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LATE NEOGENE FISH FAUNAS FROM ANGOLA, THEIR AGE AND SIGNIFICANCE

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ABSTRACT

Late Neogene ichthyological faunas are poorly known in southern Africa, and have been commonly considered as Miocene in age. A study on Angola's Late Neogene ones is presented. These faunas comprise a number of Selacians and some Teleosts that clearly belong in (or at least are closely related to) extant species. The only sure exception is *Procarcharodon megalodon*. This species is apparently outnumbered by *Carcharodon carcharias*, and that, together with the occurrence of *Galeocerdo cuvieri* and other highly differentiated forms, points out to a Pliocene age, although it was previously supposed to be Miocene and even lower Miocene (Burdigalian). Other data actually confirm this.

The whole fauna does correspond neither to a littoral and very shallow environment, nor to deep waters far away from the coast. It surely indicates warm waters. A more or less suitable model would be eastern Atlantic between Northern Angola and Cape Verde-Senegal.

Similar faunas are also present in Eastern Cape Province and Zululand in deposits related to the great Pliocene transgression. They have a very wide geographical distribution. Rio de Oro's fauna (Northwestern Africa) is perhaps also similar and would appear as an inmediate link towards european Pliocene faunas.

Marine formations from Angola's coastal basins are most interesting, mainly on account of their paleontological wealth. Some of its aspects were treated by us (Antunes, 1961, 1963, 1964, 1969-1970, 1972a, 1972b) At present, one of our main themes is the revision of ichthyological faunas, which have been found there from Lower Cretaceous until Pliocene.

Besides a more detailed account to be published soon, we think that it is useful to provide some data about the hitherto poorly known Late Neogene faunas and their regional significance, since they have scarcely been studied in Africa. This is in contrast with the much better known Miocene ones, described namely by Arambourg (1927) and Dartevelle & Casier (1943-1959); indeed the Late Neogene faunas were generally not regarded as distinct from the former.

I—GENERAL DATA

Late Neogene is present in both Cuanza's and Benguela's basins, i.e. (respectively) at Farol das Lagostas and SECIL's quarry (uppermost, algal limestones,' 'tuffeau calcaire" according to Dartevelle & Casier, or Neogene III in Antunes, 1964), on the coast at about 5 km NE from Luanda; and near Baia Farta (uppermost Neogene), some 20 km ESE from Benguela. For further data see Antunes (1964, p. 213-215).

Many fish remains, chiefly teeth and vertebrae, were found near Farol das Lagostas and at SECIL's quarry. The main collection, not studied here, is kept at the museum of Serviços de Geologia e Minas, Luanda. The bulk of the material dealt with herein was collected by the author in 1960, 1961 and 1963; some additional specimens were given to us in 1967 at SECIL's cement plant.

However, since washing and sieving methods could not be used, the smaller fossils are very scarce in the collections. Our knowledge is thus fairly adequate only in what concerns medium to large-sized forms; fortunately enough they provide quite a sound basis for discussion. As details on each species will be fully presented in a forthcoming paper, we will concentrate on some specially meaningful points.

II—LATE NEOGENE FISH FAUNA FROM FAROL DAS LAGOSTAS, SECIL'S QUARRY AND BAIA FARTA

IIa—COMPOSITION, EVOLUTION AND SOME ECOLOGICAL DATA

Preservation is not always good. At SECIL'S quarry, ripping exploitation with huge machines crush or at least damage most of the specimens. Near Farol das Lagostas, bones and teeth are generally set free from calcareous gangue by karstic erosion, either remaining *in situ* or redeposited along with Pleistocene sands, but more or less corroded and encrusted by iron oxides. No otoliths were found, and this is a serious limitation to the knowledge of Teleosts. As far as we know, the fauna comprises (Table 1):

Table 1

			Farol das Lagostas	*SECIL*	*Baia Farta*
—	* * *	Procarcharodon megalodon (+)	×	×	×
—	* * * *	Carcharodon carcharias ..	×	×	×
	* *	Isurus cf. oxyrhinchus ..	×		×
	*	Isurus benedeni (?+) ..	×		?
	* * * *	Odontaspis taurus ..	×	×	×
	*	Mitsukurina sp.	×		
—	* * * *	Galeocerdo cuvieri ..	×	×	×
	* * *	Hemipristis serra (?+) ..	×	×	×
	*	Paragaleus sp.	×		
	* *	Negaprion cf. brevirostris ..	×	×	×
	*	Scoliodon sp.	×		
—	* * * *	Carcharhinus sp. I gr. egertoni	×	×	×
	* * *	Carcharhinus sp. II gr. priscus	×	×	×
	* *	Sphyrna cf. zygaena ..	×		
	*	Pristis sp.	×		
	*	Myliobatis sp.	×		
	*	Pteromylaeus cf. bovina ..	×		
	*	Rhinoptera sp. gr. brasiliensis ..	×		
	*	Aetobatus sp.	×		
	*	Tachysurus sp.	×		
	* * *	Sphyraena cf. barracuda ..	×	×	×
	*	Sparus sp.	×	×	
	*	Cybium sp.	×		
	*	Xiphiidae ou Histiophoridae, gen. ind.	×		
	*	? Tetrodon sp.	×		

* * * very common in collection
* * * common in collection.
* * not so common in collection.
* rare in collection.
—specially meaningful species.
\+ extinct species.
?+ a species usually considered as extinct.
(see discussion in the text.)

Smaller-sized fishes are specially unsatisfactorily represented. Even so, this fauna is much richer than it could be previously acknowledged.

Nearly all forms have very close affinities with extant species, or cannot be distinguished from them. Only *Procarcharodon megalodon* is a true extinct species. Indeed it could be objected that this is also the situation of both *Isurus benedeni* and *Hemipristis serra*, however we don't think this is so:

(1) the so-called *I. benedeni* is only provisionally accepted here, since it may well correspond to a dental morphotype which does exist also in the extant *I. oxyrhinchus*, and probably is not representative of a distinct species; and

(2) Late Neogene *Hemipristis*' teeth have been reported to the fossil species *H. serra*, but it remains to be seen if they are really distinct from those of extant *H. elongatus* (Klunzinger), this being scarcely known (very rare specimens caughtin the Red Sea and Indian Ocean); the characters pointed by Leriche (1938,p. 18) as evidence for the segregation of the two species do not look very convincing, they are but minor morphological differences, probably ontogenetical (or sexual?); this could well mean that Late Neogene's highly differentiated *H. serra* and *H. elongatus* are just not distinct, the last being but a surviving population with a quite restricted distribution in contrast with its former world-wide one (perhaps to be explained by falls in sea temperature during quaternary times, specially hurting these stenotherm, warm-water sharks).

The very close affinities with modern faunas are also substantiated by the advanced stage of evolution of sharks like *Galeocerdo* (not distinct from the extant tiger shark) enormous *Isurus benedeni*, very large *Hemipristis* and *Carcharhinus* whose size largely exceeds the maximum observed in Miocene material, and do not show any significant differences towards recent specimens.

IIb—BATHYMETRICAL CHARACTERS

A quantitative approach to the composition of the whole fauna, essential to any ecological reasoning, is inclined to be biassed (Antunes & Jonet, 1969-1970, p. 225; Antunes, 1972): even if all teeth contained in a certain volume of sediment could be recovered and correctly identified, it is not possible to convert these data in terms of relative numbers of individuals since there are so many uncontrolable factors. Nevertheless we can obtain a rough estimate probably not very far from reality, at least in what concerns medium and large-sized animals.

At once we can verify that the most common dwellers of littoral, mostly shallow, brackish waters (estuaries, lagoons), or even appearing in freshwater, like *Negaprion*, *Pristis* and *Tachysurus* are scarce. This may be confirmed by *Ginglymostoma* being unknown, nurse-sharks being typical of very shallow, warm, littoral seas.

At the other end of the spectrum are *Mitsukurina* (rare), deep-water sharks that generally keep away from the littoral, and pelagic fast-swimming Teleosts such as

Cybium and Xiphiidae or Histiophoridae (both rather uncommon); *Isurus* would perhaps be included in this last group, as the remains of fishes active not very far from the surface but away from the coast tend to mix at the bottom with those from really deep-water species.

The collection comprises a relatively high proportion of large to very large sharks that cannot live in very shallow environments (*Procarcharodon*, *Carcharodon*, big *Galeocerdo* and *Carcharhinus*), although sometimes they come closer to the beaches, much like *Odontaspis*.

The Batoidea as far as known are bottom dwellers, but in general not living in great depths (*Myliobatis*, less than 60 fathoms—Bigelow & Schroeder, 1953, p. 437).

Fauna from Farol das Lagostas does correspond neither to a littoral and very shallow environment, nor to deep waters far away from the coast.

IIc—THERMAL CHARACTERS

Even if *Ginglymostoma* remains unknown, nearly all the fauna clearly indicates warm waters;: *Galeocerdo*, *Hemipristis*, *Negaprion*, *Carcharhinus* gr. *egertoni* ("bull sharks"), *Aetobatus*, *Tachysurus* and big *Sphyraena* (1). It is noteworthy to recognize the presence of young *Hemipristis*, showing that environment was well suited for reproduction—in less warm media only remains of big sized, adult animals are commonly found.

On the other side, *Isurus* and *Mitsukurina* would indicate mainly temperate (not necessarily cold) waters. *Lamna*, a genus that is an indicative of temperate to quite cold waters (Antunes & Jonet 1969-1970, p. 135-136; Antunes, 1969), is totally wanting,even if it is Common in Southern Angola's Miocene formations.

We can tentatively accept as a more or less suitable model for this fauna that of eastern Atlantic between Northern Angola (out of reach from cold current of Benguela) and Cape Verde-Senegal.

IId—AGE

The problem of the chronology of Late Neogene faunas like those from Farol das Lagostas, etc. does not concern only Angola's formations, but is of broader regional significance. In general these formations were reported to the Miocene, and more exactly to the Burdigalian stage.

These views are based on earlier works by european paleontologists like R. Douvillé (in Choffat, 1905), who correlated some deposits near Luanda to the Burdigalian of Jaen, Southern Spain, on the evidence of operculines and amphistegines. Such age was generally accepted for the whole marine Neogene formations there. Indeed those are warm-water deposits much like some lower Miocene european ones, but, owing to persistent tropical conditions, such facies lasted much longer after they had disappeared in Europe (where there has been clearly a fall of sea-water temperatures since middle Miocene times).

The views of R. Douvillé (*loc. cit.*) were adopted by H. Douvillé (1933) on the evidence of molluscs recovered at/or near Luanda, but the exact stratigraphical origin of the fossils was not stated; moreover these molluscs, as far as it is known, are a somewhat frail basis for long-range correlations. Anyway Burdigalian age was accepted without serious discussion, namely by oil geologists, for a very broad spectrum of Neogene deposits, the so-called "Luanda formation".

However other data aroused suspicion about the age. As for some fishes from upper beds of Farol das Lagostas, Casier (in Dartevelle & Casier, 1959, p. 420) admitted an "Helvetian" age, and has even stated "il n'est pas impossible qu'il s'agisse là d'une faune du début du Pliocène" (Casier, 1957, p. 287). Other fossils, like the broadly distributed and mainly Pliocene *Chlamys bollenensis*, or the echinoid *Rotuloidea vieirai*, pointed also to an age much later than Burdigalian, at least for the uppermost levels of the Neogene series.

Furthermore:

(1) Torquato & Rocha (1969, p. 46) had shown that "Luanda formation" is heterogenous and comprises Plio-Pleistocene beds that overlie unconformably Miocene ones;

(2) according to Meijer (1972, p. 152-153) there are in "Luanda formation" planktonic foraminifera corresponding approximately to *Globorotalia acostaensis* biozone, i.e. N 17 from Blow, and this zone is uppermost Miocene, upper Tortonian-Messinian (Berggren & Van Couvering, 1974, fig. 1); however, as Meijer's samples, obtained from drill cuttings, are probably not the highest in the Neogene, it seems logical that the uppermost algal limestones exposed at Farol das Lagostas, etc. are even younger;

(3) on the basis of Heteresteginid foraminifera, the data as far as known, reinforce the hypothesis of the existence in Cuanza's basin of Miocene beds higher than Burdigalian and are absolutely not in contradiction with the presence of Pliocene levels.

So we can definitely conclude that upper beds of Farol das Lagostas (Neogene III, Antunes, 1964) are at least N 17 in age, and most probably even younger—and that means Pliocene. All this corroborates our previous

(1) We gave elsewhere (Antunes & Jonet, 1969-1970, p. 223-232, 242-244) a more thorough discussion of these matters.

views (Antunes, 1963, 1964), when, for first time and mainly on the basis of fishes, we concluded these fossils to be clearly Pliocene.

IIe—FISH FAUNAS AND CHRONOLOGY

As stated above, notwithstanding earlier datations as "Burdigalian", fish faunas appealed to other interpretations. Casier (1957; also in Dartevelle & Casier, 1959) did not fail to remark the very highly evolute characters of the fauna, on which he considered it to be Helvetian in age; he stated further that it could date from early Pliocene.

Even before a more thorough study was accomplished, the identification of *Carcharodon carcharias* lead us (Antunes, 1962, p. 377) to think at an uppermost Miocene or Pliocene age, or, later on, clearly Pliocene, when we also concluded that the highly evoluted tiger shark was well the extant *Galeocerdo cuvieri* and not the common Miocene form *G. aduncus* (Antunes, 1963, p. 53). These views were reinforced by other data as shown later (Antunes, 1964, p. 214).

Let us point out the essential facts about stratigraphical distribution of the most characteristic species:

(1) *Procarcharodon megalodon*, Lower Miocene to Pliocene (or Pleistocene?), maximum size increasing to really enormous dimensions in later times. This is the situation at Farol das Lagostas, etc.

(2) *Carcharodon carcharias* is quoted for upper Burdigalian and Helvetian of Switzerland (Leriche, 1927, p. 81) by but two teeth, that appear as quite typical. As far as we can ascertain, the species does not seem to have been found again in such relatively older formations (i.e. Leriche, 1957, p. 34; Cappetta, 1970, p. 26-27; Antunes & Jonet, 1969-1970); its existence near the end of Lower Miocene is only documented by the single tooth described by Leriche, and one can feel some doubts about the correctness of the localisation. In Italy, this species is common in many Pliocene localities but it appears to be rare in late Miocene (there are a few old references, age should be checked) (see Menesini, 1968, p. 593). The species is otherwise common in Belgium but only since Scaldisian, where it seems to replace *P. megalodon* (Leriche, 1926, p. 424); but this stage is Pliocene (Pomerol, 1973, p. 164). However some teeth were also found in the Anversian, upper part of middle Miocene (Leriche, *ibid.*). In the U. S. coastal Plain, *C. carcharias* characterises Duplin marl (Yorktown formation), regarded as uppermost Miocene in Maryland (Leriche, 1942, p. 78) or "late Miocene" (Lexique Stratigraphique, 1967, p. 1184). Casier (1960, p. 14, tableau) places first appearance at upper Miocene, but with great expansion only in Pliocene.

(3) *Isurus benedeni's* very great maximum size is only known in late Miocene and Pliocene (Dartevelle & Casier, 1959, p. 401).

(4) *Galeocerdo cuvieri:* we presented (Antunes, 1972b, p. 7-9, pl. II-III) some remarks about tiger sharks' evolution. As we had shown (Antunes, 1963, p. 49-50), *G. praecursor*, described by Dartevelle & Casier, 1959, from Farol das Lagostas, is not distinct from extant species. Teeth from *G. cuvieri* were found at many localities of Late Neogene or Pleistocene age, i.e. Cyprus, Sri Lanka and Timor (collections in the British Mus. Nat. Hist.), at Santiago Island, Cabo Verde (coll. Museu Mineralógico e Geológico, Univ. de Lisboa), and in the Ashley Phosphate beds, South Carolina (Leriche, 1942, p. 55, pl. VIII, fig. 1-2), which contain many earlier fossils along with others like *G. cuvieri* and *C. carcharias* that point out to "un âge relativement récent" (Leriche, *ibid.*).

(5) *Hemipristis serra* attains a very large size, like var. *maxima* from Pliocene (Pleistocene?) of Zanzibar.

(6) *Carcharhinus* sp. I gr. *egertoni* and *C.* sp. II gr. *priscus* also attain a very large size, largely exceeding the observed maxima in many Miocene localities, as in those in the same region of Luanda.

(7) Other forms are also closely related to extant species. None of them does suggest anything that would contradict the chronological conclusion consistent with all the above presented data.

The fauna from Farol das Lagostas, etc., with *C. carcharias* very common and perhaps exceeding *P. megalodon* in number, only matches well with ichthyological faunas known elsewhere in well-dated Pliocene; at most, it cannot surely be older than Late Miocene (but nothing warrants this). Such conclusion is equally in close agreement with studies on foraminifera, among others.

III—MARINE PLIOCENE IN SOUTHERN AFRICA AND ITS ICHTHYOLOGICAL FAUNAS

Marine Pliocene is not very well known in Southern Africa, and it has been taken, in quite a lot of regions, as Miocene. Indeed the real situation is very different, as recent studies have shown that Pliocene formations are far more developed than was previously supposed: in Eastern Cape Province, "the sea extended farther inland here during the Pliocene than at any other time during the Tertiary" (King, 1972, p. 159). Then there has been a maximum of transgression which was felt also in many other regions.

In Zululand there are fish faunas seemingly identical to that of Farol das Lagostas : shark teeth found in the "Pecten bed" between Uloa and Hell's Gate belong to *Carcharodon sulcidens* (a synonym of *C. carcharias*) in "over 80 per cent" of the instances, in association with *P. megalodon*, and *Galeocerdo cuvieri*, among others (Applegate, 1970; cf. Frankel, 1972, p. 311). As for Applegate (*id.*), its age would be 'Upper Miocene at oldest", however this date seems to have been proposed under the influence of the study of Invertebrata regarded as indicating Lower Miocene. Nevertheless, as Applegate did not fail to remark, "...generally accepted Pliocene fauna from Santa Rosalia in Baja California... is amazingly close in its content to the Pecten bed", and "it could be no older than Miocene, and now I think it is even younger" (*loc. cit.*). As Frankel (*id.*, p. 312) states, the age of Zululand's Pecten bed "is most certainly post-Lower Miocene and more likely Upper Miocene-Pliocene than anything else". This situation closely parallels that of Farol das Lagostas, and it is very likely that all such deposits are very approximately synchronical and Pliocene in age.

The chronostratigraphical meaning of Southern Africa's fish faunas is of much broader significance. Owing to the enormous geographical distribution of large sharks, long range correlations are feasible. The characteristic association of predominant *Carcharodon carcharias* and *Procarcharodon megalodon*, generally together with *Galeocerdo cuvieri* and other highly differentiated forms, occur in very far away regions. This may equally be true for Northwestern Africa. At Rio de Oro, Font y Sagué found a bone bed that is but the moghrebian facies Pliocene "lumachelle a Pectinidés" (Lecointre, 1966, p. 257). L. Joleaud (1907) identified fish remains collected by Font y Sagué, among them *Carcharodon rondeleti* (=*C. carcharias*) and *P. megalodon* (less common). However *Galeocerdo aduncus*, a common Miocene form, was also recognized. One may think that, at this time, palaeoichthyologists could not distinguish between *G. aduncus* and *G. cuvieri*, since there are no clear-cut distinctive criteria (Antunes, 1972, p. 8-9, pl. II-III), only an almost constant trend in evolution. A revision of Font y Sagué's collection was needed, but unfortunately it was destroyed during Spain's Civil War. Even with some reserve, it is by no means unacceptable that Rio de Oro's Pliocene fauna is also similar to those treated above. Thus it could well represent a geographical link between Southern Africa's and Europe's Pliocene faunas.

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