Freshwater fish zoogeography in west Africa: faunal similarities between river basins

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Synopsis

Similarities between the freshwater fish faunas of 52 west African rivers have been investigated and three main zoogeographic regions recognized. The Sudanian region includes all rivers from Senegal to the Omo, as well as coastal basins from Ivory Coast to the Cross and the Wouri. The Upper Guinean region comprises the coastal basins from Guinea to Liberia and the Lower Guinean one, the coastal rivers of Cameroon and Gaboon. The Sudanian region can be sub-divided into a Sudanian region sensu stricto, including the Sahelo-Sudanese rivers, and the Eburneo-Ghanean region corresponding to coastal basins from the Cess (or Nipoué, Ivory Coast) to the Pra (Ghana). These delimitations give an highly significant within region faunal homogeneity, even if the effect of geographical proximity between rivers is removed. 21 to 71% of the fish species in each region are endemics. The present patterns of distribution are the result of past climatic and geological events affecting west Africa and, given this framework, the role of alternating wet and dry periods during the early Quarternary is emphasized as well as the importance of mountains as dispersal barriers. Role of recent river connections and links via lagoon is emphasized in explaining river faunal similarities within biogeographical regions.

Introduction

Until recently much more attention has been given to fish zoogeography in east and southern Africa (Hamilton 1982) than to that of west and central Africa. Most of the attempts to recognize different ichthyological regions or provinces in this part of the continent, have been based on superficial, and sometimes poor, knowledge of the occurrence and distribution of fish species in the dense coastal drainage network. Daget & Iltis (1965), in their major contribution to the west African fish fauna, distinguished three geographical categories of freshwater fishes: Sudanese, Guinean and indifferent.

Such a division enabled them to calculate a Sudano-Guinean index (which is the ratio of the number of Sudanese fish species to the number of Guinean ones) in order to characterize different river basins or parts of these basins. A different approach has been to use the distribution of restricted taxa as criteria for the definition of fish province boundaries in Africa. The ichthyological provinces recognized by Roberts (1975), followed by the various attempts of Blanc (1954), Matthes[1] and Poll (1974) to divide

[1] Matthes, H. 1964. La zoogéographie des poissons dulçaquicoles africains. Thesis of Amsterdam Museum April 1964, unpublished.

Table 1. The river basins studied, their code, their belonging to the biogeographical regions according to the optimization analysis and the presence-absence of rain forest in their catchment area.

| Rivers	Code	Biogeographical region		Presence of rain forest
Omo	1	Sudanian s.s.	Sudanian s.l.	no
Nil	2	Sudanian s.s.	Sudanian s.l.	no
Chad	3	Sudanian s.s.	Sudanian s.l.	no
Senegal	4	Sudanian s.s.	Sudanian s.l.	no
Gambia	5	Sudanian s.s.	Sudanian s.l.	no
Volta	6	Sudanian s.s.	Sudanian s.l.	no
Mono	7	Sudanian s.s.	Sudanian s.l.	no
Oueme	8	Sudanian s.s.	Sudanian s.l.	no
Ogun	9	Sudanian s.s.	Sudanian s.l.	in part
Upper Niger	10	Sudanian s.s.	Sudanian s.l.	no
Lower Niger	11	Sudanian s.s.	Sudanian s.l.	in part
Benue	12	Sudanian s.s.	Sudanian s.l.	no
Cross	13	Sudanian s.s.	Sudanian s.l.	yes
Wouri	14	Sudanian s.s.	Sudanian s.l.	yes
Geba	15	Sudanian s.s.	Sudanian s.l.	no
Nipoue	16	Eburneo-Ghanean	Sudanian s.l.	yes
Cavally	17	Eburneo-Ghanean	Sudanian s.l.	yes
Dodo	18	Eburneo-Ghanean	Sudanian s.l.	yes
Nero	19	Eburneo-Ghanean	Sudanian s.l.	yes
San Pedro	20	Eburneo-Ghanean	Sudanian s.l.	yes
Sassandra	21	Eburneo-Ghanean	Sudanian s.l.	in part
Boubo	22	Eburneo-Ghanean	Sudanian s.l.	yes
Bandama	23	Eburneo-Ghanean	Sudanian s.l.	in part
Agnebi	24	Eburneo-Ghanean	Sudanian s.l.	yes
Me	25	Eburneo-Ghanean	Sudanian s.l.	yes
Comoe	26	Eburneo-Ghanean	Sudanian s.l.	in part
Bia	27	Eburneo-Ghanean	Sudanian s.l.	yes
Tano	28	Eburneo-Ghanean	Sudanian s.l.	yes
Pra	29	Eburneo-Ghanean	Sudanian s.l.	yes
Little Scarcie	30	Upper Guinean		no
Tomine	31	Upper Guinean		no
Konkoure	32	Upper Guinean		no
Kolente	33	Upper Guinean		no
Jong	34	Upper Guinean		no
Sewa	35	Upper Guinean		no
Moa	36	Upper Guinean		in part
Mano	37	Upper Guinean		yes
Loffa	38	Upper Guinean		yes
St Paul	39	Upper Guinean		yes
St John	40	Upper Guinean		yes
Du	41	Upper Guinean		yes
Rockel	42	Upper Guinean		no
Mungo	43	Lower Guinean		yes
Sanaga	44	Lower Guinean		in part
Nyong	45	Lower Guinean		yes
Lokundje	46	Lower Guinean		yes
Lobe	47	Lower Guinean		yes
Kribi	48	Lower Guinean		yes
Ntem	49	Lower Guinean		yes
Rio Ekudo	50	Lower Guinean		yes
Ogowe	51	Lower Guinean		yes
Niari-Kouilou	52	Lower Guinean		yes
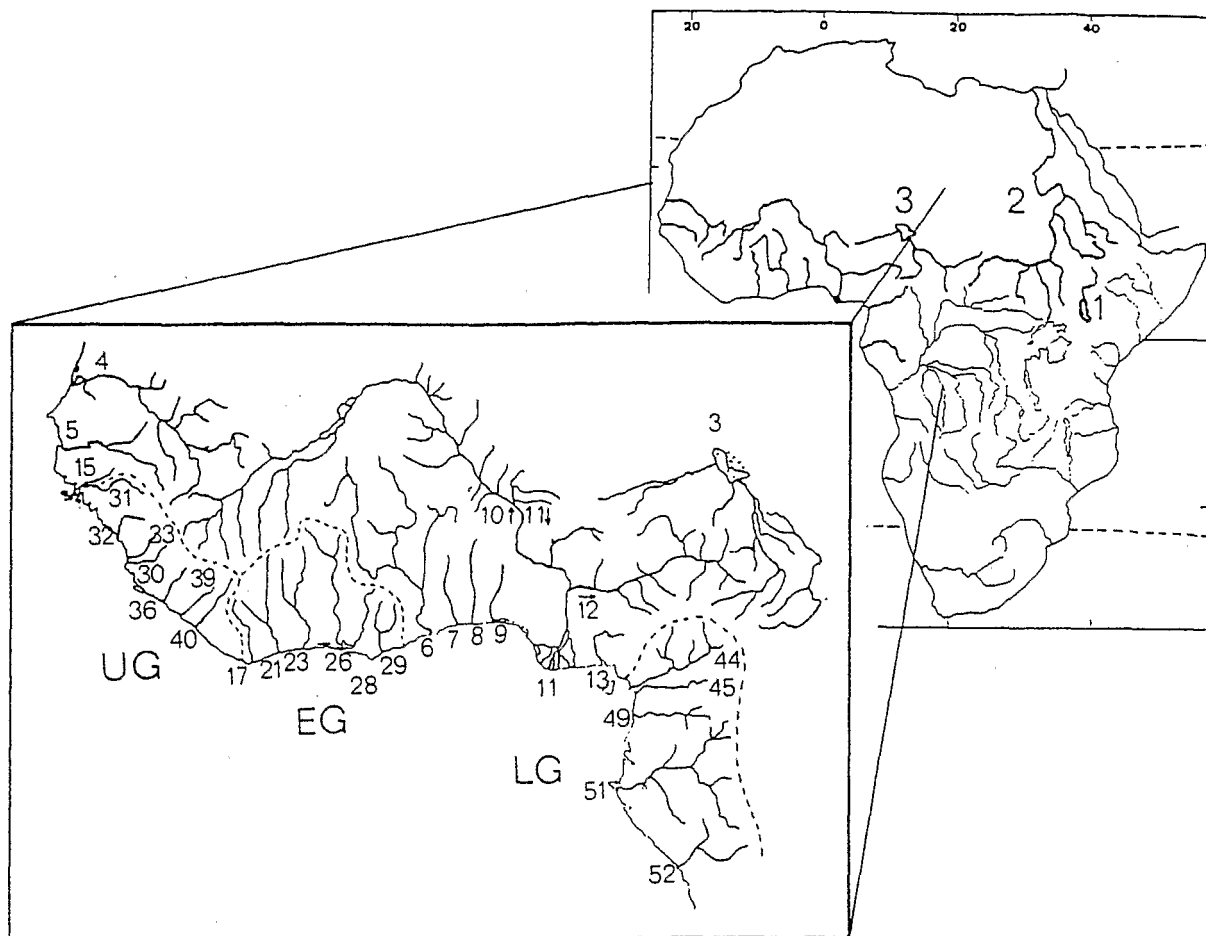
Fig. 1. Maps showing some of the river studied (bolded in the large-scale map) and boundaries of the biogeographical regions (UG = Upper Guinean region EG = Eburneo-Ghanean region LG = Lower Guinean region; Sudanian region otherwise). See Table 1 for river codes. Not mapped rivers have their mouths located in the following way: 14 and 43 between 13 and 44: 16 between 40 and 17: 18 to 20 between 17 and 21: 22 between 21 and 23: 24 and 25 between 23 and 26; 27 between 26 and 28: 34 35 and 42 between 30 and 36: 37 and 38 between 36 and 39: 41 between 39 and 40: 46 to 48 between 45 and 49: 50 between 49 and 51.

Africa into faunistic zones. He identified three main ichthyofaunal provinces in west and central Africa: the Nilo-Sudan province extending from Senegal to the Nile and Abyssinian highlands; the Upper Guinean province, including coastal rivers extending from Senegal to Ghana; the Lower Guinea from Nigeria to Zaire, including the Cross sytem. All the above geographical delimitations were more or less empirical and not supported by quantitative data. Nevertheless they reflected the state of the art at the time they were published.

The present day distribution of fish in the African basins is the result of several different factors: (1) The size of the river basin and the diversity of aq-

uatic habitats available to fish. Positive relationships between the number of fish species present and catchment area and/or river discharge were established for Africa by Daget & Iltis (1965), Livingstone et al. (1982), and Hugueny (1989). (2) The historical climatic or geological events which made possible connections or isolations of river catchments. Continual climatic changes have occurred in Africa (Hamilton 1982), but their number and nature is reasonably well established for only the past few ten thousand years. Study of lake sediments provides a large source of information on the past hydrology of Africa, but there are comparatively few data on the paleolimnology of rivers. (3) Spe-
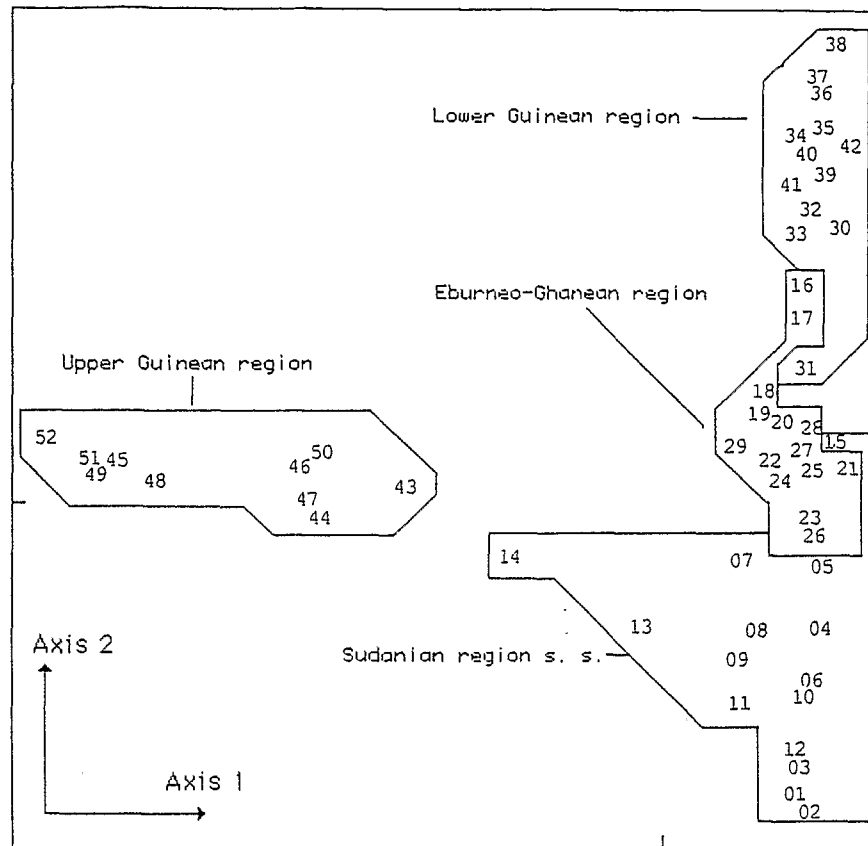
Fig. 2. The position of the river basins listed in Table 1 on the first and second axes of the correspondence analysis. Codes for river basins are given in Table 1.

ciation processes which depend on the duration of isolation and evolutionnary potential of fish families. A serious problem for biogeographic studies in Africa is the lack of knowledge of the phylogenetic relationships among species and genera (Greenwood 1983), as well as the sometimes still confused taxonomy and poor distribution data, in spite of great improvements during recent decades. (4) The existence of refuge zones during drought periods, or of relict zones usually isolated by physical barriers such as falls impassable to fish. (5) The ability of fish to disperse (Roberts 1975, Hugueny 1990a).

The aims of this paper are: (1) To investigate faunal similarities between west African river basins using their fish species compositions, to check if the use of quantified data will modify in any way the ichthyoprovinces identified by previous authors. (2) To review our current knowledge of past climat-

ic and geological events of the river catchments, with emphasis on the possible connections between catchments which could explain fish dispersion. (3) To identify the existence of barriers or refuge zones.

Origin and analysis of the data

Our knowledge of the taxonomy and distribution of fishes in Africa has improved considerably during the last two decades. This is partly a consequence of large new collections becoming available, but also of the publication of the CLOFFA, Check-List Of the Freshwater Fishes of Africa (Daget et al. 1984, 1986a, 1986b, 1991) which provided a current list of freshwater fish species with full synonymies, and subsequent revisions which introduced new taxonomic changes. Up-dated checklists for major west African river basins have also been recently pub-
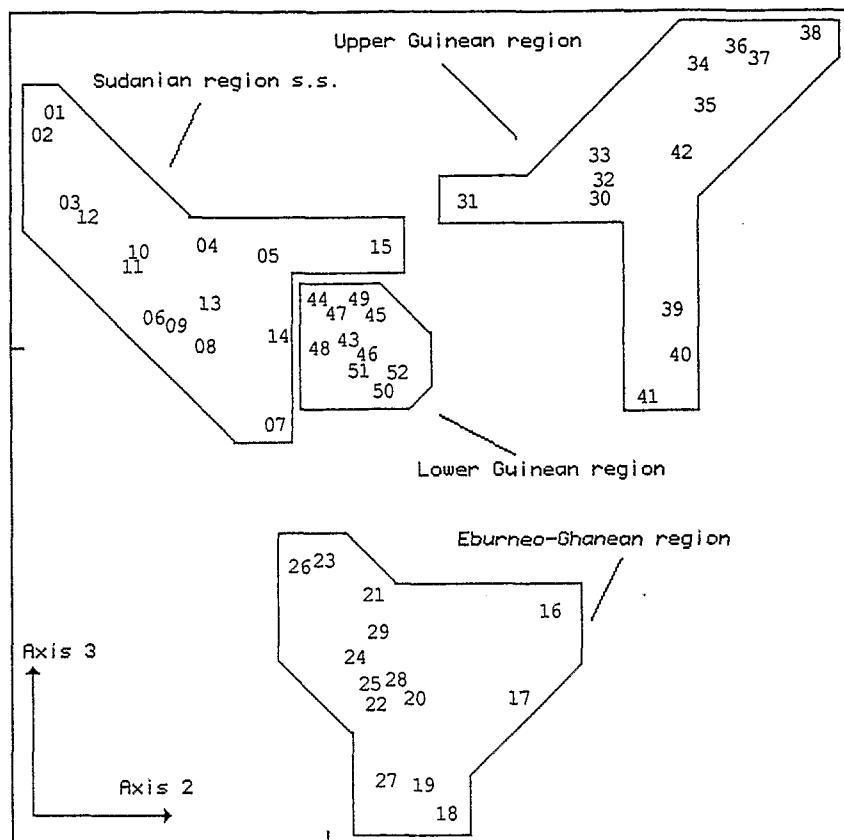
Fig. 3. Position of the river basins listed in Table 1 on the first and third axes of the correspondence analysis. Codes for river basins are given in Table 1.

lished (Lévêque et al. 1989, 1991, Paugy & Benech 1989, Paugy et al. 1990; Teugels et al. 1988), providing a useful database for further ecological and zoogeographic studies. An identification guide with distribution maps covering west Africa is now available (Lévêque et al. 1990, 1992). There are no updated checklists for rivers from Cameroon and Gabon, except for the Cross River (Teugels et al. 1992), but bibliographic data were summarized by Hugueny (1990b). Given that Museum collections were not examined, such inventories based on published papers are possibly less exhaustive than the lists established for the other west African rivers. All the data analysed in this article are available from the authors on request.

⸱Fifty river systems were considered but the Niger, given its size and peculiarities, was divided, following Lévêque et al. (1991), into the Upper and Middle Niger (from the headwaters to Kainji

Lake), the Lower Niger (from Kainji Lake to the delta) and the Benue. Thus, 52 geographical units were considered (hereafter named 'rivers'). Species recorded in only one of those rivers were not included in the analysis because, if phylogeny is unknown, they provided no information on the relationships between river systems. Fish species tolerant to salt water (classified as peripheral according to Myers 1951) and lacustrine endemics species have also been discarded. Consequently 443 species were considered from a total of 743 known to occur in 52 rivers included in this study. Rivers studied are listed in Table 1 and most of them are mapped in Figure 1. In Table 1 is also indicated if rivers run through rain forests, according to maps given by White (1983).

Data analysis was conducted in five steps: (1) A correspondence analysis, or reciprocal averaging (Gauch 1982a, Digby & Kempton 1987), was ap-
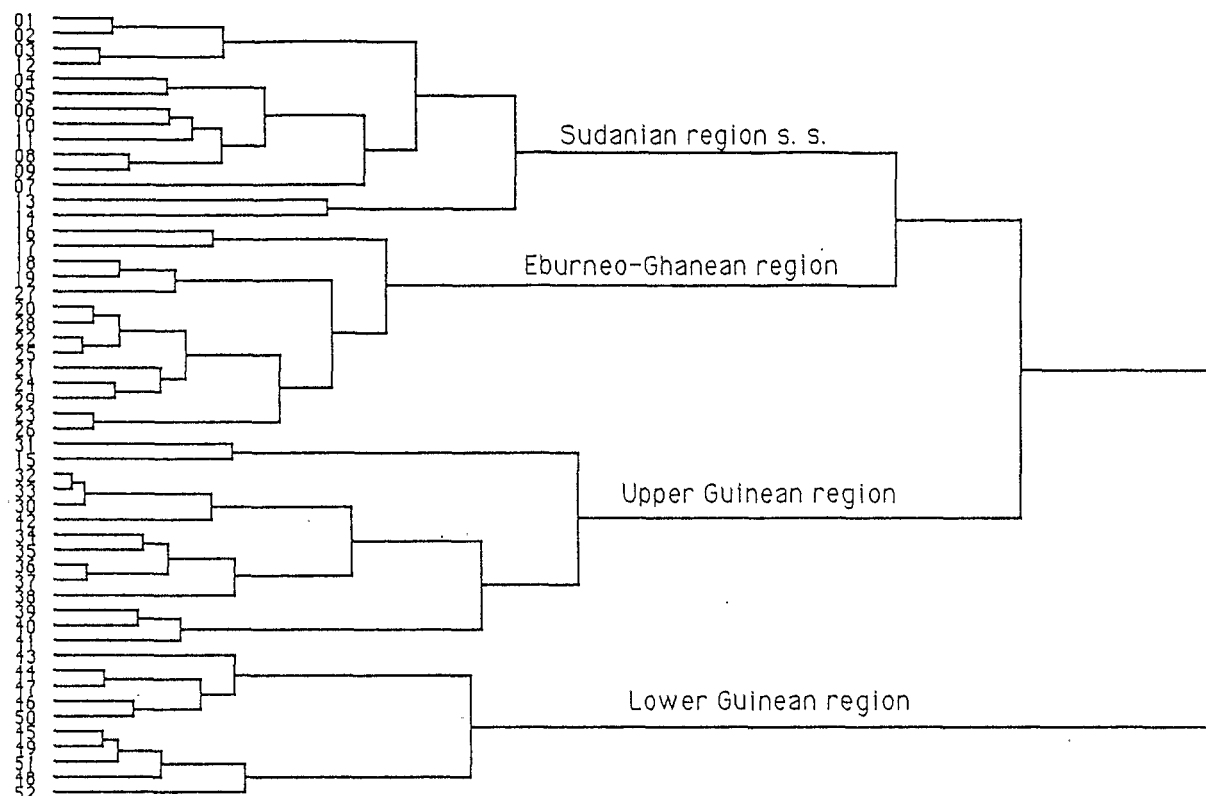
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Sudanian region s. s.

Eburneo-Ghanean region

Upper Guinean region

Lower Guinean region

Fig. 4. Dendrogram (UGPMA using Euclidian distances from the three first axes of correspondence analysis) showing relationships between rivers. Codes for rivers are given in Table 1.

plied to presence-absence data for the 52 rivers. This ordination method uses the chi-squared metric which is insensitive to zero matches in the data (contrary to principal component analysis, for instance), a recommended property in ecological. or biogeographical. multivariate analyses (Legendre & Legendre 1984). Following this analysis, a limited number of axes is retained. those which have an obvious biogeographical significance. (2) A faunistic distance between rivers was computed starting from the coordinates on factors retained in the previous step and using the euclidian distance. Using the correspondence analysis factor scores instead of the real data provides a way to smooth the dataset by eliminating the variations which are not taken into account by the factor scores retained and which are assumed to be non informative from a biogeographical point of view. Gauch (1982b) has demonstrated the ability of correspondence analysis to recover meaningful pattern in early ordination axes and to defer noise to later axes. Consequently ordi-

nation is useful even when the percentage of variance accounted for by the first few ordination axes is small. (3) Using the faunistic distance described above, a hierarchical cluster analysis was performed in order to check how many clusters (biogeographical regions) can be clearly recognized within our dataset and to display relationships between them. Dendrogram is produced by an unweighted pair groups method using arithmetic averages (UGPMA). One of the property of the UGPMA is to give a dendrogram in which relationships between units (ultrametric distances) are highly correlated with relationships between units in the original distance matrix (Gauch 1982a). (4) Partition obtained in the previous step is submitted to an optimization analysis, a moving center algorithm, which moves units among clusters until the average of within-cluster distances shows no decrease. Number of cluster is maintained constant along the analysis. This analysis is performed using the faunistic distance defined in the third step. (5) Since

fish can only emigrate from a river to its immediate neighbours, we might expect faunistic distance and ·geographic distance to be positively related even if biogeographical processes such as immigration, speciation or extinction occur in a random way. The aim of this study is to find faunistic relationships between rivers greater than expected on the basis of their spatial position and which could be the result of meaningful processes such as dispersal barriers, speciation centers and so on. Since the partition obtained in the fourth step may be a result of the geographical position of rivers, we have to assess if it still have a significance if the effect of geographical relationships between rivers is removed. In this aim a geographical distance between two rivers was computed as the minimum number of catchment divides separating them. This distance, having discrete values, ranges in our case from 1 to 8. Another distance matrix (biogeographical membership matrix) was computed in which cells have two values, zero if the two rivers considered belong to the same biogeographical region and one if they are located in two different regions. So we have 3 matrices: the geographical distance matrix (A), the faunistic matrix (B) and the biogeographical membership matrix (C). If the partition obtained is only a result of spatial position, we can expect the relationship between matrices B and C to be non significant if the effect of matrix A is removed. Statistical relationship between two distance matrices can be evaluated using the Mantel's test (Mantel 1967). Dependency between two distance matrices when the effect of a third matrix is removed was analyzed using the Mantel's test as described by Smouse et al. (1986). As Mantel's test uses correlation coefficient between matrix cells, this is like performing a partial correlation analysis. Statistical significance is evaluated by randomization (Dietz 1983) with 1000 permutations of matrix rows.

For these analyses the following softwares has been used: MacMul 2.14 (J. Thioulouse, Université Lyon I, Laboratoire de Biométrie, URA CNRS 243, 69622 Villeurbanne cedex, France), MacDendro 1.01 (ibid.), GrahMu 4.1 (ibid.) and R package (P. Legendre & A. Vaudor, Département de sciences biologiques, Université de Montréal, CP 6128, succursale A, Montréal, H3C 3J7, Canada) respective-
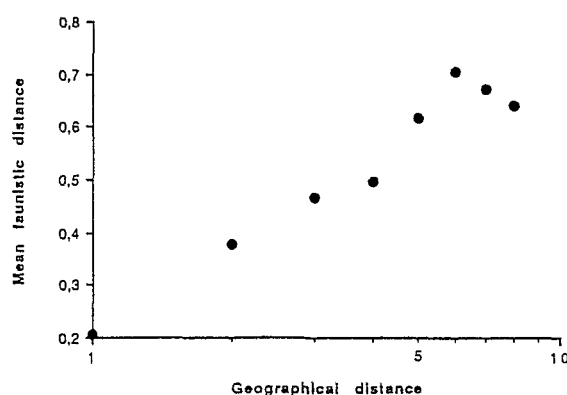

Fig. 5. The relationship between the mean faunistic distance for river basins separated by a given geographical distance and the geographical distance (1, 2, 3, etc.).

ly for correspondence analysis, analyses with distance matrices (computation of euclidian distances, UGPMA and moving center analysis), graphic displays (factorial maps and dendrograms) and Mantel's test.

Results

For the 52 rivers defined above, the first axis of the correspondence analysis (13% contribution to total inertia) separated the Cameroon and Gabon rivers from the rest. The second axis (10% contribution) displays rivers along a gradient from a group of coastal rivers located in Guinea, Sierra Leone and Liberia to a group of rivers from the sahelian belt (Fig. 2). The third axis (7% contribution) clearly identified a group of rivers from Ivory Coast and Ghana (Fig. 3). Remaining axes do not provide useful biogeographic information, consequently analyses will be conducted on the 3 first axes. Hierarchical cluster analysis (Fig. 4) reveals a first dichotomy between rivers of a Lower Guinean region (Cameroon and Gabon) and the other ones. Within these remaining rivers a second dichotomy separates rivers of an Upper Guinean region (Guinea, Sierra-Leone and Liberia) from rivers which are mainly Sudanian (Sudanian region sensu lato). Within the Sudanian region (sensu lato) a third dichotomy separates rivers of an Eburneo-Ghanean region (Ivory Coast and Ghana) from rivers of a Sudanian region sensu stricto. When these four groups of rivers are

Table 2. The characteristics of the biogeographic regions described in this study. The % endemics is the ratio (× 100) from the number of species occurring only in the region to the total number of species encountered in that region. Results are given with (between brackets) and without single river endemics.

Biogeographical regions	Mean faunistic distances between adjacent rivers	% endemics in the region
Upper Guinean	0.086	19 (35)
Lower Guinean	0.153	49 (71)
Sudanian	0.112	36 (53)
Eburneo-Ghanean	0.117	13 (21)

submitted to a moving center algorithm the solution is obtained in one step: the Geba River moves from the Upper Guinea to the Sudanian region sensu stricto. The final partition is displayed in Figures 2 and 3 and in Table 1.

The three main clusters of rivers recognized in our study (Upper Guinean, Lower Guinean and Sudanian sensu lato regions) are more or less similar to the provinces recognized by Roberts (1975): our Sudanian region, Upper Guinean region and Lower Guinean region matches respectively his Nilo-Sudan, Lower Guinea and Upper Guinea provinces. But the Nilo-Sudan province is not homogeneous because it is possible to distinguish the riverine ichthyofaunas of Ivory Coast and Ghana from the remainder.

Only a sub-set of all African rivers have been considered in this paper. As a result, some limits of the ichthyofaunal regions were not clearly identified. For example, the eastern boundary of the Sudanian region is unknown given that no river basin east of the Omo was included in the analyses. A similar situation occurs for the southern limit of the Lower Guinea, the rivers south to the Niari-Kouilou are not included in the analyses. Figure 1 shows the boundaries between regions obtained in this study.

As expected, a clear positive relationship between faunistic distance and geographic distance was observed, which is better if geographic distances are log-transformed (Fig. 5). The closer the rivers are, the more similar their fauna. Correlation coefficient between geographical distances (log-transformed) and faunistic distances is 0.414, value highly significant from Mantel's test result (p < 0.001). This suggests that the proposed partition may be no more than a grouping of rivers on the basis of their geographic position without any significant biogeographical boundaries. However, Mantel's test reveals that when the effect of geographical distance (in log.) is removed, the partition proposed still provides a statistically significant within group homogeneity: the partial correlation between faunistic distances and biogeographical distances is 0.754 (p < 0.001). This result confirms the existence of meaningfull boundaries between our biogeographic regions.

Table 2 gives the characteristics of the biogeographic regions identified. Each one includes a large number of endemic species, and could be considered as a center of endemism. If species occurring in only one river, which have been discarded in the multivariate analyses, are included in the computation, endemism increases steeply. This table gives also the mean faunistic distance between adjacent basins (geographical distance of one) within each biogeographical region.

Discussion

Our delimitation of ichthyological regions based on comparison of faunistic lists of the different river basins, partially confirms the empirical division proposed by Roberts (1975) but the boundaries have been slightly modified. The Nilo-Sudan province (our Sudanina region s. l.) remains almost unchanged but, according to our analyses, following river should be members of this region: Gambia and small Ivorian rivers (previously included in Upper Guinea by Roberts), and Wouri and Cross (previously included in the Lower Guinea).

The Upper Guinea province sensu Roberts is not homogeneous according to fish repartition. It

should be divided into our Upper Guinean region, including coastal basins from the Tomine in Guinea to the Saint John River in Liberia, and an Eburneo-Ghanean region, from the Cess (Nipoué) in Ivory Coast, to the Pra in Ghana which is faunistically closer to the Sudanian region than to the Upper Guinean one. The distinction of the Eburneo-Ghanean region results from the existence of fish species with geographical distribution restricted to this area such as: *Marcusenius furcidens, Marcusenius ussheri, Citharinus eburneensis, Barbus trispilos, Amphilius atesuensis, Schilbe mandibularis, Synodontis bastiani,* and *Aethiomastacembelus nigromarginatus.* But the fish fauna as a whole is very similar to that of the Sudanian region (s.s.).

The major difference from Roberts' zoogeographical division, lies therefore in the larger Nilo-Sudan province, including parts of what he placed in his Guinean provinces (the Cross and Wouri rivers and the Eburneo-Ghanean region). It is not clear why Roberts included the small coastal basins of Ivory Coast in Upper Guinea, but the reason could be their location in the forest area. However, from the results above, it is clear that there is no direct correlation between biogeographical regions based on fish species distribution and the present extent of the rain forest (Table 1).

The biogeographical regions described in this study are also centers of endemism. In west Africa, observed endemism for fish seems to be higher than for other vertebrates. For instance, the percentages of forest-dwelling endemic species of birds in areas corresponding to the Lower and Upper Guinea, are respectively 5 and 6 (Diamond & Hamilton 1980), for mammals these values are 25 and 34 (Grubb 1982) which is lower than for fishes (respectively 71 and 35, see Table 2). This endemicity pattern reflects the dispersal ability of these taxonomic groups: birds are better dispersers than mammals which have better dispersal abilities than fishes.

There is few biogeographic studies dealing with aquatic organisms other than fish in west Africa. A study of aquatic birds (Guillet & Crowe 1985), gave different results but that is not really surprising given that birds are not dependent upon connections between watersheds for migration. For aquatic molluscs, Van Damme (1984) recognized different bio-geographic areas in Africa which agree only in part with our results. At the generic level, Van Damme identified the equivalent of the Eburneo-Ghanean region, where there is high endemicity. The same is true for the Lower Guinea, whereas the Upper Guinea does not appear to be different from the Sahelo-Sudanian area. The zoogeography of some Monogenea (branchial parasites of freshwater fishes), is fairly similar to that observed for fish (Guégan 1990). *Dactylogyrus afer* and *D. brevicirrus* groups are mainly distributed in Nilo-Sudan rivers and not recorded from Upper Guinea. Conversely, the *D. ruahae* and *D. archaeopenis* groups are present in the Guinean zones. As a result of an enzymatic study of different populations of the siluroid *Chrysichthys maurus,* three main groups were distinguished: western Guinean province, Eastern Guinean province, and Ivory Coast (Agnèse 1989). The Nipoue or Cess River appears to be the boundary between the Guinean groups and the Ivorian group, and this agrees with our observations that this river separates the Guinean and Eburneo-Ghanean regions. These studies suggest that delimitations proposed in this paper are, at least in part, shared with other taxonomic groups or other approaches and consequently have without doubt a biogeographical meaning.

One way to explain the similarities between the fish faunas of some rivers is to consider the present day distribution of fish as the result of geological and historical climatic events. The river basins could indeed be considered as isolated islands as long as no physical connection exists between them at the present time. Although some species are probably able to enter other basins by crossing the sea, most of them colonized those basins when physical connections existed between basins in the past, or when a river was captured by another basin.

At the present time, most of west Africa consists of flat sedimentary basins and upland plains ranging from 150 to 600 m above sea level, with disjunct patches of highlands above 1000 m. Among the most important of these, the Fouta Djalon and the Guinean range along the western coast, separate those northward flowing rivers which form the sources of the Niger, Senegal and Gambia rivers, from the rivers of the Atlantic side (Guinea, Sierra

Leone and Liberia) which constitute the Upper Guinean region, and are relatively short, partly torrential in their upper courses. The Lower Guinean region is also a mountainous area. According to the vicariant model of speciation, the long term presence of barriers to migration and dispersal, can explain the existence of high endemicity areas on both sides of these barriers. The appearance of barriers can occur on such an occasion as the upthrust of mountains. For example, the Guinean range, including the Fouta-Djalon, could have isolated the southwestern Upper Guinea fauna from the north western Nilo-Sudan one. Similarly, Mounts Cameroon and Adamoua isolates the Lower Guinea area from the Nilo-Sudan province. Such events are rather old (between the end of Jurassic and the end of Eocene for the Fouta Djalon) and could explain the presence of endemic genera in the Guinean regions. Species known as amphiguineans (Daget 1962) are present on each slope of the Fouta Djalon. However, only a few species belong to this category. In fact only two, *Amphilius rheophilus* and *A. platychir*, have a restricted Upper Guinean distribution and are also present in the Upper courses of the Niger. This suggests that the Guinean range is a barrier uncrossable for almost all species of fishes. We can expect faunistic distance between adjacent rivers to be greater in mountainous area than in flat terrain where the incidence of river capture is more likely (Livingstone et al. 1982). However, mean faunistic distance between adjacent rivers within biogeographical regions does not fit this scheme: similarity between contiguous rivers is greater in Upper Guinea (a mountainous region) than in the Sudanian region (located in a rather flat area) as indicated by Table 2.

Communication between watersheds could be the result of climatic changes (extension and recession of water bodies) or tectonic activities such as earth movements, faulting, volcanism, and erosion which could result in captures. Species represented in almost all the tropical African rivers (such as *Malapterurus electricus* or *Hepsetus odoe*) demonstrate that each African river has been connected to some other rivers in the past. In order to explain present distribution of fishes it is therefore important to know not only if rivers has been connected but also

if it is a recent event. Knowing that some river basins had physical connections in the recent past (Quaternary), is it possible to observe a greater faunal similarity between them than between other adjacent ones? In our set of rivers, four such connections are documented or assumed on a geographical basis: (1) Connection between the Chad and the Benoue. At present, part of the flood water of the Logone (a tributary of Chari River, Chad basin) overflows to the west into the Mayo Kebi and over the Gauthiot Falls and joins the Benue (Reid & Sydenham 1979). There is good geological evidence that during pluvial periods this connection was already functioning. (2) Connection between the Chad and the Niger. During the late Pleistocene and Upper Holocene (12000–8000 years BP) the major river systems of western Africa had a much greater effective catchment (Talbot 1980). A number of prominent watercourses in the central Sahara, such as the Tilemsi, Dallol Bosso, Dallol Maouri, and Tarka, flowed directly into the Niger River or joined seasonally active tributaries of those rivers. Under present climatic conditions, they are essentially relict features but during the humid phases, these rivers were active (Lévêque 1990). At the height of the humid phases, the Niger-Benue system had a much greater catchment and probably received a large amount of water from the overflowing Chad basin. (3) Connection between the Niger and the Senegal. It is assumed that the Baoule (previously flowing to the Niger) is a capture by a small tributary of the Bakoy (Senegal catchment) which intervened 18000 BP (Michel 1973). (4) Connection between the Nile and the Chad. Williams et al. (1980) and Adamson & Williams (1980) established that a major change in the western margin of the Nile basin occurred as a result of Tertiary and Quaternary volcanism. The eruption of the Jebel Mara volcanic complex which commenced in the Miocene, resulted, in their view, in a westward diversion to Chad of a previously eastward flowing drainage. A catchment of more than 60000 km^2 was thus deleted from the Nile basin.

From Table 3 it appears that the faunistic distance between adjacent watersheds for which past connections are documented or assumed is always less than the mean distance between adjacent basins lo-

cated in the same biogeographical region. In that case, the presumptions outlined above are corroborated by the affinities of the freshwater fish fauna.

Apart from fish species particularly tolerant to salt water (classified as peripheral according to Myers 1951 and not included in this study), freshwater fish could hardly disperse across the sea. Nevertheless, one can observe at present a series of coastal lagoons along the west African coast often in connection with two river basins. Many species that tolerate brackish water, at least for a short period, are therefore able to migrate from one basin to another and, eventually, to colonize a new basin. That is probably the case for *Brycinus longipinnis* (present in coastal rivers from Senegal to Zaïre) and *Chrysichthys maurus* (present in coastal rivers from Senegal to Pra). Such exchanges could be facilitated during flood periods when input of freshwater diminishes the salinity of the lagoon waters. Bearing in mind the past climatic changes, there were probably pluvial periods during which high floods provided suitable conditions for fish to disperse coastwise between river mouths, either through very dilute brackish waters, or through freshwater marshes extending between two adjacent lower river courses. In Table 3 we have reported faunistic distances between adjacent rivers

Table 3. The faunistic distance between contiguous rivers assumed to have been in recent contact (C) or linked via a lagoon creek network (L). For comparison, mean faunistic distance between contiguous rivers located in the same biogeographical region is given (between brackets, see Table 2).

Connections		Faunistic distances
Jong-Sewa	L	0.051 (0.086)
Sewa-Moa	L	0.066 (0.086)
Bandama-Agnebi	L	0.108 (0.117)
Agnebi-Me	L	0.042 (0.117)
Me-Comoe	L	0.145 (0.117)
Comoe-Bia	L	0.230 (0.117)
Bia-Tano	L	0.087 (0.117)
Mono-Oueme	L	0.109 (0.112)
Oueme-Ogun	L	0.043 (0.112)
Ogun-Lower Niger	L	0.075 (0.112)
Upper and Middle Niger-Chad	C	0.091 (0.112)
Benue-Chad	C	0.026 (0.112)
Chad-Nile	C	0.084 (0.112)
Upper and Middle Niger-Senegal	C	0.077 (0.112)

which are linked via a lagoon creek network. It appears that 80% (8/10) of these distances have a lesser value than the mean distance between adjacent rivers located in the same biogeographic area. These data confirm the importance of connections via lagoons in order to explain similarity between rivers despite the fact that only some kind of species (lower course species) are able to take advantage of this immigration way.

The present day distribution of organisms, can be partly explained by climatic changes which occurred in the past. It is now well known that during the Quaternary, the African climate changed considerably, with humid periods alternating with droughts. The last 30 thousand years are fairly well documented. Perrot & Street-Perrot (1982) presented evidence of a wet period between 25000 and 22000 BP in many tropical closed-basin lakes north of the equator. They concluded that the Upper Pleistocene wet phase in northern intertropical Africa resulted from a combination of cooler temperatures and slightly greater precipitations than at present. Results from Servant & Servant-Vildary (1980) and Maley (1983) also provide evidence that there was a wet climatic phase between 30000 and 20000 BP, and numerous lakes in the Chad basin. Between 26000 and 20000 BP, these lakes were shallow, with extensive development of aquatic plants. In Ghana the level of Lake Bosumtwi was relatively high between 28000 and 20000 BP (Maley 1987).

From 20000 to 15000 BP, aridity became general over west Africa, and field-dunes covered a major part of the Sahel (Van Zidderen Bakker 1982). For the Central Sahara, there is evidence that temperatures dropped as much as 10–14° C in January and 6–8° C in July. In the southern Sahara the climate was hyperarid and lakes like Lake Chad dried up. In western Africa, the lowering of temperature was estimated to be 4–5° C or 8–9° C. The climate was arid and rivers did not flow in Senegal and Mauritania.

After 12000 BP, humidity increased. Abundant rainfall permitted the existence of permanent lakes and ponds as well as large rivers crossing the Sahara. From 12000 to 8000 BP, the major sahelian river systems probably passed through their maximum development with permanent high waters (Talbot 1980). During the late Pleistocene and Upper Holo-

cene, the rivers Niger, Senegal and Lake Chad had a much greater effective catchment. A number of prominent watercourses in the Central Sahara such as the Tilemsi, Azaouak, Dallol Bosso, Dallol Maouri and Tarka flowed directly into the river Niger. Under present climatic conditions, they are essentially relict features. The largest lacustrine expansion of Lake Chad occurred 6000 BP and the so-called Mega-Chad covered 300–400000 km² (Servant 1983).

In equatorial west Africa, a major change occurred around 8500 BP: the sudden reappearence of the humid dense forest in the area it now covers (Maley 1987). The ice age aridity had reduced the area of the rain forests and humid montane forests, savannas, grassland and semi-deserts spread over vast regions. Grassland became dominant in the Niger Delta while forest decreased significantly. The longitudinal vegetation belts of the Sudan and the Guinean coast were compressed southward and tropical rainforest could only survive in certain refugia which were exposed to the onshore westerly winds. Palynological studies in the surroundings of Lake Barombi-Mbo, Cameroon, confirm the presence of rain forest since 25000 BP (Maley 1987). Data are still poor for Sierra Leone, but for Lake Bosumtwi, south-west Ghana, the forest disappeared from 25000 to 9000 BP, indicating a recession of the western side of the dense forest.

During a dry phase we can expect: (1) high extinction rates of fish species in Sudanian rivers because of a high decrease in river flow and catchment area (Livingstone et al. 1982); (2) restricted ranges of species associated with forest due to contraction of forested areas and (3) reduced probability of connections between rivers via swamps, floodplains or lagoons.

During dry phases Sudanian rivers should have been highly depleted in species and recolonized during wet phases from aquatic refuge zones. These aquatic refuges are still to be located precisely in the Sudanian region. One hypothesis is that large river basins such as the Nile and the Niger were not totally dry and served as refuges, as was suggested for aquatic birds by Guillet & Crowe (1985). Another hypothesis is that fish took refuge in the more humid mountainous areas: Upper Nile, Upper Benue

(Roberts 1975), Upper Chari and Logone rivers, as well as Guinean range. Taking into consideration the number of endemics, the Niger and the Nile are much better candidates with about 10 percent endemics each (Hugueny 1990b, excluding lacustrine species) as refugia than the Chad where only one dubious endemic species is known. Such a situation could result from severe droughts and the drying up of most of the Chad basin, involving extirpation of the fish fauna. In comparison, the relatively large number of endemics in the Nile and the Niger suggests the existence of aquatic refuges. Other hypothetical refuge zone for Sudanian species is the Eburneo-Ghanean region.

One of the most popular, but also discussed (Endler 1982, Connor 1986), theory linking present distribution of organisms to past climatic variations is the theory of forest refugia (Haffer 1969, 1982). According to this theory, centers of speciation (or endemism) for forest organisms should be located at the sites of the last forest refugia during the last dry period when the uniform dense forest divided into smaller patches. Forest species are able to survive only in those refugia during unfavourable climatic conditions. They can therefore evolve separately, allowing speciation. When climatic conditions allow the recovery of the dense forest, some organisms extend their ranges of distribution, repopulating formerly depopulated areas. If the period of time since the last regression phase is not too long (or if organisms are poor dispersers like fishes), part of the species remain in the refuge zones or their surroundings, such areas being consequently characterized by a high degree of endemicity. In western Africa, two main centers of endemism were identified and assumed to be forest refuges for birds, mammals, and butterflies: one in Sierra Leone, and another one in Cameroon-Gabon (Diamond & Hamilton 1980; Grubb 1982; Endler 1982; Mayr & O'Hara 1986). Hamilton (1982) identified another less important refugium, covering the south-east of Ivory Coast and south western Ghana. Such centers fit relatively well with the Upper and Lower Guinean regions and with the Eburneo-Ghanean region identified for fish and it is tempting to suppose that they are the result of similar processes. According to Mayr & O'Hara (1986) one of the best evidence

supporting the forest refuge hypothesis is the existence of species having a disjunct distribution and localized in western and eastern forested blocks. This distribution suggests a formerly ininterrupted forested area along the west African coast. The western and eastern forested blocks share fish species such as *Marcusenius mento* (Jégu & Lévêque 1984), *Mormyrops caballus* (Bigorne 1987), *Mormyrus tapirus* (Lévêque & Bigorne 1985), *Isichthys henryi* (Bigorne 1989), *Brienomyrus longianalis* (Bigorne 1989) and *Ctenopoma kingsleyae* (Norris & Douglas 1992). However, only *M. tapirus* and *I. henryi* are exclusively distributed in forested areas and can be considered as unambiguous evidences supporting the theory of forest refuge. Dispersal probably occurred during wet periods, when humid forest extended all along the coast, but at an unknown date. One can imagine at that time, a more or less continuous distribution of forest-dwelling species from the Congo to Upper Guinea. Climatic events later interrupted this distribution, and savanna biota extended to the coast in lowland areas. The so-called Dahomey gap illustrates this situation. The forest-related fish species disappeared and were replaced by savanna ones in coastal basins from the Cross to the Cavally and this situation still prevails.

However, the forest refuge hypothesis faces the following difficulties in order to explain endemicity patterns observed in west African fishes: (1) Available palynological data confirm the position of only one forest refuge in west Africa: the region surrounding the lake Barombi-Mbo in Cameroon (Maley 1987, see above). Palynological or geological data are lacking to confirm or refute the position of the other ones. (2) The western part of the Upper Guinean region (including Tomine and Konkoure rivers), as delimited in this study, is not located in present forested area (Table 1) and a fortiori in forested area during past dry phases. Consequently endemism in this area cannot totally be explained by the forest refuge theory. (3) Endler (1982) considered that centers of endemism can be explained by current environmental characteristics, and he concluded that assumed refuge zones are uniform areas, without major geological, climatological or geographical discontinuities. The Guinean regions

have been highland areas for many millions of years and the observed endemism is possibly the result of adaptation of fish species to prevailing ecological conditions (cooler waters, torrential hydrological regimes, etc). It is true that many fish species adapted to turbulent conditions encountered in rapids and swift flowing reaches have distributions more or less restricted to the Guinean rivers (Welcomme & de Merona 1988). That is particularly the case for various Amphiliidae (*Amphilius*, *Paramphilius*, *Doumea*), some Mochokidae (*Chiloglanis*), Cyprinidae (*Labeo*), as well as different anguilliform fishes belonging to different families (see Lévêque et al. 1989, 1991, Paugy et al. 1990). (4) The nature of the relationship (if any) between Guinean fish and forest is unknown. Obviously, the existence of a forest gallery provides particular ecological conditions required by some fish species. But our knowledge of their biology is still too poor to allow anything other than speculation. (5) The fact that present faunas in Guinean zones are mainly the result of speciation events not taking place before the Quaternary is debatable. It is known that alternate wet and dry phases occurred in the Miocene with a parallel fluctuation in extent of the Congo basin rain forest (Lewin 1985). Splitting of forested area and parallel speciation events may have occurred at this time. (6) In so far as forest refuges are very probably dependent on heavy rains, they correspond also to aquatic refuges allowing speciation of any aquatic organisms, even if they have a weak relationship with forest.

In summary, the faunistic divergence between Sudanian and Guinean regions can be attributed to three plausible factors: upsurge of geographical barriers separating Sudanian region from Guinean regions (Guinean range and Adamoua range), distinct ecological conditions (forests and mountains in Guinean regions opposed to savanna and rather flat areas in Sudanian region) and the existence of distinct refugias for Sudanian and Guinean fishes during pleistocene dry phases. Given our limited present knowledge of phylogenetic relationships between species and their ecology, it is difficult to evaluate the importance of each of these factors.

The endemicity of the Eburneo-Ghanean region cannot be easily explained as there is no obvious

physical barriers separating it from Upper Guinea and from the Sudanian region. Its endemic species can have originated from Sudanian ones invading this zone during a dry phase, as suggested by the faunistic similarity between the Eburneo-Ghanean and the Sudanian regions, or from Guinean ones if we accept the hypothesis of a forest refuge covering the south-east of Ivory Coast and south western Ghana (Hamilton 1982). Phylogenetic studies are needed at this step.

The delimitation of faunal provinces can be considered as a basic stage in the elaboration of biogeographical hypotheses, allowing the recognition of areas with a high cladogenic activity. Biogeographical analyses like the one performed here are usefull and are probably the better way to point out objectively areas of endemicity. For instance our analysis reveals the existence of an Eburneo-Ghanean region, neglected in previous studies. However, these analyses can only infer relationship between regions from shared species and consequently are highly sensitive to recent immigration events, occurring without species differentiation. Other conclusions can be drawn if phylogeny is knwon permitting the elaboration of an area cladogram (Wiley 1988) based on older speciation events. Based on their study of bariliin cyprinid fishes (genus *Raiamas* and *Leptocypris*) and the few other phylogenetic studies available for African freshwater fishes, Howes & Teugels (1989) suggested an area cladogram displaying a first dichotomy between Sudanian region and Guinean regions, a second one between Zaire and remaining Guinean regions and a third one between Lower and Upper Guinea (see also Norris & Douglas 1992). This area cladogram obtained from phylogenetic studies confirms that Upper and Lower Guinean regions result probably from a splitting of a formerly undivided Guinean (forested?) region as suggested also from the disjunct distribution of a few species.

There are still many unresolved questions about west African fish biogeography: at which date occurred the main vicariant events (such as the postulated splitting of some species range in two Guinean populations)? Which are the closer relatives of the endemic species in each biogeographical region? Are area cladograms different between taxonomic groups composed of indifferent species or a mixing of savanna and forest dwelling species? Phylogenetic (morphological and genetical) studies are needed to help in the resolving of these points (among others), and the claim of Greenwood (1983) for a more phylogenetically orientated biogeography is still valid.

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