Convergent and divergent evolution in rain-forest populations and communities of cyprinodontiform fishes (*Aphyosemion* and *Rivulus*) in Africa and South America

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Abstract: When the African and American continents separated 65–125 million years ago, populations and communities of plants and animals of the same lineage became isolated and evolved independently. Today, however, the cyprinodontiform fishes on the two sides of the Atlantic Ocean are morphologically similar, especially the American genus *Rivulus* and the African genus *Aphyosemion*. The evolutionary-inertia hypothesis is rejected as an explanation of this similarity because of evidence that the speciation process is ongoing. This study concerns processes that are probably responsible for the convergent and divergent evolution in the composition, structure, and dynamics of populations and communities, respectively. Basic data were obtained during a long-term study in the field, at the M'Passa biological station in Gabon and the St. Elie biological station in French Guiana. At the same time, rearing experiments were conducted from the Laboratoire d'Écologie at the Muséum National d'Histoire Naturelle in Paris. The composition, structure, and dynamics of the populations at M'Passa and St. Elie are similar. Parallel evolution of the habitats may explain the parallel evolution of the populations of cyprinodontiform fishes in Africa and America, leading to similar fish populations in similar habitats. Conversely, the composition, structure, and dynamics of the communities at St. Elie and M'Passa are different. The cause of this divergent evolution may be the absence of specific predators and competitors at M'Passa and the presence of highly specialized predators and competitors at St. Elie. The predators and competitors present at St. Elie all belong to the Characidae, a very successful group of fishes in America, without an equivalent in the Old World. Analogous processes of competitive exclusion are also observed in other orders of tropical American vertebrates: batrachians, reptiles, birds, and bats.

Résumé : Quand les continents africain et américain se sont séparés, il y a 62–125 millions d'années, les populations et les peuplements de plantes et d'animaux d'origine commune se sont retrouvés isolés et ont suivi par la suite une évolution indépendante. Aujourd'hui, les poissons cyprinodontiformes sont morphologiquement très semblables des deux côtés de l'Atlantique, en particulier les *Rivulus* américains et les *Aphyosemion* africains. Pour expliquer cette similarité, l'hypothèse d'une inertie évolutive doit être écartée, vu la richesse spécifique des deux genres et parce tout indique que des processus de spéciation sont toujours en cours. Les populations et les peuplements de cyprinodontiformes américains et africains présentent-ils eux aussi une composition, une structure et une dynamique similaires sur les deux continents? C'est la question à laquelle le présent travail s'efforce de répondre. Les données de base ont été obtenues au cours de deux études à long terme sur le terrain, l'une à la station biologique de M'Passa au Gabon, l'autre à la station biologique de Saint-Élie en Guyane française. Pendant la même période, des expériences en élevage se sont poursuivies au Laboratoire d'Écologie du Muséum National d'Histoire Naturelle de Paris. Les résultats de ces études sont les suivants: la composition, la structure et la dynamique des populations sont similaires à M'Passa et à Saint-Élie. À une évolution parallèle des habitats semble correspondre une évolution parallèle des populations de poissons cyprinodontiformes en Afrique et en Amérique. À l'inverse, la composition, la structure et la dynamique des peuplements sont différentes à Saint-Élie et à M'Passa. La cause de cette évolution divergente des peuplements paraît être l'absence de prédateurs et de compétiteurs spécifiques à M'Passa et l'existence de prédateurs et de compétiteurs hautement spécialisés à Saint-Élie. Les prédateurs et compétiteurs à Saint-Élie sont tous des characidés, un groupe dynamique de poissons américains sans équivalent dans l'Ancien Monde. Des processus d'exclusion compétitive analogues sont aussi observés chez des vertébrés néotropicaux autres que les poissons, batraciens, reptiles, oiseaux et chauves-souris.

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Introduction

When the African and American continents separated 65–125 millions years ago, populations and communities of plants and animals of the same lineages, unable to disperse across a marine barrier, became isolated and evolved independently. To understand the evolutionary processes responsible for the present-day organisation and dynamics of populations and communities in tropical Africa and South America, we compare groups of species that are probably derived from common ancestors and characterized by a limited potential for geographical expansion. The cyprinodontiform genera *Aphyosemion* in Africa and *Rivulus* in America exhibit these characteristics and constitute a good system for comparison. From 1970 to 1978 in Gabon (M'Passa biological station) and from 1979 to 1997 in French Guiana (St. Elie biological station), the populations and communities of these fishes were regularly censused, special attention being paid to their composition and dynamics. At the same time, their behaviour and reproduction were studied in captivity. In this paper, we compare the results of the two studies to assess the processes that might explain the evolutionary trends, i.e., parallelism, divergence, or convergence, in the populations and communities of cyprinodontiform fishes inhabiting the rain forests of Africa and South America.

Material and methods

The fishes

Parenti (1981) classified the African cyprinodontiform genus *Aphiosemion* (202 species) and the American genus *Rivulus* (293 species) in two different families, based on such morphological differences as "supracleithrum fused to post temporal in the African fishes, not fused in the American one; first postcleithrum present in the former, absent in the latter" (Nelson 1994).

Nevertheless, their external morphology, size, shape, coloration, and sexual dimorphism, as well as their ecology and behaviour, are so similar that splitting them into two families has been questioned (Nelson 1994; Huber 1998). The similarity in external morphology between *Aphyosemion* and *Rivulus* is illustrated in Fig. 1.

Habitats

The M'Passa biological station is located in northeastern Gabon (1°N, 12°E) and the St. Elie biological station in northwestern French Guiana (5°18′N, 53°04′W). The study areas extended for about 2 km around the M'Passa biological station and for approximately 1 km around the St. Elie biological station. The two locations, situated in blocks of primary forest, have an extremely dense network of small streams, the habitat of cyprinodontiform fishes.

At M'Passa and St. Elie the composition and dynamics of the populations and communities of cyprinodontiform fishes are closely related to their habitats. Some habitats are permanent and stable, while others are subject to temporary changes.

During recent periods, the Ivindo Basin, where M'Passa is situated, and the forested coastal area in French Guiana, where St. Elie is situated, seem to have had similar climatic histories, characterized by relative stability of their habitats. According to Maley (1996), the Ivindo Basin was a part of the Central African "refugia" during glaciations. It seems improbable that the ice age significantly changed the nature of the habitats in French Guiana (Clapperton 1993; Colinvaux 1989), and according to de Granville (1982, 1992), the composition of the flora in the St. Elie area does not suggest recent modification of the habitats due to climatic changes. Thus, at both M'Passa and St. Elie, equilibrium in the composition of populations and communities results from the environment having remained unperturbed for a relatively long time, at least along the forest streams where these fishes live.

Table 1 shows the biotic and abiotic components of the habitat of the cyprinodontiforms at St. Elie and M'Passa that are most significant in the long term. These components, which are almost identical on the two sides of the Atlantic Ocean, are characterized by their permanence and stability.

Changes in habitat components

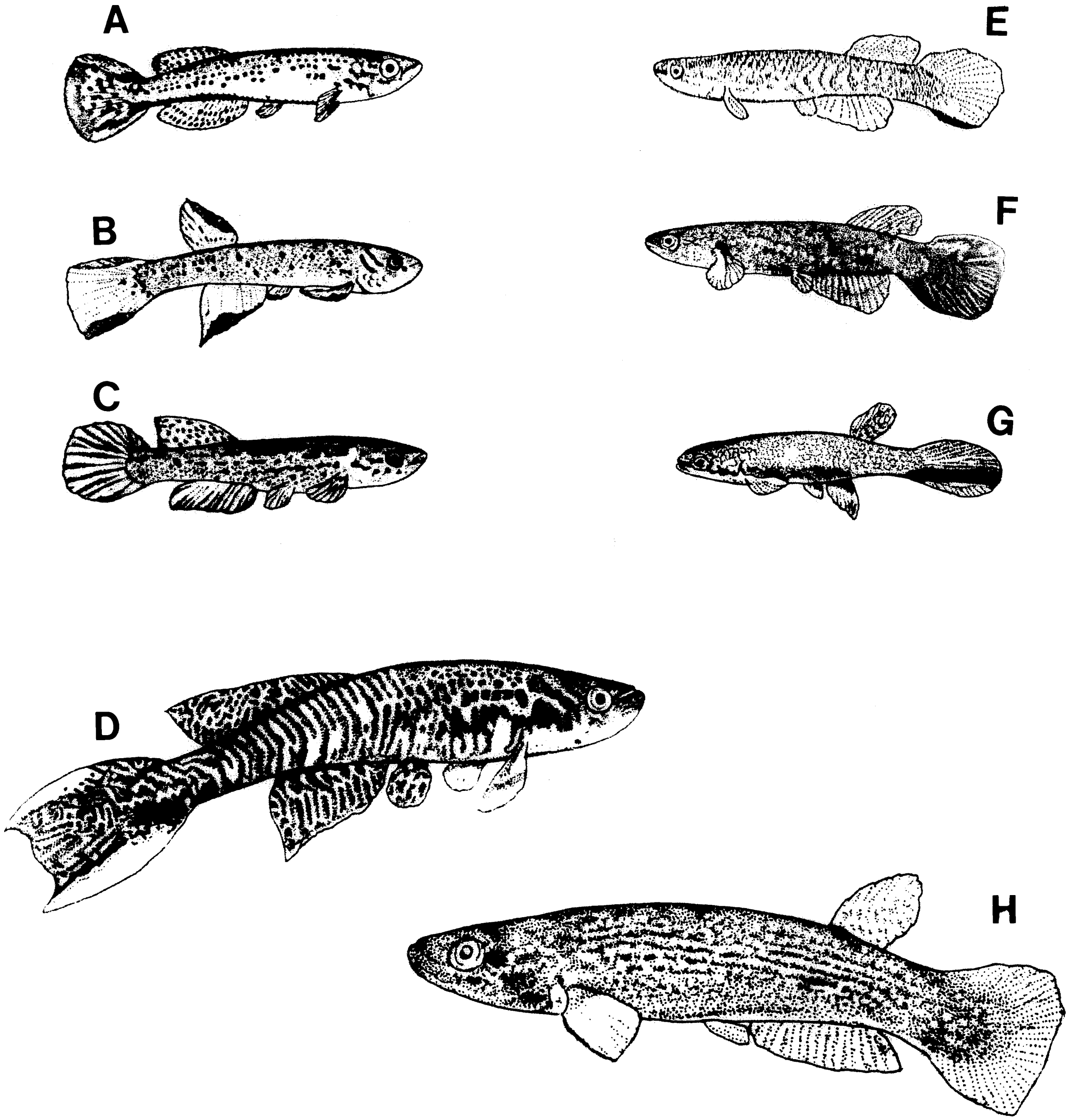
At the microhabitat scale and in the short term, I noticed important natural disturbances. At both M'Passa and St. Elie, the main disturbance is flooding after heavy rains, while biotic disturbance results from elephants, *Loxodonta africana*, trampling and wallowing in the stream course at M'Passa and from identical behaviour by tapirs, *Tapirus terrestris*, in the St. Elie region.

Methods

At M'Passa and St. Elie, the following habitat features were analysed in the field: temperature and chemical composition of the water, air temperature, and light intensity. Fishing by means of different techniques, nets, poison, or draining streams and pools, was conducted once a month over a period of 8 years at M'Passa in nine different microhabitats (the term microhabitat is used here to designate a section of stream about 40 m long, each study section being separated from the next by a distance of about 300 m). At St. Elie, fishing took place in eight different microhabitats once a year for 8 years. The captured fish were identified, counted, sexed, and measured, and most of them were released after examination. In the field we studied the specific composition of the community in each microhabitat, and the ecological specialization of each species, the social organisation of the populations, relationships with other syntopic species, especially predators and competitors, and food and feeding behaviour. Seven hundred and sixty-six individuals (belonging to all studied species) were exported to France and kept alive at the Laboratoire d'Écologie at the Muséum National d'Histoire Naturelle, some of them for 4–5 years. About 2300 individuals born in captivity were reared. We examined age at sexual maturity, sex ratio, sexual behaviour, size and periodicity of the clutch, duration of incubation, and longevity (Brosset 1982; Brosset and Lachaise 1995).

To establish the diet of the fish and their parasite load, the stomach contents and parasites from 1771 wild-collected individuals were examined with the help of specialists from the Muséum National d'Histoire Naturelle in Paris. Voucher specimens and their parasites are stored in the collection of this museum.

Fig. 1. Similarity in external morphology between the African genus *Aphyosemion* at M'Passa and the American genus *Rivulus* at St. Elie. All are adult males, drawn to the same scale. At M'Passa, the genus *Aphyosemion* (A–D) comprises three medium-sized non-annual species and one large semi-annual species. Similarly, at St. Elie, the genus *Rivulus* (E–H) comprises three medium-sized non-annual species and one large semi-annual species. (A) *Aphyosemion cameronense*. (B) *Aphyosemion punctatum*. (C) *Aphyosemion herzogi*. (D) *Aphyosemion* (*Raddaella*) *batesii*. (E) *Rivulus agilae*. (F) *Rivulus cladophorus*. (G) *Rivulus xiphidius*. (H) *Rivulus igneus*.



Results

Populations

The ecological niche occupied by the cyprinodontiform populations at M'Passa and St. Elie

The role of short-term modifications of the habitat

In the short term, the habitats of both communities are modified by seasonal flooding. Water spreads out from the streams and covers the low-lying parts of the forest. Many cyprinodontiform fishes leave the streams and pools to occupy the flooded zone, which considerably increases their foraging area. Most often this seasonal habitat and the adaptive behaviour of the fishes are of short duration, a few hours only; the cyprinodontiforms then leave this zone as it dries and return to the main stream by jumping (Seghers 1978). Numerous observations at M'Passa and St. Elie suggest that these phenomena are too brief to have much of an impact on the structure of the communities. Nevertheless, a few observations at M'Passa revealed changes in the composition of communities in the microhabitats after flooding (Brosset 1982).

More important are the deep and enduring perturbations of the habitats at M'Passa caused by the passage of groups of elephants and buffalo (*Syncerus caffer*), which use the stream courses as pathways to penetrate the thick parts of

Table 1. Comparison of the habitats of the cyprinodontiform fishes at the M'Passa and St. Elie biological stations.

M'Passa	St. Elie
Dense network of small streams inside the equatorial primary forest	Dense network of small streams inside the equatorial primary forest
Streams 5–300 cm wide and 2–25 cm deep	Streams 5–300 cm wide and 2–25 cm deep
Water level stable except during very brief seasonal flooding	Water level stable except during very brief seasonal flooding
Water transparent, almost devoid of mineral and organic components	Water transparent, almost devoid of mineral and organic components
Water temperature stable (22 ± 1 °C)	Water temperature stable (23 ± 1 °C)
pH 5.1–6.2	pH 5.0–6.6
Average light intensity at the border of the stream is 1/100 of the light above the forest canopy	Average light intensity is 3/100 of the light above the forest canopy
Overhanging vegetation above the stream, from where the trophic resources of the fish (mostly ants) come	Overhanging vegetation above the stream, from where the trophic resources of the fish (mostly ants) come

Note: The biotic and abiotic components of these habitats are similar. The slight differences in light intensity and water temperature are due to the fact that the forest canopy is more open above the prospective sites at St. Elie.

the forest, wallowing in the pools, destroying numerous microhabitats and creating new ones. During the study, the spatial configuration of the observed microhabitats and the structure of the cyprinodontiform communities were considerably modified (Brosset 1982; Brosset and Lachaise 1995).

Food resources and parasitism

The food resources available to the cyprinodontiform populations are the same in tropical Africa and South America. The forest-dwelling African genus *Aphyosemion* and the American genus *Rivulus* feed almost exclusively on invertebrates, i.e., insects and spiders, that fall from overhanging vegetation into the streams and pools. Ants are their basic food (Fig. 2), followed by spiders, then Diptera, Coleoptera, and Ephemeroptera.

No systematic study of parasitism was made; observations are related only to large parasites extracted from the digestive tracts of collected specimens. Heavy infestation by such parasites was observed in *Rivulus igneus* at St. Elie and *Aphyosemion cameronense* at M'Passa. The local environment was the same for both: drying pools with a high concentration of individuals in a state of starvation. This type of parasitism may depend on host density and may destroy a generation of fish, which may be condemned to disappear as a result of the seasonal drying of the pools. At St. Elie and M'Passa, the nematode species responsible for the infestations all belong to the genus *Porocecum* (Brosset 1982). Parallel evolution concerns not only the host, but also the specific parasites!

The composition and dynamics of the cyprinodontiform populations at M'Passa and St. Elie

Composition of the populations

At the two stations, the sex ratios of the species vary according to space and time (Brosset 1982). However, adding together all individuals captured during the study yielded balanced numbers of males and females for most of the species.

Social organisation varies according to species and characteristics of the microhabitat. But the same social structure was observed in the African genus *Aphyosemion* and the American genus *Rivulus*: promiscuity in all species living along running streams, harems in *A. cameronense* and *Rivulus agilae*, and multimale groups in *Aphyosemion* (*Raddaella*) *batesii* and *R. igneus* living in closed pools. Everywhere the social groups are made up of different-sized individuals.

Population dynamics

Reproduction. Data concerning reproduction were obtained mostly in the laboratory: age at sexual maturity, sexual behaviour, periodicity of clutches, number of eggs, dry mass of eggs, and duration of incubation. In all the studied species, both African and South American, the onset of sexual maturity is independent of size (observations of individuals in captivity and the existence of dwarf breeding individuals in spatially restricted habitats are reported in Brosset 1982). The age of an individual cannot be estimated from its size. In captivity, the age at sexual maturity (between 3 and 6 months) remains the same for all sibling males independently of their size. These peculiarities are observed in both African and American cyprinodontiforms.

Males exhibit elaborate sexual displays (Ewing and Evans 1973). Depending on the species, these displays may vary in detail but they remain similar in general structure, especially in the genera *Aphyosemion* and *Rivulus*, whose sexual displays have been studied comparatively using individuals originating from M'Passa and St. Elie. There are striking convergences between the sexual displays of the African and American species (Silva-Amador 1987).

Considerable differences exist between species in the tempo of emission of clutches, the number of eggs in each clutch (Table 2), and parental investment in each egg (Fig. 3). On the other hand, the duration of incubation is the same for all species: 17 ± 1 days at 23 °C. Similarities and differences between species are of the same order at St. Elie and M'Passa (Table 3). The conservative character of the traits related to reproduction is remarkable when the African and American cyprinodontiform populations are compared. On the other hand, the small number of eggs and large investment in each egg are general characteristics of tropical rain-forest vertebrates (for birds see Brosset and Erard 1986).

Fig. 2. Similarity between the stomach contents of *Rivulus* spp. at St. Elie (A) and *Aphiosemion* spp. at M'Passa (B) (*n* is the number of stomach contents analysed).

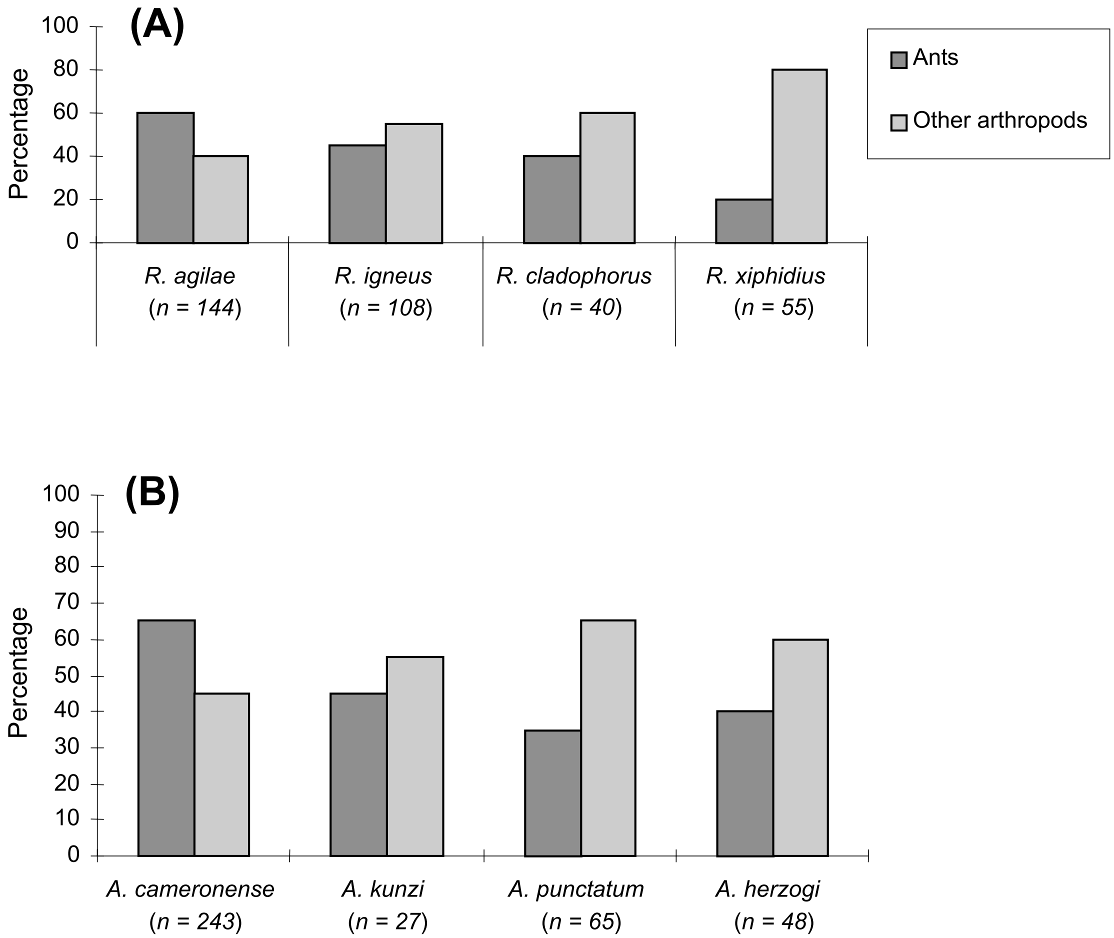


Table 2. The number of eggs in each clutch[a] for *Aphyosemion* spp. at M'Passa and *Rivulus* spp. at St. Elie.

	No. of females	Avg. no. of eggs/female	Range
Aphyosemion cameronense	41	26	5–58
Aphyosemion punctatum	30	9	3–23
Aphyosemion kunzi	28	13	2–48
Aphyosemion herzogi	16	7	1–10
Rivulus agilae	15	18	5–42
Rivulus igneus	19	18	3–51
Rivulus cladophorus	8	9	3–22
Rivulus xiphidius	6	4	2–5

[a]A clutch is the total number of ovocytes in the ovary of the wild-collected females. This number varies according to the species and individual, but the differences are similar in scale in the two communities.

Longevity. In the field, no obviously senescent individuals were seen. Individuals born and reared in captivity became senescent when 4–5 years old.

Two species, *R. igneus* at M'Passa and *A.* (*R.*) *batesii* at St. Elie, have a shorter life-span (a maximum of 26 and 21 months in captivity, respectively). Both are semi-annual species, with a peculiar reproductive cycle: they lay large eggs and exhibit long pre- and post-incubation diapauses (Wourms 1972). The eggs may remain in the mud without hatching for more than 6 months, an adaptation resulting from the fact that the parents lay their eggs in temporary habitats, especially drying pools, where the old adults may die several months before the return of the seasonal rains. At that time, the pools are filled again and upon contact with water the young immediately hatch and the development of a new generation begins (Brosset 1982).

The communities

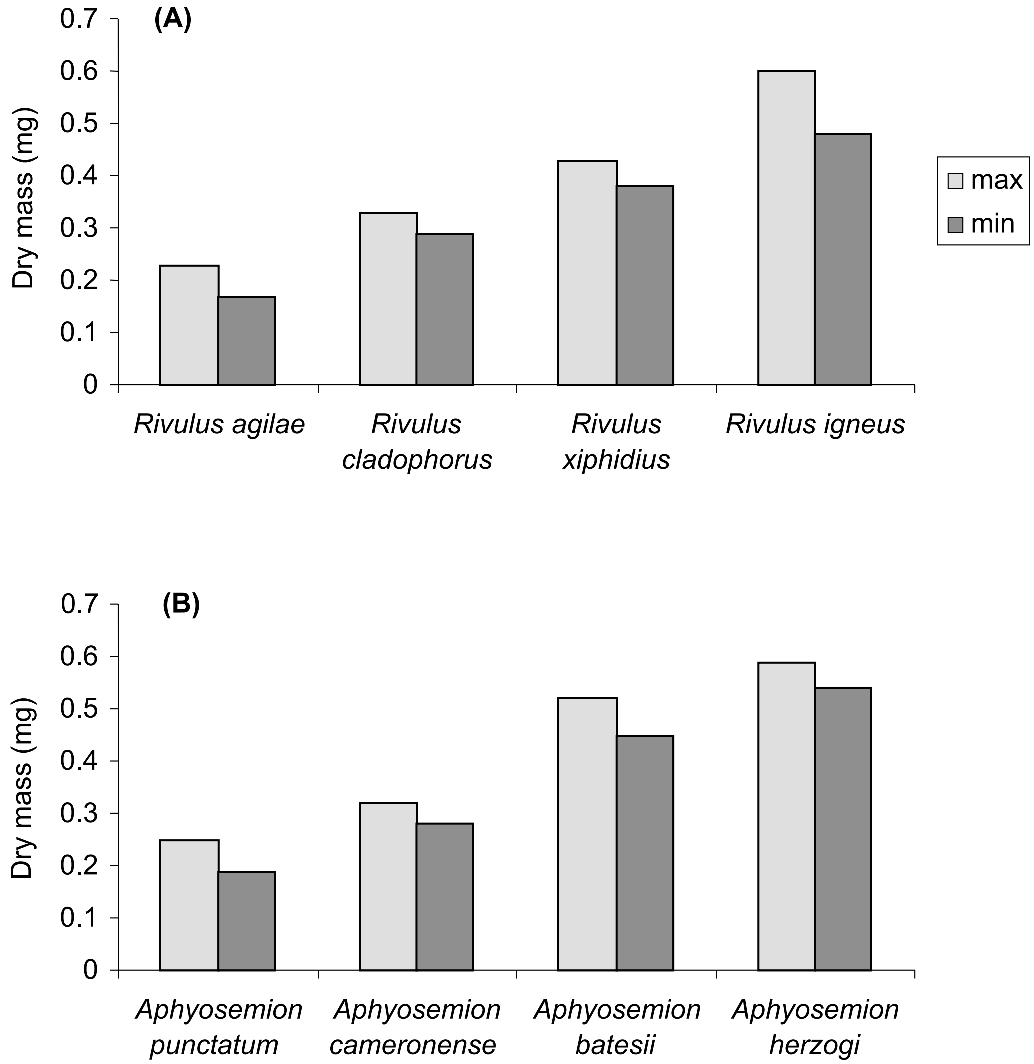
Composition

Generic diversity differs between the communities at St. Elie and M'Passa: eight species and four genera at M'Passa and four species and one genus at St. Elie. The community at M'Passa is made up of three *Aphyosemion* species, two *Diapteron* species, one *Aphyosemion* (*Raddaella*) species, one *Epiplatys* species, and one *Hylopanchax* species. At St. Elie, only four *Rivulus* species were found (Table 4).

Numerical uniformity of individuals in the M'Passa community at the specific level and presence of one numerically dominant species and one rare species at St. Elie

The long-term field study at M'Passa did not allow us to establish the presence of any one species as numerically

Fig. 3. Female investment in each egg, shown as the dry mass of 10 eggs, all from different clutches laid by different females. The differences between species are similar in scale in the American genus *Rivulus* (A) and the African genus *Aphyosemion* (B).



dominant or rare. The regular fishing effort at nine microhabitats produced equivalent numbers of captures of each species. Discrepancies in location and time were corrected by adding together the numbers of individuals of each species in the community caught during the study.

At M'Passa, the spatial distribution of the species is as follows: one or two species are found in closed pools at the border of a given stream, but all species are present in the stream itself. Examples obtained from drying streamlets and pools and a complete census of local cyprinodontiform communities are given in Brosset (1982) and Brosset and Lachaise (1995).

The same fishing effort at St. Elie gave different results. *Rivulus agilae*, which was present in all microhabitats, is numerically dominant in the community at St. Elie, with 2220 individuals captured out of a total of 3632 for the whole community. Conversely, one species is present at only one of the sites sampled at St. Elie, in a microhabitat 25 m long × 2 m wide. This species, *Rivulus cladophorus*, is considered rare everywhere (Huber 1998), and we caught only 43 individuals.

Predation and competition as evolutionary determinants of the communities' evolution

Absence of specialized predators of the cyprinodontiforms at M'Passa

At M'Passa, the fishes inhabiting the small forest streams do not seem to be regularly exploited by predators. These streams are tributaries of large rivers, which are particularly rich in specialized fish predators: three species of mammals, nine species of birds, and at least three species of snakes (Brosset 1982, 1990; Brosset and Erard 1986). At M'Passa, we observed these predators many times along the rivers, small and large, but never along the small streams where cyprinodontiforms live. One predatory fish, *Epsetus odoe*, is represented in these small streams by juvenile individuals 5–6 cm long. But these individuals are quite rare, and their stomachs were devoid of fish remains. Some cyprinodontiform remains were found in the stomach contents of the giant water shrew, *Potamogale velox* (Dubost 1965), but the majority of the species preyed upon by this shrew were identified as belonging to other families.

Table 3. The duration of incubation at 23 °C, which is the same for all the species (17 ± 1 days).

Fish species from M'Passa	*n*	No. of days	Fish species from St. Elie	*n*	No. of days
Non-annual species					
Aphyosemion cameronense	48	16–18	*Rivulus agilae*	7	17
Aphyosemion punctatum	50	16–18	*Rivulus cladophorus*	9	17–18
Aphyosemion hertzogi	34	17–19	*Rivulus xiphidius*	9	17–21
Annual or semi-annual species					
Aphyosemion (*Raddaella*) *batesii*	46	Development may be preceded by an embryonic diapause (maximum length 135 days) or followed by a post-embryonic diapause (maximum length 180 days)	*Rivulus igneus*	25	Development may be preceded by an embryonic diapause (maximum length 30 days) or followed by a post-embryonic diapause (maximum length 92 days)

Note: Pre- and post-incubation diapauses may introduce considerable delays between laying and hatching in semi-annual species, one at M'Passa and one at St. Elie. Note that during the experiments, the post-embryonic diapause was experimentally interrupted by immersing the eggs in water (they had previously been kept in humid peat). This diapause may be longer under natural conditions. *N* is the number of clutches. For details of the study see Brosset (1982).

At M'passa, predators of cyprinodontiforms were occasionally observed in recently disturbed habitats: a large spider (Brosset 1982) and a group of mandrills, *Mandrillus sphinx* (Jouventin 1975). Owing to the rarity of these observations, it is doubtful whether the fish *E. odoe*, the water shrew, the spider, or the mandrill play any role in the dynamics of the cyprinodontiform communities at M'Passa.

Presence of one specialized predator and one cannibalistic Rivulus *species in the St. Elie community*

We noticed taxonomic–morphological and ecological similarity between the fish predators, crocodiles, snakes, and birds, in the large rivers at M'Passa and St. Elie. Among the mammals, the South American counterpart of the African water shrew is a marsupial, the yapock, *Chironectes minimus* (Brosset 1989). All these fish predators at St. Elie and M'passa were located in streams and rivers that are larger and deeper than the small shallow pools and streams occupied by cyprinodontiforms. No regular predators were observed in the specific microhabitats of these fishes at M'passa; two such predators are present at St. Elie.

The specialized cyprinodontiform predator Erythrinus erythrinus *at St. Elie*

We demonstrated experimentally that the characoid fish *Erythrinus erythrinus* aggressively mimics *R. agilae* at St. Elie. When they are 2–6 months old, juvenile *E. erythrinus* temporarily share the habitat of the cyprinodontiforms. During this stage the predator exhibits the coloration pattern of the female *R. agilae*. The imitation is so perfect that some juvenile specimens of *E. erythrinus* have been classified by specialists as *R. agilae*! Various experiments have demonstrated the process of predation by young *E. erythrinus*: when a male *R. agilae* discovers a *E. erythrinus* mimicking its females, it approaches and begins to display, vibrating its open tail close to the head of the *E. erythrinus*. The predator suddenly catches the tail of the *R. agilae* and swallows the whole fish (Brosset 1997).

Table 4. Composition of the communities (four genera and eight species at M'Passa and one genus and four species at St. Elie).

M'Passa	St. Elie
Aphyosemion cameronense	*Rivulus agilae*
Aphyosemion punctatum	*Rivulus cladophorus*
Aphyosemion herzogi	*Rivulus xiphidius*
Aphyosemion (*Raddaella*) *kunzi*	*Rivulus igneus*
Diapteron cyanostictum	
Diapteron georgiae	
Epiplatys neumanni	
Hylopanchax stictopleuron	

A cannibalistic Rivulus *species*, R. igneus

None of the stomachs of 1265 cyprinodontiforms captured at M'Passa contained fish remains. The stomachs of 506 cyprinodontiforms from St. Elie mostly contained remains of invertebrates and some traces of plant matter. However, large specimens of *R. igneus* with remains of small fish in their stomachs were collected at St. Elie. These remains were identified as belonging to *R. igneus*. Also, my colleague P. Gaucher, who was trying to catch *E. erythrinus* with a fishing line baited with small *R. igneus*, caught large *R. igneus* that were concentrated in drying pools. Cannibalism also occurs regularly in captivity, when large *R. igneus* are deprived of food. This observed cannibalism only occurs when and where food is lacking. The data confirm the description of cyprinodontiform cannibalism in Huber et al. (1998).

No competitor is present at M'Passa, but two competitors are present at St. Elie

Juvenile silurids and cichlids were collected in the specific habitat of the cyprinodontiforms at M'Passa. Based on observations in the field and in captivity, these juvenile fish are bottom feeders and, based on stomach-content analysis, their prey species are different from cyprinodontiform prey. No competitor was recorded at M'Passa.

The situation is different at St. Elie, where two species belonging to the family Lesbiasinidae (order Characiformes) share the ecological niche of the cyprinodontiform community. These two mimetic species, which are difficult to separate in the field, are *Copella carsevennensis* and *Pyrrhulina filamentos* (Fig. 4). These fishes are known to be ant eaters and to live side by side with the cyprinodontiforms (Planquette et al. 1996). The stomach contents of 188 individuals confirm that the basic food is ants. The behaviour and diet of *C. carsevennensis* and *P. filamentos* at St. Elie are very similar to the behaviour and diet of the cyprinodontiform *Epiplatys neumanni* at M'Passa (Fig. 5).

I noticed that two ecologically equivalent species, *E. neumanni* in M'Passa and *C. carsevennensis* at St. Elie, exhibit a bright silvery spot on their body, on the top of the head in *E. neumanni* and at the base of the dorsal fin in *C. carsevennensis*. In the field this reflector is visible to the human eye at a distance of 4–5 m. The biological function of this spot, observed in fish species that are very distant taxonomically and geographically, but have the same ecological requirements, is unknown. It is unlikely to be a social or sexual signal (Planquette et al. 1996), or to be used for recognition between the two otherwise mimetic species *C. carsevennensis* and *P. filamentos*, because the signal is not directed towards creatures living below or at the same level as the transmitting fish. It is clearly directed upwards and towards aerial recipient species, probably invertebrates in flight or standing in the overhanging vegetation. This interpretation, that the spot acts as a luminous trap to attract prey, awaits experimental study, which must be carried out in the field because the spot loses its luminous quality in captivity.

Discussion

To explain the evolutionary determinants of this similarity in the composition, structure, and dynamics of forest-dwelling populations of cyprinodontiform fishes in tropical Africa and America, two main hypotheses may be proposed. Firstly, the similarity could result from evolutionary inertia, the modern cyprinodontiforms expressing conservative traits of the primitive stock from which all African and American fishes are derived. The second hypothesis is that these fishes evolved in parallel ways on the two sides of the Atlantic Ocean, the observed similarity of the populations being the result of convergent evolution of habitats.

If we consider the evolutionary history of the Cyprinodontiformes, the two hypotheses are not mutually exclusive. According to Huber (1998), the common ancestor of the major genera *Aphyosemion* in Africa and *Rivulus* in America would be an aplocheilid that gave rise to these two genera (and their allies) before the continents divided and Gondwana drifted. Molecular and osteological evidence, as well as recent paleobiogeographical knowledge, support the view that a number of morphological and ethophysiological peculiarities of modern cyprinodontiforms represent conservative traits inherited from the ancestral stock (Parenti 1981; Costa 1990; Murphy and Collier 1996; Huber 1998).

Nevertheless, in the present situation, two points argue against evolutionary inertia. The first is the explosion of the species groups: 202 species are described in the New World

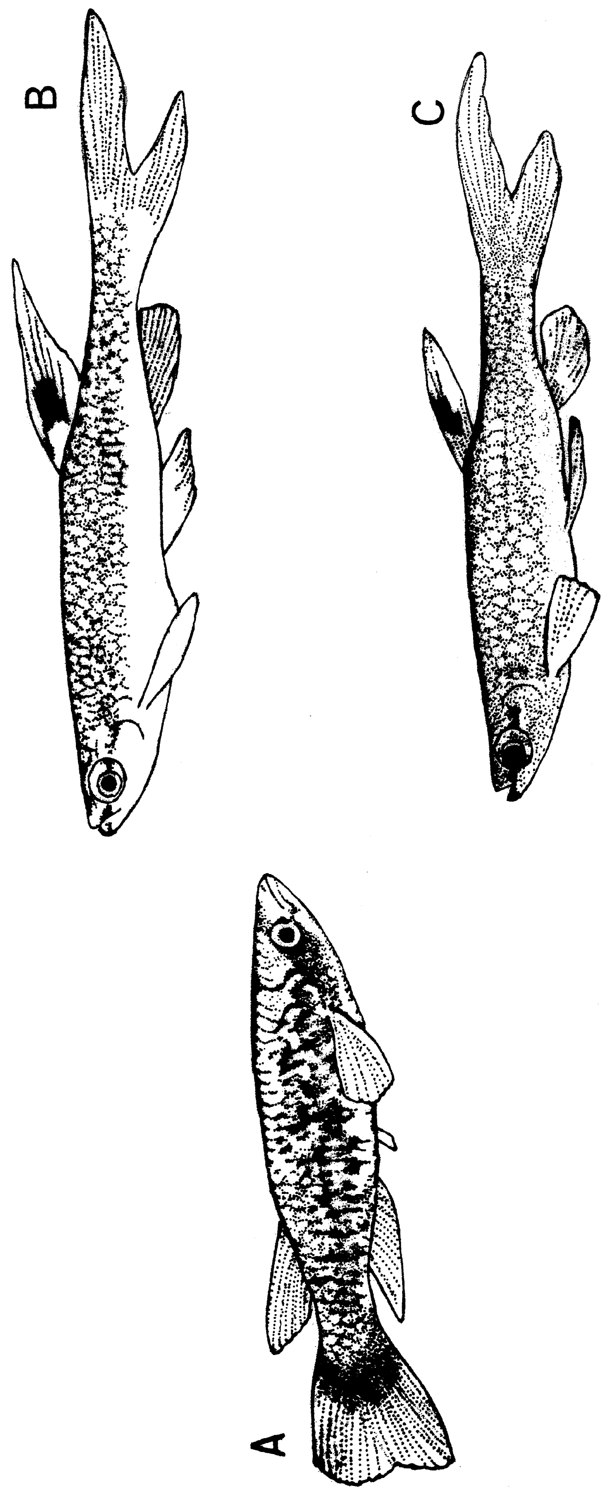


Fig. 4. (A) The cyprinodontiform *Epiplatys neumanni* at M'Passa, Gabon. (B and C) The twin characiforms species *Pyrrhulina filamentosa* and *Copella carsevennensis* in French Guiana, which occupy the same ecological niche as *E. neumanni* in Gabon, i.e., the same type of prey, the same feeding behaviour.

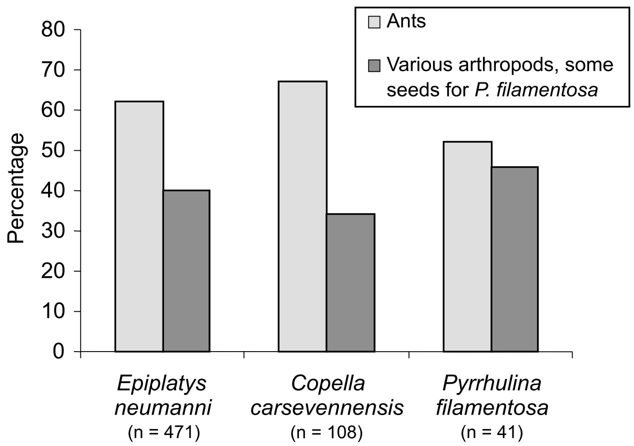


Fig. 5. Similarity in the prey (mostly ants) of the American characiforms *P. filamentosa* and *C. carsevennensis* and the African cyprinodontiform *E. neumanni*. The three species, belonging to three different genera, occupy corresponding ecological niches in Africa and America.

and 293 in the Old World (Amiet et al. 1987; Huber 1998; Murphy et al. 1999). Such species abundance is not compatible with evolutionary inertia of the primitive stock. If the evolutionary-inertia hypothesis is rejected, the second reason is related to the high probability that speciation is ongoing, especially in Africa. The role played by glaciations in the radiation of African species (Huber 1998), and the present genetic instability and variability in morphologically identical species (Brosset and Lachaise 1995), do not support the evolutionary-inertia hypothesis. As far as the composition, structure, and dynamics of the populations are concerned, we may conclude that the striking similarity between the African genus *Aphyosemion* and the American genus *Rivulus* results from the convergent evolution of habitats on both continents, i.e., similar situations, similar responses (Huber 1998).

Convergent evolution may explain the similarities in composition and dynamics between the M'Passa population and the St. Elie population

Among the fishes present in Africa and America, remarkable morphological similarity is exhibited by two dominant genera: *Aphyosemion* in Gabon and *Rivulus* in French Guiana.

The main factor responsible for this similarity, noted by Sioli (1964), Fittkau (1967), and Roberts (1972) in the Amazonian and Congolese basins, may be parallel evolution of the specific habitats of these fishes on the two sides of the Atlantic Ocean.

Table 1 presents the significant physical (abiotic) and biotic components of the habitats occupied by these fishes at M'Passa and St. Elie. The similarity of the ecological niches is obvious.

Divergent evolution may explain the differences between the two communities of cyprinodontiform fishes inhabiting the tropical forests of Africa and America

Convergent evolution with the habitat, which characterizes the history of the population, does not, however, characterize the evolution of the communities. Important differences exist between the composition, organisation, and dynamics of the communities at M'Passa and St. Elie.

Ecological determinants of the divergent evolution of the cyprinodontiform communities at M'Passa and St. Elie: predation and competition

Since Darwin, predation and competition have been considered important factors in the evolution of communities. This has been studied mostly in birds (Dawkins and Krebs 1979; Lima and Diff 1990). Do the cyprinodontiform communities studied here conform with this general rule?

The role of predation as an evolutionary determinant may be ascertained by comparing the opposite situations at M'Passa and St. Elie. According to our data, no specific regular predator of cyprinodontiforms exists at M'Passa. At St. Elie, the cyprinodontiform community is regularly exploited by two predators whose predation techniques are highly specialized: aggressive mimicry in *E. erythrinus* directed against *R. agilae*, and selective cannibalism in *R. igneus*.

Predation has often been considered to be a factor favouring species diversity in a given area (Cramer and May 1972; Roughgarden and Feldman 1975; Holt 1984; Blondel 1986). Predation pressure will contribute to the occupation of new niches, and protective behaviour against predation will lead to ecological isolation. These processes were not prevalent at St. Elie. Conversely, at M'Passa, the absence of regular predators may have contributed to the equilibrium in the numbers of individuals in populations of sympatric species and to the species richness of the cyprinodontiform community.

Competitive exclusion, which has been described in tropical stream fishes (Zaret and Rand 1971), evolved in divergent directions at M'Passa and St. Elie. A regular, specialized competitor of the cyprinodontiforms seems to be absent at M'Passa. The opposite situation was noted at St. Elie, where the typical cyprinodontiform feeding behaviour is shared by two highly specialized, very common competitors: *C. carsevennensis* and *P. filamentosa*. According to field observation and analysis of stomach contents, *C. carsevennensis* and *P. filamentosa* at St. Elie and the cyprinodontiform *E. neumanni* in M'Passa have similar diets (Fig. 5) and the same feeding behaviour. Having similar ecological niches, *E. neumanni* in Africa and *C. carsevennensis* in America would have developed similar sophisticated devices for catching prey. In the case of the American cyprinodontiforms, the presence of a competitor utilizing a luminous spot may have prevented the evolution of this device, which exists in the African cyprinodontiforms.

Conclusion

The close similarity between the forest-dwelling cyprinodontiform fish populations in Africa and America may be explained by convergent evolution of habitats. Divergent evolution in the communities would result from the absence of a regular predator and competitors at M'Passa and their presence at St. Elie. Finally, I and my co-workers noted that the specialized predators and competitors that were represented only at St. Elie all belong to the Characiformes, a group of fishes represented by families, genera, and species in all inland fresh waters in tropical South America. The dominant Characiformes probably occupied all the vacant ecological niches, displacing or eliminating other orders and families. Analogous processes of competitive exclusion may be observed in various groups of tropical American vertebrates: Leptodactylidae contra Ranidae in anurans, Iguanidae contra Lacertidae in reptiles, Tyrannidae and Furnaridae contra Sylvidae in birds, and Phyllostomatidae contra Vespertilionidae in bats.

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