Miocene catfishes (Ariidae, Bagridae) from Lisbon: a Nilotic (or Sudanian) type fauna

M. T. ANTUNES *

* Author's address: Prof. Dr. M. Telles Antunes, Centro de Estratigrafia e Paleobiologia da Universidade Nova de Lisboa, Quinta da Torre, 2825 Monte de Caparica, Portugal.

Ciências da Terra (UNL)	Lisboa	N.º 10	pp. 9-22 figs. 1, 1 pl.	1989

RESUMO

Palavras-chave: Bagres — Associação de tipo nilótico/sudaniano — Ecologia — Paleobiogeografia — Miocénico — Portugal.

Restos de bagres e de *Lates* (Pisces, Teleostomi) foram colhidos nalgumas das divisões do Miocénico de Lisboa. Aqueles, estão representados por pterigióforos (1.os raios, espinhosos, de barbatanas) peitorais e dorsais que correspondem a dois conjuntos: o do Langhiano, divisão V-*b*, pertencente a um *Arius* sp., provavelmente próximo da espécie actual *A. heudeloti;* o outro, do Burdigaliano terminal V-*a*, é atribuível a um Bagridae, cf. *Chrysichthys* sp., identificado pela primeira vez no Neogénico português.

No que diz respeito a ambientes dulçaquícolas, a associação de bagres com *Lates* é muito semelhante a associações africanas de tipo nilótico ou sudaniano. Em ambientes marinhos costeiros estavam presentes formas estenotérmicas de água quente (Polynemidae, grandes barracudas e certas espécies de tubarões) que correspondem, como modelo, a faunas atlânticas desde Cabo Verde ao Norte de Angola. Há, também, ambientes salobros, constituindo termos de transição (fig. 1).

Bagres e *Lates* imigraram na Península Ibérica provavelmente no Miocénico inferior. São desconhecidos após o Langhiano V-*b*, ressalvada a reaparição de *Arius* no Tortoniano VII-*b*. A extinção local é explicável por decréscimos de temperatura e aumento de aridez, durante parte do Miocénico superior.

A expansão daqueles peixes pode ter sido facilitada pela deslocação de massas continentais que estreitaram (ou fecharam) braços de mar entre a Europa e a África. A tolerância quanto à salinidade de peixes dos grupos em causa, relativamente eurihalinos, não é necessariamente a única explicação das migrações.

As associações de bagres e *Lates* colonizaram as águas interiores de ambos os lados do Paleomediterrâneo. Extinções locais podem ter afectado mais a evolução da distribuição geográfica do que as migrações.

RÉSUMÉ

Mots-clés: Poissons-chats — Association de type nilotique/sudanien — Écologie — Paléobiogéographie — Miocène — Portugal.

Des restes de poissons-chats et de *Lates* ont été récoltés dans des unités du Miocène lisbonnais. En ce qui concerne les premiers, on peut distinguer deux lots de pterygiophores pectoraux et dorsaux, l'un desquels (du Langhien V-*b*) appartient à un *Arius* sp. probablement voisin d'*A. heudeloti*. L'autre (du Burdigalien terminal V-*a*) peut être rapporté à un Bagridé, cf. *Chrysichthys* sp., identifié pour la première fois dans la région.

En ce qui concerne des milieux dulçaquicoles, l'association de poissons-chats avec *Lates* est très semblable à des associations africaines de type nilotique ou sudanien. Dans des environnements marins côtiers, la présence de formes sténothermes d'eau chaude (Polynemidae, de grands barracudas et certains requins) indiquent comme modèle des faunes qui existent dès le Cap Vert jusqu'au Nord de l'Angola. Il y a des stades intermédiaires quant à des eaux saumâtres, correspondant à des passages graduels (fig. 1).

Des poissons-chats et des *Lates* ont probablement immigré dan la Péninsule Ibérique au Miocène inférieur. Ils sont inconnus après le Langhien V-*b* à l'exception d'une réapparition d'*Arius* au Tortonien moyen VII-*b*. Des températures en décroissance et l'aridité expliquent leur extinction locale.

L'expansion des poissons en cause peut avoir été facilitée en conséquence du déplacement de masses continentales ayant rendu plus étroites (ou fermé) des passages marins entre l'Europe et l'Afrique. La tolérance à des salinités très variables n'est nécéssairement pas la seule explication des migrations.

Des associations en question ont colonisé des eaux intérieures des deux côtés de la Paléoméditerranée. Des extinctions locales ont pu peser davantage dans l'évolution de la distribution géographique que des migrations.

ABSTRACT

Key-words: Catfishes — Nilotic/Sudanian type association — Ecology — Paleobiogeography — Miocene — Portugal.

Miocene catfishes from Lisbon are dealt with. Two distinct sets of pectoral and dorsal pterygiophores are described. That from the Langhian V-*b* is referred to *Arius* sp. probably close to *A. heudeloti*. Another set from the uppermost Burdigalian V-*a* may be ascribed to a bagrid, cf. *Chrysichthys* sp., identified for the first time in this region.

The catfish and *Lates* association is strikingly similar to African, nilotic or sudanian ones as far as freshwaters are concerned. In marine, coastal environments, stenotherm warm-water forms (Polynemids, large barracudas and several sharks) indicate, as a model, faunas like those from Cape Verde to northern Angola. There is some gradation for brackish waters (fig. 1).

Catfishes and *Lates* probably migrated into the Iberian Peninsule in the lower Miocene. They are unknown after Langhian V-*b* except for a reappearance of *Arius* in the middle Tortonian VII-*b*. Decreasing temperatures and aridity account for local extinction at least in freshwaters.

Expansion of these fishes have been made easier owing to the displacement of land masses that narrowed or closed the marine waterway between Europe and Africa. Salinity tolerance is not necessarily the sole explanation for migration.

Catfishes plus *Lates* associations colonized inland waters from both sides of the Paleomediterranean. Local extinction may have weighed more in the development of modern distribution patterns than migration.

1. INTRODUCTION

Fossil fishes, mostly marine, have been reported since the 19th century in several Miocene units in the Tagus basin near Lisbon. This would be expected, as marine beds largely predominate.

However there are freshwater, large river sediments that distally grade into estuarine or even marine ones, early Burdigalian to Langhian in age.

Non marine beds yielded fish remains. Most were found in sands rich in land mammal fossils. In association with more or less worn and probably redeposited marine fish teeth and vertebrae, there are spines and bones less or not at all abraded. These do not belong in the fish associations so far known in marine facies; their peculiar character went unnoticed until we recognized (Antunes in GINSBURG & ANTUNES, 1968, p. 29) a large actinopterygian, *Lates,* in association with catfishes. Among these, *Arius* was identified on fin spines (ANTUNES & TORQUATO, 1969, p. 29) and otoliths (JONET, 1973, pp. 140-141).

Arius was the more likely to be expected among catfishes. Ariidae is indeed the sole mostly marine catfish family although its representatives are not at all confined to tropical, littoral, shallow, muddy bottom marine environments. Many are commonly found in brackish or freshwater or are permanent freshwater dwellers.

All catfish occurrences so far reported concern uppermost Burdigalian V-*a* division (one of the units of the Lisbon Miocene series) and next V-*b* division, Langhian. No traces were ever found in the Langhian V-*c,* Serravallian VI-*a* to VI-*c,* or in early Tortonian VII-*a.* Their absence is conspicuous in the deeper marine facies that correspond to the maximum of the Serravallian transgression, as well as in shallower ones until the lower Tortonian.

Arius otoliths are common in the middle Tortonian VII-*b* (JONET, 1979, pp. 108-109), the last Miocene unit deposited in normal marine conditions. The reappearance of *Arius* may be related to the development of shallow, muddy bottoms adequate for them (as indicated by the curious French trivial name «Fouille-m...» — cf. CADENAT, 1950, p. 133). It maybe conspecific with the extant *A. heudeloti* (STEURBAUT & JONET, 1981, p. 197). These deposits are related to a large-scale regression that marks the late Miocene.

Miocene catfishes are not well known in western Europe. Hence we will concentrate on Burdigalian and Langhian ones, which are particularly interesting for their paleoclimatical meaning as well as their African-type association with *Lates.*

2. MATERIAL AND METHODS

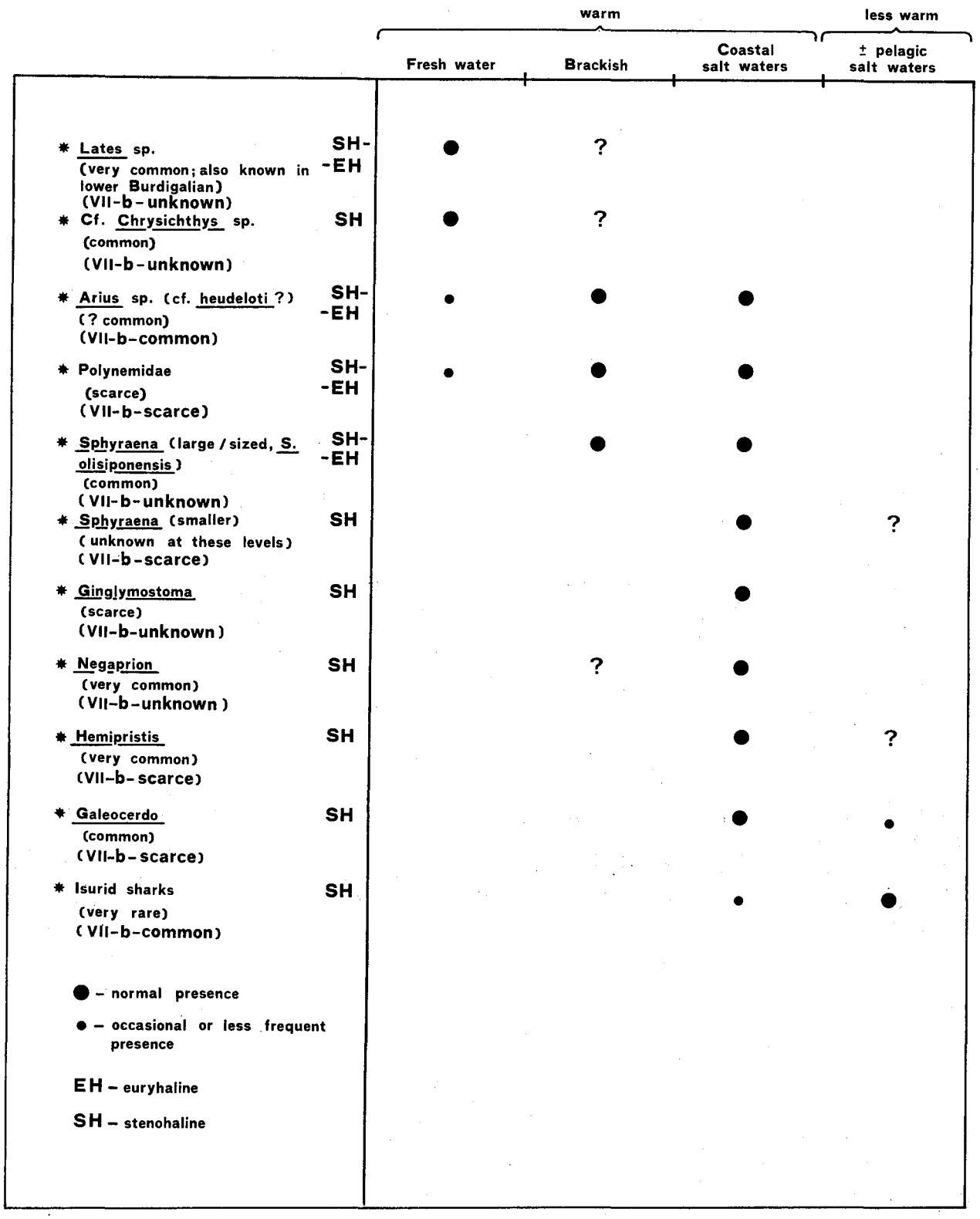
Identification of catfish bones and specially of pterygophores has been discussed (GREENWOOD, 1972, pp. 42--43). It is usually possible at the family level, but not always so since spine characters may be shared by at least two living families, such as the Ariidae and the Bagridae. More accurate determination at the genus level may not be feasible owing to close similarities between genera, as well as to poor osteological knowledge of extant forms. Even if different fossil spine types may be recognized, we cannot ascertain how meaningful they are in species identification.

Some authors indulged in comparative analysis (GREENWOOD, 1972; GAYET, 1983). We took their results into account, as well as our own comparisons with African siluroids. A memoir from POLL (1967) has been useful.

Specimens studied here (table 1) were collected by us between 1958 and 1967 at sandpits near Lisbon. All exploitation has been discontinued since, and no new collecting could be done.

TABLE 1

Distribution of some fishes in the Miocene of Lisbon according to environments and salinity (uppermost Burdigalian Va and Langhian V b vs. Tortonian VII b)



List of catfish pterygiophores (d, dorsal; p, pectoral) and other bones

A. Uppermost Burdigalian, V-*a* division.

* Quinta das Pedreiras, near Lumiar

— 8 specimens (p), right side

— 11 specimens (p), left side

— 3 specimens (p), side?

Only three are near complete; some are rather worn but others not so.

— 10 specimens (d), small to medium-sized, some near complete, unworn

— further tentatively referred specimens (a) left cleithrum, anterior part with articular cavity for pectoral pterygiophore, (b) ? 2 vertebrae.

* Quinta do Pombeiro, near Chelas
  — 9 specimens (p), right side, uncomplete but showing all important characters, small to medium sized
  — 4 specimens (p), left side
  — 1 specimen (d) and maybe another one, uncomplete.

There are no apparent differences between Quinta das Pedreiras and Quinta do Pombeiro samples. The Quinta das Pedreiras one shows a ratio dorsal: pectoral spines of 10:22, or about 1:2; this (as well as morphological characters and size) strongly suggests an homogeneous population from a single species. The sample from Quinta do Pombeiro is poorer and less significant — dorsal spines are scarcer, as it would be expected.

B. Langhian, early Middle Miocene, V-*b* division
  * Olival da Suzana, near Charneca do Lumiar
    — 1 specimen (p), left side, near complete
    — 1 specimen (p), right side, articulation lacking, from a very large individual
    — 2 specimens (p), side? (right and left), distal parts only
    — 1 specimen (d), with near complete articulation, distal portion lacking
    — 1 specimen (d), somewhat larger than the preceding one but with articulation more uncomplete
    — tentatively referred specimen, posterior part of (right?) opercular.

The ratio dorsal: pectoral pterygiophores is of 1:2 as it could be expected (however the number of specimens is too low to be significant). The whole sample from Olival da Suzana also suggests the presence of a single form.

3. DESCRIPTION AND COMPARISONS

Pterygiophores can be sorted into two morphological types. The fact that each tpe has only been found in one of the concerned V-*a* and V-*b* units has nothing to do with the distinction itself.

Even if no specimen from V-*a* is complete, reconstruction from dorsal and pectoral spines is possible. This also holds for the V-*b* sample.

All specimens from V-*b*, either dorsal or pectoral, are larger than the corresponding ones from V-*a* sample. This difference seems meaningful, as there are no reasons to suspect any bias in collecting. Morphology is not identical either, as it will be shown below. Hence V-*b* spines can be included in a single type, however distinct from the preceding one.

Both types comprise pectoral and dorsal pterygiophores that are compatible in size, in shape and in number. This excludes all catfish groups lacking a dorsal spine as the Clariidae; nothing indicates their presence, even if elsewhere they can be found in association with Ariids, Bagrids and other catfishes with dorsal pterygiophores.

— Type 1, from Quinta das Pedreiras and Quinta do Pombeiro.

* *Dorsal spines* — in a nearly complete specimen (Pdr), the shaft is nearly straight in anterior view and gently curved in lateral view; it shows an anterior rugose ridge, with a single row of small rugae but no acute serrations, flanked at each side by a pair of weaker ridges with minute, vestigial rugae; posteriorly there is a longitudinal depression with a single row of downward oriented serrations, larger distally; distal end acute; lateral surfaces with ornamentation consisting of narrow longitudinal but more or less anastomosed ridges; proximal articular surface (best preserved in other specimens) without any specially remarkable features. This description may well apply to the whole collection. Maximum observed length is 32 milimeters; minimum length about 20 mm. Ornamentation in lateral ridges seemingly more marked in larger spines. Rugae are less conspicuous in worn specimens. The articular surface for the posterior face of the reduced first fin spine has a median ridge, which is always distinct and even evident in the best preserved specimens.

* *Pectoral spines* — all are similar. Shaft somewhat curved with anterior ridge flanked by a pair of longitudinal depressions at the proximal part; this ridge is not marked in any one and shows faint rugae. Posterior ridge is serrated; the upper and lower surfaces have an ornamentation similar to that of dorsal spines. Distal end is acute. The major articular surface of the spine head, as viewed from its medial aspect, has a rounded outline, so it differs clearly from the «Species A» (GREENWOOD, 1972, fig. 1) that «... compares most closely with that found in living species of Ariidae, and with the spines of *Auchenoglanis* species (Bagridae); there is also fairly close agreement with the pectoral spine of certain extant Mochokidae (*Synodontis* spp.)» *(ibid.)*. Our specimens conform most closely with the «Species C» (GREENWOOD, *id.*, pp. 44-45, fig. 3), that approaches extant species of the genus *Clarotes* (Bagridae) *(ibid.)*.

— Type 2, from Olival da Suzana

* *Dorsal spines* — in the two best specimens, the shaft is straight in anterior view and nearly so laterally. This distinguishes types 1 and 2. Another distinctive feature is the coarsely rugose anterior anterior face; instead of the type 1 anterior ridge as described above, here it is distinctly stronger, with rugosities that tend to be in pairs or grouped as 3 or 4 basally coalescent small transverse ridges giving the shaft a bluntly serrated appearance. Lateral surface ornamentation is also different — posterior parts have a quite regular pattern with longitudinal ridges by shallow and equally narrow grooves, while anterior parts have a more irregular pattern as uncomplete and wavy longitudinal ridges tend to develop minute tubercules or rugae. The articular surface for the first spine has a barely distinct vertical ridge. The articular end is different too: in anterior view, the shape is triangular but with a narrower base with external tuberosities which define a more irregular profile than in type 1. It does not seem these differences can be related to individual variation or to ontogeny (and thus enhance the distinction of two dorsal spine types). Length is 38 mm in both specimens as preserved. If the spines were complete, overall length would attain about 60 mm. There is a fragment of a third dorsal spine from a somewhat larger specimen; it is similar to the other ones.

* *Pectoral spines* — the larger specimen is uncomplete (58.5 mm as preserved). Anterior border with a keeled ridge made of paired small tubercules, transverse to the length (single near the distal end); shaft somewhat curved distally

(malformation? accident?); posterior border with strong oblique serrations directed towards the base; upper and lower surfaces with irregularly ridged, vermiculated ornamentation, denser towards the anterior border and tending (specially in the upper surface) to present small tubercules. The head of the spine is not preserved. The characters of this spine and the ornamentation in special are compatible with those of the dorsal spines. A left spine from a smaller fish does not show well the articular surface; shaft is rather curved; ornamentation is similar but not so strongly accentuated; there is a distinct tendency to form small tubercules. Two distal fragments, dorso-ventrally compressed, show an acerate point and rather strong, downward oriented serrations in a posterior ridge; there is a distinct anterior ridge, also with downward oriented (if closer by and weaker) serrations.

4. DISCUSSION

Type 2 is clearly close to the Ariidae and can be ascribed to *Arius*. Inspite of the above stated difficulties, as well as the scarcity of comparison material, the presence of *Arius* seems well established.

Type 1 is open to discussion. All the so far available data are enough to eliminate *Arius*. It also differs from *Synodontis* (GAYET, 1983, p. 198, pl. XVII, fig. 1), particularly in the development in this genus of acute serrations in the anterior border of the pectoral pterygiophores. This is not so evident as for the pectoral spine ascribed to *Synodontis?* sp. by GAUDANT (1987, fig. 1 I), unless the specimen is worn enough to have the anterior border serrations nearly obliterated.

There may be a closer relationship to pectoral spines classified as *Chrysichthys* sp. (id., p. 198, pl. XXI, fig. 10), a Bagrid; at least we do not have any distinctive criterium between them. These spines are more like (even if perhaps not very closely) the «Species C» considered by GREENWOOD (1972, *loc. cit.*). «Species C» has been regarded as approaching extant species of *Clarotes*. Hence our type 1 spines do not belong in the Ariidae and probably correspond to a Bagrid we tentatively name cf. *Chrysichthys* sp.

This last opinion seems warranted by comparison with fishes from Angola (POLL, 1967): Amphilidae and Mochokidae are very different. This also holds for the Schilbeidae. There is no similarity to the Clariidae, so the only really comparable family is the Bagridae, and *Chrysichthys* among them since both *Leptoglanis* and *Auchenoglanis*, despite some similarities, are most unprobable hypotheses.

Atribution of type 1 to *Arius* and of type 2 to *Chrysichthys* is further supported by comparison with pterygiophores from modern representatives of these genera.

5. A NILOTIC (OR SUDANIAN) TYPE FISH FAUNA, BIOGEOGRAPHY AND ECOLOGICAL REMARKS

The tropical character of some among the Miocene fish faunas from Lisbon has long been recognized (Antunes in GINSBURG & ANTUNES, 1968). We stressed the presence of stenotherm, warm water forms such as the lemon shark *(Negaprion), Hemipristis,* the tiger shark *(Galeocerdo)* and most specially the nurse shark *(Ginglymostoma).* The latter is known in V-*a* and V-*b* units. Others are common, in contrast with the near absence of *Isurus.* Large tropical barracudas *(Sphyraena olisiponensis)* reinforce these viewpoints. An eastern Atlantic, Senegal-Guinea Gulf type of marine littoral environment prevailed during the late Lower and early Middle Miocene.

A distinctly lower thermal character correspond to the lower Tortonian VII-*a,* more or less like the Atlantic from about the Canaries to Mauretania (ANTUNES & JONET, 1970, p. 244). Changes in water temperatures were mainly interpreted on ichthyological evidence (ANTUNES & PAIS, 1984, pp. 80-81); data about teleosts (JONET, 1973, pp. 275-276) are generally in good agreement with that from sharks. A moderate increase can be assumed (ANTUNES & PAIS, *id.,* p. 81) for the middle Tortonian VII-*b.*

Revision of otoliths (STEURBAUT & JONET, 1981) led to the recognition in VII-*b* of an *Arius* close to the west African *A. heudeloti* and of Polynemidae. Both are very common coastal sea dwellers from Senegal to Angola. Polynemids such as *Polydactylus quadrifilis* prefer brackish waters and enter the rivers into freshwaters, as do Ariids. Large barracuds are commonly found in brackish environments.

These data show an unmistakably nilotic or sudanian character — not unlike that of some Tunisian Miocene associations (GREENWOOD, 1972) — for the ichthyological fauna as far as fresh- (or brackish) water elements are concerned (*Lates, Crysichthys* and *Arius* in particular).

Deteriorating thermal conditions and (perhaps even more) growing aridity in the Upper Miocene may explain *Lates*-first (*Lates* being much more demanding in well oxigenated, large water masses) extinction in Iberia of stenotherm, warm water fishes that could survive in Africa.

Reappearance of the Ariidae (and of a few Polynemidae) in the VII-*b* was not accompanied by any increase in large *Sphyraena* (unknown at this level) and of other warm water forms that are either rare, as *Hemipristis* and *Galeocerdo,* or entirely wanting *(Negaprion, Ginglymostoma).* As no other ecological uncompatibilities are evident in comparison with older levels, only a very moderate increase in water temperatures seems acceptable. However it was not enough for a full return to late Burdigalian and Langhian optimal tropical conditions (table 1) (fig. 1).

Cyprinids are today the major indigenous components of Iberian freshwater fish fauna. They are known in Portugal in inland deposits (which yielded no catfishes nor *Lates*) during the upper Middle Miocene (GAUDANT, 1977), and are well known in the Spanish Upper Miocene. Close affinities to African fish faunas are no more evident since then.

If we judge from the salinity tolerance of living representatives, migrations through coastal seas cannot be excluded and probably occurred. Otherwise migration into the Iberian peninsula certainly did occur in the Lower Miocene. Prior environments during the Oligocene were marked by aridity and perhaps by lower temperatures which would not allow catfishes (and *Lates* for stronger reason) to live there.

Catfishes and *Lates* are interesting from a paleogeographical viewpoint. Ariids were common in the Eocene as far north as in the London and Paris basins. This also applies for *Lates* or similar forms. Distribution was then Mesogean.

Taking into account our own data on the Miocene *Lates* from Lisbon, SORBINI (1970, p. 40) acknowledged that

these fishes were adapted to freshwater. Further research failed to show any *Lates* in Lisbon's Miocene marine levels (with the possible exception of very rare and worn vertebrae in littoral facies — most probably redeposited along with very scarce land mammal remains). This also points out to life in freshwater.

Associations of *Lates* and siluroids are known in Neogene formations of North Africa: Beglia Fm, Upper Miocene, Tunisia; Sahabi Fm, late Neogene, Libya; and in several Miocene and Pliocene localities in Egypt (GAUDANT, 1987). We fully agree with GREENWOOD's (1972, p. 70) statement «during the Miocene there was a fairly uniform freshwater fauna widely distributed in Africa north of the Equator»; however this distribution is even broader, and comprised western Iberia as well during at least late Lower and early Middle Miocene.

SORBINI *(loc. cit.)* did not consider migration from westernmost Europe to have had any role in the *Lates* expansion in Africa, which was explained by him *(ibid.;* fig. 10) through migration from the Egyptian region.

According to GAYET (1983, p. 195), who described Holocene freshwater fishes from the Sahara, including siluroids and a new *Lates maliensis,* «Il est donc possible de concevoir le peuplement de la «Région occidentale» de l'Afrique... par l'Est... ou par l'Ouest (par mer puis bassins du Sénégal et du Niger)». For the same author *(ibid.),* the Messinian salinity crisis may have accounted for the *Lates calcarifer* extinction in the Mediterranean. This is not uncompatible with the disappearance of *Lates* from Portugal well before the Upper Miocene.

GAYET *(ibid.)* also considers «... rien n'empêche de supposer le déplacement de cette forme (ou d'un ancêtre de cette forme) le long des côtes portugaises, puis africaines, jusqu'à l'entrée du fleuve Sénégal, puis de là au fleuve Niger. Ce trajet marin... est plus satisfaisant pour cette forme malienne que l'on ne peut rapprocher que de l'espèce marine *L. calcarifer*». This hypothesis should be taken cautiously. The Lisbon *Lates* has not yet been fully studied, so its affinities are still unknown. Marine migration through coastal waters seems possible, yet it does not look very

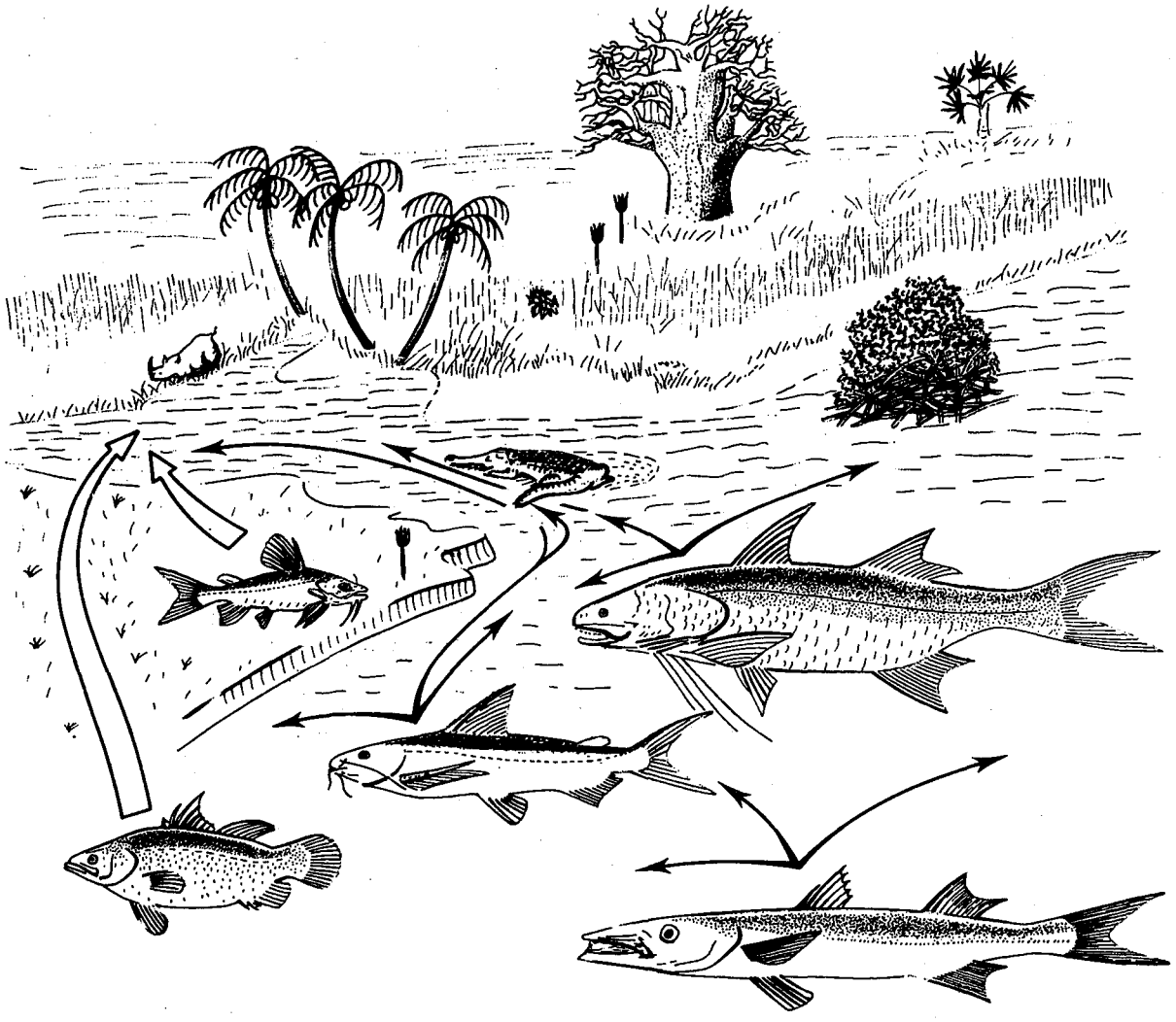


Fig. 1 — Tentative schematic representation of river, estuarine and coastal sea conditions corresponding to the uppermost Lower Miocene V-a_2 subdivision of Lisbon's Miocene series:

— essentially freshwater fishes (white arrows), *Lates* (bottom left) and cf. *Chrysichthys* sp., inspired respectively in the extant *L. niloticus* and *C. cranchii.*

— rather euryhaline, estuarine or coastal marine bony fishes eventually intruding into low salinity or even freshwaters (black arrows), from left to right *Arius* sp., *Polynemus* sp. and large barracudas, *Sphyraena olisiponensis,* inspired respectively in the modern species *A. heudeloti, P. quadrifilis* and *S. guachancho.*

Other elements depicted: the rhinoceros *Gaindatherium (Iberotherium),* the large crocodilian *Tomistoma (Gavialosuchus) lusitanica,* palm trees, a Bombacaceae as the baobab *(Adansonia),* and mangrove.

probable owing to the lack of otherwise unexplained suitable evidence in Lisbon's marine levels. Furthermore, even if there were Miocene praecursors of the Senegal and Niger rivers, this is not enough to warrant it.

Another fact has been overlooked or undervalued, the collision between the Betic and Hesperic massifs (that make up a large part of Iberia) in the late Lower and early Middle Miocene. Land (or freshwater) basin communication did then occur, thus allowing mammalian migrations (ANTUNES, 1979; ANTUNES & GINSBURG, 1983, p. 46), but no evidence for direct, land communications with North Africa was found (ANTUNES & GINSBURG, *ibid.*). Western opening of the Paleomediterranean (and perhaps other waterways as well) may episodically have been much narrower so as to allow these more or less euryhaline fishes to migrate during some particularly favourable events.

Miocene *Lates* plus catfish associations may have colonized both sides of the Paleomediterranean in southern Europe and in Africa, and so their modern distribution has more to do with local extinctions (for the European side) than to migration. Their presence in Africa was more or less constant ever since at least, but more limited in time as far as Europe is concerned.

CONCLUSIONS

1. Two sets of catfish pterygiophores from the uppermost Burdigalian and Langhian are described: one belongs to an *Arius* species close to *A. heudeloti*, whereas the other set may be ascribed to a bagrid cf. *Chrysichthys* sp. recorded for the first time in the Lisbon region.
2. The catfish plus *Lates* association is definitely similar to nilotic or sudanian freshwater ones; contemporary marine facies yielded warm water associations like those from the Coastal Atlantic between Senegal and northern Angola, while brackish facies show intermediate characters (fig. 1).
3. The catfishes probably migrated into the western Iberian peninsula during the Lower Miocene, as *Lates* certainly did, however they are unknown after the Langhian except for a reappearance of *Arius* in the middle Tortonian.
4. A general decrease in temperatures towards the Upper Miocene and growing aridity may account for local extinction, at least as far as freshwaters are concerned.
5. Migration may have been made easier through the displacement of land masses during the lower Middle Miocene, hence tolerance to lower salinites is not the only explanation for migration.
6. Catfish plus *Lates* associations spread into inland waters both north and south of the Paleomediterranean; local extinctions during the Middle and Upper Miocene may have weighed more in the development of modern distribution than migration.

ACKNOWLEDGMENT

The author thanks Dr. Donald E. Russell for the revision of the text.

BIBLIOGRAPHY

ANTUNES, M. T. (1979) — «*Hispanotherium* fauna» in iberian middle Miocene, its importance and paleogeographical meaning». *Annales Geologiques des Pays helléniques*, Tome hors série, fasc. I, pp. 19-26, 1 fig. Athens.

ANTUNES, M. T. & GINSBURG, L. (1983) — «Les rhinocérotidés du Miocène de Lisbonne — systématique, écologie, paleobiogéographie, valeur stratigraphique». *Ciências da Terra (UNL)*, n.º 7 pp. 17-98, 31 figs., 16 pl. Lisboa.

ANTUNES, M. T. & JONET, S. (1970) — «Requins de l'Hélvetien supérieur et du Tortonien de Lisbonne». *Rev. Fac. Ciên. Lisboa*, 2.ª sér., C, vol. XVI (fasc. 1), pp. 119-280, 14 figs., 20 pl.

ANTUNES, M. T. & PAIS, J. (1984) — «Climate during Miocene in Portugal and its evolution». *Paléobiologie continentale*, vol. XIV, nº 2, pp. 75-89, 2 figs. Montpellier.

ANTUNES, M. T. & TORQUATO, J. R. (1969) — «Notes sur la Géologie et Paléontologie du Miocène de Lisbonne VI — La coupe de Quinta da Silvéria (Helvétien V-*b* et V-*c*): Stratigraphie et évolution morphologique». *Boletim da Sociedade Geológica de Portugal*, vol. XVII, pp. 1-30, 7 figs., 12 pl. Lisboa.

CADENAT, J. (1950) — «Poissons de mer du Sénégal». *Initiations africaines III*, 345 pp., 241 figs., Institut Français d'Afrique Noire. Dakar.

GAUDANT, J. (1977) — «Contributions à la Paléontologie du Miocène moyen continental du bassin du Tage II — Observations sur les dents pharyngiennes de poissons cyprinidés — Póvoa dé Santarém». *Ciências da Terra (UNL)*, nº 3, pp. 129-141, 7 figs., 1 pl. Lisboa.

——— (1987) — «6. A preliminary report on the osteichthyan fish-fauna from the upper Neogene of Sahabi, Libya». *Neogene Paleontology and Geology of Sahabi*, pp. 91-99, 4 fig. Alan R. Liss, Inc.

GAYET, M. (1983) — «Sahara ou Sahel? Quaternaire récent du Bassin de Taoudenni (Mali) 5 — Poissons». Laboratoire de Géologie du Quaternaire du Centre National de la Recherche Scientifique. *Publ.* sous la dir. de N. Petit-Maire et J. Riser. Pp. 183-209 + 1 p. bibl., figs. 32-49, pl. XVI-XVIII. Paris.

GINSBURG, L. & ANTUNES, M. T. (1968) — «*Amphicyon giganteus* carnassier géant du Miocène». *Annales de Paléontologie*, Vertébrés, t. LIV, fasc. 1, pp. 3-32, 31 figs., 1 pl. Masson & Cie, Paris.

GREENWOOD, P. H. (1972) — «Fish fossils from the late Miocene of Tunisia». *Notes du Service Géologique*, nº 37, *Travaux de Géologie tunisienne* nº 6 (1971) Formation Beglia, fasc. 2, pp. 41-72, 9 figs, Tunis.

JONET, S. (1973) — «Étude des otolithes des téléostéens (Pisces) du Miocène des environs de Lisbonne». *Comunic. Serv. Geol. Portugal*, t. LVI, pp. 107-328, 14 figs., 4 pl. Lisboa.

——— (1979) — «Le Tortonien supérieur (T VII b) des environs de Fonte da Telha (Péninsule de Setubal) et ses faunes. 2ᵉ partie: Les otolithes des Poissons Téléostéens, 3ᵉ partie: Les Invertébrés». *Comunic. Serv. Geol. Portugal*, t. 65, pp. 105-130, 4 pl. Lisboa.

POLL, M. (1967) — «Contribution à la faune ichthyologique de l'Angola. Museu do Dundo/subsídios para o estudo da biologia na Lunda. Companhia de Diamantes de Angola (DIAMANG)/Serviços Culturais/Dundo-Lunda-Angola. DIAMANG/*Publicações Culturais*, nº 75, 381 pp., 162 figs, 20 pl. Lisboa.

SORBINI, L. (1970) — «Evoluzione e distribuzione del genere fossile *Eolates* e suoi rapporti con il genere attuale *Lates (PISCES-CENTROPOMIDAE): Studi e richerche sui giacimenti terziari di Bolca*». Vol. II, pp. 1-43, 10 figs., 10 pl. Museo Civico di Storia Naturale di Verona.

STEURBAUT, E. & JONET, S. (1981) — «Revision des otolithes de Téléostéens du Miocène portugais». *Bull. Soc. Belge de Géologie*, t. 90, fasc. 3, pp. 191-229, 1 fig., 6 pl., Bruxelles.

DOCUMENTAÇÃO FOTOGRÁFICA

PLATE 1

Ariid and Bagrid (Pisces, Teleostomi) dorsal and pectoral fin spines and some other bones

Arius sp.

All the following specimens have been collected at Olival da Suzana, near Charneca do Lumiar (now under the main runway of the Lisbon Airport); in sands included in the «Areias do Vale de Chelas», V-*b* Division from the Lisbon Miocene series, Langhian (lower Middle Miocene).

Fig. 1 — Dorsal pterygiophore, right side view (× 2).
Fig. 2 — Another specimen, left side showing ornamentation (particularly median anterior tubercules) (× 3).
Fig. 3 — Left pectoral pterygiophore from a large-sized individual, dorsal view (× 2).
Fig. 4 — Another left pectoral pterygiophore, dorsal view (× 2).
Fig. 5 — Distal portion of left pectoral pterygiophore, dorsal view (× 2).
Fig. 6 — Tentatively referred specimen: densely ornamented, left opercular bone, external view (× 3.5).

Chrysichthys sp.

Large specimen from Africa probably to be ascribed to *C. cranchii* (Leach), an extant species. To compare with the fossil specimens ascribed to cf. *Chrysichthys* sp.

Fig. 7a — Dorsal pterygiophore, right view, showing ornamentation and specially the median series of small tubercules (× 2).
Fig. 7b — Left pectoral pterygiophore from the same individual, dorsal view (× 2).

Cf. *Chrysichthys* sp.

All specimens were found in sands from the *V-a* divison («Areias com *Placuna miocenica*»), uppermost Lower Miocene (uppermost Burdigalian), at two localities: Quinta das Pedreiras, near Lumiar, Lisbon (QPE); and Quinta do Pombeiro, near Chelas (QPB).

Fig. 8 — Subcomplete dorsal pterygiophore, right side view (× 2). QPE.
Fig. 9 — Another one as that of the fig. 8, right side view (× 2).QPE.
Fig. 10 — Still another specimen, same view (× 3). QPE.

Remark ornamentation differences in comparison with dorsal pterygiophores ascribed to *Arius* sp.

Fig. 11 — Subcomplete left pectoral pterygiophore, dorsal view (× 2). QPB.
Fig. 12 — Subcomplete, rather curved left pectoral pterygiophore, dorsal view (× 2). QPE.
Fig. 13 — Fragment of right pectoral pterygiophore, anterior view to show articulation for the cleithrum, particularly the shape of the antero-inner process (× 3). QPE.
Fig. 14 — Uncomplete left pectoral pterygiophore, posterior/somewhat oblique view showing the articular process for the cleithrum (× 3). QPB.
Fig. 15 — Right pectoral pterygiophore, ventral view (× 3). QPE.
Fig. 16 — Right pectoral pterygiophore, ventral view (× 2). QPB.
Fig. 17 — Left cleithrum, external view (× 3). QPE.

All the specimens were collected by M. T. Antunes between 1958 and 1967, in old sandpits near Lisbon. Photographs by C. Ladeira.

PLATE 1