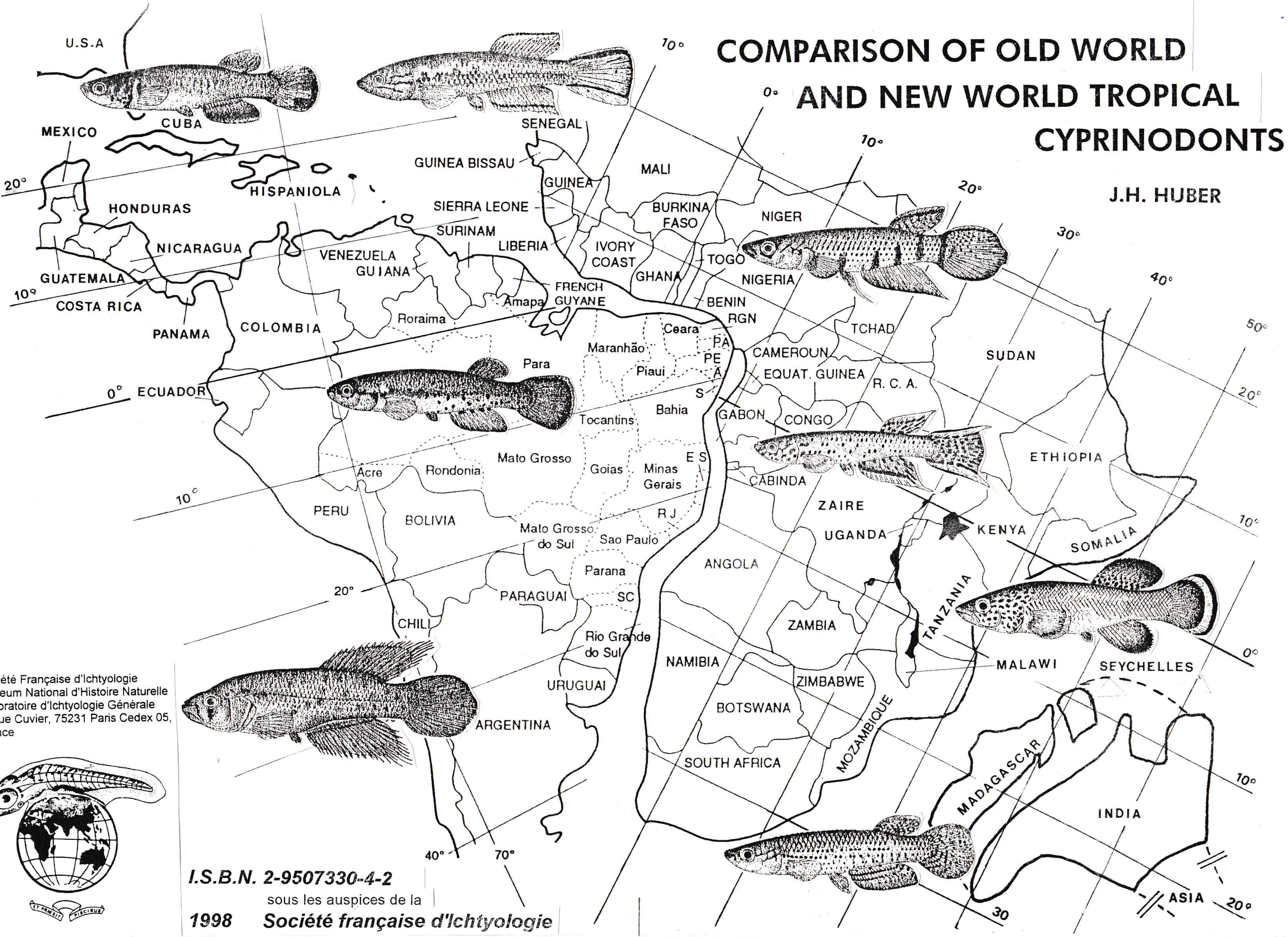
COMPARISON OF OLD WORLD AND NEW WORLD TROPICAL CYPRINODONTS

J.H. HUBER



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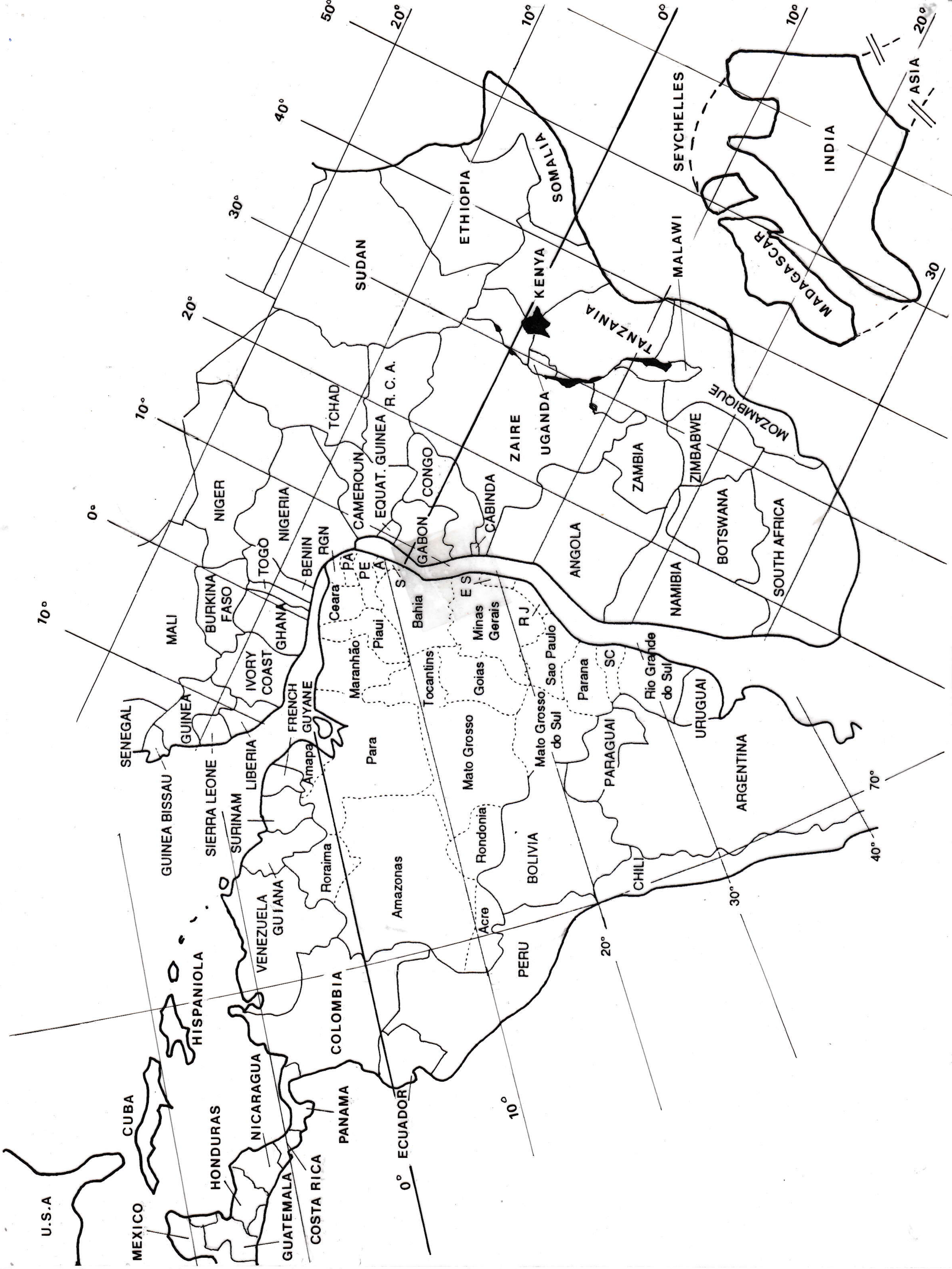


Fig. 1. Paleogeographic reconstruction (about 110 MYA) of the area under study with the present States political borders and local names (modified from Trompette, 1994).

COMPARISON OF OLD WORLD AND NEW WORLD TROPICAL CYPRINODONTS.

A PARALLEL OUTLOOK OF SIMILAR AND DISTINCTIVE CHARACTERISTICS REGARDING DISTRIBUTION, EVOLUTION, ECOLOGY, BEHAVIOR, MORPHOMERISTICS, GENETICS AND COLOR PATTERN.

J.H. Huber *

ABSTRACT.

A comprehensive and detailed comparison of Old World and New World tropical Cyprinodonts (oviparous Cyprinodontiformes, Pisces) is proposed, based on the most recent knowledge in paleogeography and palynology. It covers biogeographical aspects, from the analysis of a data base of over 3500 localities-species in tropical countries (Huber, 1996) of Africa, America and Indo-Asia (fig. 1, with local country names). It synthetizes, with a novel transversal perspective, the already published information by the author, since 1978, and by others, on systematics, genetics, external morphology, live coloration, behavior and ecology of tropical Cyprinodonts, to emphasize the many similarities and the few differences. The many similarities are hypothesized to be the result, from a process of convergence after the continental drift, of the limited capacity of these reclusive fishes, quasi exclusive in their highly uncertain biotopes, to produce a diversity of responses in the face of similar environmental changes.

Several novel biogeographical and evolutionary models are hypothetically proposed for the first time for Cyprinodonts, to replace those which failed, like the present types of soil, the present river basin outlines (...), all featuring today characteristics.

All these models refer to past periods and notably the dramatic climatic changes of the Quaternary. They explain and correlate well with our present knowledge on Cyprinodont in the New and Old Worlds:

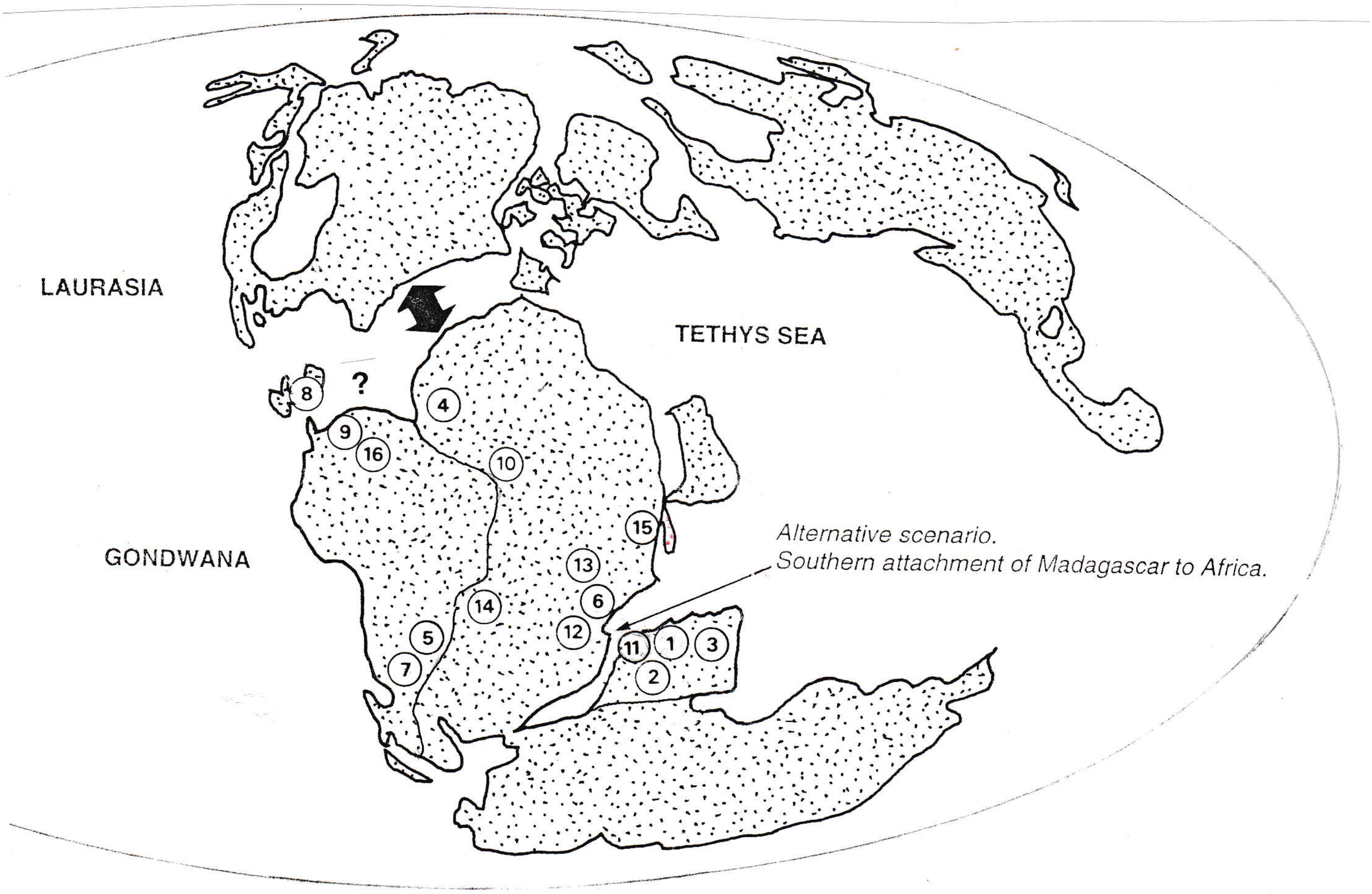
- the refugia of previous glaciation periods, in relation with major extinctions;
- the impacts of the dramatic water mass fluctuations, exemplified by the old epicontinental seas, and the islands off the coast or the huge freshwater lakes, of more recent past;
- the migration patterns in low gradient regions, within and in-between the coastal plain and the inland plateau, materialized by strates and patches of distribution, respectively;
- the tectonic and volcanic activity, exemplified by the Rift Valley lakes or by river reversals;
- the northern drift of the African continent and its impact on terrestrial flora.

Schematically, a two-scaled evolutionary history of these fishes is hypothetically proposed. One, old, for the creation and diversification of the major morphotypes along millions of years. Another, recent, along thousands of years only and linked to climatic disorders, for the explosion of the genotypes and a vicariant speciation from slightly different morphotypes which had not suffered a previous extinction.

INTRODUCTION.

In our Review of *Rivulus* (1992: 50), after having studied in depth all groups of Cyprinodonts from tropical Africa and America (since 1978, op. cit.), we emphasized the similarity in basic phenotypes, that were available both in the Old World and the New World, with 3 profiles:
- The "*Aphyosemion-Rivulus*" profile of non annual to semi-annual cylindrical species, inhabiting the primary forest creeks ("marigots") in the shade and in the mid layers of acid brown to clear waters.
- The "*Nothobranchius-Cynolebias*" profile of annual deeper-bodied species, bottom-spawners of temporary pools in the savanna, with an open landscape and muddy alkaline waters.
- The "*Epiplatys/Aplocheilus*-?" profile of non annual species, with a rather pointed mouth and a flat upwards-oriented snout, living in the upper levels of non restrictive waters and in opportunistic landscapes.

No sure component was available in the New World, at that time.
However, one species with a decided similarity with *Aplocheilus*, but annual, was subsequently discovered in the Paraguayan Chaco. It was then described and named *Trigonectes aplocheiloides* Huber, 1995.



Alternative scenario.
Southern attachment of Madagascar to Africa.

Fig. 2. The still single Gondwana continent (148 MYA), origin of the Aplocheilids and Aplocheilichthyins. Note that the hypothetical position of the Madagascar-India block is attached to Antarctica and maintained that way after the African drift. This hypothesis is different from the more traditional position of that block, with the southern part of Madagascar being attached to Africa at the level of Tanzania (modified from Smith *et al.*, 1994). Primitive (by external characters) morphotypes, Aplocheilids: 1.*Pachypanchax*; 2.*Aplocheilus panchax*; 3.*Aplocheilus lineatus et al.*; 4.*Callopanchax*; 5.*Rivulus caudomarginatus*; 6.*Paranothobranchius*; 7.*Cynolebias s.s.*; 8.*Millerichthys*; 9.*Austrofundulus-Rachovia-Pituna*; 10.*Fundulopanchax*. Aplocheilichthyins: 11.*Pantanodon*; 12.*Lamprichthys*; 13.*Laciris*; 14.*Aplocheilichthys s.s.*; 15.*Micropanchax s.s.*; 16.*Fluviphylax*.

In addition, we dedicated a chapter of that book (1992: 51) to the parallel comparison of the major characteristics of the genera *Rivulus* of the New World and *Aphyosemion* of the Old World, in a synthetic way. The many disclosed similarities induced, in conclusion (1992: 54), two possible schematic explanations:

- A close common Aplocheilid ancestor which gave birth to those two genera (and their allied), before the continental divide and drift of Gondwana (fig. 2); a similar dispersalism scenario could have been forwarded for the annual deep-bodied and the flat snout basic profiles: then at least 2-3 pre-divide ancestors, linked to the 3 basic profiles.
- A process of convergence, as a quasi-identical response to the parallel evolution and variations of the available niches and environments, both in the Old and New Worlds: then 2-3 post-divide ancestors, linked to each basic continent, the third one being the Indian-Madagascan block, separated from Africa long before the disconnection of Africa and South America (respectively circa 135 MYA -million years ago- and 90 MYA, although possible arcs of islands and earthbridges may have remained much later, for example until 65 MYA in the southern Atlantic, e.g. the Walvis Ridge-Rio Grande Rise) (fig. 3). Then, an opposite pure vicariance scenario is applicable.

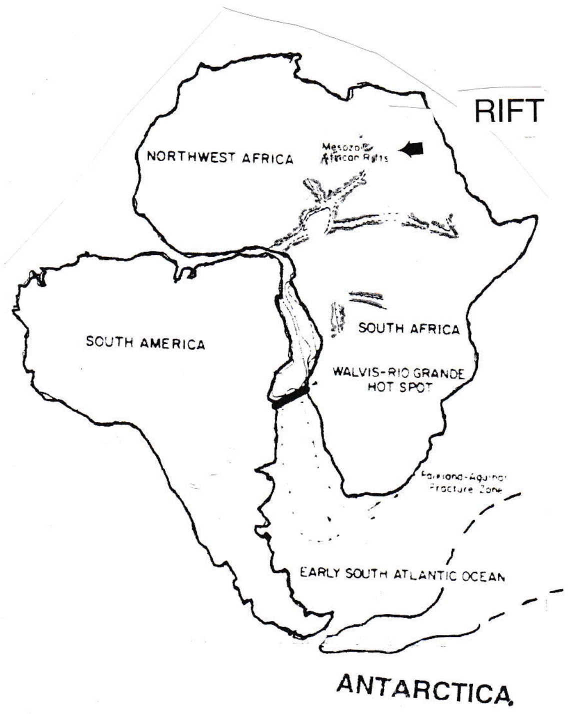


Fig. 3. The relative position of Africa with respect to South America (120 MYA). The South Atlantic, south of the Niger delta has opened up by rifting that entered the Bénoué Trough. Africa, north of the Niger river, has remained fixed with respect to South America. The mesozoic Rift is also drawn as a putative paleo-migration route (Goldblatt, 1993).

Osteological studies with a cladistic approach (Parenti, 1981; Costa, 1990) had already favored the second explanation by exemplifying only 2 ancestors, one for each continent. But cladistics were not universally accepted in those days and these studies were first based on very limited material. In addition, they placed annual forms as derived from non annuals, which we did not follow (Huber, 1996).

It was only in 1997 that Murphy & Collier (op. cit.) were able to demonstrate by the molecular analysis of three genetic fragments (12S-RNA, 16S-RNA, Cytochrome-b) that the osteological results were fundamentally correct, with a major exception. The *Aplocheilus-Pachypanchax* genera from Madagascar, Seychelles and Indo-Asia are shown to be basic to all Aplocheilids, with two descendants, one in Africa and one in South America, each producing all the extant, annual or non annual, species. A primary consequence of this result was not pursued by these authors: the extant presence of *Aplocheilus-Pachypanchax*, only in regions that drifted away before the continental divide, and of several externally primitive morphotypes in today Guinée, Nigeria, Tanzania and Colombia-Venezuela, Sertao do Brasil, Uruguay-Argentina (fig.2), implies that the entire pre-drift or early post-drift Gondwana -or at least all its coastal parts- could have been inhabited by tropical Cyprinodonts before the Tertiary (more than 90 MYA) or even since the early Cretaceous (135 MYA). However, because of the coastal origin of these extant morphotypes and because of the older versatility of tropical Cyprinodonts to marine environments, it seems unreasonable to speculate more precisely on these dates (see further, § 4.3.3).

The recent paleobiogeographical knowledge, outside Cyprinodonts, concurs with the molecular and the osteological evidences.
The present paleontological knowledge is much behind. The ancient basic morphotypes and their fossil relatives are associated with a minimum age (circa 30 MYA), much younger than the two major continental disconnections quoted above (90-135 MYA).

The purpose of this study is then to deepen comprehensively the parallel comparison undertaken for *Rivulus* and *Aphyosemion*. And to extend it to all Aplocheilids. It stands as a transversal analysis, and, as an evidence of the potentials of the basic ancestor to opportunistically respond to the variations in environment (similar situations-similar responses) and then... survive through its diversified descendants (distinctive responses). Its scope is also extended to the very different Aplocheilichthyins, which are the second group of (oviparous) Cyprinodonts inhabiting the tropical waters. Being better swimmers, they either live in different niches of the same biotopes or along edges of larger bodies of water, with also components in the Old and the New Worlds (with unfortunately a single group, *Fluviphylax*, in South America). It would have been interesting to add, to the analysis, the New World viviparous Poeciliins, which are the sister group of the Aplocheilichthyins, as ecological counterparts, but their knowledge is not available to the author.
The geographical scope of this study is then the tropical countries of Africa, America and Indo-Asia, where these two groups of Cyprinodonts are recorded (fig. 1, paleogeographic reconstruction of the two continents with the present countries local names). It excludes the temperate regions of these continents (e.g. the Mediterranean sector of Africa) or the very high mountains of tropical regions (e.g. the Andes).

The parallel comparison will be treated, for the sake of clarity, into independent topics:
1- The altitudinal and geological dimensions.
2- The past climatic variations and their impact on water mass.
3- The past climatic variations and their impact on terrestrial flora.
4- The local dimensions, the biodiversity and the ecology.
5- The behaviors, non sexual and sexual.
6- The morphotypes and the morphomeristics.
7- The color patterns and the genotypes.
Obviously these topics are fully interdependent. We shall attempt to avoid too many redundancies, by referring to other further or previous sections within the text.

On top of the point-to-point comparison, it appears primarily important to present one concept, one duality, one hypothesis that are federative to all Cyprinodonts, that are a key to their phylogeny and that need to be kept in mind all along the analysis.
* The superspecies concept.
* The sympatry-allopatry duality.
* The climatic-biogeographic hypothesis.

* The superspecies (or species-complex) represents a group of species which share a single direct common ancestor (a clade) *and* which show a strictly identical external profile. These very closely related, vicariant species are characterized by similar distribution schemes, by identical subniches preference, by similar shapes of body and fins, by sharing dominant micromorphological characters, by similar meristics and notably of the Dorsal/Anal relative deviation levels, by identical behavior, by the similar dominant choice of food (etc); they share key color pattern features and genetic mainframes, but are distinguished by details in them, inducing ethological (pre-mating) and sexual (post-mating) barriers. A superspecies, as a witness of recent explosive speciation of the Cyprinodonts, comprises many (three to over a dozen) presumably valid names. These are cryptic species (i.e. isomorphic and vicariant), although extremely rare, distinct and isolated, morphospecies have been attached to them, after DNA studies, as sister species to form a clade. A superspecies is rather easy to build up from living material in the field or in the aquarium. It is much more difficult to

define with preserved only, especially old, material (Scheel, 1968; Huber, 1978, 1992, 1996).

* The sympatry-allopatry duality is the major force in populations dynamics of Cyprinodonts (sympatry is used in its restricted sense, also termed syntopy by some authors). This duality is enacted in two complementary rules (Huber, 1978). First, the isomorphic components of the same superspecies are strictly allopatric and they replace each other vicariantly. Second, the components of distinct superspecies are sympatric (obviously, if they occur in the same biological region). Females of each sympatric component will select the right male of her own species (and not the reverse) from characteristics of his color pattern, fin shape, behavior (etc.) (Brosset, 1982). Most frequently, two congeners of two distinct heteromorphic superspecies are sympatric, whereas it happens only occasionally and in restricted ranges for other groups of fishes (Huber, 1978, 1992). Even more, up to five species of distinct superspecies of the same ancestry have been reported sympatric, both in the today permanent (non annual fishes) and seasonal (annual fishes) biotopes, and seven if other Cyprinodont lineages are included (Huber, 1978, 1992, 1995).

* The paleoclimatic hypothesized relative stability and the geomorphological instability of the mid-late Tertiary after the continental drifts of the Mesozoic era, and, the paleoclimatic disorders and the relative geomorphological stability of the Quaternary are hypothesized here for the first time to be responsible for the evolutionary history of tropical Cyprinodonts. This is based on five key observations:
- first and primarily on the relict distribution of the oldest (by external morphology) extant forms of Aplocheilids all around the split Gondwana (fig. 2). For example, *Callopanchax* in northwestern regions, as an indirect consequence of the northern drift of Africa (the old Paleo-equator line was at the level of Sénégal-Guinée, associated with the early development of forest coverage), *Austrofundulus, Millerichthys* in the proximal region of America; also, *Cynolebias s.s.* in southeastern South America.
- second, on the correlation of the embryologically older annual forms with the climatically older seasonal biotopes, that were initially available before the development of the forest coverage;
- third, on the available fossils (unfortunately for Cyprinodonts of presently temperate regions) which show a much closer morphology to the extant forms, when dated from the Pliocene than the Miocene-Oligocene;
- fourth, on parallel trends for other groups of animals (including the viviparity of the related Poeciliins, acquired during the mid Tertiary, 45-25 MYA on several occasions);
- fifth, on the availability of the same fauna with distinct populations or closely related young species in not distant islands, off the coast, disconnected from the nearby continent after the glaciation periods.

Then, this hypothesis induces two *theoretical* periods with two different types of events, even if many of these events were recurrent. The former, along the geomorphological events (earth uplifts, earth drifts, river reversals, epicontinental seas), with cumulative effects. The latter, along the climatic oscillations with sweeping effects (water maintenance in the generalized refugium). The former, for the basic morphotypes, progressively along the Cretaceous-mid Tertiary and then their somewhat derived morphotypes. The latter, for the explosion of cryptic species and of the genotypes from the then extant morphotypes, along the Pleistocene and early Holocene (at least, later than 2.5 MYA; probably also, even from as late as after the last glacial maximum, at 18000 BP- years before present). The former, for the migration patterns of large groups and subgroups. The latter, for the extension patterns of superspecies. However, the difference in time scale for these two theoretical periods must be stressed. The framework of the former is tens of millions years and may aggregate many heterogeneities and uncertainties (and major unknown extinction waves). The framework of the latter is thousands to a few millions of years and its history is being known with far more details.

These three federative characteristics are probably not shared (at least the first two) by most other groups of freshwater fishes. This is because, for ages, Cyprinodonts have been all, with variations, dwellers of rather reclusive biotopes, under cover, where they are dominant or even exclusive. They live in small shallow bodies of slow-moving or stagnant waters, often temporary or seasonal (non annual and annual Aplocheilids) or else in small or larger -but at their margins, only- rather moving waters (Aplocheilichthyins). So they tend not to encounter the group of populations that are neighboring them, each being compartmentalised a few kilometers apart. They are absent (or rare, even for the erroneously hypothesized riverine *Fluviphylax*) in the deep mid-waters of large rivers, where most fishes live. This is also because Cyprinodonts, much more the Aplocheilids than the Aplocheilichthyins, are poor swimmers. The result of these two related factors (reclusive biotopes and slower mobility) is that the modes of distribution, evolution, survival and migration (...) have their specificities and are rather different from the standard groups of fishes. Some groups of fishes -in small numbers- do indeed live at some age or stage in the Cyprinodonts reclusive biotopes. This is by chance (e.g. an invasion from the nearby river after the floods) or by specialization (e.g. the predatory behavior against the adults Cyprinodonts or their offspring), since the majority of their counterparts are to be found in the standard biotopes. None to our knowledge truly competes with the Cyprinodonts, in either the Old or New World, in terms of space, population density, food. It is of utmost importance to emphasize the reclusive character of the tropical Cyprinodonts (which cannot escape from this constraint, like the temperate more sea-tolerant Cyprinodonts): unlike standard riverine fishes, their waters are the first to suffer disturbances, up to desiccation in case of an unusually long drying period. This has major implications in both the Old and New Worlds, and for both non annual and annuals groups, in terms of evolution, speciation and expansion patterns.

Finally, for the reader who is not a Cyprinodont specialist, let's recall a point of systematics and nomenclature for the concept of species (Huber, 1996). The diversity of phenotypes, or even, of the so important male live color patterns, is lower than the genetic diversity. This implies that the number of biological species surpasses by far the number of distinguishable phenotypes (see the suggested reasons, § 2 and 3, in the past climatic fluctuations). This has led to a practical species concept (Huber, 1996) which limits species naming to isolated populations with at least one stable distinguishing external character. Then a species-name (i.e. a taxon at the species level) often encompasses several biological species that cannot be distinguished by phenotype.

The major paleontological dates, associated with putative biogeographical events affecting tropical Cyprinodonts, are given in Table 1, as a vital lead in the present study.
In addition, also as a vital lead for the reader, the postulated superspecies are characterized, in Table 2, according to their primitive (plesiomorphic) or derived (apomorphic) external characters, separately for the Aplocheilids and for the Aplocheilichthyins. And their biogeography is comparatively associated, within a vicariance approach.
Both tables also contain information and data that are not found in the text and provide with a different and supplemental viewpoint.

Abbreviations of taxa at the generic level follow Huber (1996). Generic and subgeneric names are alternatively used for argumentation purposes, clearly without a systematic objective. It goes without saying that the precision "ancestor of" is mostly omitted when extant species are mentioned within an historical context. This is for simplicity sake. Country names are given with their local spelling. Sources are given in the bibliography, which is intentionally limited to general references.

PARALLEL COMPARISON OF OLD WORLD AND NEW WORLD TROPICAL CYPRINODONTS.

1- The altitudinal and geological dimensions.

1.1- The altitude: the duality coastal plain-inland plateau.

1.1.1- The geomorphological data of the plain and the plateau.

The first similarity, and a fundamental one, between the Old and the New Worlds, concerns the presence of lowlands along the ocean, the coastal plain, and in parallel, not far, of highlands, the plateau at about 350 m altitude and above. This rise of lands is a long and ancient process (since the Pre-Cambrian, see further § 1.2) and has suffered considerable erosion through time (fig. 4a).

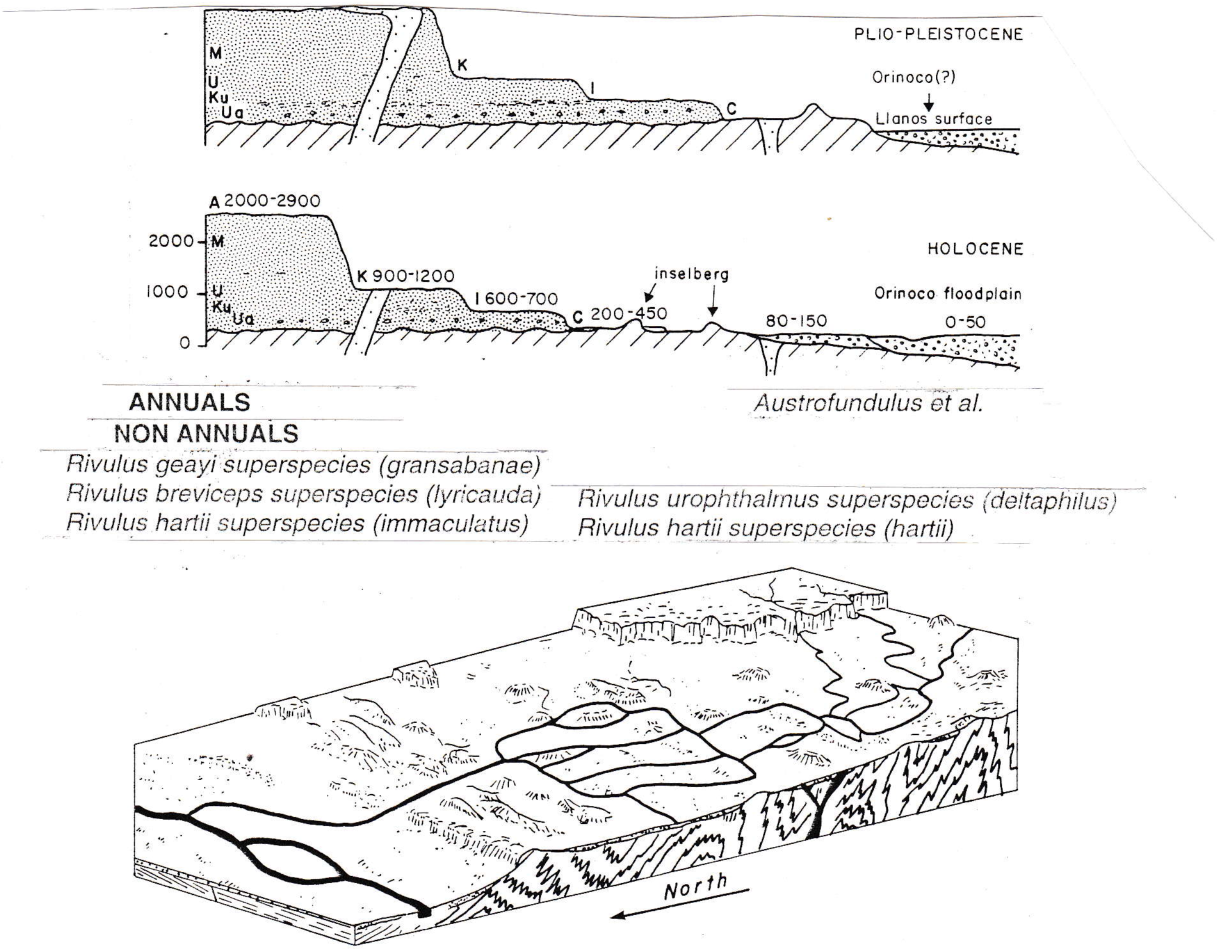


Fig. 4a. Example of the erosion of the pre-Cambrian Guyana shield: above, the evolution of table-top surfaces, finalized inselbergs where Cyprinodonts have become isolated like *Rivulus immaculatus, Riv. lyricauda*. A: Auyan-Tepui; K: Kamarata; I: Imataca; C: Caroni-Aro. Below, the Caroni basin, tributary of the Orinoco, with intricated channels which suggest a climatic change from arid to humid, probably less old than 2.5 MYA (Clapperton, 1993a).

The rise of land today occurs (fig. 4b):
- in Atlantic Africa from Guinée to central Angola (more southernly also, but then the coastal plain is desertic and no Cyprinodont has been reported);
- in Indian Africa from southern Somalia to eastern South Africa (about 28°S);
- in Atlantic South America from Venezuela (east of the Orinoco delta) to southeastern Brasil (about 30°S);
- in Pacific South America from western Colombia (Barranquilla, independently of the insertion of the isthmus of Panama) to western Peru (about 8°S).

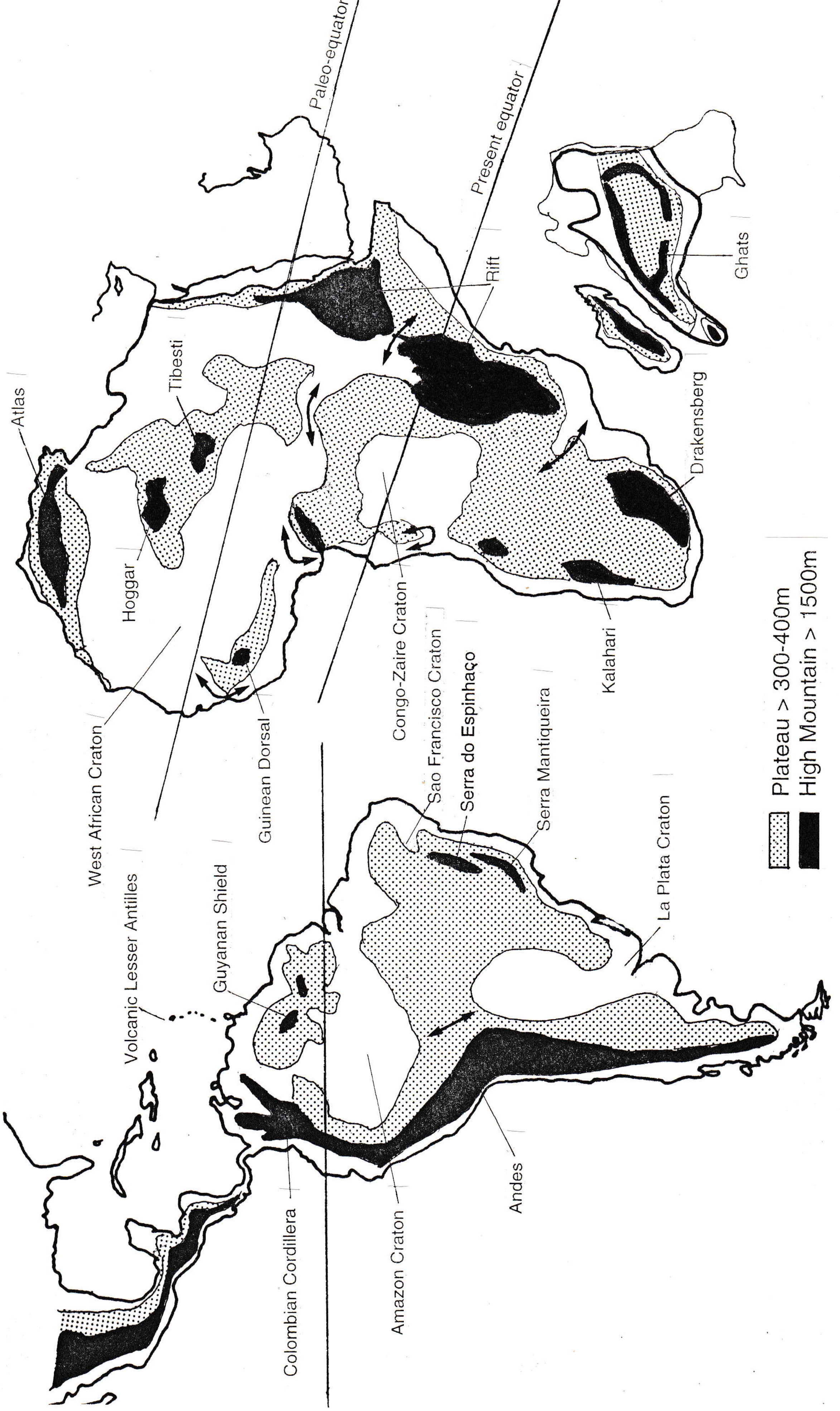


Fig. 4b. Paleogeographic reconstruction (circa 80 MYA) of the area under study with the present limit of the coastal plain and inland plateau (original drawing by Chauche). Putative migration routes between today plain and plateau are given by arrows.

In Africa, the coastal plains are usually narrow, between 20 and 100 km. They can occasionally widen to 200-300 km in relation to the mouth of large rivers (the Ogooué-Komo in Gabon, the lower Ecucu in Ecuatorial Guinea, the lower Sanaga in Cameroun, the Niger in Nigeria, the Volta in Ghana, the Zambezi in Mozambica, the Morogoro in Tanzania, the Uebi in Somalia). Some of these widenings with a deep carving into the highlands are important lowland bridges (see further § 1.1.2). In South America, the coastal plain is much wider (200-400 km) from Guiana to the Brazilian state of Maranhao (42°W), then narrow (20-100 km) southerly on the Atlantic coast, and also narrow on the Pacific coast. Lowland bridges are rarer.

Obviously, coastal lowlands are available all over the world, but such a parallel-to-coast, exchange-proof, limited band is seldom seen in the other continents.

Comparatively, the interior plateau is huge: wide by 1400 km to 5500 km in Africa, and, by 1600 km to 3500 km in South America.

The rise of lands which constitutes the interior plateau is ancient i.e. pre-Cambrian (see further, geology § 1.2). However, some less old tectonic and volcanic upheavals have modified this simple pattern: for example, in Africa, since circa 5-10 MYA, the Mont Cameroun volcano, the Killimandjaro volcano, the Mount Kenya volcano, in America, the Andes, since circa 20 MYA, with its many volcanic systems, from 1 to 10 MYA. In these higher mountains (above 2000 m) tropical Cyprinodonts are absent.

The present transition between the low and the high lands can be smooth (e.g. in western Nigeria, in Côte d'Ivoire/Ivory Coast to Bénin, in northern Kenya-Somalia, in the eastern Guyanan shield, in eastern Venezuela) or sharp (e.g. from Cameroun to Angola, in southeastern Brasil), with obviously intermediate situations. This is a major issue for Cyprinodonts distribution.

1.1.2- Correlation with the Cyprinodonts distribution and its evolutionary consequences.

The fauna of tropical Cyprinodonts is highly dependent on the transition plain-plateau, all the more that it is sharp (Huber, 1978). This is not only valid for Aplocheilids in both the Old and the New Worlds, but also for the African Aplocheilichthyins. However, this phenomenon is less conspicuous for the latter, because they are better swimmers and they can invade some, usually limited, highland regions upstream, along the edges of a large river course, and reciprocally, downstream in the coastal plain. A sharp rise in altitude constitutes an overwhelming constraint for Cyprinodonts, whereas a more progressive transition offers the possibility even to some Aplocheilid species to extend. However, these exceptions are rare, compared to the rule. And even in the case of a smooth transition and a consecutive inland invasion, the distribution appears desequilibrated (abundance, speciation) in favor of the lowland, as if the extension dynamics were getting less and less strong from its nested origin (e.g. the *Scriptaphyosemion* lineage in Guinée, the *Zononothobranchius* lineage in eastern Africa).

The distinctiveness of the Cyprinodont fauna between the coastal plain and the interior plateau in freshwaters has been shown on several occasions.

- In Atlantic Africa, for the genus *Aphyosemion s.l.*, the superpecies of the coastal plain are different from those of the plateau and no introgression is known (*A. petersi* is a relict from the past more widely distributed *Archiaphyosemion* before the Mont Nimba uplift, Huber, 1978). All Cyprinodont superspecies of the coastal plain from Ecuatorial Guinea to Cabinda are not reported in the neighboring plateau, except the Aplocheilichthyin *Plataplochilus terveri* (Huber, 1981a). In Cameroun, the *Procatopus* species are unable to climb up the hills where *"Micropanchax" camerunensis* is established (Huber, 1998a). Another way of exemplifying this is to mention that some species have exceptionally managed to invade the neighboring foothills from their standard range but they were quickly stopped in their incursion which remained very limited (e.g. *Epiplatys esekanus*, up in the Cameroun plateau, *Aphyosemion cameronense* down to the Ecuatorial Guinea foothills).
- In Indian Africa: the *Nothobranchius* from the Tanzania plain (subgenera *Nothobranchius*,

Adiniops, Aphyobranchius, Paranothobranchius) are not collected in the plateau (Huber, 1996). However, the distinction does not apply to components of the subgenus *Zononothobranchius* (Seegers, 1985) or to Aplocheilichthyins of the *Cynopanchax* lineage, present both in the coast and the plateau (Huber, 1998a), but rarer outside their nested origin, as already mentioned. In that part of Africa, as in South America, east of both continents, the Cyprinodont fauna is dominantly annual: the change in faunal status, from non annual to annual, does not eliminate the duality between the plain and the plateau (see further § 3.1, the forest and non-forest coverages).

- In Atlantic South America: the Aplocheilid genera *Campellolebias* and *Cynopoecilus* in the coastal plain, from Rio de Janeiro to Porto Alegre, are not found inland and the *Simpsonichthys whitei* superspecies is distinct from the distantly related species of central Brasil (Huber, 1995). Similarly, the *Rivulus* superspecies over the coastal range are separate from those inland (Huber, 1992) with the exception of the lowlands of the Amazon basin (see further the interior lakes: § 2.4).

The duality of the fauna between the coastal plain and the plateau is then well documented. In total, when the transition is sharp, not a single superspecies is significantly distributed in either the plain and the plateau.

However, one question remained open and unresolved by standard morphomeristic techniques (Huber, 1978, for Africa, 1992, for America): are superspecies from the plain phylogenetically related to those from the plateau facing them? Collections in the foothills areas have not been able to materialize precisely the boundary in fauna. Then, what does actually happen there? Strict allopatry? Occasional sympatry?
To suggest a possible answer, let's point out first that even if the altitudinal transition is sharp, this is not a wall. This wall would erroneously imply that no Cyprinodont fauna is living within the rising transition. Or that no contact is possible between the two faunas. Rather, it appears that facing groups of allopatric superspecies in the plain and in the plateau may well be phylogenetically related. This is here hypothesized for the first time, based on the following observations:
- the distributional differentiation appears to be purely geographic, when the transition is sharp. It fails when it is smooth (providing with circumventing patterns of distribution, drawn like a "U") and in the lowland bridges (the exceptions quoted above). These bridges may be the centers of origin and of extension of the plateau superspecies (see further § 1.1.3 and § 4.3 the biodiversity), in relation with refugia (see further § 3.3.2);
- the major barrier on both sides does not appear to be altitude *per se*, but the preemption of the niches by closely related groups or by strict ecological counterparts, mutually rejecting each other (see further the local distribution schemes, § 4.1 and the frontier species concept, § 4.4).

In addition, this hypothesis is strengthened by earlier observations of possible phylogenetic links between isomorphic superspecies of the two faunas (e.g. the *Aphyosemion calliurum* and *cameronense* superspecies sharing morphological, coloration and subniche characteristics in Huber, 1978 and similarly the *Chromaphyosemion*, *Diapteron* and *Kathetys* lineages in *Aphyosemion*) and by the results obtained through modern systematic softwares applied to external phenotypic characters (Huber, 1998a for Aplocheilichthyins and Huber, 1998c for American Aplocheilids).

In terms of species extension, the analysis of the over 3500 localities-species (Huber, 1996) supports the thesis that the coastal plain and the plateau are very different, similarly, in both the Old and the New Worlds. The coastal plain is a corridor, stopping in some cases at a dead-end, whereas the much larger plateau leaves space for new horizons. It can be then assumed that the colonization has developed in the plain by waves of migration from one of these dead-ends or from a lowland geographical bridge of interpenetration between plain and plateau or from a refugium. Whereas it has radiated from a center in the plateau (see further the frontier species concept: § 4.4 and the refugium theory: §3.3). Then, in the plain,

several strates of allopatric parallel-to-coast invasions are seen.
In the corresponding plateaus of Africa and South America, the distribution is distinct from the "banded" one on the coast. In theory, it is unlimited: it is flat (though hilly, locally) or rising smoothly until the break of the reciprocal plain, if the Rift valleys and the Andes are not taken into account. However, additional constraints limit considerably the distribution of superspecies, like the forest coverage (§ 3.1), the internal lakes (§ 2.4). These constraints explain clearly but not completely the vertical patches of each superspecies distribution. The reasons for the precise extension of one patch and of the change from one patch to another of an allopatric superspecies remain obscure. This is all the more so that patches of sympatric superspecies of the same biological region are not superimposed: unknown and cumulative local factors in the past may be dominant, if not a simple pre-emption of the concerned subniches (see also further the refugium theory, § 3.3, and the frontier species concept, § 4.4). In no case (but one, see further the interior lake of Zaïre, § 2.4), does a superspecies show a very large "banded" distribution in the plateau, as it does along the coastal plain.

To exemplify this model, let us examine in detail the "good case" of central west Africa, for two reasons. First, it is better known by field collections (Huber, 1996). Second, the transition plain-plateau is sharp, between the Niger and the Congo-Zaïre river deltas (Huber, 1978, 1981a). Similar, but less documented, situations exist throughout the rest of Africa and in South America. A short comparative note for the region between Fortaleza and Porto Alegre is also presented to point out the similarity in South America.

1.1.3- The model illustrated in coastal central west Africa.

This west African region is not only homogeneous by the well contrasted plain and plateau, but also by its limits, the two deltas, where the transition between the high and low lands is, on the contrary, progressive and where then exchanges are possible, by the continuous primary or derived forest coverage (§ 3.1), and by the sandy coastal fringe where lagoons and seasonal biotopes are frequent (see further the climatic variations, § 2.5).
In the northern limit, there is a real but uneasy interconnection due to the presence of a chain of the high mountains of West Cameroun: the *Aphyosemion gardneri* superspecies is present on both sides, in the plain and in the plateau, with an inversed, somewhat oblique, "U"-distribution. In the southern limit, there is a strong interconnection with a "U"-distribution of the components of the two closely related *Aphyosemion* superspecies, *striatum* and *ogoense* (Huber, 1982), with the overall occurrence of components of the *Epiplatys multifasciatus* superspecies (Huber, 1980a), with the link between the Congolese cuvette and the coastal Aplocheilichthyins of the *Congopanchax-Poropanchax* lineages (*myersi-scheeli*: Huber, 1998b).

From the immediate surroundings of the sea to the foothills of the plateau, and not beyond, 3 strates of Cyprinodonts, 21 distinct superspecies, 3 of them being annual, are reported:
- 2 Aplocheilichthyins, in brackish water (*Aplocheilichthys spilauchen*, *Poropanchax scheeli*).
- 1 Aplocheilichthyin (*Porop. macrophthalmus et al.*), 3 annual Aplocheilin lineages (the *Fundulopanchax s.s.-Gularopanchax* lineages with 6 species-names, the *Paludopanchax* lineage with 4 species-names), 3 non annual Aplocheilins (the *Aphyosemion calliurum* superspecies with 7 species-names; the *Aphyosemion bitaeniatum* superspecies with 4 species-names; plus, the monotypic relict *Foerschichthys flavipinnis*); all are rather close to the coast, with, though, some inland isolates (e.g. *A. celiae*); some can even stand very weak salt contents (e.g. *Foe. flavipinnis*). Two species-names from two distinct lineages are also endemic to the Niger delta, *Epiplatys longiventralis* and *biafranus*, remnants of two Sahelian invasions.
- 2 Aplocheilichthyin and 8 non annual Aplocheilin lineages, distributed all over the plain (the *Procatopus* superspecies with 3 species-names, the *Plataplochilus* superspecies with 4 species-names; the *Epiplatys sexfasciatus* superspecies with 6 species-names; the *Epiplatys multifasciatus* superspecies with 2 species-names, replacing *sexfasciatus*, south of

Lambaréné; the *Epiplatys singa* superspecies with 3 species-names; the *Aphyosemion striatum* superspecies with 5 species-names; the *Aphyosemion gabunense* superspecies with 3 species-names; the *Aphyosemion loennbergii* superspecies with 3 species-names; the *Aphyosemion oeseri* superspecies with 3 species-names; the *Aphyosemion pascheni* superspecies with hypothetically 4 species-names, discontinuously distributed: see further the extinction dimension: § 3.2).

This is the richest (62 species-names) and the most diversified (21 superspecies) region over the entire distribution of Cyprinodonts. It is remarkable to notice that, among them, 4 superspecies lineages cover the entire coast length (1800 kms): the *Aphyosemion calliurum* superspecies, *Aply. spilauchen*, *Poropanchax scheeli*, the *Epiplatys singa* superspecies.
In addition to this static picture, a more dynamic view discloses several waves of invasions from a single ancestor or several ancestors, with possibly relict forms having restraint and not parallel-to-coast distributions:
- at least two in *Chromaphyosemion* (*bitaeniatum et al.* and *loennbergii et al.*), not taking into account the relict melanistic sublineage (*bivittatum*, *lugens*).
- at least two in the *striatum* superspecies (*striatum et al.*, *microphtalmum*), not taking into account the three isolated forms of *gabunense*, endemic to the lower Ogooué river.

These successive waves of invasions may be linked to climatic fluctuations (see further § 2.1), with the strate confined along the coastal lineage, hypothesized to be more ancient. At least, as it appears from the analysis of the polarity of primitive-derived external characters (Huber, 1998a,b).
A more dynamic view also assesses the possibility of a past wider range in the plain, as for the interior components of the *calliurum* superspecies (*edeanum*, *heinemanni*, *celiae*) or as for superspecies with a disjunct distribution (e.g. *A. raddai*).

This very rich fauna can only be explained by several additional factors that brings a "lasagna" structure:
- a dead-end effect for groups originating from the south, hypothetically stopped by the epicontinental sea (see further § 2.3) and/or the dramatic changes in the forest coverage exemplified by the Dahomey/Bénin gap (see further, § 3.1) and/or the quicker preemption of these regions after these events by other superspecies. And, reciprocally for those from the north (stopped by the stable, dryer and narrowing plain in Angola);
- a conflicting effect for groups coming from the north and the south, in competition at various points (e.g. the *striatum* superspecies has been unable to extend north of the Sanaga river, with *A. raddai*);
- a lateral instability effect due to variations along time of the sea levels, with the present levels being close to the maximum by about two meters, along the Pleistocene-Holocene (see further § 2.1) and consequently of the surface of the coastal plain;
- and a related fluctuation effect in the lateral coverage of the primary forest (fragmentation, expansion) and, to the contrary, of the seasonal biotopes (see further the refugium theory: § 3.3).

Where does the origin of the coastal superspecies finally stem?
Presumably, not in the plateau. Because all the presently recognized primitive superspecies -usually annuals- are only present in the plain and the plateau non annual superspecies show derived characters; even, for the two superspecies at the dead-end of the distribution (*gardneri* and *striatum*, plus their relatives). And lowland bridges should play a major role for the superspecies of the plateau, as already stated (§ 1.1.2), like, presumably, the Ecucu for *A. cameronense* and the Ogooué for *Diapteron*.

1.1.4- The model illustrated in coastal southeastern South America.

On the other side of the Atlantic, a very similar situation occurs. The coastal corridor from Fortaleza to Porto Alegre is narrow, with a sharp transition with the highlands which are dry (similar to east Africa). No interconnection by lowland bridges is known to be relevant,

except perhaps the Rio Sao Francisco, which has not been prospected. Its two borders are also associated with a progressive transition into the highlands. In the north, the Amazon basin (with the same role as the Congo-Zaïre basin in Africa, see § 2.4). In the south (and dead-end), the lowlands of the Parana-Paraguay mouth, where another epicontinental sea has been recorded (see § 2.3). The resulting pattern of distribution of the Cyprinodonts is identical to Africa (Huber, 1981c, 1992). However, the diversity of fauna is essentially different and much less high in South America -8 superspecies, 23 species-names over circa 3500 km- than in Africa - 1800 km. The following potential reasons are suggested:
- the historically more southern position of the American continent;
- the absence of any lowland bridge into the plateau (with the possible exception of the lower Rio Sao Francisco);
- the absence of forest in the nearby plateau, which prevents a continuum of coverage;
- the less conspicuous coverage of the primary forest;
- the past drier climate offering less numerous suitable biotopes and inducing more extinction, in *Rivulus* at least;
- the direct competition of the related viviparous Cyprinodonts.

Except for the first, second and last reasons, the south American condition is similar to that of the Indian coast African plain, circa 4000 km long, between Maputo and Mogadiscio, with frequent sharp transitions between the plain and the plateau. It results in a similarly less rich diversity of the Cyprinodont fauna, which is dominantly annual.

Anyhow, in southeastern America, four different superspecies of the genus *Rivulus* are reported on the plain (Huber, 1992). Only one, *Riv. marmoratus et al.*, occupies the total range, but this is a brackish marine form. Another, the *Rivulus* santensis superspecies, restricted to the coastal fringe, is present over two thirds of the plain, south of Rio Itapemirim, Espirito Santo State and is the only one to be diversified (5 species-names). The other two are single species, belonging to northern groups: the relict *Riv. brasiliensis* only known from Rio de Janeiro area, far away from its hypothesized counterpart, *campelloi*, from the lower Amazon; *Riv. bahianus*, probably isolated from the other components of the *urophthalmus* superspecies of the Amazon basin. Four superspecies of annual fishes, all restricted to pocket zones. First, the related *Campellolebias*, *Cynopoecilus* and *Leptolebias* lineages, replacing each other allopatrically, from Porto Alergre to Rio Mucuri, Bahia State; second, the *Simpsonichtys whitei* superspecies, partly sympatric to *Leptolebias*, between Rio de Janeiro and Ilheus, Bahia State. This whole coastal fauna is distinctive from the central arid Brasilian plateau, which encompasses only one non annual superspecies, *Rivulus punctatus*, and a great variety of annual species in the lineages of *Simpsonichthys*, *Cynolebias s.s.*, *Plesiolebias*, *Stenolebias*, *Spectrolebias*, *Maratecoara*, *Neofundulus*, *Trigonectes*, *Pterolebias*. No component of them is present in the coastal plain: even, *Cynolebias porosus* which has Recife, on the coast, for type locality is in fact recorded only on the nearby plateau.

1.2- The geology, the tectonic and volcanic activities and their consequences.

The geomorphological landscapes of the Old and the New Worlds have followed a parallel history: in early times (pre-Cretaceous) and in nearer times (mostly during the Miocene). In between these two active periods of general uplift, a long period of stability took place during which erosion sculptured the present old terrains: no high mountains, smooth low plateaus.
The pre-Cretaceous activity (2000 MYA - 500 MYA) in the pre-divide western Gondwana has resulted in three characteristic situations of present contrasted importance, in both the Old and the New Worlds (Trompette, 1994):
- the striking similarity in the corresponding soils of both sides of the Atlantic (fig. 5). But, there is no correspondance in the Cyprinodont fauna, either between the Old and New Worlds, or between two different soils in each continent (see further the failure of the local barriers § 4.1).

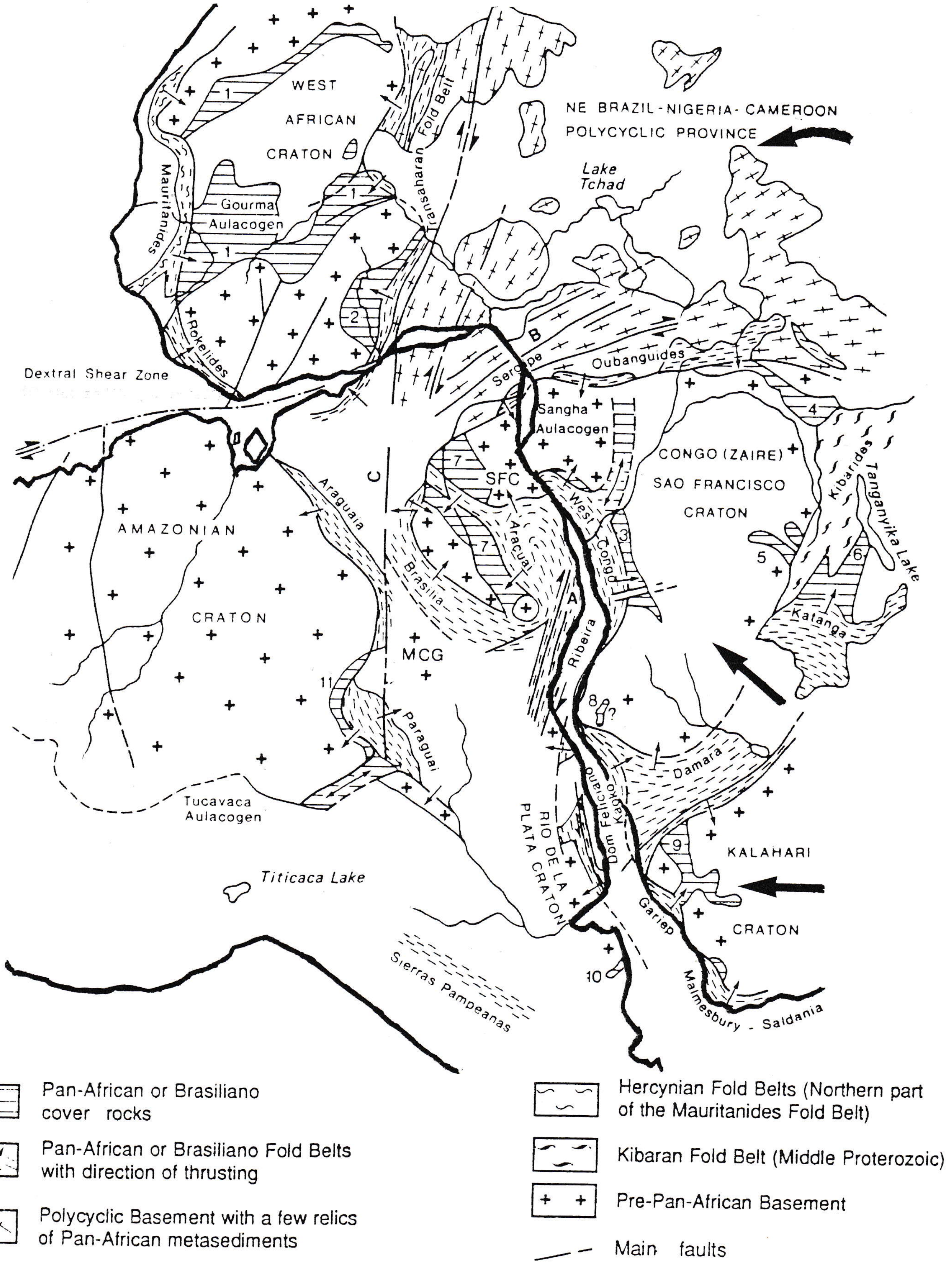


Fig. 5. Major structural units of pre-drift western Gondwana after the pan-African or Brasilian orogeny (circa 600 MYA). Putative paleo-routes via cratons are given by arrows in a vicariance scenario. Abbreviations: MCG, Goias central massif (partly cratonic); SFC, Sao Francisco craton massif (modified from Trompette, 1994).

This lack of link between fauna and geology stems from, first, the very different time scales, second from the northward drift of Africa, while South America remained static, third from the poor influence of the typicality of soils on water composition; probably, climate has been a dominant factor;
- then, the striking analogies in modeling the landscape, with the occurrence of several cratons in which some extant Cyprinodont groups have been found subsequently endemic. Like the Amazonian craton and its adjacent belts (see § 2.3), the Congo-Zaïre Sao Francisco craton (see § 2.3), the west African craton, the Kalahari craton (now semi-desertic), the Rio de la Plata craton (see § 2.2) and the particular case of northeastern Brasil and its African extension;
- last, the more general duality of coastal lowlands and presently more or less flat highlands (see previous § 1.1; fig. 4a, 4b).

Much later, during the Miocene (circa 15-30 MYA), a strong tectonic activity started in eastern Africa with the following consequences (Lévêque, 1997):
- a general upgrading of the eastern plateau, basic at 1000 m;
- volcanic eruptions in western, northeastern and eastern Africa: the Jebel Mara, in between the Tchad and the Nile drainages;
- the formations and depressions of the Rift Valleys, separating Somalia from the rest of Africa: in the north of the present lake Malawi through the western and eastern Gregory Rifts into Ethiopia and further north towards the Red Sea and the Jordan Valley (fig. 6a);
- the subsequent and progressive creation of the Rift lakes (fig. 6a) (see further § 2.6);
- the sudden reversal in some river courses: the Jebel Mara volcano has resulted in a westward diversion into lake Tchad of previously eastward flowing drainages (more than 60000 square kilometers deleted from the Nile catchment).

All these dramatic changes imply that components of the genus *Epiplatys*, which are absent in coastal eastern Africa, were either present before these events but then became extinct (unable to survive very dry conditions, unlike the *Micropanchax loati* superspecies), or more probably had not yet reached the Tibesti and the upper Nile. This incomplete distribution, with no non annual Aplocheilid in northeastern Africa, whereas they are present in all other parts of the Old World, has also been noticed for other groups of fishes, like Mastacembeloidei, Bariliinae, Notopteriidae (Lévêque, 1997).

Other east African river courses have been interrupted or changed, with consequences mainly on the Aplocheilichthyins colonization (fig. 6a). Previously west flowing rivers of central Africa, towards the Congo craton have changed their courses eastward, resulting in the creation of internal drainages of lakes Victoria and Kyoga or, for more southern rivers, in Indian Ocean rivers, like Malagarasi, Rungwa, the great Ruaha and many others. Thence, the Sahelian *Micropanchax loati* superspecies has been capable of invading the Indian Ocean coast biotopes in eastern Africa, e.g. *Mic. kongoranensis*. And the distribution of *Cynopanchax* in Aplocheilichthyins appears chaotic or disjunct for some species e.g. *maculatus* (Huber, 1998a).
Further, rivers of the Tanzanian shield, between the Athi and Zambezi mouths, have been captured and decapitated, allowing confluences of today separated rivers. Finally, the history of the upper Zambezi and the upper Lualaba has also been hectic (Lévêque, 1997). For example, before the tectonic events, the upper Zambezi, the upper Cunéné, the Okavango, the upper Kafue, the Bangwelu and the upper Lualaba rivers all flowed into a common basin, part of the Zaïre cuvette (fig. 6b). Then, reversals and various changes allowed the (re)invasions of some Aplocheilichthyins into southern Africa and the present southern distribution of *Hypsopanchax*.

Somewhat before, during the Eocene (35-50 MYA), the latest uplift of the Guinean Dorsal, resulted in the changed course of the eastward Sénégal basin, towards the northwest, up to a marine gulf around Bakel (i.e. much more to the north than today). This implies a disconnection of the coastal fauna from the Sahelian fauna and the development of

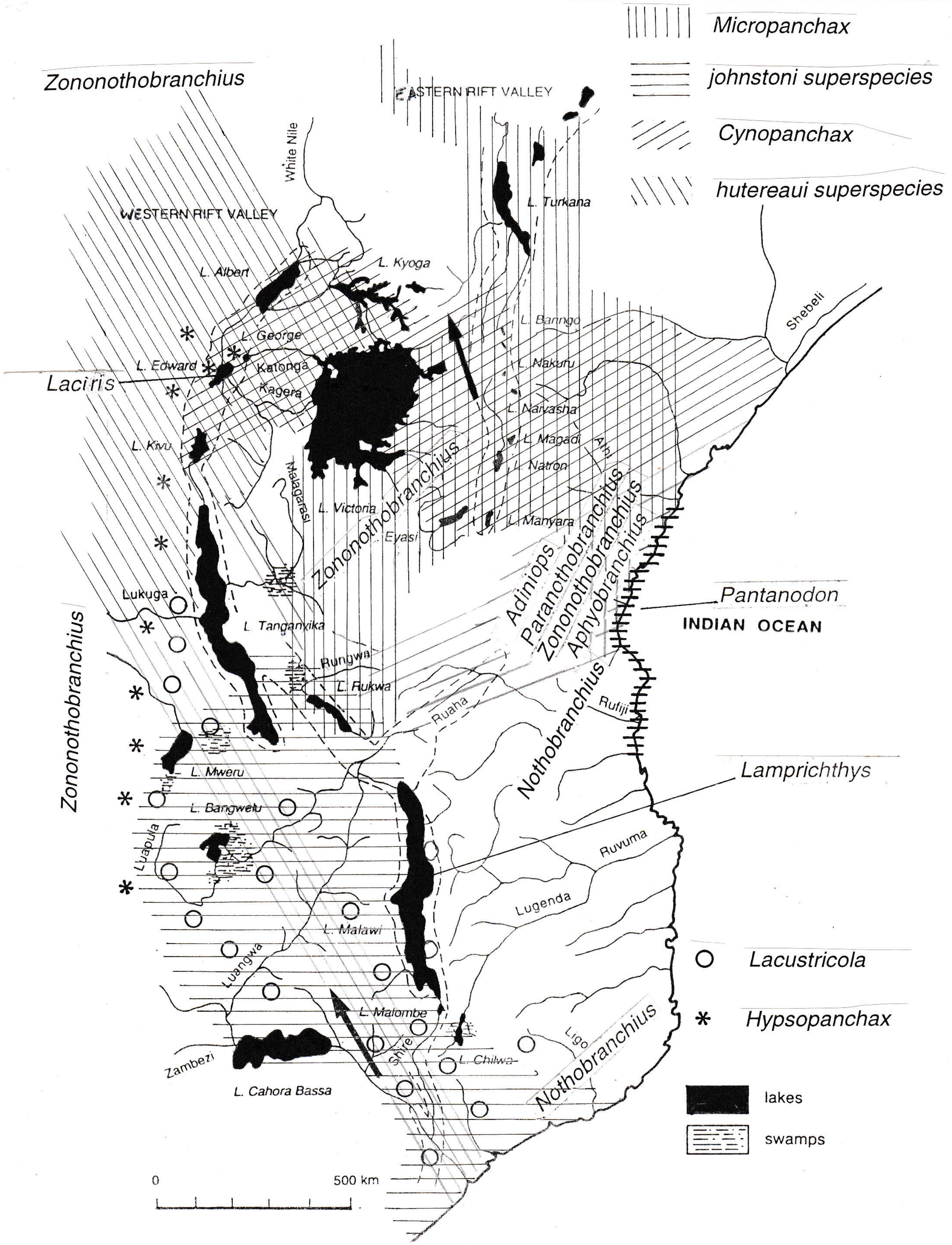


Fig. 6a. The two Rift valleys of eastern Africa and their associated lakes. The Cyprinodont fauna distribution is indicated (approximately, only for visual appraisal) with putative migration routes (modified from Lévêque, 1997).

endemicity, with the Aplocheilichthyin *nimbaensis* superspecies and part of the *Archiphyosemion* lineage (Huber, 1998a) (see further also the Guinean Dorsal as a refugium, § 3.3).

In South America independently, but also in the Miocene, began the sudden rise of the Andes, from a string of islands within a marine geosynclinal basin (Goldblatt, 1993). Before that major event, the north-south Pacific coast exhibited a much larger plain, with possible suitable habitats for annual (and non annual) Cyprinodonts. This may be one possible explanation for the present disjunct distribution of *Pituna* and *Pterolebias* (see also further § 3.2, the climatic alternative hypothesis). More importantly some rivers, including the Amazon, flowed westwards (Gayet *et al.*, 1993; fig. 10a) into the marine basin (the epicontinental sea, see further § 2.3). This may reverse the traditional view of expansion of *Rivulus* up to Peru, from the eastern present delta of the Amazon and upstream along the river. Lots of fossil fishes -unfortunately not identified, in the Cyprinodont lineages, yet- have been disclosed in that western paleo-plain, south of the present Magdalena river, e.g. at La Venta, in Colombia (Lundberg, *in litt.* 1997). Later (25 MYA), began the uplift of the Sierra de Perija, at the tip of northern Colombia and, during the Pliocene (5-10 MYA), the last uplift of the Serras of northern Colombia, along the present Cauca and Magdalena rivers, together with the Proto-Panamean connection. These mountains separated the fauna of Choco western Colombia from that of the Llanos of Venezuela and that of the Amazon: a then 3000-4000 m barrier. For Cyprinodont, not surprisingly, this barrier is not exchange proof. Indeed, the *Cynodonichtys* and *Vomerivulus* non annual lineages are restricted to west of the Sierra de Perija (and mainly in Central America), but annual populations referable to *Rachovia* are found both sides and it is unknown if a speciation has occurred.

Similar reversals of rivers, but not east-west, may have also played a role for neotropical Cyprinodonts, at least in easing colonization (fig. 6b). During part of the Tertiary (not precised: Costa, 1995a), the upper Parana at the level of the Sete Quedas falls (border of Brasil and Paraguay) and the upper Paraguay rivers reversed completely from northward to southward. This may explain the further southern expansion of the *punctatus* superspecies in *Rivulus* and, conversely the older, hypothetical, northern expansion of the *Cynolebias* superspecies (i.e. *porosus et al.*), along the western side of the highland Brasilian plateau, culminating with the Serra Mantiqueira and the Serra do Espinhaço (see further, § 4.3.2).

Finally, it is worth mentioning that, apart from some localized volcanic eruptions that occurred in both continents, within existing highlands, during the late Pliocene and the Quaternary, no recent earth disruption is reported.

Geomorphological events within each continent are important for the understanding of the older evolution of the tropical Cyprinodonts (orogenic vicariance).
- Understandably, the pre-Cretaceous events bear little direct importance. However, indirectly and despite erosion, they affected the presumably east-west routes of the old morphotypes, before and/or just after (depending on extinction factors that are untouchable today) the continental divides (see also further § 4.3) and the expansion mode of extant species (see previous, § 1.1, the plain-plateau transition).
- The about-Miocene events bear much more importance. They trapped ancestors of some older phenotypes in restricted areas of both the Old and New Worlds, after the uplift (e.g. some Rift lakes Aplocheilichtyins, see further § 2.6, and *Aphyosemion bamilekorum* in West Cameroun or *Rivulus derhami* in a remote Andean valley). They facilitated or prevented or interrupted migrations of old morphotypes (see also further § 4.3).

The geomorphological events are as important as the climatic events (see further, § 2), but they took place during long step wise processes. They are also very different in practice and can be regarded as barriers, transfer bridges, exchange platforms (see also the two-scaled evolutionary history of tropical Cyprinodonts that is hypothesized in the introduction).

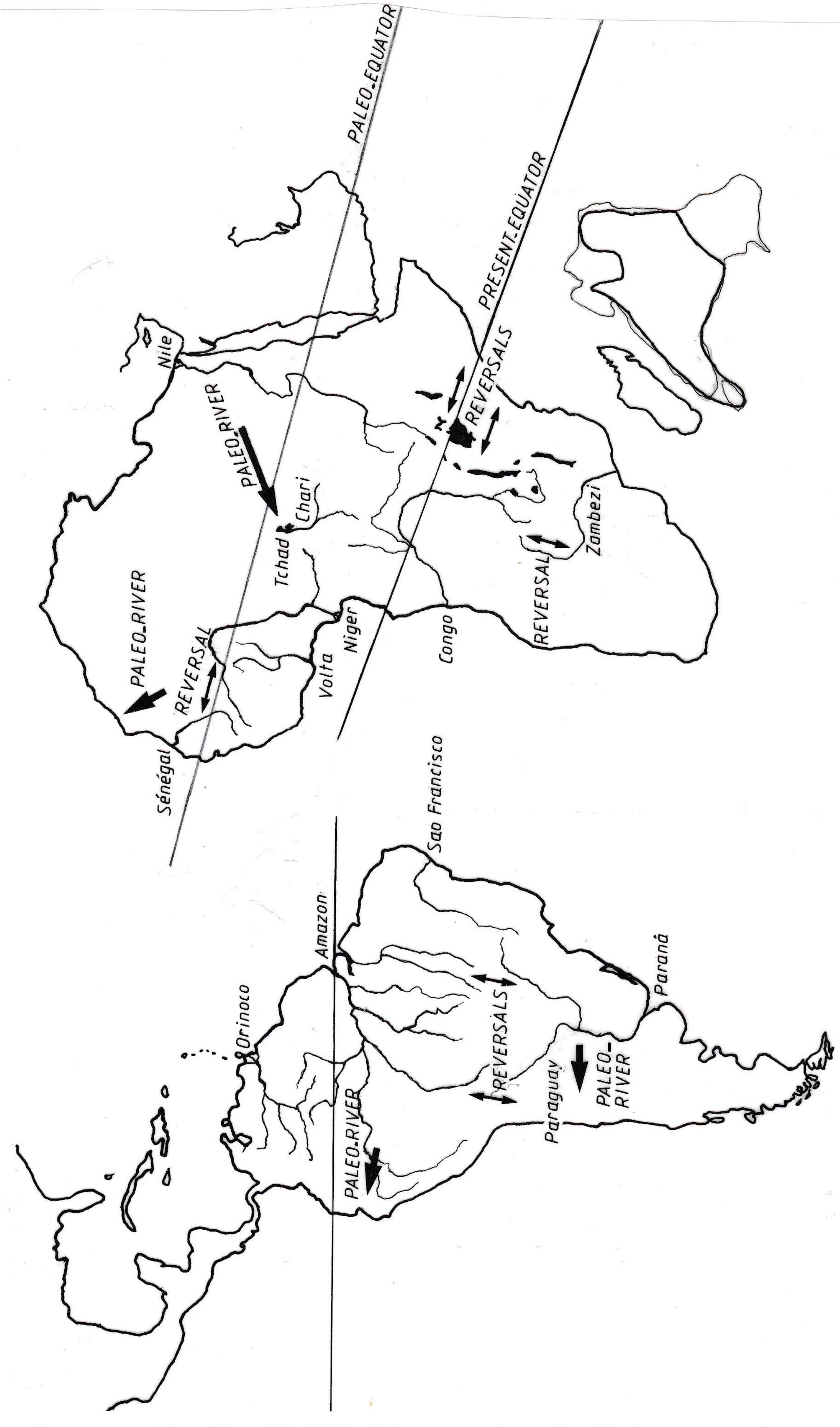


Fig. 6b. Paleogeographic reconstruction (circa 80 MYA) of the area under study with the present main rivers and indications of past river flows and past reversals by arrows (original drawing by Chauche).

On the other hand, these two types of events -geomorphological and climatic- are locally related and their effects are superimposed (additive or attenuative). Geomorphologic events, like drifts and mountain uplift, do influence strongly the climate. For example, the Andean uplift has modified conspicuously the climate of South America, with major winds and rain coming on the upper Amazon from the south and not from the Pacific or the Alantic coast (see further, $ 2 for further details).
The climatic events can be analysed from two dependent view points -water and coverage- but we shall cover them separately for clarity sake (§ 2 and § 3).

2- The past climatic variations and their impact on water mass.

Three major lowland phenomena have also contributed strongly to the present pattern of distributions of tropical Cyprinodonts: the rise in sea level with the corresponding shrinkage of the coast outline, the epicontinental seas, the huge interior freshwater lakes. These three events may have occurred at the same time(s), but the epicontinental seas were not as frequent and recurrent as the two others. All are direct consequences of higher temperatures in the air and in the sea.
In practice, this has resulted (amended from Lévêque, 1997):
- in the melting of ice near the poles or inland glaciers (e.g. in the poles, in the Andes, in the Rift mountains);
- in a significant reduction of the coastal plain band, e.g. like today;
- in the transgression of the sea far inland (e.g. in the Brasilian Sertao), up to create epicontinental seas;
- in the disconnection of a part of land from the coast, resulting in islands which are presently isolated, or, in the disconnection of landbridges between arcs of islands (e.g. in the Caribbean lesser Antilles);
- in the sudden increase of the permanent and seasonal overfloods (e.g. in the Amazon basin), of lacustrine water levels in the Rift Valleys lakes;
- in the considerable extension of river basins, e.g. the Sénégal-Niger rivers, the internal lakes of Congo and Amazon, with possible interchange between neighboring basins;
- in the dramatic development of the rain forest coverage (see further, § 3.1) and of the non forest ephemeral biotopes.

And reciprocally, during cool and dry periods. With two exacerbated specificities for the New World (Clapperton, 1993b) in comparison to the Old World, at that time. The more important role of the Andes and its many glaciers (as low as 1800 m), to retain water subsidy. The less important role of the on-shore Atlantic winds in bringing rain which resulted in an unusually greater weight of the seasonality of climate than today.

These oscillations in climate have been theorized and generalized over the entire history of the Earth, although our knowledge of climatic variations is only established in detail, for the late Quaternary, following palynologic studies.
On the one hand, the palynologic records tend to emphasize two major facts (Maley, 1996a):
- a progressive increase of the amplitude of the glacial periods with two major steps, the first about 2.5 MYA (Pleistocene) and the second 800 000 BP.
- a peak of glacial maximum repeated each 100 000 years, since 800 000 BP.

It is thought (Maley, 1996b) that the changes of magnitude are due to the appearance of the northern ice cap in relation to the African drift, towards the end of the Tertiary (6 MYA).
On the other hand, glacial cycles have been hypothesized by Milankovitch (Lowe & Walker, 1997) to be due to astronomical variables related to the earth relative position to the sun and to planets, with three combining cycles: the eccentricity cycle (periodicity: 100 000 years), the obliquity cycle (periodicity: 41 000 years), the processional cycle (periodicity: 23 000 or 19 000 years).

Did these short term climatic oscillations also take place during much older periods? No data can confirm this. However, it is presently considered, based on the analysis of sediments

and of fossil vegetation, that:
- prior to Quaternary (2.5 MYA) and up to the Oligocene (40 MYA), the eventual oscillations were not of the same magnitude;
- before 60 MYA, the climate was much more uniform, with a reversal in comparison to the Quaternary (warmer poles, cooler paleo-equator and low gradient between them);
- between 40 and 60 MYA, a warmer and wetter climate in the tropics is congruent with the development of forest (see further § 3.1).

Then, if the climatic variations which are suggested by the general eustatic sea level fluctuations between 10 and 2.5 MYA (see further, § 2.1) did actually occur, it appears that their amplitude did not reach the same climax and their frequency was not as high (although some rare peaks of 100 m below present level have been recorded, probably in relation with the Antarctic ice cap).

Anyhow, the established climatic oscillations of the Quaternary strongly affected the vulnerable reclusive waters and the tropical Cyprinodonts of both the Old and New Worlds. In addition, since the glacial periods (especially the last one) induced strong extinction (see further § 3.1), it is of poor interest to consider the older glaciation periods in absence of any fish fossil record: most of their effects have been swept off, along time.

Finally, another phenomenon influenced strongly the climate (see further the difference in coverage, § 3): the movement of the African plate with a twofold process:
- a northern drift from a paleo-equator line at the level of the present southern Sahara (late Cretaceous, 70 MYA) and the present southern border of Egypt, to a line close to the present latitude of 5° North (50 MYA); a total of circa 1650 km drift has been accomplished between 70 MYA and the continent stabilization (14 MYA);
- a clockwise rotation along an axis lying off the Sénégal coast, with a more important impact at the periphery, in East Africa.

However, it should be noted that the magnitude and speed of this drift is subject to discussions among specialists.

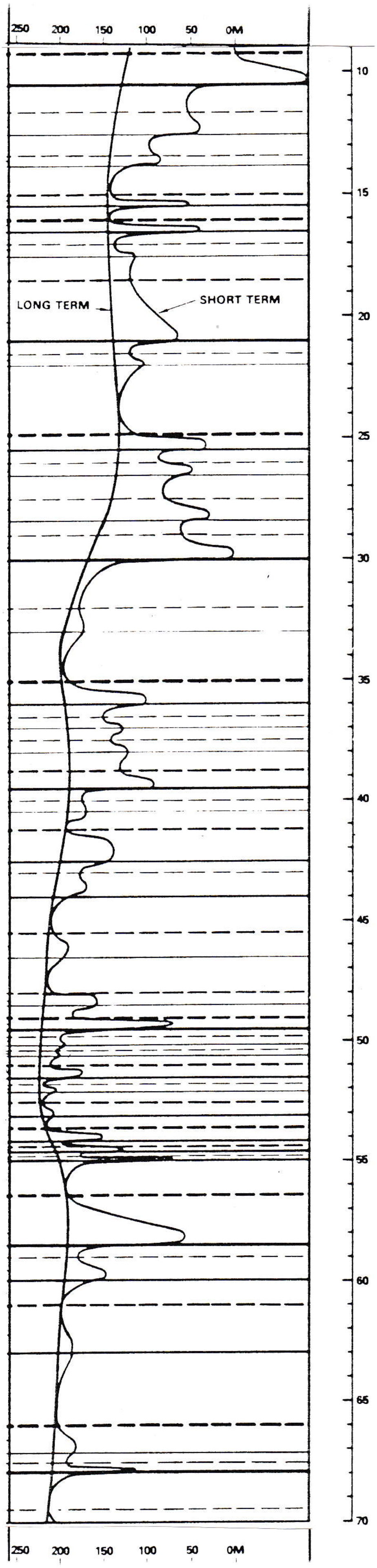
2.1- The sea and the lacustrine water levels and their fluctuations.

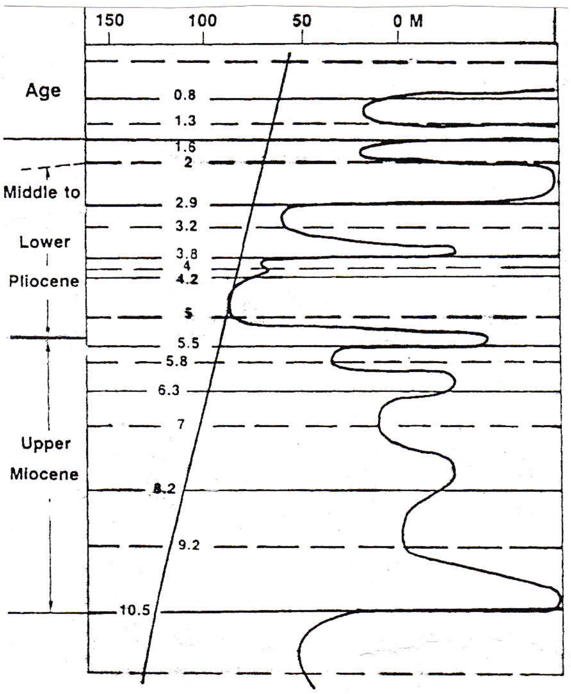
Fluctuations of the water levels, either salt or fresh, are then consequences of climatic variations over time: during cooling periods of the weather, the glaciation times, ices appeared considerably increased and extended in the polar regions of the Earth and in the mountains. This resulted in lowered level of the seas and rain decreases.

They are much more known in details for the Quaternary: at least 21 glaciation periods are recorded over a period of about one to two million years only. During the last -and apparently most severe- glacial period at its peak (L.G.M.: circa 18000 BP):
- the northern Atlantic ocean was a polar sea; the mean drop of the surface temperature was 3.5 to 10°C at the Canary Islands;
- all mountains of both the Old and the New Worlds were covered by large glaciers;
- evaporation from sea was much reduced;
- atmospheric CO2 was reduced to circa 170 ppm;
- evapo-transpiration and convective condensation in the forest was also much reduced, creating a negative spiral to forest coverage (see further § 3.1);
- drier winds from the sea brought less rain and humidity: mean rainfalls decreased by 30%;
- mean air temperatures fell sharply by 4°C in the lowlands and 10°C in the mountains.

For relatively short periods, circa 3000 years at a time, during the glacial periods, peak temperatures were lowered by as much as 7.5°C in the Cyprinodonts environment.

This temperature decrease in the air had a direct effect on water temperature, but this must not have stressed the Cyprinodonts significantly. Only, the air dryness and the subsequent rain decrease had severe consequences.





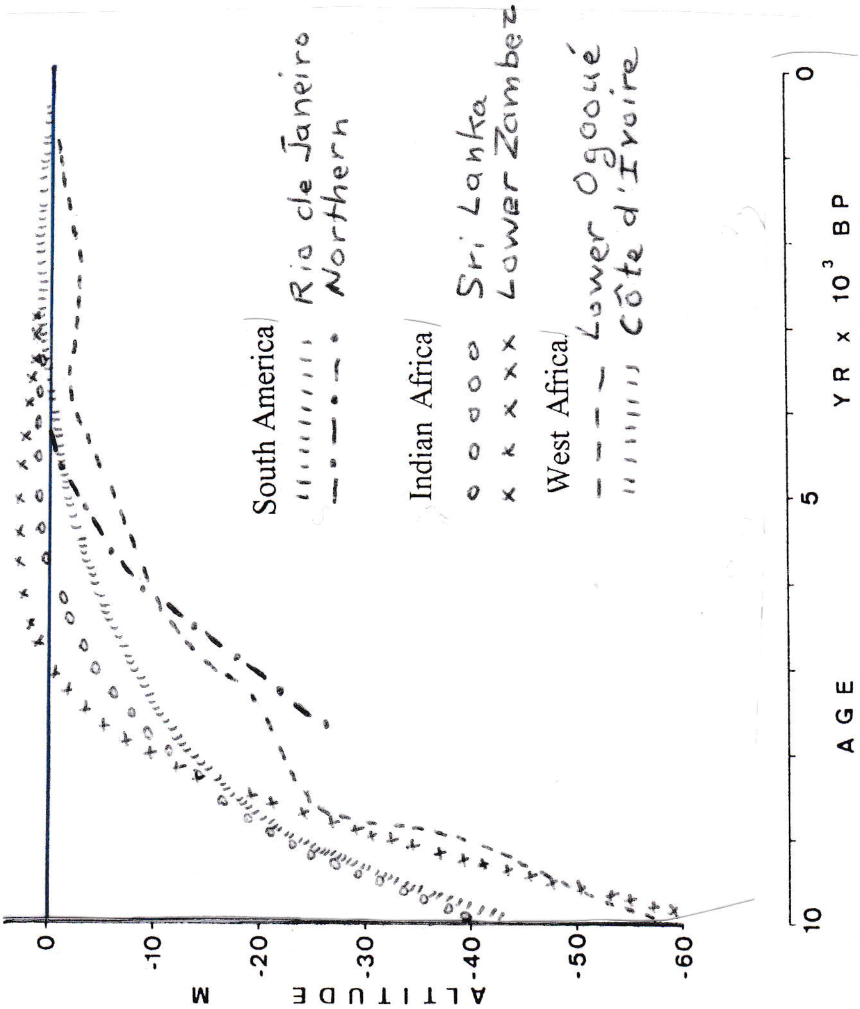


Fig. 7a. Absolute sea levels between today and 10000 BP, in West Africa, Indian Africa and Atlantic South America (modified from Pirazzoli, 1991).

Fig. 7b. Long term and short term eustatic sea levels variations during the last 70 MYA. Several very low levels are reported since the Miocene (Haq *et al.*, 1988).

During the last glacial period, between 75 000 BP and 10 000 BP, and especially its maximum (L.G.M.), between 24 000 BP and 14 000 BP, tropical waters cooled down by 3-4°C and sea levels decreased by up to 120 meters with fluctuations: minus 85 meters, at 25000 BP, minus 50 meters between 70 000 BP and 25 000 BP, minus 120 meters between 24 000 BP and 14 000 BP.
As an illustration (fig. 7a), the relative sea levels at some spots of western Africa, eastern Africa and India, eastern South America are given for the last 10 000 years BP. More generally, the sea levels have changed over history with an inversally proportional incidence in non-marine areas (Haq *et al.*, 1988). For example, the eustatic sea level has been decreasing on a long term trend during the last 70 MYA (Haq *et al.*, 1988). Understandably, the short term fluctuations are less well documented over that period. But several very low sea levels (minus 100 m) are also reported during the Miocene (10 MYA) and the Pliocene (2.9 MYA), similar to those of the Quaternary (fig. 7b).
These Quaternary fluctuations in the sea level and thus in the coastal outline have had direct and indirect (§ 2.2, off the coast islands, § 2.3, epicontinental seas, and § 2.5, the extinction dimension) consequences on the Cyprinodont fauna.

The direct consequence concerns the surface of the coastal plain.

- At the peak level of the last dry period (L.G.M.), the sea retreated by at least 120 m (e.g. fig. 8 for Asia) and the coastal line may have been not too far from the sea continental shelf (circa 200 m depth). The coastal plain gained some 40 to 120 km of width. Coastal lakes, like Maracaibo, were dried out. Large "avenues" of extension for Cyprinodonts could have then been offered, if only the forest coverage was not reduced in parallel. However, the relict presence of annual forms in both the Old and the New Worlds testify that these species had in the past a much larger distribution: in Africa, the taxa *Callopanchax* in Sénégal to Liberia, *Paludopanchax* in Bénin to Cameroun, *Fundulopanchax-Gularopanchax* in Bénin to Ecuatorial Guinea (and possibly Gabon) and, because these annual species are older than those non annual, this should have also occurred in earlier times (see the ephemeral dimension, § 2.5). This is probably also the case with the more opportunistic non annual *Epiplatys* species, e.g. the *sexfasciatus* and the *singa* superspecies. More importantly, these fluctuations have induced disruptions in the brackish water mangrovian biotopes of highly specialized species: *Aplocheilichthys spilauchen* and *Poropanchax scheeli* in western Africa, *Pantanodon stuhlmanni* and *madagascariensis* in Indian Africa, *Rivulus marmoratus* in Atlantic America. For certain periods, the mangrove has been continuous which explains the huge distribution of these species, if a dispersal process is excluded (see further § 2.2).

- At the peak of the last wet period (H.C.O. at circa 9000 BP), the sea water levels were about 2 meters above present, which corresponds to the poorest and smallest recent availability of coast land and reciprocally to the best conditions of speciation (see further § 3). Cyprinodont species density is the highest and species distribution is strongly compressed in a "lasagna" structure along the coast. This lateral structure suggests to hypothesize here for the first time that the oldest sublineages are those located nearest to the sea. Two examples in Aplocheilichthyins and Aplocheilids: the brackish species *Porop. scheeli* invaded its niche before the further wave of the related *Porop. macrophthalmus* superspecies from freshwaters. The *bitaeniatum* superspecies in *Chromaphyosemion* is confined to the fringe of the coastal plain, whereas the *loennbergii* superspecies in the same subgenus is more inland and may correspond to a second migration scheme.

2.2- The island species as witnesses of the evolution clock.

In both the Old and the New Worlds, there are several islands, situated not far from the coast, say less than 100 kms, and with a less than 120 meters depth of the in-between sea. Because, as mentioned above (§ 2.1), the lowest levels of the sea were about 120 meters below present during the severe glacial periods, these islands are witnesses of the past

distribution of tropical Cyprinodonts. Conversely, some species became fully isolated from the continent forms since the last pluvial period (11 000-8 500 BP). They may have developed speciation during that period. These remarkable islands can be regarded as speciation clocks and they are studied as such for the first time here.
Bioko and the Bijagos in western Africa, Zanzibar and Mafia in eastern Africa, Nosy Bé and Nosy Boraha in Madagascar, Sri Lanka, the Andamans and thousands of islands off Indonesia, in Indo-Asia, Puna off Guayaquil, Margarita, Trinidad, Tobago, Santa Catarina, close to Florianopolis in southern America. Two additional more distant islands -Pemba, north of Zanzibar (700 m deep strait) and Grenada, north of Tobago (650 m deep strait)- are worth consideration.

For some of these islands only, collections of Cyprinodonts are known:
- Bioko is situated off the Cameroun coast, with a present 35 km wide strait and 66 m depth of the sea at a maximum. At least, between 18 000 BP and 11 000 BP, Cyprinodonts were present on the coastal plain, now submersed by water. Today, some of them are slightly different on the island from those on the coastal plain, with one nearly definite speciation for the component of *Aphyosemion*, the poorest swimmer of all: *A. oeseri* in Bioko, *A. marmoratum* in western Cameroun, with distinctive color patterns, but similar karyotypes and partial interfertility. The other Cyprinodonts are either brackish (*Aply. spilauchen*, *Porop. scheeli*) or freshwater dwellers (*Aphyosemion bitaeniatum*, *Epiplatys infrafasciatus*, *Procatopus similis*), with slightly different characters from their inland counterparts at the border of Cameroun and Nigeria. Surprisingly, *A. calliurum* is not present on the island, and no annual forms either, because suitable biotopes are lacking.

- Zanzibar is situated off the Tanzania coast, with a 30 km wide and 53 m maximum deep strait. The two lands have been separated since 9 000 BP, at the level of Dar es Salaam. Two annual *Nothobranchius* species are found on the island. The first, *N. guentheri*, distinctive by color pattern and karyotype from its main land counterpart, *N. foerschi*. The other, *N. melanospilus*, apparently not, although no detailed comparative genetic and interbreeding study has been performed. Unfortunately, the island of Pemba has not been prospected.

- Mafia is situated off the Tanzania coast, at the level of the Rufiji river delta, with a 20 km wide and 33 m maximum deep strait. The two lands have been separated since circa 8 500 BP. One species of *Nothobranchius* with yellow and red phases, *N. korthausae*, appears to be endemic to the island. On the facing mainland, another similar species, with blue and red color phases is reported *N. eggersi* which is related to *korthausae*, according to its morphomerictics. Not far on the coast and far upstream of the Rufiji are recorded the single two locations of its presumed more primitive counterpart, distinctive by morphology and, but much less so, by color pattern, *N. lourensi*, with also a yellow phase.

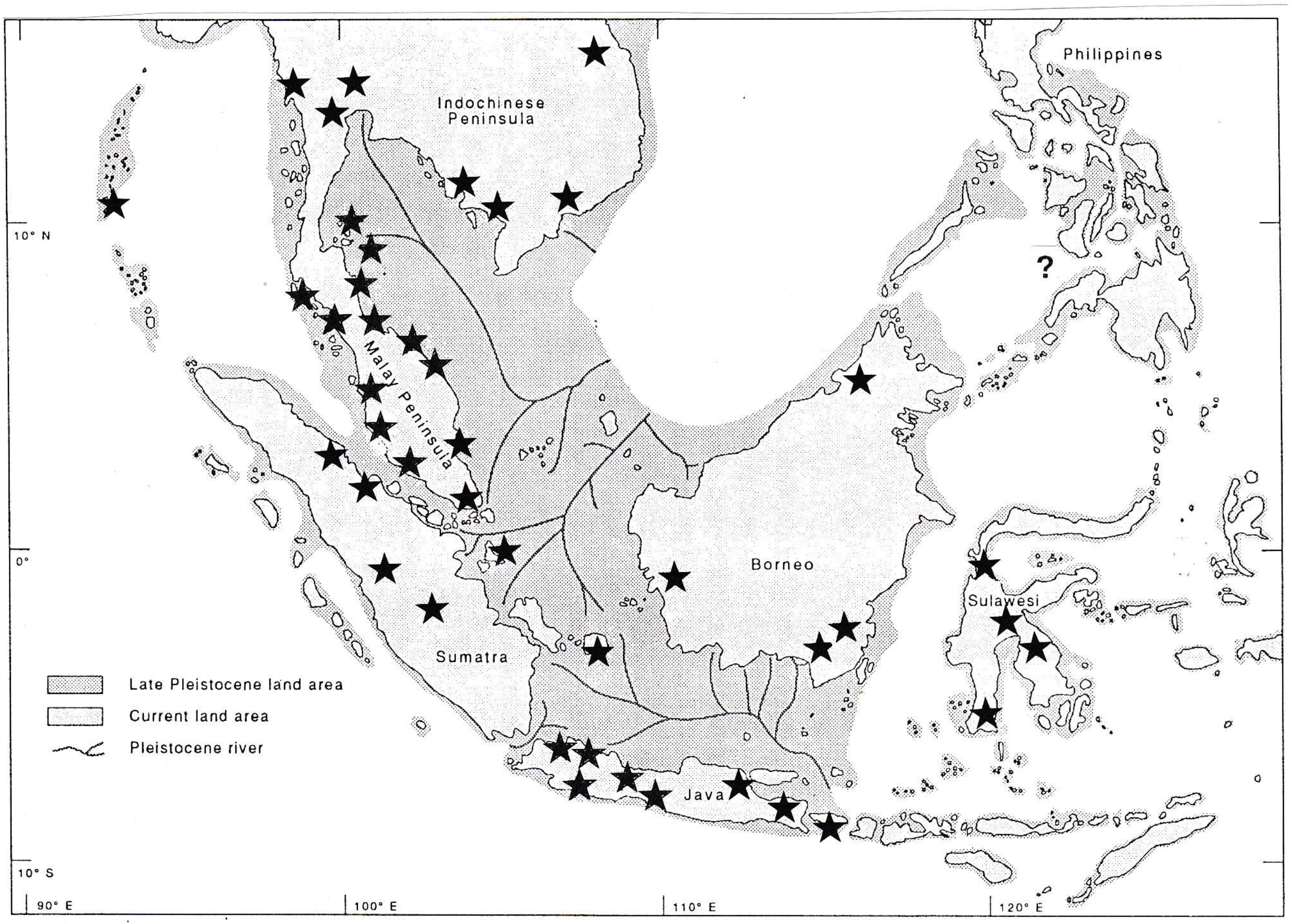
- Nosy Bé is situated off the northwestern coast of Madagascar, with a 15 km wide and 24 m maximum deep strait: the same *Pachypanchax omalonotus* with the two color phases has been collected on both lands, which have been separated since circa 8500 BP. Unfortunately, Nosy Boraha has not been prospected on the eastern forested side of Madagascar. It should be very interesting, since it falls within the putative range of the strange *Pantanodon madagascariensis*.

- Sri Lanka is situated off the southeastern coast of India, with a 40 km wide and 64 m maximum deep strait. Its history as an island appears to be much older than those of Africa. Sri Lanka has been separated for a long time from the continent, which itself collided with Asia about 25 MYA. But circa 12 000 BP, it was connected to India for the last time. Two species of *Aplocheilus* are reported from the island: *Apl. parvus*, nearly all around the coasts and *Apl. dayi* (with two subspecies) only in the southwestern coastal region. The counterparts of *parvus* in India have been named *blockii* (Madras, eastern India) and *kirchmayeri* (Margao, western India), but there are suspicions that all three taxa are interfertile. Color patterns of the Indian forms are poorly or not at all known, especially from the corresponding mainland facing Sri Lanka. On the other hand, *Apl. dayi* is well separated by color patterns, by morphomeristics and by haemoglobine types from the inland form, *Apl. lineatus*. It may be that these two groups of species have a different history and that *parvus*, only, was isolated from its counterparts during the last pluvial maximum.

- The Andamans are situated off the Malaysian coast at 350 km distance. Similarly, the Indonesian archipelago is made of very large (Sumatra, Java, Borneo, Sulawesi) to smaller islands (Bali, Belitung, etc.). All have been colonized by the very opportunistic species, *Apl. panchax*, from India after its connection to Asia. There is no surprise in this situation since the whole region was a continuous land during the late Pleistocene (fig. 8), except for Sulawesi (unknown landbridge? human transplant of *panchax*?). This paleo-land includes Malaysia and Indonesia, up to the Lombok island. Whether it includes the Philippines or not is unknown precisely and no collection of *panchax* has been reported yet from the southern Philippines, vicariantly arrived from Sulawesi or Borneo. The population of Andamans has been given the subspecies status (*andamanicus*), but it is not known alive and, in general, geographical variations of *Apl. panchax* are poorly known, so that it is difficult to raise further conclusions. However, the fact that the more derived (smaller species with lower meristics and with a derived behavior) *blockii* superspecies has been unable to extend more northernly than Madras in eastern India suggests the hypothesis of a more northeastern origin for *panchax* than the two other *Aplocheilus* sublineages in the paleo-block of Madagascar-India.

- Trinidad, Margarita, Tobago and Grenada are situated off the Venezuela coast in a decreasing order of proximity, respectively by 15, 20, 30 and 120 km from the coast. The strait is respectively 40, 54, 75 and 650 m maximum deep, today. Due to the much deeper strait, the phenomenon for Grenada is clockwise much older. It may be argued that Grenada is part of the southern Proto-Antillean arch, made of volcanic smaller islands (see further here). The first three islands have been separated from the main land since the last pluvial maximum (circa 8000 BP). On all islands and on the nearby continent, *Rivulus hartii* has been reported. The Grenada population only is slightly different by color pattern from the more proximal ones. However, no comprehensive genetic study has been performed and speciation may have occurred between that population and the others. On the Venezuelian mainland, the populations of *Riv. hartii* are not variable, relatively to the standards of the genus (Huber, 1992).

Because Cyprinodonts are known as secondary freshwater fishes (i.e. tolerating sea waters for short times but breeding mainly in freshwaters), it has been argued that they invaded their territories by dispersal through sea (Lundberg, in Goldblatt 1993). We do not believe in such a pattern for tropical Cyprinodonts, i.e. those belonging to the lineage of the Aplocheilids and Aplocheilichthyins (to the contrary to the dominantly temperate Cyprinodonts, for example). This can be established on extreme cases like the present African brackish dwellers, *Aplocheilichthys spilauchen*, *Poropanchax scheeli* on the west coast and *Pantanodon stuhlmanni* and *P. madagascariensis* on the east coast. If these species were able to disperse, then they would have colonized long distance, deep sea islands. For example Cabo Verde, Sao Tome (2200 m depth), Principe (2900 m depth), for the former. The Comores, the Seychelles, and the group of islands around Juan de Nova (1100 m depth) in the Mozambica channel, for the latter. Moreover, *P. madagascariensis* would have a different present distribution in Madagascar. Murphy and Collier (1996) have confirmed through molecular analysis that the greater Antillean island *Rivulus* species have vicariantly reached, through landbridges Cuba (*Riv. cylindraceus*) and Hispaniola (*Riv. roloffi*) from South America. Even, according to us, at a later stage, the lesser Antilles, Martinique and Sainte Lucie (*Riv. cryptocallus*) and Grenada (*Riv. hartii*). However, the time of these migrations is uncertain like the dating of the proto-Antillean plate (circa 80, 65 and/or 40 MYA). Anyhow, the hypothetical migration route is well established during the Miocene (27 MYA), as derived from animal invasion from North or South America (fig. 9).



In addition, we infer that *Rivulus marmoratus*, a crab holes dweller, also swimming in reef hypersaline waters from Florida to southeastern Brasil has not invaded its mangroves by dispersal, because otherwise, it would have reached easily -and if not easily, at least discontinuously- the Mexican Gulf. It is missing from west of Tampa to Campeche and also on the Pacific coast, that could have been reached by dispersal up to 3 MYA. It is only known not far from the two putative extensions of the plate, in Florida and Yucatan/Belize (see also the obscure case of *Millerichthys* from eastern Mexico, § 4.3.2).

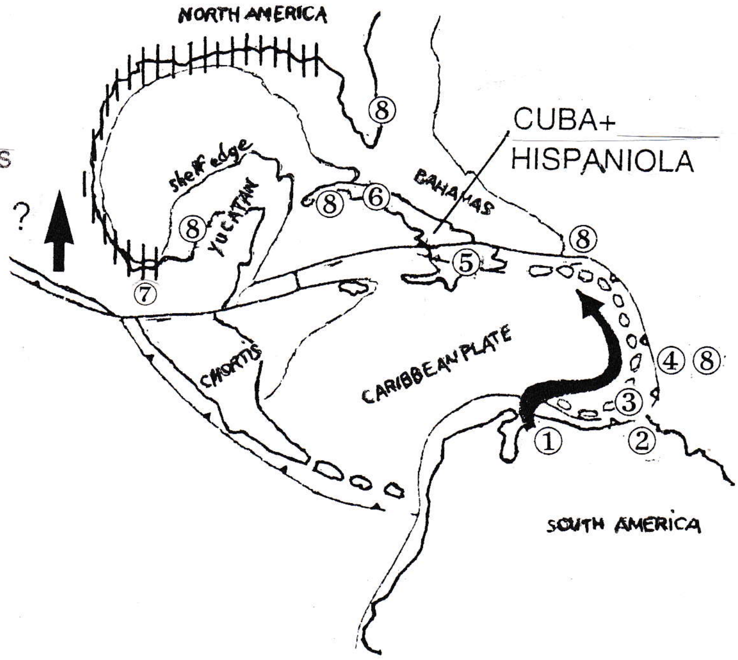


Fig. 8. Southeastern Asia, showing current land areas and the late Pleistocene land coverage, as estimated from the 120 m bathymetric line. The distribution (stars) of *Aplocheilus panchax* follows that Pleistocene land except for the Sulawesi (unknown landbridge? human transplant?). The attachment to it of the Philippines is still a question mark: no collection of *Aplocheilus panchax* has been reported from there yet, but the southern present islands are little prospected (modified from Heany, 1991).
Fig. 9. Putative configuration of the Caribbean zone during late Oligocene-early Miocene (27 MYA). The island arc is an established migration route for animals (Goldblatt, 1993). Cuba and Hispaniola used to be united, in line with the species differentiation of *Rivulus*.
1- *hartii* (main land); 2- *deltaphilus*; 3- *hartii* (Grenada); 4- *cryptocallus*; 5- *roloffi*; 6- *cylindraceus*; 7- *robustus*; 8- *marmoratus*.

Allopatric vicariance is indeed the key distribution and speciation model. Certainly most of these islands, remnants of low water levels, have been connected to the main land on several occasions. But the weak differentiation in morphology, if any, between the corresponding faunas suggests a relatively recent event, only. This implies that the eventual previous faunas must have faced extinction during subsequent dry periods. This is also confirmed by the absence of any relict, more primitive forms in the mountainous areas, if any, of these islands (e.g. even in Sri Lanka for *Aplocheilus*).

The off-the-coast islands are then privileged witnesses of speciation: some species, but not all, have separated from the main land forms and become endemics since the last glacial maximum. Like the other fish groups (Haffer, 1993; Lévêque, 1997), Cyprinodonts may have then developed genetic isolation in about 10 000 years. However, this hypothesis has to be checked in depth on species that have not similarly developed a distinctive color pattern. When two congeners are available in the same island, it is puzzling to observe that one has faced speciation with color differentiation, the other apparently not, as in Zanzibar and in Sri Lanka: the present situation may result from more complex past events, where partial extinction may have played a role (see also further, the speciation dimension, § 4.2). From this point of view, the islands off-the-coast promotes a similar scenario to the main land (see further the refugium theory, § 3.3) with "island" species: series of opportunistic colonizations, partly swept off by waves of extinction, as a consequence of climatic desiccation.

2.3- The epicontinental seas.

The frequent variations of the sea levels over history have resulted in transgressions (advance of the sea) or regressions (retreats of the sea). During high amplitude times, the sea has been able to invade large portions of the coast, creating marine cuvettes, such as in the neighboring parts of the Brasilian Sertao during the Pliocene (5 MYA) or Somalia/Ethiopia (10-12 MYA) and many other poorly known regions. During very high amplitude times, the occurrence of epicontinental seas has been intermittently permitted for very long periods in regions combining the two characteristics of extended very low lands and limited freshwater inflow (fig. 10b). These introgression seas must have represented an impassable barrier for all tropical Cyprinodonts (except the brackish species) and, if they could not be circumvented, they isolated their populations on both sides.

Three epicontinental seas are established in the Tropics (Smith *et al.*, 1994; fig. 10b).
- The west African sea longitudinally split the continent at the level of the Niger delta from circa 80 MYA to 60 MYA. At that time, the Mediterranean sea was not formed and Africa was an island continent, broken into two parts. Further, this epicontinental sea has not always been continuous from south to north and has occurred with a much smaller extension in more recent times in place of the present Niger delta, up to circa 5 MYA. Murphy and Collier (1997) have hypothesized that the phylogenetic relationships of *Epiplatys* and *Callopanchax et al.* in the west, and their phylogenetic separation from *Aphyosemion* and *Fundulopanchax* in the east, can only be explained by this epicontinental sea. An alternative explanation, also recurrent, would be materialized by the more western Bénin/Dahomey Gap of dry savanna between coastal forests of the Quaternary (as per Clausen, 1967 and subsequent authors). But this would be less coherent with the -much older- morphological differentiation. The limited westward present extension of the *Paraphyosemion* (?) lineage (*A. walkeri* only) and of *Poropanchax* (*Porop. macrophthalmus et al.*), when the sea was dried out, promotes the more recent event. Conversely, the western-stemmed genus *Epiplatys* (see further § 4.3.1), more opportunistic and better swimmer than *Aphyosemion*, has re-invaded partly the regions west and east of the epicontinental sea: the *spilargyreius* superspecies is represented in coastal Bénin and Nigeria and in the Sahelian regions to the east, the *bifasciatus* superspecies has exactly the same range. Indeed, the two events may be supplemental, not exclusive explanations, especially since they occurred during similar late periods (e.g. 5 MYA). Besides, an unusual dead-end accumulation of superspecies is observed today in the area of the present Niger delta (with in addition five endemic species in

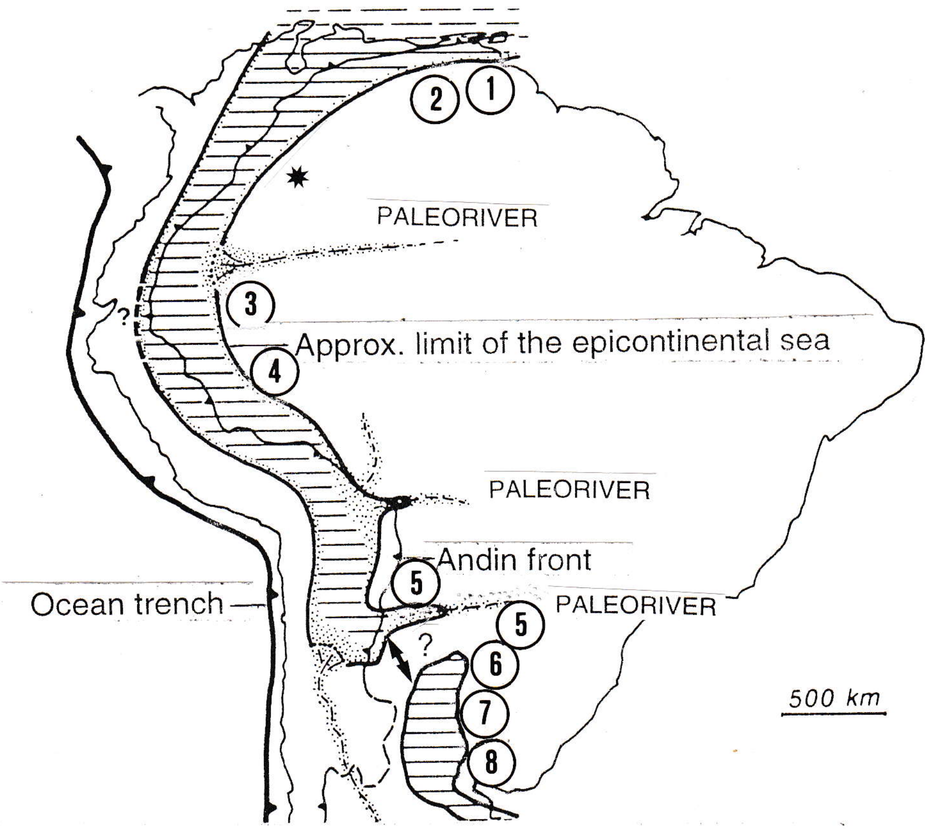


Fig. 10a. Paleogeographic reconstruction of western South America (70 MYA), showing the peculiar position of the Bolivian region at the southern tip of an elongated marine basin (horizontally hatched) connected to the open sea at the level of today Venezuela. Several large rivers, including the paleo-Amazon, were contributing clastics (dots) and freshwater to the basin. Aplocheilids collected near the basin: 1.*Austrofundulus-Rachovia*; 2. *Pterolebias zonatus* superspecies; 3. *Rivulus*; 4. *Pterolebias peruensis*; 5. *Trigonectes*; 6. *Simpsonichthys*; 7. *Neofundulus*; 8. *Cynolebias s.s.* (modified from Gayet *et al.*, 1993).

Fig. 10b. The epicontinental seas at their approximate maximum (60 MYA) in western Africa and South America (modified from Smith *et al.*, 1994).

Fundulopanchax, Paludopanchax, Epiplatys, Foerschichthys), after the sea has dried out since long.
- The northern South American sea which deeply introgressed the continent at the level of the lower Magdalena river. It was conspicuously available from 95 MYA (or earlier) to 37 MYA, with a variable size, and much less so, later, up to the Andes lift (45-20 MYA). Its maximum hypothetically corresponds to 60 MYA (about 1800 kms long, up to the present southern Bolivia, see also fig. 10a). This sea should be responsible for the colonization of the *Orestias* lineage which was later trapped in the Andes uplift and should be a paleo-migration route, along its coast, for the tropical Cyprinodonts (see further § 4.3.3, the implications for the supposed pattern of expansion of the non annual *Rivulus* and the annual *Pterolebias*). The absence of any annual Cyprinodont (*Rachovia, Austrofundulus*) west of it, up to the Pacific coast, and the poorer diversity of *Rivulus* species lineages (the *Vomerivulus* and the *Cynodonichthys* closely related lineages) west of it, may witness this barrier, although the land, west of it, is hypothesized to have been submersed occasionally. On the contrary, the fauna is richest to the north-east, in the Llanos and the lower Orinoco, with many sympatric annual Cyprinodonts (6 endemic species) and the opportunistic *Rivulus urophthalmus* superspecies.

- The southern South American sea which deeply introgressed at the level of the present La Plata and the Paraguay-Parana river mouth. It occurred recurrently (e.g. 60 MYA), but showed apparently a maximum much later (from 12 MYA to 10 MYA) and was also present during the last high sea levels (circa 5 MYA). However, no report yet has suggested a link between the two South American epicontinental seas (fig. 10a). This sea may explain, after its desiccation, the presence, still today of hypersaline lakes and of many more paleo-lakes (Clapperton, 1993a), west of it. The Cyprinodont species richness seems much lower where it was embedded. On the contrary, a very high diversity in the annual Cyprinodont fauna is seen in the peripheral regions where 6 sympatric superspecies have accumulated: the Uruguay coastal plain, east of it, the La Plata region in Argentina, south of it, and the mid Paraguay, north and west of it.

From these three cases, we hypothesize here that the epicontinental seas concerned more the primitive and annual Cyprinodont morphotypes and have had at least two major consequences:
- the older opening of migration routes along their coastal plains;
- the much later dead end accumulation of species, often rather primitive, very often annual, with a strong diversification, on their sides, once they were dried out, all the more that the sea retreat in two of them at least (La Plata and the Niger delta) is known to have been much greater than usual (see also further § 3.3, the ephemeral refugium as a supplemental explanation).

2.4- The huge interior freshwater "lakes".

Whereas the epicontinental seas are saline, the huge interior lakes are freshwaters. Africa and South America both witnessed (at the same time and on several occasions) the occurrence of the so-called huge interior lakes within their low-altitude largest river basins (Goldblatt, 1993).
The term "lake" is controversial and expert paleo-biogeographers are not in agreement concerning the continuity of waters and their limits. But the controversy is without interest for tropical Cyprinodonts, because no species that inhabits those regions, is lacustrine. What is important for the Cyprinodont distribution and speciation is to emphasize the alternance, in the concerned homogeneous regions, of periods of high, nearly continuous overflows of water during wet climates and of low fragmented waters and seldom suitable biotopes during dry climates (see also the refugium theory, § 3.3). One such "lake" is available in Africa -the Congo basin- and another in South America -the Amazon basin- with strikingly similar consequences regarding their interior and peripheral fauna distribution for Aplocheilids and Aplocheilichthyins. And also, striking differences.

Both regions are inhabited by specific superspecies which have not invaded deeply into neighboring regions. In the Congo, the *Aphyosemion elegans* superspecies, the *Epiplatys multifasciatus* superspecies, plus the forest annual, much less abundant group *Raddaella*. In the Amazon, the *Rivulus urophthalmus* and *ornatus* superspecies, plus the forest annual, much less abundant group, *Moema*. Within the basin, one can only observe a total mixture of genetically independent populations and of distinctive color patterns of the various components of the non annual superspecies, following the alternate conditions of the biotopes. Plus, the occasional, though rare, sympatric occurrence of components of the same superspecies, leading to a seemingly inextricable systematic puzzle. Whereas the distribution is back to normal allopatric vicariance of stable color patterns in the peripheral rising lands of the cuvettes (belts). In addition, both regions contain relict often dwarf endemic species. In the Congo, *Adamas formosus* (counterpart of *Aphyosemion*), *Aphyoplatys duboisi* (resp. of *Epiplatys*), *Hylopanchax stictopleuron* (resp. of *Hypsopanchax*), *Congopanchax myersi* and *brichardi* (resp. of *Poropanchax*). In the Amazon, *Rivulus* (*Anablepsoides*) *atratus* and *obscurus* (resp. of *Rivulus ornatus*), *Fluviphylax pygmaeus et al.* (resp. of Poeciliins). All these strange forms belonging to monotypic (sub)genera or to small species flocks are only found in these two basins and nowhere else. Their limits of distribution are probably associated with the greater extensions of these "lakes" and their forested periphery. However, these two regions are distinct by their position and by their link to the coastal plain:

- The Congo region is extended parallel to the coast, which means that its western highlands belonging to the plateau represent another lateral line. There, the Cyprinodont distribution of the plateau draws exceptionally a longitudinal band, as for the *Aphyosemion widekampi* superspecies. Besides, although the Congo cuvette was created in an ancient craton that was frequently invaded by the sea during the Mesozoic, it was subsequently isolated by a peripheral uplifting during the Pliocene (first huge lake theory: 5-6 MYA). Then, it was later (beginning of the Pleistocene, 2.3 MYA) captured by a coastal stream at the level of Kinshasa-Brazza to flow into the ocean (Lévêque, 1997) and establish its present coverage (4 million square kilometers). As a consequence, no poor swimmer Cyprinodont, like those of the *elegans* superspecies, has been capable to invade the coast (or the reverse). Whereas the other endemic lineages (and less poor swimmers) have, like *Epiplatys multifasciatus s.l.*, *Hypsopanchax zebra*, the *Poropanchax s.l.* lineage.

- The Amazon basin, on the contrary, is extended transversally (west-east) to the coast and the lower Amazon delta has always been present during the Quaternary (although its position varied quite a lot and it was dry during the L.G.M., see fig. 15). As a consequence, the Amazonian Cyprinodont superspecies have been able to migrate deeply into or from (depending on their actual origin, western or eastern, at the time of the paleo-Amazon, before the Andes uplift) the neighboring regions like the Guyanan shield, the upper Orinoco drainage in Venezuela. And no internal lateral distribution of Cyprinodonts is present in the plateau. Moreover, it should be stressed that the Amazon bed has historically been below sea level (Clapperton, 1993b). First, the main Amazon trunk is incised into the late Tertiary sediments for as much as 2000 km from its mouth, like the lower courses of its main tributaries. Second, the present bed level is at about 80-100 m below modern sea level, as far upstream as Manaus and this level is similar to that of the L.G.M. sea level, so that a specific "cone" was available at that time in place of the delta (fig. 15). Two consequences of this unique situation can be forwarded. During high sea levels periods, a deep introgression of salted waters may have indirectly disrupted the Cyprinodonts dynamics in the reclusive freshwater courses: for example, *Rivulus* is richly represented north of the Amazon, but poorly, south of it. Reciprocally, during low sea levels, a high fragmentation of freshwaters (if any) specifically produced large stagnant zones ("varzea" and finger lakes, termed "fluvial rias"), perennial for the annual fauna.

A third example of a huge lake, not controversial, is available in Africa -the Mega Tchad- but its history is completely different (Lévêque, 1997). It is situated in a dominantly dry area with savannas, although it was forested during the wet climate periods. In terms of Cyprinodont distribution, its expansion (up to 300 000 square kilometers with waters to the foot of the Ennedi-Tibesti) and its alternate regression (up to the present 25 000-10 000 square kilometers) have permitted the link between the eastern Nilotic, the southern Zaïrean and the western Guinean faunas, like a distributional platform. This is especially valid for Aplocheilichthyins of the *normani* superspecies (*Poropanchax*?) west and east, of the *loati-pfaffi* superspecies (*Micropanchax s.s.*) west, east and southeast and the *kingii* superspecies, somewhat deeper bodied, east and west. It is valid too for *Epiplatys* with the two, often sympatric, *spilargyreius* and *bifasciatus* superspecies and for *Zononothobranchius*, west, east and southeast. Conversely, the relict distribution of *Nothobranchius rubroreticulatus* in the present surroundings of the lake may witness its extinction, more distantly and the refugium status of the lake (in a generalized understanding, § 3.3) with a non complete desiccation. Two additional events have played a key role in the biogeography of the Tchad routes (Lévêque, 1997). Both broke the past link with the lower Nile drainage: The Jebel Mara eruption (see previous, the tectonic activity §1.2) and the regression and desiccation of the ancient Mayo Kebi River (in relation with the ancient Mesozoic Rift, fig. 3), which flowed from the Red Sea, southwestward into lake Tchad, the present Benoué river and finally the Niger delta (over 4 500 km) during 20 MYA (from mid-Eocene-30 or 40 MYA -to mid-Miocene-15 MYA). For Cyprinodonts, it explains why only the ancient lineage of the *loati-pfaffi* superspecies (Huber, 1998a) is present in the entire subsaharan region up to the lower Nile river in Egypt (*Mic. schoelleri*, now presumably extinct).

In total, these three "lakes" have all a role of faunal exchange platform for the tropical Cyprinodonts, but not in the same directions for the Old and the New Worlds: mainly south-north for the Congo (and west, when its outflow to the Ocean was secured), east-west for the Amazon, and southeast-northwest for the Tchad. This new hypothesis is supported by their so important characteristic of being flat lands, like the coastal plain (see further the putative migration routes, § 4.3.3).

2.5- The inland waters and the ephemeral dimension.

Whether they are present forest or savanna dwellers, tropical Cyprinodonts are very dependent on inland water masses, because all live in reclusive biotopes with shallow waters. This choice -or defensive deportation- of small bodies of waters is probably very old (i.e. at the Pangean level) because the temperate groups of Cyprinodonts are also characterized by shallow fresh or brackish waters. This is valid not only for the rather poor swimmers belonging to the Aplocheilids, but also for the better swimmers belonging to the Aplocheilichthyins. When the latter are found in larger bodies of waters, then they follow their edges and, in case of overflows, are much more abundant, in the neighboring flooded areas (Costa, 1996a in South America; Huber, 1998a in Africa).

These inland waters are highly uncertain, even if they are permanent for long periods. This is because several parts of a permanent slow-moving creek may rapidly become isolated from the rest and dry out within a few days (see accordingly, the jumping behavior, § 5.1.3 and fig. 17). A situation that has nothing to do with the large "stable" biotopes represented by the rivers hosting the standard ichtyofauna.

This level of uncertainty is increasing in stagnant permanent waters, up to the seasonal ephemeral waters that completely dry out once or twice in a year. Ephemeral waters are facts of life for Aplocheilids, for a long time. They have developed, in both the Old and the New Worlds, annual adaptations to survive (embryologic diapauses). We may even hypothesize here that the annual behavior, with its continuum dimension, preceded the continental drift, because:

- the morphomeristical data and the first molecular results, but not the osteological results, concur in placing the strict annual species in primitive positions, relatively to their own

phylogenetic lineage which encompasses non annuals;
- the tropical forest development is posterior to the savanna landscape (see further § 3.1) and annual species are found in both territories, with a much greater biodiversity in the savannas (see further § 4.3), which implies that they are relict in the present rain forests and their populations are today progressively segregated and then threatened.

However, this does not mean that strict annualism is a single shot event. As it has been shown by inducing artificial diapauses (Huber, 1992) and by the phylogenies obtained from the molecular analysis (Murphy & Collier, 1997) and by several marked monsoonal periods during the history of the Earth, the mechanism which produces annualism occurred on several occasions.

The past variations in the extension of freshwaters courses, following climatic fluctuations, explain in part the distribution of tropical Cyprinodonts, whenever they live in permanent or ephemeral waters. Satellite photos (Landsat) have disclosed that in slowly moving water courses, with either large or narrow beds, a dramatic increase of rainfall does not result in the increase of the speed of the water current or in an increased erosion of the bed, getting deeper. Instead, it results in an extension of the water course, which creates temporary overflows and links with other water courses near their sources or secondary arms. This very important phenomenon bears two major consequences for Old World and New World Cyprinodonts, of distinct time scale.

During the past history:
- wet periods have induced expansions of the water courses, through floods, in flat regions for temporary and permanent waters;
- dry periods have reciprocally shrunk water mass, sometimes to complete dryness. This purely means species extinction for Cyprinodonts, because they are unable to survive in large deep bodies of water (see further § 3.4). In consequence, the distribution of some groups appears to be disjunct, such as *Pituna*, with *stellifer* in Venezuela and *compacta/poranga* in Central Brasil (fig. 13a). Some species have in addition been trapped in closed systems with no or little water outflow (see further, the depression lakes, § 2.6).

Indeed, floods of shallow waters represent a key factor of extension and of survival for non annual and annual tropical Cyprinodonts. They provide the necessary continuity between permanent (and ephemeral) subsystems.

This correlates with the following three observations:
- first, the Cyprinodont fauna is homogeneous and uniform in the present Sahel, as a witness of the past forest coverage well into the Sahara (for example at 9 000 BP, see fig. 12). Six species are present all over, *Poropanchax normani*, *Micropanchax pfaffi*, *Epiplatys bifasciatus* and *Ep. spilargyreius*, together with the two annual species *Fundulosoma thierryi* and *Nothobranchius kiyawensis*. And, two of them, the components of *Epiplatys*, have been able to reach the lower Congo (Kinshasa), with little speciation contingencies, through the Tchad basin;
- second, annual species have been able to survive within the rainforest, with the availability of temporary water overflows among dominant permanent waters. In central western Africa, the taxon *Raddaella*, and in deep Amazonia, the taxon *Moema*, are strictly annuals. In Biafra, the *Aphyosemion gardneri* superspecies is a forest semi-annual, like the *Rivulus hartii* superspecies in the Guyanan shield;
- third, the typical floods, that occurred along the coastal line of western and eastern Africa and eastern South America, materialized by lagoons of freshwaters, are colonized by annual species of the taxa *Fundulopanchax*, *Paludopanchax*, *Campellolebias*, *Cynopoecilus*, etc., and by specialized Aplocheilichthyins (and Poeciliins). Respectively brackish lagoons are inhabited by *Aplocheilichthys spilauchen*, *Poropanchax scheeli* and *Pantanodon* sp. in Africa and, partly, by *Rivulus caudomarginatus/marmoratus*. This strengthens the single vicariant mode of speciation, along freshwaters overflows in flat lands or along the continuous line of coastal brackish lagoons.

Today, too, the monsoonal structure of climate, in Africa more than in South America, offers the alternance of permanent and temporary waters that are requisite for tropical Cyprinodonts dynamics. The fragility of their biotopes provides them with a protection against the standard ichthyofauna, which cannot invade for long these biotopes because of their inability to delay embryological development in damp or even dry conditions.

The major role of floods (or overflows) over flat lands in Cyprinodonts history is hypothesized here for the first time. It has important implications on migration patterns for annuals (see further, § 4.3.3) and is associated with the single rather effective barrier of the altitude. Another consequence is their link with the non forest ephemeral refugium (see further § 3.3).

2.6- The depression lakes.

The Rift valley lakes (fig. 6a) of eastern Africa are unique in that most are very old, with limited or no outflow and with a chaotic history. Some lakes are closed like today Malawi, Tanganyika, Victoria, Turkana, their water level being the balance between inflow and evaporation. Some are today very extended like Tanganyika (33000 square kilometers), Victoria (68500 square kilometers), Malawi (25000 square kilometers). All are situated at high altitude levels, between 400 m (Malawi, Turkana) and 1800 m (Nakuru, Naivasha). All are filled with alkaline waters (mean pH values between 8.1 and 9.5). Some are today shallow lakes, such as Turkana, Bangwelu, Georges, Chilwa, Chiuta, Nakuru, Naivasha and these lakes (like lake Tchad, Ngami, Bosumtwi..., far away) have suffered desiccation during dry periods (especially the last one L.G.M.). However, the presence of annual species in their surroundings (e.g. *Nothobranchius kirki*, near lake Chilwa; *N. rubroreticulatus*, near lake Tchad), and only there, suggests that some water remained whatever happened.
There are several other lakes with very high salt contents in water and no fish life.
From north to south: Turkana (over 20 MYA), Kyoga (over 10 MYA), Albert/ Mobutu (over 20 MYA), Edouard/ Rutanzige (less than 5 MYA), Kivu (over 5 MYA), Tanganyika (over 20 MYA), Mweru (over 5 MYA) and Malawi (over 20 MYA), plus some smaller lakes such as Baringo, Nakuru, Naivasha, Rukwa.

The homogeneous climatic and heterogeneous tectonic histories of these lakes have induced a complex pattern of distribution for the available Cyprinodonts, belonging to Aplocheilichthyins, the rare Aplocheilins being restricted to temporary marshes outside the lakes (*Nothobranchius* sp.).
- First, the water levels have varied considerably according to the wet and dry periods. For example, Tanganyika started as a large area of shallow marshes (the proto-lake), then changed into small independent lakes (12 MYA), rivers shallow depressions (5 MYA), one single large lake (2 MYA), three discrete lakes with a 600 m drop in water level (relative to today) from 200 000 BP to 40 000 BP, with only a 150 m relative lesser level at 35 000 BP, or 300 m at 15 000 BP (L.G.M.) and finally the present situation since 12 000 BP (H.C.O.). This explains that two species, highly specialized, have been trapped into two of them and become endemics: the lithophylous *Lamprichthys tanganicanus*, with no significant morphologic variability over 600 kms and the plankton-feeding, pelagic *Laciris pelagicus* in lake Edouard deep waters. However, this does not say why no similar endemics are present in the other lakes, outside their shores and tributaries, since similar rising and falling waters have occurred too in some of them with steep slopes and deep waters.
- Second, the interconnection between these lakes has varied considerably. During the last wet period (H.C.O.), Turkana, Rukwa and Victoria were connected and flowed into the Nilo-Sudan drainage (Lévêque, 1997). This explains that some relict species of these lakes are related to that ichthyofauna: *Micropanchax loati* in Victoria and the river Nile, *Mic. fuelleborni* in Rukwa and *Mic. jeanneli* in Turkana. Besides, Victoria was connected to Edouard via the Katonga valley from 60 000 BP to 30 000 BP. Today, the interconnection concerns also Edouard, Albert, Kyoga which explains the later colonization of all by *bukobanus*, a component of the *Cynopanchax* lineage and by *vitschumbaensis/kassenjiensis* belonging to another superspecies (Huber, 1998a). Thus, the sympatry of these three phylogenetic

lineages. Kivu used to be connected with Edouard by the Rutshuru river which has been cut by lava produced by the Kironga volcano, but today it is linked with Tanganyika by the Ruzizi river. No Cyprinodont has been collected yet in Kivu (also close to a refugium, see further § 3.3.3), but the third typical Rift lineage of Aplocheilichtyin, more southern, is present with *pumilus*, in Tanganyika and the Ruzizi river. Besides, the fourth lineage, also southern, is present in Malawi (*johnstoni*) and in Mweru (*moeruensis*) and also in Rukwa (*matthesi*), due to the interconnection with Malawi, via the Rukwa overflow (Huber, 1998a). Finally two cases affected by the Rift tectonics can be suggested. First, *Hypsopanchax*, distributed all over the Congo cuvette, has been trapped in part in lakes Edouard and George: *Hypso. deprimozi* has been endemic to their western slopes since the elevation of the western wall of the depression. It has been synonymized with the very similar *Hypso. modestus*, from the upper Ituri river, northeastern Zaïre (i.e. west of the Rift). Since the separation of the two series of populations occurred a long time ago, this should be confirmed by genetic experiments. Second, the species "*Micropanchax*" *hutereaui* which should be present in fold belt regions, upstream the Congo river has suffered from the Rift disruption and is replaced by sister species easterly: its distribution is disjunct, in the north and in the south only.

Even if the Rift lakes are unique and no corresponding counterpart is to be found in tropical South America, it is tempting to regard the Andean depression lakes as an homologous situation. Lake Titicaca and surrounding lesser lakes are trapped at a very high altitude (4000 m). There, the Cyprinodont fauna belongs to the temperate lineage of Cyprinodontins with a single genus, *Orestias*, showing an explosive differentiation rate in morphology, like the many Cichlid lacustrine flocks in the Rift lakes. This implies that the dominant Cyprinodont dwellers of the African Rift lakes, the Aplocheilichthyins, were unable to develop morphological diversifying strategies over many distinct subniches, like *Orestias* (and their cousins *Aphanius* in Turkish lakes and *Cyprinodon* in North America, or, in lake Chichancanab of Mexico). Another explanation is that maybe the Rift Cichlids were already dominant in these lakes when the reclusive Aplocheilichthyins managed to enter from their surroundings. It is purely theoretical to consider the case in South America, since the drastic cold conditions in Titicaca and its marine origin (see § 2.3) before the Andes uplift, rule out the co-presence of tropical Cyprinodonts or have enforced their extinction.

3- The past climatic variations and their impact on terrestrial flora.

3.1- The forest development and its coverage as a faunal border.

3.1.1- The rain forest development.

The history of the rain forest coverage is represented by the progressive decline of the Gymnosperms (ferns) and their partial replacement by the Angiosperms, since their appearance, 120 MYA (Maley, 1996b).

Angiosperm actually began to dominate the Gymnosperms, only adapted to hot aridity, from 90 MYA, with the progressive change in global climate in the splitting Gondwana (induced by the ocean opened by the drift). Angiosperm abundance and diversity increased explosively during the pre-paleoforest construction (80-70 MYA), but this resulted in small trees and shrubs. Multistratal rain forest is in its infancy. The next 10 million years witness its expansion (e.g. in Africa, fig. 11, in relation to the paleo-equator). The peak of Angiosperm closed forest is estimated at the early Eocene (53 MYA), when very wet conditions promoted rain forest as far north as present 30°N of latitude. Africa and America were largely forested, except in their most southern parts (e.g. the Kalahari sands, then up to the present Congo), benefitting from their island conditions (e.g. the north African Channel, within the warm Tethys sea, fig. 10b). Tropical Cyprinodonts were probably at the maximum of their welfare, then. The large rain forest, as today, with the present floral genera, is hypothesized from the mid Eocene (45 MYA), which should be an important period for expansion and diversification of tropical Cyprinodonts ancestors. In total, a very long process (over 60 Million years) and a striking difference with the short term major disruptions of the Quaternary.

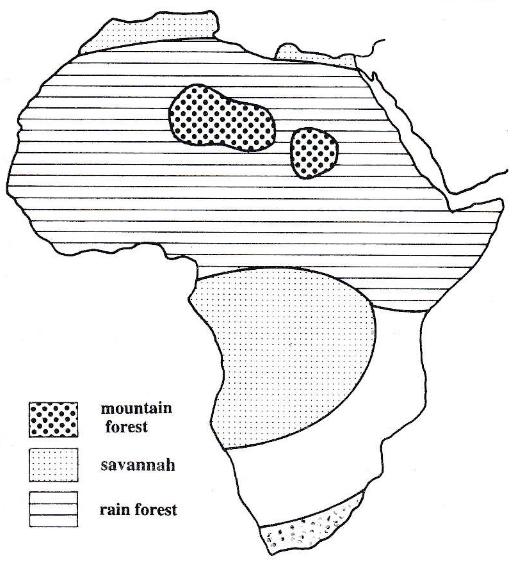


Fig. 11. Distribution of the main floras in Africa, during the wet period of circa 60 MYA. The equator is further north than today. The rain forests have developed along the northern coast (Bonnefille, 1993 in Lévêque 1997).

The comparison of the wet tropical flora between the Old and the New Worlds shows a marked impoverishment of Africa, probably due to the more severe arid conditions that endured that continent (Maley, 1996b) and to its northern drift, ended by the closure of the Tethys sea. The main stages of this impoverishment is associated with the Cretaceous Tertiary (C/T) boundary (circa 65 MYA), the end of Eocene (30 MYA), the end of the Miocene (7-9 MYA), the end of the Pliocene (2.5 MYA), which must have affected the African Cyprinodonts. A marked difference in the floral composition is also observed between the Old and New Worlds (Goldblatt, 1993): for example, white Palms declined considerably in Africa in the course of the Tertiary (65-2.5 MYA), whereas they have persisted in large numbers in South America (Maley, 1996b).

This fact must not be overlooked in the comparison of the Cyprinodont faunas characteristics between the Old and the New Worlds. During over 50 MYA (from circa 65 to 14 MYA), the biotopes and especially the waters of the forest Cyprinodonts have been influenced by distinct pollens, plus many other floral materials, fallen from the vegetation above. If it is accepted that most local factors are not discriminant between Africa and South America, e.g. soils, then this specificity in flora may be a key dimension into the differentiation of these fishes. In addition, over time, the southern move of the equator line in Africa must have had consequences over the climate and over Cyprinodonts dynamics.

Finally, near the sea, the mangrovian plant, *Rhizophora*, appears in coastal western Africa (e.g. in Gabon) during the Miocene and it can be hypothesized that the history of *Aplocheilichthys spilauchen* is associated to its expansion.

3.1.2- The forest and non forest, as faunal borders (fig. 12, 13a, 13b).

The present coverage of primary rain forest, and conversely of drier savanna, for those groups of tropical Cyprinodonts bound to each, has been proposed to be the most important factors of general and local distributions and speciation (Clausen, 1967). This is equally documented in both the Old and the New Worlds. For example the *Aphyosemion* distribution is included within the regions of at least 1600 mm rainfall per year (Lévêque, 1997).

Traditionally, tropical Cyprinodonts, both from the Old and New Worlds, have been allocated to two biological groups, the forest and the savanna bound groups:

- To strict forest adaptative forms belonged the following taxa: *Aphyosemion, Rivulus, Procatopus, Poropanchax, Hylopanchax* and *Plataplochilus* in non annuals. These fishes were hypothesized to be dependent on the forest shelter.

Today, central western Africa including the Congolese cuvette, Guinean Africa, Amazonian America including the upper Orinoco and the Guyanan shield, and coastal fringes (fig. 12) are covered by forests;

- To savanna adaptative forms belonged the annual taxa, as *Nothobranchius s.l., Cynolebias s.l.* Today, eastern and southern Africa, northern Venezuela and Colombia (Llanos), central Brasil and the Chaco in Bolivia-Paraguay-Argentina are characteristic savannas (fig 13a).

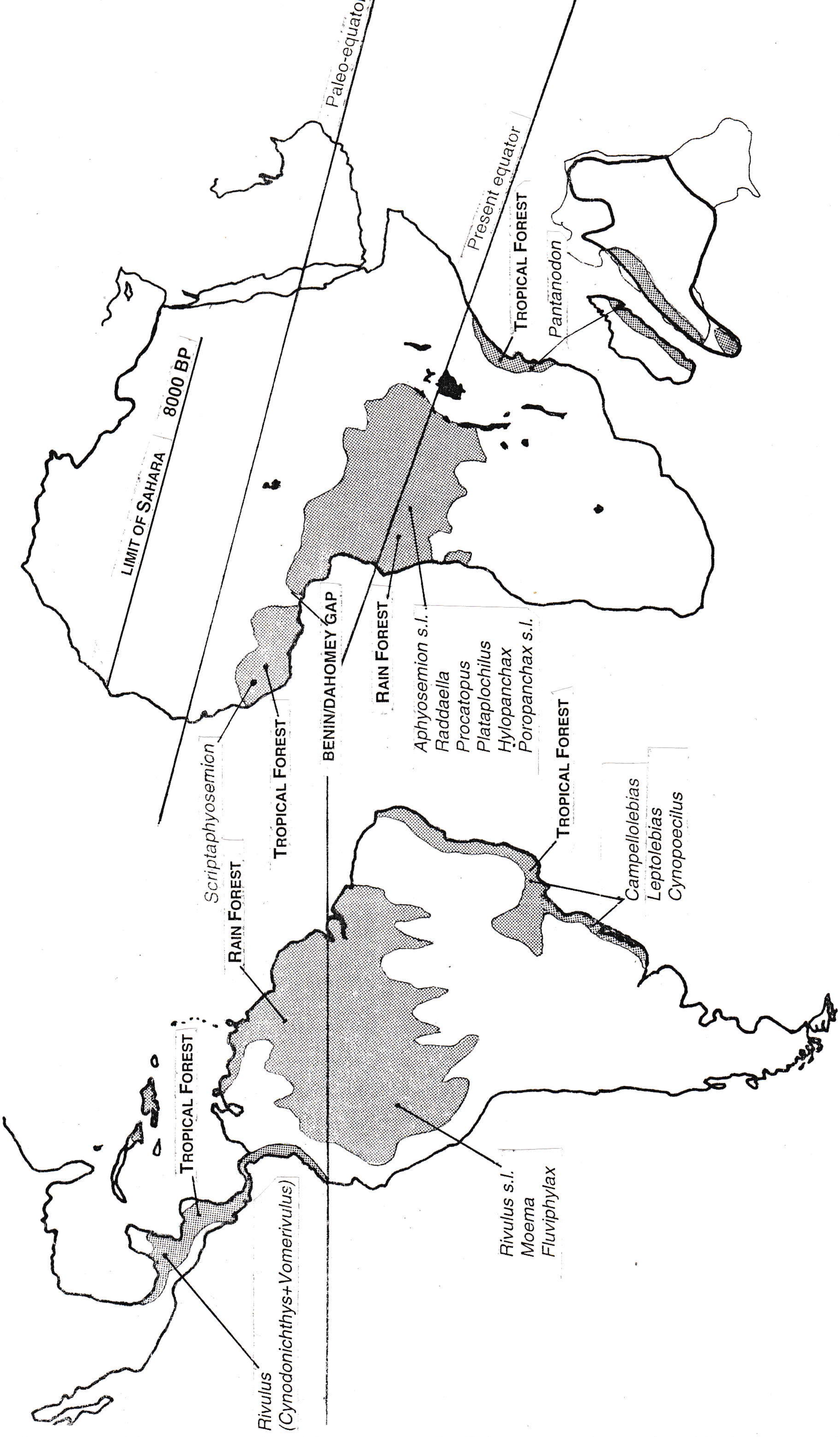


Fig. 12. Paleogeographic reconstruction (circa 80 MYA) of the area under study with the present limit of the forest coverage. The northern limit of forest coverage at 8000 BP is given by a line, as the African Paleo-equator (original drawing by Chauche).

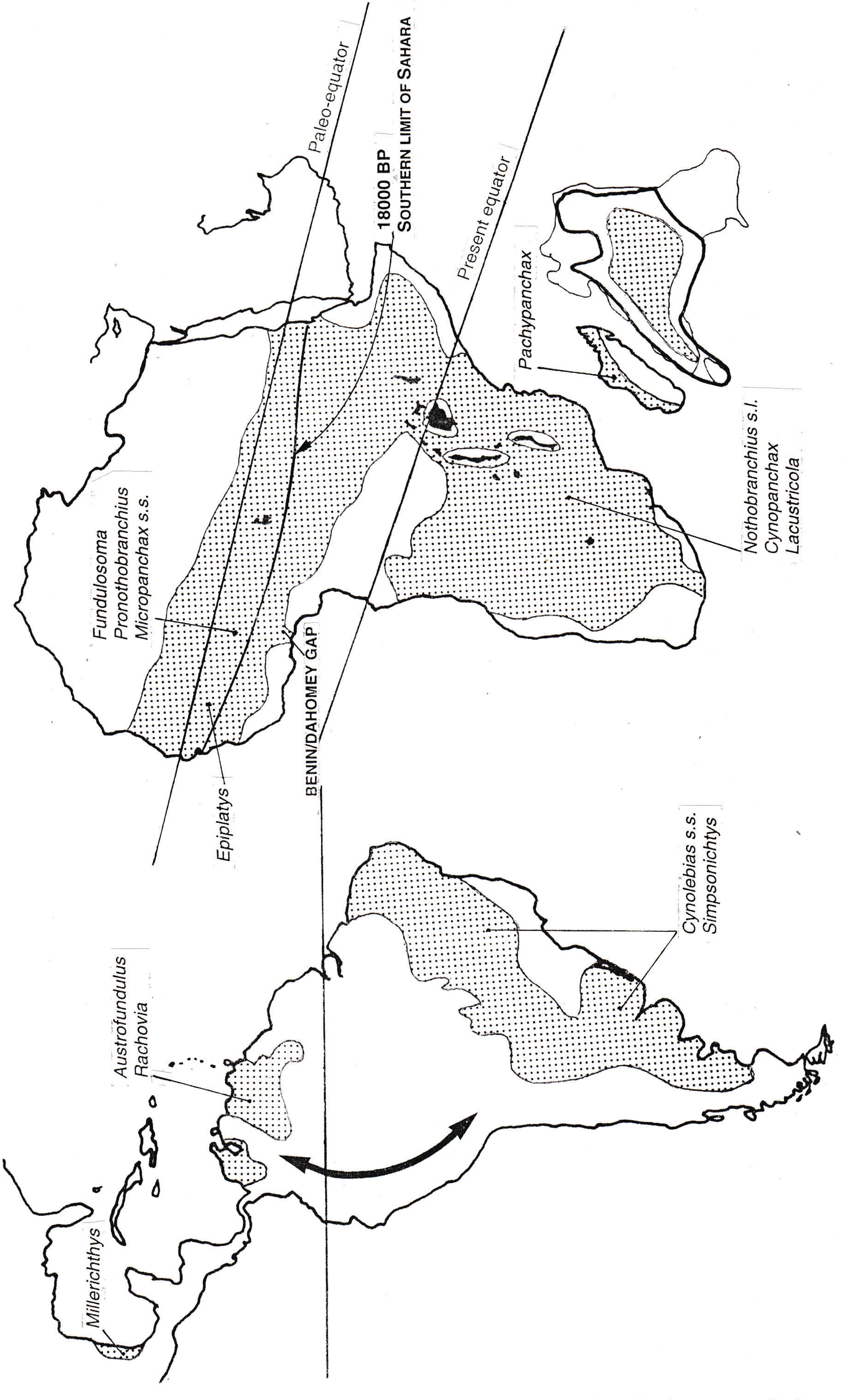


Fig. 13a. Paleogeographic reconstruction (circa 80 MYA) of the area under study with the present limit of the savanna coverage. The southern limit of Sahara at 18 000 BP is given by a line, as the African Paleo-equator (original drawing by Chauche).

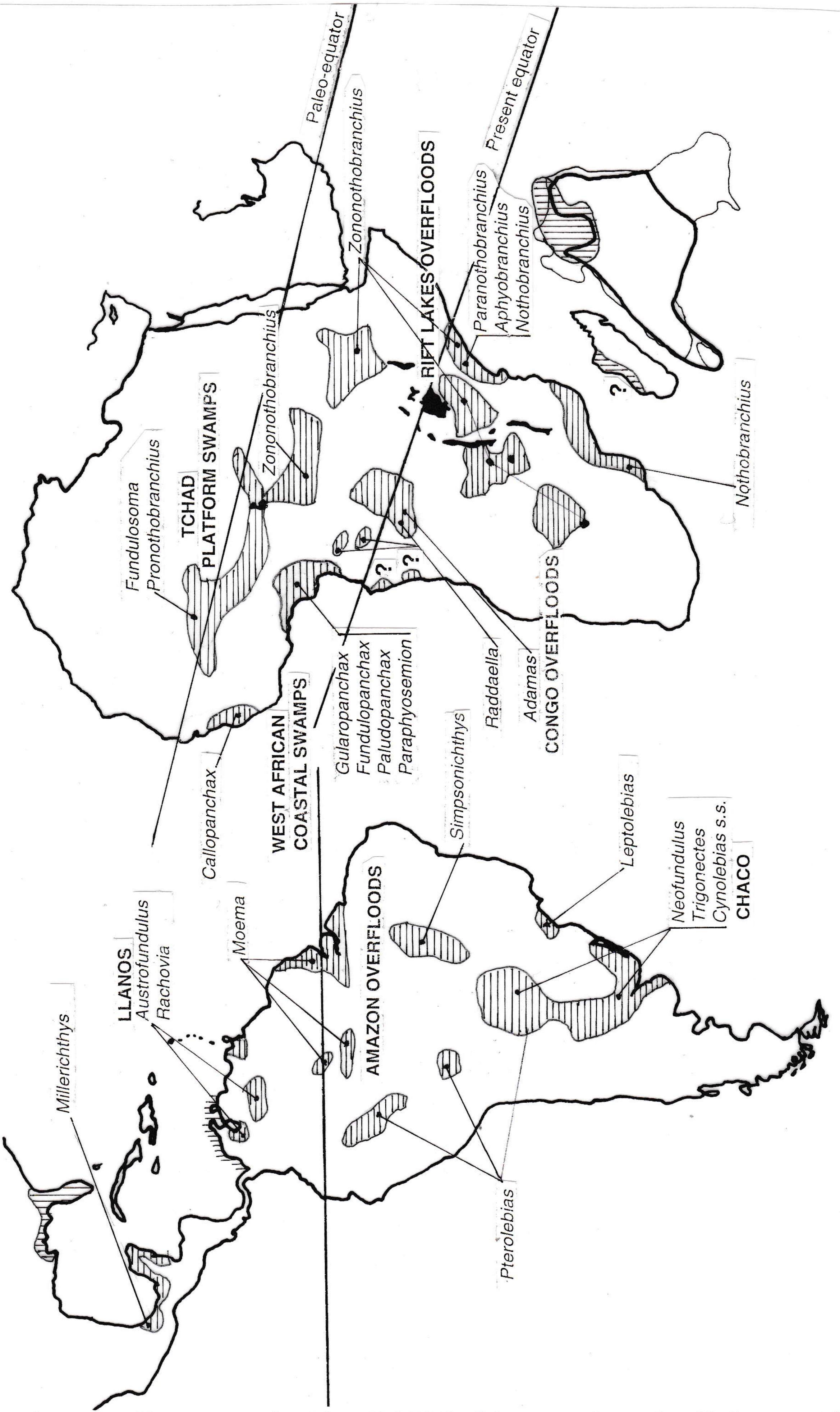


Fig. 13b. Paleogeographic reconstruction (circa 80 MYA) of the area under study with the present limit of the ephemeral biotopes. Major brackish regions are also drawn (vertical lines) (original drawing by Chauche).

However, a more detailed analysis reveals that counter-examples are numerous and that this interesting hypothesis is biassed by the present situation and only explains parts of the reality. This is sustained by the following arguments:

- the distribution of *Aphyosemion* in Africa and *Rivulus* in America (Huber, 1992) is not strictly superimposed with the present forest coverage and border. Exceptions, like *A. bualanum* in northern Cameroun, *A. rectogoense, A. schioetzi* in the sandy Batéké plateau of Congo, *A. nigerianum* in the dry Jos Plateau of Nigeria, *Riv. gransabanae* in the dry plateau of Venezuela, the single *Rivulus punctatus* superspecies in central Brasil witness some adaptability of the said forest-bound Cyprinodonts; similarly, present forest species are also collected in very old savanna pockets, as A. *lamberti* in the Booué area;
- the forest-bound components are in fact restricted to the primary forest maximum limit of the last wet period and became extinct or recessive in the today derived savanna or gallery forests;
- some non annual genera, as *Epiplatys, Hypsopanchax* and *Micropanchax s.l.*, are more opportunistic, since their today distributions are superimposed with the largest expansion of the past forest and some micro-populations are still surviving isolated in very dry regions, like *Ep. spilargyreius* in the Tibesti. Strict savanna adaptative forms are not properly known in tropical Cyprinodonts, even in the non annual Aplocheilichthyins, which thrive in gallery forests. Notably, the presently Sahelian *Micropanchax* species have developed and expanded during past pluvial times.
- for annuals, the driving force is the availability of the necessary ephemeral biotopes made of marshy and temporary bodies of water, not the savanna or the present lack of forest (fig. 13b);
- annual forms, although dominantly present in today savanna landscapes, are widely present in primary forests, even in their parts with little seasonality in both the Old and New World (*Raddaella* sp., *Moema* sp.); the annual taxa related to *Rivulus*, e.g. *Pterolebias, Pituna*, which follow the north-south western forest belt of the Amazon, are less strict savanna dwellers;
- the alternate regions between the two historical core categories, colonized variably by forest (wet periods) or savanna (dry periods) represent ubiquitous examples, such as the Dahomey-Bénin Gap in west Africa, the Tchad basin, the western Amazonian belt; they may represent exchange platforms, that witness present disjunct distributions as for *Aphyosemion s.l., Nothobranchius s.l., Pterolebias/Pituna* respectively;
- phylogenetic groups are not congruent with the present forest coverage, as for example the related *Epiplatys, Callopanchax, Scriptaphyosemion*, with distinct adaptation to coverage;

We hypothesize here for the first time that:

- the present coverage of rain forest provides with an incomplete explanation to the distribution of the strictly forest-bound groups; rather, the present situation is recessive of a much wider coverage at the peak of the Holocene wet climate (H.C.O.);
- the present coverage of the savanna rather features a less strictly bound forest coverage for non annual tropical Cyprinodonts: the distribution of *Epiplatys*, for example, encompasses what is understood to have been the widest recent forest coverage (maybe older than the H.C.O.). Remains of this past wealth, as in the Sahel or the Tibesti populations, just witness a better resistance to drying conditions than their *Aphyosemion* relatives, but the situation is recessive, too (*Epiplatys* is then not adaptative to savanna);
- the present distribution of all extant non annual groups should be better looked at by following the past forest borders, not the present one;
- conversely, annual groups should not be interpreted as savanna dwellers; rather, they inhabit ephemeral biotopes, i.e. seasonal waters over clay water-proof soils which dries out periodically. Their distribution which can match present savanna (mostly) and present forest (occasionally) rather witnesses a much larger coverage of ephemeral biotopes of an old past. These ephemeral biotopes, which may have existed prior to the forest coverage are hence labelled here "non forest" and are more often associated to overflows of large bodies of water;

- the maintained combination, over time, of these ephemeral biotopes with their possible expansion, during wet past periods, and of a quasi-permanent drier landscape (and muddy waters) are the actual keys for species richness of most annual fishes;
- the present forest-savanna duality should be replaced by a past forest-non forest duality; hence, the maximum past distributions of the forest and non forest groups are similar and mostly superimposed in Aplocheilids, with the exceptions of the Indian coastal plain of Africa, of Asia and of the Rio Paraguay delta in South America (for unknown reasons);
- the present distribution of forest and non forest groups is the result of the complex history of these environments (e.g. the past distribution of non forest is unknown);
- the availability of protected reclusive waters is much more important for tropical Cyprinodonts than the presence of coverage. Man's organized habitats more than modern deforestation have then fatal consequences on these fishes.

Understandably, forest and non forest environments are expanding inversally. But the tropical Cyprinodont groups bound to each show a remarkable adaptability to adverse changes. Two examples can be proposed: first, as already mentioned, the labile character of the annual embryological development (see previous, the ephemeral dimension § 2.5), second the nested position of some annual groups within non annual branches of phylogenetic trees.

Ultimately, it appears that this duality between forest and non-forest Cyprinodonts is more practical than comprehensive: the common denominator is the reclusive character of all biotopes. The various types of the egg membrane and the various schemes of diapauses, which both end up in a continuum of states from non annual to annual forms (pers. observations; Seegers, 1985; Zee & Wildekamp, 1995; Wourms, 1972) confirm the lability of the mechanism of annualism, in line with this continuum in biotope characteristics and with the variable availability of the seasonal biotopes or the fragility of parts of the permanent biotopes.

3.2- The forest-non forest reciprocal variations along climatic fluctuations.

The history of the general climate in the Tropics is presently understood to have followed two opposite schematic patterns.
First, a globally warmer period (with higher sea levels) is hypothesized from the unique Gondwana continent of the Jurassic to the Paleocene (60-65 MYA, fig. 11), after the drift, with a low gradient all over the Earth. Near the paleo-equator and in low latitude regions, monsoonal dry climate is supposed to have been dominant, even very dry and hot in the center of the pre-divided Gondwana (which is now the heart of the rain forest). This is in line with an hypothesized very old initial appearance of annualism in Cyprinodonts.
Second, a globally less warm period (with a general trend to declining sea levels) is hypothesized after. This corresponds with the initial development of the forest coverage. This second period can in turn be divided into two subperiods, a relatively stable period up to the mid Miocene (10-15 MYA) and a growingly unstable period, afterwards and especially from the end of the Tertiary (2.5 MYA), with high gradients all over the Earth. The second sub-period is hypothesized to have been induced by two factors. On the one hand, the further development of the glacial Antarctic pole (15 MYA with previous maximums during Oligocene, 30 MYA, and Miocene), then the initial development of the glacial Arctic pole (6 MYA). On the other hand, the strong difference in thermal gradient between the equator and each pole, and the mean temperature difference -11°C, yearly- between the two hemispheres (Maley, 1996b).
However, as already mentioned, the thermal gradient between the two hemispheres has occurred since the initial development of an ice cap in Antarctic, during the Oligocene (30 MYA) and this has resulted in the creation of monsoons and seasonal biotopes, then of another (among others, unknown) hypothesized phase of annualism among Cyprinodonts.
The impact of the northern drift of Africa, i.e. a southern move of tropical climate, was

compensated, though, by the antagonistic effect of monsoon and their northern rains (Maley, 1996b).

Parallel and synchronically to the climatic oscillations following water mass and rain variations, the terrestrial flora has varied in composition and in extension. Yearly rain supports dense forest when total amount is above 2000 mm, semi-deciduous forest, savanna woodland or bushy savanna, according to local factors, between 2000 mm and 1500 mm, bushy savanna and grassland, below 1500 mm, in the Tropics (Bush, 1994). Consequently, two types of forests have been available, for a long time, according to altitude: the lowland rain forest and the mountainous deciduous forest (see the refugium theory, § 3.3). On the contrary, savannas are characterized by herbs, mainly from the family Graminae (except along the bodies of water: gallery forest).
Modern lowland forest currently extends to 800 m altitude. A mean decrease of 4°C (or even 5°C) in air temperature is thought to induce lowland deforestation of about 800-900 m. Even if the eustatic level of the sea could reach 120 m below present during glaciation maximums, this is consistent with the disappearance of forest, except in rare coastal pockets or in places with some water inflow (e.g. deltas). Conversely, a mean decrease of 7-8°C in mountains led to the downwards migration of montane forests by 1400-1500 m (see further the lowland and the montane refugia, § 3.3).

The study of pollens contained in paleo-deposits by palynologists, from carrots taken from lakes, in volcanic mountains or off-shore, have provided many useful and detailed information on the past flora extension (e.g. Haffer, 1993; Maley, 1991, 1996b; Maley *et al.* 1990). Such as:
- the climatic oscillations of the Quaternary (and with a lower amplitude of prior periods) are cyclical, recurrent events;
- the climatic oscillations locally induce similar consequences, due to the fact that the geomorphological condition remained the same from the late Miocene;
- the two major glacial periods occurred between circa 24 000 BP and 12 000 BP and between 160 000 BP and 130 000 BP;
- the two warmest and wettest periods occurred between circa 13 000 BP and 3 000 BP and between 128 000 BP and 118 000 BP, with a similar duration of 10 000 years each;
- the maximum extension of forest since 800 000 BP in Africa corresponds to lake Victoria to the east (not taking into account the Indian coast) and in South America to the central Brasilian plateau;
- the phase of maximum fragmentation of forest and of maximum extension of forest concern only 5-10% of the period from 800 000 BP, each; the remaining 80-90% of time relates to intermediate status with less extreme oscillations.

Besides, the recurrency of climatic events does not mean identical consequences, due to a memory effect of the previous events, even if this effect was much reduced in the case of the severe L.G.M.- on the floral composition and on the destiny of the Cyprinodont fauna within the most stressed regions.

Dozens of similar palynologic studies and results have been published from various parts of Africa and South America, which confirm the parallel -but not identical- evolutions of the situation in both continents.
For example, during the last Quaternary period of the African Rift lake Edouard (alt. 900 m) the oscillations in climate have induced the following variation in flora:
- from 29 900 BP to 25 350 BP, cool and dry climate creates a mountain forest;
- from 25 350 BP to 14 700 BP, even drier (very arid) climate reduces flora to terrestrial herbs and swamp plants; then, the lake is restricted to shallow marshy pools;
- from 14 460 BP to 12 530 BP, a wet climate promotes the progressive re-installment of the lowland forest, but the montane forest remains dominant;
- from 12 530 BP to 2 920 BP, a slightly wetter climate induces the full extension of the primary forest with a maximum at 9 000 BP (H.C.O.).

These climatic variations have generally had a major impact on forest coverage and on the possible expansion of forest dwellers. During the warmest and wettest periods, present dry regions were quite humid and completely or partly forested (fig. 13a).
As in Africa:
- the Sahara belt (except in its northern regions);
- the so-called Bénin/Dahomey gap;
- the Mayombe and Batéké hills of southern Congo;
- the northern Cameroun and neighboring Centrafrique;
- the lake Tchad surroundings.

And in South America:
- the Bolivian, Paraguayan and Argentinan western Chaco;
- the central Venezuelian Llanos;
- the Brasilian Sertao.

Several non annual Cyprinodonts were probably present in these today very dry regions, like the Sahara, as extension of the neighboring fauna (e.g. *Epiplatys, Micropanchax*) and most have now become extinct. But, because this phenomenon occurred at the margins of the distribution of tropical Cyprinodonts, and for a relatively short while, it had a limited impact on speciation. Indeed, the analysis of the distribution and of the diversity of the Cyprinodonts in these territories reveals that non annual Cyprinodonts are not endemics there. The major driving force lies within the forest itself of dry periods... or in the perennial survival of ephemeral biotopes for annuals: this is hereafter detailed as the generalized refugium theory.

3.3- The generalized refugium theory and the fragmented forest of glacial times.

3.3.1- The refugium theory: historical and extended dimensions.

The forest coverage has long appeared a critical determinant for a large variety of animals, which are dependent on its characteristics: shade, more constant temperature and humidity levels of air and consequently of freshwaters. Haffer (1969) is attributed to have been the first to theorize this observation and its consequences to the fauna distribution and speciation, for Amazonian forest birds. However, this theory, termed as the refugium theory, did not start to widespread before 1982 when Prance's book (op. cit.) was in part dedicated to it: today the concept of the theory is finding a growing consensus. It is studied in many faunal (e.g. various birds, Nymphalid butterflies, some lizards, some amphibians, scorpions, stingless bees) and floral groups (e.g. *Begonia*, Angiosperms).
The refugium theory "proposes that vegetational changes following climatic reversals during any period of the earth's history cause the fragmentation of species ranges and the isolation of a portion of the respective biotas in ecological refugia, where species populations, either become extinct, or survive unchanged, or differentiate to the level of the species or subspecies, with genetic and/or morphological variations" (Haffer in Prance, 1982). During the corresponding warmer and wetter periods (i.e. interglacials), forest regained previously lost ground, but probably not to the identical.

The evidence of a refugium should be derived from five different and independent sets of data on the physical environment: topography, paleoclimate, geomorphology, soils and vegetation structure (Whitmore & Prance, 1987). Animal endemicity does not make a priori a refugium, but a posteriori confirms one, when areas are superimposed (i.e. when biogeography fits).

For forest bound animals, these refugia areas -or enclaves, or species "islands"- are presently characterized by endemic faunas (centers of endemicity) and often in addition by a high rate of speciation (centers of diversity). However, a refugium is not an "island" of stability, but instead an island of concentration and survival, for fishes like tropical

Cyprinodonts, both annuals and non annuals (see further, the generalized sympatry, § 4.5 and the neutralist behavior). This is not either an "island" of exclusion, the present sympatric occurence of up to 5 congeners supports this, together with the similar today persistance of forest plants from the Eocene, Oligocene and Miocene in the same place.

The refugium has been subsequently better defined by practical climatic and altitudinal specifications (Maley, 1987, 1991, 1996a,b; Maley *et al.*, 1990).
Cooler weather was characterized by strong stratiformes blankets of clouds with limited sun radiation and poor potential rains, which allowed the maintenance of a high degree of humidity, with two possible intricated and simultaneous consequences during peak glacial maximums:
- in permanent forests of lowlands (and of inland rising plateau), as in central western Africa including the Congolese cuvette, as in the Guyana Shield and the Amazon and its belts, a fragmentation into independent compartments, up to the restriction to galleries along large rivers or a shrinkage in certain pockets, e.g. near the sea, where on-shore winds could still bring some rains;
- in foothills of high mountains, the persistence and the downward expansion, with more rainfalls, of montane deciduous trees and herbaceous flora as near the Rift or the Andes.

Indeed, there is a remarkable correlation between the postulated refugia and the present yearly rain record of over 2000 mm, not far from the foothills of highlands, in South America (Bush, 1994). However, short term local climate is very difficult to appraise in the past. This may be illustrated by the present complexity of predicting Amazonian rainfall: during the last El Nino event of 1982/83, northeastern Brasil experienced terrible droughts, whereas Ecuador and northwestern Peru experienced record rainfalls and no dry season (Bush, 1994).

Forest dwellers are then isolated in these relict forest zones, termed as refugia in a broader (and more relative) sense, which are much more numerous, but smaller, than in the original, more biological meaning. They should also be more difficult to characterize by palynologists, because of their less ultimate status and their more scattered localizations.

The materialization of the concept in precisely delineated refugia zones has been somewhat controversial in the restricted sense, because of insufficient data (e.g. sampling artefacts in Amazonian plants, Nelson *et al.*, 1990), of non quality data, of contrary observations (e.g. the evidence of forest alterations, even in refugia, as per Colinvaux, 1989; Colinvaux *et al.*, 1989), of a possible deviation in the localization of refugia and the coastal core areas of endemicity for some fauna (Hamilton & Taylor, 1991), of a possible amalgamation between endemicity and species diversity, of the not always superposition of the endemicity for various faunas and floras.

The refugium concept is indeed intellectually attractive and, as such, as led to hasty generalizations and/or to misinterpretations (Haffer, 1993). In addition, it is impossible in practice to determine very small refugia (i.e. the "mini-refugia"), where an extant endemic fauna is or will be disclosed, simply because of the field and logistic difficulties in the Tropics. It may face much less ambiguity in its broader sense, especially for the coastal refugia, knowing the facts that the coast line, during the L.G.M., was about 120 m below (with shore rains being captured by the gradient) and 30-40 km off the present line, and also if the concept is not requested to explain every cases. Besides, future studies should aim to better correlate refugia and fossil records, and refugia and species richness and endemicity (Whitmore & Prance, 1987). Anyhow, it is not our intention to take part into the controversy but to bring data that fits -or not- with the concept.

The refugium theory is applied here for the first time to tropical Cyprinodonts and generalized to the ephemeral non-forest biotopes. The reclusive biotopes of shallow waters

of these fishes have been adversely affected by the climatic reversals. And five important observations strengthen the concept:
- even during better and wetter periods, like today, tropical Cyprinodonts are recorded in these vulnerable places and never outside of them;
- the fragmented forest or non-forest correlates well with the enormous genotypic plasticity, unlike the standard ichthyofauna (see further, § 7.4);
- the maintenance, even during the dry maximums, of relict vulnerable biotopes is the sole explanation for the non complete extinction of these fishes, either annual or non annual;
- the extension models of these fishes from their putative centers of origin, either in strates or patches, is congruent with the concept of refugium;
- the two types of refugia, in lowlands and at the foothills of highlands, is congruent with the two types of endemic species in tropical Cyprinodonts.

Many refugia delineations fit remarkably with the Cyprinodont distribution of endemic forms and with the higher diversity of species, in both the Old and New Worlds. Exceptions are rare. They may be due to insufficient collection data, or to undisclosed refugia, or, why not, to other explanations. For example, the survival of some tropical Cyprinodonts may have been insured by their specialized choice for a niche, such as brackish lagoons (*Aplocheilichthys, Pantanodon*) or even marine reefs (*Rivulus marmoratus* and some viviparous Cyprinodonts) which performed as refugia. In addition, there are several examples of primitive (by external morphology) deeper-bodied Cyprinodonts, confined to the highlands described in the extended dimension of the theory. These species are related to more derived lowland forms: *Aphyosemion bamilekorum* in Cameroun (Bamiléké plateau), *Rivulus magdalenae* in Colombia (upper Magdalena basin), *Riv. hildebrandi* in Panama, *Riv. corpulentus* in Colombia, as survivors of relict montane forest of past dry periods.

Major criticism of the refugium concept has concentrated on Amazonia and recent analysis (Clapperton, 1993b, fig. 15; Hammen & Absy, 1994; Bush, 1994) favors that:
- the western Amazon basin may have stayed as forest, continuously during L.G.M.;
- fragmented forest was the rule in the central Amazonian cuvette;
- refugia could only be located in the flanks of uplands close to northern, southern belts. In that case, the postulated independant refugia of the upper Amazon would be replaced by a very extended region of permanent forest. The rare and scattered collections of Cyprinodonts in that region do not allow to take a definite position in favor of several refugia or not. The presence of relict *Rivulus* species in isolated Andean remote valleys, the richness of the *Rivulus* fauna, with an important variability in color pattern, at the foothills level, favors the presence of fragmented forest, at least. However, the total absence of endemic atypical species, but one (*Pterolebias peruensis*) and the presence of the same superspecies than in the mid Amazon basin weaken the hypothesis of distinct refugia.

A final aspect of the refugium theory deserves consideration: the "suture zone" (Haffer in Prance, 1982) which represents the point of contact of fauna from two different postulated refugia. Indeed the frontier species (see further, § 4.4) is congruent with that conceptual approach, although, as already mentioned, the borders of distribution of sympatric superspecies are not superimposed. Within the much prospected region of coastal western Africa, three major faunal changes linked to lowland bridges, are observed which can be associated in theory with these "suture zones":
- at the level of the lower Ogooué (the *Chromaphyosemion* lineage first appearance, the change between the *Epiplatys sexfasciatus* and *multifasciatus* superspecies);
- at the level of Rio Muni (the change between the *Plataplochilus* and *Procatopus* lineages);
- at the level of the Mont Cameroun (the southern disappearances of the *Paraphyosemion* and *Paludopanchax* lineages).

However, reality must be much more complex than the "suture zone" model, since in the same regions other Cyprinodont groups have not been affected and are continuously present (with speciation, though).

We hereby generalize the extended theory of refugium to some core zones of ephemeral biotopes that have been constantly maintained during past glacial times. Conceptually, the attached annualism and the refugium endemicity derive from the same survival process. Because the climatic variations had also a major and similar impact on the reclusive ephemeral biotopes of the annual forms in the less humid savannas, as in forests, it can be supposed that these areas were linked to the large rivers galleries, as it is presently exemplified in South America, where annuals are frequent in river overflows, dead arms and river islands. And also to flatland lakes surroundings, as around the present Tchad (e.g. *Nothobranchius rubroreticulatus*), or the past lagoons north of the Niger river (now dried out: Lévêque, 1997) or in eastern Brasil, or near the large river deltas (e.g. the Niger delta) or around each Rift valley lake (e.g. the lake Victoria, with *Nothobranchius taeniopygus*), with past flat surroundings or in core marshy areas as the Pantanal or the Goias. However, the precise delineation of these "annual" refugia will only be possible when more collection data are available for these fishes and when molecular experiments have proposed candidates for the more primitive forms.

To avoid any misunderstanding, the refugium theory is only discussed hereafter within the places established by palynologists.

For future in depth studies, tropical Cyprinodonts will represent one of the best model for the refugium concept because their reclusive biotopes can be hypothesized to be one of the first to dry out along rain sharp decrease, because their poor mobility (unlike terrestrial fauna and birds) and because their food requirement (ants) enhance their dependence to their biotopes.

3.3.2- The presently postulated localisation of refugia (fig. 14).

The today presumed refugia are available in parallel in both the Old and the New Worlds (fig. 14, with corresponding numbers).

In Africa, from west to south (Maley, 1991, 1996b):

1- the Fouta Djalon and the Guinean Dorsal;
2- the attached -or not- coastal region of Liberia-Sierra Leone;
3- the border region between Côte d'Ivoire and Ghana (i.e. west of lake Bosumtwi);
4- the coastal pockets from Biafra to the Sanaga delta, and probably also to Ecuatorial Guinea and Gabon;
5- the West Cameroun highlands, including the lake Barombi Mbo and the Mont Cameroun, and the attached region south of the Sanaga river;
6- the Cristal Mountains and the du Chaillu Massif, and possibly the Monts Doudou in Gabon;
7- the galleries along some major rivers of the Congolese cuvette, especially in the area of lake Tumba and more upstream the Congo river, up to Yangambi, and the Kasaï river, up to Ilebo;
8- the hilly area, west of the Kivu mountains in northeastern Zaïre, and southerly up to lake Tanganyika;
9- the upper Nile river region in connection with the Rift Dorsal;
10- the Mayombe coastal highlands of Congo-Cabinda and the inland pockets of Angola;
11- the Tanzanian coast, in connection with the Uluguru mountains (region of Morogoro).

In South America, from north to south (Clapperton, 1993a,b; Whitmore & Prance, 1987):

12- the Pacific Choco coast in northwestern Colombia (including the extreme northwestern hills);
13- the lower Magdalena and Cauca, in northern Colombia;
14- the western shores of lake Maracaibo and the upper Apure river in Venezuela;
15- the highlands of Guiana (Pakaraima) and of Suriname;
16- the coastal inlands of Guyane and Amapa, in Brasil, independent or attached to the previous refugium;
17- the Napo in Ecuador and the upper Amazon in northern Peru;
18- the upper Rio Purus and Jutai, in southern Peru;

19- the upper Rio Madeira, in northern Bolivia;
20- the upper Amazon, at the three-countries corner (Brasil, Colombia, Peru);
21- the middle Amazon, at the Rio Negro confluence, nearby Manaus; at the Obidos level; the lower Rio Tocantins, south of Belem; the middle Rio Tapajos; the middle Rio Madeira near Porto Velho, all areas being in Brasil;
22- the savanna pocket near Brasilia;
23- the coastal pockets in eastern and southeastern Brasil, from Recife to Porto Alegre;
24- the upper Araguaia basin;
25- the western slopes of Serra Mantiqueira and Serra do Espinhaço;
26- in central America, small refugia, yet poorly -and only- known in Mexico.

3.3.3- The evidence of refugia for Old World and New World Cyprinodonts.

We hypothesize here that the refugium theory, in its present generalized sense, is the major driving force in the speciation and in the distribution of superspecies of tropical Cyprinodonts. From a restricted, isolated position during a glacial maximum, a surviving species began to expand by radiation in the plateau and by linear migration in the corridor coastal plain, following the forest increase in coverage for non annuals or the extension of ephemeral biotopes for strict annuals taking the opportunity of overflows. With recessive phases, since it is known that short milder dry periods did occur within generally wet periods (e.g. 3000 BP and several others prior to the L.G.M.).

Theoretically, a species could expand, until it gets into contact with:
- a closely related congener, a component of its own superspecies which has been split (strict mutual rejection if the speciation process has reached the irreversibility);
- a less related congener, a component of a different superspecies: here, the result is ambiguous, since both phylogenetic lines may remain allopatric (mutual rejection, when presumably recent relatives are concerned) or accept sympatric coexistence (see the neutralist theory, § 5.1.2);
- an impassable barrier, materialized by the highend altitude, by the limit of the forest coverage, by the limit of climatic and orogenic availability of ephemeral biotopes, by the sea water (...).

In the second case -a foreign contact- this helped in the creation of vicariant frontier species (§ 4.4), with or without color convergence (§ 7.3). The model is even more complicated, because more than one Cyprinodont species may start for expansion from a given refugium, which probably is the most important cause of the generalized sympatry.
Anyhow, the frontier species model with peripheral speciation (see further § 4.4) corroborates well with that expansion model of the refugium, even if it is not reasonable to ask for a total explanation from it.

The present patterns of distribution are indeed complex:
- since that process of expansion with wet climate (and the reciprocal recession during dry climates) has repeated itself several times, during the Quaternary interglacial/glacial periods and before;
- since the originating refugium may not have been exactly the same, each time;
- since some (or most?) species of the previously created species during the preceding interglacial may have become extinct;
- since only fragmented forests have resulted during less dry periods than the maximums (e.g. L.G.M.) and thence isolated populations may have enjoyed or not speciation (see further the genotypic plasticity, § 7.4).

This complexity is especially exemplified at borders of distribution of each superspecies. In the plateau, it results in patches of distribution for each superspecies. In the plain in strates of distribution (see previous, § 1.1). And these patches and strates, when concerning sympatric groups, are not superimposed, i.e. sympatric species do not show the same borders of distribution (and even more for sympatric superspecies).

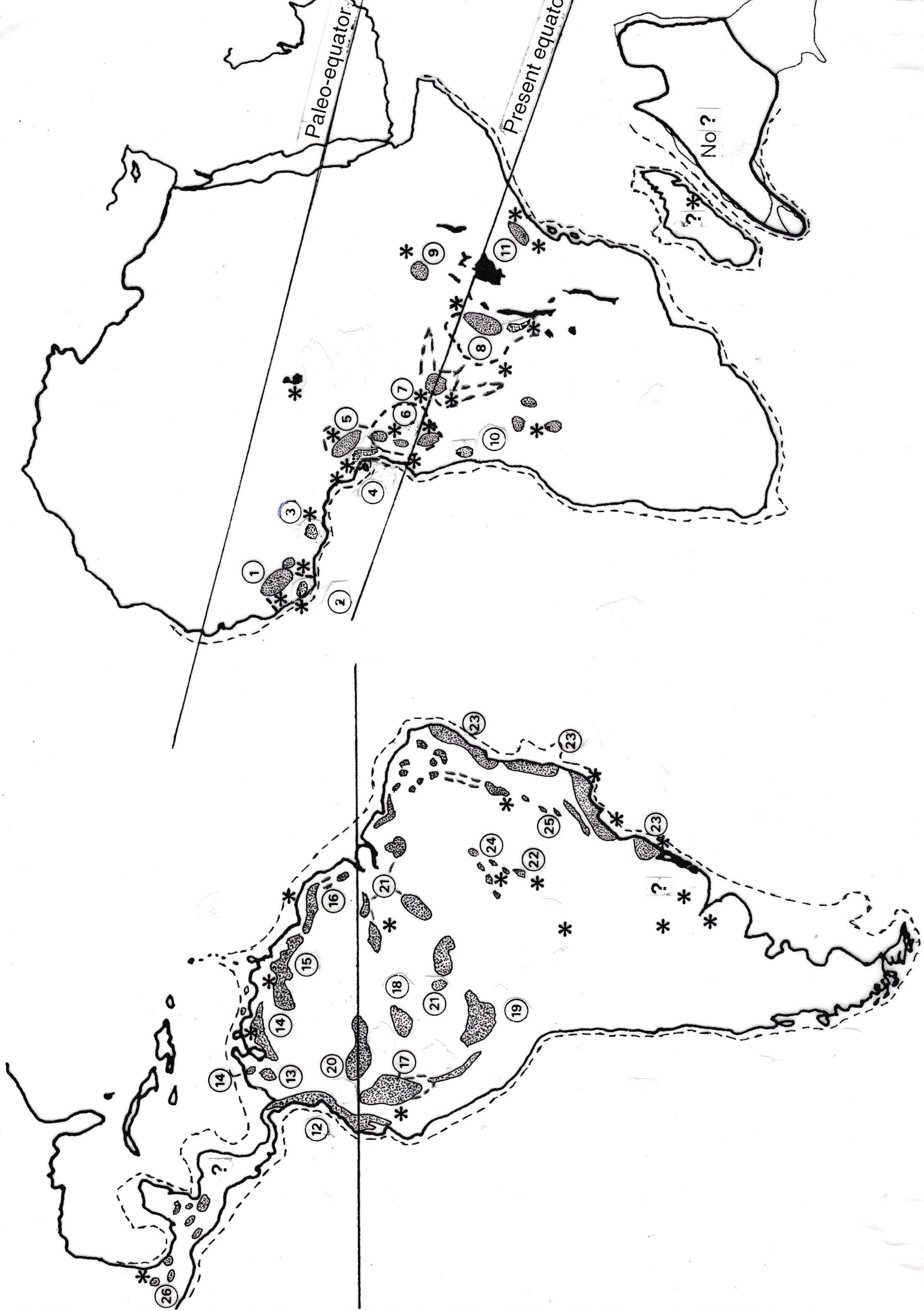
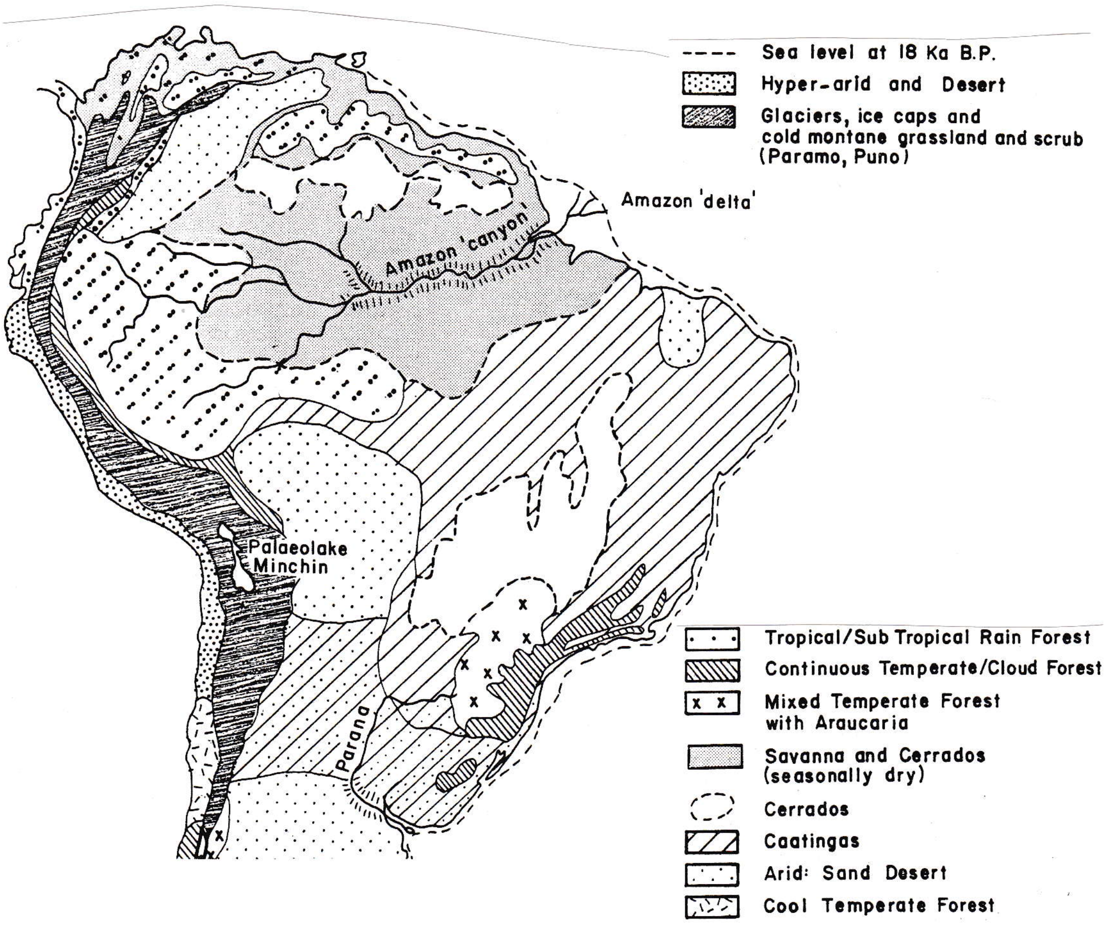


Fig. 14. Diagram of the main rain forest refugia in the Old and New Worlds, at the L.G.M. (numbers refer to text and stars to endemic phenotypes) (original drawing by M. Chauche, from Maley, 1991, 1996b in Africa and Whitmore & Prance, 1987 and Clapperton, 1993b in America).



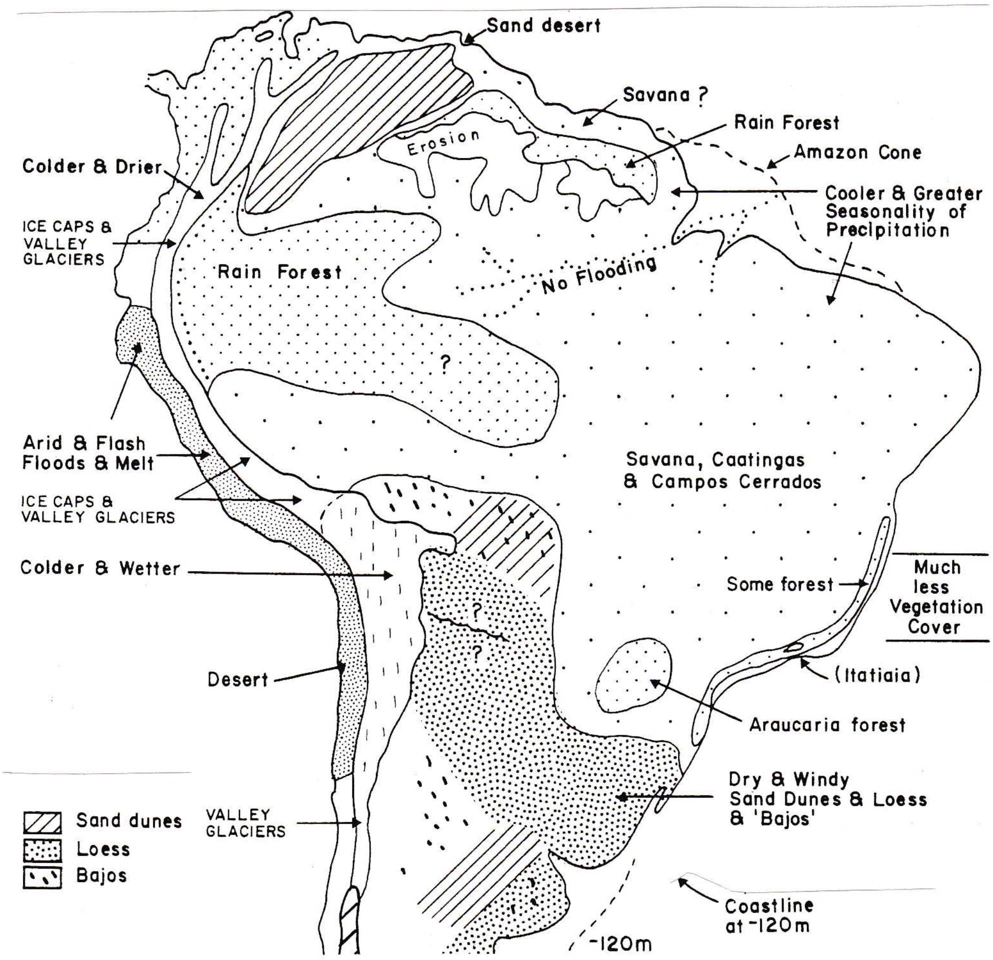


Fig. 15. Alternative reconstruction of South America at L.G.M., especially for upper Amazonia (Clapperton, 1993b).

Invasions, retreats and reinvasion from refugia are documented by the presence of relict endemic species in montane refugia or lowland refugia, and by the diversity of fauna in fragmented-forest or gallery-restricted refugia (e.g. in the present cuvettes). Conversely, it may be hypothesized that actual refugia for Cyprinodonts must have existed in both the coastal plain and the inland plateau. This stems on the old pre-emption of the niches by distinctive phenotypes in the lowlands and the highlands. For example, *Chromaphyosemion* and *Diapteron*, two ecological counterparts, have present disjunct distributions, which do not originate from a single refugia (even if the two refugia, one in the plain, the other in the plateau, may not be very distant).

Although tropical Cyprinodonts are known from an extensive number of collecting localities (over 3500 localities-species, more often in Africa than America, are reported in Huber, 1996), the situation is far from satisfactory for the following reasons:

- collections are being made in the reclusive biotopes along roads and this rarely corresponds with distributional limits or with the outline of refugia;
- no interpolation can easily be performed in complicated cases, because, contrary to other groups of fishes, Cyprinodonts are not distributed along the delineation of river basins (see further, § 4.1).

Here is a full account of the presumed known cases for Cyprinodonts in the presently postulated refugia (fig. 14).

From the Old World:

- in the Fouta Djalon and the Guinean Dorsal, the species *Aphyosemion guineense* and its allied and the Aplocheilichthyin *nimbaensis* superspecies are endemic, with their primitive components being isolated in highlands. From there, several species have radiated that are today known only in the neighboring regions. The strong speciation is also exemplified by three small-range *Epiplatys* species, *Ep. lamottei*, *roloffi* and *hildegardae*;
- in the attached coastal region of southern Guinée to Liberia, with the endemic presence of the *Callopanchax* variable species flock, the endemic and relict *Epiplatys* (*annulatus, dageti, barmoiensis, njalaensis*, and *lokoensis* if valid) and the general high diversity of the *Scriptaphyosemion* superspecies and of the *Epiplatys fasciolatus* superspecies;
- in the border region between Côte d'Ivoire and Ghana, only one Aplocheilid species, annual and variable -*Aphyosemion walkeri*- and three Aplocheilichthyins -*Micropanchax bracheti* and *keilhacki*, *Poropanchax rancureli*- are endemic, because this region is lacking highlands. To this region may also be linked the high diversity of the *Epiplatys chaperi* superspecies and the scattered populations of the relict *A. petersi*. The remaining Cyprinodont fauna corresponds to insiders from the west, the north and the east;
- in coastal pockets from Biafra to the Sanaga delta, and probably also to Ecuatorial Guinea, several species are endemic, mainly within the rivers delta: *A. raddai, A. franzwerneri, A. pascheni*, the *Paludopanchax* species, the *Fundulopanchax-Gularopanchax* species, the last two being annuals; each pocket contains components which have developed the species status. Two *Epiplatys* insiders, *Ep. longiventralis* and *biafranus*, have lost connections with their Sahelian relatives;
- in the lake Barombi Mbo region, there are species which are rather distinctive from the nearby regions and received separate names: *Aphyosemion lacustre, Epiplatys infrafasciatus rathkei*, *Procatopus lacustris*; also, near the Mont Cameroun, with *A. poliaki, A. volcanum*; also in West Cameroun highlands and foothills, with a high diversity of *Aphyosemion* superspecies (the *gardneri, ndianum* superspecies);
- in the Cristal mountains of Gabon, one monotypic species is relict and endemic, *Episemion callipteron* and another has adopted a restricted niche of very shallow waters (*Aphyosemion herzogi*). In their southeastern part, this is also the nested shelter of the *Diapteron* superspecies. In the Massif du Chaillu, the *coeleste* and the *hofmanni* superspecies are endemic. A southeastern origin of the endemic *Aphyosemion thysi* superspecies is congruent with some odd short range species, as *A. caudofasciatum* and *Hypsopanchax catenatus*. More generally, Gabon is amongst the richest countries in terms of speciation (53

species-names, despite the fact that the promising northern Massif du Chaillu is left unexplored, due to the lack of roads) and that the postulated refugium in the Monts Doudou has not been prospected;
- in the galleries along the Congolese cuvette and especially in the area of lake Tumba, there are several relict dwarf species, most in monotypic (sub)genera: *Adamas formosus, Aphyoplatys duboisi, Hylopanchax stictopleuron, Congopanchax myersi* and *brichardi*;
- in the Mayombe coastal hills, no endemic Cyprinodont fauna is reported yet and that region cannot be considered as a refugium for Cyprinodonts. However, further studies are needed in order to better evaluate the high diversity of *Plataplochilus* species there, the presence in highlands (up to 800 m) of *Aphyosemion microphtalmum*, as a possible originator of the two related *striatum* and *ogoense* superspecies (see also previous the lowland bridges, § 1.1.3). Collections in the region of the mid Louessé, i.e. west of the known localities of *A. louessense* are strikingly missing and could fill the gap.
- in the inland plateau of Angola, there are several mini refugia near the sources of tributaries (Cuilo, Cuango, Lua) of the Kwango, Kouilou, Kasaï rivers or in the highlands near Kuito (upper Cuanza river) where the diversity and endemicity of Aplocheilichthyins appears to be unexpectedly high, from our limited knowledge.
- in the Tanzanian coastal plain and nearby highlands, the richness and the diversity of the Cyprinodont fauna are great, with some endemic lineages like the *Paranothobranchius* species and the *Aphyobranchius* species, which are distinctive from the standard lineages of *Nothobranchius*, and Aplocheilichthyins that have migrated inland (or returned to their origin) from the refugium (the *Cynopanchax* lineage).
- in the hilly area, west of the Kivu mountains, from Bukavu to Tanganyika in eastern Zaïre; in the upper Nile river region; unfortunately no significant Cyprinodont collection is available to confirm these important montane refugia.

On the contrary, there are some pocket regions which are known for their endemicity and diversity in Cyprinodonts and are not presently regarded as refugia:
- in the Niger delta in southwestern Nigeria, there are several endemic annual species in the *Paludopanchax* lineage (*arnoldi*) and in the *Fundulopanchax* lineage (*powelli*), in addition to the strange *Foerschichthys flavipinnis*. But, this region had been considered a refugium previously (Maley, 1987), this region is also seen as a deadend linked to the epicontinental sea (see previous § 2.3), this region holds annual species which are also reported from the Biafranan neighboring lowland refugium in western Cameroun;
- in the Ogooué delta, in the surroundings of Lambaréné, there are several relict species as *Aphyosemion gabunense et al.*, *A. hera* and the diversity in *Epiplatys* is high, but this fits with the generalized concept of refugium and, as mentioned above, the northern Massif du Chaillu is not prospected and future collections may explain that situation;
- in the Kasaï province of southeastern Zaïre, there are several endemic and primitive *Nothobranchius* annual species and variable Aplocheilichthyins. But, again this may be related to the neighboring Kivu montane refugium up to the lake Tanganyika and to its downward extensions (Maley, 1996b).

From the New World:
- in the Pacific Choco coast in Colombia (including the extreme northwestern hills), the fauna is poorly known and presently two superspecies of *Rivulus* only are available that are related to the central American fauna; however, the high variability in the preserved material available leads one to suspect a higher diversity (Huber, 1992);
- in the lower Magdalena and Cauca basins, in Colombia, no significant Cyprinodont collection is available;
- in the western shores of lake Maracaibo and the upper Apure river in Venezuela, there are probably the shelter places of the relict coastal annuals belonging to the *Rachovia*, *Austrofundulus* (?) lineages for the former, and the *Pituna*, *Terranatos* and deep-bodied *Pterolebias* lineages for the latter;

- in the highlands of Guiana (Pakaraima) and of Suriname, where the highest *Rivulus* diversity is recorded (whereas, in Guyane, diversity stems in the lowlands); in this region is reported a high speciation level (*Rivulus immaculatus, lyricauda, amphoreus, holmiae*, and in the foothills, *waimacui, breviceps*, plus annuals of *Austrofundulus* and of *Moema*);
- in the coastal inlands of Guyane and Amapa, in Brasil, are recorded six species of *Rivulus*, one being probably relict (*cladophorus*) and the atypic oviparous Poeciliin, *Tomeurus gracilis*;
- in the Napo in Ecuador and the upper Amazon in northern Peru, strong speciation is reported; e.g. 5 species of sympatric *Rivulus* (including one odd, with external primitive characters, *elongatus*) and an annual, *Pterolebias peruensis*, in the area of Iquitos, Peru; in remote valleys of the upper Amazon, near the Andes foothills, are relict endemic species of *Rivulus*, like *Riv. derhami, jucundus, monticola*;
- in the upper Rio Purus and Jutai, in southern Peru, no significant Cyprinodont collection is available;
- in the upper Rio Madeira, in northern Bolivia, a strong endemicity is suspected with distinctive forms of widely distributed superspecies like *Rivulus christinae*, *Riv.* aff. *beniensis*, *Riv.* aff. *rectocaudatus*, the annual *Pterolebias rubrocaudatus*;
- in the upper Amazon, at the three-countries corner (Brasil, Colombia, Peru), no Cyprinodont collection is available;
- in the middle Amazon, at the Rio Negro confluence, near Manaus, several short range *Fluviphylax* sp. with osteological differentiation, two endemic species of *Rivulus* (*obscurus, xanthonotus*) and a strong diversity of the standard *Rivulus* sp. (*atratus, ornatus*) are observed in addition to annuals of the *Moema* lineage; at the Obidos level, at the lower Rio Tocantins, south of Belem, at the middle Rio Tapajos and at the middle Rio Madeira near Porto Velho, few Cyprinodont collections are available and it is not easy to confirm the refugium theory. We may expect the maps of Cyprinodont endemism to be improved in central Amazonia, as collections are made in these little accessable areas;
- in the savanna pocket near Brasilia, two distinctive species, relative to their own sublineages, are reported: *Simpsonichthys boitonei* (without ventrals) and *Rivulus pictus* (more massive);
- in coastal pockets in eastern and southeastern Brasil, from Recife to Porto Alegre, the number of relict forms is high; for example, only in the refugium of the region of Rio de Janeiro, 3 species of the *Leptolebias* lineage, *Rivulus brasiliensis, Simp. whitei* and *constanciae* are registered, all endemics; south of Santos, another refugium hosts the *Campellolebias* lineage and *aureoguttatus* of the *Leptolebias* lineage, but no other Cyprinodont has been collected in between these two refugia, except the widely distributed *Rivulus santensis* superspecies;
- in the upper Araguaia, with the single known locality of the dwarf monotypic genus, *Spectrolebias*, and with a high species diversity and endemicity of groups as *Stenolebias*, *Maratecoara, Plesiolebias, Pituna*, (in the Goias, too, with limited data);
- in the western slopes of Serra Mantiqueira and Serra do Espinhaço (eastern Brasil) (Clapperton, 1993b), a high diversity of *Simpsonichthys* and *Cynolebias s.s.* species, plus the relict *Rivulus decoratus* and the odd *Simpsonichthys trilineatus*, southerly.

The Mexican refugia are not known enough to be studied in conjunction with the tropical Cyprinodont fauna, all the more that additional groups of these fishes are distributed there, originating from North America (several endemics: *Garmanella pulchra, Fundulus grandissimus, Floridichthys polyommus*, and the lake Chichancanab *Cyprinodon* species flock, etc.). Anyhow, the single endemic Aplocheilid is restricted to a small area of coastal eastern Mexico, *Millerichthys robustus*, which is not far from those refugia (although it may be an annual fish).

In central America from Guatemala to Panama, no refugium has been studied yet. The Rivulin fauna (*Rivulus*) is distributed everywhere with a high speciation pattern, near the Atlantic and Pacific coasts and in the highlands, since the Cyprinodont invasion (circa 2.5 MYA). However, the relict presence of two endemic species near two old lakes (*weberi* and *fuscolineatus*), the isolated populations in high altitude volcanoes (*frommi, volcanus*), the presence of a diminutive species flock (the *glaucus* superspecies), the strong variability in the populations of the *isthmensis* superspecies, with or without speciation, suggest that severe glacial periods have occurred and species have survived in refugia and fragmented forests.

On the contrary, there are some pocket regions which are known for their endemicity and diversity in Cyprinodonts and, up to now, are not described as refugia:
- in the Goias, near Aruana, where the diversity in species and the endemicity (*Stenolebias, Plesiolebias*) of relict species is very high, especially in annuals forms. However, here, the generalized definition of the refugium would fit, since these ephemeral marshes are very old and permanent, like the Venezuelian Llanos;
- in the Paraguayan Chaco, where up to 6 annual species, two being endemic, "*Plesiolebias*" *bitteri* and *Trigonectes aplocheiloides*, are sympatric with the non annual distinctive *Rivulus punctatus*;
- in the coastal lowlands and nearby highlands of Uruguay, where up to 5 annual species are sympatric, with one endemic form, *Cynopoecilus melanotaenia*.

All these places, extremely rich in annual forms, should be studied by palynologists to explore their refugium status, seeing that the older deadend effect of the southern epicontinental sea -and its reverse, during dry periods- has also been proposed for the last two mentioned (see previous § 2.3).

3.4- The extinction dimension in line with climatic fluctuations.

For the reclusive Cyprinodonts, the extinction dimension must have been a major character of glacial periods, especially the last one which is today understood as the most severe of the Holocene.

We hypothesize here for the first time that the extinction dimension is a major feature for tropical Cyprinodonts. The best illustration is the very low diversity among the basic morphotypes, especially if the relict monotypic genera are excluded, in comparison to the very high genetic variability: *Rivulus* or *Aphyosemion s.l.* are homothetic genera with at least 100 species-names (Huber, 1996). Long desiccation periods are fatal to tropical Cyprinodonts, although most non annual species can develop delayed embryological hatching, similarly to annuals.

Speciation often started recently, but extinction could occur just before:
- for all presently arid zones, like the Sahara, the Kalahari in Africa, central India or the western Chaco in South America, a near-to-total extinction;
- for all very dry areas during L.G.M., as in the upper and mid Niger basin in Africa, or the Llanos in northern Venezuela, a partial extinction, the annual forms being only able to survive in refugia, too;
- reciprocally, for all regions that were submersed by sea during wet times (H.C.O.), a complete extinction; but species may have been able to survive in the remaining islands or along the coast;
- and, for all areas with long term dried out biotopes during the L.G.M., except in the refugia, a near-to-total extinction.

More ancient extinction processes must have been numerous for Cyprinodonts, like for other faunas and floras, such as for:
- major changes in climate: the reversal from a cooler equator to a warmer equator (the C/T boundary, 65 MYA);
- major geomorphological events: the Andean and the Rift uplifts, the postulated meteorite crash (65 MYA) with also consequences on climate;
- major tectonic events: the continental divide, the continental drifts of Africa and India, with also consequences on climate.

The extinction dimension is rarely exemplified with tropical Cyprinodonts. This comes from

the lack of fossils, for these very small fishes. Also, because the last wet period provided them with ideal conditions for expansion. There are, however, some key cases:
- either relict, witnessing a much larger distribution, like *Aphyosemion raddai*, a presumed component of the *striatum* superspecies, in the Old World or like *Rivulus brasiliensis* in the New World;
- or showing a disjunct distribution, like *Aphyosemion pascheni*, near Kribi in Cameroun and *hera* from Benguié in Gabon, like *Aphyosemion petersi* in Côte d'Ivoire/Ivory Coast and in Ghana, both in the Old World, like *Pituna compacta*, in Brasil and *stellifer* in coastal Venezuela, in the New World.

However, the extinction must have been more than compensated by the speciation rate during interglacials. The general sympatry, today, of two congeners, and sometimes even more, favors a positive balance. Then, the neutralist theory (see further § 5.1.2) must have been exacerbated in the refugia, by overall promiscuity, with a low extinction rate. While strong passive extinction could occur outside refugia.

Even today, with our wet climate, Cyprinodonts become extinct in temperate regions when biotopes definitely dry out (e.g. some *Cyprinodon* species in desertic remote lakes of California and Texas or of highlands of Potosi in Mexico).

Finally, another state of discontinuity is poorly understood: the rare occurrence, both in the Old and New Worlds, of populations with a color pattern similar to a distant species, within the distribution of a related species. Polymorphism can be excluded, because these populations are extremely rare and because they are stable in aquarium generations. They might be relict populations of the distant species which had a past much larger range. Or they might be the consequence of egg transfers by birds (see further, § 4.1.5) or less unlikely, they might be the fruit of a similar genetic mutation. For example, the *geayi*-like population in Suriname or Guiana, within the *Rivulus agilae* range, the *hartii*-like population in the *Rivulus igneus* range in Guyane, the scattered *halleri* populations (with an orange zone on peduncle), within the *Aphyosemion cameronense* range.

4- The local dimensions, the biodiversity and the ecology.

4.1- The failure of the present traditional barriers for the standard ichthyofauna.

Several attempts have been undertaken to explain the present structural distribution of Cyprinodonts by the traditional barriers that are effective for other groups of fishes: these are materialized by a local highland, the geology of soils, the water temperature and composition, the river basins. In addition, some exceptional external accidents have been otherwise proposed.
All have failed to be significant for individual species of tropical Cyprinodonts, as established hereafter.

4.1.1- The local highlands.

The altitude is not a 100% proof barrier, even in the case of a sharp transition between the coastal plain and the plateau:
- first, in some cases as already stated (§ 1.1), some intermediate bridges do occur allowing some invasion;
- second, some contact still exists or has existed in the foothills between two vicariant superspecies, one from lowlands, the other from highlands, as it is exemplified in the color convergence of frontier species (see further, § 7.3);
- third, even if they are morphologically distinctive, those superspecies may still have a recent common ancestor, as in the highland *Rivulus amphoreus* and the lowland *Riv. stagnatus* (Murphy & Collier, 1996).

It is probable, even if *Rivulus* fishes are good climbers (Huber, 1992), due to their unique jumping and aestivating capacities (see further, § 5.1.3), better than other Aplocheilids, that all tropical Cyprinodonts follow the same scheme. For example, the poor swimmer *Aphyosemion microphtalmum* has been able to reach the 800 m altitude from his standard coastal range in southern Congo (Huber, 1978).

We have already hypothesized here that phylogenetic relationships, based on external morphology and ecology, exist between vicariant facing isomorphic superspecies in the plain and the plateau and that they were permitted by those intermediate bridges in case of a sharp transition: e.g. between the *calliurum* and the *cameronense* superspecies at the level of the Rio Ecucu bridge.

4.1.2- The geology of the soils.

Contrary to Clausen (1964) and Scheel (1990), the geology of the soils is not at all, for us, a barrier to species, e.g. according to the basement complex, the sediments, the volcanic soils. Although one may accept that the soil has indeed a limited influence on water chemical composition that may induce speciation, but not a barrier. For example, the distribution of various components of the taxon *Chromaphyosemion* has been hypothesized to be attached to soil determinants, but the availability of additional populations with their color patterns compared to soil characteristics has denied this: the *loennbergii* component is found on sediments and not only on the pre-Cambrian complex, the volcanic soils are inhabited by two distinctive phenotypes, *volcanum* and *poliaki*, which replace each other on a different basis (see the Mont Cameroun refugium, § 3.3).

It may be argued that the composition of the soil constitutes a barrier to annual Cyprinodonts, for which the ephemeral biotopes can only retain water longer if bottom is waterproof, as clay. However, very different types of clay are characteristic of biotopes of annuals and the presence of clay does not imply the associated presence of annuals. For annuals, the first necessity is reccurent waters, mostly but not compulsorily seasonal.

4.1.3- The physico-chemical variables of the water.

The humic contents of the water have also been proposed to be a characteristic of certain species and not of others (e.g. Poll & Lambert, 1965). Black waters have been reported to be specific to *Hylopanchax stictopleuron* (in contrast to *Hypsopanchax* sp., in the Congolese cuvette), to *Moema* sp. (in contrast to *Trigonectes* sp., in the Amazon basin). However, there are reports of *Hylopanchax* in white waters, where it is abundant (the Ivindo basin), and it is replaced by the related *Procatopus terveri*, in the same waters to the south. There are reports of *Moema* sp. in white waters in Guiana. On the other hand, the specificity of the chemical composition of water has long been abandoned to explain species distribution. Tropical Cyprinodonts biotopes contain very similar waters throughout the range, with high variations and pollutions that are tolerated.

The water temperature has also been proposed to be a characteristic of some evolutionary groups. But this fails to be demonstrated, apart from very high temperatures (as in hot springs) or very low (below freezing). Tropical Cyprinodonts are encountered in waters of 38°C in extreme cases (e.g. annuals of the savanna in the Old and New Worlds, *Rivulus pictus* in central Brasil, reported in Huber, 1992). And in waters of 4-9°C in Argentina, when the air temperature is about 0°C. Single species can be found in warm lowland waters and cool highland ones, like *Rivulus isthmensis* (Huber, 1992). In this case, the gradient is not less than 15°C. This last remark is another indirect clue that dryness -and not fall in temperature of 4 to 6°C- is responsible for the disruption caused to Cyprinodonts, during glacial periods.

4.1.4- The limits of the river basins.

The river outlines have also failed to represent limits for species. All species are capable of crossing large rivers, even poor swimmers like *Aphyosemion* or *Rivulus*. *A. cognatum* is present on both sides of Congo-Zaïre, at the level of Brazza-Kinshasa (Huber & Scheel,

1981), *Riv. geayi* and *Riv. urophthalmus* live on both sides of the Amazon at the level of Belem where the river is, today, 3 kms wide (Huber, 1992). During glacial maximums, all rivers must have been reduced enormously, compared to our present rather wet period and transfers have been easy, even before or after these maximums.
River basins, conversely, have no influence on Aplocheilids and even Aplocheilichthyins, although this may be not obvious, at first sight, because of biasses induced by the evidence of other groups of fishes. Indeed, no Cyprinodont species distribution is delineated by the border of a basin of a large river, of a group of smaller tributaries, or of a single tributary.
A few examples will hopefully sweep away the contrary:
- the coastal plain corridor species are not associated with a specific basin; their distribution is much larger (see the examples in § 1.1) and lateral, not transversal to the coast, like coastal rivers;
- several species of Aplocheilichtyins may be living in the same river (Huber, 1998a). At least, four species of *Fluviphylax* inhabit the middle Amazon and its nearby large tributaries in Brasil, replacing each other allopatrically without the explanation of a river swap (Costa, 1996a);
- large river basins, near their sources, are occupied by components of distinct phylogenies: for example, in the upper Ogooué in Gabon-Congo, *Procatopus terveri* is dominant whereas *Hypsopanchax zebra* is linked mainly to the upper Kouilou, but also to the neighboring area, flowing into the Ogooué, and finally, a frontier species is present in between, *Hypso. catenatus* (Huber, 1981b). This is an extreme example in the less poor swimmers that are Aplocheilichthyins: unlimited examples are available for Aplocheilid species on the plateau;
- temporary pools, although many can be associated with a river basin, are inhabited by annual species, with an independent distribution;
- sympatric congeners, by no means, have exactly superimposed distributions in both the Old and the New Worlds, some included in some drainages, others in different ones, even if some drainages are common.

It has been argued for Cyprinodonts that species may expand from one sub-basin to another along the overflows of a large river, but not at the most upstream levels of the inhabited marigot. The hilly landscape would act there as a dead-end and prevent the connection. We believe that this is biassed by the present situation. During past wetter periods, waters were much more importantly extended than today, with many more interconnections. Even now, the structure of a river is rapidly disrupted, as it has been experienced in a Peruvian upper Amazon small river with 3.7% of its floodplain being reworked in only 13 years; or with a different angle, 27% of the total forest surface in Peru occupies floodplains that are no more than a few hundred years old (Goldblatt, 1993). Even now, elephants may rapidly disorganize a sector inhabited by Cyprinodonts and create links between subsystems (Brosset, 1982; Brosset & Lachaise, 1995). This instability promotes variability in genotype (see further § 7.4, its plasticity) and vicariant speciation.

4.1.5- The external accidents.

Some external accidents are known to have exceptionally modified the distribution of standard fishes, like "fish rains" or species transfers out of water, through birds or man (artificial transplants for malaria control, in the case of *Nothobranchius*). They may have affected micropopulations of Cyprinodonts, too (see, the extremely rare cases of discontinuous populations, § 3.4). But no species, except *Nothobranchius* (*taeniopygus*), has been established on that basis over the entire distribution of tropical Cyprinodonts. These appear to be minor anecdotal events, in contrast wih the generalized models of expansion that are developed here.

In total, it is hypothesized here for the first time that the local distribution of the Cyprinodonts should be better looked at with an eye to the past local barriers, specific to reclusive animals, than with an eye on the present barriers that prevail for standard fishes. And, as already mentioned, this remark concerns also the forest and non forest coverage.

4.2- The speciation dimension.

In a static conjecture, like that of the islands off the coast (§ 2.2), speciation seems to be reached, as for other groups of fishes (Lévêque, 1997) in a time scale of circa 10 000 years. In a much more dynamic conjecture, like the post glacial expansions with the competitive pressures materialized by frontier species, this time scale may be shortened. This implies that most components of a superspecies may be only a few thousand years old, even if they are descendants of much older, extant or more probably extinct, phenotypes. This hypothesis of a recent speciation is supported by two considerations:
- first, as already stated (§ 3.4), the last glacial maximum (L.G.M.) was probably the hardest, and complete dryness of most shallow water biotopes has resulted;
- second, the expansion of Cyprinodonts is stopped by the availability of related congeners. This is established by two facts: the ranges of various allopatric superspecies are not identical in size, although the expansion clock has started about simultaneously with the arrival of a new wet period; the patchy distributions, in the plateau, of two related sympatric superspecies do not overlap fully.

This time scale can be reasonably illustrated for poor static swimmers, like *Diapteron* in Gabon. If the refugium of the southeastern part of the Monts de Cristal is the nested origin of that unique group in the Ivindo and neighboring basins, then its present distributional limit corresponds to an eastern expansion of 350 km, with *Kathetys,* another lineage with similar subniche characteristics, as a border. Since the last L.G.M., it has expanded by at least 20 m per year, or 2 km per century, an acceptable rate in comparison with the standards of other groups of fishes. On the other hand, the supposed expansion rate of rain forest -300 km per thousand year- promotes an even quicker process: the circa 350 km would have been reached in less than 1200 years, which would mean that the eastern frontier species of that lineage (*D. abacinum, D. seegersi*) could be unexpectedly very young.
Further, an indirect example in temperate Cyprinodonts can be forwarded. A recent intra lacustrine speciation -8000 BP- for the 5 sympatric species of *Cyprinodon* of lake Chichancanab in Mexico, has been suggested by molecular experiments (Strecker *et al.*, 1996). This Yucatan lake was linked with the Caribbean sea, after the L.G.M.

As for other living organisms, speciation among Cyprinodonts appears to be "stress-driven" (Bush, 1994), i.e. linked with environment disruptions that occurred along the history of the Earth, and especially for the extant species during the Quaternary and late Tertiary. For Cyprinodonts in particular, their reclusive niche promotes a recent event, like the last glacial period (L.G.M.) which had a sweeping effect on previous events. This is congruent with the refugia, with endemic species and strong diversity. In addition, the last sub-glacial period (3000 BP), posterior to the L.G.M., has induced fragmented forests in independent compartments which are also congruent with the genotypic plasticity and color pattern diversity, with or without the development of genetic or behavioral barriers between populations of the same (super)species (e.g. *Aphyosemion ahli*; *Chromaphyosemion*). An idealized model would then be twofold, 18 000 BP and 3000 BP, in line with a very young age for many extant species. The very short subterminal branches in the phylogenetic trees within one superspecies support this model. However, the experience of the complexity of these fishes should push one to some reservation, all the more that the variation in karyotype is huge (e.g. the haploid number varies from 20 to 10 in the species-name *Aphyosemion ahli,* with no stable external character of differentiation) and it may be unreasonable to accept for granted such a short time, on a general basis. Besides, the complexity of distributional patterns among sympatric superspecies suggests that our present observations are the result of several superimposed events and not only the L.G.M. or the very last two periods, although their weight should be high.
Then, the response is not simple and complexity should be case driven.

Speciation is, in all tropical Cyprinodonts, an allopatric vicariant process, when the extension of a phenotype is stopped by a constraint of space occupation. The other basic mechanism of speciation in fishes, the sympatric process, when a mutation is fixed within a population then segregated, is not reported in those tribes or schools of reclusive fishes. Indeed, the biotopes are already crowded with sympatric, not directly related congeners. Conversely, some sort of gene exchange (during the less stable rainy season?) must occur between independent tribes or schools that maintains the gene pool, and this reduces the probability of sympatric speciation.

The frontier species concept (see further § 4.4), the refugium theory (see previous § 3.3) and the neutralist theory (see § 5.1.2) prevailing in the structural relationships of the micropopulations (see further § 5.1.2) all promote a parapatric mode of speciation. For example, the above idealized twofold model provides with parapatric speciation. First, the re-expansion from a refugium with well characterized frontier species at the periphery (e.g. from the L.G.M.). Second, the vicariant speciation in isolated populations inhabiting fragmented forests or non forests with less characterized biospecies (e.g. from the last subglacial period). The population records at the border of two allopatric components of the same superspecies or of two isomorphic allopatric superspecies, are scarce, because obviously the roads where the collections are obtained do not follow these borders. However, the number of sympatric occurrences of two species of the same superspecies is extremely low (3 cases out of thousands of localities among non annuals, except in the huge freshwater lakes, see previously § 2.4 and Huber & Scheel, 1981). It may reflect the narrow zone of contact, as near Malinga in southern Gabon, where *Aphyosemion coeleste* and *ocellatum* have been collected together in the same marigot (Huber, 1996). It may result from more complex events, as, near Akok in western Cameroun, with *A.* aff. *lugens* and *A.* aff. *loennbergii* of the *Chromaphyosemion* lineage (Eberl, pers. comm. 1997). And as, near Makokou in Gabon, with *Diapteron georgiae* and *cyanostictum* (then, Brosset, in 1982, has shown a strong aggressivity of the female of one species towards the male of the other, in the neighboring tribe, see further, § 5.1.2). But these cases may be probably transient (mutual rejection within a superspecies), this assessment being shared by Amiet (pers. comm.).

The general rule is hypothesized here for the first time as a rapid faunal swap, within a few hundred meters of a series of marigots or temporary pools, of one species by another of the same superspecies. Even in annuals, cases of such sympatry are extremely rare, and probably under pressure of the end of the dry season, when collections are undertaken.

In no case has a species been reported with a significant range, carving into that of another related species which would support sympatric speciation. Even, some rare cases of mutational deviation in color pattern (e.g. *Rivulus violaceus*, *Aphyosemion dargei*) appear at the border of two related components of the same superspecies: *pictus* and *modestus* for the first case and *bualanum* and *exiguum* for the second case, with a concomitant change in color phase (see further § 7.2).

Speciation of tropical Cyprinodonts, non annuals and annuals, corresponds with the genetic explosive plasticity (see further, § 7.4). The best match is the male color pattern, but it is far from being perfect (Brosset & Lachaise, 1995, as a lottery process). A specific phenotype may encompass several genotypes. But these genotypes may or may not be associated with actual complete speciation in crossing experiments (Scheel, 1974).

4.3- The biodiversity and abundance.

The biodiversity of tropical Cyprinodonts reflects, like their relative abundance in homogeneous regions, the past history of these fishes, the older periods of morphological differentiation, the latest periods of the explosive speciation after several expansions and recessions (especially linked to the L.G.M.). Clearly, the biodiversity and abundance are strongly correlated: richness increases with the long record of perfect adaptation to environment. For example, *Aphyosemion* in the Old World and *Rivulus* in the New World depend on the present (or more importantly past) forest coverage (Huber, 1992). Historical permanent forest, like in refugia (fig. 14), marks the highest density. On the contrary, at the periphery of present forest, only one or two species, with less frequent populations, are recorded (Huber, 1978). Or likewise in central America, for new territories of recent expansion (less than 2.5 MYA).

If, besides, the two following postulates are accepted:
- the number of phylogenetic lineages and the number of named species, with primitive external characters, available in a given region are correlated to the history of distribution;
- the climatic variations, although not identical, had a similar spectrum of implications.

Then, we can hypothesize the origin of some groups (see also table 2)..

Let us, first, record the number of superspecies and presumably valid species-names in the various homogeneous regions (statistics extracted from Huber, 1996). Because South America is much less prospected than Africa, the number of species-names is not the same, despite the greater surface: 202 in the New World and 293 in the Old World. A strong disequilibrium is seen between Aplocheilichthyins (respectively 4 versus 61) and Aplocheilids (198 versus 232), also when Poeciliins are added (200 species-names).

4.3.1- The biodiversity in the Old World.

In Africa (Huber, 1978) and Asia, 9 homogeneous regions can be disclosed (fig. 16, with corresponding numbers):

1- in the upper Sénégal-Sahel-upper Niger-Tchad homogeneous regions. Dominant fauna: 2 superspecies of *Epiplatys*, the *spylargyreius* superspecies (1 species-name), the *bifasciatus* superspecies (1 species-name); 1 superspecies of *Micropanchax*, the *loati* superspecies (3 species-names); 3 annual superspecies, 2 being relict, *Fundulosoma thierryi* (1 species-name) and *Pronothobranchius kiyawensis* (1 species-name) and 1 *Nothobranchius* lineage, as insider of southeastern origin, *Nothobranchius (Zononothobranchius) rubroreticulatus* and *virgatus* (2 species-names). Insiders: two Aplocheilichthyin lineages, with two opportunistic species, *Poropanchax normani* from coastal forest lowlands and "*Micropanchax*" *hutereaui* from the Congolese fold belts. In this region, Aplocheilichthyins and *Epiplatys* are dominant although poorly diversified. Annuals are relict, with 2 of them being monotypic. This region appears to be the center of origin of no extant Cyprinodont group, but the extension of savanna groups when better conditions were available in the past.

2- in the coastal and neighboring graded highlands of Sénégal, Guinée to Ivory Coast, west of the Bénin/Dahomey gap. Dominant fauna: 4 superspecies of *Epiplatys*, with the *fasciolatus* superspecies (16 species-names), the *chaperi* superspecies (with 5 species-names), the *dageti* superspecies (2 species-names), *Ep. (Pseudepiplatys) annulatus*; 5 superspecies of *Aphyosemion s.l.* (in the *Callopanchax* phylogenetic lineage, according to Murphy & Collier, 1997), the *guineense* sublineage in the Guinean Dorsal (5 species-names), the *guignardi* superspecies in northern derived savanna (1 species name), the *liberiense-roloffi* superspecies in eastern coastal lowlands (6 species names), the *geryi* superspecies in western coastal lowlands (3 species-names), the annual *occidentale* superspecies (3 species-names), 3 Aplocheilichthyin superspecies with the endemic *nimbaensis* superspecies in the Guinean Dorsal and derived slopes (4 species-names), the *Poropanchax* superspecies (2 species-names), *Aplocheilichthys spilauchen* in brackish waters. Insiders, *Epiplatys bifasciatus* (3 species-names, 2 being relict), *Ep. spilargyreius*, the semi-annual *Aphyosemion walkeri* from the Bénin-Dahomey gap. This region is rich and diverse in *Epiplatys*: if the first molecular results are confirmed, which join *Epiplatys* and *Callopanchax* in ancestry (Murphy & Collier, 1997), then this region may well be its origin. Two factors sustain this hypothesis. First, the past equatorial position of that region and its past forest coverage (60 MYA, fig. 11) supports the presence of very old species by external morphology (*Callopanchax s.s.*, "*Aphyosemion*" *guineense*). Second, the past pre-drift position of that region links it to the herein hypothesized neotropical origin of *Rivulus*-like forms in Venezuela-Guyanas.

3- in the Bénin/Dahomey gap of dried savannas. Dominant fauna: the semi annual *Aphyosemion walkeri* superspecies, which has relatives in Nigeria (1 polytypic species-name), 2 Aplocheilichthyin relict species which are linked to the Sahelian fauna, *Micropanchax bracheti* and *keilhacki*. Insiders: the Sahelian fauna of *Epiplatys*, of *Micropanchax*, plus *Pronothobranchius kiyawensis* and *Fundulosoma thierryi*. Migrations of the western and eastern Cyprinodont faunas are sporadic, depending on gallery forest. This region is very poor in endemic Cyprinodonts, despite previous favorable forest, and extinction rate is assumed to have been high. This region may also be seen as a mere sub-region of the Sahel (except the coastal fringe).

4- in the coastal forested lowlands from Nigeria (and attached Togo-Bénin) to Cabinda. Dominant fauna (as already detailed, § 1.1): 11 superspecies of *Aphyosemion*, with the *calliurum* superspecies (7 species-names), the *bitaeniatum* and the *loennbergii* superspecies in *Chromaphyosemion* (9 species-names), the *oeseri* superspecies (3 species-names), the *franzwerneri* superspecies (4 species-names), the *striatum* superspecies (5 species-names), the *gabunense* superspecies (3 species-names), the *arnoldi-filamentosum* annual superspecies (4 species-names), the annual *sjoestedti* superspecies in *Fundulopanchax* (2 species-names), the annual *gulare* superspecies in *Gularopanchax* (4 species-names). Only, 2 superspecies of *Epiplatys*, the *singa* superspecies (2 species-names), the *sexfasciatus* superspecies (6 species-names) and the relict dwarf species *Foerschichthys flavipinnis* which, like *Adamas formosus*, is an Aplocheilid of obscure phylogeny with an Aplocheilichthyin behavior. In total, 5 Aplocheilichthyin superspecies, with *Procatopus* (3 species-names), *Plataplochilus* (4 species-names), *Poropanchax* (2 species-names) and the brackish species, *Aplocheilichthys spilauchen* and *Poropanchax scheeli*. Insiders: the two Sahelian *Epiplatys* species in the Niger delta, with two relict forms (4 species-names) and, south of the Ogooué river, the *Epiplatys multifasciatus* superspecies, more diversified in the Congolese cuvette (2 species-names). This region is much richer in *Aphyosemion* and in annuals, related to *Fundulopanchax*. It contains several primitive forms of that genus: it may be the center of origin of that genus that invaded the interior plateau from bridges with the coastal plain (see also the Congolese cuvette). The precise origin, either northern and/or southern, for both, depending on subgroups, cannot be proposed. The southern part has not been searched for annual forms and the Cabinda-Angola coastal plain is unprospected. The Aplocheilichthyins are well established and diversified, but they may have penetrated this region through the Congolese cuvette.

5- in the corresponding forested plateau of Nigeria, Cameroun, Ecuatorial Guinea, Gabon, and the neighboring southern and northwestern Congo, western Centrafrique. Dominant fauna: 12 superspecies of *Aphyosemion*, with the *gardneri* superspecies (10 species-names), the *ndianum* superspecies (3 species-names), the *exiguum* superspecies in *Kathetys* (4 species-names), the *cameronense* superspecies (7 species-names), the *herzogi* superspecies (2 species-names), the *wildekampi* superspecies (3 species-names), the *ogoense* superspecies (9 species-names), the *coeleste* superspecies (6 species-names), the *thysi* superspecies (2 species-names), the relict *hofmanni* superspecies (2 species-names), the annual *batesii* superspecies in *Raddaella* (1 to 3 species-names), plus the related *Diapteron* flock (5 species-names) and the maybe related relict *Episemion callipteron*. Only 1 *Epiplatys* superspecies, the *sangmelinensis* superspecies (2 species-names). Only 1 Aplocheilichthyin, "*Micropanchax*" *camerunensis*, related to the opportunistic *hutereaui* or *normani*. Insiders: *Plataplochilus* from the coast of Gabon-Congo (1 species-name), and several invasions from the Congolese cuvette belt, with the *Aphyosemion elegans* superspecies (2 species-names), the *Epiplatys multifasciatus* superspecies (2 species-names), in Aplocheilichthyins the *Hypsopanchax* lineage (2 species-names) and the monotypic *Hylopanchax* lineage (1 species-name). This region, very rich in *Aphyosemion,* contains only 1 annual superspecies (*Raddaella*) that is also present in the Congolese cuvette and may have invaded from there. Many superspecies are correlated to coastal

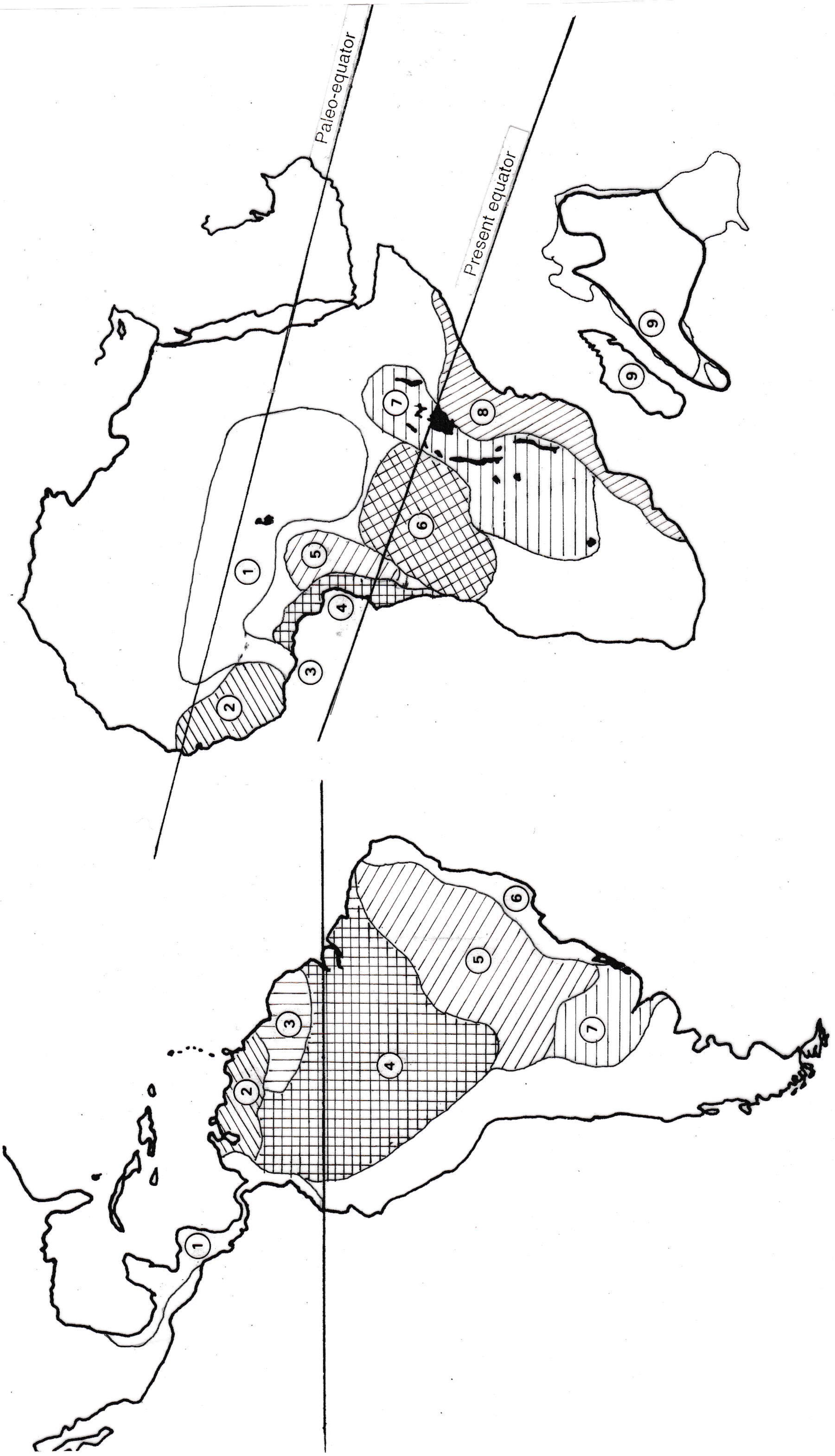


Fig. 16. Paleogeographic reconstruction (circa 80 MYA) of the area under study with the present limit of the regions of homogeneous biodiversity (numbers refer to text) (original drawing by Chauche).

counterparts: for example, *Chromaphyosemion*, *Kathetys* (the *exiguum* superspecies) and *Diapteron* are dwellers of the same subniche.

6- in the Congolese cuvette and its attached belts (including hypothetically the poorly known plateau of Angola). Dominant fauna: only the *Aphyosemion elegans* superspecies (7 species-names) plus the relict dwarf, externally related, *Adamas formosus*; only the *Epiplatys multifasciatus* superspecies (4 species-names), plus the relict, dwarf, maybe related *Aphyoplatys duboisi*. The annual *batesii* superspecies may originate from the cuvette lowlands. In total, 5 Aplocheilichthyin superspecies with the *Hypsopanchax* superspecies (3 species-names), the *Congopanchax* superspecies (2 species-names) and the monotypic *Hylopanchax stictopleuron*, within the cuvette, and the *Lacustricola* superspecies (5 species-names), the *hutereaui* superspecies (6 species-names) within fold belts. Insiders: the 2 Sahelian *Epiplatys* superspecies with two endemic forms (4 species-names), the *Aphyosemion ogoense* superspecies from the plateau (at least, 2 species-names related to *ogoense* or forming an independent sublineage linked to *labarrei*) and *Nothobranchius* (4 species-names) in the Kolwezi area of southeastern Zaïre. This region is rich in endemic and relict species. It also plays an exchange-platform role for other groups, like maybe the Aplocheilichthyins. It is the limit of the *Nothobranchius* series and could be the origin of the *Aphyosemion* series but very primitive phenotypes are missing (in the *Adamas* ancestry?).

7- in the Rift valley and the Zambezi corresponding region. Dominant fauna: 6 superspecies of Aplocheilichthyins, with the *Lacustricola* group (2 species-names), the *Cynopanchax* group (3 species-names), the *johnstoni* superspecies (4 species-names), the *hutereaui* superspecies (3 species-names), the *loati* superspecies (6 species-names) and the 2 monotypic lacustrine genera, *Lamprichthys tanganicanus* and *Laciris pelagicus*. *Aphyosemion et al.* and *Epiplatys* are completely missing. Insiders: annual *Nothobranchius* (5 species-names) in surrounding marshes, 2 species of *Hypsopanchax*, one being trapped in the Rift valley after tectonic movements. This region is very rich in Aplocheilicthyins groups and also in species restricted to single lakes, because of their disrupted histories: it might be the center of origin of these fishes, because their recent coastal counterparts of western Africa appear to have migrated through the Congolese cuvette and those of eastern Africa are the same species which would have downstreamed. But, this needs further confirmation: in contrast, a coastal east African origin is more in line with paleogeography and with the relict presence of *Pantanodon*.

8- in the east African coastal plain and grading plateau. Dominant fauna: 5 superspecies of annual *Nothobranchius* in the available subgenera, *Nothobranchius s.s.* (7 species-names), *Paranothobranchius* (4 species-names), *Aphyobranchius* (3 species-names), *Adiniops* (6 species-names), all restricted to the coastal part, *Zononothobranchius* (7 species-names) in the plateau also. Aplocheilichthyins are either the same species as in the Rift Valley or derived species of the *Cynopanchax* group (3 species-names), of the *johnstoni* superspecies (1 species-name), of the *loati* superspecies (1 species-name). The specialized brackish Aplocheilichtyin *Pantanodon* (1 species-name) dwells the Tanzanian coast. This region appears clearly the center of origin of *Nothobranchius*, the richest fauna corresponding to the coastal refugium of Tanzania, with older phenotypes like *Paranothobranchius* being endemic. Maybe, also, of Aplocheilichthyins.

9- in the Madagascar-Indo-Asian continent: in Madagascar and the Seychelles, 2 superspecies, *Pachypanchax* (4 species-names) and, in brackish biotopes, another, seemingly very different, *Pantanodon* species (*madagascariensis*); in Asia, 2 superspecies of *Aplocheilus*, the *panchax-lineatus* superspecies (4 species-names) and the *blockii* superspecies (3 species-names). This region is poor in Cyprinodonts, although this is relative. Madagascar holds only 2 freshwater fish families (Lévêque, 1997). The Indo-Asian biotopes are competitively occupied by the related group of Beloniformes (*Oryzias*, *Adrianichthys et al.*) (Huber, 1996) and they have suffered much less from the climatic upheavals of the Quaternary which induced speciation.

4.3.2- The biodiversity in the New World (see also table 2).

In Central and South America, 7 homogeneous regions can be disclosed:

1- in Central America, from Mexico (Campeche) to the Choco Pacific coast in northwestern Colombia. Dominant fauna: 2 superspecies of *Rivulus*, the *isthmensis* superspecies in *Cynodonichthys* (11 species-names) and the *elegans* superspecies (11 species-names) in *Vomerivulus*, which correspond to two successive migrations in central America from northern Colombia (Murphy & Collier, 1996) when the Panamean isthmus was established (later than 2.5 MYA). A previous invasion of Mexico is witnessed by the possibly annual, relict, monotypic *Millerichthys robustus*, through the Caribbean arc (another alternative could be studied: a northern drift of a microplate from northern South America, older than 95 MYA, in relation to its very old morphotype, as in fig. 2, but this is highly speculative). Additional Caribbean Cyprinodont fauna followed that route, like the 2 *Rivulus* endemics to Cuba and Hispaniola (once united in a single island), and the brackish *Riv. marmoratus*, which reached the Yucatan and Florida, plus *Riv. cryptocallus*, which later reached the Martinique and Santa Lucia islands and *hartii*, Grenada respectively. This region is poor in tropical Cyprinodonts, not because of an unsuitable environment, but because it was preoccupied by components of northern temperate oviparous groups and the viviparous Cyprinodonts.

2- in the ephemeral biotopes of the lower Orinoco, in northern Venezuela and northeastern Colombia. Dominant fauna: 5 annual superspecies in groups related to *Rivulus* or to *Cynolebias*. To the former, the *Pterolebias longipinnis* superspecies (2 species-names), the *Rachovia* superspecies (4 species-names), the *Austrofundulus* superspecies (at least 2 species-names), the *Pituna* superspecies (1 species-name). To the latter, the monotypic dwarf *Terranatos*. Insiders: 2 *Rivulus* superspecies, *hartii* and *urophthalmus*, with only 1 species-name for each. This region with a long history of ephemeral biotopes is the richest for annuals related to *Rivulus* and maybe their center of origin (Huber, 1998c). Additional evidence is that counterparts of these groups are present south of the Amazon cuvette (*Pituna*; *Pterolebias*).

3- in the Guyanan shield, from eastern Venezuela to Amapa, in Brasil. Dominant fauna: 6 *Rivulus* superspecies, with the *hartii* superspecies (5 species-names), the *urophthalmus* superspecies (4 species-names), the *geayi* superspecies (4 species-names), the *frenatus* superspecies (3 species-names), the *breviceps* superspecies (2 species-names). All along the coast, *Rivulus marmoratus* is present in the brackish marine biotopes, likewise the oviparous Poeciliin, *Tomeurus gracilis* in freshwaters. Insiders: 2 components of annual superspecies, 1 *Austrofundulus* species-name in the western regions, 1 *Moema* species-name in the eastern regions. This region is very rich in superspecies and in species of *Rivulus*, which are often sympatric, with 1 superspecies, being probably semi-annual. It maybe its center of origin for that reason and also because of the presence of more primitive related species in the highlands. With this hypothesis, the centers of origin of non annual *Rivulus* species and annual species in genera related to *Rivulus* are vicariant, not superimposed, if especially *Riv. hartii* and *Rachovia* sp. are considered. The geographical proximity, in conjunction with the 2 long since established stagnant marshes and primary forest, strengthens this hypothesis (*marmoratus* being excluded from the analysis).

4- in the Amazon basin and its tributaries in the fold belts of Brasil, Peru, Colombia, Venezuela and northern Bolivia. Dominant fauna, 4 endemic superspecies of *Rivulus*, in addition to the Guyanan superspecies which are also represented in parts: the *Rivulus rectocaudatus* superspecies (3 species-names), the *ornatus* superspecies (3 species-names), the *peruanus* superspecies (3 species-names), the *limoncochae* superspecies (3 species-names), plus the odd species like *atratus*, *obscurus* and *elongatus*. The single neotropical Aplocheilichthyin is endemic with the same niche as its African counterparts, *Fluviphylax* (4 species-names). All of them prefer to inhabit the cuvette, likewise the single annual group *Moema* (4 species-names), whereas the other annuals are restricted to its fold belts: *Pterolebias* (7 species-names), *Renova* (1 species-name) and probably components of the *Cynolebias s.l.* lineage which are unknown yet, as insiders (*Terranatos* being a witness as a relict form). This region appears to represent no center of origin, but rather a platform of exchange.

5- in the savanna plateau of central Brasil and neighboring Paraguay and Bolivia. Dominant fauna: only 1 superspecies of *Rivulus*, the non annual *punctatus* superspecies (7 species-names), compared to only 2 superspecies allied to *Rivulus* and 8 superspecies allied to *Cynolebias*, all annuals. To the former, *Trigonectes* (5 species-names), *Neofundulus* (4 species-names) which have become extinct in the northern parts of this region. To the latter, *Cynolebias s.s.* (6 species-names), the *Simpsonichthys* lineage (Costa, 1996b) with the *boitonei* superspecies (5 species-names), the *notatus* superspecies (4 species-names), and the *flammeus* superspecies (6 species-names), *Plesiolebias* (4 species-names), *Stenolebias* (2 species-names), and the dwarf relict, *Maratecoara* (2 species-names) and the monotypic *Spectrolebias*. Insiders: *Pterolebias* (2 species-names) and *Pituna* (2 species-names). The richness of this region in annual species related to *Cynolebias* (*Simpsonichthys* included) reflects its long history of ephemeral biotopes. However, those species appear to have migrated from a proximal coastal region. More primitive *Cynolebias s.s.* and *Simpsonichthys* superspecies are today present in two regions. For the former group, in the lower Paraguay. For the latter, between Ilheus and Rio de Janeiro (the single interconnection bridge, the Rio Sao Francisco, being unprospected). On the other hand, annual *Rivulus*-like forms are much rarer and less diversified. They are confined to western parts of the region, which they probably reached via the western belts of the Amazon (*Pterolebias* and *Pituna*) and from the Amazone itself (*Trigonectes*) from a *Renova*-like ancestor.

6- in the coastal corridor from Recife to Porto Alegre in eastern and southeastern Brasil (as already detailed in § 1.1). Dominant fauna: the relict annual superspecies restricted in refugia, like *Leptolebias* (7 species-names), *Campellolebias* (3 species-names), the *whitei* superspecies (4 species-names) and the monotypic *Cynopoecilus*; only 1 endemic *Rivulus* lineage, the *santensis* superspecies (5 species-names) and the brackish *Rivulus marmoratus*, with an odd offshoot exhibiting external primitive characters, *caudomarginatus*. Insiders: 3 *Rivulus* superspecies, *frenatus* (1 species-name) and *urophthalmus* (1 species-name) from the north, *punctatus* (1 species-name) from the south. The eventual relationships of the phylogenetic lineage *Cynopoecilus-Leptolebias-Campellolebias* with some central Brasilian are yet undetermined (Huber, 1995). As in Africa, the center of origin of *Simpsonichtys* appears to be in the coastal plain, but the precise location can only be hypothesized from geography, as yet. Three theoretical options are possible, at the northern dead-end, at the southern dead-end and at the level of the Rio Sao Francisco bridge, which have not been prospected. Southern collections of *Simpsonichthys* would be an important contribution, because the primitive forms by external characters appear to be southern. But, many forms must have faced extinction in that corridor, as for the coastal African *Fundulopanchax* and *Gularopanchax*.

7- in the Chaco regions of Paraguay, central and southern Bolivia, northern Argentina, in Uruguay and the neighboring southern Brasil. Dominant fauna: the primitive superspecies allied to *Cynolebias*, the *Cynolebias s.s.* superspecies (6 species-names), the *Cynolebias bellotii* superspecies (9 species-names), the *Cynolebias nigripinnis* superspecies (6 species-names). Insiders: *Trigonectes* (1 species-name), *Pterolebias* (1 species-name), "*Plesiolebias*" *bitteri* (1 species-name), the *Simpsonichthys chacoensis* superspecies (2 species-names), *Neofundulus* (2 species-names), *Rivulus punctatus* (1 species-name). This region, although less rich than the central Brasilian plateau, contains all more primitive *Cynolebias*-like groups, and within these groups, the more ancestral forms, according to external characters (Huber, 1998c). It is hypothesized to be the center of origin of the *Cynolebias* related groups. Annual groups are dominant, while non annuals are represented by only 1 species-name in *Rivulus*.

4.3.3- The suggested dipolarity of the centers of origin of tropical Cyprinodonts, with remarks on vicariance, dispersalism and putative migration routes (see also table 2).

The diversity, abundance and endemicity, when taken as reference for the identification of origins of phylogenetic groups, are strongly correlated with their characteristics in biogeography, morphology, and genotypes. Seven assemblages of individual phylogenetic lineages can be proposed with a center of origin:
- *Callopanchax* and *Epiplatys*, in northwestern Africa, correlated with the old equator;
- *Aphyosemion*, non annual and annual, in western central Africa, in the coast, either northerly, near the Niger delta or southerly, in relation to the Congolese cuvette (which has a key role in the origin of many other groups of fishes, as suggested in Lévêque, 1997);
- *Nothobranchius* in (south)eastern Africa, near the coast, with a pre-Rift east-west flow. *Pronothobranchius* and *Fundulosoma* are then its western final offshoots;
- Aplocheilichthyins in (south)eastern pre-Rift Africa (i.e. before the many east-west and north-south river reversals affecting the Congo cuvette and the Zambezi);
- *Rivulus*-like forms, annual and non annual, in northern South America, the Venezuelian Llanos and the neighboring Guyanan shield, respectively, if the primitive and marine *Riv. marmoratus-caudomarginatus* is not taken into account;
- *Cynolebias et al.* in southern South America, near to the epicontinental sea and the present Rio de la Plata;
- *Fluviphylax* in western Amazon and upper Orinoco in Brasil and Venezuela, as a relict primitive close to the viviparous Poeciliins (the paleogeography fits with the West African craton).

Many of these centers of origin correspond to a north-south dipolarity in both the Old and New Worlds.

However, it must be stressed that the above considerations are unfortunately not sustained by fossil records and that coastal fringes might be a route to circumvent that dipolarity (see further, here): molecular experiments will be a first test for them.

The dipolarity of extant Aplocheilid morphotypes is apparently in line with the further subdivision into two distinct lineages in both Africa and South America, each containing annual and non annual components:
- in Africa, the northern lineage comprising *Epiplatys* and *Callopanchax* and the southern lineage of *Aphyosemion*, *Fundulopanchax* and *Nothobranchius*;
- in South America, the northern lineage comprising *Rivulus*, *Austrofundulus* and *Trigonectes* and allied lineages, and, the southern lineage of *Cynolebias* and allied lineages.

The suggested dipolarity of the centers of origin favors a vicariant mode of expansion of tropical Cyprinodonts of both Aplocheilid and Aplocheilichthyin lineages as proposed by Murphy and Collier (1997), and not dispersalism. Besides the present distribution of some taxa in very old isolated regions raises a lot of important biogeographical issues that also promote a vicariance scenario, and not a pre-drift or early post-drift dispersal. The following new biogeographical arguments may be proposed:
- the presence of *Pachypanchax* in the Seychelles Islands that were attached to India until circa 66 MYA (Malod *et al.*, 1997) and in Madagascar that was not deeply separated from India before 70-75 MYA;
- the absence of *Pachypanchax* in East Africa, but presence in Madagascar which is thought to have been off Africa-Antarctica since 135 MYA;
- the presence of the brackish *Pantanodon* in both Kenya-Tanzania and eastern Madagascar, but not on the islands in between;
- the non-phylogenetic correspondance of brackish to marine extant species on both sides of the Atlantic Ocean, among Aplocheilids and Aplocheilichthyins (Huber, 1998b);
- the non-availability of the brackish, primitive by external characters, *Rivulus marmoratus*, on the Pacific coast of central and northern America;
- the presence of *Millerichthys*, north of Yucatan, which might be a very old region;
- the absence of salt tolerant Aplocheilichthyins in the African Horn (a land, since 40 MYA).

This growing biological evidence is congruent, as mentioned in the introduction, with the osteology, even if not all morphotypes have yet been studied in depth, and with the preliminary results of molecular biology. It is non-the-less worth to consider the implications of a pure dispersal scenario. A single marine ancestor for each of the two lineages, the Aplocheilids and the Aplocheilichthyins (within the larger scope of Poeciliids), either pre-drift or post-drift (but not too long after, in order to avoid deep sea channels which are not compatible with the shallow waters inhabited by the Cyprinodonts):
- the pre-drift option is not in agreement with the basic position of *Pachypanchax* and *Aplocheilus*, relatively to all other Aplocheilids, in the molecular tree (Murphy & Collier, 1997) and with the nested position of *Fluviphylax* with Poeciliids and of *Pantanodon* with mainland African taxa, in the phylogenetic trees (Parenti, 1981; Huber, 1998a; Costa, 1996a);
- the post-drift option is not in agreement with the distinct dates of the two drifts which implies that a dispersal scenario could only be suggested between Africa and South America, circa 85-90 MYA. However, the high degree of separation of the branches between the Old World and New World lineages of the two groups (Parenti, 1981; Costa, 1995b) is in contradiction.

More importantly, vicariance is congruent with the division of the Cyprinodontiformes into two large lineages, i.e. two suborders, sensu Parenti (1981), the Aplocheiloidei (here, the Aplocheilids) and the Cyprinodontoidei for all others (including the Aplocheilichthyins). However, this division raises the unanswered question of the origin of the Poeciliids/Aplocheilichthyins: their phylogenetic relationship with the temperate Cyprinodonts implies a more northern origin near the Tethys sea (see further below). From the Indian-Madagascan origin of Aplocheilids, all three techniques of phylogeny (external morphology, osteology, molecular biology) concur to hypothesize an east-west flow of expansion in Gondwana. The dipolarity of extant presence of primitive morphotypes (by external morphology criteria), the plate tectonic drifts, the related global climate before the continental divide, the hypothesized arid and continental climate in the center of Gondwana and the prefered flatland pattern of migration of these fishes immediately suggest two putative major paleo-routes, a northern and a southern routes from southeastern Gondwana, along the coastal plain.

A supplemental and distinct approach to the problem of the migration routes is karyotypic. This is proposed here for the first time and it is congruent with the above considerations.
Scheel (1968, 1974) has established that the number of haploid chromosomes (n) and of arms (A) is to decrease along the evolution time, from a basic haploid number of chromosomes of 24 in Teleosts. The analysis of the data base of published karyotypes (Huber, 1996) reveals that:
- all known species with old karyotypes are presently inhabiting in coastal plains;
- all known species with oldest karyotypes are presently scattered at the periphery of Gondwana. For example, in Aplocheilids: *Pachypanchax playfairii* from the Seychelles with n= 24 and A= 48; *Aplocheilus dayi* from Sri Lanka with n= 24 and A= 44; *Nothobranchius melanospilus* from Tanzania with n= 19 and A= 38 (no *Paranothobranchius* has been studied yet); *Callopanchax occidentalis* from Sierra Leone with n= 23 and A= 44; *Aphyosemion microphtalmum* from Cabinda with n= 20 and A= 38; *Simpsonichthys whitei* from southeastern Brasil with n= 23 and A= 46; *Cynolebias nigripinnis* from Argentina with n= 24 and A= 37 (no *Cynolebias s.s.* has been studied yet); *Rachovia maculipinnis* from Venezuela with n= 22 and A= 38; *Pterolebias hoignei* from Venezuela with n= 23 and A= 36; *Pituna stellifer* from Venezuela with n= 24 and A= 37. In addition, those species which have more than 24 haploid chromosomes (n= 25 to 27) are distributed also near the periphery of Gondwana, as *Epiplatys dageti*, *Pseudepiplatys annulatus* and *Pterolebias peruensis*;
- within a large phylogenetic group (i.e. a speciose genus or a group of related genera) with a distribution on the plain and the plateau, the older karyotypes correspond to species from the coastal plain;
- all known species with older karyotypes are distributed from northern or southern regions

of Gondwana, which is congruent with the above suggested dipolarity.

Unfortunately, because of much less old events, tropical Cyprinodonts are today absent in North Africa (Sahara *s.l.*), South Africa, and southern and western South America. Besides, fossils from those regions have not been found yet. It is then impossible to have a more complete picture of older phenotypes from the periphery of Gondwana.
Another scenario of flatland migration routes, which is compatible with above, concerns flat inland parts of paleo-Africa and then shortcuts the extreme northern and southern regions of Africa. At least, two routes can be proposed which corresponds to older morphotypes:
- a Nilo-Sahel route, with the Mesozoic Rift subroute, which takes into account the older morphotypes of Aplocheilichtyins (with poorly studied karyotypes), including *Micropanchax s.s.* and *Laciris,* and those of Aplocheilids (with *Fundulopanchax-Gularopanchax*);
- a Zambezi-Congo cuvette route, with then the La Plata craton, which also takes into account the older morphotypes of Aplocheilichthyins (the deep-bodied lineage with *Lamprichthys*).

These two alternative migration paleo-routes are more in line with those of the standard ichthyofauna (Lévêque, 1997), but they may not be of the same time scale than the two above. And the two sets of scenarios are not exclusive and are supported by the combined analysis of vicariance and external characters of extant species (see table 2).

Another major biogeographical issue of discussion -still unresolved- is the actual origin of separation of the Indo-Madagascar block from Gondwana, since it is inhabited by the most primitive Aplocheilid species and the very isolated Aplocheilichthyin genus *Pantanodon*:
- either, as an offshoot from Antarctica (then warm), with a deep gulf introgression by the paleo-Indian ocean, at the level of present southern Mozambica (fig. 2). In that case, a very southern origin of Aplocheilichthyins is not coherent with the Tethys sea, as the origin of the temperate Cyprinodonts (Parenti, 1981 and several earlier authors) or else would mean a considerable early extinction in between. It implies also that the Madagascar island actually drifted in the same way as Africa mainland. On the other hand, this hypothesis may be rather coherent with a southern scenario for the lineages allied to *Nothobranchius* and *Cynolebias*.
- or, more traditionally (fig. 2), as an offshoot from middle east Africa, at the present level of Kenya (which was already 15 latitude degrees more to the south than today), with the reverse consequences.

Finally, it is worth adding that a southern route vicariance scenario, either coastal or inland via the Congolese craton, for example, implies that the migration could only occur during late Jurassic (circa 140-135 MYA: opening of the southern Atlantic Ocean) and that this event is congruent with the hypothesized separation of the Madagascan-Indian block from Antarctica (135 MYA). Then, it may not be too provocative to suggest that Antarctica played a major role in the paleo history of Cyprinodonts, in line with the related Australasian Beloniformes.

4.4- The frontier species concept.

As stated in the introduction, the elementary phylogenetic unit in Cyprinodonts is the superspecies, made of several cryptic (i.e. vicariant and isomorphic) components that are separated by genetic isolation and named when a stable difference at least can be disclosed in male color pattern, especially on fins and posterior sides, so important for pre-mating recognition. The distributional structure of a given superspecies is not due to chance. There is usually one (occasionally two or more) widely distributed phenotype with a central range, exhibiting a rather generalized color pattern. There are several phenotypes, usually with a small range, occurring at the periphery of the superspecies, exhibiting a more derived and less variable color pattern. These small-ranged phenotypes are never found in the middle core range of the superspecies, but rather at its border. More importantly, these short-ranged species do not appear all along the periphery of the superspecies (like in the peripatric speciation of standard river fishes), but only in precise areas. Hypothetically, these areas witness a friction conflict with another superspecies.

This phenomenon was termed by us (Huber, 1980b, 1981b) the "frontier species" concept for the *Aphyosemion ogoense* superspecies. As an example of the color pattern diversity, those of that superspecies are detailed hereafter:

- the *louessense* male is the most variable: it is characterized by series of longitudinal irregular blotches and a single broad mid-line, more or less conspicuous, on the sides; the caudal fin pattern is flamed and asymetrical;
- the *ogoense s.s.* male shows a series of red longitudinal spots on the sides including a broad basal red line from the anal insertion to the lower caudal and also an asymetrical organization of external bands on the caudal fin (red margin and yellow/blue submargin on the upper part; the reverse on the lower part), plus a flamed pattern in the center of the fin;
- the *ottogartneri* male is similar to *ogoense*, but without the typical basal line on the sides;
- the *pyrophore* male is similar to *ottogartneri*, but the red longitudinal lines on the sides are replaced by thin red bars, posteriorily;
- the *caudofasciatum* male is similar to *pyrophore*, but with a red fasciated, instead of a flamed caudal fin;
- the *zygaima* male is similar to *louessense*, without the mid-line, but the caudal organization of external bands is symetrical (red margins on the upper and lower part of caudal);
- the *labarrei* male is similar to *zygaima* but the irregular spots are replaced by vertical blotches and the caudal fin is lacking the yellow submargins and the margins are black, not red;
- the *joergenscheeli* male is vaguely similar to *ottogartneri*, but the series of side spots are arranged rather vertically and the caudal pattern is unique with a red circumcaudal submargin on a plain deep blue background;
- the male of the yet undescribed Tirbak's species is vaguely similar to *joergenscheeli*, but the series of irregular red bars on the sides are broader and there is a symetrical organization of external bands on the caudal fin, comprising a yellow margin and a red submargin.

From the western-central asymetrical phenotype, the variable *louessense*, are hypothetically derived more stable phenotypes with an asymetrical caudal pattern (*pyrophore, ogoense, ottogartneri*) to the east, then more divergent phenotypes with a symetrical caudal pattern (*joergenscheeli, tirbaki, zygaima, labarrei*) at the northern and southern periphery. Within each frontier species, the variability in the male color pattern is remarkably low.

All species, for which the karyotype has been studied, are determined by separate fundamental numbers of chromosomes and/or of arms. They breed true to their characteristics, which excludes the possibility of simple color variations or natural hybridization.

Since then, lots of examples of frontier species have been forwarded to strengthen the concept in many Cyprinodont genera of both the Old and the New Worlds, in the non annual and in the annual groups, in the coastal lowlands and in the interior plateau. The cases of frontier species are especially numerous in the forest regions of today or of the last pluvial periods, which implies that the concept is associated with the refugium theory (see previous, § 3.3). The immediate modelization of the frontier species concept would push the central phenotype as the primitive candidate to the other components of the superspecies, and a derived status for the frontier species themselves. However, the precise location of the refugia is not known precisely to validate with certainty this hypothesis and collecting localities of the various components are not numerous enough either. If valid, then *Aphyosemion louessense* (the *ogoense* superspecies), *A. cameronense* (the *cameronense* superspecies), *A. guineense* (the *guineense* superspecies) would be primitive in their own groups and the eastern Mayombe (or southern Massif du Chaillu), the inland upper Sanaga and the Fouta Djalon would be respective candidates for refugia .

The geographical structure of the frontier species implies that it is not promoted by the groups occurring sympatrically. Rather, it is promoted by the change in fauna between two allopatric vicariant superspecies, which presumably reject each other because they are closely related and/or ecological counterparts, in contrast to sympatric superspecies.

This is an allopatric competitive exclusion (pre-emption) process. The observation is especially striking when two -and not only one- frontier species are recorded vicariantly, as offshoots of the two conflicting superspecies and when this is accompanied by color convergence, as for example in the genus *Aphyosemion* (see further § 7.3).

All yet known examples of frontier species schematically possess:
- in comparison to their own superspecies, a distinctive color pattern, a similar but different karyotype;
- in comparison to the facing superspecies, a distinctive morphology (size, body and fins shapes, fin ray counts and especially D/A deviation) and a very different karyotype.

However, this concept:
- must not be extended to all taxa with a restricted range and a similar morphology to their vicariant counterpart: there are taxa -like *Aphyosemion dargei*, *A. etzeli*, *Rivulus cladophorus*- which occur at the border of two widely distributed, related species and may have developed by accidental mutation or maybe a trace of an unknown past situation. There are taxa -like *Aphyosemion bamilekorum*- in particularly isolated areas (mountains) or -like *A. franzwerneri*- in coastal pockets, with a reduced distribution due to a hypothesized partial extinction;
- should need a further support in terms of local distribution data; due to the lack of roads, and then of collections, we have no idea of the present populations dynamics at the border of the distribution of two vicariant superspecies where friction occurs. Not to mention, the dynamics of the past periods, in the Quaternary, with the cover of the primary forest linked to climatic variations (see previously § 3.2). Because it is known that the *Aphyosemion* populations are made of isolated, static, pyramidal tribes in reclusive biotopes (stable, slow-moving shallow streams towards the dry season; less stable, strongly flooded brooks during the rainy season, see further § 4.5) it can be inferred that bordering populations of two frontier species may be occasionally sympatric or may have been so in the past, at the time of their rejection and speciation, making then plausible the color convergence (see further § 7.3).

4.5- The ecological subniches and the generalized sympatry.

The differentiation of the ecological niche into several subniches has been proposed, following field observations (Huber, 1980b, 1992, 1996; Nico & Thomerson, 1989; Amiet, 1987; Brosset, 1982), to explain rationally the sympatric occurrence of tropical Cyprinodonts and their biodiversity. Four subniches have been disclosed both for non annuals and annuals of both the Old and the New Worlds:
- the clear, sandy, shallow places of the marigot in shady zones, with slow to very slow current;
- the dirty, shallow places of the marigot or the pool, over beds of leaves or mulm in shady zones, with slow or no current;
- the open, more sunny zones of the biotope, with stagnant and less shallow waters over a muddy bottom;
- the open, more sunny zones of the biotope with an active current, over sand or gravel.

The first two subniches are inhabited by large genera, like *Aphyosemion* in Africa and *Rivulus* in America; the second and the third are characteristic of annual species (no current, clay bottom) and *Epiplatys* (some current) and the last, of Aplocheilichthyins. In addition, the prefered localization within the biotope has been forwarded (Huber 1979, 1992; Nico & Thomerson, 1989) to exacerbate differences: near the surface, near the bottom, near the edge, in midwater, both for annual and non annual Cyprinodonts of the Old and New Worlds, although this is not enough documented and it may concern more odd (by external morphology) species or species flocks.

These many separate subniches, insufficiently precise and studied and anyhow relative, do not give a complete explanation of the extreme biodiversity in certain places, with up to 5 sympatric congeners. Even if a behavioral differentiation is added (e.g. crepuscular activity

in contrast to day time activity). Even if food is considered: food is the same for most Cyprinodonts of the old and the New Worlds which share the same habitat -ants and insect larvae (Brosset, 1982; Nico & Thomerson, 1989)- and this food is available equally, i.e. by chance, over all subniches. Only a few species have a special diet like some Aplocheilichthyins, some annuals (Nico & Thomerson, 1989), *Laciris* (Huber, 1998a) and *Diapteron* (Brosset, 1982) (...). This infers that the niche differentiation, as well as all other differentiations (in color pattern, in morphotype...) and the rare specificities (in behavior, in food...) are not sufficient to warrant such a level of achieved co-existence.
Only a neutralist interspecific behavior can explain this very limited competition (see further, § 5.1.2), not enhance it. The flexibility of the Cyprinodonts in their contingent reclusive biotopes is then a rule of conservation for adaptation and survival. No clear cut separation exists between the species and the subniches, only tendencies (Brosset, 1982; fig. 17). And even the annual versus non annual duality is full of present intermediates (the "semi-annual" species) and of past changes (e.g. from an annual dominant type, into a less annual), as evidence of the lability of the concept.

Both in the Old and New Worlds, and in Aplocheilids and Aplocheilichthyins, the sympatry of 2 congeners is the general rule. Cases of 3 or 4 congeners do occur regularly in the old primary forest or historical ephemeral regions, especially when collections are exhaustive, over 200 m of the biotope. In certain, not rare localities, apparently not far from refugia, the diversity of sympatric Cyprinodonts is so high that the mutual non-rejection achieves an idealized model. For example, in the Old and New Worlds:
- in the Ivindo basin, are frequently collected in the same marigot 5 species in the *Aphyosemion* lineage (*A. punctatum*, *A. cameronense*, the annual *Raddaella*, the crepuscular *Diapteron* with *georgiae* and/or *cyanostictum*, *A. herzogi*), 1 species of *Epiplatys* (*Ep. neumanni*) and 1 species of Aplocheilichthyin (*Hyl. stictopleuron*) (fig. 17);

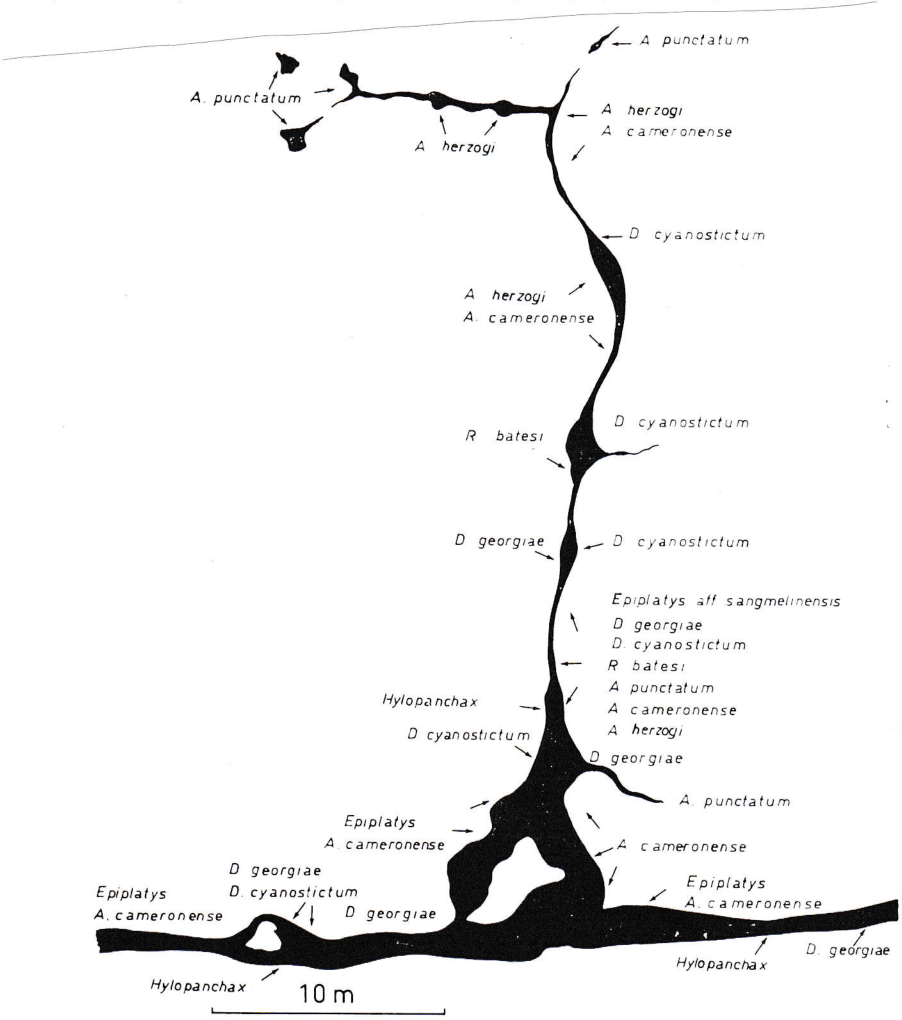


Fig. 17. Independent micropopulations in sympatry (Brosset, 1982).

- in the Niger delta, around Lagos, in purely freshwaters, 5 species in the *Aphyosemion* lineage (*A. calliurum*, the annual *Fundulopanchax* with *sjoestedti*, *gulare* or *powelli*, the annual *Paludopanchax* with *arnoldi*, *A. gardneri*, *A. bitaeniatum*), 2 species in the *Epiplatys* lineage (*grahami, togolensis*), 2 Aplocheilichthyins (*Aplocheilichthys spilauchen*, *Poropanchax macrophthalmus* or *hannerzi*), and the relict *Foerschichthys flavipinnis*;
- in the Tanzanian floodplains of east Africa near Dar es Salaam, 4 (potentially 5) annual species of *Nothobranchius* (in the *Adiniops*, *Aphyobranchius*, *Paranothobranchius, Zononothobranchius* and *Nothobranchius* subgenera) and 2 Aplocheilichthyins (*Micropanchax kongoranensis* and *Cynopanchax maculatus* or *lacustris*);
- in the Kourou area of Guyane, 5 species of *Rivulus* (*agilae, lungi* or *urophthalmus*, *xiphidius*, *igneus*, plus the odd species *Rivulus cladophorus*), without forgetting the probable occurrence of the annual *Moema* lineage and *Tomeurus gracilis*, the single oviparous Poeciliin;
- in the Iquitos area of Peru, 5 among 7 species of *Rivulus* (*rubrolineatus*, *elongatus*, *rectocaudatus*, *iridescens*, aff. *intermittens*, the surface dweller *Anablepsoides (Riv. atratus)* and a poorly identified component of the *ornatus* superspecies), 1 annual species of *Pterolebias* (*peruensis*) and probably an undisclosed *Moema* component;
- in the Venezuelian Llanos, 5 among 6 annuals, 1 species of *Pterolebias* (*zonatus* or *hoignei*), 1 species of *Austrofundulus* (e.g. *transilis*), *Terranatos dolichopterus, Rachovia maculipinnis, Pituna stellifer.*
- in the Paraguayan Chaco, in temporary bodies of water, 1 species of *Rivulus* (*punctatus*) and 5 among 8 annual species, in *Cynolebias* (*vandenbergi*, *monstrosus*, an unidentified component of the *nigripinnis* superspecies), in *Simpsonichthys* (*chacoensis*), in "*Plesiolebias*" (*bitteri*), in *Trigonectes* (*balzanii* or *aplocheiloides*), in *Pterolebias* (aff. *longipinnis*), in *Neofundulus* (*ornatipinnis*) (Huber, 1995);
- in the Araguaian floodplains of Brasil, 6 annual species in *Simpsonichthys* (*costai*), *Maratecoara* (*lacortei*), *Plesiolebias* (*aruana* and *lacerdai*), *Spectrolebias* (*semiocellatus*) and *Trigonectes* (*rubromarginatus*), plus a probable component of *Pituna*. And similarly, in the historical ephemeral biotopes of the Goias.

The local diversity of Cyprinodonts is well ahead of the ecological richness and is equally valid in the Old World and the New World.

5- The behaviors, non sexual and sexual.

The behaviors reflect the adaptation of a given phenotype to its environment. For Cyprinodonts, the diversity of the reclusive biotope is low.
Between the Old and New Worlds, similarities in behavior are then the rule, and differences are the exceptions, which are most, for unknown reasons, recorded in the neotropics. In addition, there are specificities that will not be covered here, because they are yet restricted to isolated examples only, such as a crepuscular behavior (*Diapteron*: Brosset, 1982) or a filtering behavior (*Pantanodon*: Huber, 1998a).

5.1- The non-sexual behavior.

5.1.1- The tribe structure and the schooling structure.

Both in Africa and South America, the two major lineages of Cyprinodonts exhibit the same general organization in groups (Huber, 1996):
- a pyramidal tribe for all Aplocheilids. Each tribe is made of a few dozens of individuals, with one or very few dominant males, a lot of dominated, usually subadult immature males, a large lot of mature and maturing females and the remaining bulk of juveniles. To a lesser degree with annuals, all sizes of juveniles may be seen, even if the very young fry is not trapped in the standard collecting nets. The old dominant male(s) with longest extensions in fins and the very large females (a pair or two) are often hidden in the roots of the overhanging vegetation on the edges of the marigot or pond.

- a loose school (or shoal) for all Aplocheilichthyins. The school is made of a few dozen to hundreds of individuals of all sizes with also dominant and dominated members, although not in a vertical hierarchy like the Aplocheilids. The fish swim parallel and synchronistically. Their reactions to a danger is collective as for any shoaling groups.

The Aplocheilichthyin school is dynamic, whereas the Aplocheilid tribe is static, in line with their choices of the water current subniches. Only two known major exceptions to that rule are the monotypic Aplocheilid genera *Adamas*, restricted to the Congo-Zaïre cuvette and *Foerschichthys* to the Niger delta surroundings. These diminutive fishes gather in large schools with community behavior along the banks of gently flowing rivers (Huber, 1979; Scheel, 1990).

5.1.2- The neutralist behavior.

Both major lineages of tropical Cyprinodonts, all over their range, are found in micro-populations (tribe or school) of different species that are sympatric (see the sympatry dimension, § 4.5). In fact, the sympatry (i.e. syntopy for some authors) is not strict so that the members of the various micro-populations, belonging to different generic lineages or to different superpecies are not mixed altogether. They remain within their community group, each separated from another by a short distance (a few meters or less) and, not always, by characteristics of the niche (see the variety of niches, § 4.5).
A major ethological consideration is that the sympatric superspecies within a single biotope do not exhibit reciprocal conflicting behavior whatsoever, although:
- most are competing in terms of food (see § 4.5) and most are food limited: stomachs contents have been disclosed to be frequently empty and then the fish are food dependent (Brosset, 1982). Although food is often scarce and not restricted to special parts of the biotope where competition could be exacerbated -terrestrial insects fall by chance anywhere in water, from the overhanging plants or trees or from the banks- the groups of Cyprinodonts occupy all parts of the biotope;
- the available space in the biotope is limited, somewhat more during the dry season for non annuals, and especially at the end of the dry season for annuals: the fish density is a clue to promiscuity;
- an intraspecific aggressivity -but no interspecific aggressivity- may have developed: fin displays (Ewing, 1975), up to bites (Brosset & Lachaise, 1995), especially in annual species in the drying biotope (Huber, 1981e). Intraspecifics are antagonistic and hierarchical, whereas interspecifics are agonistic.

Actually each tribe or school ignores the next. The organization within each tribe or school seems to be much more imperious than the relationships with the other groups, whether they belong to the same species or to a different superspecies. This situation is probably linked to the reclusive character of the Cyprinodonts and we would like to conceptualize it here as the neutralist behavior. This neutralism results from observations in the artificial obliged conditions of the aquarium, but also in the field (pers. observations).

To support the concept further, with a different approach, it may be stressed that (except cannibalism, see further) the only reported case of a strong interspecific aggressivity concerns two related species, *Diapteron georgiae* and *cyanostictum*, in the rare occasions when they are found sympatric. Then, females develop repulsive ethological barriers with the males of the other species (Brosset, 1982). According to the limited available information, the neutralist behavior of the groups is maintained during the rainy season, because, then, little is changed in terms of the water current and the organizational structure may not be disrupted. Groups get more separated in terms of space and migrate to shallower parts of the overflows. Conversely throughout the dry season, space between groups may be shrunk.

5.1.3- The particularities in non-sexual behavior: jumping-aestivating, non-swimming, cannibalism.

In addition to the above standard behavioral organisational patterns, there are some specificities, which appear just extreme deviations of standard behaviors.

- The jumping behavior is shared by all non annual Aplocheilids, in the Old and New Worlds, in response to a presumed danger (Huber, 1979). This is an uncontrolled passive escape behavior that is commonly reported on collections of fishes of the genera *Aphyosemion*, *Epiplatys*, *Aplocheilus*. components of the neotropical genus *Rivulus* exhibit a derived behavior in that they jump actively out of the water to swallow prey and to move, via the damp ground, from one biotope to another (various reports in Huber, 1992). More importantly, this behavior is linked with their unique aestivating and sexual egg-stranding abilities. Aestivating is again, for *Rivulus*, another extreme of a general posture, namely the lazy motionless attitude with the rest of the body loosely abandoned downwards from the obliquely oriented head. When aestivating, *Rivulus* are just motionless out of the water, in the damp for a -sometimes- long period or in-between jumps. Active jumping and aestivating do not occur in their Old World counterparts. This is all the more remarkable that it is an excellent specific response to the reclusive nature of their biotopes and niches, which cannot be differentiated for *Rivulus* and for *Aphyosemion*. The absence of a similar evolution in Africa may be due to chance or, if not, lies more in the higher variations in the water levels and in the extension of floods in America, rather than in the presumably more ephemeral character of the biotope in America. However, this locomotion capacity is not associated with a better range extension for species. In Africa, *Aphyosemion* species show similar sizes of ranges, highly dependent on other external constraints.

Reciprocally, annuals, which usually inhabit lower parts of the biotopes, exhibit the opposite behavior to jumping, the burying behavior and this is also associated with the sexual behavior.

Aplocheilichthyins do not jump at all, even in case of a major danger, but react like other schooling groups of fishes. They flee in all directions for some short time and reintegrate the disintegrated school as soon as possible. Otherwise, the school is maintained as much as possible (Huber, 1980b).

- The non-swimming behavior appears to be just a strange exceptional adaptation to the standard poor capacity of swimming of Aplocheilids. It concerns differently two species, or maybe only some populations of these. The Old World *Aphyosemion franzwerneri*, restricted to extremely shallow biotopes with a deep blanket of loose substrate, is not able -and do not need to- swim in the upper layers. Inversely, the New World *Rivulus atratus* is a top-layer, often collected in mid-river deep waters. Individuals have difficulties to swim downwards and especially to remain near the bottom. They are immediately disequilibriated and lifted to the surface (Huber, 1992).

- The cannibalistic behavior, although rare, has appeared on both sides of the Atlantic for two groups of Aplocheilid fishes with similar morphological characters, featuring a possible remarkable convergence. In both the Old and the New Worlds, the cannibalistic forms are characterized by a very large size, a rounded massive morphology, an obvious widely opened and protruded, gape-formed, mouth with stronger teeth, a very long head, a relatively smaller eye, a strong depression at the frontal level, a strong reduction of body depth behind the anal fin level, all fins rounded and advanced, a generalized color pattern and an annual condition. Many of these characters are assumed to be primitive, relative to the other components of their phylogenetic lineage. Whether the cannibalistic is a relict primitive behavior or not is unknown. However, the predatory behavior is not shared by other primitive species in temperate Cyprinodonts and it is likely that it is adaptative. In the Old World, these are the adults of *Paranothobranchius s.s.* which eat their sympatric small-sized congeners of the other subgenera *Zononothobranchius* and *Aphyobranchius* (Wildekamp, pers. comm.). In the New World, these are the adults of the subgenus *Cynolebias s.s.*

(Huber, 1995) which eat -not exclusively- their small congeners of the *nigripinnis* superspecies, of the *Simpsonichthys*, *Plesiolebias* lineages. For example, *Cynolebias* monstrosus feeds on "*Plesiolebias*" *bitteri* and *Simpsonichthys chacoensis* (Huber, 1995). Actually, cannibalism not only concerns the juvenile fishes of the predated species, but also the adults 4-5 cms long and the young of their own species. In this regard, this behavior is an extreme of the cannibalistic behavior that has been observed with many Aplocheilids under aquarium conditions when food has been restricted for a long period, between parents and their fry, or, among fry of very different sizes.

5.2- The sexual behavior.

5.2.1- The shared general postures.

Both in Africa and South America, the two major lineages of Cyprinodonts exhibit the same sexual behavior types, as for the non sexual behavior. This is verified whatever the dedicated substratum for egg-laying is (Huber, 1996):

- water plants and overwhelming terrestrial plants (roots, small branches with leaves) for non annual Aplocheilids and most Aplocheilichthyins, in the upper layers of the water;
- bottom mulm, debris and dead leaves for annual Aplocheilids;
- rock holes for a special group of forest Aplocheilichthyins of the lowland, in (sub)genera *Procatopus*, *Plataplochilus* and for the lacustrine *Lamprichthys* in lake Tanganyika.

All Aplocheilid species lay eggs one by one among the substratum in a typical posture: an elongated "S" features the parallel close contact of both sexes (Ewing & Evans, 1973). Eggs develop within 3 weeks for non annuals and in 2 to 9 months for annuals, with optional diapauses for the former, that are compulsory for the latter. However, as stated previously (§ 3.1), intermediates are known in the egg membrane structure or in the incubation period (4-6 weeks in semi-annuals). Premating behavior is also the same on both sides of the Atlantic. First, the mutual recognition process based on the female's choice of the displaying male of her own species. Second, the male drives the female to the decided spawning place from above, nearly chin to chin.

All Aplocheilichtyin species lay eggs, also one by one, on their chosen substratum. However, the contact is not real or imperious, since the pair remains aside although parallel. Premating signals are poorly known, although the same display of male fins and colors occurs too. This scenario appears a priori to be less successful than the Aplocheilid one. Since the abundance of both groups is similar in the preferred niches, it is probable that the prolificity of the Aplocheilichthyin is greater.

The sexual behavior of the tropical Cyprinodonts is rather of a primitive type, although stringent environmental conditions, like seasonality in the biotopes, have pushed the ancestor to an adaptative behavior and thus to annualism. This is not truly primitive as in pelagic fishes (however, the breeding of the single fully pelagic tropical Cyprinodont, *Laciris pelagicus*, is unknown), this is not advanced either like in the fish families where parent care occurs, e.g. in Cichlids, in Anabantids.

5.2.2- The particularities in sexual behavior: eggstranding, diving, dancing and viviparity (Huber, 1996).

All particularities in sexual behavior are, as for non sexual behavior, rather extremes of a general behavior.

Eggstranding is, as mentioned above, a direct consequence of the unique ability of *Rivulus* species to jump out of the water and remain in the damp for a while (Huber, 1992). There, the eggs can be laid with a better safety ratio, than in the upper layers of the water, as for all other non annual species.

Diving too is an extreme of the general behavior of bottom spawning: the pair dives completely and disappears in the substratum to lay each egg. This unique behavior depends on the willingness of the pair (i.e. some pairs or some species simply do not dive within the same phylogenetic lineage) and obviously on the structure of the substratum. However, this behavior is only known for some neotropical annuals. And there is no immediate explanation, since the substratum of the annual biotopes is similar in Africa and in South America, and more importantly, there are non divers in South America that are sympatric with divers. This behavior appears none the less superior to the bottom spawning: better protection of the parents, of the egg, more deeply buried. Even if the parents lose mutual contact by sight, their numerous contact organs on scales and fins, present in all annuals, must compensate this deficiency. However, this superiority appears slight, because males of pure bottom spawners move the substratum a good deal around the egg by a sweeping movement of the tail.

Dancing is a particular case of the premating display of fins of the courting male with competing males and the laying female. This dancing strategy is only documented in some rare cases like *Procatopus* (parallel to their viviparous couterparts of *Xyphophorus*; Clausen, 1967), in the *Aplocheilus blockii* superspecies (Scheel, 1968), in the "*Plesiolebias*" *bitteri* superspecies (Huber, 1995), i.e. parallel in the 3 continents.

Viviparity is also observed in both lineages of tropical Cyprinodonts and in both continents, although it is a rare character. Likewise, it can be considered as an extreme of the general oviparity, with intermediate cases: true viviparity is only observed in the neotropical Poeciliins and in one (or two) species of Sahelian *Epiplatys*, for only some far eastern populations (Guma'a, 1982 for *Ep. bifasciatus* and Werner, 1919 for *Ep. marnoi* in Sudan).
All Aplocheilichthyins from Africa and South America are oviparous. But one Poeciliin species, *Tomeurus gracilis*, is decidedly oviparous (as a reversal example?). Most Aplocheilids do not exhibit internal fertilization. But one neotropical genus does, *Campellolebias*, for which the male has an active gonopodium-like modified anal fin. An intermediate, with oviparity, is the vicariant genus *Cynopoecilus*, for which only a transient folding of some anal fin rays fails to provide the internal fertilization capacity. A different response to the same adaptative process concerns *Rivulus*: most species are oviparous, but one, *Riv. marmoratus* is self hermaphroditic: hermaphrodites, female-like, lay not only fertilized but also nearly ripe eggs, a significant part of the 3 weeks' embryological development being internal.
Further, the availability of sex chromosomes, as yet only known for three tropical species (*Nothobranchius guentheri*, *Pterolebias hoignei* and *Aphyosemion mirabile*), in the Old and New Worlds, is probably a general matter. This derived character goes in the same direction as viviparity.

6- The major phenotypes and the morphomeristics.

Basic morphotypes of the Old and the New Worlds not only look alike, as stated in the introduction, but also their derived phenotypes. This is especially striking with the dwarf relict species, usually in monotypic (sub)genera. Like *Adamas formosus*, *Aphyoplatys duboisi*, *Episemion callipteron*, *Congopanchax myersi* and *brichardi*, *Hylopanchax stictopleuron*, *Epiplatys (Pseudepiplatys) annulatus*, *Foerschichthys flavipinnis*, *Poropanchax scheeli* in Africa. And like *Rivulus (Anablepsoides) atratus*, *Terranatos dolichopterus*, *Maratecoara lacortei* and *formosa*, *Spectrolebias semiocellatus*, *Cynopoecilus melanotaenia*, "*Plesiolebias*" *bitteri* in America. These phenotypes clearly relate, by morphology, to those of nearby diversified Cyprinodonts (phylogenetic relationship or convergence).

6.1- The global stability dimension, together with the local variation (see also table 2).

Stability of the morphology ends up in genera of over fifty species, like *Aphyosemion s.l.*, *Rivulus*, *Micropanchax s.l.*, *Cynolebias s.l.*, *Nothobranchius*, in the Old and New Worlds to the same extent. This is certainly the opposite among temperate Cyprinodonts. Especially among the lacustrine components of the Cyprinodontins (*Aphanius*, *Cyprinodon*, *Orestias*), the morphological differentiation is high and the genetic differentiation is low (Strecker *et al.*, 1996). The evolution of the tropical Cyprinodonts is then completely distinct from them. The reclusive biotopes, the generalized sympatry have surprisingly not promoted morphological differentiation to a great extent, but, genetic plasticity (see further § 7.4).

To the overall stability of the tropical Cyprinodonts basic morphotypes, corresponds an unexpectedly higher variability in the detailed characteristics of downstream lineages and of their member species. A striking resemblance between old and New Worlds tropical Cyprinodonts lies indeed in this variability, that overlaps from one species to the other or from one superspecies to another:
- most morphomeristical characters are more variable within a species or within a population than their corresponding averages between distinct species. And these variations overlap, as in the number of rays in fins, the proportions of the body, the scale counts. For example, the dorsal fin count averages vary from 6.7 to 8.1 among the 8 components of the *Rivulus urophthalmus* superspecies, whereas the fin count varies by 4 rays on average for each species (Huber, 1992);
- all micromorphological characters show the same variability, like the frontal scalation system, the cephalic neuromasts structure and organization, the ctenoid-like spines on scales and fin rays (Huber, 1998a,c). This situation is a priori somewhat unexpected, since these micromorphological characters may only vary discontinuously (e.g. frontal scalation of type D or E; 2, 3 or 4 supraorbital pores). However, a closer study of these micromorphological characters reveals that minor progressive changes induce the modification from one type to the other (Huber, 1981, 1998a) (see further, § 6.2);
- for all Cyprinodonts species, there are populations (Brosset, 1982), with a reduced average size, on a hazardous basis ("nano-populations");
- most Aplocheilichthyins exhibit an allometry in growth.

6.2- Major presumably primitive and derived characters of body and fins.

Relative to their own groups, species with presumably primitive external characters can be defined by a larger size, a deeper body, a set of rounded short fins, rather advanced fins (shorter predorsal and preanal lengths) and rather superimposed (a lower deviation of the dorsal fin insertion to the anal insertion), long-based fins, an annual behavior (see also Table 2). Reciprocally, derived forms exhibit the reverse state of these characters. In addition, primitive color patterns tend to be generalized: rare scattered red markings, more frequent yellow or blue markings (Huber, 1998a). However, derived characters tend to be different in the Old World and the New World, especially fins shapes and extensions. Lyretails and filamentous posterior rays are the specificities of Old World Aplocheilids like *Aphyosemion et al.* Whereas filamentous fins with the extension of anterior and central rays are for neotropical annual genera like *Pterolebias*, *Simpsonichthys*. And likewise, for the micromorphological characters: frontal scalations, generally of the G-H-types in the Old World, of the D-E-F-types in the New World. Conceivably (Huber, 1998a; Scheel, 1990), the primitive frontal type would be the A-type, since the A scale is overwhelming the pineal organ. However, this pattern is not seen in tropical Cyprinodonts, whereas it is frequent in the temperate Fundulid Cyprinodonts. It is therefore difficult to determine which of the available types is more ancient in each continent and between them. The same remarks would apply if the cephalic neuromasts patterns were considered (especially, for Aplocheilichthyins: Huber, 1998a) (see details in table 2).

It is hypothetized here that the differences in the occurrence and types of derived characters between the Old and the New Worlds result from the longly separation of the continents: chance overcomes the similar responses to similar environmental constraints. In total, evolution has combined as much as possible this limited diversity in derived morphological characters. It results in limited major lineages -less than 15 in over 400 Aplocheilids- if one excludes the dwarf relict, usually monotypic species. And only 2, in Aplocheilichtyins, a slender and a deep-bodied lineage.

7- The color patterns and the genotypes.

Within a species or a population (a series of tribes or schools in the same continuous biotope), the color pattern and the genotype are rather stable, in contrast to the morphomeristical overlapping variability. This relative fixity is probably a necessity in the environment of sympatric and similarly built species.

7.1- The limited color pattern portfolio, together with a highend combinations level.

Most species of tropical Cyprinodonts (notably Aplocheilids) are "produced" from a limited number of patterns in the various parts of the body and fins of the male, the female being subdued (i.e. with dark brown reduced markings at the same place). These are (Huber, 1992): series of continuous or discontinuous spots or lines, complete or interrupted, series of vertical or oblique bars, series of chevrons, series of bands, various blotches, in different colors (generally red, rarely yellow-green, exceptionally blue), in different places (anterior sides, posterior sides, dorsal and anal fins, caudal fin, marginal or submarginal, on the opercle or behind it). A superspecies develops all these possibilities to create up to twelve well identified isomorphic phenotypes (i.e. with a similar morphology, with comparable meristic data, with similar fin extension types): see the example of the *Aphyosemion ogoense* superspecies and its 9 components in § 4.4. Indeed, no case of two components of the same superspecies, with disjunct and significant ranges, and the same color pattern, has been reported: rather, each component with a definite color pattern is replaced by another, with little continuity in between, which along with the high genotypic variations leaves little place for the subspecies concept. As mentioned already, each component breeds true to its characteristics, even in the closed and artificial environment of the aquarium. Finally, each superspecies may be characterized by a specificity in color pattern which is seldom seen elsewhere. For example, the so conspicuous and banal lower red band on sides of the *cameronense* superspecies can only be disclosed in three other Aplocheilid species, never sympatric with it, over the entire range.

This highend capacity of combining a limited set of colors and patterns in an astronomical number of species, each being unique, is a major characteristic of the Cyprinodonts basic lineages which, besides, do not have many contrasting morphologies, biotopes, foods, behavior types, but two or three.

However, a detailed analysis reveals that Old World and New World Aplocheilids have developed, as for fin shapes and extensions, specificities. The ocellus is more a neotropical character (*Rivulus*) although this is faint in *Aphyosemion* of the western groups (*Scriptaphyosemion*, *Archiaphyosemion*). The post-opercular, the pre-opercular and the mid-side blotches are more neotropical characters (respectively in *Rivulus/Pituna* and *Cynolebias/Simpsonichthys*), but they are not exclusive (*Scriptaphyosemion*, *Nothobranchius*). The oblique bars on sides are more African than American (*Epiplatys*), although it is seen in one odd *Rivulus* species (*atratus*). The red or dark reticulations on the lower head (the "shield") is frequent in most African species, although it is only seen in *Campellolebias* and *Leptolebias* species of southeastern Brasil or somewhat reduced in some *Rivulus* (the *geayi* superspecies). The conspicuous margins and submargins in fin patterns are more emblematic of *Aphyosemion* species and rare in *Rivulus* (the *urophthalmus* and *isthmensis* superspecies). Specificities per superspecies are in table 2.

The separate and different "choices" that have been made since their drifts in the three disjunct zones in terms of color characteristics seems, as for fin appendages, to be the result only of the long separation.

However, two historical differences should be studied in more detail:

- the 15 degrees northern drift of Africa, while America was static, has had major impacts on the composition of the flora and consequently on distinctive pollens that yearly fell by tons

on Cyprinodonts biotopes;
- the repeated stronger monsoon climate in the Old World than the New World has had major impacts on the biotopes discontinuity, variability and structure.
In this context, it is worth mentioning that unlike African *Aphyosemion*, the American *Rivulus* surprisingly lose their bright colors after a while in aquarium (Huber, 1992), although they live in identical biotopes with the same water composition, near to pure rain (see also the major difference in floral composition and richness between the Old and New Worlds, § 3.1.1, which must have impacted the biotopes over time).

7.2- The sympatric and allopatric color phases.

Both in the Old and New Worlds, sympatric individuals or allopatric species occur with identical color patterns, except for the external margins of fins which are either yellow or white/blue. This is an additional variability dimension, that has been established in numerous cases, but this is not universal. Sympatric individuals of yellow and blue color phases have been reported for *Aphyosemion cameronense*, *A. gardneri*, *A. ogoense*, *A. pyrophore*, *A. calliurum*, *Rivulus urophthalmus*, *Riv. pictus*, *Epiplatys sexfasciatus*, *Pachypanchax omalonotus*, *Nothobranchius korthausae*, *N. kafuensis*, *Aplocheilus panchax*, *Procatopus similis*, *Lacustricola pumilus*, *Poropanchax hannerzi, Procatopus similis, Cynopanchax bukobanus*, etc. Vicariant related species with two color phases have been reported for *A. bualanum* (blue) and *A. exiguum* (yellow), *A. lamberti* (blue) and *rectogoense* (yellow), *A. chauchei* (blue) and *schioetzi* (yellow), *A. toddi* (blue) and *occidentale* (yellow), *Riv. geayi* (blue) and *Riv. agilae* (yellow), usually with a transition between forest and derived savanna. Then, reproductive barriers have been established between these vicariant components following genetic exclusion, whereas there are none in the first case of sympatry.

7.3- The color convergence.

The color convergence is a mysterious but established phenomenon in tropical Cyprinodonts. It could be argued that it is only the result of chance, because of the limited portfolio of color patterns and their combinations. However in that eventuality, cases of color convergence would have been reported among sympatric components of sympatric superspecies. Rather, all cases of color convergence correspond to facing frontier species of distinct superspecies and to derived singular color patterns.

As in *Aphyosemion*:
- *celiae* is the frontier species of the *calliurum* superspecies in the Cameroun coastal plain, facing *cinnamomeum*, the frontier species of the *gardneri* superspecies in the plateau, both with a unique shared color pattern of the caudal fin: a crescent shape organisation of colors;
- *marmoratum* is the frontier species of the *oeseri* superspecies in the Nigeria/Cameroun coastal plain, facing *mirabile*, another frontier species of the *gardneri* superspecies in the plateau, both with a marbled pattern of posterior sides and vertical fins;
- *exigoideum* is the frontier species of the *striatum* superspecies in the Gabon coastal plain, facing *joergenscheeli*, the component of the *ogoense* superspecies in the plateau, both with a circumcaudal red line on a blue-green background;
- *rectogoense* is the frontier species of the *elegans* superspecies in the Gabon/Congo savanna plateau, facing *ogoense*, the frontier species of the *ogoense* superspecies in the same but forested plateau, both with a basal red line on lower sides and a flamed caudal pattern;
- Tirbak's undescribed species is the frontier species of the *ogoense* superspecies in the Gabon forest plateau, facing *coeleste*, both with a deep blue side pattern and a broad yellow and a thin red submargin in the vertical fins.
And this does not concern *Aphyosemion* only. For example, in the New World, *Pterolebias phasianus* is the frontier species of the *longipinnis* superspecies, which shows the same pattern in details than *Trigonectes* (see also table 2, for additional examples).

7.4- The genotypic plasticity, as a witness of flexibility in a stringent environment.

The highend spectrum of definite species-color patterns is the external picture of the genotypic plasticity in Cyprinodonts, in contrast with other major groups of fishes which have eventually differentiated themselves on the basis of morphology and/or behavior and/or habitats, but not -or much less- on genotype.

The genotypic variation has been exemplified on karyotypes (Scheel, 1968 et subseq., Mallabarba *et al.*, 1988 et subseq.), on protein phase contrast (Etzel, 1981 et subseq.) and on DNA-RNA contents (Bernardi *et al.*, 1990; Murphy & Collier, 1996 et subseq.), for both the Old and New Worlds. It has been interpreted as a lottery process (Brosset & Lachaise, 1995), along the still today frequent ecological disruptions. It is a major characteristic of the tropical Cyprinodonts, more so for the static Aplocheilids than the dynamic Aplocheilichthyins. For example, the haploid chromosome number varies between 10 and 20 among the components of the already mentioned *Aphyosemion ogoense* superspecies (Scheel, 1990), which is a huge variation, unique among fishes. Unlimited parallel examples could be forwarded both in the Old and New Worlds, and among annuals and non annuals. These variations proceed from 2 basic genomic combinations: centric fusion and pericentric inversions (Scheel, 1974). This often results in a sterile crossing between species and even between populations of the same "species-name".

In tropical Cyprinodonts, the highest known genotypic plasticity corroborates with species richness (sympatry of several superspecies) and consequently to refugia. Based on similar observations for other reclusive animals (frogs, *Corydoras* fishes and, according to Clapperton -1993a-, grasshoppers, butterflies), it is hypothesized here for the first time that the genotypic variation is a recent event in Cyprinodonts. It would be due to the extreme climatic fluctuations and to the consecutive restriction of the environments of these fishes (forest coverage fragmentation, ephemeral biotopes discontinuity), for those phenotypes that have survived to extinction.

The genotypic plasticity, as mentioned in the introduction, is even higher than the color pattern typicality. For example, several identical phenotypes that can be attributed to *Aphyosemion ahli* in coastal Cameroun have been shown, although collected in not distant localities, to have very different, not compatible karyotypes. The fragmentation of the biotopes during the milder period of glacial times and the consecutive isolation of populations for long times can only explain this situation. When more normal ecological conditions returned, there was no fusion of populations, which had become intersterile biospecies, with no need of mutual rejection (see the neutralist theory, § 5.1.2). The extreme of complexity is obtained in the Congolese cuvette (Huber & Scheel, 1981), and probably also in the Amazon basin, where the return of wetter periods induced a continuity of waters (see previous, the huge freshwater lakes § 2.4) which mixed the distribution of the already intersterile *Aphyosemion* populations. The observed complexity in the coastal *Chromaphyosemion* (Scheel, 1974) or the inland *Diapteron* (Brosset & Lachaise, 1995), is very high, although less puzzling in nomenclature.

Is this recent event of explosive genotypes even as recent as the Holocene?

With Cyprinodonts, reality always ends up in a more complex pattern than anticipated and indeed the non rationality in the distribution of the sympatric superspecies and the huge karyotypic spectrum are examples of that complexity and of a supposed accumulation of recurrent events.

Still, most considerations that have been analysed here, from the island clocks to the generalized refugium theory, from the twofold effect of the two last glacial periods to the still present regular disruptions of the reclusive biotopes, concur, for at least many species, to a positive response.

CONCLUSION.

This thorough detailed and parallel comparison of the characteristics of Old World and New World tropical Cyprinodonts is the first transversal and global analysis in this group.
Of course, the modern knowledges in tectonic plates and in palynology are better founded. They have permitted that this comparison is structured and argumented.
Even if still a lot has to be understood, deepened or simply confirmed by experiments.

Finally, we would like to synthesize the various aspects of this comparison with a different viewpoint and in two segments. The similar responses to the same changes, the different and apparently specific responses to these changes. The former may be reflecting the memory of the ancient Cyprinodont phenotype, the latter may be its first true differentiation between the three aggregate regions, after probable considerable extinction intervals.
Similar responses to similar changes or situations:

- The various potential niches are occupied similarly in Africa and America, either by annual or non annual Aplocheilids in reclusive passive waters or by Aplocheilichthyins in somewhat less reclusive active waters. It is a shame then that no annual component has been transferred into Asia along the northern drift of Madagascar and India.
- The general distribution pattern is clearly the same in all regions, with 5 possible longitudinal strates along the coast (marine, brackish, freshwater coastal lagoons, internal lowlands including the cuvettes, and the neighboring plateau). Within the plateau itself, vertical patches of superspecies are similarly observed. This major shared asset is all the more important that it is not seen, to our knowledge, in the other major groups of fishes, which are linked to river drainages. Apart from the key roles of the transition coastal plain-plateau and of the fluctuations of the sea level, the major driving force appears to be the forest coverage -or conversely, the ephemeral biotopes continuity- over past periods.
- The general response to disturbances is the same, whatever it stems from climatic fluctuations (here the key role of refugia can be exemplified) or from tectonic disruptions creating constraints and opportunities.
- The general speciation mode, by vicariance, is the same whatever the basic group is concerned: diversification of superspecies at borders with frontier species as a direct consequence of migration from relict places of the past dry maximums.
- The same local structure of independent micropopulations -of the same species or of sympatric distinctive superspecies- is a consequence of the defensive selection of reclusive biotopes and of the neutralist behavior, by these fishes, contrary to other groups of fishes.
- The global evolutionary response is the same in terms of general morphotype. The observed stability is associated with a detailed variability of morphomeristics and a highend diversity of color patterns and of genotype. The dwarf relict specialized species occur similarly in the three continents. The potentiality of the viviparity and of sex chromosomes is available in the Old and New Worlds.
- The general behavior in tribes or schools is the same, whatever the position in the continuum of annualism to non annualism.

Distinctive responses to similar changes or situations:

- The combination of derived characters is clearly not the same in the Old and the New Worlds. This concerns details of morphology (head shapes, fins shapes and extensions, the cylindrical or deep profile of body, frontal scalations, cephalic neuromast patterns, etc.), of color patterns (organization, specificities), of behavior (particularities, like aestivating). However, each specificity disclosed in one continent for one group also occurs in the other, less exacerbated.

Nobody will now contradict the fact that African, American and Indo-Asian Cyprinodont faunas are separated for so long -at least 90 million years- that resemblances are more the result of convergence than anything else. But these convergences occur everywhere among the two very homogeneous phylogenetic groups, the Aplocheilids and the Aplocheilichthyins. The resemblances are so numerous that the homoplastic characters, derived from a similar or a different response to similar situations, should be related to each of the two basic ancestors. And much less to a stochastic chance.

No doubt these fishes are in every way very different from the standard river fishes and opposite by major traits:
- independent micropopulations of sympatric congeners in reclusive fragile biotopes where they are quasi-exclusive;
- explosive recent genotypes and typified color patterns, together with an amazing basic morphological stability (only 5 basic morphotypes, 3 in Aplocheilids, 2 in Aplocheilichthyins);
- probable recurrent extinction episodes except in refugia, from where a brand new expansion process started again.

The important finding of this study is that, by combining data of paleogeography, paleoecology, vicariance, endemicity, diversity and external characters of extant phylogenetic lineages, it is possible to hypothesize their centers of origin as well as plausible scenarios of the long term history and migration patterns of tropical Cyprinodonts.

The main additional finding of this study is that, contrary to previous publications, the explosive evolution of the tropical Cyprinodonts, is to be found in the near past. Apart from the very old development of the few distinguished morphotypes linked to major Earth events, most of the evolution spur is hypothesized to be recent, linked to climatic fluctuations and especially to the late glacial maximums of the Pleistocene-Holocene. The evolution of these fishes, pushed by similar and severe constraints, is playing with a limited number of options. The many similarities between the Old and the New Worlds characteristics change then somewhat the picture from a purely haphazard convergence into the disclosure of very few options, variably combined as much as possible.

Stronger constraints make necessity more imperious.

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The modern paleo-reconstructions reflect a high correlation ratio with our present knowledge on extant Cyprinodonts. But, they will need to be updated along any improvement. And obviously, these complex themes, such as plate tectonics, paleo-climates, refugia, orogenic migration patterns, could only be superficially tackled in this global, then limited comparison. No doubt that the renown experts of these fields will understand the constraints and limitations. In addition, the herein modelization approach bears in essence a limitation. It is comparative and global and naturally tends to generalizations. Although many of these may be correct, the biological complexity will surely point out the limits of generalizations and also some erroneous reasoning. More importantly, these models have been designed to be tested over by the new and promising, but not ultimate, molecular techniques as well as by the other basic approaches in osteology and external morphology, now that computer softwares (e.g. PAUP) provide an impressive support (Huber, 1998c). Together with its synthetic and unique transversal approach, and its spur to undertake additional collections, especially in the putative refugium areas, in lowland bridges and in frontier zones of superspecies distributions, this is surely the key target of this work.

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Tab. 1. Major paleontological dates (tectonic, orogenic, climatic, floristic) with their possible biogeographical consequences on the tropical Cyprinodont fauna, according to the present knowledge.

205-170 MYA	The unique Pangean supercontinent, with two subunits Gondwana in the south and Laurasia in the north, enforced from the east by the Tethys sea, possible origin of the Cyprinodontiformes ancestor, with an alternative scenario in Antarctica for the Aplocheilids, at least. Inferred monsoonal circulation of air and absence of polar front, induced by persistently or seasonally drier conditions in low to mid latitude (early and mid Jurassic).
170-150 MYA	First fragmentation of Pangea. Opening of the northern proto-Atlantic ocean. The Antarctic continent with the modern Madagascar and India, still attached to rest of Gondwana (last hypothesized connection of Africa and Antarctica, 148 MYA). Global climate is warm in Antarctica. Temperature gradient is low from equator to pole. Equatorial region appears dry, even arid (mid-late Jurassic).
145-138 MYA	Opening of the southern proto-Atlantic ocean, northward from South Africa (late Jurassic), in 3 phases: south, up the Porto Alegre-Walvis-Montbasa discontinuities; central, to the level of Pernambuco-Ngaoundéré sediments; more northern, with the (then) equatorial domain. Dominant flora: ferns (Gymnosperms). Gondwana is hypothesized to be seasonal and dry, before drift. The minimum age for a southern vicariant scenario of Aplocheilids (at least) stems there (just before the widening of the southern proto-Atlantic).
135-130 MYA	First fragmentation of Gondwana, into western and eastern Gondwana. A rifting process, similar to the present Rift lakes, in Africa. Disconnection of the united block Madagascar-India from Antarctica, drifting northward. The minimum ages of the Aplocheilid lineage of *Pachypanchax* (and possibly of the Aplocheilichthyin lineage of *Pantanodon*) are derived from the Madagascar separation. An alternate, and probably less old origin of Madagascar-India lies at the level of Kenya-Tanzania. Proto-Cordillera in South America. Southern tip of South America, still attached to Antarctica until circa 130 MYA (early Cretaceous).
120-105 MYA	Africa and South America, only connected by a land bridge at the level of the present coast between Cameroun-Sierra Leone and finally of, either Liberia or more probably Nigeria at the level of the Niger delta (early Cretaceous). The minimum age for an east-west vicariant scenario stems here, between Africa and South America. Most Cyprinodontiformes basic morphotypes may exist, although the oldest fossils in Atherinomorpha, their upper level relatives, are dated early Tertiary or 60 MYA, as a minimum.
105-90 MYA	Complete separation of Africa and South America (about 90 MYA, 200 km between the two coast lines, approximately the present distance between Africa and Madagascar). But still island bridges, up to 65 MYA (the total separation process has been very long, circa 80 Million years). South America is an island (until 3.5 MYA). Occurrence of epicontinental seas at the Niger and the Magdalena rivers levels in western Africa and northern South America (late Cretaceous).
90-85 MYA	Complete separation of Madagascar and India, the latter drifting northwards. The minimum age of the Indo-Asian extant genus *Aplocheilus* lineage stems there. Temporary regression and closure of the African epicontinental sea

	(late Cretaceous). The absence of highlands (yet), the presence of a northern seaway (north of Morocco) and the warmer temperature of ocean induce (also in America) moisture air masses to penetrate well inland of Africa. Angiosperm diversity increases explosively.
80-65 MYA	Re-opening of the epicontinental sea in Africa and its definitive regression and desiccation: during 20 MYA, Africa is split into two subunits with a north-south cut between the present Maghreb and Niger delta (late Cretaceous-Paleocene). A smaller southern epicontinental sea occurs along peaks of sea levels, including during the late Tertiary, at least, with consequences on Cyprinodonts. Separation of Seychelles from India (66 MYA) at the level of the Deccan Traps, with associated volcanism, after the opening of the Mascarene basin (78 MYA). During late Cretaceous, Seychelles were an integral part of India (hypothesized minimum age of separation of the two lineages *Aplocheilus* and *Pachypanchax*). Climate progressive change with further establishment of Angiosperms rain forest. Continuous northward drifting of the African continent, the equator being about 15 degrees more to the north, while South America stayed in the same position. Equatorial or tropical climate being prevalent in Sahara (late Cretaceous and early Tertiary, from Paleocene to early Eocene).
65-60 MYA	The C/T boundary. Massive extinction in fauna and flora. Collision of a large asteroid with a probable major impact in the Caribbean (65 MYA). Proto-Antilles arch, connecting South America to Mexico and Florida (uncertain dating: may be earlier, 70-80 MYA, or much later 40-45 MYA). The Caribbean plate is thought to have arisen in the Pacific Ocean and drifted eastward from 80 MYA. Progressive break of the Greater Antilles into the present Cuba, Hispaniola and Puerto Rico. Longitudinal asymetry: much more surfaced islands from north to south, i.e. from Greater Antilles to Lesser Antilles. Ancestors of *Rivulus roloffi* from Hispaniola and *Riv. cylindraceus* from Cuba are about that age. *Millerichthys*, from coastal eastern Mexico, should be too (or trapped in a drifting earlier microplate).
53-32 MYA	Rain forest with extant floral taxa well established. The Guinean dorsal uplift results in the isolation of the Sahelian and west African coastal fauna. The Andean uplift reaches an altitude of 5000 m (45 MYA). The Eocene "stability" period: forests, well established with extant flora. Equatorial African flora moves with the continent northern drift. Dry seasonal climate, south of a line Paraguay-Argentina. Viviparity in Poeciliins.
30-20 MYA	The late Eocene boundary with major extinction (30 MYA). Putative first appearance of an ice cap on the Antarctic pole (30 MYA). Closure of the Colombian epicontinental sea. First disclosure of Cyprinodont fossils (but none in the Aplocheilid or the Aplocheilichthyin lineages). Connection of India with Asia (25 MYA), with the Himalayan uplifting (India remained an island during 60 MYA). Strong tectonic activity in Africa, after a long period of stability: rifting and uplifting of domes with further depression of the Rift valleys, and eruption of volcanoes. Strong tectonic activity in South America, with the Andes crisis uplifting (20 MYA). The Andes barrier induces a significant cooling and drying climatic change in South America, especially in Central Brasil.

	(Oligocene-early Miocene).
20-18 MYA	Late Oligocene cooling period: rain forest is fragmented by open woodlands and savannas.
17-15 MYA	The "Miocene Climatic Optimum". High sea levels. Asia is about 3.5 latitude degrees, south of its present position (a drift of 400 km).
14-12 MYA	Africa stabilized in its present latitude position. Equator fixed in northwestern Gabon (Middle Miocene). Arabia and northeastern Africa come into contact with the Iranian and Turkish position of southwestern Eurasia allowing faunal exchange between Africa and Asia (for Cyprinodonts, only the southern invasion of the temperate genus *Aphanius*). Reversal of climate and temperature towards aridity and cooling (the northern seaway is now reduced to the Proto-Mediterranean sea): extension of savanna, restriction of forest to between Sahara and southern Zaïre, and, to between central Venezuela and central Brasil.
10-9 MYA	Proto-Panamean arch, irregularly connecting south to central America, at Costa Rica level. Opening of a southern epicontinental sea at the present La Plata, well into Argentina-Uruguay-Paraguay. Cooler period: a Mediterranean climate in Africa and South America. Creation of the oldest Rift valley lake, the Tanganyika. The fossils show the same morphology as the extent forms in the genera *Fundulus* and *Aphanius*: their minimum age is estimated 5-10 MYA (late Miocene).
8.8-6.4 MYA	Stable climate in Africa, warm: West Africa, humid. A gigantic lake probably occupies the entire Zaïre basin (early Pliocene).
6.4-2.5 MYA	Drier and cooler climate with major extension of the savanna in Africa, South America and Asia, but not with full synchronicity. Putative first appearance of an ice cap on the Arctic pole (6 MYA). Another major extinction wave and a drastic cooling with a 70 m drop in sea level occurs at terminal Miocene (5.2 MYA), inducing the dryness of the Mediterranean sea, followed by a warmer period with the sea level 80m above present. Marked climatic fluctuations between warm and humid periods and cool and dry periods. Irreversible connection of South America and Central America, originating from the latter, due to the uplift of the Panama isthmus (mid-Pliocene, end of Tertiary, 3.5 MYA). Concomittant last uplift of the Serras of northern Colombia. Drastic cooling with a 100 m sea level drop (2.9 MYA).
2.5 MYA	Another extinction wave and first major glaciation period in the northern Hemisphere, with stringent consequences in tropical Africa and South America (early Pleistocene). Sahara is definitely established as desert (1.2 MYA). Six older glacial periods of early-mid Pleistocene in both continents (exemplified in Bogota samples).

Up to today, 21 glacial to near glacial periods with aridity, alternating interglacial warmer and wetter periods, with melting of ices and upheaval of the Atlantic and Indian oceans levels (Pleistocene to early Holocene). For example, drop of 600 m in water level of lake Tanganyika which is split in three smaller lakes (200 000 BP).
However, faunal migration patterns and pollen data for tropical Asia suggest that forest, rather than savanna, is dominant during that period

	and glaciation less severe (ocean sea levels decrease to the same level, though).
18000 BP	Peak of last glacial period (L.G.M.= "Last Glacial Maximum") which started about 75000 BP (previous severe glacial period between 160 000 BP and 130 000 BP): north Atlantic is a polar sea, glaciers in Atlas, Hoggar and east Africa and the Andes, drop of 3.5 to 10°C in temperature of the sea and land, mean annual rain fall decreased by 25-30% in South America and 30-50% in Africa, hyper arid Sahara (Sahel shifted 300 km southward), "desiccated" lake Tchad, the Congo and Amazon basins strongly shrunk, grassland dominant in past forest, which only remains in refugia, drop in sea levels by 110-120 m, allowing coastal land extension and last connection to islands (e.g. Bioko, Mafia, Zanzibar, Trinidad). Last considerable extinction in tropical Cyprinodonts.
12000 BP	Abundant rainfalls inducing increased humidity, numerous lakes, ponds and marshy areas, many rivers crossing the previous desertic regions. "Holocene Climate Optimum (H.C.O.)", circa 8500 BP, peak of wet warm climate and sudden reappearance of the humid dense forest, with its present delineation; 7500 BP, rainfall decline in Sahelian zone; 6000 BP, the Mega Tchad (300 000 square kilometers); huge extension of the Amazon rain forest and varzeas; 2500 BP, dryness extension north of the 14 degrees northern latitude line.

In total, this historical model highlights:
- the late Jurassic-early Cretaceous congruence of the splitting of Madagascar-India, Africa and America, all from an Antarctica base (150-135 MYA);
- the mainly Tertiary orogenic limited disruptions (70-5 MYA);
- the mainly Quaternary dramatic climatic disruptions (2.5 MYA).

It supports the origin(s), the migration patterns, the morphological stability and the genotypic/speciation explosive diversity of the tropical Cyprinodonts.

Tab. 2. Synthetized data on Aplocheilids and Aplocheilichthyins, at the superspecies level, with putative primitive (p) or derived (d) characters for a quick identification based on *external characteristics*, in relation to the biogeography. Polarized states are given for each character and cautiously recalled for each lineage in view of its quick appraisal. By no means can this be regarded as an effort of a phylogenetic reconstruction for 3 reasons. First, states cannot be considered in absolute terms, but relatively to each analysed clade. Second, the main problem with the external morphology approach (and also with the osteological and molecular approaches) concerns frequent homoplasies (convergence and reversion). Third, the major objective of phylogenetic reconstruction -to recognize synapomorphies at nodes of each group- often meets proper difficulties with Cyprinodonts, because of their morphological uniformity and because of the limited options combined ad libitum by these fishes. The number of presumably valid species-names is given in parenthesis, updated from Huber, 1996. Specificities are mentioned relatively to a greater monophyletic lineage: if derived (d), they may be considered as autapomorphies. The analysis is based on a primitive lineage of temperate Cyprinodonts, as an outgroup.

Characters:
Maximum total length: very large, over 10 cm (pp); large, between 8 and 10 cm (p); small, between 3 and 4 cm (d); dwarf, less than 3 cm (dd). Upper limits are about 10% lower in Aplocheilichthyins.
Relative body shape (vertical): deep (pp), compact (p), elongate (d), slender (dd).
Lateral relative body shape: rounded (pp), slightly compressed (d), strongly compressed (dd).
Upper body line: with a hump back, especially in old male (pp), smooth (p), with at least one disruption (d).
Lower body line (in relation to allometry): smooth (p), with a discontinuity at vent (d), with a disruption at fin insertion (dd).
Front shape: convex (pp), flat (dd).
Relative peduncle shape: very deep (pp), deep (p), low (dd).
Mouth shape: rounded and wide (pp), pointed (dd).
Snout shape: equal to subequal (p), disproportionate (d), oblique (dd).
Frontal scalation: no type or simple (S) type (pp), pineal (A) or circular type (E/F/D) (p), upper type (G/H) (d). Alternative (not studied): upper circular, F-type (d), upper G/H-type (dd).
Frontal neuromasts: in 4 pores (pp), in 2/3 pores (p), limited in often discontinous grooves (d), numerous in lyre-shaped channels (dd). The polarization is tentative.
Interorbitar (relatively): large (p), narrow (d).
Relative eye diameter: very small (pp), very large (dd).
Relative counts at Dorsal and Anal fins: very high and equal (pp), high for Anal, lower for Dorsal (p), low at Dorsal (d), very low (dd).
Relative position of Dorsal versus Anal (D/A): very low or negative (pp), very high (dd).
Insertion of Dorsal fin: advanced, less than 60% of S.L. (pp), remote, over 75% of S.L. (dd).
LL scale count: very high (over 45 for Aplocheilids, over 35 for Aplocheilichthyins) (pp), very low (dd).
Scales covering bases of fins: all (pp), only Caudal fin (p), none or very little (dd).
Side scales, irregularly positioned (pp), in regular lines (d).
Sexual dimorphism in body shape: none or little (p), present (d).
Sexual dimorphism in fin shape: none or little (pp), present (dd).
Sexual dimorphism in fin ray count: none or little (pp), limited (d), strong (dd).
Shape of male Caudal fin (not considering extensions): high and short (pp), low and long (dd).
Sexual dichromatism: none or little (pp), present, usually female subdued (d), strong, distinctive patterns (dd).
Supracaudal ocellus (mainly in female): absent (pp), faint (d), present (dd).
Dark band through eye: extensive and angular (pp), present and limited (p), none (dd).
Dominant markings on male sides and fins: golden (pp), none, except a silver/blue hue (p), blue (d), red (dd).
Melanism: strongly present in both sexes (pp), absent (dd).
Dark bars on sides: absent (p), present (d). The important dark lateral band (permanent or mood dependent) cannot yet be polarized, especially since it may be represented in various forms (median,

lower, upper, anterior, posterior).
Color pattern: generalized, with irregular and more variable markings (pp), derived, with specific design (dd).
Swimming: in mid waters (pp), near bottom (p), near surface (d), at surface (dd).
Breeding: in bottom substrate (pp), dives (p), among plants (d), egg-strander (dd).
Biotope: brackish to marine (pp), ephemeral and stagnant (p), permanent or slightly seasonal with low current (d), permanent with some current (dd).
General posture: straight in less reclusive areas (pp), straight near edges (p), passive, in protected areas (d), loose and downward (dd).
Behavior: no jumper, in schools (pp), no jumper, in tribes (p), some jumping activity in tribes (d), strong jumping and aestivating activity in tribes (dd).
Egg development: compulsorily delayed (strict annual) (pp), possibly delayed (semi-annual) (p), maybe artificially delayed (non-annual) (d), short and hardly delayed (strict non-annual) (dd).
Coverage: today in savanna and gallery forest (p), today in primary forest (d).
Biogeography: an east (pp) to west (dd) global flow is hypothesized. A south (pp) to north (dd) global flow can also be hypothesized, at least for Aplocheilids (the Aplocheilichthyins history is unclear in relation with that of temperate Cyprinodonts). Locally, a brackish/marine (p) to freshwater (d) flow can be hypothesized, as well as a plain (p) to plateau (d) flow, with the exception of some primitive forms trapped in montane highlands.

Groups:
- Old World Aplocheilins (227/232). Frontal neuromasts (limited) in often discontinous grooves (d). Remote insertion of Dorsal fin (dd). No sexual dimorphism in fin ray count (pp). No supracaudal ocellus in female, except in *Archiaphyosemion*, *Scriptaphyosemion*, and in median position, *Paranothobranchius s.s.* (pp). Behavior: some jumping activity in tribes, except *Adamas*, *Foerschichthys* (d).

1- Indo-Asian and Madagascan Aplocheilins (10/12). Smooth upper and lower outlines (pp). No sexual dimorphism in body shape (p). No dark band through eye (dd). Breeding: among plants (d). Biotope: permanent or slightly seasonal with low current (d). Posture: straight in less reclusive areas (pp). Egg development: maybe artificially delayed (non-annual) (d). Specificities: an antero-dorsal black spot, especially in female and juveniles (d); transverse dark lines on throat reminding *Epiplatys*, but different (d).
1.1- *Pachypanchax* (4). Large (pp). Deep body shape (pp). Convex frontal shape (pp). Rounded lateral shape (pp). Very deep peduncle (pp). Rounded and wide mouth (pp). Equal snout opening (p). Circular frontal scalation (p). Interorbitar, unusually large (p). Very high counts at Dorsal and Anal fins (pp). Low D/A ratio (p). Side scales, irregularly positioned, even angled-away for *playfairii* (pp). No sexual dimorphism in fin shape (pp). High and short male Caudal fin (pp). Little sexual dichromatism (pp). Color pattern: generalized (pp). Swimming in mid waters (pp). Coverage: today in savanna and gallery forest (p). Specificity: two series of discontinuous spots at mid Anal fin of male (d). In total, a very primitive lineage, much more by external morphology than *Aplocheilus*. Distribution: endemic to plain and plateau of Madagascar and Seychelles (pp); absent from India and Africa (artificially introduced in Zanzibar).
1.2- *Aplocheilus* (6/8). Flat front (d). Slightly compressed (d). Oblique snout (dd). High count at Anal, much lower at Dorsal fin (p). Very high D/A ratio (dd). Marked sexual dimorphism in fin shape (dd). Sexual dichromatism, with subdued female (d). Swimming at surface, except *blockii* (dd). Coverage: today in primary forest (d). Specificities: pike-like morphology, similar to *Epiplatys* (d); an oval golden shining spot on front (also in *Epiplatys*) (d).
1.2.1- *blockii* superspecies (1/3). Compact body shape (p). Upper frontal scalation type (d). Very low LL scale count (dd). Color pattern: derived, with specific design of gold and red discontinuous chevrons (dd). Swimming near surface (d). Specificities: a pre-mating dancing behavior (independently acquired at least also by *Aphyoplatys*, *Plesiolebias*, *Procatopus* and some viviparous Poeciliins) (d); always shorter Ventral fins (p). Distribution: near the coast of western and eastern India, and all around Sri Lanka (pp); vicariant to *panchax*, with which it may be related, as a specialized smaller-sized sublineage; often sympatric with *lineatus*.

1.2.2.1- *panchax* superspecies (2). Very large (pp). Elongate body (d). Deep peduncle (p). Rounded and wide mouth (pp). Occasionally, circular frontal scalation (p). High and short male Caudal fin (pp). Blue conspicuous markings on male sides and fins (d). Color pattern: derived, with specific design of discontinuous lines of blue and red spots (dd). Specificities: lanceolate Caudal fin shape (d); opportunistic, with sympatric color phases and variability. Distribution: all over Indo-Asia (northerly vicariant to *blockii*), up to Sulawesi (p/d).
1.2.2.2- *lineatus* superspecies (3). Very large (pp). Elongate body (d). Deep peduncle (p). Rounded and wide mouth (pp). Occasionally, circular frontal scalation (p). Low and long male Caudal fin (dd). Color pattern: generalized (pp). Golden conspicuous markings on male sides and fins (pp). Strong melanism in both sexes (pp). Dark vertical bars on (posterior) sides (d). Specificities: dark lower band on posterior sides (d); extended Ventral fins in male. Distribution: similar to *blockii* (pp). In total, the most primitive *Aplocheilus*, close to the paleo-junction with *Pachypanchax* (Deccan Traps).

2- African Aplocheilins (217/220). Smooth upper and lower outlines (pp). No hump back, except *Paranothobranchius* and occasionally *Nothobranchius s.s.* (d). Disproportionate snout, but oblique in *Epiplatys* (d). No sexual dimorphism in body shape (p). Sexual dichromatism, with subdued female, much less so in *guineense* superspecies and *Foerschichthys* (d). No dark band through eye, except the *Nothobranchius* series (minus *ocellatus*) and *Adamas, Foerschichthys* (dd).

2.1- *Nothobranchius* series (42). Convex frontal shape (pp). Very little compressed, except *Paranothobranchius* (not) and *Fundulosoma* (more). No or simple frontal scalation type, with scales more planted than slated (pp). Very high counts at Dorsal and Anal fins, except *Aphyobranchius*, *Fundulosoma* (pp). Very low or negative D/A ratio, except *Aphyobranchius* (pp). Advanced insertion of Dorsal fin, except *Aphyobranchius* (pp). Little sexual dimorphism in fin shape, except *Fundulosoma* (pp). High and short male Caudal fin (pp). Swimming near bottom, except *Aphyobranchius* (p). Breeding: bottom substrate (pp). Biotope: ephemeral and stagnant (p). Posture: passive, in protected areas, except *Paranothobranchius s.s.* (d). Egg development: compulsorily delayed (strict annual), except *Aphyobranchius* (pp). Coverage: today in savanna and gallery forest (p). The most primitive major lineage of the African Aplocheilins (notably *microlepis*) by external morphology, in line with biogeography.
2.1.1- *Nothobranchius* (41). Specificity: red "net" on male sides, delineating the scale border (except *Paranothobranchius*) (d).
2.1.1.1- *Paranothobranchius* (4). Very large (pp). Deep body shape (pp). With a hump back (pp). Side scales, irregularly positioned (pp). Color pattern: generalized (pp).
2.1.1.1.1- *ocellatus* superspecies (1). Very large (pp). Compact body shape (p). Very deep peduncle (pp). Rounded lateral shape (pp). With a discontinuity at vent (pp). Rounded and wide mouth (pp). Interorbitar, unusually large (p). Very small eye diameter (pp). No dark band through eye (dd). Very high LL scale count (pp). Golden conspicuous markings on male sides and fins (pp). Strong melanism (pp). Grey spotless female (p). Posture: straight near edges (p). Specificities: a mid-caudal peduncle ocellus (gold ringed) on female (dd); red blotches on male preopercle (dd); a crescent-shaped color pattern at Caudal fin, gold bordered with black (also in *Neofundulus* and *Rivulus caudomarginatus*, independently acquired); cannibalistic (dd); gape-shaped mouth (dd), with prominent enlarged teeth, as *Cynolebias s.s.*. Distribution: relict, not far from the Tanzanian refugium (p/p).
2.2.1.1.2- *microlepis* superspecies (3). Large (p). Deep body shape, deeper than all other lineages (pp). With a hump back (pp). With a discontinuity at vent, similar to *Cynolebias porosus* lineage (pp). Golden conspicuous markings on male sides and fins (pp). Strong melanism (pp). Grey spotless female (p). Extensive and angular dark band through eye (pp). Specificities: prominent comb-shaped Dorsal and Anal fins in male (d); no red markings on male sides (p). Distribution: restricted to coastal plain of Somalia-Tanzania (p/p); unfortunately, a southern component of this mostly primitive lineage has not yet been collected (South Africa-Mozambica). Remark: this superspecies may also be linked with *Nothobranchius s.s.*, leaving *Paranothobranchius* monotypic.
2.1.1.2- *Nothobranchius s.s.* (8). Very large (pp). Deep body shape (pp). Occasionally, with a hump back (pp). Color pattern: generalized (pp). Specificities: prominent comb-shaped Dorsal and Anal fins in male, as *microlepis* (d); black peppered dots on male preopercle (d); wine red dominant color of male sides (d); black peppered dots on female sides (d). Distribution: coastal plain of Indian Africa,

northwards from South Africa (pp).

2.1.1.3- *Adiniops* (8). Compact body shape (p). Red conspicuous markings on male sides and fins (dd). Specificities: dark wide-angled chevrons on male sides (d); a bright red Caudal fin on male (d); a pre-opercular red "shield" on male, as in *Aphyosemion s.l., Rivulus geayi, Aphyobranchius* (dd). Distribution: similar to *Aphyobranchius* in Indian coastal Africa (p/p), as a derived offshoot of the primitive *Nothobranchius* lineage and in connection to the Tanzanian refugium.

2.1.1.4- *Aphyobranchius* (3). Small (d). Elongate body (d). Slightly compressed (d). Long Anal but somewhat shorter Dorsal fin base (p). Red conspicuous markings on male sides and fins (dd). Color pattern: derived, with specific design (dd). Swimming near surface (d). Specificities: a prominent dark "net" on female sides (d); less strict annual development (semi-annual) (d); higher D/A ratio than the other lineages (d); spawns among plants (p); small papillae on the upper lip of both sexes (d). In total, the most derived, by external morphology, eastern *Nothobranchius* lineage. Distribution: as *Adiniops*, but smaller and not superimposed (p/p).

2.1.1.5- *Zononothobranchius* (17). Compact body shape (p). Red conspicuous markings on male sides and fins (dd). Color pattern: derived, with specific design (dd). Specificities: several conspicuously colored bands on male unpaired fins, notably all around Caudal fin (dd); light brown spotless female (p); strong vertical markings irregularly on male sides (d). Distribution: the largest in *Nothobranchius*, in eastern African plain and plateau (Rift valley) (p), northerly to Sudan and lake Tchad (d).

2.1.2- *Pronothobranchius* (1). Small (d). Compact body shape (p). Short based and rounded unpaired fins (p). Very low LL scale count (dd). Red conspicuous markings on male sides and fins (dd). Specificities: red "net" absent on male, replaced by red spots on scale centers (d). Distribution: as *Fundulosoma*, the strongly derived final western offshoot of *Nothobranchius* in western Sahelian Africa, westerly from lake Tchad (d). In the Mesozoic Rift scenario, it may be the grading vicariant link between *Nothobranchius* and *Fundulopanchax*.

2.1.3- *Fundulosoma* (1). Small (d). Elongate body (d). Slightly compressed (d). Long Anal but somewhat shorter Dorsal fin base (p). Very low LL scale count (dd). Marked sexual dimorphism in fin shape (dd). Color pattern: generalized (pp). Blue conspicuous markings on male sides and fins (d). Specificities: dark, not red, partial "net" (d); a lyre-shaped Caudal fin, with filaments in old male (dd); shape (fan opening) and color (broad submargin) of Caudal fin in male, similar to the vicariant *Aphyosemion walkeri* (convergence). By external morphology, *Pronothobranchius* and *Fundulosoma* may be considered as two independent successive (and often sympatric) sister groups of the *Nothobranchius* series, the latter being more derived. Accordingly, the distribution of the latter is more western and reaches more the coast than the former. *Fundulosoma* has been hypothesized to be closer to *Paludopanchax* (pigments, Caudal fin shape) but this is less supported by osteology and ecological distribution. *Fundulosoma* vicariantly replaces *Paludopanchax* (Togo) and *walkeri* (Côte d'Ivoire/Ghana) when the landscape becomes Sahelian.

2.2- *Aphyosemion-Fundulopanchax* series (108/110). Smooth upper and lower outlines (p). Upper frontal scalation type (d). Marked sexual dimorphism in fin shape, except *ogoense* superspecies and *microphtalmum* (dd). Red conspicuous markings on male sides and fins, except *Diapteron, Episemion, Foerschichthys* (dd). Posture: passive, in protected areas, except *Adamas, Episemion, Foerschichthys* (d). Specificity: a red preopercular pattern of reticulations ("shield") on male (except *Foerschichthys*, and weak on *Adamas, Episemion, Diapteron*). Also seen, weak, in the derived *Nothobranchius* lineages. In *Callopanchax et al.*, the pattern is also present, but differently drawn. By external characters, most -but 2- *Aphyosemion* lineages are strongly derived, in contrast to the *Fundulopanchax* lineages. These 2 lineages live in regions that are candidates as a center of origin for *Aphyosemion*: *Adamas* in the Congo cuvette and *Foerschichthys* in Nigeria. Because of insufficient collection data, because both regions record intermediate forms between *Aphyosemion* and *Fundulopanchax* (respectively *Raddaella* and the *oeseri* superspecies) and primitive endemic forms in other Cyprinodont groups (respectively *Aphyoplatys/Lamprichthys/Laciris* and *powelli*), because both regions also record very derived forms in *Aphyosemion* (respectively *elegans* and *calliurum/bitaeniatum*) and because they are both associated to old migration patterns (respectively the pre-Rift connection and cuvette and the Mezosoic Rift), it is yet hazardeous to select one of the two.

2.2.1- *Aphyosemion et al.* (80). Slightly compressed (d), except *Foerschichthys*. High count at Anal, lower at Dorsal fin, except *Raddaella* (p). Low and long male Caudal fin, much more than

Fundulopanchax et al. (dd). Color pattern: derived, with specific design, except *Adamas* (dd). Swimming near surface, except *Raddaella*, near bottom and *Adamas*, in mid waters (d). Breeding: among plants, except *Raddaella*, near bottom and *Adamas*, *Foerschichthys* (d). Biotope: permanent or slightly seasonal with low current (d). Egg development: maybe artificially delayed (non-annual), except the semi-annual *Raddaella*, *Adamas* (d). Coverage: today in primary forest (d).

2.2.1.1- *elegans* superspecies (*Aphyosemion s.s.*) (12). Slender body (dd). Very high D/A ratio (dd). Specificities: complete correspondance of color patterns on male sides and inner unpaired fins (dots for dots; lines for lines) (d); lyre-shaped Caudal fin in male, with filaments, as in *calliurum* (d). By external morphology, the most derived lineage with *calliurum* and *bitaeniatum* in *Aphyosemion* (convergence? phylogenetic value?). Distribution: endemic to the Congo cuvette and its belts (p/d).

2.2.1.2- *batesii* superspecies (*Raddaella*) (1/3). Very large (pp). Elongate body (d). Very high counts at Dorsal and Anal fins (pp). Low D/A ratio (p). Swimming near bottom (p). Breeding: bottom substrate (pp). Egg development: possibly delayed (semi-annual to strict annual) (p). Specificities: red chevrons on male sides, anteriorily (d); filaments on upper and lower Caudal fin and posterior rays of Dorsal and Anal fins of male (d); lyre-shaped Caudal fin in male (d). Usually placed among the *Fundulopanchax* lineages: distinguished from them by the shape of the Caudal fin (not bilobate or trilobate), by the extended rays on Dorsal and Anal (not the anterior rays), by the fins red color (less generalized), by the peduncular depth (less deep). Shares with them the equal and high number of Dorsal and Anal fin rays (rather superimposed) and the semi-annual development. Confirmed in *Aphyosemion* by molecular experiments (Collier, pers. comm.). Distribution: endemic to the northern Congo cuvette and its belts, plus the neighboring plateau of Gabon and Cameroun (d), probably in line with the lake Tumba refugium.

2.2.1.3- *ogoense* superspecies (10). Elongate body (d). High D/A ratio (d). No sexual dimorphism in fin shape (pp). Specificity: most (but not all) components with a flamed, asymmetrical red Caudal fin in male (d). Distinguished from the related *striatum* superspecies (except *microphtalmum*) by the rounded Caudal fin in male. Distribution: forms a "U" with the *striatum* superspecies (*ogoense* in the plateau, *striatum* in the plain); the most southern distribution for an *Aphyosemion* superspecies, in the Congo plateau, maybe in line with the Mayombe refugium (p), and in the cuvette southern belts (p).

2.2.1.4- *striatum* and *gabunense* superspecies (8). Slender body (dd). High D/A ratio (d). No sexual dimorphism in fin shape for the primitive component, *microphtalmum*, only (pp). Specificities: regular red continuous lateral lines on sides (d); double red band, parallely on Dorsal, Anal and Caudal fins of male (d). Distribution: coastal plain from Cabinda to Ecuatorial Guinea (p) and maybe Cameroun.

2.2.1.5- *coeleste* (4) and *wachtersi* (2) superspecies. Slender body (dd). Very high D/A ratio (dd). Specificities: a conspicuous golden, red contrasted or not, post-opercular zone in male for *coeleste* (d); blue dots on upper sides for *wachtersi* (d). Distribution: at least southern Massif du Chaillu in Gabon (d), in partial sympatry with the *ogoense* superspecies (maybe a northern derived offshoot); may be linked to the Massif du Chaillu refugium.

2.2.1.6- *thysi* superspecies (2). Slender body (dd). High D/A ratio (d). Specificities: thin red or dark vertical bars on male sides (d); short extensions on unpaired fins like *gabunense*. Distribution: relict to the southern Massif du Chaillu, where it is graded (p/d).

2.2.1.7- *wildekampi* superspecies (3). Elongate body (d). Very high D/A ratio (dd). Specificities: a spade-shaped Caudal fin in male (d); near peduncle, the red lines or spots in male agglomerate in a mozaic pattern (d). Distribution: longitudinal, along the western belts of the Congo cuvette (d), in-between the *cameronense* and the *elegans* superspecies. Remark: the southern third component, *aureum*, may also be regarded as a frontier species of the *coeleste* lineage, showing color convergence.

2.2.1.8- *cameronense* superspecies (7). Elongate body (d). High D/A ratio (d). Specificities: most components with a basal red band between Anal fin and peduncle (d); variable color pattern and phases, sympatrically and allopatrically (d). Distribution: the plateau between southern Cameroun and northern Gabon (d), its center of origin being hypothetically linked to one of the lowland bridges (Ogooué, Ecucu, Sanaga...).

2.2.1.9- *calliurum* superspecies (7). Slender body (dd). High D/A ratio (d). Specificities: a black rounded spot on throat of frightened specimens (d); an asymmetrical color pattern between Dorsal and Anal fins on male (d). Distribution: coastal plain from Cabinda to Togo, mainly restricted near the coastal fringe in freshwaters (p/d), but also locally inland; prefers stagnant waters on dead leaves, as *cameronense*, its ecological counterpart.

2.2.1.10- *franzwerneri/pascheni* superspecies (4). Slender body (dd). High D/A ratio (d) for *franzwerneri* and low (p) for the others. Restricted to bottom for *franzwerneri* which besides shows a post-opercular dark blotch (p). Specificities: a black lateral band on female sides (and sometimes male) (d); lives in very shallow waters, as its counterparts *herzogi* and *hofmanni* in the plateau (d). Distribution: restricted to pocket zones in relation to coastal refugias of Gabon and Cameroun (p). Probably an older lineage, related to *calliurum*.

2.2.1.11- *herzogi* superspecies (2). Elongate body (d). High D/A ratio (d). Specificity: divided color pattern of Caudal fin in male (d). Distribution: endemic to shallow waters of the Monts de Cristal in Gabon and neighboring regions of the plateau (d), in line with the refugium.

2.2.1.12- *hofmanni* superspecies (2). Small (d). Slender body (dd). High D/A ratio (d). Specificity: red and blue lateral continuous lines, fading before peduncle (d). Distribution: endemic to shallow waters of the (southern) Massif du Chaillu (d), in line with the refugium.

2.2.1.13- *bivittatum, bitaeniatum* and *loennbergii* superspecies (*Chromaphyosemion*) (9). Slender body (dd). Very low or negative D/A ratio (pp). Very low LL scale count (dd). Specificities: a double temporary black lateral band on sides of both sexes (d); a series of gold or blue-green colored scales on upper anterior sides of male (d); angel-shaped unpaired fins in male (d). Distribution: coastal plain from the Ogooué river in Gabon (p) to Togo (d), in cristal clear waters over sand, as its ecolgical counterparts in the plateau, *exiguum* and *georgiae* superspecies. The older sublineage, *bitaeniatum*, restricted to coastal fringes, the melanistic sublineage, *bivittatum* to the Mont Cameroun refugium, the flamed sublineage, *loennbergii*, including the larger-sized *riggenbachi*, to the lowland bridges pocket refugia.

2.2.1.14- *exiguum* superspecies (*Kathetys*) (5). Slender body (dd). High D/A ratio (d). Specificities: red and blue vertical bars on sides and fins of male (dark on female) (d); smaller mouth opening, as in *Chromaphyosemion* and *Diapteron* (d). Distribution: Camerounian plateau and neighboring regions (d); a possible center of origin in the Cameroun mountains may be hypothetically proposed if the primitive *bamilekorum* from the Bamiléké plateau is confirmed to be related to *exiguum*, but a more attractive hypothesis lies in connection with *Episemion*.

2.2.1.15- *georgiae* superspecies (*Diapteron*) (5). Small (d). Slender body (dd). Very low or negative D/A ratio (pp). Very low or negative D/A ratio (pp). Blue conspicuous markings on male sides and fins (d). Specificities: reverse color pattern on sides and fins of male: blue spots on red background (d); temporary dark thin bars on sides (also *Kathetys*) (d); crepuscular behavior (d); feeds on crustaceans (p). Distribution: endemic to northern Gabon (d) (north of the Ogooué river and east of the Monts de Cristal, with which it may be associated as a refugium).

2.2.1.16- *Episemion* (1). Small (d). Slender body (dd). High D/A ratio (d). Blue conspicuous markings on male sides and fins (d). Specificities: a temporary black lateral band on sides (also in *Kathetys*) (d); a fan-shaped Caudal fin in male (d). Placed in the *Aphyosemion* series of clear waters (and not in *Epiplatys* series) for the first time. Distribution: endemic to the Monts de Cristal in Gabon and neighboring regions of the plateau (d), in line with the refugium. If phylogenetic relationships with *exiguum* are established, instead of *bamilekorum*, then it may be a relict, less derived lineage positioned near the center of origin of the 3 ecological counterparts, *Chromaphyosemion, Kathetys* and *Diapteron*.

2.2.1.17- *Adamas* (1). Small (d). Slender body (dd). Very high D/A ratio (dd). Dark limited band through eye, as in the *Nothobranchius* series (p). Strong melanism in both sexes (pp). Color pattern: generalized (pp). Swimming in mid waters (pp). Breeding: bottom substrate (pp). Behavior: no jumper, in schools (pp). Egg development: possibly delayed (semi-annual) (p). Specificities: a heart-shaped diamond spot on front (d); "lampeye" state (d); larger eye diameter (d); external profile of body and fins, similar to the frequently sympatric *elegans* superspecies, but superficially (hypothetical convergence of *elegans*, when entering into competitive pressure with *Adamas*). In total, an externally primitive and specialized phenotype, with a behavior similar to Aplocheilichthyins (as *Foerschichthys*): the single *Aphyosemion*-like phenotype to have a vicariant distribution with *Nothobranchius*. Distribution: endemic to the entire Congo cuvette including its southeastern part (p/d), in line with the lake Tumba refugium and extended river refugia.

2.2.1.18- *Foerschichthys* (1). Small (d). Slender body (dd). Rounded lateral shape (pp). Very low count at Dorsal (d). Very high D/A ratio (dd). Little sexual dichromatism (pp). Color pattern: generalized without red markings (pp). Behavior: no jumper, in schools (pp). Specificities: a blue shine on sides, like Aplocheilichthyins (p), white margins on unpaired fins of male, as *Poropanchax* (color and morphological convergences in sympatry, similar to *Adamas* and *elegans*) (d); "lampeye" state (d); also, a narrow black line on mid-side as in Aplocheilichthyins (d). Distribution: freshwater lagoons, west of the Niger delta up to Togo (i.e. west of the epicontinental sea) (d).

2.2.2- *Fundulopanchax et al.* (27). Slightly compressed (d). Deeper peduncle than *Aphyosemion et al.* (p). Very high counts at Dorsal and Anal fins (pp). Very low or negative D/A ratio, except *Paraphyosemion* (pp). Anterior rays of Anal (and less so of Dorsal) fins, longer than posterior rays (d). Color pattern: derived, with specific design, except *Gularopanchax, walkeri, arnoldi, powelli* (dd). Larger red spots on male sides, except *oeseri* (d). Swimming near bottom (p). Breeding: bottom substrate (pp). Biotope: ephemeral and stagnant, less so for *Paraphyosemion* (p). Egg development: possibly delayed (semi-annual) (p). Coverage: today in primary forest, except *walkeri*, which lives also in savanna (d). At least, 2 of the 4 lineages seem to have evolved independently from an unknown probably extinct (*powelli* like?) ancestor distributed in the Mezosoic Rift.

2.2.2.1- *Fundulopanchax* (2). Very large (pp). Deep body shape (pp). Specificities: red bars on posterior sides of male (d); filamentous trilobate Caudal fin in male (d); conspicuous red post-opercular blotch (d) (all for *sjoestedti*). The poorly known (from juveniles only) *powelli* is assigned here tentatively (strong melanism and rounded fins in both sexes as very primitive features). Disjunct distribution for *sjoestedti* in two coastal pockets: western Niger delta in Nigeria and lower Ndian river in western Cameroun (d), probably in connection with refugia.

2.2.2.2- *Gularopanchax* (4). Very large (pp). Deep body shape (pp). Color pattern: generalized (pp). Specificities: bilobate Caudal fin in male (d): a broad continuous (or not) red mid-line on male; divided color pattern at Caudal fin (d). Distribution: in coastal pockets (linked with micro-refugia?) between Bénin and Ecuatorial Guinea (and probably Gabon) (d). The Ecuatorial Guinea new phenotype shows less primitive characters (lower fin ray counts, very low circumpeduncular scales, smaller size, derived color pattern), compared to northern components, and may witness the northern origin of that lineage.

2.2.2.3- *Paraphyosemion* (17). Large (p). By external morphology, *Paraphyosemion* is an intermediate between *Aphyosemion* and *Fundulopanchax.*

2.2.2.3.1- *gardneri* (including *mirabile*) superspecies (10). Large (p). Compact body shape (p). Low D/A ratio (p). Specificities: lyre-shaped Caudal fin in male with short extensions (d); symmetrical unpaired fins pattern in male (also in *walkeri*) (d). Distribution: inland Nigeria (up to the Jos plateau, northerly) and foothills of the West Cameroun mountains (d), the derived species-names being more eastern and relict, close to the refugium.

2.2.2.3.2- *ndianum* superspecies (3). Compact body shape (p). Elongate body (d). Low D/A ratio (p). Specificities: a symmetrical red flamed patten on male Caudal fin (d); a red mid-line on male Anal fin (d). Distribution: endemic to foothills at the border of Nigeria and Cameroun (d), in connection with the refugia of the Cameroun mountains and of the Sanaga.

2.2.2.3.3- *oeseri* superspecies (3). Elongate body (d). High D/A ratio (d). Rounded fins without extensions (p). Specificities: red spots on male sides, as in *Aphyosemion* (d); asymmetrical color pattern of Dorsal and Anal fins in male as in *calliurum* (d); tendancy to a reticulated pattern on posterior sides (d) (similarly to *mirabile,* as a color convergence). Distribution: similar to *ndianum,* sometimes sympatrically (d). Remark: tentatively placed here and not among *Aphyosemion,* because of the color pattern, the deeper head, the higher number of circumpeduncular scales, but lacks the so important character of the extended anterior rays of Anal fin in male; also, traditionally placed close to the *calliurum* superspecies, which it replaces inland, vicariantly. An example of the grading variation between *Fundulopanchax* and *Aphyosemion* and more generally between Cyprinodont major lineages.

2.2.2.3.4- *walkeri* superspecies (1). Compact body shape, similar to *gardneri* (p). Low D/A ratio (p). Color pattern: relatively generalized and variable (p). Specificities: a broad yellow orange submargin on unpaired fins of male (d); a post-opercular dark blotch in male (irregular in *gardneri*) (d); a fan-shaped Caudal fin, as *Fundulosoma* (d). Distribution: coastal plain and grading plateau of Ghana and Côte d'Ivoire (d), not vicariantly to *gardneri.* A phylogenetic relationship with *Paludopanchax (filamentosum)* would be more coherent with the biogeographical vicariance.

2.2.2.4- *Paludopanchax* (4). Very low or negative D/A ratio (pp). Advanced insertion of Dorsal fin (pp). Distinguished from the other related lineages by its much smaller size. According to karyotype (*powelli* is unknown), the most primitive lineage: may be in line with the Mesozoic Rift.

2.2.2.4.1- *arnoldi* superspecies (1). Elongate body (d). Color pattern: generalized (pp). Specificity:

symmetrical pattern of bilobate Caudal in male (d). Distribution: relict, like *powelli*, in western Niger delta (d).
2.2.2.4.2- *filamentosum* superspecies (3). Compact body shape (p). Specificities: fan-shaped Caudal fin (d); asymmetrical pattern of trilobate Caudal in male (d); less derived color pattern than *arnoldi*. Disjunct distribution, as for *sjoestedti*, in two coastal pockets: western Niger delta in Nigeria (to Togo) and lower Ndian river in western Cameroun (d). May have invaded from the eastern shores of the epicontinental sea.

2.3- *Callopanchax* series (18). Large (p). Slightly compressed (d). Smooth upper and lower outlines (d). Upper frontal scalation type, except *guineense* (d). Marked sexual dimorphism in fin shape (dd). Swimming near surface, except *Callopanchax s.s.* (d). Breeding: among plants, except *Callopanchax s.s.* (d). Biotope: permanent or slightly seasonal with low current, except *Callopanchax s.s.* (d). Posture: passive, in protected areas (d). Egg development: maybe artificially delayed (non-annual), except *Callopanchax s.s.*, a strict annual (d). Coverage: today in primary forest (d).
2.3.1- *occidentalis* superspecies (*Callopanchax s.s.*) (3). Large (p). Deep body shape (pp). Deeper peduncle than other components (p). Interorbitar, unusually large (p). Very high counts at Dorsal and Anal fins (pp). Very low or negative D/A ratio (pp). Comb-like anterior Dorsal fin (d). Advanced insertion of Dorsal fin (pp). Color pattern: derived, with specific design (dd). Swimming near bottom (p). Breeding: bottom substrate (pp). Biotope: ephemeral and stagnant (p). Egg development: compulsorily delayed (strict annual) (pp). Specificities: a white to blue border and red sub-border around Dorsal, Anal and Caudal fins of male (not margin) (d); mid to lower head, deep blue in male, during pre-mating (d); gold and blue markings (except *monroviae*, red) on male sides over a brown red background (d); rectangular shaped unpaired fins without extensions (d). Distribution: coastal Guinée to Liberia (d), in line with the refugium.
2.3.2- *guineense* and *petersi* superspecies (5). Elongate body (d). High count at Anal, lower at Dorsal fin (p). High D/A ratio (d). Little sexual dimorphism in fin shape (pp). Little sexual dichromatism (pp). Color pattern: generalized (pp). A faint supracaudal ocellus in female (d).
2.3.2.1- *guineense* superspecies (*Archiaphyosemion s.s.*) (4). Large (p). Circular frontal scalation (p). Blue/green conspicuous markings on male sides and fins (d). Specificities: dark lower head during (pre)mating (d); no red marking on sides or fins (p). Distribution: the Guinean Dorsal (d), in line with the refugium.
2.3.2.2- *petersi* superspecies (*Archiaphyosemion*, part.) (1). Some melanism in both sexes (p). Thin dark bars on sides (maybe convergently acquired from the sympatric *Epiplatys*) (d). Specificities: a red post-opercular spot in male (d); a gold lower band at male Caudal fin (d). Distribution: relict in isolated coastal pockets of Côte d'Ivoire and Ghana (d), after probable extinction during the last dry period.
2.3.3- *liberiense, geryi* and *guignardi* superspecies (*Scriptaphyosemion*) (10). Slender body (dd). High count at Anal, lower at Dorsal fin (p). High D/A ratio (d). Stronger sexual dimorphism in fin shape than the rest (dd). Low and long male Caudal fin, as *Aphyosemion et al.* (dd). A faint supracaudal ocellus in female (d). Red conspicuous markings on male sides and fins (dd). Color pattern: derived, with specific design (dd). Specificities: a dark mid-lateral band on female sides (also in primitive *Aphyosemion* lineages, as *franzwerneri/pascheni*) (d); contrary to *Aphyosemion*, the Caudal fin pattern is closed by a red border, uniting the two margins (d); red dots (*liberiense*), red reticulations (*geryi*) and brown dots (*guignardi*) characterize male color pattern for each superspecies. Distribution: coastal Guinée to Liberia (d), in line with the refugium, and grading inlands for *guignardi*, north of the Guinean Dorsal.

2.4- *Epiplatys* series (49/50). Breeding: among plants (d). Biotope: permanent or slightly seasonal with low current (d). Egg development: maybe artificially delayed (non-annual) (d). Color pattern: derived, with specific design (dd). The proposed systematic changes are derived from a more detailed (non published) study. Although these fishes are more opportunistic than *Aphyosemion*, in terms of the biotope characteristics and forest coverage, they appear to be exclusive to lowlands and extremely rare in the plateau (*sangmelinensis* being the exception), opposite to *Aphyosemion*. It is hypothesized here for the first time that this circumventing non-climbing property is associated with their standstill pike-like behavior, except *Aphyoplatys*, in stagnant waters.
2.4.1- *Epiplatys* (48/49). Flat front (d). Slightly compressed (d). Rounded and wide mouth, except *Pseudepiplatys* (pp). Oblique snout (dd). Upper frontal scalation (d). Closed frontal neuromast system,

as in the *Callopanchax* series (except *Epiplatys* s.s.). High count at Anal, lower at Dorsal fin (p). Very high D/A ratio (dd). Remote insertion of Dorsal fin (dd). Marked sexual dimorphism in fin shape (dd). Swimming at surface (dd). Posture: straight in less reclusive areas (pp). Coverage: today in primary forest (opportunistic), except *bifasciatus, spilargyreius* (d). Specificities: pike-like outline and posture (d); an oval golden shining spot on front (also in *Aplocheilus*) (d); a dark lateral wide band, posteriorily (d). The *fasciolatus, bifasciatus, spilargyreius, grahami* superspecies may represent a monophyletic group, defined by the absence of broad dark cross bars anteriorily and of a complete peduncular bar, by the lack of "tear" drop dark blotch below eye, by the oval shape of the Caudal fin, by the golden spots on upper sides, by the thinly-lineated chin pattern. This slenderer, less derived, major lineage has a northern center of origin and may receive the subgenus name *Parepiplatys.* A second major lineage contains all the other superspecies with opposite characteristics (*Lycocyprinus* and *Pseudepiplatys*, in the west, *Epiplatys,* in the east). The two groups have the same distribution, all around lowland regions, avoiding the plateau.

2.4.1.1- *fasciolatus* superspecies (16). Very large (pp). Elongate body (d). High D/A ratio (d). Golden conspicuous markings on male sides and fins (pp). Specificities: slightly oblique dark markings on sides (also seen, somewhat differently, in the related *spilargyreius*) (d); double converging red lines on the Anal and Caudal fins of male (d); oval shaped Caudal fin in male (d). Distribution: coastal plain and grading inland of Guinée to western Côte d'Ivoire (d), in line of the coastal refugium; derived phenotypes (*lamottei, coccinatus, roloffi*) are located in a pocket region near Nzérékoré (also endemic for *nimbaensis*, in Aplocheilichthyins), in line with the Guinean Dorsal refugium (Mont Nimba).

2.4.1.2- *spilargyreius* superspecies (hypothetically including *sangmelinensis* superspecies) (5/4). Slender body (dd). Low and long male Caudal fin (dd). Golden conspicuous markings on male sides and fins (pp). Coverage: today in savanna and gallery forest (p). Specificities: regular oblique dark lines on sides and Caudal fin (d); a dark border on male Caudal fin (d). Distribution: vicariant to *fasciolatus,* northeasterly in the Sahel, up to Sudan and the Congo cuvette (Kinshasa) (d); locally insiding into coastal pocket regions, with or without speciation, as *bifasciatus*.

2.4.1.3- *bifasciatus* superspecies (hypothetically including *chevalieri* superspecies) (4/5). Slender body (dd). Low and long male Caudal fin (dd). Red conspicuous markings on male sides and fins (dd). Coverage: today in savanna and gallery forest (p). Specificities: a double lateral dark band on sides of both sexes (d), as in *Chromaphyosemion* (independently acquired), the lower band being just slightly below the sub-median band of *spilargyreius-fasciolatus* (d); a series of red spots along lower body base (also shared by *grahami*) (d); extended Ventral (and rarely Pectoral) fins in male (d); filaments in Dorsal and Anal fins of old male (d); internal fertilization in some Sudanian populations at least (d). The sister species *bifasciatus-barmoiensis* form the most derived, by external morphology, sublineage among the above three lineages. The attached *chevalieri* superspecies shows only the dark lower band. Distribution: occasionally sympatric to *fasciolatus-spilargyreius*, in the coastal plain from Guinée to Bénin, in the Sahel, up to Sudan and the Congo cuvette (d). The hypothesis of *chevalieri* closer to *bifasciatus* than to *spilargyreius* is congruent with the relict presence of *spilargyreius* in the Kinshasa area (unless it has been artificially introduced there).

2.4.1.4- *grahami* superspecies (*Parepiplatys s.s.*, a previous synonym of *Lycocyprinus*, part.) (2/3). Slender body (dd). Low and long male Caudal fin (dd). Red conspicuous markings on male sides and fins (dd). Specificities: red pattern in chevrons (d); dark thin oblique bars or chevrons, temporary or only in juveniles and females (d); a series of red spots along lower body base (also shared by *bifasciatus/chevalieri*) (d). Distribution: easterly vicariant to *dageti* and *chaperi*, in the coastal plain from Cabinda to Togo; restricted near the coastal fringe up to Lambaréné (p/d), due to the competitive pressure of *sexfasciatus*, then more widely expanded to the south.

2.4.1.5- *dageti* superspecies (*Lycocyprinus s.s.*) (2). Slender body (dd). Low and long male Caudal fin (dd). Red conspicuous markings on male sides and fins, but not numerous (dd). Specificities: a red throat pattern (also seen in the species *phoeniceps* of the *multifasciatus* superspecies) (d); the last black bar on male peduncle extends downward and becomes a broad lower margin at Caudal fin of male (d); 5 bars in total, bar number 1, oblique and the longest, bars number 2 and 3 extend slightly into Anal fin of male (similarly in *chaperi*) (d); pointed lower Caudal fin in male (similarly in *chaperi*) (d). Distribution: relict and restricted to coastal fringes of Liberia to Ghana (d).

2.4.1.6- *chaperi* superspecies (*Lycocyprinus*, part.) (5). Elongate body (d). Red conspicuous markings on male sides and fins (dd). Specificities: similar to *dageti* superspecies, but somewhat less slender and with more derived color markings (strong red pigments). Moved, here for the first time, from the *sexfasciatus* series to a close relationship with *dageti*, the species *etzeli*, locally sympatric with *dageti*, being intermediate. Distribution: northerly vicariant to *dageti* superspecies in coastal inlands and foothills of Côte d'Ivoire to Ghana (d).

2.4.1.7- *sexfasciatus* superspecies (*Epiplatys s.s.*) (5). Large (p). Elongate body (d). Red conspicuous markings on male sides and fins (dd). Specificities: 6 dark bars on sides, all rather vertical, the upper part being more variable (straight in the southern populations or oblique in the northern ones). Distribution: in the coastal plain of western Africa (d), limited by *chaperi* in the north and *multifasciatus* in the south, two distinctive lineages with a similarly barred pattern. Speciation may be in line with microrefugia (as *Gularopanchax*). Frequently sympatric to components of the *grahami* superspecies).

2.4.1.8- *multifasciatus* superspecies (*Epiplatys* part.) (8). Elongate body (d). Red conspicuous markings on male sides and fins (dd). Specificities: intermediate thinner and temporary bars on sides (in total over 12, also seen in some populations of *sexfasciatus* and of *dageti*) (d); red flamed Caudal fin (d). Very similar to *sexfasciatus* in body and fin shapes, but may be separated by the number and design of the vertical bars, the closed frontal neuromast pattern (as all other *Epiplatys*). Distribution: southern vicariant of *sexfasciatus*; in the coastal plain of Gabon (south of Lambaréné) to Cabinda and in the Congo cuvette and its belts (p). Frequently sympatric to components of the *grahami* superspecies and to *chevalieri*).

2.4.1.9- *Pseudepiplatys* (1). Small (d). Slender body (dd). Low peduncle (d). Low and long male Caudal fin (dd). Golden, if any, conspicuous markings on male sides and fins (pp). Posture: straight near edges (p). Specificities: no dark bars but broader 3 rings (d); dark head (d); elongate sword shaped Pectoral and Caudal fins (d); 3 median and inner red lines on male Caudal fin (d). Distribution: relict near the coastal fringe from Liberia to Guinée (d), vicariantly to *dageti* superspecies, with which it may be related (in contrast to the sympatric *fasciolatus*).

2.4.2- *Aphyoplatys*. (1) Small (d). Slender body (dd). High D/A ratio (d). Low and long male Caudal fin (dd). Strong melanism in both sexes (pp). Blue conspicuous markings on male sides and fins (d). No dark bars on sides, unlike *Epiplatys* (p). Swimming near surface (d). Posture: passive, in protected areas (d). Specificities: a pre-mating dancing behavior (independently acquired at least also by the *Aplocheilus blockii* superspecies, *Plesiolebias*, *Procatopus* and some viviparous Poeciliins); lanceolate Caudal fin shape (d); not oblique mouth (p) and a shorter snout; black lower lip, as in *panchax* (d); a dark and gold lateral line from snout to behind eye (d); a blue submarginal line all around male Caudal fin. Distribution: endemic to the Congo cuvette (p/d), in connection with the lake Tumba refugium. An externally rather primitive phenotype, as *Adamas*, with which it is occasionally sympatric.

3- South American Rivulins (195/198). Smooth upper and lower outlines (pp). No hump back, except *Cynolebias s.s.*, *Austrofundulus* (d). Disproportionate snout, but oblique in *Trigonectes*, *Moema* (d). Sexual dichromatism, with subdued female, except *atratus* and some components of *Cynolebias s.s.* with no dichromatism and *Cynolebias nigripinnis* and *bellottii*, *Simpsonichthys*, with a dichromatic distinctive pattern (d).

3.1- *Rivulus* series (119/121). Flat front (d). Circular frontal scalation, except *Millerichthys*, *Anablepsoides* (p). High count at Anal, lower at Dorsal fin, except *Austrofundulus*, *Millerichthys*, *Neofundulus*, more primitive and *Anablepsoides*, *marmoratus* superspecies more derived (p). No sexual dimorphism in body shape, except *Pituna*, *Millerichthys*, *Pterolebias* (p). No sexual dimorphism in fin ray count (pp). Posture: passive, in protected areas, except *Rivulus* and the oblique mouth group with *Trigonectes*, *Moema*, *Renova* (d) (details in Huber, 1998c).

3.1.1- *Austrofundulus* (2). Very large (pp). Deep body shape (pp). Slightly compressed (d). Occasionally with a hump back (pp). Very high counts at Dorsal and Anal fins (pp). High D/A ratio (d). Marked sexual dimorphism in fin shape (dd). A faint and rare supracaudal ocellus in female (d). Dark limited band through eye (p). Golden conspicuous markings on male sides and fins (pp). Strong melanism in both sexes (pp). Color pattern: generalized (pp). Swimming near bottom (p). Breeding: dives (p). Biotope: ephemeral and stagnant (p). Behavior: some jumping activity in tribes (d). Egg development: compulsorily delayed (strict annual) (pp). Coverage: today in savanna and gallery forest (p). Specificities: darkly pigmented anal papillae (d); a very high transversal scale count (over 12) (pp); separated from the closely related *Rachovia* by the deeper body shape, the diving behavior, the spade shaped Caudal fin (with upper and lower extensions) and the hump back in male. In total, a very primitive lineage, by external characters. Distribution: coastal plain of northern South America, in relation with the Maracaibo, Apure and Guiana refugia (d).

3.1.2- *Rachovia* (4). Compact body shape, occasionally with a curved back (p). Slightly compressed (d). High D/A ratio (d). Very low LL scale count (dd). Marked sexual dimorphism in fin shape (dd). A faint supracaudal ocellus in female (d). Dark limited band through eye (p). Golden conspicuous markings on male sides and fins (pp). Color pattern: generalized, but less than *Austrofundulus* (especially the species *pyropunctata*) (pp). Swimming near bottom (p). Breeding: bottom substrate (pp). Biotope: ephemeral and stagnant (p). Behavior: some jumping activity in tribes (d). Egg development: compulsorily delayed (strict annual) (pp). Coverage: today in savanna and gallery forest (p). Specificities: lyre-shaped Caudal fin with a black border in male (d); a lower orange margin at Caudal fin in male (d) (also independently acquired in *Trigonectes et al.*). Distribution: similar to *Austrofundulus*, but not superimposed (more westerly, but less easterly, in line with its more derived status).

3.1.3- *Pituna* (3). Compact body shape, occasionally with a curved back (p). Rounded lateral shape (pp). High D/A ratio (d). Marked sexual dimorphism in fin shape (dd). A faint supracaudal ocellus in female (d). Dark limited band through eye (p). Color pattern: generalized (pp). Swimming near bottom (p). Breeding: bottom substrate (pp). Biotope: ephemeral and stagnant (p). Behavior: some jumping activity in tribes (d). Egg development: compulsorily delayed (strict annual) (pp). Coverage: today in savanna and gallery forest (p). Specificities: a conspicuous black post-opercular blotch (d); golden spots all over body sides and fins of male (p). Distribution: disjunct, in northern coastal Venezuela and in the central Brasilian plateau (d), the southern components with a relatively less primitive status; in-between, the Amazon cuvette has been invaded by another distinct lineage (*Moema*). No western component yet known in the Amazon belt, unlike *Pterolebias*. Probably relict of a past much wider distribution and restricted to small regions not far from putative refugia (Apure, Araguaia...).

3.1.4- *Millerichthys* (1). Small (d). Compact body shape, occasionally with a curved back (p). Rounded lateral shape (pp). No or simple frontal scalation (pp). Very high counts at Dorsal and Anal fins (pp). High D/A ratio (d). Little sexual dimorphism in fin shape, with rounded Caudal fin (pp). No supracaudal ocellus in female, but a series of black spots along the peduncle (pp). Dark limited band through eye (p). Golden conspicuous markings on male sides and fins (pp). Color pattern: generalized (pp). Swimming near bottom (p). Breeding: hypothesized bottom substrate (pp). Biotope: ephemeral and stagnant (p). Behavior: some jumping activity in tribes (d). Egg development: maybe compulsorily delayed (strict annual) (pp). Coverage: today in savanna and gallery forest (p). Specificities: 2-3 golden bands on male mid Anal fin (d). In total, a very primitive phenotype by external characters (maybe the most in the *Rivulus* series). Distribution: relict in a small pocket in coastal eastern Mexico (d/p), that may be linked to a micro refugium. It should have colonized its place in very old times (i.e. long before the Panamean isthmus).

3.1.5- *Pterolebias* (10). Strong sexual dimorphism in fin shape (dd). Dark limited band through eye (p). Swimming near bottom (p). Breeding: bottom substrate (pp). Biotope: ephemeral and stagnant (p). Posture: straight near edges (p). Behavior: some jumping activity in tribes (d). Egg development: compulsorily delayed (strict annual) (pp). Specificities: a post-opercular marking (d), specific to sublineages: black in *peruensis* or red in *wischmanni*, orange, gold ringed (like a butterfly) in *longipinnis*.

3.1.5.1- *peruensis* superspecies (6). Very large (pp). Compact body shape (p). Slightly compressed (d). High D/A ratio (d). A faint and rare supracaudal ocellus in female (d). Color pattern: generalized except the species *peruensis* (pp). Coverage: today in primary forest (d). Specificities: unique broad dark bars on sides and fins of both sexes in *peruensis* (d); orange lower margin in male Caudal fin (d); extended Pectoral fins in male (d). Distribution: western belts of Amazon cuvette, along the paleo epicontinental sea (p/d).

3.1.5.2- *longipinnis* (2) and *zonatus* (2) superspecies. Very large (pp). Deep body shape (pp). Strongly compressed (dd). Very high D/A ratio, up to +17 (dd). No supracaudal ocellus in female (pp). Golden conspicuous markings on male sides and fins in vertical bars (northern) or chevrons (southern) (pp). Coverage: today in savanna and gallery forest (p). Specificities: a very long and filamentous Caudal fin in male (d); very extended Ventral fins in male (also in *Trigonectes*, independently acquired). Distribution: disjunct, vicariantly from the *peruensis* superspecies in the south. In the north (*zonatus*), sympatric with *Austrofundulus/Rachovia* with a similar distribution in the Llanos (d) and in the south (*longipinnis)*, along the northern and southern paleo epicontinental seas, up to northern Argentina (p) (also locally, near Santarem-Belem in the lower Amazon: relict??).

3.1.6- *Rivulus* (89/92). Slightly compressed (d), except *marmoratus*. Marked sexual dimorphism in fin shape but less so than the other groups, and except *atratus* and *marmoratus* superspecies (dd). No extension or filaments in male fins, except *rectocaudatus* superspecies (ventrals) and one component, *gransabanae*, of the *geayi* superspecies (p). No dark band through eye (dd). Color pattern: derived, with specific design, except *marmoratus, cylindraceus* (dd). Swimming near surface, except *atratus*, at surface (d). Breeding: egg-strander (dd). Biotope: permanent or slightly seasonal with low current (d). Posture: loose and downward, except *atratus* and *frenatus* superspecies (dd). Behavior: strong jumping and aestivating activity in tribes, except *atratus* (dd). Egg development: maybe artificially delayed (non-annual), except *hartii* (d). Coverage: today in primary forest, with exceptions (d).

3.1.6.1- *hartii* superspecies (5). Very large (pp). Elongate body (d). Very high D/A ratio (dd). Remote insertion of Dorsal fin (dd). Very high LL scale count (pp). High and short male Caudal fin (pp). A distinctive but irregular supracaudal ocellus in female (dd). Red conspicuous markings on male sides and fins (dd). Breeding: bottom substrate (pp). Egg development: possibly delayed (semi-annual) (p). Specificities: 3 series of dark spots on posterior sides of female (d); broad transversal dark bars on back and upper sides (d). Distribution: the Guiana Shield and the northern Amazon belts (d), usually sympatric with components of the striated lineage.

3.1.6.2- *peruanus* superspecies (5). Large (p). Compact body shape (p). Shorter head (p). Very high D/A ratio (dd). Very high LL scale count (pp), but not high transversal count. High and short male Caudal fin (pp). A distinctive supracaudal ocellus in female (dd). Gold conspicuous markings on male sides and fins (pp). Specificities: irregular large red brown blotches on sides and fins of male (d). In total, a rather less derived phenotype. Distribution: restricted to highlands and their foothills at the periphery of the *hartii* superspecies (d).

3.1.6.3- *urophthalmus, limoncochae* and *micropus* superspecies (22). Elongate body (d). Very high D/A ratio (dd). Remote insertion of Dorsal fin (dd). A distinctive supracaudal ocellus in female (dd). Red conspicuous markings on male sides and fins (dd). Specificities: red striations in 10 lines on male sides (striated lineage, but maybe polyphyletic), continuously or fused in 3-4 broader lines, posteriorly (d); unpaired fins with a symmetrical pattern of dark margin and light submargin (d). Distribution: opportunistic all over northern South America in the Amazon cuvette and its belt and the coastal plain, up to Bahia (d); probably older phenotypes in remote Andean valleys, along the paleo epicontinental sea (p/d). Remark: the distribution of *Rivulus elongatus* (with very high scale counts) along the paleo epicontinental sea, may also mark up the origin of the group.

3.1.6.4- *santensis* superspecies (4). Slender body (dd). Very high D/A ratio (dd). Remote insertion of Dorsal fin (dd). A faint and rare supracaudal ocellus in female (d). Golden conspicuous markings on male sides and fins (pp). Color pattern: generalized (pp). Specificities: gold/green series of spots on male sides and fins. Distribution: in the Brasilian coastal plain (p/d), with speciation in line with putative refugia.

3.1.6.5- *isthmensis* superspecies (*Cynodonichthys*) (11). Elongate body (d). Remote insertion of Dorsal fin (dd). Sexual dichromatism (subdued), with distinct pattern for *weberi* only (d). A distinctive but irregular supracaudal ocellus in female (dd). Red conspicuous markings on male sides and fins (dd). Specificities: unpaired fins with an asymmetrical pattern of dark margin and light submargin, contrary to *Vomerivulus* (d). Distribution: central America (dd), as a first invasion wave up to Mexico (*tenuis*), with speciation in line with putative micro refugia. The species, primitive in northern South America, is still unknown.

3.1.6.6- *elegans* and *glaucus* superspecies (*Vomerivulus*) (11). Elongate body (d). Very high D/A ratio (dd). Remote insertion of Dorsal fin (dd). No supracaudal ocellus in female (pp). Red conspicuous markings on male sides and fins (dd). Specificities: red discontinuous lines of spots on male sides (d); a crescent-shaped (white, blue or gold/red) colored Caudal fin in male (d). Distribution: central America (dd), as a second invasion wave up to Costa Rica (*glaucus*), with speciation in line with putative micro refugia. The primitve species in northern South America is in highlands of Colombia: *magdalenae*.

3.1.6.7- *cylindraceus* superspecies (*Rivulus s.s.*) (2/3). Small (d). Compact body shape (p). High D/A ratio (d). Side scales, irregularly positioned (pp). A faint supracaudal ocellus in female (d). Strong melanism in both sexes (pp). Color pattern: generalized (pp). Specificities: upper dark post-opercular blotch in both sexes, contrasted with shining blue in male (d). Distribution: relict, as an old lineage, confined to 2 Caribbean islands (d).

3.1.6.8- *marmoratus* superspecies (2). Large (p). Compact body shape (p). Rounded lateral shape (pp). Very low count at Dorsal and Anal fins (dd). High D/A ratio (d). Very high LL scale count, up to 55 (pp). Very high transversal scale count (about 15) (pp). Side scales, irregularly positioned (pp). No sexual dimorphism in fin shape (pp). Little sexual dimorphism in fin shape (pp). A distinctive supracaudal ocellus in female and also male (dd). Golden conspicuous markings on male sides and fins (pp). Strong melanism in both sexes (pp). Color pattern: generalized (pp). Biotope: brackish to marine in mangrove (pp). Specificities: simultaneously, a black post-opercular blotch and a supracaudal ocellus in both sexes (d); a black circumcaudal border in male (also in *Neofundulus*, independently acquired?) (d); one component, *marmoratus*, is a selfing hermaphrodite (d). In total, maybe the most primitive lineage within *Rivulus*. Distribution: discontinuous from Santos in Brasil to Florida, along the coast depending on the presence of mangrove (pp/p); the southern component (*caudomarginatus*) is, by external morphology, even more primitive. Its extension is probably linked to that of *Rhizophora et al.*

3.1.6.9- *frenatus* superspecies (3/4). Slender body (dd). High D/A ratio (d). Low and long male Caudal fin (dd). No supracaudal ocellus in female (pp). Blue conspicuous markings on male sides and fins (d). Specificities: a lateral black lower band on sides of both sexes (d), permanent in female; a blue iridescence on male sides (d); straight posture, more in mid-waters (p). A very derived lineage. Distribution: the coastal plain of the Guianan Shield (d), with speciation in line with putative refugia.

3.1.6.10- *geayi* superspecies (4/5). Small (d). Slender body (dd). Low peduncle (d). High D/A ratio (d). Low and long male Caudal fin (dd). A faint supracaudal ocellus in female (d). Red conspicuous markings on male sides and fins (dd). Specificities: a pre-opercular red shield on male, as in *Aphyosemion s.l.*; red and blue chevrons on male sides (d); a dark temporary mid-line band on sides of both sexes, with a prominent post-opercular blotch (d). Distribution: the coastal plain and neighboring highlands of the Guianan Shield and the mid to lower Amazon (d), with speciation in line with putative refugia.

3.1.6.11- *punctatus* superspecies (7). Small (d). Elongate body (d). Very high D/A ratio (dd). Remote insertion of Dorsal fin (dd). Sexual dichromatism, with distinct pattern for *punctatus*, only (dd). A distinctive but irregular supracaudal ocellus in female (dd). Red conspicuous markings on male sides and fins (dd). Specificities: darker chevrons on male posterior sides (d). With many similarities in terms of external charcters to the geayi superspecies. Distribution: the Brasilian plateau and surroundings up to northern Argentina (p), in southern vicariance to the *geayi* superspecies.

3.1.6.12- *ornatus* (3) and *beniensis* (3) superspecies. Small (d). Slender body (dd). Low peduncle (d). Very low count at Dorsal (d). Very high D/A ratio (dd). Remote insertion of Dorsal fin (dd). Low and long male Caudal fin (dd). A distinctive and exceptionally large supracaudal ocellus in female (dd). Red conspicuous markings on male sides and fins (dd). Seemingly prefers stagnant lake surroundings (p). Specificities: the unusual size of the ocellus (d); for *ornatus*, gold and red squarish spots on posterior sides (d); for *beniensis*, the fewer continuous lines than *urophthalmus*. Remark: *beniensis* may also be considered as a southern offshoot of *urophthalmus/limoncochae* in Bolivia. Distribution: *ornatus* is restricted to the Amazon cuvette and the upper Orinoco (d).

3.1.6.13- *breviceps* superspecies (2). Elongate body (d). High D/A ratio (d). No supracaudal ocellus in female (pp). Red conspicuous markings on male sides and fins (dd). Specificities: spade shaped Caudal fin in male (also in the related *rectocaudatus*) (d); dark temporary lower (not median) band on sides of both sexes (d). Distribution: the western Guianan Shield (d), in the coast and the neighboring plateau.

3.1.6.14- *rectocaudatus* superspecies (3). Elongate body (d). Very high D/A ratio (dd). A distinctive supracaudal ocellus in female and in male (dd). Red conspicuous markings on male sides and fins (dd). Specificities: a supracaudal ocellus in both sexes (d) and no dark band, contrary to *breviceps*. Distribution: vicariant to *breviceps* in the Venezuelian plateau and Amazon western and northern belts (d).

3.1.6.15- *atratus* (and *obscurus*?) superspecies (*Anablepsoides*) (2). Dwarf (dd). Slender body (dd). Low peduncle (d). No or simple frontal scalation (pp). Very low count at Dorsal and Anal fins (dd). Very high D/A ratio (dd). Remote insertion of Dorsal fin, with Dorsal fin insertion behind Anal ending (dd). No sexual dimorphism in fin shape for *atratus* only (pp). Low and long male Caudal fin (dd). No sexual dichromatism for *atratus* only (pp). No supracaudal ocellus in female (pp). Strong melanism in both sexes for *atratus* only (pp). Dark bars on sides (d). Swimming at surface, unable to stay downwards (dd). Specificities: for *atratus*, head broader than deep at interorbitar (d), upward orientation of Pectoral fins (d), 4 to 6 oblique bars (d), a very low permanent and prominent black band on sides (d). Remark: *obscurus* is assigned here because a common osteological character has been disclosed and because of its coherent meristics, distribution and ecology; its color pattern, though, is closer to *frenatus* superspecies. Distribution: the Amazon cuvette (d) in a specialized niche.

3.1.7- *Trigonectes* (6). Very large (pp). Elongate body (d). Slightly compressed (d). Pointed mouth (dd). Oblique snout (dd). High D/A ratio (d). Remote insertion of Dorsal fin (dd). Strong sexual dimorphism in fin shape (dd). No supracaudal ocellus in female (pp). Dark limited band through eye (p). Red conspicuous markings on male sides and fins (dd). Color pattern: derived, with specific design (dd). Swimming near surface (d). Breeding: bottom substrate (pp). Biotope: ephemeral and stagnant (p). Posture: straight near edges (p). Behavior: some jumping activity in tribes (d). Egg development: compulsorily delayed (strict annual) (pp). Coverage: today in savanna and gallery forest (p). Specificities: slightly flattened body at Anal fin level (d); the very extended Ventral fins (also in *Pterolebias longipinnis*) (d), the fused lines on posterior sides (also in *Moema* and *Rivulus limoncochae* superspecies), the orange lower band on male Caudal (also in *Rachovia, Moema*), the oblique snout (also in *Moema*, but less marked). Distribution: the Brasilian plateau, south of the Amazon belts (p/d). The older species, by external characters (*aplocheiloides*) appears to be southern.

3.1.8- *Moema* (4). Very large (pp). Elongate body (d). Slightly compressed (d). Pointed mouth (dd). Oblique snout (dd). Very high D/A ratio (dd). Remote insertion of Dorsal fin (dd). No supracaudal ocellus in female (pp). Dark limited band through eye (p). Red conspicuous markings on male sides and fins (dd). Color pattern: derived, with specific design (dd). Swimming near surface (d). Breeding: bottom substrate (pp). Biotope: ephemeral and stagnant (p). Posture: straight near edges (p). Behavior: some jumping activity in tribes (d). Egg development: compulsorily delayed (strict annual) (pp). Coverage: today in primary forest (d). Specificities: acuminate Pectoral fins in male (d); discontinuous red lines on male sides and fins (d). Distribution: the Amazon cuvette and its belts near the Guianan Shield (d), in northeastern vicariance to *Trigonectes*.

3.1.9- *Renova* (1). Large (p). Elongate body (d). Slightly compressed (d). Pointed mouth (dd). High D/A ratio (d). Marked sexual dimorphism in fin shape (dd). A faint supracaudal ocellus in female (d). Dark limited band through eye (p). Red conspicuous markings on male sides and fins (dd). Swimming near surface (d). Breeding: bottom substrate (pp). Biotope: ephemeral and stagnant (p). Posture: straight near edges (p). Behavior: some jumping activity in tribes (d). Egg development: compulsorily delayed (strict annual) (pp). Coverage: today in primary forest (d). Specificities: a similar outline (except the head) to *Rivulus* (*hartii* superspecies) (d); a red continuous line near the base of male Anal fin (d), discontinuous in *Moema* and *Trigonectes*; distinguished from the two related lineages of *Trigonectes* and *Moema* by the less derived morphology and color pattern. Distribution: only known from one locality in Venezuelian Amazon (d); probably, a western vicariant of *Moema*.

3.1.10- *Neofundulus* (5). Large (p). Compact body shape (p). Rounded lateral shape (pp). Very high counts at Dorsal and Anal fins (pp). Very low or negative D/A ratio (pp). Little sexual dimorphism in fin shape (pp). High and short male Caudal fin (pp). No supracaudal ocellus in female (pp). Dark limited band through eye (p). Golden conspicuous markings on male sides and fins (pp). Color pattern: derived, with specific design (dd). Swimming near bottom (p). Breeding: bottom substrate (pp). Biotope: ephemeral and stagnant (p). Posture: loose and downward (dd). Behavior: some jumping activity in tribes (d). Egg development: compulsorily delayed (strict annual) (pp). Coverage: today in savanna and gallery forest (p). Specificities: a crescent shaped color at Caudal fin of male (gold and black), also in Anal fin (d). Distribution: the Brasilian plateau and southern surroundings (p). The older species, by external characters (*ornatipinnis*) appears to be southern.

3.2- *Cynolebias* series (70). Convex frontal shape (pp). Circular frontal scalation, except *Cynolebias* (p). Frontal neuromasts (numerous) in lyre-shaped channels (dd). Strong sexual dimorphism in fin shape, except some components of *Cynolebias s.s.* (dd). No supracaudal ocellus in female (pp). Dark limited band through eye, extended only in *Cynolebias s.s.* (p). Swimming near bottom, except *Plesiolebias* (p). Biotope: ephemeral and stagnant (p). Posture: passive, in protected areas except *Cynolebias s.s.* (d). Behavior: no jumper, in tribes (p). Egg development: compulsorily delayed (strict annual) (pp). Coverage: today in savanna and gallery forest, except *Campellolebias* (p).

3.2.1- *Cynolebias* (26). No or simple frontal scalation (pp). Very high counts at Dorsal and Anal fins (pp). Advanced insertion of Dorsal fin, except *porosus* superspecies (pp). High and short male Caudal fin (pp). One to several dark blotches in the center of female sides, except *porosus* superspecies (d). Breeding: dives (p). Strongly primitive, by external characters.

3.2.1.1- *porosus* superspecies (*Cynolebias s.s.*) (12). Very large (pp). Deep body shape (pp). Rounded lateral shape (pp). With a hump back (pp). With a discontinuity at vent (pp). Very deep peduncle (pp). Rounded and wide mouth (pp). Very small eye diameter (pp). Very low or negative D/A ratio (pp). Very high LL scale count (pp). Scales covering bases of all unpaired fins (pp). Little sexual dimorphism in body shape (p). Some limited sexual dimorphism in fin ray count (d). Little sexual dichromatism (pp). Extensive and angular dark band through eye (pp). Golden conspicuous markings on male sides and fins (pp). Color pattern: generalized (pp). Posture: straight near edges (p). Specificities: cannibalistic (dd); gape-shaped mouth (dd), with prominent enlarged teeth, as *Paranothobranchius ocellatus*; a conspicuous upper spine at operculum margin (d). A very primitive lineage, by external characters, with specialization: the most primitive in the *Cynolebias* series. Distribution: the western slopes of Serra Mantiqueira and related highlands, from Brasilian Sertao (d) to Parana and Paraguayan Chaco (pp); stemmed from the Uruguayan and Argentinan coastal plain, where it is sympatric with the 2 other lineages. The older species by external characters (*elongatus/monstrosus/prognathus*) appear to be southern.

3.2.1.2- *bellottii* superspecies (7). Deep body shape (pp). Strongly compressed (dd). Low D/A ratio (p). Strong sexual dimorphism in body shape (d). Strong sexual dimorphism in fin ray count (4 more rays in female Anal fin) (dd). Sexual dichromatism, with distinct pattern (dd). Blue conspicuous markings on male sides and fins (d). Color pattern: generalized (pp). Specificities: distinguished from *nigripinnis* superspecies by the larger size (p), the higher D/A ratio which is never negative (d), the presence of ctenoid scales on male sides and fins (also in *porosus* superspecies) and the more derived color pattern. As *nigripinnis*, it lacks red pigments. Distribution: lowlands of Uruguay, Argentina, Paraguay and neighboring Brasil, along the paleo epicontinental sea (pp).

3.2.1.3- *nigripinnis* superspecies (9). Small (d). Deep body shape (pp). Strongly compressed (dd). Very low or negative D/A ratio (pp). Strong sexual dimorphism in body shape (d). Strong sexual dimorphism in fin ray count (4 more rays in female Anal fin) (dd). Sexual dichromatism, with distinctive pattern (dd). Blue conspicuous markings on male sides and fins (d). Color pattern: derived, with specific design (dd). Specificities and distribution: see *bellottii*, with which it is almost always sympatric (pp).

3.2.2- *Simpsonichthys* (19). Strongly compressed, even flattened (except *whitei*) (dd). Circular frontal scalation (p). Very high counts at Dorsal and Anal fins (pp). Advanced insertion of Dorsal fin, except *whitei* superspecies (pp). Strong sexual dimorphism in body shape (d). Strong sexual dimorphism in fin ray count (4 more rays in female Anal fin) (dd). Sexual dichromatism, with distinct pattern (dd). One to several dark blotches in the center of female sides, except *porosus* superspecies (d). Red usually vertical conspicuous markings on male sides and fins, except the species-names *chacoensis*, *costai*, *constanciae* and *whitei*, which are more primitive and distributed at the southern periphery (dd). Color pattern: derived, with specific design (dd). Breeding: dives (p).

3.2.2.1- *boitonei* superspecies (5). Compact body shape (p). Low D/A ratio (p). Specificities: blue bars on preopercular region and below eyes (d); blue markings on brown/red body background (p), dark bars on female sides (d). Distribution; the Brasilian plateau, west of Serra Mantiqueira and related highlands, between Brasilia and the Sertao (p/d) (rare, if any, in Pantanal), except the central part of the region, occupied by *notatus*.

3.2.2.2- *notatus* superspecies (4). Small (d). Compact body shape (p). Very low or negative D/A ratio (pp). Specificities: 3 anterior bars, darker than posterior bars in male (d); female, with dark markings, not bars. Distribution: see *boitonei* (in part sympatric, from the limited knowledge).

3.2.2.3- *flammeus* superspecies (6). Small (d). Elongate body (d). Very low or negative D/A ratio (pp). Specificities: red reticulations on male front and predorsal region (d), often filamentous unpaired fins in male (d). Note: the southern species, *trilineatus*, is hypothesized here to show a remarkable color pattern convergence with a former species, *Neofundulus (acutirostratus)*. Distribution: similar, but not identical, with *boitonei/notatus* superspecies with which it is often sympatric.

3.2.2.4- *chacoensis* superspecies (2). Small (d). Compact body shape (p). Low D/A ratio (p). Specificities: body and unpaired fins of male, intensely black or brown with white dots (independently acquired also in *bellottii* and *nigripinnis*) (d); elongate Dorsal and Anal fins in male (except *costai*) (d), blue submarginal line on all unpaired fins of male (d). Note: the newly described species, *filamentosus*, from central Bolivia, is a northern component, according to us. Distribution: the western part of the Brasilian plateau and neighboring Paraguay/Bolivia in vicariance to the Brasilian plateau lineages (p/d).

3.2.2.5- *whitei* superspecies (4). Compact body shape (p). High D/A ratio (d). Specificities: not deep bodied (d) and compressed lineage; short head; light markings on male sides (except *myersi*, red and derived) (p). A relatively more primitive lineage by external characters, especially its southern components. Distribution: coastal plain of southeastern Brasil (p/d) (components are missing to exemplify the vicariance in the north with other *Simpsonichthys* lineages and in the south with *Cynolebias*).

3.2.3- *Terranatos* (1). Small (d). Elongate body (d). Slightly compressed (d). Low peduncle (d). High count at Anal, lower at Dorsal fin (p). Very low or negative D/A ratio (pp). Advanced insertion of Dorsal fin (pp). Little sexual dimorphism in body shape (p). No sexual dimorphism in fin ray count (pp). Blue conspicuous markings on male sides and fins (d). Color pattern: generalized (pp). Breeding: bottom substrate (pp). Specificities: male with twisted unpaired fins during mating (d), extended Dorsal, Anal and Caudal fins, the latter being bilobate (d), extended Ventral fins (d). Distribution: little known; 2 distinct regions, the Llanos and the Venezuelian Amazon/Orinoco (d).

3.2.4- *Maratecoara* (2). Compact body shape (p). Slightly compressed (d). Deep peduncle (p). High count at Anal, lower at Dorsal fin (p). High D/A ratio (d). Little sexual dimorphism in body shape (p). Strong dimorphism in fin shape (dd). Red conspicuous markings on male sides and fins (dd). Color pattern: derived, with specific design (dd). Breeding: dives (p). Specificities: deep blue branchiostegal membrane that is projected during mating (d), lozenge-shaped Caudal in male only (d). Externally similar to *Terranatos*, except the Caudal fin shape and the subdued female (d). Distribution: little known; both species in the swampy Pantanal/Araguaia of Brasilian plateau (d).

3.2.5- *Spectrolebias* (1). Dwarf (dd). Slender body (dd). Slightly compressed (d). Low peduncle (d). Very high counts at Dorsal and Anal fins (pp). High D/A ratio (d). Little sexual dimorphism in body shape (p). Some limited sexual dimorphism in fin ray count (d). Low and long male Caudal fin (dd). Pointed Dorsal fin in male (but not Anal) (d). Blue conspicuous markings on male sides and fins (d). Color pattern: derived, with specific design (dd). Breeding: dives (p). Specificities: body, translucent (similarly to some Aplocheilichthyins) (p?); a semi-circle shaped black blotch at Anal fin edge in male (d). Distribution: only known from one locality in Araguaia basin (swampy Pantanal of Brasilian plateau) (d).

3.2.6- *Stenolebias* (2). Dwarf (dd). Elongate body (d). Slightly compressed (d). Low peduncle (d). High count at Anal, lower at Dorsal fin (p). High D/A ratio (d). Some limited sexual dimorphism in fin ray count (d). Low and long male Caudal fin (dd). Red conspicuous markings on male sides and fins (dd). Color pattern: derived, with specific design (dd). Breeding: dives (p). Specificities: red flamed basal Dorsal fin in male (d). Distribution: known from a few localities, only in Goias and in Araguaia basin (swampy Pantanal of Brasilian plateau) (d). *Stenolebias, Plesiolebias, Papiliolebias* form a monophyletic assemblage, which may be vicariant.

3.2.7.1- *Plesiolebias* (3). Dwarf (dd). Compact body shape (p). Strongly compressed (dd). High count at Anal, lower at Dorsal fin (p). Very low or negative D/A ratio (pp). Very low LL scale count (dd). Some limited sexual dimorphism in fin ray count (d). Red conspicuous markings on male sides and fins (dd). Color pattern: derived, with specific design (dd). Breeding: bottom substrate (pp). Specificities: a pre-mating dancing behavior (independently acquired at least also by *Aphyoplatys*, the *Aplocheilus blockii* superspecies, *Procatopus* and some viviparous Poeciliins); a red stripe on anterodorsal part of male sides (d); oblique, but not complete bars on male sides (d). Distribution: known from a few localities, only in Goias and in Araguaia basin (swampy Pantanal of Brasilian plateau) (d).

3.2.7.2- *Papiliolebias*, subgenus of *Plesiolebias* (1). Small (d). Deep body shape (pp). Strongly compressed, even flattened (dd). High D/A ratio (d). Very low LL scale count (dd). Strong sexual dimorphism in body shape (d). Some limited sexual dimorphism in fin ray count (d). Golden conspicuous markings on male sides and fins (pp). Color pattern: derived, with specific design (dd). Breeding: bottom substrate (pp). Specificities: oblique bars, completely on male sides (d); a post-opercular blue marking on male (d); rectangular shaped Anal fin in male (d); female equal to larger than male (p). Distribution: the Paraguayan and Bolivian Chaco (p/d), in southern vicariance to *Plesiolebias s.s.*

3.2.8- *Campellolebias* (3). Small (d). Compact body shape (p). Slightly compressed (d). Deep peduncle (p). Very high counts at Dorsal and Anal fins (pp). Very low or negative D/A ratio (pp). Advanced insertion of Dorsal fin (pp). Very low LL scale count (dd). Little sexual dimorphism in body shape (p). Red conspicuous markings on male sides and fins (dd). Some limited sexual dimorphism in fin ray count (d). Color pattern: derived, with specific design (dd). Breeding: bottom substrate (pp). Coverage: today in primary forest (d). Specificities: internal fertilization (d); male urogenital papillae is elongated and connected to Anal fin (d). Distribution: southeastern Brasilian coastal plain (pp), vicariantly to the southern *Cynopoecilus* and the northern *Leptolebias*.

3.2.9- *Cynopoecilus* (1). Small (d). Compact body shape (p). Slightly compressed (d). Deep peduncle (p). High count at Anal, lower at Dorsal fin (p). Very low or negative D/A ratio (pp). Advanced insertion of Dorsal fin (pp). Little sexual dimorphism in body shape (p). Some limited sexual dimorphism in fin ray count (d). Strong melanism in both sexes (pp). Color pattern: derived, with specific design (dd). Breeding: bottom substrate (pp). Specificities: the first Anal fin rays of male are put together to form a non-operative gonopodium, but no internal fertilization (d); a wide mid-lateral dark band on sides (d). Distribution: see *Campellolebias* (pp).

3.2.10- *Leptolebias* (7). Small (d). Compact body shape (p). Slightly compressed (d). High count at Anal, lower at Dorsal fin (p). Low D/A ratio (p). Little sexual dimorphism in body shape (p). Some limited sexual dimorphism in fin ray count (d). Golden conspicuous markings on male sides and fins (pp). Color pattern: derived, with specific usually vertical design (dd). Breeding: bottom substrate (pp). Specificities: Ventral fins with a united base (p?); red "shield" in preopercular region of male, as in *Aphyosemion et al.* and *Rivulus geayi* superspecies (d). Distribution: see *Campellolebias* (p/d).

4- African and Madagascan Aplocheilichthyins (61). Disproportionate snout (d). Upper frontal scalation type, except *Pantanodon, Aplocheilichthys* (d). Frontal neuromasts (limited) in often discontinous grooves, except *Pantanodon, Laciris* (d). Very large eye diameter (dd). Marked sexual dimorphism in fin shape, except *Laciris*, *Micropanchax s.s.* and *Aplocheilichthys* (dd). No sexual dimorphism in fin ray count (pp). No supracaudal ocellus in female (pp). No dark band through eye (dd). Swimming near surface, except *Lamprichthys, Laciris, Aplocheilichthys* (d). Breeding: among plants, except *Procatopus, Lamprichthys* on rocky substrate and *Laciris* which is pelagic. (d). Posture: straight in less reclusive areas (pp). Behavior: no jumper, in schools (pp). Egg development: short and hardly delayed (strict non-annual), except *Lamprichthys* (dd). Coverage: today in primary forest, except *Micropanchax* (d). Specificities: blue shine on sides (except *Lacustricola, Aplocheilichthys*) (d); "lampeye" state (d); a dark "net" around side scales, not red as in *Nothobranchius* (d); a thin dark median line on sides and another, not always, along lower body base, behind Anal fin (d); frequent allometry in growth, except *Micropanchax s.s.* and *Laciris* (d) (details in Huber, 1998a,b).

4.1- *Pantanodon* (2). Small (d). Compact body shape (p). Flat front (d). Strongly compressed (dd). Disrupted upper outline (d). Circular frontal scalation (p). Frontal neuromasts in deep grooves (p). High D/A ratio (d). Advanced insertion of Dorsal fin (pp). Very low LL scale count (dd). Strong sexual dimorphism in body shape (d). High and short male Caudal fin (pp). Color pattern: generalized (pp). Biotope: brackish to marine (pp). Biotope: permanent or slightly seasonal with low current (d). Specificities: nearly closed opening of mouth (d); no external teeth (d); filtering activity (d); 3 spines at Ventral fins in male (d); a short Dorsal fin base, with the largest Anal fin base (d); a marked disruption in body outline at the Dorsal fin level (d); wing shaped Dorsal fin in male (d), distinctive from Anal (d). Distribution: disjunct, in coastal eastern Africa (*stuhlmanni*) and at least northeastern Madagascar (*madagascariensis*), the 2 species being very different by external characters, seemingly from the limited knowledge (pp).

4.2- *Lamprichthys* (1). Very large (pp). Deep body shape (pp). Convex frontal shape (pp). Strongly compressed (dd). Deep peduncle (p). Pointed mouth (dd). Equal snout opening (p).Frontal neuromasts in 4 pores (pp). Very high counts at Dorsal and Anal fins, but not equal (pp). Very high D/A (+27) ratio (dd). Very high LL scale (and vertebrae) count (pp). Side scales, irregularly positioned (pp). Strong sexual dimorphism in body shape (d). Stronger sexual dimorphism in fin shape (dd). Very high insertion of Pectoral fins (p). High and (very) short male Caudal fin (pp). Golden conspicuous markings on male sides and fins (pp). Strong melanism in preserved material of both sexes (pp). Color pattern: derived, with specific design (dd). Swimming in mid waters (pp). Breeding: on rocky substrate (p). Egg development: longer than other Aplocheilichthyins, maybe artificially delayed (non-annual) (d). Specificities: strictly lacustrine (d); crescent-curved Caudal fin shape in male; striation of golden and blue spots on male sides and unpaired fins (d). In total (with *Laciris*), the most primitive phenotype by external characters, knowing the fact that coastal east African more primitive phenotype may still be discovered. Distribution: endemic to shore waters of lake Tanganyika (p).

4.3- *Laciris* (1). Very large (pp). Elongate body (d). Rounded lateral shape (pp). Frontal neuromasts, absent (dd?) and vestigial channels (dd?). High count at Anal, lower at Dorsal fin (p). Very high D/A ratio, with Dorsal insertion at or behind Anal fin ending (dd). Very high LL scale count (pp). Little sexual dimorphism in body shape (p). No sexual dimorphism in fin shape (pp). Strong melanism in both sexes (pp). Color pattern: generalized (pp). Swimming in mid (even deep) waters (pp). Specificities: vestigial sensory system (dd?); strictly lacustrine (d); pelagic (d); a broad dark vertical border on male Caudal fin (d). Distribution: endemic to deep waters of lake Edouard (p).

4.4- *Micropanchax* (7). Convex frontal shape (pp). Low peduncle (d). Interorbitar, unusually narrow (d). High count at Anal, lower at Dorsal fin (p). High D/A ratio (d). Little sexual dimorphism in fin shape (pp). Little sexual dichromatism (pp). Color pattern: generalized (pp). Biotope: permanent or slightly seasonal with low current (d). Coverage: today in savanna and gallery forest (p). By external morphology, the older phenotype appears to be in eastern Africa, where diversity and endemicity of the lineage is highest (center of origin?).

4.4.1- *loati* superspecies (*Micropanchax s.s.*) (5). Slender body (dd). Rounded lateral shape (pp). Little sexual dimorphism in body shape (p). Specificities: tendancy of the male to be smaller than female (d); little, if any, shine on male sides in some species (p); no allometry in growth (p). A primitive lineage. Distribution: primitive, from eastern Africa to northwestern Gambie, through the entire Sahelian zone (p/d).

4.4.2- *kingii* superspecies (2). Elongate body (d). Somewhat deeper than the other component and with preopercular pores (p). Distribution: heterogeneous and poorly known, at the northern (Nile) and maybe southwestern periphery (lake Tchad and coastal Togo) of *Micropanchax*.

4.5- *Lacustricola* (22). Convex frontal shape (pp). High count at Anal, lower at Dorsal fin (p). Little sexual dimorphism in body shape (p). Sexual dichromatism, with subdued female (d). Color pattern: derived, with specific design (dd). Distribution: in the Rift valley and surrounding regions, including Angola, resulting in a complex pattern, with partial sympatry and allopatry, following tectonics.

4.5.1- *Lacustricola s.s.* (5). Elongate body (d). Slightly compressed (d). High D/A ratio (d). Specificities: a broad lateral mid-side band in both sexes (d); a moderate upward disruption in body outline at front of old male (d). Distinguished from the 3 other sublineages by its larger size. Distribution: probably originating from eastern Angola/Zaïre, where it is highly diversified (p).

4.5.2- *Cynopanchax* (6). Compact body shape (p). Rounded lateral shape (pp). Somewhat deeper peduncle (p). Low D/A ratio (p). Specificities: a short and rounded, fan-shaped Caudal fin in male (d); a vertically oblong post-opercular dark blotch (d). Distribution: eastern Africa in the coastal plain and the neighboring plateau, up to the Rift lakes (included) (p).

4.5.3- *hutereaui* superspecies (7). Compact body shape (p). Slightly compressed (d). High D/A ratio (d). Specificities: dark transversal-to-rays markings on the posterior half of unpaired fins of male (d); mozaic markings on male sides (d). Distribution: western Rift (including some tributaries of lakes, down to southeastern Africa) and mainly the Congo cuvette belts (up to the Cameroun plateau, with *camerunensis*) (pp/d). Southerly vicariant to *Poropanchax normani.*

4.5.4-*johnstoni* superspecies (4). Slender body (dd). Slightly compressed (d). High D/A ratio (d). Blue conspicuous markings on male sides and fins (d). Specificities: well separated blue spots on male sides of both sexes (without gold spots, as in *Lamprichthys*) (d). Distribution: along the southern Rift valley to coastal southeastern Africa, via the Zambezi river (pp).

4.6- *Poropanchax* (7). Convex frontal shape (pp). Slightly compressed (d). Low peduncle (d). Frontal neuromasts in 2/3 pores (p). Very low count at Dorsal and Anal fins (dd). High D/A ratio, except *Congopanchax* (d). Little sexual dimorphism in body shape (pp). Low and long male Caudal fin (dd). Sexual dichromatism, with subdued female (d). Color pattern: derived, with specific design (dd). Biotope: permanent or slightly seasonal with low current (d). Specificities: a posteriorily cut Caudal in female (d); extended Ventral fins in male at least (d); the overall shining blue zone on male sides is divided into 2 bands, except *normani* (also in *Plataplochilus*, independently acquired) (d). Because of the lack of collections in the southern range, its possible center of origin cannot be established but the somewhat less derived characters of *Congopanchax* and the presence of frontal pores (instead of channels) in southern populations of *scheeli* promote a southern center of origin (in the plain or the cuvette).

4.6.1- *Congopanchax s.s.* (2). Dwarf (dd). Slender body, but somewhat less than the related lineages (dd). Very low or negative D/A ratio (pp). Specificities: bilobate Dorsal and Anal fins in male, with filaments (d). Distribution: endemic to the (western?) Congo cuvette (p/d), in line with the lake Tumba and the lower Kasai refugia.

4.6.2.1- *macrophthalmus* superspecies (*Poropanchax s.s.*) (3). Slender body (dd). Blue conspicuous markings on male sides and fins (d). Specificities: a colored (blue, rarely red) border on male Caudal (d). Distribution: coastal plain from Cameroun to Côte d'Ivoire (d), with speciation in line with putative refugia, near the coastal fringe in freshwaters.

4.6.2.2- *scheeli* superspecies (*Poropanchax* part.) (1). Slender body (dd). Biotope: brackish to marine (pp). Specificities: a more greenish hue on male sides (d); extremely long Ventral fins in male (also extended in female) (d). Distribution: coastal plain from Gabon to Nigeria (at least), in brackish waters, notably near estuaries (d/p).

4.6.2.3- *normani* superspecies (*Poropanchax* part.) (1). Elongate body (d). Somewhat deeper than the other *Poropanchax* components. Specificities: overall blue/silvery shining on sides (p); dark transversal-to-rays markings on the posterior region of unpaired fins of male (d). Distribution: coastal plain from Liberia to Guinée and the Sahelian neighboring zones, north of the Guinean Dorsal and easterly to the upper Nile (d); occasionally sympatric with *Micropanchax s.s,* but apparently not with the *nimbaensis* superspecies (competitive exclusion?).

4.7- *Aplocheilichthys* (1). Very large (pp). Deep body shape (pp). Slightly compressed (d). Very deep peduncle (pp). Pointed mouth (dd). Equal snout opening (p). Circular frontal scalation (p). Interorbitar, unusually large (p). Very low count at Dorsal (d). High D/A ratio (d). Little sexual dimorphism in fin shape (dd). Strong body shape dimorphism and dichromatism (d). High and short male Caudal fin (pp). Golden conspicuous markings on male sides and fins (pp). Color pattern: derived, with specific design (dd). Swimming in mid waters (pp). Biotope: brackish to marine (pp). Biotope: permanent or slightly seasonal with low current (d). Specificities: pin-pointed profile of upper maxillary (d); somewhat extended Ventral fins in male (as *Poropanchax*, independently acquired) (d); dark and gold transversal bars on sides and Caudal fin of male (d); mid-Anal fin rays extended, then truncated posteriorily in male (d). Distribution: brackish and even marine waters (spawning may be obtained in pure sea water) from Angola to Gambie (p/p) (and opportunistically upstream in inland waters, up to 150 km); frequently in sympatry with *Poropanchax scheeli*; the putative center of origin is southern, in line with less derived populations in Congo.

4.8- *Hylopanchax* (1). Dwarf (dd). Elongate body (d). Slightly compressed (d). Low peduncle (d). Branchiostegal appendages in adult male (d). High count at Anal, much lower at Dorsal fin (p). Very high D/A (+13) ratio (dd). Remote insertion of Dorsal fin, posterior to Anal ending (dd). Very low LL scale count (dd). Strong sexual dimorphism in body shape (d). Sexual dichromatism, with subdued female (d). Color pattern: derived, with specific design (dd). Biotope: permanent with some current (dd). Specificities: very low transversal scale count for a relatively deep-bodied phenotype (d); post-opercular scales, strongly enlarged (d); dark "net" more prominent (shared with *Hypsopanchax*). Distribution: the Congo cuvette and its western belts, in Congo and Gabon. Seemingly, a derived northwestern offshoot of the vicariant *Hypsopanchax* (p/d), maybe in relation with the lake Tumba refugium.

4.9- *Hypsopanchax* (6). Deep body shape (pp). Strongly compressed (dd). Disrupted upper outline (d). Pointed mouth (dd). High count at Anal, lower at Dorsal fin (p). High D/A ratio (d). Strong sexual dimorphism in body shape (d). High and short male Caudal fin (pp). Sexual dichromatism, with subdued female (d). Color pattern: generalized (pp). Biotope: permanent with some current (dd). Specificities: the most deep-bodied and flattened lineage (d); a strong disruption in the frontal outline and in the lower body behind Ventrals, forming a keel in old male (d); frequent dark wide chevrons on male sides and markings along scale margins in both sexes (d). Distribution: the northeastern, eastern and southern belts of the Congo cuvette, southwards up to the Zambezi basin (p/d).

4.10- *Procatopus* (12). Flat front (d). Strongly compressed, even flattened (dd). Disrupted upper outline (d). Pointed mouth (dd). High count at Anal, lower at Dorsal fin (p). Strong sexual dimorphism in body shape (d). Stronger sexual dimorphism in fin shape (dd). High and short male Caudal fin (pp). Sexual dichromatism, with subdued female (d). Red conspicuous markings on male sides and fins (dd). Color pattern: derived, with specific design (dd). Biotope: permanent with some current (dd). Distribution: the west African coastal plain, rather inland, and neighboring foothills or grading plateau

(d): the three lineages replace each other vicariantly. Sympatric with *Poropanchax*, near the coastal fringe. Similarly to *Poropanchax* and *Aplocheilichthys*, a southern center of origin may be hypothesized (cephalic pores in southern lineage).
4.10.1- *Procatopus s.s.* (3). Deep body shape (pp). Branchiostegal appendages in adult male (d). Very high D/A ratio (dd). Breeding: on rocky substrate (p). Specificity: a pre-mating dancing behavior (independantly acquired at least also by *Aphyoplatys*, *Plesiolebias*, the *Aplocheilus blockii* superspecies and some viviparous Poeciliins). Specificities: Ventral fins, closer to the Pectoral fins insertion (d); red back in dominant male (d); red markings crossing rays of male unpaired fins (d); Anal fin, with extended posterior rays in male (d). Distribution: Bénin (east of the Dahomey gap) to northern Ecuatorial Guinea (d).
4.10.2- *Plataplochilus* (5). Compact body shape (p). Branchiostegal appendages in adult male (d). Frontal neuromasts in 3 pores (pp). High D/A ratio (d). Specificities: the overall shining blue zone on male sides is divided into 2 bands (also in *Poropanchax*, independently acquired) (d); red markings on mid-posterior sides of male (d); a temporary dark lower band on sides of male (d). Distribution: Cabinda (and maybe Angola) to southern Equatorial Guinea (p/d).
4.10.3- *nimbaensis* superspecies (4). Small (d). Compact body shape (p). Disrupted lower outline (d). High D/A ratio (d). Specificities: an additional break in body outline at the lower opercle level (d); vertical red markings on male posterior unpaired fins (d); combines uniquely in *Procatopus* a lower D/A ratio with a high ray count at Anal (p). Distribution: west of the Dahomey gap, from Ghana to Gambie and notably diversified in the Guinean Dorsal, in line with the refugium (d); closer to the coast in its eastern range (due to probable *normani* pre-emption, westerly). Note: this systematic move is established in Huber (1998a).

5- American Aplocheilichthyins (4) (the all -but one- viviparous Poeciliins are dominant, with circa 200 species, according to Parenti, 1981).
5.1- *Fluviphylax* (4). Dwarf (dd). Convex frontal shape (pp). Slender body (dd). Slightly compressed (d). Low peduncle (d). Upper frontal scalation type (d). Frontal neuromasts (limited) in often discontinous grooves (d). Interorbitar, unusually narrow (d). Very large eye diameter (dd). Very low count at Dorsal and Anal fins (dd). High set Pectoral fins (p). Very high D/A ratio (dd). Remote insertion of Dorsal fin, behind Anal ending (dd). Very low LL scale count (dd). Little, if any, sexual dimorphism in body shape (p). No sexual dimorphism in fin shape (pp). No sexual dimorphism in fin ray count (pp). Low and long male Caudal fin (dd). Little sexual dichromatism, if any (pp). No supracaudal ocellus in female (pp). No dark band through eye (dd). Strong melanism in both sexes (pp). Color pattern: generalized (pp). Swimming near surface (d). Breeding: among plants (d). Biotope: permanent or or slightly seasonal with low current (d). Posture: straight in less reclusive areas (pp). Behavior: no jumper, in schools (pp). Egg development: short and hardly delayed (strict non-annual) (dd). Coverage: today in primary forest (d). Specificities: "lampeye" state (d); very few markings, if any (p); feeds on algae and invertebrates (d). A strongly derived lineage in comparison to African Aplocheilichthyins, but not as much as its sister group, the viviparous Poeciliins. Distribution: endemic to the Amazon cuvette and its main tributaries (including the Amazonian Orinoco) (d).

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