



**Huge Miocene Crocodilians From Western Europe:
Predation, Comparisons with the “False Gharial” and Size
Crocodilos Miocênicos de Grande Tamanho do
Oeste Europeu: Predação, Analogias com “Falsos Gaviais” e Tamanho**

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Resumo

Dentes de mastodonte mordidos, inéditos, demonstram que a predação pelos enormes *Tomistoma lusitanica*, que existiram na região de Lisboa e Península de Setúbal do Miocénico inferior ao início do superior, incluía os maiores mamíferos terrestres de então: os mastodontes *Gomphotherium angustidens*, mesmo adultos e senis, um dos quais teria, em estimativa não rigorosa, uns 50 anos à morte.

São discutidos efeitos de dentadas, bem como os caracteres de impressões devidas ao impacte, intenso atrito e eventual esmagamento. A dentição de indivíduos de porte muito grande desempenharia papel de prensão e, também, de verdadeiros moinhos de dentes para triturar peças duras. Efeitos de esmagamento, não derivado de causas tectónicas, foram também observados num suídeo.

Os resultados podem significar que a razão básica da ictiofagia prevalecente nos “falsos-gaviais” actuais, *Tomistoma schlegelii*, pode estar relacionada com a pressão humana que os inibe de atingirem o máximo tamanho possível e, por conseguinte, de capturarem presas maiores.

É realçada a importância da imigração a partir da Ásia e das afinidades biogeográficas, a qual parece óbvia dada a presença simultânea de *Tomistoma* e *Gavialis* no extremo ocidental da Eurásia. Dados muito diferentes acerca da África do Norte não contradizem este ponto de vista.

Extrapolações baseadas nos falsos-gaviais miocénicos contribuem para melhor conhecimento da espécie actual. As semelhanças são ainda maiores tendo em conta os caracteres cranianos de *T. lusitanica* comparativamente ao maior crânio conhecido dentre todas as espécies actuais, o de um *T. schlegelii*.

A estimativa do comprimento total de *Tomistoma lusitanica*, que algo excedia os 8 metros, confirma que se trata de animais gigantes, predadores de topo capazes de atacar presas de porte muito grande. Também aproveitavam cadáveres.

O porte máximo parece ter atingido o de *Ramphosuchus crassidens* dos Siwaliks, há muito considerado como o *nec plus ultra*, em tamanho, dentre todos os crocodilos do Neogénico.

Tomistoma lusitanica foi um dos maiores crocodilos de sempre, e mesmo o maior réptil do ocidente europeu após a Era dos dinossauros.

Palavras-chave: *Tomistoma lusitanica*; Miocénico; Predação; gonfotérios; *Tomistoma schlegelii*

Abstract

As shown here on the basis of bitten teeth, the diet of the huge, lower to early upper Miocene *Tomistoma lusitanica* included some of the largest contemporaneous, terrestrial mammals, including adult or senile gomphotheres (*Gomphotherium angustidens*). One of the latter would be, in a rough estimate, about 50 years old at death. Bite impressions are discussed, including marks resulting from impact, intense attrition and eventual crushing. The teeth of very large-sized tomistomines would have a not restricted to prehension role, they also acted as true cone devices for crushing hard parts. Crushing - non-tectonic effects - have also been observed on a suid fossil.

The so far obtained results may point out that the very basic reason of the extant false-gharial, *Tomistoma schlegelii*'s prevailing ichthyophagy may be human pressure that prevents them to attain their possible maximum size, and hence to capture larger prey.

The importance of immigration from Asia and biogeographic affinities is stressed. This seems obvious after the simultaneous presence of *Tomistoma* and *Gavialis* in westernmost Eurasia. Different data from North Africa do not contradict these views.

Extrapolations based on the Miocene false-gharials contribute to a better understanding of the surviving species. Similarity is even greater if account is taken of the closer morphological cranial features between the fossil forms under study and the largest known skull of all extant crocodilians, a *T. schlegelii*.

Estimations of *Tomistoma lusitanica*'s overall length, somewhat in excess of 8 meters, confirm this form attained a giant size. These top predators undoubtedly preyed or scavenged upon very large prey. They also scavenged on corpses.

Tomistoma lusitanica undoubtedly was one of the largest crocodilians that ever existed and whose maximum dimensions seem to have attained those of the Siwaliks' *Ramphosuchus crassidens*, long regarded as the Neogene *nec plus ultra* in size.

Tomistoma lusitanica was one of the largest crocodilians from all times, and even the largest western Eurasia reptile after the age of the dinosaurs.

Keywords: *Tomistoma lusitanica*; Miocene; Predation; gomphotheres; *Tomistoma schlegelii*

1 Introduction

Tomistomine crocodylians are represented by the “false gharial” *Tomistoma schlegelii* (Müller, 1843). Small populations survive in Malaysia and Indonesia (Borneo, Sumatra), but the species seems extinct elsewhere in Southeast Asia. It occurred in Southern China in historical times.

A long snout is one of *Tomistoma*'s most conspicuous characters, hence some similarity to another longirostrine crocodylian, the Indian gharial *Gavialis gangeticus*.

Long snout is related to large supratemporal openings and with the development of the *musculi temporalia*, partly lodged in each of the same openings. Temporal muscles enable fast lateral head movements. With the mouth partly open and numerous teeth, such a movement becomes a terrible trap for fish. It has therefore been accepted that both *Gavialis* and *Tomistoma* are mainly ichthyophagous. Phylogeny has been discussed, mainly in order to clarify the supposedly close or not so close affinities between these two genera.

The Tomistomine crocodylians had a much broader distribution as they reached Europe, Africa and even America. The European ones probably arrived from Asia by Upper Oligocene times (Antunes & Cahuzac, 1999). During the Miocene, large-sized ones have been found from Poland to Austria, the former Yugoslavia, Italy, Malta, France, Spain including Balears islands (Mas & Antunes, 2008), and Portugal.

In Portugal, *Tomistoma lusitanica*'s teeth and bones occur since lower to early middle Miocene in Algarve and mainly in the Lisbon basin. No remnants have been found in later beds with the sole exception of one individual from lower Tortonian. Tomistomines were the predominant crocodylians over scarce gharials and *Diplocynodon* relicts (Antunes, 1994). A skull and mandible were described (Vianna & Moraes, 1942; version in French, 1945) and reported to a new variety *lusitanica* of *Gavialosuchus americanus* (Sellards, 1915). This was revised taking also into account a new complete specimen (Antunes, 1961), the former being taken as holotype of *Tomistoma lusitanica* (Vianna & Moraes); see Antunes (1987), Antunes & Ginsburg (1989).

The success of these Tomistomines is related to several factors as a thermal optimum along with excellent swimming capacities. Remnants occur in large river, estuarine or coastal sea facies.

What kinds of prey would these animals take? Let us pose that question under the light of some hitherto unpublished paleontological hints as well as comparisons with data on extant species.

2 Material and Methods

All the specimens described here were collected by the author during his field researches carried on since 1957 in Lisbon's neighbourhood. Then, there were many sand pits commercially exploited for the building industry, mostly in upper Lower Miocene and lower Middle Miocene units. In this context, no organized palaeontological excavation could be done. Vertebrate fossils were found dispersed in sands. We have done what indeed was possible: to buy the specimens secured by the sandpits' workers.

Exploitation was often very risky; accidents were common, and several workers died. This situation therefore justified Government's decision in 1967 to cease all exploitations of this kind. This rich source of palaeontological material ended then. Material became part of some collections: the most meaningful one of large-sized vertebrates, comprising a large number of proboscideans (Gomphotheres and a few Deinotheres), rhinoceroses and others, is that of the Geological Museum of the former Geological Survey in Lisbon, another (mostly including specimens collected by us) being that of the Lisbon University Natural History and Science Museum.

3 Tomistomines as Predators

An interesting coprolite from Quinta das Pedreiras near Lumiar, Lisbon (uppermost lower Miocene, ca. 17.5 Ma) contains an undigested fish vertebra. It may be ascribed to a locally common (albeit with a very broad geographic distribution) teleostean apparently of the same genus as the giant Nile perch, *Lates niloticus* (Antunes & Gaudant, 2003). A mammalian predator would completely digest it. By comparison with *L. niloticus*, the fossil vertebra is from a specimen

about 5 kg in weight. Predation by Tomistomine crocodilians would be expected.

As is usually referred in the literature, the “false-gharial” thrives mostly on fishes. Its maximum length has been stated as attaining at least 4 meters (Ross, 1990: 72), but these viewpoints are changing.

Indeed the largest known modern crocodilian skull, kept in the Natural History Museum, London, is from *Tomistoma schlegelii* (Internet, Darren Naish, 2008). Curiously enough, this giant *T. schlegelii* skull looks much similar in shape and proportions as the *T. lusitanica* ones. Although we cannot be sure how measurements were taken, it is possible to estimate its total length: the skull length vs. total body length ratio is about 1:7, as commonly recognised even if this relationship is not accurate, especially for very large individuals. Hence the corresponding total length would be about 7 m. Furthermore, in the same blog the author states “Based on these giant skulls, we can be fairly confident that *Tomistoma* exceeds 6 m in total length and is one of the largest extant crocodilians”.

All this suggests the total length of the individuals represented by the two complete *Tomistoma lusitanica* skulls (see Table 1) would attain 6.5 to slightly in excess of 7 metres. As I will show, additional mandibular fragments point out to a still much larger individual.

If comparisons with the indo-pacific crocodile, *Crocodylus porosus*, are valid, weight could attain about 1 ton for very large individuals at least 7 m long.

Localities →	Quinta da Farinheira	Quinta dos Durões
Length from the tip of the snout to the rearmost point of the occipital condyle	1037	996
Length from the tip of the snout to the distal border of the cranial table	930	932

Table 1 *Tomistoma lusitanica*, measurements (in mm) of the two complete skulls so far known: the holotype from Quinta da Farinheira near Chelas/ Lisbon (Langhian, ca. 15.5 Ma) and another from Quinta dos Durões near Mutela (lower Tortonian, ca. 11.6 Ma) (Antunes, 1961:41)

On the other hand, crocodilians diet widely varies with ontogeny (Ross, 1990: 76-84). Shortly after hatching, small individuals take worms, insects, etc., while larger ones prey on fishes and other small vertebrates, older adults being able to attack large living mammals or corpses.

Preying on monkeys and deer has been recorded for *T. schlegelii*, but until recently there was no record of attacks on humans. According to Orangutan Foundation Blog, a man disappeared in a creek December 31st 2008 near Pondok Ambung Research Station in Kalimantan (Indonesian Borneo). Seventeen hours later, a large, barely reaching 5 metres in length, probably more than 50 years old female “false Gharial” was killed there; it contained remains from the missing person. Authors wonder how a “false gharial” could survive for so long in an area under strong human pressure.

Larger size enables *T. schlegelii* to hunt larger prey. This was the case for the even larger *Tomistoma lusitanica*.

4 A Predator Becomes a Prey

A high ranking predator can become a prey. This is obvious as far as corpse remnants - skull and mandible in anatomic connexion, vertebrae and limb bones – from Quinta dos Durões at Mutela near Almada are concerned (Antunes, 1961)/age: lower Upper Miocene/ lower Tortonian, ca. 11.6 Ma [all ages in Ma according to available data from the CICEGE, Faculdade de Ciências e Tecnologia/ Universidade Nova de Lisboa].

The Mutela mandible was crushed on its right side, this kind of fossilization being discussed in a next chapter. Only a violent blow, enough as *causa mortis*, could result into spectacular fracturing of such a large and very robust structure. Which predator could have produced it?

One, first hypothesis points out to another very large individual from the same species as a result of a fight between competing males during the breeding season. Intense bleeding could lead to death as a consequence of aggression, followed by drowning of the disabled animal.

Who could apply such a huge force in a marine environment? Three strong candidates seem possible:

(a) another very large crocodilian, probably from the same species;

(b) the giant shark *Carcharocles megalodon* which was frequent nearby;

(c) large odontocete Cetaceans akin of the extant *Physeter catodon* or of the killer-whale *Orcinus orca*, some being also present.

As no evidence supports (b) and (c), (a) is almost certain.

Sinking to the bottom, the corpse was attacked by smaller predators. Indeed, a sand shark *Odontaspis taurus* tooth was found in the gangue very close by the upper surface of the skull. Bones served as a base and shelter to a lot of invertebrates.

All in all, a powerful predator was killed by another of its own kind only to become a scavengers' prey.

5 New Evidence

When revising gomphothere's teeth, we noticed: y sample (A) a *Gomphotherium angustidens* tooth collected by us about 1963 at the Olival da Susana sandpit, near Charneca do Lumiar, in sands from the Vb division of the Lisbon Miocene series/“Areias do Vale de Chelas com *Ostrea crassissima*”, Langhian, ca. 15.5 Ma - a site that disappeared as a result of Lisbon airport main runway's enlargement, and, sample (B) a gomphothere tooth fragment collected by us the same year or a little later at the nearby Quinta da Silvéria sandpit; stratigraphic unit and age are the same. Both (A) and (B) belong to our private collection.

Additional, partly non-gomphothere specimens, will be referred.

Further comparisons were made to a mastodon left second lower molar y sample (C) from the LNEG Geological Museum in Lisbon that has been partly crushed while still fresh and shows some impressions that most probably can be ascribed to crocodilians; previous taphonomic studies and observations on modern material support this statement. The concerned molar was collected still longer ago at Vale Formoso de Baixo, near Marvila in marine beds from the VIc unit from Lisbon's Miocene series, upper Serravallian, ca. 12 Ma.

As far as occurrence in Serravallian marine beds is concerned, there are other, rare mastodon findings: an upper 1st molar from the same VIc

unit at the former Mitra quarry; and a lower m3 fragment from the next underlying VIb unit, ca. 12.5 Ma (Cotter, 1904: 16-17; Roman, 1907, pl. IV, figs. 1, 1a, 1b, 2 and 2a, 3 and 3a; Zbyszewski in Bergounioux, Zbyszewski & Crouzel, 1953: 17-18), plus an undescribed fragment from Quinta do Prior Velho.

In their memoir, Bergounioux, Zbyszewski & Crouzel (1953) state:

- (p. 17), “L'horizon Vc n'a pas livré de Mammifères terrestres” [Jonet (1981: 49) reported otherwise a mastodon tooth fragment from a marine, Vc site at Portela de Sacavém (Langhian ca. 15 MA)].

- (p. 17), “VIb -” “cette formation, qui a livré vers sa base, un fragment de molaire de *T. angustidens*, trouvée ... en face de l'ancien couvent de Grilos. ... Un fragment de molaire de *T. angustidens* a été également recueilli, dans une sablière de Q.^{ta} do Prior Velho (Sacavém) probablement vers le sommet de la formation”.

- (p. 18) “VIc ... C'est le calcaire supérieur de la zone 2 qui a donné la dent de *Serridentinus* [that we also report to *Gomphotherium*] ..., ainsi que celle de *Trilophodon* trouvée à Quinta do Vale Formoso (250 m SO du signal géodésique de Desterro)”.

Indeed all but one of the so far known mastodon teeth from Serravallian beds seem devoid of the progressive, apomorph evolutionary characters that could be expected at those times. They do not present any meaningful size or other differences from homologous teeth from the Langhian localities and can be ascribed to the same taxon, i.e. *Gomphotherium angustidens*. This plus the presence of a marine gangue including mollusc casts that (C) still keeps (our direct observation) allow us to regard the concerned teeth as Langhian fossils that later were re-deposited in a marine environment. The status and interest of re-deposited terrestrial fossils in marine beds has been unrecognized, undervalued or just ignored.

Lastly, we will refer a probable bite crushing on an associated set of upper premolars (P2, P3) from the suid *Listriodon (Bunolistriodon) lockarti* that we collected by the same epoch at Quinta da Farinheira sand pit near Chelas, Langhian Vb (D).

6 Discussion

The concerned tooth is a left second lower molar y, sample (Figures 1 and 2). Full root development and abrasion point out to an adult yet not senile individual. The proximal root is missing; the corresponding fractures seem old and prior to fossilization. The distal root is nearly complete. Dental abrasion is severe, even on the cingulum tubercles.

Measurements are as follows (mm):

- maximum length, > 100.4 (it should be a little longer, since the mesial extremity lost some matter);
- maximum width, > 56.8 (there is loss of part of the enamel);
- maximum height from the tip of the distal root to the abraded by use, occlusal surface, 93.3.

This tooth shows bite marks. A gomphothere remnant with evidence of crocodylian bites is a rarity, but this could be expected: crocodylian attacks on elephant corpses have been shown (Ross, 1990, p. 90), an *Elephas* carcass being eaten by several *Crocodylus palustris*.

Bite marks are most clear on the internal side of the distal root. Sets of successive, spaced holes seem compatible with several bites from the same crocodylian. This indicates a dentition with no important size or pattern differences between teeth, as in a longirostrine crocodylian (Figure 4).

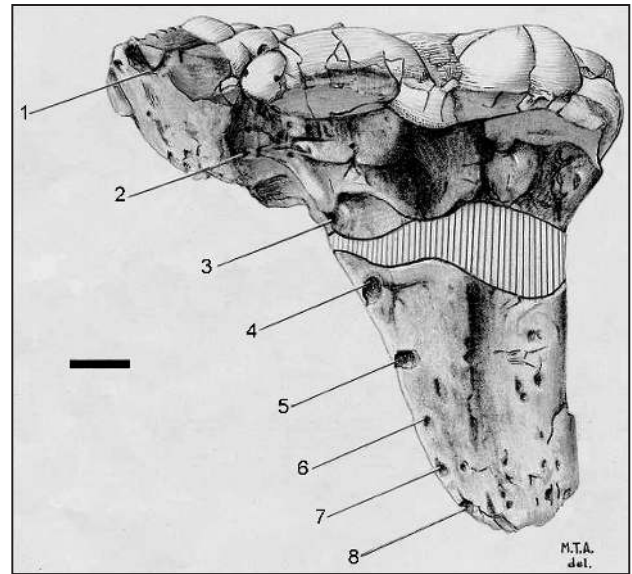


Figure 2 *Gomphotherium angustidens*, y sample A labial view. Scale: bar, 1 cm. An 8 teeth impacts' bite series (1 to 8) is shown (there are other, less complete ones). Intensive fracturing and enamel losses; underlying dentin, dark grey. Stripped area – plaster infill (but lingual side keeps all natural contacts, hence there is no deformation).

The two successive larger and best preserved ones do not present a regular, rounded outline; both show small, outside facing irregularities that may be interpreted as impressions produced by the pair of descendant crests that begin near the crocodylian tooth apex and fade towards the base (Figure 3).

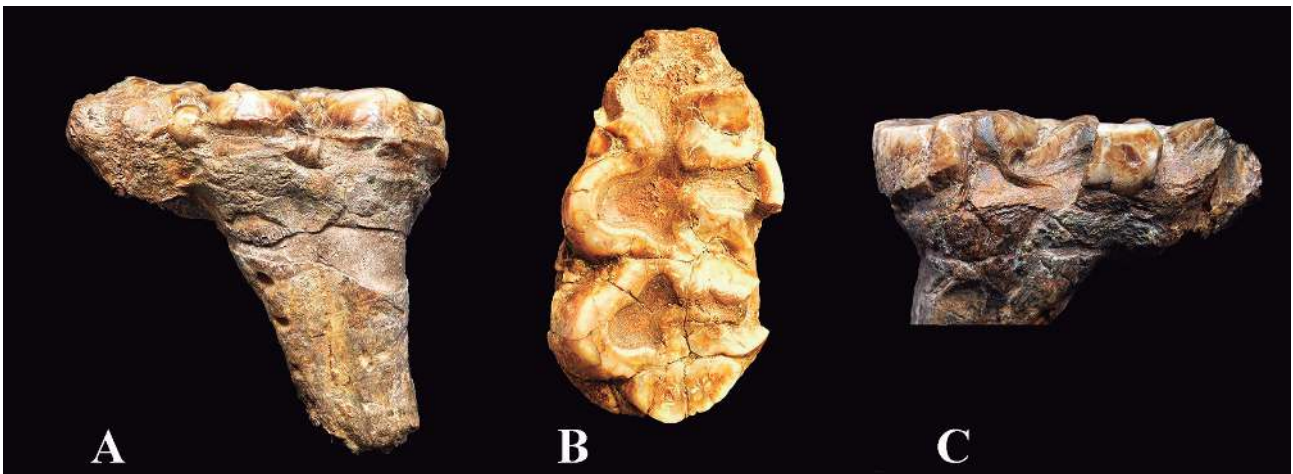


Figure 1 A. *Gomphotherium angustidens*, sample (A), left lower M2, labial view. Scale: maximum length, 100.4 mm. The specimen shows several crocodylian (cf. *Tomistoma lusitanica*) bite impressions, and especially a series of 8 ones; the impressions 4 and 5 preserve marks left by tooth crests (compare with impressions on plaster of mandibular teeth of the largest, giant specimen of *T. lusitanica* dealt with this paper). See Figure 2 (drawing) for more evidence. Intense fracturing. Enamel is shown white, lighter grey areas exposing dentine after enamel loss. Stripped area has been filled with plaster, but there is perfect contact on the (not shown) lingual side, hence the position is correct; B. The same, occlusal view; crown fractures are distinct; C. The same, labial view to show specially the main bite impressions (and other ones).



Figure 3 Two *Tomistoma lusitanica* isolated, near unused teeth to show the enamel longitudinal wrinkles and one crest in each side; wrinkles and crests produce impressions on hard parts when gliding. Same scale (fig. 3B, maximum dimension from the bottom to the point, 42.2 mm). Quinta das Pedreiras, Lisbon. Uppermost Burdigalian, late lower Miocene. M. T. Antunes collection.

The bite impressions apparently were produced as the beast tried to dilacerate tissues by shaking it with violence.

However, the whole set of teeth from a very large crocodilian is not used only for grasping prey and helping into tearing its body. It also could be used, as indeed it was, as a mechanical teeth or cone crushing machine as used for rock, concrete, ore and other hard materials.

The whole pattern is not easy to interpret. Impact points and impressions produced by sliding of the crocodilian's tooth on a slippery, quite flat enamel surface may be seen (Figure 3).

The near even pattern of teeth impact depressions suggest that those impressions cannot have been produced by premaxillary teeth, whose differences in size and in the spaces between them are more heterogeneous. It also is consistent with the need for a longirostrine crocodilian to bite a resistant part well inside the mouth where force is maximum, not with the end of the elongated rostrum. Hence we may admit those impressions were produced by the rear mandibular teeth, since the mandible is the only movable part of the head during biting. Of course, maxillary or premaxillary teeth could produce counter-imprints, even if probably less distinct.

Interpretation is difficult as there are superposed bites. The teeth sometimes glided on the surface, producing more than a single imprint. This task is even more complicated because teeth hit parts of the gomphothere tooth whose mechanical resistance is widely distinct. Enamel is much harder but may crack under pressure, while dentin and cement behaviour are different. Impact points on the enamel could often result into radiating fractures, gliding marks, displacement and ripping away of enamel fragments.

One of the bites comprises not less than eight teeth impacts (Figure 2), and further crocodilian teeth in the series may just have missed the target. Let us remark that some teeth may have produced minor effects or no effects at all if they were amidst their replacement process. Other bites resulted into vertical, strong stress accompanied by crushing, intense enamel fracturing, and loss of enamel chunks.

The large, strong and rather thick-teethed crocodilian most probably was a large *Tomistoma lusitanica* (see next chapter). No confusion is possible with a gharial, also present in the same area, nor with the rare and by far too small *Diplocynodon*.

Another specimen y, sample (B) (Figures 4 A,B,C and 5) also shows crocodilian bite marks. It is a fragment of one upper right third molar (M^3) from a senile *Gomphotherium angustidens*. It was incomplete when collected. The distal root is lacking.

The specimen consists of the third and fourth lochs, severely abraded by use (more heavily so on the lingual side), plus the talon.

The enamel cap retains small quantities of cement in depressions and shows on the labial side's surface some defects that may be regarded as hypoplasies. The remaining portion of dentine suffered severe losses of matter; its pattern somehow recalls the extraction of splint fragments from a flint nucleus to produce artefacts, as it was commonly done by ancient men.

The larger fracture surfaces show successive, alternating yellowish (thicker) and dark red (thinner) dentine growth bands. Such a feature does not seem to have been described and interpreted. A hypothesis to try to explain it is based on the evidence that growth proceeded at an uneven pace during the development

of the molar’s crown. We counted 15 to 16 bands, a small error being possible. Do these bands represent seasonal growth changes? If so, the M3 took at least about 16 years to conclude its growth. Of course, we cannot ascertain the approximate age when the last molars form in *Gomphotherium*, but a rough approach may be attained through comparison with extant elephants (Table 2).

Molar	Molar Appearance (years)	Molar loss (years)
D2	Birth	2
D3	Birth	6
D4	1	13-15
M1	6	28
M2	18	43
M3	30	>65

Table 2 Jugal teeth replacement in extant elephants, all produced by the first dental blade – D, milk teeth; M, molars

In the case of an elephant, we could estimate (with reserve, hence we underline it with ??) a time span of $15+16 \approx 31$ years until the M3 appearance, followed by abrasion by use that went along even until the piercing of the last loph’s enamel. This is really a very advanced abrasion stage, only attainable in a

senile individual. Difficulties in food chewing would imply starvation and death not long after.

Even if the abrasion pace was faster than in elephants, maybe the M3 was used for about 20 years after its appearance, and therefore the animal would be roughly about 50 years old at death. Crocodilian attack would have been possible either on a decrepit gomphothere, or on its dead body.

Detailed observation shows several impact points with dentine fracturing around and longitudinal losses of matter that seem to have been produced by intense attrition related to the displacement of a conical tooth. These are placed at intervals compatible with the arrangement of teeth in a crocodilian mandible (or maxilla), the impact points being at rather even spaces. Three corresponding impacts are recognizable. Around impact points there are small radial fractures. Dentine may break irregularly, but generally produces more or less curve, concave surfaces. These surfaces present longitudinal striae that seem to result from attrition by the surface of the teeth. In one case, the impression of the tooth crest is distinct (Figure 5, div.).

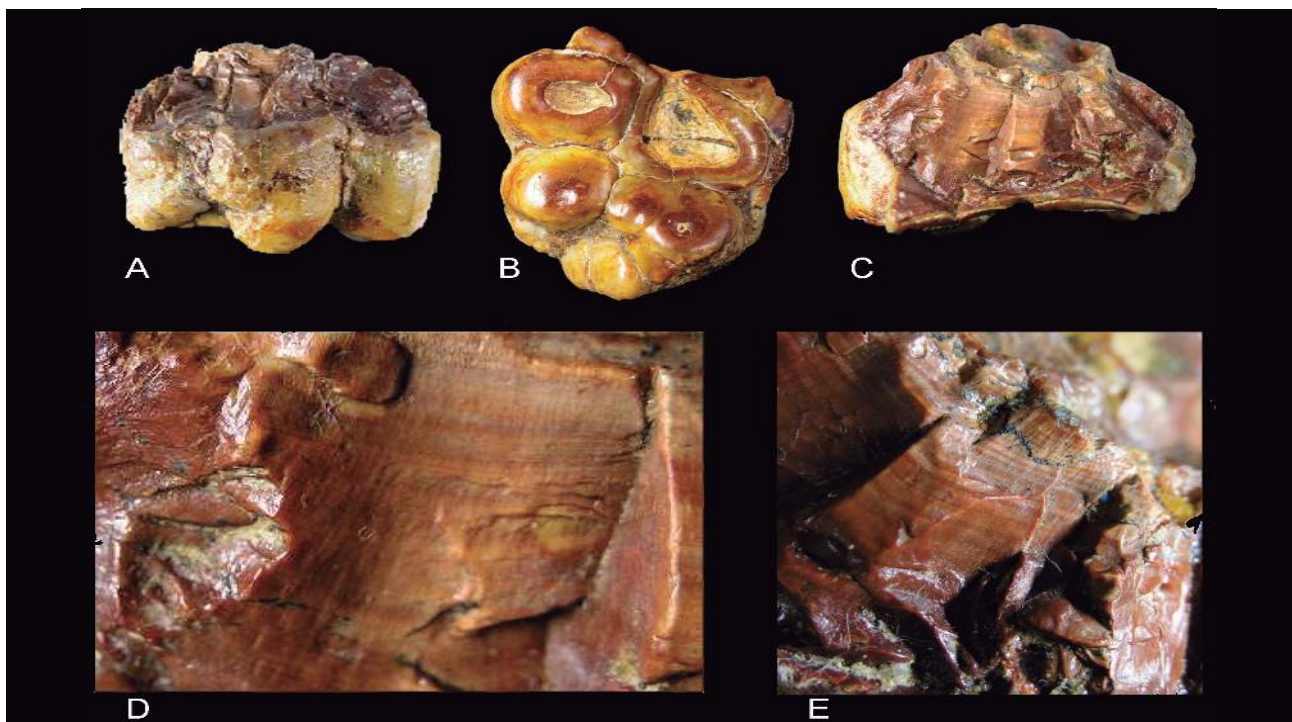


Figure 4 A. *Gomphotherium angustidens*, sample (B), Quinta da Silvéria sandpit, Vb unit, Langhian; M. Telles Antunes collection. Mesial view. Several crocodilian (cf. *Tomistoma lusitanica*) bite impressions; B. The same, occlusal view. Measurements as preserved: maximum length, 68.3 mm; maximum width, 63.2 mm; C. Idem, whole labial view; D. Idem, labial view, enlarged detail to show irregular, bitten, with longitudinal striae that can have resulted from attrition to the tooth wrinkled surface, mesial surface; & radial fracturing (to the left). Scale: approximately x 5; E. Enlarged detail to show concave surfaces (rounded section) produced by crocodilian teeth, distinct darker (thinner) and lighter (thicker) growth bands; a seemingly thin prismatic structure (upper center); an impression diverticule produced by a tooth’s crest of a gliding crocodilian tooth; and an tooth point impact hole (bottom center right). Scale: approx. x 2.5.

As far as we can recognize because distinction is much less obvious than in the specimen (A), two sets of imprints show the following spaces in millimetres between consecutive ones: 15.72 – 15.41; 18.35 – 18.38. Impact points describe in both sets a gentle rounded curve. Differences do not necessarily imply bites from different individuals since they may be related to different positions in the mandible or in the maxillaries.

The Vale Formoso specimen is a left mandibular M2. The specimen was referred as *Trilophodon* by Zbyszewski (Bergounioux, Zbyszewski & Crouzel, 1953: 18). Despite its special interest owing to its later geologic age, it was not dealt with in the paleontological chapter the same reference. This large memoir includes but an ambiguous reference that probably concerns it (Fig. H, “Schéma évolutif des mastodontes portugais, p.132): *Tr. angustidens* is indeed referred for the VIc unit.

We observed again (December 2011) the same specimen, N° 5447 from the LNEG Geological Museum. A description was given by Roman (1907: 53-54, pl. IV figs. 2-2a), who also provided excellent photos accurately reproduced by phototypy. This was indeed a chance because the specimen as it stands now underwent some destruction (certainly by accident) accompanied by losses of fragments that more or less concern the mesial third part, especially under the crown in the lingual side. Furthermore, a rather unhappy restoration added plaster that covered some underlying features that may indeed have been

destroyed. Hence we have to base some reasoning on the more than a century old figures.

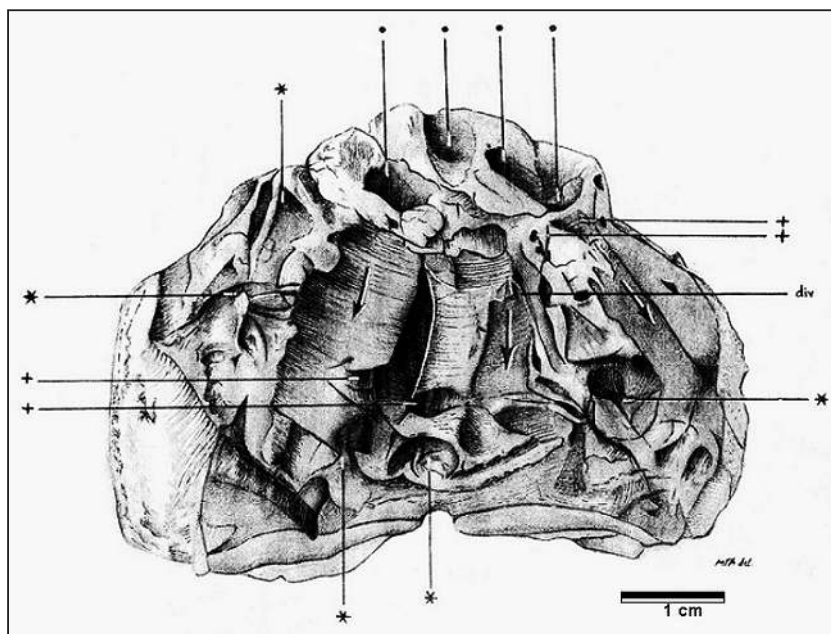
The specimen had previously been identified as *Trilophodon angustidens*. As far as we are concerned, these former interpretations may be accepted on the base of the tooth’s size (maximum length, 125.3 mm; maximum breadth, 65.0 MM) and shape, with rather blunt and low elements of the crown – and not distinctly higher and with a distinct if moderate tendency to hypsodony. In our opinion, it belongs to a *Gomphotherium angustidens* at the normal evolution stage as recognized among the Langhian Vb specimens. Its stratigraphically higher occurrence means but a later deposition during another sedimentary cycle.

Most of the roots have been lost, but the crown is complete except for a bit at the proximal, lingual corner.

The badly broken crown suggests it was strongly compressed upside down, with some parts displaced in an offset way but happily were not lost, so the tooth still was quite fresh. Crocodilian bites seem similar to the results of a cone crushing device; they caused this damage. Bites are further indicated by several holes on two more or less equally spaced rows (3+4) on the lingual surface of the root, well distinct in the photograph. Would these alternating impressions mean a single bite resulting in maxillaries and dentaries’ teeth? We do not try to reply on the basis of the available data.

The crushing process certainly occurred before the first fossilization, while the tooth still was

Figure 5 The same specimen represented fig. 4, drawing to show: - recognizable teeth impact points associated to radiate fractures (*); - simple impact points (+); - arrows (↓), recognizable sense of displacement of a gliding tooth; - div, diverticle in a bite surface scar produced by a tooth crest; points (•), depressions of the pulpar chamber under the two last loph. Scale: bar, 1 cm.



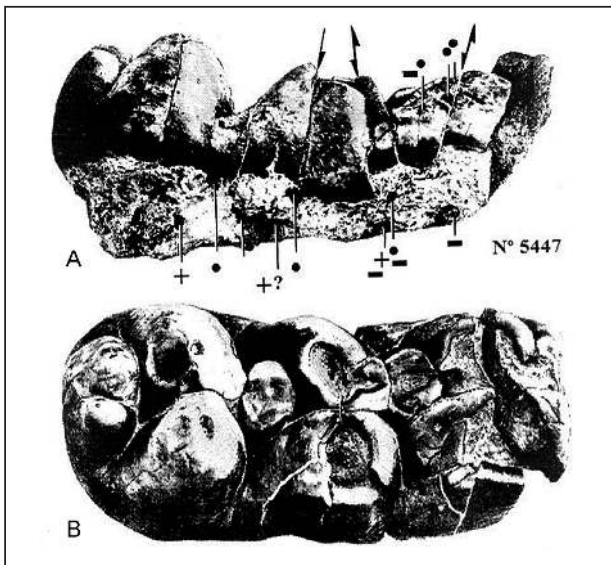


Figure 6 *Gomphotherium angustidens*, sample (C), lingual (above) and occlusal views according to Roman (1907, pl. IV, 2 and 2a), modified by M. T. Antunes. Scale: approx. x 0.5. Intense fracturing by sub vertical crushing with displacement of fragments prior to fossilization, most probably by crocodilian (cf. *Tomistoma lusitanica*) bites. **Arrows**: recognizable senses of displacement of tooth fragments. **Dots**: rather regularly spaced holes in root tissues (lingual side) may be ascribed to crocodilian teeth apex's impressions; two sets of such impressions may be seen in rows just under the crown and below. Another set is placed above on enamel. **Crosses**: set of impressions still below, one (?) being doubtful; there may be further, not so distinct further ones, especially rear part (to the left of the figure). **Black rectangles**: impressions still seen on Roman's (1907) figure but lost subsequently (see text).

associated to soft parts; if dry, a similar procedure would broke it apart in multiple fragments. Most of the root was lost. These features were not accounted for by Roman (loc. cit.) or anybody else until now.

New observation of the specimen (N° 5447, Geol. Museum) shows indeed a sorry reality, as the specimen underwent long ago (but after the times of Roman) an accident, maybe a fall. Enamel chunks and most of the root remnants from the mesial part of the specimen were lost.

A quite imperfect restoring was attempted: added plaster filled some parts, i.e. concealing the valley between the 1st and 2^d lophids. Nearly all the mesial third part of the lingual side root surface was lost. It therefore is no more possible to verify the corresponding features, including bite impressions that were there according to Roman's figures. Observation is rendered even more difficult because the whole was covered with a thick resin coating. Hence it became even more necessary to observe and rely on the Roman (1907) photographs.

Nevertheless, direct observation was very useful. It confirmed our long ago recognition of a gangue with fragments of marine molluscs. Even more, some more impressions were detected (Figure 7).

Let us underscore that all the concerned fossil-bearing beds, as well as some thousands of vertebrate remnants collected there show no evidence of tectonic deformation. Fossilization with crushing of mechanically resistant teeth as shown above, explained through the intervention of crocodilians, is not common in the Lisbon Miocene series.

Besides the *Tomistoma* skull in connection to its crushed mandible (see “*A predator that becomes a prey*”), and the gomphothere tooth, we found long ago at Quinta da Farinheira (Langhian, Vb unit) two associated, right upper premolars (P2-P3) of the suid *Listriodon* (*Bunolistriodon*) *lockarti* (Figure 8).



Figure 7 A. *Gomphotherium angustidens*, sample (C), lingual view as now (Dec. 2011). Photograph by M. T. Antunes. Scale, 5cm. Black stars: right side of impressions on enamel; G, plaster; White stars: impressions on roots' tissues, some doubtful (?). Black triangle plus white star: the lower vertex points out to an impact point from which start radiating fractures that are clearly seen (a classical impact demonstration); B. *Gomphotherium angustidens*, sample (C), labial view as now (Dec. 2011). Photograph by M. T. Antunes. Scale, 5cm. G, plaster. About the middle part of the 3^d lophid there is a shallow, nearly vertical, descending sulcus that describes a small turn in distal sense and ends at a depressed impression; it seems to have been produced by gliding of a tooth along the enamel's surface until it stopped, producing a deeper imprint.



Figure 8 *Listriodon* (*Bunolistriodon*) *lockarti*, sample (D), lingual (Fig. 8a) and occlusal views. Intense fracturing by sub vertical crushing with displacement of fragments prior to fossilization, most probably by a crocodylian. Enlarged. Scale in mm.

This specimen, deeply fractured by crushing, is most uncommon since it differs from all other teeth from the same species (Antunes & Estravís, 1986): all in all, only these two associated teeth were crushed before fossilization in a total of 61 molars and premolars.

Suids certainly were among the commonest middle-sized mammals preyed upon by mammalian carnivores, but the latter invariably did not crush their victim's teeth. In the specimen under study, the teeth crowns show displaced offset enamel chunks in an unusual hard, carbonated gangue, while in this site all or nearly so specimens were collected in loose sands. Even if in this case we cannot be as sure as with the preceding ones about which predator did it, but a crocodylian also is most likely.

As a consequence, nothing suggests that the impressions as described above to have been produced by large-sized, flesh-eating mammals: the only surviving Creodont, i.e. the huge and very rare *Hyainailouros*, or bear-dogs as *Amphicyon*. We don't see any among the contemporary mammalian carnivores risking his dentition to break a mechanically resistant matter as dentine, much harder than bone, with no meaningful profit as far as edible matter is concerned.

On the other hand, teeth damage is not a problem for crocodylians since dental replacement takes place during their whole life. A crocodylian most clearly seems the author of the crushing bite impressions.

7 How Giant was *Tomistoma lusitanica*?

Total length was discussed above after evidence from the two already described skulls and mandibles. Very large as they are, these specimens do not attain the maximum size for *Tomistoma lusitanica*.

Indeed, we obtained in 1967 two fragments of a left hemimandible from a much larger individual (Figure 9) in a sand pit at Quinta das Pedreiras near Lumiar, Lisbon (uppermost Burdigalian Va unit, ca. 17.5 Ma).

Found and carelessly collected by workers, it certainly was broken by them. We could buy but these fragments, the lacking parts being destroyed, lost or taken away by somebody.

Assuming that the total number (18) of mandibular teeth is the same in each side as in the *T. lusitanica* mandibles, there is evidence of the rear part of the 11th tooth alveolus followed by a short space; the 12th is also separated from the 13th by a short space; a somewhat longer space separates it from the 14th; this tooth is followed by the 15th at a shorter space; this one is followed by the decreasing, smaller and very close-by 16th (missing), 17th (broken) and 18th, the last one.

One fragment is the proximal part of the dentary with the first and second teeth (Figs. 9a, 9b). It much exceeds in size the corresponding parts of the mandibles previously referred to. Measurements as preserved: maximum length, measured on bone, 86.0 mm; width at the level of the 2d tooth, 52.9

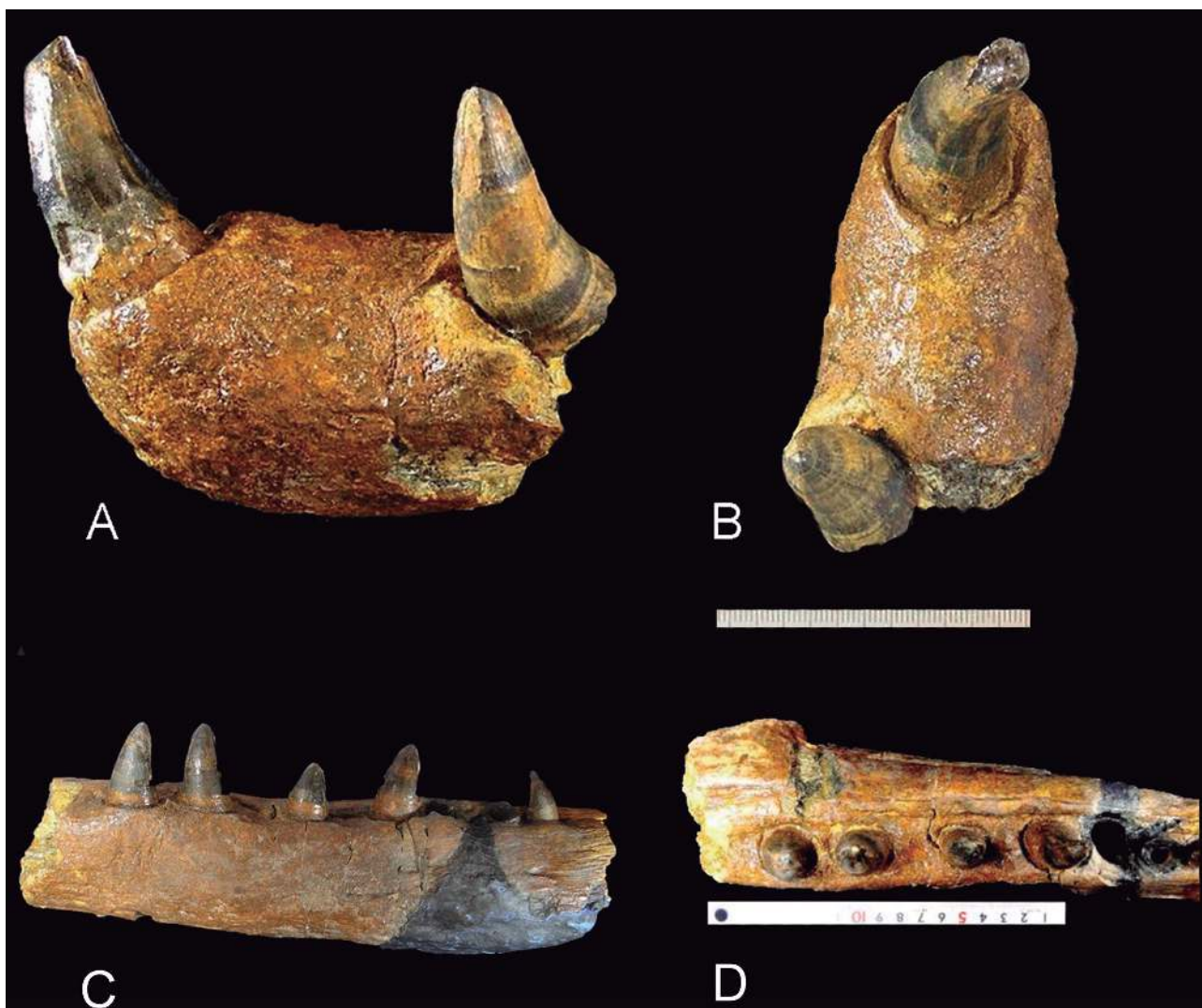


Figure 9 A. *Tomistoma lusitanica*, tip of left dentary with the first and second teeth from the largest known mandible, external view. Quinta das Pedreiras. Scale: much reduced (ca. x 0.17). Ruler in cm and mm; B. The same, dorsal view. Scale in cm and mm; C. Distal portion of symphysis and part of the left mandibular ramus, lateral (external) view with the rear part of the 11th tooth alveolus, teeth 12th to 15th, 16th alveole (tooth is missing), the broken 17th and the 18th and last. Very much reduced; ruler in cm; D. The same as for Figure 9 C, dorsal view.

mm; height of dental bone at the same, 2d tooth level, 52.8 mm. The symphyseal articular surface is well preserved.

The larger fragment (Figures 9 C and D) comprises part of the distal portion of the symphysis (left splenial and dentary bones) as well as part of the mandibular ramus until the proximal tip of the surangular. No special features have been noticed beyond massive character and impressive size: maximum length, 309.0 mm; width at the rear (distal) part of the symphysis, 89.4 mm (hence the total width of the symphysis at this level would be ca. 17.9 mm); height at the same level (that is just after the 12th tooth), 68.2 mm. The deep ‘penetration’

of the splenials into the symphysis is a constant character of the crocodilians under study.

The large, somewhat arched teeth are in full agreement to those already described. Spaces between teeth tips as measured on a plaster cast impressed by the specimen (Figure 10) are (in mm):

– 11th - 12th, 38.2; 12th - 13th, 29.1; 13th - 14th, 52.1; 14th - 15th, 44.2; 15th - 16th, 26.3; 16th - 17th, 23.1; 17th - 18th, 23.6.

The total length from the 11th to the 18th is 235.5.

The same measurements taken on the 8 clear teeth points (plus less distinct, one or two



Figure 10 Bite impressions on plaster obtained with the hemi mandible fragment described this chapter. Scale in cm and mm.

ones) of the more complete bite impression on the *Gomphotherium* molar have been recorded:

- 11th – 12th, 17.2; 12th - 13th, 18.3; 13th – 14th, 12.0; 14th – 15th, 13.0; 15th – 16th, 10.5; 16th – 17th, 8.3; 17th – 18th, 9.1.

The total distance from the 11th to the 18th is 83.3 only. These bites have therefore been produced by a much less large individual than the huge preceding one, i.e. more or less a third (83.3: 235.5 = 35.4 %) of the giant’s size.

The same portion of mandible allows comparisons with the *T. lusitanica* holotype. The length of the fragment dealt with here exceeds that of the same mandibular portion by about 30%!

Taking into account that the length of the holotype’s skull from the extremity of the snout to the rear border of the cranial table is 930 mm, the skull of the Quinta das Pedreiras ‘super giant’ may be estimated at about 930+30% or about 1209 mm.

Let us stress again that results are not accurate, but indeed we can obtain a rather correct, non-exaggerated value for the ‘super-giant’s total length as approximately 7 times the skull length: 1209 x 7 = 8463 mm. The estimated total length would most probably exceed 8 meters and may nearly have attained 8.5 meters!

We thus can grossly estimate the volume and weight. For a linear dimensions’ increase factor of about 0.3, the volume and weight factors would be ca. $(1.3)^3 = 2.197$.

For comparison purposes we may take into account length and weight of very large individuals from:

- *Gavialis gangeticus*, the Gharial from India, 6 m (attaining perhaps 7.6) and 1000 kg (estimated);

- *Crocodylus niloticus*, the Nile crocodile, 6.45 m total length and 909 kg;

- *Crocodylus porosus*, the Salt-water crocodile, 7 m and 2000 kg (estimated), longer records of 8.1 and 8.4 m being somewhat doubtful;

- *Melanosuchus niger*, the Black caiman or ‘jacaré guaçu’, 7.7 m and 1310 kg.

If we admit figures of the same order of greatness as a weight of about 2 tons for a 7 m specimen, an 8 m overall length *T. lusitanica* would weigh about $2 \times (2.197) \approx 4.394$, or grossly more than 4 tons.

Comparisons can be made with another neogene Tomistomine, *Rhamphosuchus crassidens* Lydekker 1840 from the Siwaliks, Pakistan, from which we observed a cast of a snout at the Muséum national d’Histoire naturelle, Paris. This species was based on fragmentary, incomplete material that pointed out to the longest reptile after the age of dinosaurs, whose length was estimated in 15 to 16 meters.

Nevertheless this last figure seems an exaggeration. More recent estimates merely point out to ca. 8-9 meters for *Rhamphosuchus*, a value that is about the now known maximum for *Tomistoma lusitanica*.

8 Conclusions

1. New evidence indicates that diet of huge *Tomistoma* included not only fishes but also

some of the then largest terrestrial mammals as *Gomphotherium angustidens*. The individual that produced the bites described here was about 3.5 to 4 m in total length, or maybe half the maximum size of the largest ones. This is a rather large size for the extant “false-gharial”, yet less than its possible maximum. Moderately large-sized *Tomistoma lusitanica* were perhaps not large enough to attack a living adult gomphothere, but could well scavenge on their corpses (Figure 11).



Figure 11 Hypothetical reconstruction of a possible environment during Miocene times – the mouth of a large river not much far away from sea near a palm-rich, subtropical area. On the bank, a swollen by decay *Gomphotherium* corpse is attacked by a huge ‘false-gharial’ while other ones and a vulture wait. Two albatrosses remind the closeness of the sea.

2. These results may indicate that the main reason for *Tomistoma schlegelii*'s alleged ichthyophagy may simply be human pressure that would impeach the false gharials to attain its true maximum size, much in excess of what had been acknowledged. Giant skulls in collections, including the largest one that belonged to a false-gavial, are evidence enough.

3. Evidence points again to the importance of immigrations from Asia and geographic affinities, as shown by both *Tomistoma* and *Gavialis* in westernmost Europe. This is also the case for the immigration of the rhinoceros *Hispanotherium* at lower Middle Miocene (Antunes & Ginsburg, 1983, Antunes, 2003), preceded by those of ‘Oriental vipers’ and other thermophilous snakes (Szyndlar, 2000). Lack of adequate data and differences from North African faunas does not contradict these views (see Piras *et al.*, 2007).

4. Extrapolations based on the Miocene false-gharials contribute to a better understanding of the surviving *T. schlegeli*. Similarity is even greater if account is taken of the closer cranial features between the large-sized fossil forms under study and the above referred massive, largest of all extant crocodilians’ skulls.

5. Overall length in excess of 8 meters confirms *Tomistoma lusitanica* as one of the largest crocodilians that ever existed. These huge predators undoubtedly attacked very large prey, including gomphotheres, maybe still in life and not only as corpses.

6. A true giant, *Tomistoma lusitanica*'s dimensions seem to have attained those of the Siwaliks’ *Rhamphosuchus*, long regarded as the Neogene maximum in size.

7. *Tomistoma lusitanica* was one of the largest crocodilians from all times, and even the largest reptile from western Eurasia after the age of the dinosaurs.

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