

Relict tropical fish fauna in Central Sahara

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Following a taxonomic revision of freshwater fishes recorded from the Sahara, an updated species list is given. It appears that most species collected in small water bodies are relict populations of widespread species occurring in surrounding river basins, except for *Barbus apleurogramma* which might be a relict of a more ancient fish fauna. Distribution patterns are discussed in view of the supposed extent of river catchments during the Holocene.

Une révision taxinomique des espèces de poissons récoltées dans le Sahara a permis de dresser une liste actualisée prenant en compte les connaissances récentes. Il apparaît que la plupart des espèces collectées dans les petites collections d'eau sont des populations reliques d'espèces largement répandues dans les bassins hydrographiques voisins, à l'exception de *Barbus apleurogramma* qui pourrait être un vestige d'une faune plus ancienne. La distribution actuelle est discutée, à la lumière des données sur l'extension supposée des bassins hydrographiques durant l'Holocène.

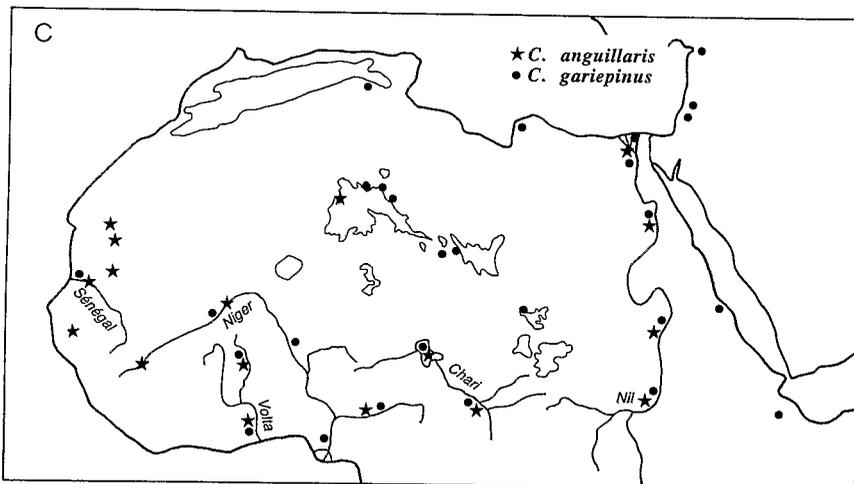
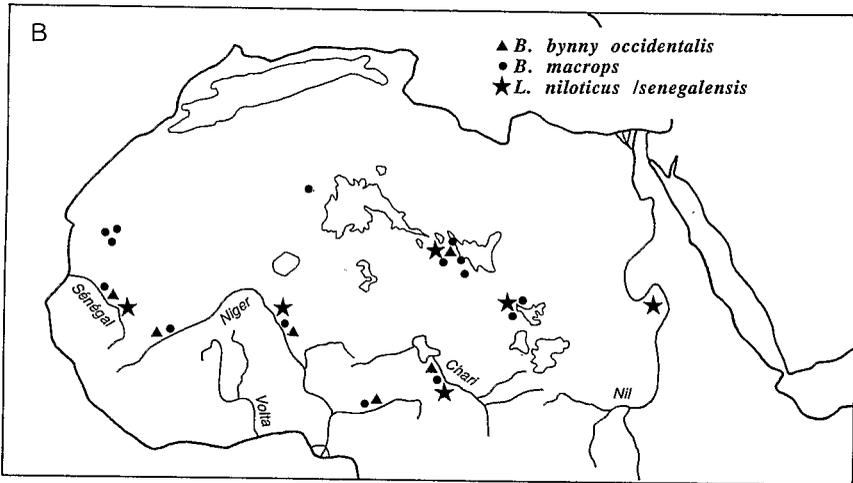
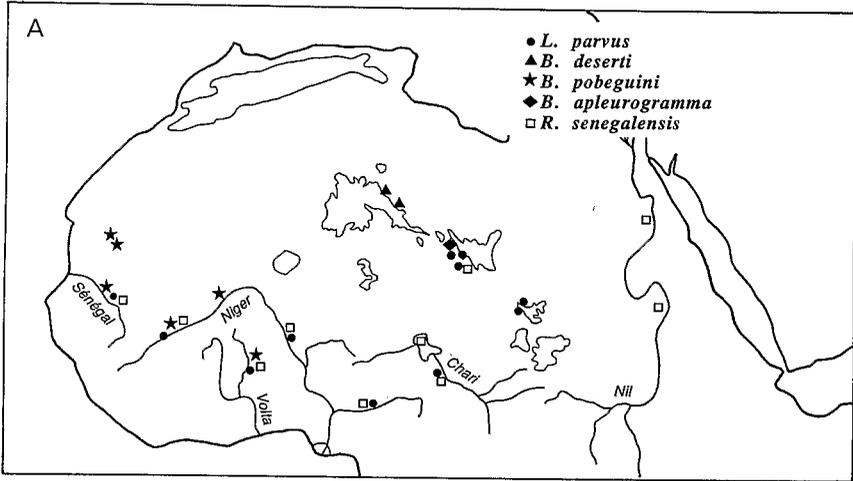
Introduction

Since the beginning of this century, numerous Saharan expeditions were able to collect several fish species in the widely scattered and isolated small patches of water in this area (Daget, 1959a, 1968; Dumont, 1979, 1987; Estève, 1949, 1952; Fowler, 1949; Le Berre, 1989; Monod, 1951, 1954; Pellegrin, 1913, 1919a-b, 1931, 1934, 1936). If the occurrence of species known from Sudanese rivers far south was quite surprising for the first discoverers, it is nowadays obvious that their occurrence results from the dynamics of changing climates over the area (Dumont, 1982; Maley, 1983).

As a result of the improvement of our knowledge on African fishes, and following recent

taxonomic revisions, it turned out that confusion existed in the identification of some species, often based on small specimens, sometimes poorly preserved. The aim of this paper is to give an updated taxonomic review of the relict fish populations in the Sahara, and to discuss their significance. This paper only deals with fish of afrotropical origin, bearing in mind that northern Africa is nowadays mainly colonized by Palaearctic or Mediterranean species. Many of the specimens collected are housed in the Muséum national d'Histoire naturelle, Paris (MNHN), the British Museum of natural History, London (BMNH) and the Musée royal de l'Afrique centrale, Tervuren (MRAC), and part of those collections were examined.

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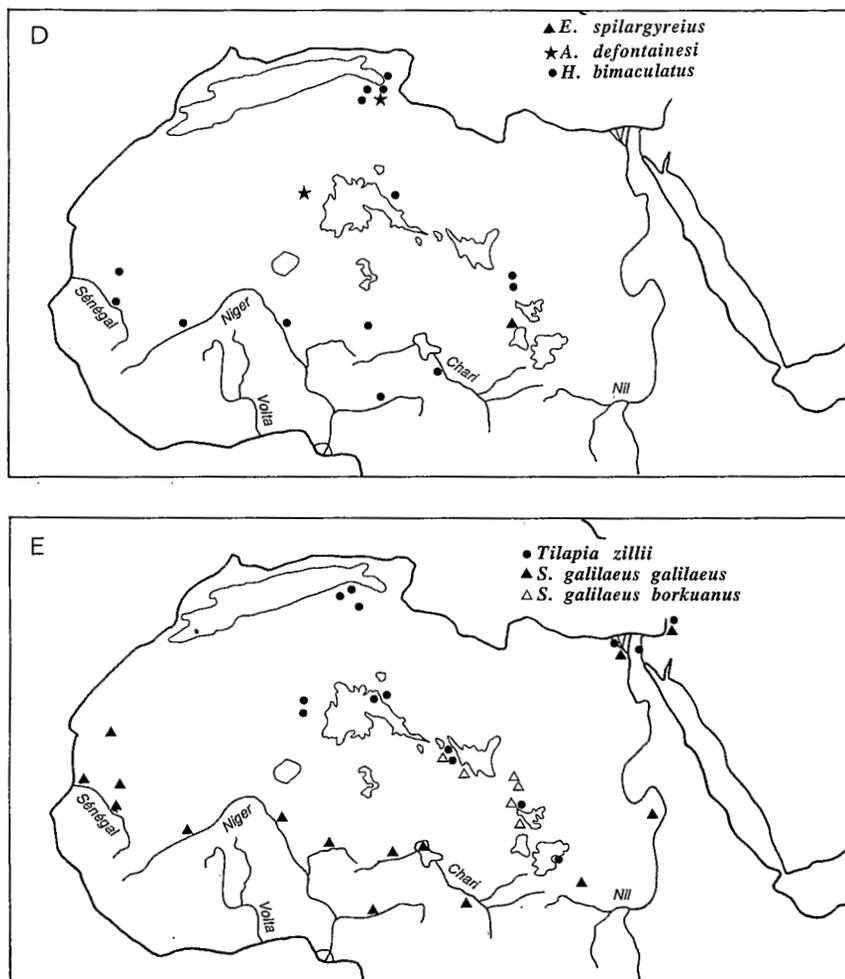


Fig. 1. Distribution of relict tropical fish species in Sahara and surrounding river basins. Data on *Clarias* from Teugels (1986) and on *S. galilaeus* from Trewavas (1983).

List of species collected in Central Sahara

On Figure 1 all known Saharan records are reported. For surrounding river basins, scattered symbols give an idea of the distribution range for each species. Detailed distribution record for these basins are published by Lévêque et al. (in press), Paugy & Benech (in press) and Teugels et al. (1988).

Cyprinidae

Barbus apleurogramma Boulenger, 1911 (Fig. 1A)

Reported by Daget (1968) from Aoué, on the western side of the Ennedi (MNHN n° 1967-647). The specimens examined exhibit the following characters: mouth terminal, at the level of the middle of the eye; only one barbel on each side, its tip reaching the anterior margin of the eye; last simple dorsal ray bony and slightly denticulated behind (clearly marked only in large specimens);

7 branched dorsal rays; 22 to 23 scales in longitudinal series, 8 around caudal peduncle; no lateral line; a black spot at the base of the caudal and anal fins; scales edged with dark brown. This description is diagnostic for *B. apleurogramma* as described by Boulenger (1911).

The presence of *B. apleurogramma* on the south-western side of the Ennedi is surprising (see discussion) as the species was only known from Lake Victoria and related streams.

Barbus bynni occidentalis Boulenger, 1911 (Fig. 1B)

Daget (1959a) and Blache et al. (1964) reported *B. batesi* from Totous (Tibesti). For Trewavas (1974) the identification is doubtful and Lévêque & Guégan (in press) reidentified the three juvenile specimens as *B. bynni occidentalis*. The latter is present in the Chad basin, whereas *B. batesi* is known from Cameroun.

Barbus deserti Pellegrin, 1909 (Fig. 1A) and *Barbus macrops* Boulenger, 1911 (Fig. 1B)

For a long time, there has been considerable confusion between both species. Re-examination of the type specimens of *B. deserti* allowed Hopson & Hopson (1965) and Lévêque (1989) to conclude that both are valid species. They share similar scale counts, and show a black spot on the dorsal fin. But the black spot covers the tip of the fin in *B. macrops*, whereas *B. deserti* bears a spot on the distal half of the first branched rays, distantly set from the distal margin. *Barbus deserti* was described on the basis of four specimens collected in Tassili n'Ajjer at Redir de Sfedil (Pellegrin, 1909) which is apparently a pool of the river Edefil (or Idefil, or Efedil), a seasonal tributary of the river Imirhou which carries the periodical rainfall of the northern part of the Tassili. Skorepa (1977) examined 36 specimens of *B. deserti* collected in two "gueltas" of the Imirhou river, and a series in MNHN (n° 1959-120) originates from Oued Djerat, few kilometers north to the Imirhou river. Specimens of *B. deserti* were also collected at El Barcat (Barkat) near Ghat, and are housed in MNHN (n° 1935-59) and BMNH (n° 1937.7.8: 4-6) (see Hopson & Hopson, 1965; Lévêque, 1989). *Barbus deserti* is apparently restricted to northern slopes of Tassili n'Ajjer. As a result, most of the other series previously identified as *B. deserti* in literature, are in fact *B. macrops* which is a widely distributed species

known from most West African river basins.

Barbus anema Boulenger, 1903 was reported from Totous (Tibesti) by Pellegrin (1919a). According to Daget (1959a) this identification is doubtful. The specimens are badly preserved and Daget (op. cit.) observed posterior barbels in one specimen. I was able to observe anterior and posterior barbels in two of the Totous specimens (MNHN n° 1919-65). The tip of the dorsal fin is blackish and there are some remains of a black longitudinal band. I consider these specimens as juveniles of *B. macrops* which has already been collected at Totous.

Barbus pobeguini Pellegrin, 1911 (Fig. 1A)

Numerous specimens were collected in different sites of the Adrar area (Mauritania). The species was identified *Barbus (Capoeta) pobeguini mauritanica* Pellegrin, 1937, by Estève (1952), and *Barbus (Hemigrammocapoeta) mirei* Estève, 1952, a junior synonym of *B. pobeguini* (see Monod, 1954). This species is known from the Niger, Senegal and Volta basins but has never been collected in the Chad and Nile basins.

Labeo niloticus (Forsskål, 1775) / *Labeo senegalensis* Valenciennes, 1842 (Fig. 1B)

The specimens from Totous (Tibesti) identified as *Labeo horie* by Pellegrin (1919a) were juveniles. Daget (1959a) mentioned that they were in poor condition and reidentified the series, as well as another sample collected in the same water body, as *L. niloticus*. The three specimens from Totous examined by Daget have 15 branched dorsal rays, 42 scales in longitudinal series, 8.5 scales between lateral line and dorsal fin, 5 to 5.5 between lateral line and base of pectoral fin, 20 scales around caudal peduncle. The number of scales, as well as the number of dorsal rays, are characteristics of *L. niloticus*, compared to *L. horie* and *L. senegalensis*, according to Reid (1985).

Daget (1968) also reported specimens identified as *Labeo* sp. from Ennedi, and mentioned that they were close to *L. horie* / *L. niloticus* from Tibesti. The specimens (MNHN n° 1967-658) have meristic counts slightly different from the Tibesti ones: 13-15 (mode 14) branched dorsal fin rays; 38-40 scales in longitudinal series; 6.5 scales between lateral line and dorsal fin origin; 4.5 scales between lateral line and base of pectoral

fin; 16 scales around caudal peduncle. The Ennedi specimens are therefore very close to *L. senegalensis* occurring in Chad basin and distinguished from the Nile species by lower scale counts (see Reid, 1985). In fact, it may well be that *L. senegalensis* present in the Chad and western basins, and *L. horie* and/or *L. niloticus* are local populations of the same species. Nevertheless, the Ennedi specimens appear to be related to the Chad fauna whereas the Tibesti *Labeo* are closer to the Nile ones.

Labeo parvus Boulenger, 1902 (Fig. 1A)

For Reid (1985) *L. tibestii* Pellegrin, 1919 is a junior synonym of *Labeo ogunensis*. According to Jégu & Lévêque (1984) *L. ogunensis* as well as *L. chariensis* are synonyms of *L. parvus*, a widespread species known from the West African river basins, including Chad, but absent from the Nile. Daget (1959a) already considered *L. tibestii* to be close to *L. annectens* which could be a synonym of *L. parvus* according to Reid (1985).

Raiamas senegalensis (Steindachner, 1870) (Fig. 1A)

A single specimen was collected in the Yezei (Tibesti) and identified *Barbus loati* by Pellegrin (1919a). Daget (1959a) reidentified the specimens as *B. senegalensis*. For Lévêque & Bigorne (1983), *R. loati* is a junior synonym of *R. senegalensis*.

Clariidae

Clarias anguillaris (Linnaeus, 1758) (Fig. 1C)

C. senegalensis Valenciennes, 1840 reported from Adrar (Mauritania) and central Sahara, is a junior synonym of *C. anguillaris* (see Teugels, 1986).

Clarias gariepinus (Burchell, 1822) (Fig. 1C)

Clarias lazera Valenciennes, 1840 reported from Ennedi and Tibesti is a junior synonym of *C. gariepinus* (see Teugels, 1986).

Cyprinodontidae

Epiplatys spilargyreus (Duméril, 1861) (Fig. 1D)

Specimens collected at Tigui (Borkou) were identified as *Aplocheilus marni* (incorrect spelling for *Haplochilus marnoi* Steindachner, 1881) by Estève (1952) and reidentified as *Epiplatys senega-*

lensis (Steindachner, 1870) by Daget (1959a). Scheel (1968) introduced the synonymy with *E. spilargyreus*.

Cichlidae

Astatotilapia desfontainesi (Lacépède, 1803) (Fig. 1D)

The species previously identified *Haplochromis desfontainesi* is restricted to Tunisia and Algeria (Regan, 1922), despite the wide distribution range of the genus in Africa (Greenwood, 1979). The mention of *A. desfontainesi* from Chad basin by Dumont (1982: Tab. 1) is erroneous. It is *A. bloyeti* Sauvage, 1883 which is known from the Chad area and Upper Niger (Greenwood, 1979).

Hemichromis bimaculatus Gill, 1862 (Fig. 1D)

Reported from different localities up to the Atlas.

Sarotherodon galilaeus (Linnaeus, 1758) (Fig. 1E)

According to Trewavas (1983), *Tilapia borkuana* Pellegrin, 1919 which was reported from many localities in the Borkou-Ennedi-Tibesti is a subspecies of *Sarotherodon galilaeus*. The most striking character is the pigmentation. Another subspecies, *Sarotherodon galilaeus galilaeus* is known from the Adrar (Mauritania) (Monod, 1951; Estève, 1952).

Tilapia zillii (Gervais, 1848) (Fig. 1E)

The species is reported from numerous localities up to the Atlas. It is widespread and apparently resistant to salinity.

Discussion

At the present time, as throughout the Pleistocene, the Atlas watershed is a geographical barrier between Sudanian fish in the desert and those of Eurasian origin in the Maghreb. But Greenwood (1973) found in fish remains from late Miocene deposits of Tunisia (Bled el Douarah), a diversified freshwater ichthyofauna showing strong affinities with the contemporary fauna of Egypt and tropical Africa. Among identified fossils, representatives of the genera *Polypterus*, *Lates*, *Heterobranchus* and *Clarias*, ? *Clarotes* and ? *Synodontis* are present. Thus the

Table 1. Occurrence of afrotropical fish species in different areas of the Sahara. Modified from Dumont (1982). 1, Adrar (Mauritania); 2, Tunisia and south Algeria; 3, Aïr; 4, Ahaggar; 5, Tassili N'Ajjer; 6, Ghat; 7, Tibesti; 8, Ennedi; 9, Borkou.

	1	2	3	4	5	6	7	8	9
<i>B. apleurogramma</i>								*	
<i>B. occidentalis</i>							*		
<i>B. deserti</i>					*	*			
<i>B. macrops</i>	*			*			*	*	
<i>B. pobeguini</i>	*								
<i>L. niloticus</i>							*		
<i>L. parvus</i>							*	*	
<i>R. senegalensis</i>							*		
<i>C. anguillaris</i>	*								
<i>C. gariepinus</i>					*		*	*	
<i>E. spilargyreus</i>									*
<i>H. bimaculatus</i>		*			*			*	*
<i>S. g. galilaeus</i>	*								
<i>S. g. borkuanus</i>							*	*	*
<i>T. zillii</i>		*		*	*		*	*	

fish fauna of the late Miocene in Tunisia, contrasts strongly with that of the present, which is extremely depauperate and show affinities with species in Europe and Asia Minor (*Barbus capito*, *Aphanius* and *Phoxinella*). The cichlid *Astatotilapia desfontainesi* is the only species of unquestionable African affinities. The Miocene fauna from Tunisia is fairly similar to contemporary records from Egypt (Priem, 1914, 1920), Syrte Major, Cyrenaica (Arambourg, 1963) and East Africa (Greenwood, 1951; Greenwood & Howes, 1975). Van Couvering (1982) also reported that *Palaeochromis*, a late Miocene cichlid discovered in the Seybouse Valley near Guelma (Algeria), is closely related with Central and West African *Pelmatochromis*. According to Greenwood (1973), "the faunal similarity between different Miocene deposits, gives the impression that during the Miocene, there was a fairly uniform freshwater fauna (at least at the generic level) widely distributed in Africa north of the equator. Due to the relative paucity of materials, it is difficult to determine just how widespread this fauna was or when it made its first appearance. But Eocene deposits in Libya (Arambourg & Magnier, 1961) have a very simi-

lar fish fauna (*Polypterus*, *Lates* and unidentified Siluriformes)". *Protopterus* sp. were also identified in Lower Eocene fossils from El Kohol, near Brezina, on the southern flank of the Saharan Atlas, Algeria (Mahboudi et al., 1984). The fossil records from Lake Edward (Greenwood, 1959; Greenwood & Howes, 1975) revealed that during Pliocene to late Pleistocene, the fish fauna was more similar to the Nile one than it is today and included several of the genera now absent. For Lake Victoria, only few data indicate that some Nile type elements (now absent) were present before the modern lake was formed (Greenwood, 1951, 1974).

As a result of taxonomic revisions, it appears that the relict fauna of the Borkou-Ennedi-Tibesti area which exhibits the highest diversity (Table 1), is clearly related to that fauna existing in the Chari and Nile basins. All species reported from this area, except for *B. apleurogramma*, are found in those basins. There is good evidence that during the last Holocene humid period, the Chad basin extended to the foot of the Ennedi-Tibesti whose drainages had flowed into the so-called mega-Chad (see Talbot, 1980; Servant, 1973). The iso-

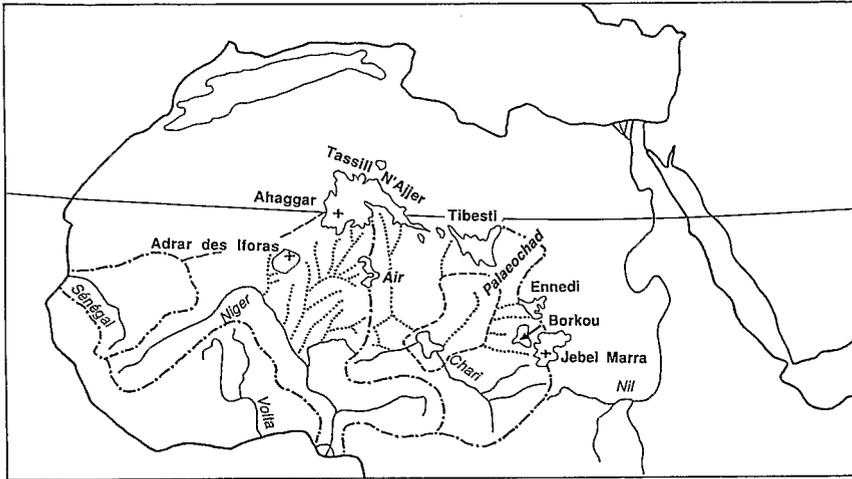


Fig. 2. Estimated limits of potential catchments of the Senegal, Niger and Chad systems during the earlier Holocene when the whole catchment areas were probably active. Modified from Talbot (1980) and using informations from Riser & Petit-Maire (1986).

lation of these populations happened 5-6,000 yrs ago and this apparently explains the relative richness of the ichthyofauna. It is also clear that in spite of the present extreme isolation of the area, this time period is apparently insufficient to allow speciation and appearance of endemics, even if some morphological variability can be observed.

The record of *B. apleurogramma* in the Ennedi, is nevertheless more surprising as this species is nowadays only known from L. Victoria and the connected river systems. Until now the importance of this record and its significance have rather been neglected. Knowing that the species no longer occurs in the Chad and the lower Nile, it could well be the relict of a more ancient fish fauna extending northwards, and whose representatives later disappeared from Sudanese river basins. There are many other evidences of faunal exchanges during the geological times.

It should also be noted that *B. apleurogramma* belongs to a group of *Barbus* showing a serrated last simple dorsal fin ray. Without giving to much emphasis to this morphological feature as its phylogenetic significance is not yet known, I can nevertheless ascertain that nowadays this group is represented by only few species, with a limited distribution, in Africa north of the equator: *B. cadenati*, *B. dialonensis* and *B. guineensis*,

restricted to the upper courses of the rivers Konkoure, Gambia and Senegal in the Fouta Djalon (Guinea) (Daget, 1962); *B. miolepis* known from the upper reaches of the Chari in Central African Republic but widespread in Zaire and coastal rivers in Cameroon; *B. kerstenii*, *B. neumayeri* and *B. pellegrini* occurring in the Nile drainage only in the Lake Albert-Edward region, but widespread in East Africa (Banister, 1987). It could then well be that *B. apleurogramma* from Ennedi, was part of an ancient fauna which was more widely distributed than nowadays, and whose representatives disappeared probably during an arid climatic phase, relict populations subsisting in particular zones. That could imply that the isolation of *B. apleurogramma* would be older than the last humid period.

The phylogenetic affinities of *B. deserti* known from the northern slopes of the Tassili n'Ajjer are not clear, but morphologically it appears to be related to the small tropical *Barbus* with which it was confused. There are superficially close similarities with Sudanese species and comparing morphometric characteristics and colour pattern, *B. deserti* resembles *B. callipterus*, a presently widespread species in Niger and Chad basins. Some other tropical species were also collected in the Tassili: *Clarias gariepinus*, *Tilapia zillii* and *Hemichromis bimaculatus*.

latus. It is possible that the above species are relict fauna of the Chad basin fauna which were able to survive severe droughts and to colonize the northern slopes of the Tassili. To support this idea, it should be recalled that the Tassili represents the northern limit of the maximum potential catchment of Chad (see Talbot, 1980 and Fig. 2). During periods of maximum humidity, including the earlier Holocene, the whole catchment was probably active and relict drainages from Tassili to Chad are still apparent. *Barbus biscarensis*, a northern colonizer, is also present on the northern slopes of Tassili.

The relict fish fauna of the Ahaggar is poor compared to the Tibesti-Ennedi one and there is no record from Aïr or Adrar Ifora. That is surprising if we consider the dense relict drainage of the central Sahara including prominent watercourses such as the Tilemsi, Dallol Bosso, Dallol Maouri and Tarka which were active during late Pleistocene and upper Holocene (Talbot, 1980). During the early Holocene, there were large tropical lakes (Riser & Petit-Maire, 1986) and a diversified fossil fish fauna was collected all over this area (Daget, 1959b, 1961; Gayet, 1983). *Lates maliensis* Gayet, 1983 was described from the Taoudeni depression of Malian Sahara, but is now considered as a synonym of *L. niloticus* (Van Neer, 1987). The paucity of the present fish fauna could be explained by the scarcity of suitable perennial habitats of the area, but this hypothesis can hardly be tested.

Bailey-Watts & Rogers (1970) provided some information on the fish fauna of the Jebel Marra. The samplings were restricted to a stream (Wadi Golol) tributary of the Wadi Azum, and an adjacent pool. Such habitats are connected to the main river during the flood and the fish fauna collected is therefore representative of the Chari basin. Green et al. (1984) also provided fragmentary information on fish fauna inhabiting Lakes Keilak and Kundi, respectively in south Kordofan Province and southern part of Darfur in Sudan. *Clarias lazera* (= *C. gariepinus*), *Tilapia zillii* and *Schilbe mystus* were caught in those isolated water bodies from the Upper White Nile basin, which nevertheless probably contribute water to the Nile system in exceptional wet seasons.

The Saharan relict tropical fish fauna survived for thousands of years in isolated small

water bodies. But one could expect that some of the records will become of historical interest, as long as man impact (mainly water pollution) will progressively modify the present distribution, in eradicating fish species in some of the water bodies.

Acknowledgements

This work was part of PEDALO programme (Poissons d'eau douce d'Afrique de l'Ouest) sponsored by ORSTOM and PIREN (CNRS). The author is grateful to D. Paugy and G. Teugels for their valuable comments.

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Received 29 September 1989

Revised 16 November 1989

Accepted 17 November 1989