The cyprinodont fish *Rivulus* (Aplocheiloidei: Rivulidae) in Trinidad and Tobago: molecular evidence for marine dispersal, genetic isolation and local differentiation

M. J. Jowers1,2, B. L. Cohen3 and J. R. Downie2

Abstract

Mitochondrial DNA sequences (756 bp) were obtained from the cytochrome *b* gene of 36 *Rivulus* individuals collected from 10 sites in Trinidad and one site in Tobago. Eight haplotypes were identified. Low genetic divergence (0.5%) between one western Trinidad (Blue Basin) haplotype and *Rivulus hartii* from north-western Venezuela (Paria peninsula) and high genetic divergence (c. 11%) between these and the remaining other Trinidad and Tobago haplotypes suggests that the islands were colonized by two lineages. The commoner haplotype is distributed throughout lowland Trinidad, possibly a reflection of flooding of the Orinoco River leading to high dispersal between watersheds. *Rivulus* from higher altitude (Northern Range) localities that would not have been affected by such flooding show high genetic divergence between sites. The genetic differentiation between northern and southern watersheds suggests isolation between some of these drainages.

Key words: Altitude – cytochrome *b* – population – *Rivulus hartii* – Trinidad

Introduction

The island of Trinidad lies east of the South American mainland (off northern Venezuela), separated by an 11-km-wide strait, while the island of Tobago lies about 36 km further east. It has long been recognized that the rivulidine freshwater fishes of these islands may have come from South America, perhaps when the sea level was higher than it presently is, or by crossing the straits at times of reduced marine salinity when the Equatorial current causes high, wet season discharges from the Amazon and Orinoco rivers to flow past the islands (Kenny 1978; Alkins and De Souza 1984; Boos 1984; Kenny 1995).

The inter-relationships of many South American, Antillean and Caribbean species of Rivulidae have been explored using cyt *b*, COI, 12S and 16S rDNA mitochondrial sequences (Murphy and Collier 1996; Collier et al. 1998; Murphy et al. 1999). Two phylogenetic studies have shown that *Rivulus hartii* from Trinidad (Murphy and Collier 1996) and from Paria peninsula, northern Venezuela (Murphy et al. 1999), are closely related to other Rivulidae from Venezuela and Guianas. Collier et al. (1998) included both of these specimens in a wider but modest *R. hartii* population study. Their results show high genetic divergence between *R. hartii* from the mainland and Trinidad, suggesting isolation at these localities. There has been no attempt in this or other prior work on these fish in Trinidad and Tobago to assess the level of within-species variation or its possible relationship to geographical and ecological factors. Here, we present new cyt *b* sequences from 36 *Rivulus* individuals from 10 separate localities around Trinidad and one locality in Tobago, and analyse them both phylogenetically and in relation to other factors.

Biological background

*Rivulus hartii* (Boulenger, 1890), the jumping guabine, is a euryhaline fish known from eastern Colombia, the northern coasts of Venezuela, and the Caribbean islands of Trinidad, Tobago, Margarita and Grenada (Boeseman 1960; Robins et al. 1991; Huber 1996). It is the most widespread freshwater fish in Trinidad (Kenny 1995), where it occurs in estuaries, rivers both below and above rapids and waterfalls, in mountain streams, lowland swamps as well as in temporary, shallow rain pools. It grows up to 10 cm in length (Price 1955; Kenny 1995; Bührnheim and Fernandes 2003). Previous studies in Trinidad have shown that the highest population densities of *R. hartii* are found in habitats that are inaccessible to other fish (Liley and Seghers 1975; Fraser and Gilliam 1992; Gilliam et al. 1993; Fraser et al. 1995, 1999; Reznick et al. 1997; Gilliam and Fraser 2001). In Trinidad, it also is the only fish that can ascend or bypass waterfalls and rapids, and is known to move from rivers to steep rocky mountain streams (Gilliam et al. 1993; Fraser et al. 1995, 1999; Fraser et al. 2001; Gilliam and Fraser 2001). Notably, individuals are capable of jumping out of the water and may survive on, and travel substantial distances across, damp leaf-litter (Seghers 1978), so that many populations are found some distance away from rivers, in nearby pools (Reznick 1982; Costa 1987).

Materials and Methods

Taxon sampling

*Rivulus* specimens were captured using handnets during July to August 2002 and 2003. Sites sampled are shown in Fig. 1 and listed in Table 1. After collection, they were killed in 0.01% benzocaine and preserved in 95% ethanol. Freshwater fish surveys and reviews (Price 1955; Boeseman 1960; Kenny 1995) have shown that *Rivulus hartii* is the only rivulidine species present in Trinidad and thus made identification of individuals simple (specimen museum numbers are listed in Table 1). Despite careful search the only other fish found in the sampled localities was the Guppy, *Poecilia reticulata*. These were present only at Blue Basin (in the river below the waterfall, not in the steep stream where *Rivulus* was captured), and at Lopinot.

Laboratory protocols

DNA extraction protocols were similar to those described by Sambrook et al. (1989). Mitochondrial DNA (mtDNA) was extracted from caudal tail muscle and purified using standard phenol/chloroform protocols. The primers L14724 (Kocher et al. 1989) and H15557 (Hillis et al. 1996) were used to amplify a fragment of approximately 830 bp
under standard PCR conditions: 1x (94°C 2 min), 30x (93°C 1 min; 52°C 1 min and 72°C 1 min), 1x (72°C 10 min, 30°C 1 min and 4°C hold) using commercial reagents and protocols similar to those recommended by the manufacturer (Promega, UK). Amplified cyt b fragments were purified by gel electrophoresis and recovered by silica/chaotrope spin column (Qiagen, Crawley, UK). These cyt b sequences are approximately twice as long as those previously reported (Collier et al. 1998). Moreover, 12S rDNA sequences were also obtained from a few animals, but showed no variation.

Sequencing of both strands was performed by the in-house sequencing unit with the amplification primers and dideoxy chain terminators (BigDyes, PE Biosystems, Warrington, UK), and analysed in an ABI 377 apparatus (Applied Biosystems, Perkin Elmer, Warrington, UK). After removing PCR primers and incomplete terminal sequences, 756 base pairs (252 codons) were available for analysis. For DNAs T528 and T531 poor quality internal reads (respectively 62 and 81 nt long) were replaced by Ns. All nucleotide sequences could be aligned without gaps and, when translated into amino acids using the vertebrate mitochondrial code, stop codons were absent.

Phylogenetic analysis
Analyses were performed with paup*4.b.10 (Swofford 2002) and MrBayes 3.0 (Huelsenbeck and Ronquist 2001). The PTP test (Faith and Cranston 1991) was used to assess the presence of non-random structure in the data, based on a heuristic search of 100 randomisations. Trees were constructed by maximum parsimony (MP; heuristic search with TBR branch exchange), maximum likelihood (ML) and Bayesian maximum likelihood (BML) optimality criteria but only ML and BML results are shown because MP did not contribute useful information. The Akaike Information Criterion (Posada and Buckley 2004) best-fit ML model was identified using Modeltest 3.06 (Posada and Crandall 1998) for the ML analysis, and MrModelTest 2.0 (Nylander 2004) for the Bayesian analyses.

Clade support in MP and ML was inferred by bootstrapping and in BML by the frequency with which a clade appeared in the saved trees. BML analyses were performed with default priors and Markov chain settings, and with random starting trees. The gamma shape parameter and proportion of invariant sites were estimated from the data and a codon-based model of site-specific rate heterogeneity was implemented. Trees were sampled every 100 generations for 1 000 000 generations. The log-likelihood scores plateau were reached at about 5000 and 1000 generations (Figs 2 and 3, respectively) and a consensus tree was constructed from the last 1000 (Fig. 2) and 100 (Fig. 3) trees (100 000 and 10 000 generations, respectively). The likelihood ratio test (Huelsenbeck and Crandall 1997) was used to decide whether ML-clock and ML + clock trees differed significantly. Relative rate tests were performed with RRtree 1.1.13 (Robinson et al. 1998).

Saturation of substitutions was evaluated by plotting (in Excel) transition against transversion distances and fitting the linear or power regression that gave the highest $r^2$ value. TCS 1.18 (Clement et al. 2000) was used to reduce the sequences to haplotypes, and because of the observed low variability and the large number of identical sequences within and between localities, all phylogenetic analyses were performed on the resulting eight haplotypes.

Statistical analysis of population diversity and structure
The geographical structuring of genetic variation was evaluated with $\Phi$-statistics, using the analysis of molecular variance (AMOVA) in
et al. 2000), following the method of Templeton et al. (1992). A spanning network (MSN) were estimated using TCS 1.18 (Clement
with 10,000 data permutations. Haplotype frequencies and a minimum
37 variable nucleotides (36 parsimony-uninformative
indicates that there was no detectable saturation. There
base composition shows an anti-G bias
1994; Zhu et al. 1994; Martin and Bermingham 1998; Lee
A ¼ 27%; C ¼ 27%; T ¼ 32%; G ¼ 14%) (Cantatore et al.
Among the 36 R. hartii individuals sampled, eight haplotypes
first codon position, but none resulted in an amino acid
phylogeny. Specimens, location data, GenBank accessions and haplotypes
Table 1. Rivulus hartii phylogeny. Specimens, location data, GenBank accessions and haplotypes
Location Coordinates Altitude Glasgow numbers (GLAHM) Field and laboratory numbers GenBank accessions Haplotype
Trinidad (Northern Range) Blue Basin 61°33′W, 10°44′N 500 m 130048 T538 AY619607 H1
Tucker Valley 61°37′W, 10°43′N Sea level 130046 T536 AY619635 H8
El Tucuche 61°24′W, 10°44′N 300 m 130026 T516 AY619628 H5
Maracas Waterfall 61°24′W, 10°43′N 300 m 130016 T506 AY619631 H5
Mount Saint Benedict 61°21′W, 10°39′N 150 m 130014 T504 AY619608 H7
Lopinot 61°19′W, 10°41′N 150 m 128968 T458 AY619638 H7
Paria River 61°15′W, 10°47′N Sea level 130001 T491 AY619620 H3
Trinidad (Central Range) Mount Tamana 61°11′W, 10°27′N 30 m 128970 T460 AY619609 H7
Mount Harris 61°06′W, 10°30′N 10 m 130027 T517 AY619624 H6
Trinidad (Southern Range) La Lune River 61°20′W, 10°05′N 30 m 130024 T514 AY619632 H7
Tobago (Main Ridge) Argyle River 60°36–35′W, 11°17–16′N 400 m 128964 T454 AY619612 H2
128967 T457 AY619610 H2
130012 T502 AY619611 H2
All R. hartii specimens are deposited at the Glasgow University Hunterian Museum (GLAHM).
Note: Tucker Valley is located in north-western Trinidad but does not form a part of the hill formations. The approximate
altitudes are taken from topographical maps.
ARLEQUIN (Excoffier et al. 1992; Schneider et al. 2000). The
significance of variance components and Φ-statistics were assessed
with 10,000 data permutations. Haplotype frequencies and a minimum
spanning network (MSN) were estimated using TCS 1.18 (Clement et al. 2000), following the method of Templeton et al. (1992).

Results
Sequence characteristics
As in other fish, base composition shows an anti-G bias
(4 = 27%; C = 27%; T = 32%; G = 14%) (Cantatore et al.
1994; Zhu et al. 1994; Martin and Bermingham 1998; Lee
et al. 2001; Doadrio and Dominguez 2003; Peng et al. 2004).
Base composition heterogeneity was absent (Chi-squared
test, p = 0.96). The scatter-plot of transition versus trans-
version p′ distances showed a linear relationship (r2 = 0.96),
indicating that there was no detectable saturation. There
were 77 variable nucleotides (69 parsimony-uninformative
and eight informative); 63 variable sites were third codon
positions, five were second codon positions and one was a
first codon position, but none resulted in an amino acid
substitution.
Among the 36 R. hartii individuals sampled, eight haplotypes
were found (Table 1, Fig. 3). Six haplotypes occurred in
samples from the Northern Range: Blue Basin (H1 and H4);
Paria River (H3); El Tucuche and Maracas Waterfall (H5); Mount Saint Benedict and Lopinot (H7); and Tucker Valley
(H8). One haplotype (H7) occurred in both of the two Northern
Range localities (Mount Saint Benedict, Lopinot) and in the
Central (Mount Tamana, Mount Harris) and southern (La
Lune River) ranges. A single haplotype was recovered from
every sample site except Blue Basin and Mount Harris, at each
of them two haplotypes were found (H1 + H4 and H6 + H7,
respectively). In Tobago, only one haplotype (H2) was found.
Phylogenetic analyses
The eight haplotype sequences were aligned with the previous
cyt b sequences (each of 360 nt, obtained from Genbank)

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derived from specimens from western Brazil and Venezuelan or Guianese locations. The 360 nt region present in all specimens was analysed by BML to identify a suitable local outgroup for analysis of the 756 nt ingroup alignment. This analysis (Fig. 2) clearly identifies the existence of a derived *R. hartii* clade containing sister sub-clades, one clade comprising the specimen from south-eastern Caracas, the haplotype H1 and the sequence from the mainland Paria peninsula locality, a specimen from the island of Margarita and yet another comprising the remaining island haplotypes. This result indicates that H1 is an appropriate local outgroup for the main analyses that follow. The levels of divergence associated in this alignment with the various named species of *Rivulus* are given in Table 2.

The 360 and 756 nt alignments have strong non-random structure (PTP test, *p* = 0.01, respectively). From the 756 nt alignment ML and BML analyses both recovered two moderately well-supported clades, shown in Fig. 3. One clade comprises haplotypes H6, H7 and H8, from low-altitude localities in the Northern, Central and Southern Ranges, while the second comprises two sub-clades, one uniting the Tobago haplotype H2 with H3 from the nearest Trinidad locality (Paria River), the other uniting the adjacent Northern Range localities Blue Basin (H4) and El Tucuche/Maracas Waterfall (H5). Thus this analysis provides evidence for both geographical differentiation between *Rivulus* lineages in different watersheds and for communication between now-isolated sites.

Although there are no direct calibrations of molecular evolution rates in Rivulidae, the customary estimate of approximately 1.5% divergence per million years (Bermingham and Avise 1986; Bernatchez et al. 1991; Bernatchez and Dobson 1998)
1991; Zardoya and Doadrio 1999; Machordom and Doadrio 2001; Doadrio et al. 2002; Doadrio and Dominguez 2003) was used to obtain a rough idea of the likely ages of the divergences observed, given that relative rate tests found no significant differences between lineages (p > 0.05) in the rate of change in sequences from all the localities. Divergence estimates used for the molecular clock analysis are given in Table 3.

Analysis of variance

Because of the high sequence divergence observed between H1 and the ingroup, and the large contribution that this haplotype must make to variability, it was excluded from all AMOVA analyses. These located 72% of the variation between and 28% within populations (Table 4). AMOVA also revealed a significant subdivision between the northern (Tobago and Paria River) and southern drainages (all other localities) and between low- and high-altitude populations (<300 versus >300 m above sea level). Other variables, such as mountain ranges, faunal groups (Kenny 1995) or river drainages, showed no significant differentiation (p > 0.05).

Discussion

The results provide useful new information on the genetic differentiation of Rivulus in Trinidad and Tobago. The level of divergence between haplotype H1 and the remaining haplotypes (c. 11%) is greater than that between some named pairs of mainland species (e.g. R. stagnatus – R. deltaphilus; 5.7%, R. sp. Rio Supamo – R. stagnatus; 4.9%, R. sp. Rio Supamo – R. deltaphilus; 2.7%). Thus, the islands appear to have been colonised by at least two different lineages, now represented on the one hand by the specimens from the Paria peninsula on the mainland and from Blue Basin on Trinidad, and, on the other, by the remaining specimens. The approximately 11% divergence suggests that the lineages split circa 7 My, and it seems likely that H1 evolved in isolation on the mountains of either the Paria peninsula or of northern Trinidad, both of which rise over 600 m and would have provided refugia during marine high-stands. The high divergence between H1 and the remaining Trinidad and Tobago samples, if associated with diagnostic morphological variation, would probably be sufficient to justify the description of a new species. However, the morphological and meristic characters of the specimens involved have not yet been studied.

The low genetic differentiation found between H1 and R. hartii from the Paria peninsula may be the result of a recent dispersal from northern Venezuela to western Trinidad, perhaps when the Orinoco River wet season discharges reduce salinity levels in the Paria Gulf from 30% to 5–15% (Alkins and De Souza 1984; Read 1987; Kenny 1995). Similarly, some Venezuelan species of freshwater fish occur in the south-western peninsula of Trinidad, and are thought to have dispersed there during rainy season periods of reduced salinity (Price 1955; Alkins and De Souza 1984). The close genetic similarity between the Margarita Island and Trinidad and Tobago H1 and R. hartii from the Paria peninsula may be the result of a recent dispersal from northern Venezuela to western Trinidad, perhaps when the Orinoco River wet season discharges reduce salinity levels in the Paria Gulf from 30% to 5–15% (Alkins and De Souza 1984; Read 1987; Kenny 1995). Similarly, some Venezuelan species of freshwater fish occur in the south-western peninsula of Trinidad, and are thought to have dispersed there during rainy season periods of reduced salinity (Price 1955; Alkins and De Souza 1984). The close genetic similarity between the Margarita Island and Trinidad and Tobago...
Paria River samples in the guppy (1992) found a similar close relationship between Tobago and colonized by fish crossing from Trinidad. Fajen and Breden locality sampled, suggesting that Tobago may have been associated with the one found at the closest northern Trinidad notable, however, that the Tobago haplotype is most closely

type (H8) and other southern haplotypes (Table 3). It is similar to other southern regions. This claim fits well with the

valley is unlike that of the Northern Range, and is more

Tucker Valley is at the westernmost side of the Northern

region (Mount Harris), Blue Basin, Tucker Valley, La Lune River drainage, Tobago drainage (Argyle River) and Paria River drainage. Non-significant values are shown as NS.

Table 4. Hierarchical analysis of molecular variance (AMOVA). Hierarchical structures analysed: all populations; all 11 sampled localities without group structuring

<table>
<thead>
<tr>
<th>Structure analysed</th>
<th>Among groups</th>
<th>Within groups</th>
<th>Within populations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Va %</td>
<td>p</td>
<td>Fct</td>
</tr>
<tr>
<td>All populations</td>
<td>6.27 72.06</td>
<td></td>
<td>2.43 27.94</td>
</tr>
<tr>
<td>Northern versus southern watersheds</td>
<td>2.81 63.62 &lt;0.05 0.63</td>
<td></td>
<td>1.57 35.69 &lt;0.001 0.98 0.03 0.69</td>
</tr>
<tr>
<td>High altitude (&gt; 300 m) versus all other populations (excluding Tobago)</td>
<td>2.81 63.62 &lt;0.05 0.51</td>
<td></td>
<td>2.63 47.99 &lt;0.001 0.98 0.03 0.65</td>
</tr>
<tr>
<td>High altitude (&gt; 300 m) versus all other populations</td>
<td>1.10 34.36 &lt;0.05 0.34</td>
<td></td>
<td>2.07 64.69 &lt;0.001 0.98 0.03 0.39</td>
</tr>
<tr>
<td>Mountain ranges</td>
<td>0.54 18.99 NS</td>
<td></td>
<td>2.28 79.94 &lt;0.001 0.98 0.03 1.06</td>
</tr>
<tr>
<td>Kenny’s (1995) divides</td>
<td>1.19 38.70 NS</td>
<td></td>
<td>1.86 60.31 &lt;0.001 0.98 0.03 0.99</td>
</tr>
<tr>
<td>River drainages</td>
<td>1.38 46.69 NS</td>
<td></td>
<td>0.46 21.16 52.29 &lt;0.001 0.98 0.67 1.03</td>
</tr>
</tbody>
</table>

By Northern (Paria River, Tobago) versus Southern watersheds (all other localities)

By localities 300 m above sea level (Blue Basin, El Tucuche, Maracas Waterfall, Tobago) versus below 300 m above sea level (all other localities).

By mountain ranges (Tobago Main Ridge, Trinidad Northern, Central and Southern Ranges).

By Kenny’s (1995) faunal distribution (Antillean; Paria River and Tobago, Western Trinidad; Tucker Valley, Blue Basin, El Tucuche, Maracas Waterfall, Mount Saint Benedict, Lopinot, Mount Tamana, Eastern Trinidad; Mount Harris, Southern Trinidad; La Lune River).

By river drainages: Caroni drainage (Mount Saint Benedict, Lopinot, El Tucuche, Mount Tamana), Blue Basin, Tucker Valley, Oropuche drainage (Mount Harris), La Lune River drainage, Tobago drainage (Argyle River) and Paria River drainage.

By Northern (Paria River, Tobago) versus Southern watersheds (all other localities).

By mountain ranges (Tobago Main Ridge, Trinidad Northern, Central and Southern Ranges).

By Kenny’s (1995) faunal distribution (Antillean; Paria River and Tobago, Western Trinidad; Tucker Valley, Blue Basin, El Tucuche, Maracas Waterfall, Mount Saint Benedict, Lopinot, Mount Tamana, Eastern Trinidad; Mount Harris, Southern Trinidad; La Lune River).

By river drainages: Caroni drainage (Mount Saint Benedict, Lopinot, El Tucuche, Mount Tamana), Blue Basin, Tucker Valley, Oropuche drainage (Mount Harris), La Lune River drainage, Tobago drainage (Argyle River) and Paria River drainage.

Values in bold indicate significance (P ≥ 95) among groups.

Tobago haplotypes (Fig. 2) and the colonization of Trinidad and Margarita from the mainland probably result from the dispersal facilitated by coastal currents (especially the Orinoco River counter current) that flow in a circular motion around northern Venezuela, from western Trinidad to Margarita (Kenny 1995).

Apart from H1, all the other Trinidad and Tobago specimens are closely related to one another, and may reasonably be regarded as R. hartii. However, they differ substantially (mean ML distance: H2-8 – mainland species; 31.1 ± 0.5%) from all other sampled mainland species, and presumably represent genotypes derived from a common ancestor with H1 or from H1 itself, having been isolated from H1 for circa 7 My. As indicated by the analysis of genetic variance, divergence among these haplotypes shows some geographical and ecological structure associated mainly with isolation by northern and southern watersheds (Kenny 1995), or by altitude (Table 4). Because of complex historical fluctuations in the sea level, much of lowland Trinidad had been repeatedly flooded during the past few hundred thousand years (Murphy 1997), and this provides a reasonable explanation for relative lack of divergence between most low-altitude samples. Five populations from three low-altitude mountain range river drainages (east, west and south drainages, Fig. 1) share identical haplotypes (H7) which suggests that the present distribution of Rivulus in lowland Trinidad may be the consequence of the fragmentation of a once large widespread population during sea level low-stands, leading to the isolation of individuals in separate different river drainages. Although Tucker Valley is at the westernmost side of the Northern Range, Kenny (1995) argues that the faunal distribution of this valley is unlike that of the Northern Range, and is more similar to other southern regions. This claim fits well with the low genetic differentiation between the Tucker Valley haplotype (H8) and other southern haplotypes (Table 3). It is notable, however, that the Tobago haplotype is most closely associated with the one found at the closest northern Trinidad locality sampled, suggesting that Tobago may have been colonized by fish crossing from Trinidad. Fajen and Breden (1992) found a similar close relationship between Tobago and Paria River samples in the guppy Pecelia reticulata. They suggested that for this fish, the ancestral mtDNA haplotype from Venezuela could have also colonized Tobago. However, more samples from eastern Trinidad and from Tobago would be required before the direction and number of colonization events involving Rivulus could be constrained.

This study originated as a part of an investigation of interactions between the endemic Trinidadian frog, Mannophryne trinitatis and its predators (Downie et al. 2001; Jowers and Downie 2005; Jowers et al. 2006) that was extended to include the phylogenetic relations of the Golden Tree Frog, Phryllodites auratus and M. trinitatis (M. J. Jowers unpublished data). Both of these studies found evidence of the long-term isolation of populations in areas or peaks of the Trinidad Northern Range mountains and, combined with the present study, they emphasize the importance of mountain refuges as a factor in speciation.

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Resumen

El pez Cyprinodontiforme Rivulus (Apocheiloidei: Rivulidae) en Trinidad y Tobago: evidencia molecular de dispersión marina, isolamento genético y diferenciación local

Secuencias mitocondriales de ADN (756 bp) fueron obtenidas del gen citocroma b de 36 individuos de Rivulus colectados de diez localidades en Trinidad y de una localidad en Tobago. Ocho haplotipos fueron identificados. Baja variabilidad genética (0.5%) entre estos y el resto de haplotipos provenientes de Trinidad y Tobago sugiere que las Islas fueron colonizadas por dos linajes. El haplotipo mas común es...
distribuye por zonas bajas, posiblemente a consecuencia de las inundaciones del río Orinoco que facilitaron la dispersión de individuos entre ríos. Rutilus provenientes de localidades a elevada altitud (Cordillera del Norte) no afectados por estas inundaciones muestran alta divergencia genética entre localidades. La diferencia genética entre ríos del sur y del norte de Trinidad sugiere islamiento entre estos sistemas fluviales.

References


Nylander JAA (2004) Mrmodeltest 2.0. Program Distributed by the authors, Uppsala University, Uppsala.


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