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On Western Europe Miocene Gavials (Crocodylia) their Paleogeography, Migrations and Climatic significance*

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Key words: Crocodilians - Gavials - Miocene - Europe - Portugal - Paleogeography — Climate

Abstract: Crocodilian remains ascribed to an undeterminate species of *Gavialis* are described. All material was collected in several localities in the Lower Tagus basin in Lisbon and nearby. Age spans from the Lower Burdigalian to Langhian. No post-Langhian evidence is known.

References are made to the entire crocodilian fauna from the concerned region. It comprises the autochtonous *Diplocynodon* in association to immigrants, *Tomistoma lusitanica* and *Gavialis* sp. Both probably are of asiatic origin from stocks that expanded westwards. This expansion seems related to the Burdigalian transgression and to the corresponding paleogeographic and environmental changes.

Migration from westernmost Europe may account for the implantation in eastern North America of *Tomistoma* stocks that through speciation gave rise to the Upper Miocene *T. americana*.

The value of the Crocodilians is stressed as climatic indicators, and specially of *Tomistoma* and *Gavialis* as warm stenotherm forms. Increasing aridity in lower Middle Miocene and lower temperatures may account for their regional rarefaction and subsequent extinction.

Palavras chave: Crocodilos - Gaviais - Miocénico - Europa - Portugal - Paleogeografia - Clima

Resumo: São descritos restos de crocodilos atribuídos a uma espécie indeterminada de *Gavialis*. Todo o material provém de jazidas situadas na bacia do Baixo Tejo, em Lisboa e arredores, datadas desde o Burdigaliano inferior ao Langhiano, São desconhecidos em níveis mais modernos.

É considerado o conjunto da fauna de crocodilos da região, a qual inclui uma forma europeia autóctone, *Diplocynodon* sp., a par de imigrantes: *Tomistoma lusitanica* e *Gavialis* sp., ambos de provável origem asiática. A expansão para ocidente parece relacionada com a transgressão do Burdigaliano e correspondentes modificações paleogeográficas e ambientais.

Migrações a partir do extremo ocidental da Europa podem explicar a implantação de populações de *Tomistoma* na América do Norte oriental que, através de especiação, deram origem a *T. americana*, do Miocénico superior.

Salienta-se o valor dos crocodilos como indicadores climáticos e, em especial, de *Tomistoma* e *Gavialis* como formas estenotérmicas de temperatura elevada.

Aridez crescente no início do Miocénico médio e temperaturas menos elevadas explicam a sua rarefacção e subsequente extinção na região em causa.

INTRODUCTION

After Middle Eocene times, the Crocodylia underwent a sharp decline in Europe which almost surely can be ascribed to climate deterioration during Late Eocene and Oligocene. From at least six genera in the Middle Eocene, only *Diplocynodon,* an Alligatorine, survived through Oligocene. It thus became the sole autochtonous crocodilian genus in this continent, where it survived until the early Upper Miocene, probably somewhat later.

A renewal did occur in the Lower Miocene, with the immigration of long-snouted crocodilians. This irnmigration is certainly related to the great Burdigalian transgression, which opened an excellent pathway to

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good swimmers - provided that they could tolerate salinity to a certain extent, and that the temperatures were adequate.

The best known forms have been reported to the genus *Tomistoma* (whose only extant representative is *Tomistoma schlegeli*, the type species) or to *Gavialosuchus*, which has been regarded as a synonym of the former (ANTUNES, 1987).

For a long time no true Gavial was recognized beyond Asia. A «revolution» occurred when LANGSTON (1965) has shown that Gavialids lived in South America between the Oligocene and the Pliocene. Maybe as a consequence, some authors begun to see fossil Gavials where they had never been reported. This happened in Europe, albeit taking aim at the wrong target: regarding *Gavialosuchus* as a distinct genus and (still more important) including it among the Gavialids. This was previously discussed (ANTUNES, 1987; ANTUNES & GINSBURG, 1989). Indeed, facts show that (a) *Gavialosuchus* is very close to *Tomistoma* and not at all to *Gavialis*; (b) *Gavialosuchus* does not justify its distinction from *Tomistoma* at the genus level, even if it could perhaps be regarded as a subgenus from the latter; (c) Tomistomines and Gavialids are quite distinct.

Although keeping *Gavialosuchus* as a junior synonym of *Tomistoma*, there has been a minor change in our views. Whereas we regarded the Tomistomines at family rank in our earlier paper, further developments led us to adhere again to the classification of KÄLIN (1955). We thus placed *Tomistoma* Müller, 1846 in a subfamily Tomistominae of the family Crocodylidae (ANTUNES & GINSBURG, 1989, pp. 80-81).

Gavialids also arrived in western Europe in the Lower Miocene. Uncomplete and scarce material perhaps prevented an earlier identification. As far as the Lower and early Middle Miocene from Lisbon are concerned, the presence of a further and still more slender-teethed crocodilian was recognized long ago (ZBYSZEWSKI, 1949, pp. 66-67, figs. 153 and 160) as *Tomistoma calaritanus* Cappellini, 1890. Following up with some reserve, we aknowledged the presence of a *Tomistoma* cf. *calaritanus* (ANTUNES, 1961, p. 57, pl. X, figs. 30-33).

This point deserves some attention. By comparison with CAPPELLINI's figures (1890, tav. II, figs. 1-3; tav. III, figs. 1-2), it is clear that the specimen from Cagliari can be reported to *Tomistoma*; and that its smooth, not so slender teeth are well distinct from the Lisbon ones determinated by Zbyszewski as *Tomistoma calaritanus*. Hence we admitted that this form could be a true gavial (ANTUNES, 1987, p. 50), and later reported it to *Gavialis* sp. (ANTUNES & GINSBURG, 1989, pp. 87-88). In a paper on pliocene crocodilians from the Upper Siwaliks, very similar teeth were reported to *Gavialis* cf. *gangeticus* (PATNAIK & SCHLEICH, 1993, pl. VI, figs. 2-4). The attribution of our specimens to *Gavialis* seems corroborated again.

New data prompts us to discuss paleogeography, migrations and climate as far as crocodilians and some mammals (Proboscideans, Anthracotheres) are concerned. All these problematics are related indeed.

DESCRIPTION

Order CROCODYLIA Gmelin, 1788
Suborder EUSUCHIA Huxley, 1875
Family Gavialidae Cuvier, 1807
Genus *Gavialis* Oppel, 1811
Gavialis sp.

(Plate I, figures 1- 6)

Former dental descriptions (ZBYSZEWSKI, 1949, p. 67; ANTUNES & GINSBURG, 1989, p. 87) are adequate enough. Although there is some variation in shape and size, some general characters may be recognized. Teeth are long, slender, pointed, nearly straight or somewhat curved rearwards; cross-section more or less rounded or elliptical but not much laterally compressed; weak longitudinal keels (one of them, probably postero-external, being longer than the other, antero-internal one); with very distinct fine longitudinal striae, this being one of its most distinctive characters-along with general morphology and proportions. The largest teeth may reach about 35 millimeters in total crown length, and about 11 millimeters in maximum transversal diameter. In shape, size and ornamentation these teeth are closely similar to those of extant *Gavialis gangeticus*, the type species (Plate I, fig. 7-10). The teeth from *Tomistoma lusitanica* are much more thick, blunt and curved, with a nearly smooth enamel surface (Plate I, fig. 11-13).

A symphysial fragment of a worn, toothless, very slender right dentary from Areeiro do José da Graça (Langhian), with very steep forwards-directed alveoli seems to belong to a gavial. Even if it is from a large individual, it seems much too narrow to belong in a *Tomistoma*.

Among the scarce post-cranial skeletal elements so far collected, there may be some ones belonging to *Gavialis*. Huge bones probably belong to *Tomistoma lusitanica*. However, poor knowledge of the post-cranial skeleton prevents us to ascribe such remnants to one or another of these forms.

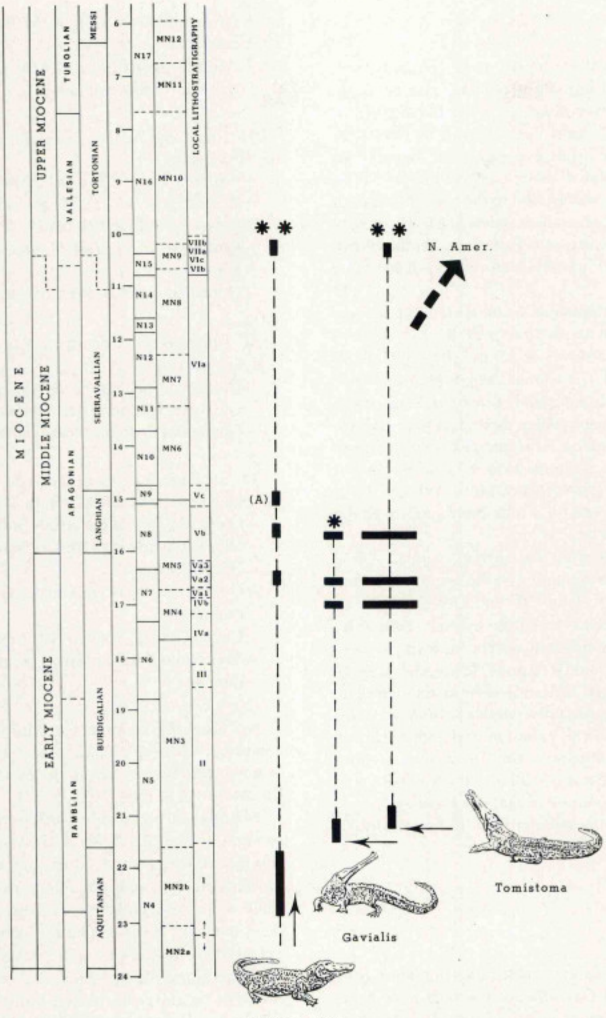


Fig. 1 — Miocene occurrences of Crocodilians in the Lower Tagus basin and at Amor, near Leiria (A). *Tomistoma* and *Gavialis* immigrated (probably from Asia) into this region, previously inhabited by a single european endemic genus, *Diplocynodon*.

Continental and marine stages; Age (Ma); Blow's zones N4 to N17; «mammal units» MN2a to MN12, as well as the hypothetical emigration of *Tomistoma* to eastern North America are shown.

narrow bars, *scarce*; medium, *common*; broad, *frequent*.—* probable regional extinction;—** regional extinctions.

AGE

In the distal, western, mostly marine Atlantic versant of the Lower Tagus basin, *Gavialis* may be recognized since the Lower Miocene: lower Burdigalian, II local unit (fig.1). Its presence is shown by rare, slender teeth from fine sands exposed at the foundations of the Universidade Católica (ANTUNES & MEIN, 1986). These sands correspond to the earliest stages of the great Burdigalian transgression. The unit II also yielded typical *Tomistoma lusitanica* teeth. Hence both genera arrived into this area roughly at the same time.

Earlier, in the Aquitanian I unit there are but some small crocodilian teeth that may be ascribed to *Diplocynodon* (ANTUNES & MEIN, 1992, p.p. 132). Both *Gavialis* and *Tomistoma*, which predominates, are fairly common in later units (upper and uppermost Burdigalian, Langhian), where they seem to be accompanied by *Diplocynodon*. This last genus occurs up to lower Middle Miocene in the Lower Tagus basin, and beyond it at Amor (ANTUNES & MEIN, 1981, p. 179), a site that seems to be still a little more modern in the lower Middle Miocene.

The regional history of *Tomistoma* is similar. A few teeth from beds corresponding to the beginning of the Serravallian transgression (Vc unit; JONET, 1981, p. 49) are probably reworked from earlier sediments; *Tomistoma* is unknown later, except for a single individual from the early Upper Miocene (lower Tortonian, VIIa unit). A dermal scute is the only evidence of a crocodilian (*Diplocynodon?*) from the more or less synchronic lower Vallesian of the inner part of the same basin in Ribatejo. Both occurrences show that the demise of the crocodilians still was not complete. None are known in Portugal since then.

No *Gavialis* was found later than the lower Middle Miocene.

LOCALITIES

Teeth, mandibular and maxillary fragments that may be ascribed to *Gavialis* are kown to have been collected in the following units and sites. Except when otherwise stated, all these sites are old sand pits, of no avail since about 1967 and almost completely destroyed as now.

A. *Lower Burdigalian*, II unit («Areolas da Estefânia»), age: see fig.l.

- Universidade Católica, Lisbon (foundations) / *Gavialis*.
- [– Quinta do Rilhafoles near Cruz do Tabuado, Lisbon/ *Tomistoma* only].

B. *Upper Burdigalian*, IVb unit («Areias da Quinta do Bacalhau»).

- Avenida Padre Cruz (ex Avenida Paulo VI - cf. ANTUNES *et al.*, 1973, pp. 462-464, 467, 500) [lower part of the IVb unit].
- Quinta da Noiva, East of Avenida Gago Coutinho, Lisbon.
- Quinta do Narigão, West of the same Avenue.

C. *Uppermost Burdigalian*, Va$_2$ unit («Areias com *Placuna miocenica*»).

- Quinta da Conceição near Alto de S.João, Lisbon.
- Quinta do Pombeiro near Chelas, NE from Lisbon.
- Quinta das Pedreiras near Lumiar, Lisbon.

D. *Langhian*, Vb unit («Areias do Vale de Chelas»).

- Quinta das Flamengas, North of Chelas.
- Quinta da Farinheira, also N of Chelas.
- Olival da Suzana, SE of Charneca do Lumiar, North of Lisbon.
- Quinta da Silvéria, also SE of Charneca do Lumiar.
- Quinta Grande, South of Charneca do Lumiar.
- Areeiro do José da Graça, South of Charneca do Lumiar.

No *Gavialis* remnants are known elsewhere in Portugal, although *Tomistoma* was recognized in Algarve (ANTUNES, JONET & NASCIMENTO, 1981, p. 16; ANTUNES & PAIS, 1993, p. 13).

Material of comparable age from the «faluns» of western France (ANTUNES & GINSBURG, *loc. cit.*) cannot be distinguished from that under study and belongs in the same unnamed species of *Gavialis*. Lack of more complete specimens prevents a better determination. It seems that the same association (not referred to before) is also present in the Middle Miocene of the Rhône valley, France: a tooth from «la molasse calcaire marine de Saint-Jean-en-Royans (Drôme)» (DEPÉRET, 1887, p. 244) may be from *Tomistoma*, and another tooth from «un niveau plus élevé encore de l'étage helvétien, dans les sables *à Nassa Michaudi* de Saint-Pierre-de-Chandieu (Isère)» (DEPÉRET, idem, p. 244-245, pl. XIII, fig. 49) seems typical of *Gavialis*.

CROCODILIAN MIOCENE FAUNA IN WESTERN EUROPE

In brief, the Miocene crocodilian fauna from western Europe (Portugal, France and probably Spain too) comprises 3 eusuchians:

Family GAVIALIDAE
  Genus *Gavialis* Oppel, 1811
  • *Gavialis* sp.

Family CROCODYLIDAE Gray, 1825
Subfamily *Tomistominae* Kälin, 1955
  Genus *Tomistoma* Müller, 1846 (including *Gavialosuchus* Toula & Kail, 1885)
  • *Tomistoma lusitanica* (Vianna & Moraes, 1945) (or undistinguishable forms)

Subfamily *Alligatorinae* Cuvier, 1807 (Kälin, 1933)
  Genus *Diplocynodon* Pomel, 1847
  • *Diplocynodon* sp.

Elsewhere in Europe, the Miocene situation is similar. There are well-represented *Diplocynodon* (as *D. styriacus*) and *Tomistoma* (as *Gavialosuchus eggenburgensis* and *Tomistoma calaritanus*), gavials being unknown as far as we could ascertain.

PALEOGEOGRAPHY

GENERAL DATA

During its long history, several representatives of the Crocodylia were adapted to life at the sea. Some authors even related their general geographic distribution to the History of the Tethys (FRANCO, 1991). However, most of the Crocodilians are inland water dwellers, although some ones may tolerate saltwaters. All are swimmers, including the more terrestrial forms. Gavials are supposedly the most aquatic of all. Migration of crocodilians does not require as much as purely land mammals the existance of land bridges. A string of islands would have been good enough, provided there was no limiting thermal barrier. Arid belts are paramount or even unfranchisable barriers for them.

This is probably true for most extinct crocodilians. They had good migration possibilities unless there were impeaching factors as aridity or temperatures under their thermic tolerance lower limits.

Paleogeographic conditions offered by the Paleomediterranean after the closure of the eastern Tethys in early Miocene, when there was a string of islands that eventually met, even allowed the immigration of land mammals into western Europe. A major transgression as that of the Burdigalian restricted arid areas in favour of more humid ones. This, coupled with climate warming, undoubtedly favoured *Tomistoma* and *Gavialis* migrations from Asia

THE PROBOSCIDEAN DATUM IN WESTERNMOST EUROPE

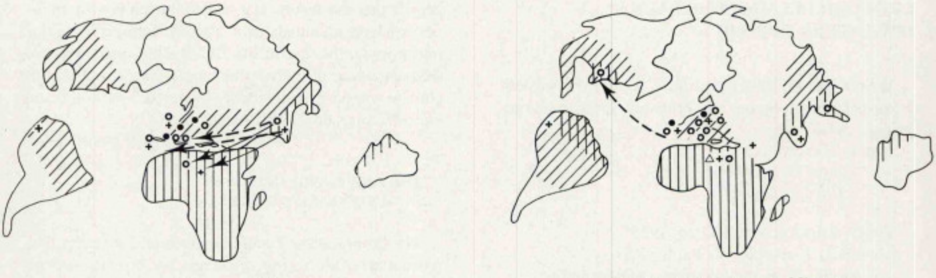
The Proboscidean Datum in westernmost Europe is a particularly interesting reference for migration from Africa to Eurasia (migrations in the reverse direction becoming therefore possible), whether it has been geologically instantaneous (as it seems) or if there was some diachronism regarding other european regions. As KOWALSKI & KUBIAK (1993, p. 279) stressed (also following BERNOR *et al.*, 1987), African mammalian faunas at about 22 Ma do not contain evident Asian immigrants; on the contrary, the African (Songhor) fauna of *ca.* 19 Ma contains numerous Asian elements, and that «will place the beginning of interchange between Africa and Eurasia and of migration of proboscideans between 23 and 18 My». The Proboscideans from Belchatów in Poland as early as at about 18 Ma (if the dating of the directly overlying tuffite is correct), from Hungary at >19.6 Ma (KOWALSKI & KUBIAK, *ibid.*), and from elsewhere undoubtedly show the early date of the African-Eurasian connection.

After our earlier paper (ANTUNES, 1990), better magnetostratigraphic, Sr dating and foraminifera data allow us to ascertain that *Gomphotherium* was common in the Lower Tagus basin near Lisbon at about 17 Ma, and that no remains at all are known in 4 earlier sites with mammals at about 21 Ma - even if proboscidean remains would have been relatively easy to detect where other rather large (*i.e.* Anthracotheres) to small mammals were found. Proboscidean first immigration took place there sometime prior to 17 and later than about 21 Ma . This is not at all uncompatible with the above referred data

THE CROCODILIAN NEOGENE DISTRIBUTION IN EUROPE

Gavialis and *Tomistoma* general distribution is shown (fig.2).

Crocodilian neogene distribution in Europe as presented by FRANCO (1991, p. 56, fig. 5) comprises *Diplocynodon, Crocodylus* and *Tomistoma*. However



Early to Lower Miocene

Middle to early Upper Miocene

Fig. 2 — General distribution of Crocodylia (Sebecosuchians not included).
Vertical bars, Crocodylinae; open circles, *Tomistoma*, including *«Gavialosuchus»*; triangle, *Euthecodon* (only in Africa); +, Gavialidae; oblique bars, Alligatorinae; full circles, *Diplocynodon*. Some migration pathways for *Tomistoma* and *Gavialis* are shown

this may be misleading since it suggests that the presence of *Crocodylus* is as warranted as that of the two other genera. No evidence of it is presented by FRANCO (ibid.). As far as we can ascertain, there is but a single reference for Europe, that of the miocene *Crocodylus bambolii* (RISTORI, 1890, according to STEEL, 1973, p. 67). Formerly, crocodilian material (often very poor) was commonly reported to *Crocodylus* without adequate proof; C. *bambolii* is «Represented by the remains of more than one animal, including very imperfect skull and jaw material, post-cranial fragments and scutes» (...) «possibly ancestral to *C. niloticus*» (STEEL, ibid.). The last statement is indeed astonishing regarding the poor quality of the material, we cannot see any valid reason to ascribe it to *Crocodylus*, much less to recognize some kind of phyletic relationship to *C. niloticus*. The distinction from *Diplocynodon* (well known in Miocene beds not so far away, i.e. in Austria and France) should have been made clear. It may thus be concluded that these are very weak grounds to demonstrate the presence of *Crocodylus* in the european Neogene.

Still another point is of interest. *Gavialis gangeticus* and *Tomistoma schlegeli* have a disjointed distribution. Both seem to be essentially fish-eaters, even if they may eat other food as available. They could thus be potential competitors.

The situation was different in Europe. An evolutive trend towards larger, more robust-teethed and less longirostrine Tomistomines (as *Tomistoma lusitanica*) resulted in animals adapted to different ecological niches. That maybe minimized competition. They coexisted with *Gavialis*. The latter would probably remain essentially fish-eaters; while these Tomistomines would be more eclectic predators. The last possibility matches equally well with the lack in Europe of Miocene *Crocodylus*, which could be competitors for larger prey.

The poorly documented presence of a rather small Alligatorine as *Diplocynodon* does change nothing about these views. *Diplocynodon* apparently lived inland in less rich but also less-competitive environments that had not been colonized by powerful large river and littoral dwellers as *Gavialis* and the very large *Tomistoma.*

There is no evidence of an african origin for the western Europe crocodilians: Lower Miocene faunas from Egypt and Lybia include *Crocodylus lloydi*, *Tomistoma dowsoni*, a *Gavialis*, and the very peculiar *Euthecodon arambourgi* (GINSBURG & BUFFETAUT, 1978). The gavial material does not allow accurate comparisons with European specimens, and the affinities of *Tomistoma dowsoni* in regard to the European forms should be cleared. The african *Gavialis* and *T. dowsoni* are therefore not yet very useful for comparison. On the contrary, none of the unmistakably African forms as *Crocodylus lloydi* (or any other species of the same genus) or the easily recognizable *Euthecodon* (see GINSBURG & BUFFETAUT, 1978) ever occurred in Europe.

An Asian source for the *Gavialis* and *Tomistoma* immigration into western Europe is much more probable. After its apogee until lower Middle Miocene, *Gavialis* became successively extinct. It still survived in the Upper Miocene in Iraq (BUFFETAUT & THOMAS, 1981).

FOSSIL CROCODILIANS AS CLIMATE INDICATORS — MIOCENE GAVIALS AND TOMISTOMINES IN WESTERN EUROPE

Crocodilians are indicators of warm and humid environments. Among extant forms even the seemingly more tolerant to less warm situations (as some alligatorines) have minimum thermic requirements of *ca.* 10 degrees C. during the coldest weather conditions. Different situations aroused according to the different requirements of the concerned species.

Other crocodilians are still less tolerant. *Tomistoma schlegeli*, the «false gavial» or «Sunda gavial» lives in the Malayan Peninsula, Sumatra and Borneo; *Gavialis gangeticus*, the gharial, lives in river systems in India and Burma; it occurs in lake Chilka which sometimes contains mixed sea and fresh water. All known evidence about fossil representatives points out equally to tropical environments.

Migration of *Tomistoma* and *Gavialis* into the Lower Tagus basin area occurred at about 21 Ma, most probably not before. Climate was a leading factor. Only it can explain optimal conditions and maximum diversity for crocodilians. There has apparently been a global change from one climatic belt to another (see MADE, 1992), thus promoting migration of many land species, and not only minor climatic changes that could at best account for the migration of a few species into areas whose conditions became within the threshold of their requirements.

In spite of good agreement with most of the interpretations from MADE (*loc. cit.*), one of his statements puts some problems: «The translation of optima of suids, tragulids and anthracotheres shows that the idea of a slow global cooling superimposed on a relatively stable pattern of humidity as the motor of migrations during the Neogene is possible» (MADE, 1992, p. 35). Reality is indeed much more complex, with several warmings and coolings as well as humid and dry episodes during Neogene times, as the rich evidence from the Lisbon area clearly shows (ANTUNES & PAIS, 1993, fig. 4). The local extinction of the last anthracothere *Brachyodus onoideus* may instead have been a consequence of (a) a dryness event a little after 17 My, and (b) to subsequent destruction of the suitable habitats for these semiaquatic mammals owing to the rather sudden flooding related to the late Burdigalian (about 16.7 My) transgression.

Shortly after the crocodilians local apogee, dryness led to crocodilian rarefaction and apparently to the extinction of *Gavialis*, which is unknown there after ≈15.7 My. Later cooling may have been unfavourable to the crocodilians as a whole and specially to *Gavialis*. Moderate warming in the early Upper Miocene could have restablished adequate termal conditions, but this was hampered by dryness. This may explain the scant evidence of the last (at ≈ 10.4 My) crocodilians *(Tomistoma,? Diplocynodon)* in the concerned region.

Western Europe miocene *Gavialis* and *Tomistoma* are excellent indicators of the tropical conditions that prevailed until the lower Middle Miocene in Portugal and probably in France too. This can be true for other european areas where (a) both *Tomistoma* and *Gavialis* were recorded, as in France: Loire basin (ANTUNES & GINSBURG (1989), probably the Rhône valley (DEPÉRET, 1887, pp. 244-245), and in Gers (BUFFETAUT *et al.*, 1984, and ANTUNES & GINSBURG, 1989, p. 90); or (b) *Tomistoma* only – as in Valencia and Catalonia (Spain) (BATALLER, 1956, p. 26; BADÍA, 1969, p. 33); Malta and Gozzo; Italy (Sardinia and elsewhere); Austria (Eggenburg); Yugoslavia (Serbia) (STEEL, 1973, *ibid.*); and at Pinczów, Poland (ANTUNES in MLYNARSKI, 1984, pp. 134- 135).

CONCLUSIONS

1. Some crocodilian dental (and other) remnants were studied again; they can definitely be ascribed to an undeterminate species of *Gavialis*.

2. *Gavialis* first appearance in the Lower Tagus basin area is placed at the lower part of the II local stratigraphic unit at about 21 Ma, and is more or less synchronous with that of *Tomistoma. Tomistoma* and *Gavialis* immigration seems to precede a little that of the Proboscideans (Gomphothere datum); immigration from Asia may have begun sometime before the closure of the eastern Tethys and subsequent humid climate conditions at *ca.* 20 Ma. There is no evidence of any immigration from Africa.

3. Both *Gavialis* and *Tomistoma* (specially the latter) are common in IVb and Va (late Burdigalian) and lower Vb (Langhian) units; *Gavialis* was never collected in higher beds in this region, whereas *Tomistoma* (represented but by a single individual) reappears in the early Tortonian VIIa. A list of localities is given.

4. The miocene crocodilian fauna in Portugal and in western Europe as well comprised a gharial, *Gavialis* sp.; *Tomistoma lusitanica* or closely related forms; and a relict from Paleogene, *Diplocynodon* sp .

5. *Gavialis* geographic distribution has then been wide in Europe, even if apparently surpassed by that of *Tomistoma,* which has spread to most of this continent.

6. *Gavialis* and *Tomistoma* coexisted extensively in large river, estuarine or even littoral areas, owing especially to differing ecological niches; the former were specialized fish-eaters, whereas robust-teethed *Tomistoma* could thrive on larger prey, moreover without competition from *Crocodylus*.

7. As *Gavialis* and *Tomistoma* are typical warm stenotherm forms; their miocene representatives are good indicators of the tropical conditions that prevailed in Portugal and probably elsewhere in areas where both genera were present since the Lower Miocene until the early Middle Miocene.

8. The apogee of such excellent indicators corroborates the rich evidence yielded by the Lower Tagus basin of a climate optimum in the late Lower Miocene; and to conditions still more or less favourable in the early Middle Miocene, even if this region became drier.

9. The spectacular demise that followed can be correlated to aridity, responsible for the rarefaction of crocodilians and ultimate regional extinction of *Gavialis*. This rather arid episode has been followed by a temperature decrease that is evident for Serravallian times. Nevertheless, relict *Tomistoma* populations survived there until the early Tortonian, or reappeared by immigration from not so far away refuge areas. No crocodilians are known later.

10. Migration to North America could be possible for good swimmers that eventually ventured into the sea: *Tomistoma americana* (Sellards), from the Upper Miocene or Pliocene of Florida, may have arisen from emigration under the stress of unfavourable conditions of *Tomistoma lusitanica* stocks, followed by speciation that led to a further step towards heavily built and less long-snouted Tomistomines. This hypothesis (ANTUNES, 1961, pp. 64-66) is compatible with our present state of knowledge. The apparently sooner extinction of *Gavialis* in western Europe may have prevented gharials to do likewise.

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Gavialis gangeticus and *Tomistoma schlegeli* skulls used for comparison purposes were provided by the Laboratoire d'Anatomie Comparée from the Muséum national d'Histoire naturelle, Paris.

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REFERENCES

ANTUNES, M.T. (1961) — *Tomistoma lusitanica*, Crocodilien du Miocène du Portugal. *Revista Fac. Ciênc. Lisboa*, 2.ª série-C - IX (fasc. 1.°), pp. 3-88, pl. I-XII.

—— (1987) — Affinities and Taxinomical Status of Miocene Longirostrine Crocodilians from Western Europe with Remarks on Phylogeny, Paleoecology and Distribution. *Comun. Serv. Geol. Portugal*, 1987, t. 73, fasc. 1/2, pp. 49-58.

ANTUNES, M.T. *in* MLYNARSKI, M. (1984) — Notes on the amphibian and reptilian fauna of the Polish Miocene. *ACTA ZOOL. CRACOV.*, 27, 8, pp. 127-148 [ANTUNES, M.T. - Order *Crocodylia*, pp. 134-135]. Kraków.

ANTUNES, M.T.; FONSECA, B. & ROCHA, R. (1973) — NOTES SUR LA GÉOLOGIE ET LA PALÉONTOLOGIE DU MIOCÈNE DE LISBONNE / XII - Coupe de l'Avenida Paulo VI, Lumiar: Stratigraphie et Paléontologie / Conclusions générales. *Revista da Faculdade de Ciências de Lisboa*, 2.ª série C - vol. XVII, fasc. 2.°, pp. 459-514. Lisboa.

ANTUNES, M.T. & GINSBURG, L. (1989) — Les Crocodiliens des faluns miocènes de l'Anjou. *Bull. Mus. natn. Hist. nat.*, Paris, 4.ᵉ sér., 11, 1989, section C, n.° 2, pp. 79-99, pl. I-III.

ANTUNES, M.T.; JONET, S. & NASCIMENTO, A. (1981) — Vertébrés (Crocodiliens, Poissons) du Miocène marin de l'Algarve. *Ciências da Terra (UNL)*, Lisboa, n.° 6, pp. 9-38, pl. I-V.

ANTUNES, M.T. & MEIN, P. (1981) — Vertébrés du Miocène moyen de Amor (Leiria) / importance stratigraphique. *Ciências da Terra (UNL)*, Lisboa, n.° 6, pp. 169-188, pl. I.

—— (1986) — Petits mammifères du Burdigalien inférieur (Universidade Católica, Avenida do Uruguay). *Ciências da Terra (UNL)*, Lisboa, n.° 8, pp. 123-138, pl. I.

—— (1992) — Les plus anciens mammifères terrestres du Miocène marin de Lisbonne - le gisement du km 10. *Ciências da Terra (UNL)*, Lisboa, n.° 11, pp. 127-140.

ANTUNES, M.T. & PAIS, J. (1993) — The Neogene of Portugal. *Ciências da Terra (UNL)*, Lisboa n.° 12, pp. 7-22.

BADÍA, S.C. (1969) — Litoestratigrafía y paleontología de unas arenas del Mioceno de Sant Pere de Ribes. (Garraf, Barcelona). *Acta Geológica Hispánica*, t. IV (1969), n.° 2, pp. 29-34.

BATALLER, J.R. (1956) — Contribución al conocimiento de los Vertebrados terciarios de España. *CURSILLOS Y CONFERENCIAS*, Fasc. III, pp. 11-28, Instituto «Lucas Mallada» de Investigaciones Geologicas, Madrid. [Identified as *Tursiops*, a Cetacean].

BERNOR, R.L.; SEN, S.; & THOMAS, H. (1987) — A consideration of some major topics concerning Old World Miocene mammalian chronology, migrations and paleogeography. *Geobios* 20 (4), pp. 431-439. Lyon.

BUFFETAUT, E.; CROUZEL, F.; JUILLARD, F. & STIGLIANI, F. (1984) — Le Crocodilien longirostre *Gavialosuchus* dans le Miocène moyen de Polastron (Gers, France). *Geobios*, Lyon, 17 (1), pp. 113-117.

BUFFETAUT, E. & THOMAS H. (1981) — Un Gavial dans le Miocène supérieur d'Irak (Jebel Hamrin, Formation Bakhtiari). *C.R. somm. Soc. géol. Fr.*, 1981, fasc. 5-6, pp. 175-178.

DEPÉRET, CH. (1887) — Recherches sur la succession des faunes de Vertébrés miocènes de la vallée du Rhône. *Archives du Muséum d'Histoire naturelle de Lyon*, T. IV. 269 pp., 25 pl.

FRANCO, F. (1991) — Crocodilian Reptiles and the History of Tethys. *Saito Ho-on Kai Spec. Pub.*, n.° 3, 1991, pp. 53-58 *(Proceedings of Shallow Tethys 3, Sendai, 1990).*

GINSBURG, L. & BUFFETAUT, E. (1978) — *Euthecodon arambourgi* n.sp., et l'évolution du genre *Euthecodon*, crocodilien du Néogène d'Afrique. *Géologie Méditerranéenne*. Tome V, n.° 2, 1978, pp. 291-302, pl. I-II.

JONET, S. (1981) — Vertébrés remaniés dans l'Helvétien V-c des environs de Lisbonne. *Comun. Serv. Geol. Portugal*, 1981, t. 67, fasc. 1, pp. 47-51, pl. I.

KÄLIN, J. (1955) — Crocodilia, *in* Piveteau, J. (ed.), *Traité de Paléontologie*, t. V, pp. 695-784. Masson & Cie. Paris.

KOWALSKI, K. & KUBIAK, H. (1993) — *Gomphotherium angustidens* (Cuvier, 1806) *(Proboscidea, Mammalia)* from the Miocene of Belchatów and the Proboscidean Datum in Poland. *Acta zool. cracov.*, 36 (2), pp. 275-280, Krakow.

LANGSTON W. (1965) — Fossil crocodilians from Colombia and the Cenozoic history of the Crocodylia in South America. *Univ. Calif. Pub. Geol. Sci.*, 52, 157 pp., 5 pl.

MADE, J. VAN DER (1992) — Migrations and climate. *Courier Forsch.-Inst. Senckenberg*, 153, pp. 27-37, Frankfurt a. M..

PATNAIK, R. & SCHLEICH, H.H. (1993) — Fossil crocodile remains from the Upper Siwaliks of India. *Mitt. Bayer. Staatsslg. Paläont. hist. Geol.*, 33, pp. 91- 117, pl. I-VIII, München.

STEEL, R (1973) — *Encyclopedia of Paleoherpetology*. Ed. by Professor Dr. Oskar Kuhn. Part 16. *Crocodylia*. Gustav Fischer Verlag. Stuttgart. Portland-USA. 116 pp.

ZBYSZEWSKI, G. (1949) — Les Vertébrés du Burdigalien supérieur de Lisbonne. *Mem. Serv. Geol. Portugal*, Lisboa, 77 pp., 22 pl.

PLATE

PLATE I

Crocodilian teeth: comparisons between fossils from stratigraphic local units IV-b (upper Burdigalian, late Lower Miocene, *ca.* 17 Ma), V-a (uppermost Burdigalian, *ca.* 16.5 Ma), and V-b (Langhian, early Middle Miocene, *ca.* 15.5 Ma) - Lower Tagus basin near Lisbon, Portugal - and the extant Gharial from Ganges river, India.

Photographs: João Pais. Bar scales: 1 centimeter.

Gavialis sp.

Fig. 1 - Tooth (adult individual), rear (distal) view showing distinct striation (cr, crest). Loc.: Quinta das Flamengas, near Chelas; unit V-b. Collection: Instituto Geológico e Mineiro museum, Lisboa; number 4789.

Fig. 2 - Tooth (adult individual), rear (distal) view. In an area (upper left of the figure) where enamel was abraded off the underlying dentine is exposed; facets are clearly distinct. Loc.: Quinta das Flamengas. Coll.: Inst. Geol. Min., n.° 4794.

Fig. 3 - Tooth (adult individual), anterior (mesial) view. This specimen (like other ones) underwent some transport in coarse sands; hence enamel is somewhat abraded. There are some fine longitudinal cracks, not to be confused with striae and facets. Loc.: Quinta das Flamengas. Coll.: Inst. Geol. Min., n.° 4794.

Fig. 4 - Tooth (adult individual), external view, showing the strongly striated and facet--like aspect of the enamel surface. Loc.: Quinta das Pedreiras, near Lumiar, Lisbon; unit V-a. Coll.: M. Telles Antunes, Lisboa. **Scale: figures 1-4, x 1.2**.

Fig. 5 - Distal tooth, rear (distal) view; strongly striated, facetted enamel surface. Loc.: Quinta das Flamengas. Coll.: Inst. Geol. Min., n.° 4794.

Fig. 6 - Tooth from a young individual. anterior (mesial) view. As in the preceding specimens, the general aspect is (even more) slender and slightly curve. Loc.: Quinta das Flamengas. Coll.: Inst. Geol. Min., n.° 4794. **Scale: figures 5-6, x 1.4**.

Gavialis gangeticus (Gmelin, 1789)

Fig. 7 - Adult, large sized male 12th left maxillary tooth, anterior (mesial) view; to show longitudinal striae. Coll.: Muséum national d'Histoire naturelle, Paris.

Fig. 8 - The same tooth, rear (distal) view. **Scale: figures 7-8, x 1.1.**

Fig. 9 - Immature specimen, sex unknown Left view of the anterior part of the rostrum showing teeth from the premaxillaries (Pmx), maxillaries (Mx) and dentary bones (D). Coll.: M. Telles Antunes. **Scale x 0.6.**

Fig. 10 - The same specimen, detail to show the 3d to 10th left maxillaty teeth, and the 7th to 14th dentaty teeth. Cutting crests and the facetted aspect are distinct. **Scale: ca. x 0.9.**

Tomistoma lusitanica (Vianna & Moraes, 1945)

Fig. 11 - Tooth (adult individual), external view, enamel with thin, longitudinal cracks, otherwise nearly smooth; more massive, blunt and curved shape. Loc.: Quinta do Narigão, near Avenida Gago Coutinho, Lisbon; unit IV-b. Coll.: M. Telles Antunes.

Fig. 12 - Tooth (adult individual), rear (distal) view; somewhat cracked but otherwise nearly smooth enamel surface. Loc.: Quinta do Narigão. Coll.: M. Telles Antunes. **Scale: figures 11-12, x 0.9**.

Fig. 13 - Distal tooth from an (?) immature individual, anterior (mesial) view, to show the nearly smooth *(post mortem* or post loss) longitudinally cracked enamel surface). Coll.: Inst. Geol. Min., n.° 4780. **Scale x 1.5**.

PLATE I


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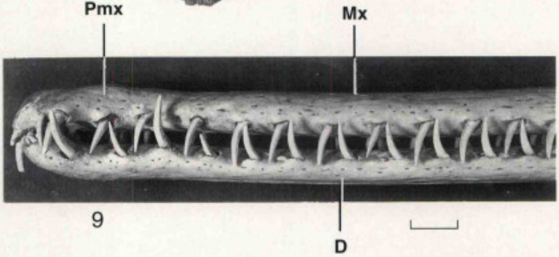

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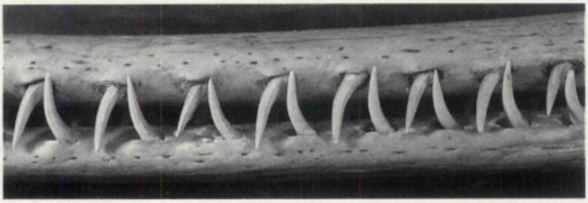
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