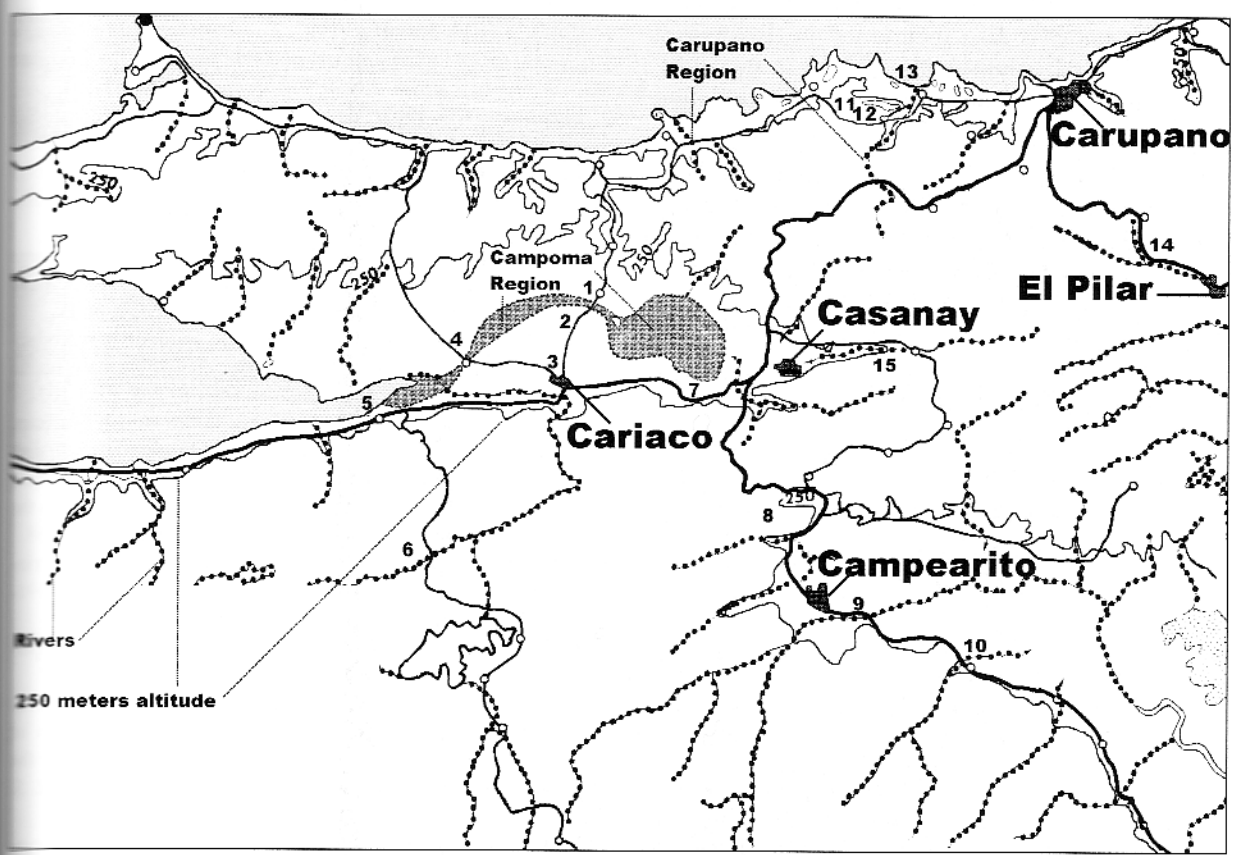

Fig. 10. Map of the collection sites in and around the Paría Peninsula, Venezuela. Indicated are river systems, the Campoma- and Carúpano regions, and the 250 m altitudes. Localities 1-4, and 7 rendered Campoma guppies, Campoma variety. Localities 11-13, and 15 rendered Campoma guppies, Carúpano variety. All other, non-Paría localities, rendered Common guppies.

be an established local population of *P. wingei*. How guppies were distributed there is unknown; they might be remains of an earlier, wider range of the Campoma guppy, but most likely they are released aquarium specimens originating from the Cariaco-Carúpano region.

The Endler's live-bearer is renamed as "Cumaná guppy" by Alexander and Breden (2004). This vernacular name is misleading because not all guppies from Cumaná they collected are named as such (Alexander and Breden, 2004: 3), only those from the west part of Cumaná. The paper of Alexander and Breden (2004) adds a lot of quantitative data to our findings, confirming *P. wingei* as a valid species. They quantified sexual isolation, adding sexual selection and different male display traits to our findings of behavioural differences (Alexander and Breden, 2004: 5). They also added clear morphological differences to the description of the two guppy species (Alexander and Breden, 2004: 4, fig. 6), as well as a full examination of the differences in colour patterns also mentioned in the present paper (Alexander and Breden, 2004: 3, 7, figs. 3-5). Finally, they recorded only common guppies in a radius of 100 km outside Cumaná, confirming the presence of exclusively *P. reticulata* populations between Cumaná and the Paria Peninsula. Alexander and Breden (2004) recorded a total lack of reproductive (postzygotic) isolation between their Cumaná guppies and other guppy populations, although they did mention the initial incompatibility of Endler's guppies with *P. reticulata*. This makes sense in the light of our hypothesis of human introduction: the initial isolation, existing in the late 1970's, is now broken down, possibly by introduction of *P. reticulata* genes into the Cumaná population of *P. wingei* by sneak copulations.

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