Stuttgarter Beiträge zur Naturkunde
Serie B (Geologie und Paläontologie)

Herausgeber:

Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart

Stuttgarter Beitr. Naturk.	Ser. B	Nr. 250	44 pp., 13 figs., 5 tabs.	Stuttgart, 31. 10. 1997

The anthracotheriid genus *Bothriogenys* (Mammalia, Artiodactyla) in Africa and Asia during the Paleogene: phylogenetical and paleobiogeographical relationships

By Stéphane Ducrocq, Montpellier

With 13 figures and 5 tables

Abstract

The revision of the dental material referred to the Anthracotheriida~~e *Bothrio*~~*genys* from the Fayum in Egypt led to consider only four distinct species of the five described at the turn of this century, and to bring up to date the diagnoses for the different species. The type specimen of *Bothriogenys parvus* belongs to a new and distinct genus, *Qatraniodon*, whose affinities are proposed. A phylogenetical study has been undertaken and the different cladograms obtained are discussed.

Comparisons of the African taxa with a southeast Asian species of *Bothriogenys* suggest phylogenetical and paleobiogeographical relations between the mammals of both landmasses. Cenograms constructed for the Fayum mammalian community most probably reflect a closed and tropical environment, and contribute to the question of the age of the Jebel Qatrani Formation.

Résumé

Une révision du matériel dentaire attribué à l'anthracothère *Bothriogenys* de la Formation Jebel Qatrani du Fayum a permis de ne conserver que quatre espèces distinctes parmi les cinq décrites par Schmidt (1913) pour ce genre et à mettre au point les diagnoses des différentes espèces. L'holotype de *Botriogenys parvus* appartient à un nouveau genre distinct, *Qatraniodon*, dont les affinités sont discutées. Une étude phylogénique portant sur le genre *Bothriogenys* du Fayum est également proposée, et la validité des différents cladogrammes obtenus est discutée.

La confrontation du matériel africain et d'une espèce d'Asie du Sud-Est conduit à suggérer que des relations phylogéniques et paléobiogéographiques existaient probablement entre les formes africaines et asiatiques. La construction de cénogrammes pour la communauté mammalienne du Fayum révèle que celle-ci vivait probablement dans un environnement forestier soumis à un climat de type tropical, et une interprétation de l'âge de la formation Jebel Qatrani est discutée.

Zusammenfassung

Die ägyptischen Arten der Anthracotheriiden-Gattung *Bothriogenys* werden an Hand von odontologischen Untersuchungen revidiert. Es wird die These vertreten, daß nur vier der fünf von SCHMIDT (1913) beschriebenen Arten zu dieser Gattung gehören. Der Holotypus von *B. parvus* gehört zu einer neuen Gattung, *Qatraniodon*, die definiert wird. Eine phylogenetische Untersuchung der Gattung *Bothriogenys* wurde unternommen, und die verschiedenen phylogenetischen Alternativen werden besprochen.

Vergleiche des afrikanischen Materials mit einer südostasiatischen Art haben ergeben, daß phylogenetische und paläobiogeographische Beziehungen zwischen den afrikanischen und den asiatischen Formen wahrscheinlich sind. Die erstellten Cenogramme für die Säugetierfauna des Fajums zeigen, daß der Lebensraum wahrscheinlich ein bewaldetes Umfeld mit tropischem Klima war. Das Alter der Jebel Qatrani Formation wird diskutiert.

Contents

1. Introduction

Since the discovery of the fossiliferous localities in the Fayum Depression (Egypt) at the beginning of the century, and until recently, the mammals from this region were thought to be mostly endemic to Africa. This assertion was based in part on the fact that these taxa were primitive representatives of their respective families and only known in the Fayum localities. But recent discoveries of mammalian faunas in North Africa (Algeria [COIFFAIT et al. 1984; MAHBOUBI et al. 1986; DE BONIS et al. 1988; GODINOT & MAHBOUBI 1992], Tunisia [COURT & HARTENBERGER 1992; HARTENBERGER & MARANDAT 1992], Libya [SAVAGE 1971; WIGHT 1980]) and in the Arabian Peninsula (Oman [THOMAS et al. 1989; GHEERBRANT et al. 1993]) led to reconsider this hypothesis. Moreover, the description of Upper Eocene ungulates and primates from Southeast Asia (DUCROCQ 1994a; DUCROCQ et al. 1995a, 1995b) reinforces the idea that Southeast Asia was an important centre of origin and evolution for several mammals (particularly anthracotheres and primitive primates), in spite of the geographical distance that separated both areas. However, the mammalian Fayum faunas are actually well known owing to the numerous geological and paleontological works made by several American teams. A complete review of the history of research is given by SIMONS & RASMUSSEN (1990). Higher primates and hyracoids are particularly well diversified in the Fayum (see for example RASMUSSEN et al. 1992). Among other mammal goups, anthracotheres occur in almost the entire Fayum Depression. These ungulates have been studied at the beginning of the century (SCHMIDT 1913), but since that time, no other work has been conducted concerning this group of mammals. Moreover, the recently described late Eocene mammalian fauna from Thailand has yielded, among others, an anthracothere which is morphologically and probably phylogenetically very close to the African species (DUCROCQ 1994a, 1995, in press). A revision of the anthracotheres from the Fayum seems therefore necessary considering the growing knowledge of this group of mammals, and of its dental variability. In addition, the discoveries of Paleogene taxa in Southeast Asia allow to reassess the hypotheses about the faunal changes between Asia and North Africa.

The following abbreviations are used in the text: SMNS (Staatliches Museum für Naturkunde Stuttgart) and NHML (Natural History Museum London). Acronyms for specimen numbers are C (= Cairo for the Geological Museum, Cairo), M (= Museum at the Natural History Museum London), TF (= Thai Fossil at the Department of Mineral Resources, Bangkok), Vm (= Vertebrate mammal at the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing).

Acknowledgements

I wish to thank Prof. Dr. B. Ziegler, Dr. O. Rieppel and Dr. E.P.J. Heizmann for having received me at the Staatliches Museum für Naturkunde and for having given me all facilities to work there. I also had the kind help of all technicians of the Museum when necessary. Dr. J.J. Hooker received me in the Natural History Museum in London and allowed me to study the anthracothere material from the Fayum in his care. I had also fruitful contacts with J. Sudre, J.-L. Hartenberger and J.-J. Jaeger from the Laboratoire de Paléontologie, Montpellier, France, during my stay in Stuttgart. Mrs. R. HARLING (Stuttgart) and Mr. M. PONS (Montpellier) helped me with photographic work, and Dr. G. Bloos helped me to prepare the manuscript in proper form . My thanks go also to the Alexander von Humboldt-Stiftung for its financial support and efficient organization, and thanks to which this work was undertaken and achieved. Publication No. 97-069 from the ISEM, UMR 5554 CNRS.

2. Geological setting

The geology of the Fayum Depression has been recently reviewed in detail by several authors (see for example BOWN & KRAUS 1988; VAN COUVERING & HARRIS 1991; GINGERICH 1993 with different interpretations). But it seems necessary to give here a short summary about the nature of the levels that yielded mammal remains.

The late Paleogene rocks in the Fayum Depression (fig. 1) consist of the nearshore marine and fluvial Qasr el Sagha Formation overlain by the mainly fluvial Jebel Qatrani Formation. The Fayum region currently displays more than one hundred terrestrial vertebrate localities (RASMUSSEN et al. 1992). These localities are mainly distributed in the Jebel Qatrani Formation, a few of them occurring in the underlying Qasr el Sagha Formation. No precise indication concerning the stratigraphical origin of the remains of *Bothriogenys* housed in Stuttgart and London is given in the literature. ANDREWS (1906: ix, table) stated that a large number of silicified trees associated with vertebrate remains (embrithopods, hyracoids, proboscideans, artiodactyls, carnivores and reptiles) comes from the lower beds of a fluviomarine series, the latter consisting in variegated sands, sandstones, clays and marls with limestone-grits and thin bands of limestone. The so-called 'fluviomarine series' now corresponds to the Jebel Qatrani Formation according to the nomenclature of SAID (1962).

In 1905–1906, MARKGRAF assembled a large collection of vertebrate fossils from the 'bone beds' of the lower part of the Jebel Qatrani Formation (BOWN & KRAUS 1988). SCHMIDT (1913) did not give further indications about the location of the fossiliferous levels. Meanwhile, fossil remains occur throughout the Jebel Qatrani Formation from about 45 m up to 250 m (BOWN & KRAUS 1988). One can consider that the anthracotheriids studied by SCHMIDT might come from the collectings made by MARKGRAF before 1911, because the very large collection of vertebrates at the SMNS in Stuttgart was assembled by MARKGRAF in the years before 1911. According to SIMONS (1968: 19) and RASMUSSEN (1989: 60), 'There is a considerable probability that none of the earlier finds [before 1906] was collected from the Upper Fossil Wood Zone'.

The lower fossil Wood zone corresponds to the lower sequence of the Jebel Qatrani Formation, and the upper fossil Wood zone corresponds to the upper sequence of the Formation. The upper and lower sequences are separated by a cliff-forming marker bed called the 'Barite Sandstone' (at about 150–160 m high on the Jebel Qatrani Formation).

Also, SIMONS (1968: 9) stated that 'Markgraf was employed by the American Museum to collect jointly with Granger's party and [...] he continued the work of exploration of the Fossil Wood Zone, bringing in scattered materials, mainly from the northeast of quarries A and B'.

RASMUSSEN et al. (1992) defined four Fayum faunal zones (FFZ 1 to 4) in the Jebel Qatrani Formation, the FFZ1 being the lowest in the series. The limit between FFZ2 and FFZ3 also indicates the Eocene-Oligocene boundary. But according to these authors, the anthracotheriids occur in the four faunal zones described by them, and the abundance of anthracotheres increases markedly in the fourth faunal zone. An-

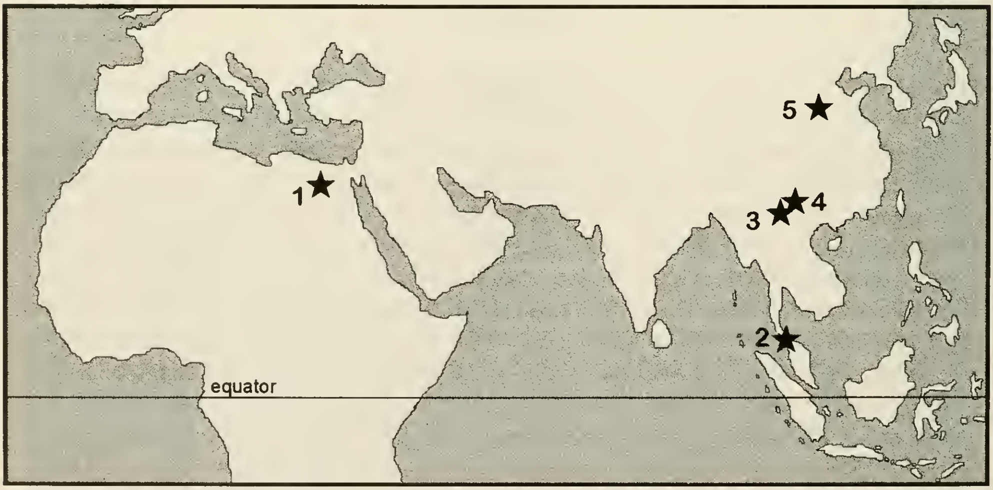


Fig. 1. Location map of the different localities that have yielded remains of *Bothriogenys*. 1: Fayum Depression (lower Oligocene of Egypt); 2: Krabi Basin (late Eocene of Thailand); 3: Xiaotun (Yunnan Province, lower Oligocene of South China); 4: Shiping (Guizhou Province, lower Oligocene of South China); 5: Baishuicun (Shanxi Province, lower Oligocene of Northeast China).

thracothere remains are relatively rare or infrequent at quarries below 100 to 150 m, but they become abundant and widespread in the upper part of the sequence. In addition, RASMUSSEN et al. (1992: 562) stressed that, together with other mammal taxa, the genus *Bothriogenys* occurred throughout the Jebel Qatrani Formation, from quarry L-41 (base of the formation) up to quarries I and M (top of the formation).

Concerning the age of the Fayum anthracotheres, VAN COUVERING & HARRIS (1991) stated that the entire Jebel Qatrani Formation was Upper Eocene in age. RASMUSSEN et al. (1992) supposed that the Eocene-Oligocene boundary was situated between FFZ 2 and FFZ 3 (at about 150 m above the base of the Jebel Qatrani Formation). This would imply that most of anthracotheriid remains are lower Oligocene in age (if one consider the time-stratigraphic correlations proposed by RASMUSSEN et al. 1992). GINGERICH (1993) used planktonic foraminiferal biostratigraphy and radiometric ages on overlying basalts of the Jebel Qatrani Formation as a basis to conclude that the Jebel Qatrani Formation is entirely Oligocene in age. However, there is still some debate as to whether the age of the basal part of the sequence is latest Eocene or earliest Oligocene.

3. The Anthracotheriidae

Anthracotheres are a group of Tertiary suiform ungulates that ranged from small, terrier-sized animals to beasts approaching the hippopotamus in size (BLACK 1978). These animals may have had a hippopotamid mode of life, and several authors moreover consider that Anthracotheriidae might have been the ancestors of extant hippopotamuses (for example COLBERT 1935, GENTRY & HOOKER 1988), although others suggested that hippopotamids could have originated from a peccary stock (PICKFORD 1993, and see DUCROCQ 1994b for discussion). The family Anthracotheriidae occurred in Asia from the late (and perhaps middle) Eocene (COLBERT 1938, DUCROCQ 1992) until the Plio-Pleistocene. They appeared in Europe during the late Eocene (HELLMUND 1991, DUCROCQ 1994a) and they became extinct in the Miocene. North America was colonized by Anthracotheriidae from the late Eocene (STUCKY 1992) until the end of the Oligocene, mainly by selenodont forms of the subfamily Bothriodontinae (MACDONALD 1956). Finally, this family also evolved in Africa from the lower Oligocene (GINGERICH 1993) or the late Eocene (VAN COUVERING & HARRIS 1991) to the Plio-Pleistocene (BLACK 1978).

The Anthracotheriidae of the Fayum fauna have been previously attributed to the Oligocene European and North American genus *Ancodon* on the basis of the resemblances they displayed with the known species (ANDREWS 1906). Then, in his monography on the Fayum artiodactyls, SCHMIDT (1913) attributed the anthracotheriids to the genus *Brachyodus* and the sub-genus *Bothriogenys*. Since that time, several authors have set up *Bothriogenys* at a generic status (BLACK 1978; DINEUR 1981). *Bothriogenys* is a genus known in the lower Oligocene of Fayum in Egypt (BLACK 1978; SCHMIDT 1913) and five species have been described from the Fayum (*B. parvus*, *B. gorringei*, *B. rugulosus*, *B. fraasi*, and *B. andrewsi*). This genus has also been recognized in the Upper Eocene of southern Thailand, with a new species, close to those known in the Fayum (DUCROCQ 1994a; DUCROCQ in press), and possibly in the lower Oligocene of southern and northern China (CHOW 1958; CHOW & CHANG 1960; XU 1962).

In a general way, the dental material attributed to the genus *Bothriogenys* housed in the SMNS in Stuttgart, in the NHML in London and to that of Thailand displays a structural pattern very similar in the different species. My aim is not to redescribe the material published by SCHMIDT, but to propose a revision of the specific and the generic status of some specimens. Only the dental material will be studied here, the postcranial elements (perhaps with the exception of the astragali) being too poorly known to be referred with certainty to *Bothriogenys*.

Order Artiodactyla OWEN 1848

Family Anthracotheriidae GILL 1872

Genus *Bothriogenys* SCHMIDT 1913

Type species: *Bothriogenys fraasi* SCHMIDT 1913; designated therein.

Emended diagnosis. – Small to medium-sized anthracotheres; skull and jaws moderately elongated; diastema between premolars and canine present, generally short, and between C and anterior lower premolars; no descending flange of the angle; no reduction in dental formula; no incisor enlargement; premolars simple, elongated; molars bunodont to bunoselenodont; enamel somewhat rugose; protoconule well developed; parastyle and mesostyle flattened; lower molars with short anterior protoconid and hypoconid arms.

Bothriogenys fraasi (SCHMIDT 1913)

* 1913 *Brachyodus (Bothriogenys) fraasi.* – SCHMIDT, p. 158–163; p. 186–190; pl. 1, fig. 13; pl. 2, figs. 1–7; pl. 3, figs. 1–5, 23–25, 29–35; pl. 4, figs. 7, 10.
1913 *Brachyodus gorringei.* – SCHMIDT, pl. 3, figs. 23–25.
1978 *Bothriogenys fraasi.* – BLACK, p. 427.

Lectotype (design. BLACK 1978): skull with left and right P^1-P^3; Nr M 10186, Natural History Museum, London.
Formation and location: Jebel Qatrani Formation, Fayum, Egypt.

Emended diagnosis. – Differs from other species of *Bothriogenys* in the association of its deeper lower jaw, with lingual convexity under molars and lingual concavity under premolars, its labial concavity of tooth row, the strong increase of size from M_1 to M_2, its lower molars with slightly bulbous and labially salient external wall, its prehypocristid in Y on fresh teeth, and strongly developed mesial and distal cingulids. Upper molars tend to be as wide as long, thus recalling those of *B. rugulosus*, but with more slanted cusps. No diastema in the upper premolar row, and long diastema between the upper canine and P^1; symphysis reaching P_1 (Annexe, table 1).

The type specimen of *B. fraasi* housed in the NHML (Nr M10186) displays dimensions and dental structure similar to those of the skull from the SMNS (Nr 44175). The only differences that can be pointed out between both specimens concern the structure of P^1-P^3: their distolingual cusp and cingulum are slightly more developed in the London skull than in the Stuttgart specimen.

B. fraasi is the second largest anthracotheriid species known from the Oligocene Fayum sediments. SCHMIDT (1913: 37) pointed out that on unworn lower molars, the prehypocristid divides into two distinct crests, the mesial one running to the posterior wall of the trigonid (= cristid obliqua), and the lingual one joining the apex of the entoconid. This morphology gives the prehypocristid a Y form. Although

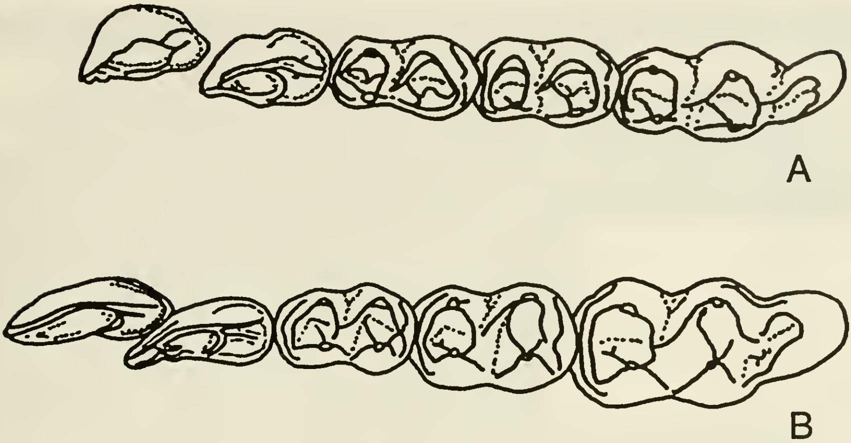


Fig. 2. Occlusal view of lower tooth row of A: *B. gorringei* (mandible 46348) and B: *B. fraasi* (mandible 44081, SMNS). Note the structure of the hypocristid on M_2 and M_3. Not to scale.

Schmidt regarded this feature as a specific character for *B. fraasi*, it lacks on the juvenile mandible Nr 11948, but it can be observed, however, in most specimens referred to *B. rugulosus*, and in some specimens of *B. gorringei*. Although Hellmund (1991) stated that the Y prehypocristid reflects a derived condition, this character should therefore be regarded as a variable feature, or as a trait that occurs only in fresh teeth in the Fayum anthracotheres (fig. 2 and 3C).

Three fragmentary mandibles housed in the SMNS that have been previously attributed to *B. gorringei* (among which one [Nr 44081] is figured in Schmidt 1913: pl. 3, fig. 23–25) can be referred to *B. fraasi* on the basis of the association of their deep lower jaw, their dimensions, the increase of size from M_1 to M_2, their bulbous labial wall of lower molars and their peculiar structure of the prehypocristid (fig. 3C).

Schmidt (1913: 37) also pointed out that the lingual face of P_2 and P_3 is simple. It seems that he took the juvenile lower jaw Nr 11948 as a basis of this assertion. As a matter of fact, this mandible displays a premolar which is triangular in shape with two slight distal crests, a very faint distal talonid, and a weak lingual cingulid. The lingual face of this tooth is concave and almost flat. If one considers the adult lower jaw Nr 44174 from the SMNS, the teeth are all very worn, but it is possible to observe the remains of a P_2 that does not display the structure described above. Although the P_2 is extremely worn, it bears a larger size, a more developed distal cingulid, two distal crests and a strong lingual cingular shelf. This stucture recalls that found on the P_2 of *B. gorringei*. It is therefore very likely that the premolar of the mandible Nr 11948 corresponds to a D_2 and not to a P_2, since the former always displays a more simple morphology than that of the latter (fig. 4 and 5).

A mandible from the NHML preserving right P_3-M_3 (Nr 9462) was labelled *as B. rugulosus*, but I here refer it to *B. fraasi*. Indeed, M9462 is too large to belong to the former species, and its deep horizontal ramus (about 38 mm under M_1 and M_3) and teeth morphology and structure distinguish it from all other Fayum species. Also, this specimen allows to better know the lower premolars of this species. The two last premolars (P_{3-4}) display a structure similar to that of the corresponding premolars of

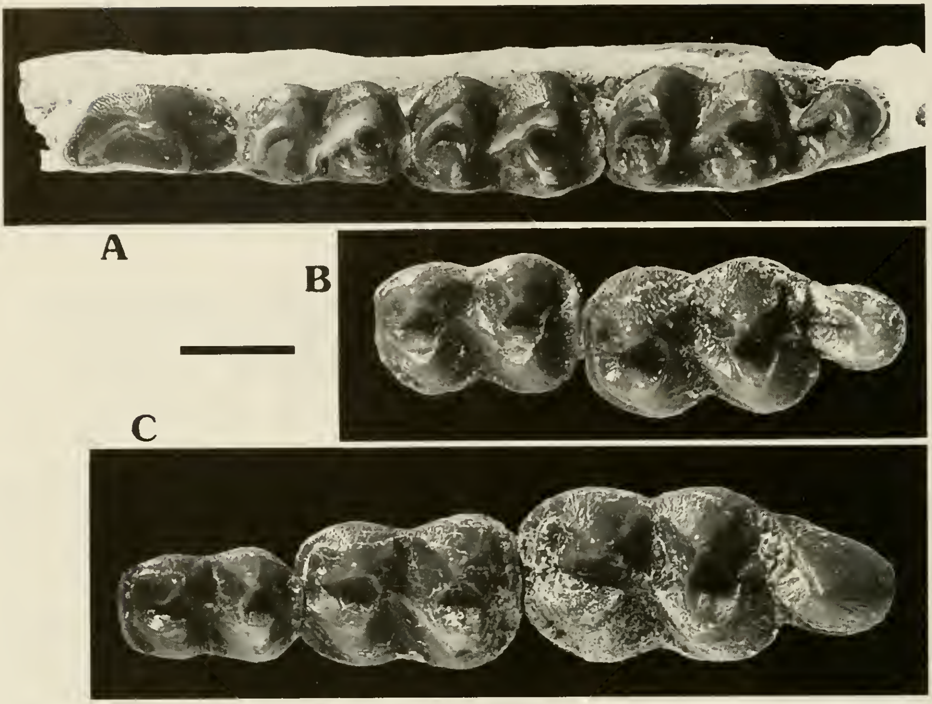


Fig. 3. Comparison between the lower molars of A: *B. gorringei* (right P_4-M_3, Nr 44101), B: *B. rugulosus* (left M_{2-3}, Nr 12636a), and C: *B. fraasi* (left M_{1-3}, Nr 44081). No left lower jaw *of B. gorringei* in the SMNS is well preserved enough for exact comparisons. All specimens housed in the SMNS. Scale bar = 10 mm.

B. gorringei, but they are somewhat more elongated than in the other species. In addition, the anterior part of the P_4 is particularly mesiodistally elongated, and it passes and lingually covers the talonid of P_3 (fig. 2). This situation is unknown in all other forms, where the P_{3-4} are shorter and more labially convex. The elongation of the lower premolars and the covering of P_3 by P_4 cannot be observed on the other lower jaws from the SMNS collections (Nr 44174 and 44176) since these teeth are so worn or they lack. On the other hand, the lower molars of M9462 illustrate that the Y prehypocristid is hidden by the wear of these teeth, thus enhancing the hypothesis according to which this structure does not correspond with a derived condition.

It must be stressed that in a general way, the overall structure of the teeth of *B. fraasi* is close to that of *B. rugulosus* (labial and lingual shape of the lower molar cusps, enamel slightly more wrinkled than in *B. gorringei* and *B. andrewsi*), thus suggesting that *B. fraasi* is phylogenetically closer related to *B. rugulosus* than to the other species of *Bothriogenys*.

Bothriogenys rugulosus (Schmidt 1913)

1906 *Ancodon gorringei.* – Andrews, p. 181 (M8424, M8425, M8423).
1906 *Ancodon* sp. – Andrews, p. 191 (C10500).
* 1913 *Brachyodus rugulosus.* – Schmidt, p. 165–168; p. 190–192; pl. 3, figs. 11–12; pl. 4, figs. 5, 8.
1978 *Bothriogenys rugulosus.* – Black, p. 427.

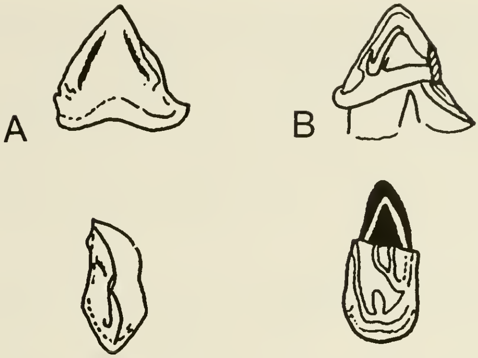


Fig. 4. Lingual (top) and occlusal (bottom) views of A: right D_2 of *B. fraasi* (mandible 11 948, SMNS), and B: left P_2 of *B. fraasi* (mandible 44 174, SMNS). Black part on B corresponds to worn root. Not to scale.

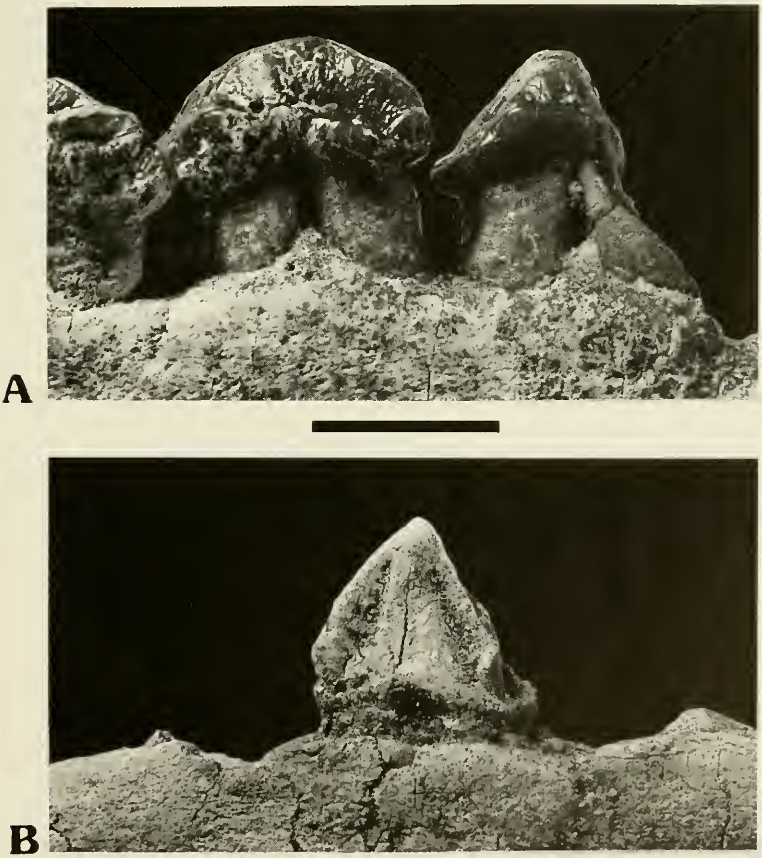


Fig. 5. Comparison between A: lingual view of left P_2 of *B. fraasi* (mandible Nr 44 174) and B: lingual view of right D_2 of *B. fraasi* (mandible Nr 11 948). All specimens housed in the SMNS. Scale bar = 10 mm.

Lectotype (design. Black 1978): a portion of left maxilla with M^2-M^3; Nr 44135, Staatliches Museum für Naturkunde, Stuttgart.

Formation and location: Jebel Qatrani Formation.

Emended diagnosis. – *B. rugulosus* can be distinguished from all other species of the genus by its smaller size, its upper molars about as wide as long without marked increase of size from M^1 to M^3, and with paracone steeper than metacone, its more massive lower molars with more rounded labial wall of the protoconid, its deeper labial sinusid between the anterior and posterior lobes of lower molars, so that the external walls of the teeth are slightly more labially salient, its more rectilinear third lobe of M_3, its almost complete cingulid on the whole labial side of the crown, and its typically strongly wrinkled enamel (Annex, table 1).

The fragmentary left maxilla with M^2-M^3 Nr 44135 was originally proposed by Schmidt (1913) as the type specimen. This specimen does not seem to be typical of the species since its dimensions and proportions (see Table 1) tend to be closer to those of *B. gorringei*: the teeth are slightly larger than the other upper molars attributed to *B. rugulosus* and they are somewhat wider than long, when one of the diagnostic characters of *B. rugulosus* is square upper molars.

The lower jaw of *B. rugulosus* is somewhat more slender than that of *B. gorringei* or *B. fraasi* and its retromolar space does not develop so much (it does not exceed 11 mm in the old specimen Nr 12636b, whereas the retromolar space can reach 15 mm in *B. gorringei* and 18 mm in *B. fraasi*). Also, a few slight dental features can distinguish the two species. In *B. rugulosus*, the M_3 displays a somewhat reduced and more straight hypoconulid than in *B. gorringei*. Also, the metaconid of *B. rugulosus* lower molars displays a marked mesial crest that descends from its apex and connects with the paracristid that extends along the anterior face of the trigonid basin. This premetacristid is either absent or very slight and does not contribute to close the trigonid basin in *B. gorringei* (fig. 6 and text-fig. 3B).

On upper molars, as stressed in the emended diagnosis, the teeth do not increase their size very much from M^1 to M^3 as in other species of *Bothriogenys*. Also, the labial styles are not so strongly developed, particularly the mesostyle, and the meta-

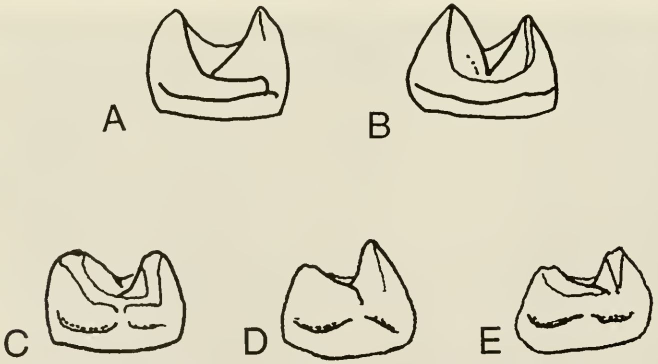


Fig. 6. Mesial views of right M_3 in A: *B. gorringei* (mandible 46348) and B: *B. rugulosus* (mandible 12636a). Both mandibles from the SMNS. Not to scale.
Distal view of left M_2 in C: *B. gorringei* (mandible 12636, inversed), D: *B. fraasi* (mandible 44081), and E: *B. rugulosus* (mandible 12636a). All mandibles from the SMNS. Not to scale.

style tends to be distally salient. SCHMIDT (1913: 14) pointed out the narrowness of the labial cusps relative to the lingual ones. This feature is well developed on the type specimen, but on other specimens (for example 44133 from SMNS, M9243 from NHML) the labial cusps tend to be more transversely developed and closer to the lingual ones.

In its overall morphology, *B. rugulosus* therefore seems to be the most primitive Fayum anthracotheriid, as SCHMIDT stressed.

Bothriogenys andrewsi (SCHMIDT 1913)

* 1913 *Brachyodus andrewsi.* – SCHMIDT, p. 168–169; p. 193–195; pl. 1, figs. 10–12; pl. 3, figs. 13–18.
1978 *Bothriogenys andrewsi.* – BLACK, p. 427.

Lectotype (design. BLACK 1978): right upper M^2, Nr 44086, Staatliches Museum für Naturkunde, Stuttgart. In the monography of SCHMIDT (1913) and in BLACK (1978), the type specimen was cited and described as a left upper M^2.

Formation and location: Jebel Qatrani Formation.

Emended diagnosis. – Large size anthracothere. Quadratic upper molars with strongly developed labial styles, and labial wall of paracone somewhat steeper than that of the metacone. P^4 with oblique labial corner. Differs from *B. fraasi* and *B. rugulosus* in its more slender lower molars. Enamel finely crenulated (Annex, table 1).

B. andrewsi is known only by isolated teeth: a strongly worn right M^2, right P^4, D_4, M_3, and I_1. The type specimen does not display much details of structure, and mainly the size allows to distinguish this species from the others.

With the exception of its larger size, the lower M_3 is identical in structure and morphology with the same tooth of *B. gorringei.* The only distinctive feature that can be observed is the slightly lower hypoconulid in the large species (although this could be related to the differences of wear). Also, the D_4 of both species are very similar. The tooth of *B. andrewsi* displays a more developed labial cingulid and two minute enamel spurs at the labial end of the transverse valleys that originate from the labial cingulid; a basal and somewhat larger spur labial to the median lobe of the tooth seems to have its own root.

The P_4 is also close to that of *B. gorringei.* Its labial wall is somewhat more oblique and mesially extended, but the overall structure is the same for both species.

No specimen from the NHML can be referred to this large species that seems to have been rather rare in the Fayum according to its relative abundance in the fossil record.

Bothriogenys gorringei (ANDREWS & BEADNELL 1902)

* 1902 *Ancodon gorringei.* – ANDREWS & BEADNELL, p. 7.
1906 *Ancodon gorringei.* – ANDREWS, p. 179–180 (M8881) and pl. 18, figs. 1–3; p. 182 (M8505a, M8505b, M8428, M8427, M8506a, M8506b).
1913 *Brachyodus gorringei.* – SCHMIDT, p. 164–168; p. 178–186; pl. 1, figs. 1, 6–8; pl. 2, figs. 8, 9; pl. 3, figs. 19, 39; pl. 4, figs. 1–4, 6, 9.
1913 *Brachyodus parvus.* – SCHMIDT, p. 169–171; p. 195–198; pl. 1, figs. 2–5; pl. 3, figs. 6–9, 20–22, 36–38.
1978 *Bothriogenys gorringei.* – BLACK, p. 427.
1978 *Bothriogenys parvus.* – BLACK, p. 427 (in part).

Holotype: lower jaw with left M_1-M_3 and right I_1, I_3, P_2-M_3; Nr C 8629, Geological Museum, Cairo (cast M8881 in the NHML).

Formation and location: Jebel Qatrani Formation.

Emended diagnosis. – Middle-sized species of *Bothriogenys*. Differs from *B. fraasi* in its smaller size, and in its lower molars with a weaker increase of size from front to rear, with more vertical distal wall of labial cusps, and poorly developed labial cingulid. Differs from *B. rugulosus* in its somewhat larger size, its lower molars with less bulbous labial walls and less developed premetacristid, its M_3 with longer and more slender hypoconulid, its upper molars wider than long, and in its somewhat less wrinkled enamel. Differs from *B. andrewsi* mainly in its smaller size (Annex, table 1).

The species *B. gorringei* has been erected by Andrews & Beadnell in 1902 on the basis of an almost complete lower jaw (figured by Andrews 1906, plate 18, fig. 1–3). *B. gorringei* is by far the most abundant anthracotheriid species within the fossil material housed in Stuttgart (24 fragmentary jaws and/or isolated teeth) and in London (13 specimens). The type specimen (cast Nr M8881) from London displays a slightly larger size than most of the other specimens attributed to this species. However, the other specimens of the NHML agree in dimensions with the SMNS material.

The type specimen displays dimensions and, in a lesser degree, proportions that remind the fragmentary lower jaw Nr 44081 from Stuttgart that I attribute to *B. fraasi* (see further). But the London specimen can be distinguished from this larger species by its M_3 with the more slanted distal walls of the labial cusps, by its inner cusps that form a more open V in lingual view, and by its weaker labial cingulid. In addition, the horizontal ramus is more slender (28 mm under P_2, 32 mm under M_1, 36 mm under M_3) than in *B. fraasi*. The type mandible might have belonged to a male specimen according to its large size and its developed diastema between C and P_1 (21 mm), P_1 and P_2 (26 mm) and P_2 and P_3 (2.5 mm). Also, the structure of the lingual face of the lower premolars is similar to that of the corresponding teeth of the mandible Nr 44080 from Stuttgart, with a lower and somewhat weaker lingual crest of P_4 in M8881 (fig. 7).

Among the dental material from the NHML that I refer to *B. gorringei*, several specimens have not been described or even cited in the litterature, particularly in Andrews (1906). The fossils have been attributed to various species of *Bothriogenys* following the work of Schmidt (1913), and several of them display the same catalogue number. I therefore give the following list of the London specimens that, according to me, belong *to B. gorringei*: M8881 (type specimen), M8426, M8427, M8428 (a right lower premolar), M8428 (a fragmentary lower jaw preserving right M_{2-3}), M8428 (a fragmentary lower jaw preserving left P_3-M_3), M8505a, M8505b, M8506, M8506a, M8506b (a fragmentary lower jaw preserving left M_{1-3}), M8506b (a fragmentary lower jaw preserving left M_3), M9462, M10350, M10351. Table 1 (Annex) displays the measurements of the dental material for all species of *Bothriogenys*.

A fragmentary lower jaw preserving a right P_2 (M8428) was previously attributed to *B. ?parvus*, but the structure and dimensions of both tooth and horizontal ramus are similar with those of *B. gorringei*. This premolar displays a weak mesial crest and lingual cingulid.

Also, a fragmentary lower jaw with right D_4-M_1 and the talonid of D_3 (M10351) labelled as *B. parvus* shows size and strong structural similarities with *B. gorringei* (M_1 size larger than that of the type of *B. parvus*, with more massive outline and stronger mesiolabial crest of the metaconid).

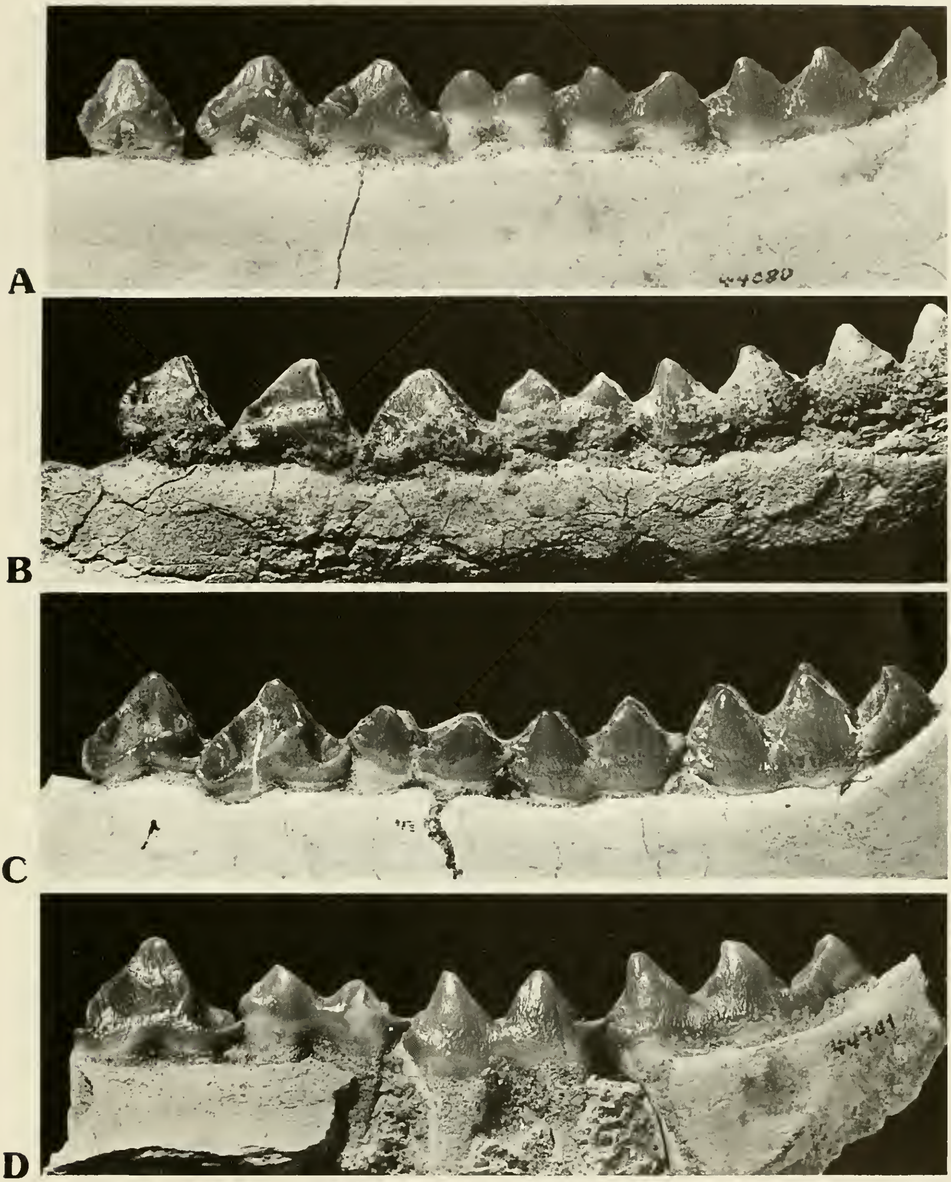


Fig. 7. Comparison of the lingual faces of P_3-P_4 in *B. gorringei*. A: mandible Nr 44080; B: mandible Nr 46349; C: mandible Nr 46348; D: mandible Nr 44101. All specimens housed in the SMNS. Scale bar = 10 mm.

The lower jaw Nr M9462 with left M_{2-3} was referred to *B. rugulosus* on the basis of its crenulated enamel and rather short hypoconulid on M_3. However, the dimensions of the London specimen are closer to those of *B. gorringei*, the premetacristid is weaker than in *B. rugulosus*, the labial wall of the protoconid is more rounded, and the lower molars lack the typical waisting between the anterior and posterior lobes.

In a general way, the lower jaw displays a constant morphology, with the exception of the retromolar space that is longer in older specimens.

Among all the fossils attributed to *B. gorringei*, the structure of the lingual face of lower premolars is variable (fig. 7). They display a mesial crest that inflates more or less at the base of the crown, and a lingual crest that goes down and evolves in a cusplet. On P_2, the mesial crest either forms a spur which is low on the crown (mandible Nr 44080), or it is developed as a strong wing that occupies the two thirds of the anterior side of the tooth (mandible without number). On the same specimens, the distolabial basin is respectively shallow or deep and wider (fig. 8).

On P_3 and P_4, the lingual crest is the most variable. It can form a triangular shelf at the mid-height level of the crown or slightly lower, and in a more or less anterior position. This lingual crest can also evolve in a high cingular shelf on the lingual base of the crown. This extreme situation is observed on the fragmentary lower jaw associated with the right M_3 Nr 44101 figured by Schmidt (1913, pl. 3, figs. 20–22) and previously attributed to *B. parvus* (fig. 7D), and in a lesser degree in the specimen Nr 8505b from London (a lower jaw with left P_4-M_3). Thus, the structure of the lingual face of the P_4 can display several stages of crest development within the same species (fig. 8). This suggests that the simple structure of the lingual face of the lower premolars cannot be used as a specific feature, but should be rather considered as a variable character in *B. gorringei*. This situation can also be observed in the European anthracotheriid *Elomeryx crispus*, in which the P_3-P_4 display different evolutionary stages on their internal wall (Hellmund 1991: 23 fig. 5). Schmidt (1913: 196) stated that the simple structure of the lingual face of the P_4 in *B. parvus* cannot correspond with individual variation, although he found an alleged P_3 that displays an analogu-

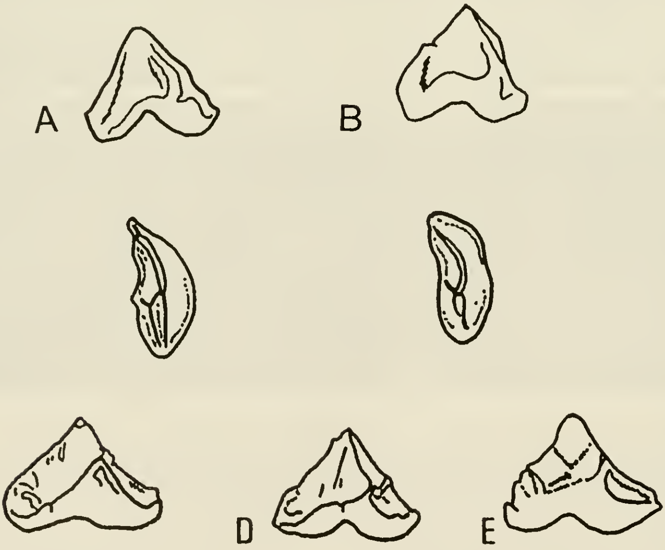


Fig. 8. Lingual (top) and occlusal (bottom) views of P_2 in *B. gorringei* (A: mandible 44080, SMNS; B: mandible Nr 46349, SMNS). Not to scale.
Lingual views of right P_4 in *B. gorringei* (C: mandible 44080; D: mandible 12636b; E: mandible 44101. All mandibles from the SMNS). Note the variation in the structure of the lingual crests. Not to scale.

ous simple lingual face. But this tooth is neither described, nor figured by SCHMIDT, and therefore cannot be referred to *B. gorringei.* The outline and dimensions of the lower molars are rather constant in *B. gorringei.*

No upper molars studied in the Collections of the NHML can be referred to *B. gorringei.* However, it is quite difficult to distinguish the upper molars of this species from those *of B. rugulosus* only by their dimensions. Structurally, the upper molars of *B. gorringei* display a typical association of features: they are wider than long, the parastyle is somewhat more labially protruding than the mesostyle, the cusps are more straightened, and the increasing of size from M^1 to M^2 is stronger than in *B. rugulosus.* As a consequence, the upper dental material from London previously referred to *B. gorringei* (M8423, M8424, M8425) should be regarded as belonging to the species *B. rugulosus.*

The type specimen of *B. parvus* is a fragmentary lower jaw with preserved M_1-M_2 (Nr C 8821). The distinctive features listed by ANDREWS (1906: 189) only apply to this specimen and not to other fossils from Stuttgart described by SCHMIDT (two fragmentary lower jaws: one with right P_4-M_2 without number associated with a right M_3 Nr 44101 and a juvenile left lower jaw with D_2-M_1 Nr 44105), which should be referred to *B. gorringei* (fig. 7D). The only difference that could be pointed out between *B. gorringei* and *B. parvus* is the weak development of the labial cingulid in *B. parvus.* This observation only applies to the material referred to *B. parvus*, with the exception of the type specimen C 8821. However, this cingulid is also poorly expressed in some other specimens of *B. gorringei* (for example on the lower jaw Nr 44101 figured on fig. 3A). The cingulid also tends to be more developed on the third lower molar in the latter species.

Another character that can be observed on relatively fresh teeth is the distal binding of the posterior cusps (entoconid and hypoconid) by a 'U' crest, that occurs only in a few specimens. In most of molars, this type of binding is different: the distal crest of the hypoconid (= posthypocristid) is lingually directed, and at the level of the posterior longitudinal valley of the molar, it runs distally and joins the hypoconulid (fig. 9).

Also, the posterior cusps of molars display a mesial binding which can be of two types. In most of the specimens, the anterior arm of the entoconid (= preentocristid) joins the anterior arm of the hypoconid (= cristid obliqua) in front of the hypocon-

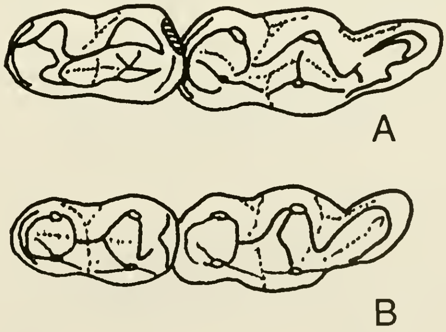


Fig. 9. Occlusal view of M_{2-3} in *B. gorringei.* A: mandible Nr 46350 (inversed, SMNS), B: mandible 8428 (NHML). Note the structure of the hypocristid on lower molars. Not to scale.

id. In three of about 15fragmentary lower jaws and/or isolated teeth (mandible M8428, 44105 and without number), there is an additional mesiolingual crest that runs from the apex of the hypoconid to join the preentocristid (fig. 9). HELLMUND (1991: 24, Fig. 6) regarded the occurrence of two distinct crests from the hypoconid as a primitive configuration, and the prehypocristid that joins to the cristid obliqua as an evolved situation.

Genus *Qatraniodon* n. g.

Type species: *Ancodon parvus* ANDREWS 1906.

Diagnosis. – Small anthracothere about the size of *Elomeryx crispus cluai*. Differs from all African species of *Bothriogenys* in its smaller size, its more elongated and slender lower molars with narrower mesial end of the trigonid, its straight and mesiolingually directed preprotocristid, and in its lack of the mesiolabial crest of the metaconid. Talonid wider than the trigonid. Talonid basin lingually open, posterior wall of the trigonid high. Cristid obliqua very low and reaching the middle of the trigonid wall. Lingual wall of the inner cusps vertical. Slight cingulid on the anterior face and on the labial end of the transverse valley on lower molars, and more strongly developed on their distal face. Horizontal ramus shallow (measurements in mm for C 8821 are: M_1 length, 12.3; M_1 trigonid width, 5.8; M_1 talonid width, 6.6; M_2 length, 14.4; M_2 trigonid width, 7.3; M_2 talonid width, 8.3).

Qatraniodon parvus (ANDREWS 1906)

* 1906 *Ancodon parvus.* – ANDREWS, p. 189–191; Text-Fig. 62.
1913 *Brachyodus parvus* (in part). – SCHMIDT, p. 195.
1978 *Bothriogenys parvus.* – BLACK, p. 427.

Holotype (by monotypy): A portion of the right ramus of a mandible with M_1-M_2; Nr C 8821, Geological Museum, Cairo.

Formation and location: Jebel Qatrani Formation.

Diagnosis. – Same as for genus.

A cast of a fragmentary lower jaw with right M_1-M_2 from the Natural History Museum in London (original Nr C8821 in the Geological Museum, Cairo) has been described as *Ancodon parvus* by ANDREWS (1906: 189–190) and then as *Brachyodus parvus* by SCHMIDT (1913: 195–196).

ANDREWS (1906: 189) gave a short description of the holotype, in which he pointed out the distinctive features observed with *Bothriogenys gorringei*. However, a description in detail is here necessary. The molars are basically quadritubercular and strongly increase in size from front to back. There is no apparent paraconid. The lingual cusps are bunodont and the labial ones are more selenodont, with their mesial and distal crest reaching only the middle of the tooth. The crowns are rather high, and their labial and lingual walls are vertical.

The trigonid cusps (protoconid and metaconid) are as high as the talonid ones and are situated close together with the protoconid being the larger of the two. The protoconid and the metaconid are joined by an almost vertical, high and distal crest that separates the trigonid basin from the posterior part of the tooth. The metaconid displays a short, low and mesially directed crest that ends at the mesial border of the molar above the slight mesial cingulid. An oblique and longer crest that originates from the protoconid apex joins the mesial end of the metaconid crest very low on the anterior face of the crown.

The talonids of M_{1-2} are somewhat wider than the trigonids. The entoconid is very slightly anterior to the hypoconid and is connected to it by a high V-crest whose head is mesially directed. The cristid obliqua is very low and joins the base of the trigonid wall at the midline of the tooth. On the M_2 (the freshest tooth), the distal crest of the hypoconid is lingually directed and stops in the midline of the tooth without connecting the distal wall of the entoconid. The latter cusp displays a slight distal crest that joins the lingual end of the distal cingulid. A well developed hypoconulid is present on both lower molars, it is laterally bounded by a distal cingulid.

The labial cingulid is developed only in the valley between the protoconid and the hypoconid. The mesial cingulid extends from the mesiolingual to the mesiolabial corners of the tooth.

Althought it belongs to a juvenile specimen, the mandible is slender, measuring 19.1 mm at its greatest depth, beneath M_2 talonid. The inferior border of the ramus angle gently runs upward from this point, and there is no indication of an expanded mandibular angle.

The generic status of *Bothriogenys parvus*

The cast Nr C 8821 displays dental dimensions and structure that distinguish it from all other fossils described as *B. parvus*. As the other fossil specimens previously attributed to *B. parvus* might belong to *B. gorringei* (see above and below), only the cast C8821 can be referred to *B. parvus*. Indeed, the molars of the cast are markedly smaller and more elongated than those of all other specimens previously referred to *B. parvus* (fig. 10).

Qatraniodon parvus is clearly an anthracotheriid. As other representatives of the family, it is characterized by the presence of strong, mesially directed premetacristids, well separated metaconids and protoconids that are subequal in size, cristid obliqua that connects the posterior trigonid wall, and V-shaped hypolophids.

The M_1 of *Qatraniodon* is smaller than that of the mandible Nr 44 105 (15.8 x 8.9) which is the smallest specimen attributed to *Bothriogenys gorringei*, and than those of all other species of *Bothriogenys*, and it further displays several differences of structure. The preserved portion of mandible C 8821 is shallower than in all other species. The preprotocristid directly joins the premetacristid mesially to the meta-

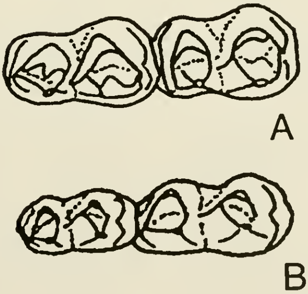


Fig. 10. Comparison of occlusal view of M_{1-2} of A: *B. gorringei* (mandible cast M8881, NHML) and B: *B. parvus* (cast of C8821, SMNS). Not to scale.

conid, so that the trigonid basin seems to be lingually closed. In addition, there is no mesiolabial crest that goes from the apex of the metaconid down to the trigonid basin, as is the case in all other species of *Bothriogenys*. Such a crest occurs on the M_1 of the mandible 44 105 on which the preprotocristid surrounds the mesial border of the tooth and connects with the mesial part of the base of the metaconid. The trigonid basin is thus crescentic in outline and seems to be lingually open. Also, the trigonid seems to be more mesially compressed than in all other species, and the cristid obliqua does not ascend the posterior trigonid wall. Finally, the talonid of M_2 is lingually open since the posthypocristid does not reach the postentocristid or the base of the entoconid. All these features are unusual in *Bothriogenys*, and therefore warrant a distinct generic status for the mandible C 8821.

Another anthracotheriid genus described by SCHMIDT (1913) from the Fayum fauna is *Rhagatherium aegyptiacum*. This species is only known by an isolated presumed M^3, and therefore direct comparisons are not possible with the fragmentary mandible C 8821. Three species of *Rhagatherium* are so far known in Europe (*R. valdense*, *R. frohnstettense* and *R. kowalevskyi*) and possibly one or two other species in India. In a general way, *R. valdense* and *R. frohnstettense* differ from the Fayum artiodactyl in their smaller size and in their wider lower molars with more labially protruding anterior and posterior lobes. *R. kowalevskyi* also is much smaller than the Fayum species. In his description of this species, HELLER (1930) pointed out that the occurrence of an intermediate cusp on the posterior arm of the hypoconid characterizes the genus *Rhagatherium*. However, no trace of such a cusp can be observed on the Fayum species. In addition, the more slender occlusal outline of the lower molar, the lack of a crest on the mesial face of the entoconid, of a labial cingulid, and the occurrence of a weaker distal cingulid set the latter form away from *R. kowalevskyi*.

The other artiodactyl known in the Fayum assemblage is *Mixtotherium mezi*. This species, that should be referred to the Mixtotheriidae, is represented by an isolated M^3 which is much larger than the corresponding teeth of the European species (SUDRE 1977: 47). The European species *Mixtotherium cuspidatum*, *M. priscum* and *M. leenhardti* differ from the Fayum mandible in their smaller size (except for *M. priscum*), their more massive lower molars, their open trigonid, their weaker distal cingulid, and their more distally situated entoconid. Therefore, on the basis of its general structure and dimensions, the specimen C 8821 cannot be referred to the genera *Rhagatherium* or *Mixtotherium*.

It must be stressed that the fragmentary mandible C 8821 displays an association of several dental features that can be found in the genus *Anthracokeryx*, a genus known exclusively in Asia: the lower molars are quite elongated with the anterior lobe somewhat wider than the posterior lobe, the preprotocristid is mesiolingually orientated, and the premetacristid is short, mesially directed, and connects lingually to the preprotocristid just above the mesial end of the crown, the talonid basin is distally open. These characters are particularly well observed in the late Eocene species from Thailand, *Anthracokeryx thailandicus* (DUCROCQ 1992*)*. However, the Fayum species differs from all species of the genus in its smaller size (with the exception of *A. tenuis* from Burma), its much shallower horizontal ramus, its more slender lower molars, its more developed distal cingulid, and in lacking the mesiolabial crest of the metaconid.

The other material previously attributed to *B. parvus*

The upper P^4 figured by Schmidt (1913, pl. 3, figs. 7–8) displays dimensions and morphology that are similar with those of the corresponding tooth of *B. gorringei*. Schmidt (1913: 19) stressed on the height and the sharp crests of this tooth as distinctive features for *B. parvus*, but the P^4 is unworn, and therefore cannot be distinguished from the morphology of the last premolar of *B. gorringei*.

Also, the descriptions and illustrations by Schmidt (1913: 17–18) of upper molars attributed to *B. parvus* fit well with the upper molars of *B. gorringei*. Indeed, the metacone more lingual than the paracone, the strongly developed barrel of labial cusps, the small paraconule close to the protocone, the metastyle not salient distally, the distal cingulum that follows the distal end of the longitudinal valley, the weakening cingulum at the base of the metaconule, and the parastyle stronger than the mesostyle are characteres that are found also in *B. gorringei*.

The right D^4 referred to *B. parvus* by Schmidt agrees very well with a milk molar of *B. gorringei*, and there is no reason to attribute it to another species on the basis of its structure.

Tab. 1. Measurements (in mm) of the dental material attributed to *Bothriogenys* from SMNS and NHML.

Bothriogenys gorringei (SMNS)

Mandible Nr 44080	Length	Width	Mandible Nr 44105	Length	Width
right P/2	13.8	6.8	left D/2	9.3	4.4
right P/3	16.2	8.4	left D/3	14.3	6.0
right P/4	17.1	9.8	left D/4	18.3	7.4
right M/1	15.0	10.3	left M/1	15.8	8.9
right M/2	18.0	12.4			
right M/3	29.0	13.9			
Mandible Nr 46348	Length	Width	Mandible Nr 12636b	Length	Width
right P/3	15.3	7.4	right P/3	16.3	9.0
right P/4	16.0	8.9	right P/4	16.7	9.6
right M/1	17.3	10.3	right M/1	16.6	10.2
right M/2	19.3	11.8	right M/2	20.4	12.3
right M/3	27.5	12.2			
Mandible Nr M 8428	Length	Width	Mandible without Nr	Length	Width
right M/2	19.2	12.3	right P/4	15.4	8.3
right M/3	31.2	13.8	right M/1	16.4	9.8
right M/2	19.3	12.3			
Isolated right M/3	Length	Width	Mandible Nr 46508	Length	Width
(associated with the above mandible)			right M/3	33.4	15.8
Nr 44101	27.2	12.3			
Mandible Nr 46349	Length	Width	Mandible Nr 46512	Length	Width
right P/2	12.5	7.4	right P/4	14.9	8.9
right P/3	16.7	8.8	right M/1	–	–
right P/4	17.0	9.9	right M/2	18.2	13.2
right M/1	17.2	10.3	right M/3	28.3	14.2
Mandible Nr 11949	Length	Width	Mandible without Nr	Length	Width
right D/4	19.3	8.3	left M/1	17.1	10.8
right M/1	17.6	10.1	left M/2	18.9	13.3
left M/3	30.7	14.2			

Isolated right M/3	Length	Width
	30.8	15.2

Isolated right M/1	Length	Width
	17.1	9.4
(enamel lacking)		

Isolated right P3/	Length	Width
	14.2	10.8

Isolated left M2/	Length	Width
	21.4	23.5

Isolated left M3/	Length	Width
(44079)	26.2	27.9
right M1/	21.1	19.5

Palate Nr 46352	Length	Width
left P4/	11.3	16.4
left M1/	17.4	18.5
left M2/	21.4	24.5

Isolated left M/1	Length	Width
	16.5	10.4

Mandible Nr 46510	Length	Width
left M/3	32.3	14.2

Isolated right M2/	Length	Width
	20.7	24.8

Isolated left M2/	Length	Width
	21.4	24.6

Palate without Nr	Length	Width
right P4/	13.0	15.3

Palate Nr 44135	Length	Width
left M2/	19.6	21.1
left M3/	20.8	22.6

Bothriogenys gorringei (NHML)

Mandible Nr M8881	Length	Width
right I/3	8.4	6.5
right P/2	15.5	9.8
right P/3	18.9	11.6
right P/4	19.3	13.2
right M/1	18.9	12.8
left M/1	18.7	12.3
right M/2	22.8	16.2
left M/2	21.8	15.4
right M/3	34.4	18.7
left M/3	35.0	18.7

Mandible Nr 9462	Length	Width
left M/2	21.3	13.4
left M/3	26.9	14.7

Mandible Nr 10350	Length	Width
left D/3	15.1	6.4
left D/4	21.4	8.3
left M/1	18.3	10.7

Mandible Nr 8505B	Length	Width
left P/4	17.8	10.2
left M/1(trigonid)	–	8.8
left M/2	19.8	12.8
left M/3	31.3	14.2

Mandible Nr 8506A	Length	Width
right M/2	22.3	13.4
right M/3	34.3	15.5

Mandible Nr 8506B	Length	Width
left M/3	31.6	14.8

Mandible Nr M8506B	Length	Width
left M/1	15.3	9.9
left M/2	18.9	11.4
left M/3	26.3	13.5

Isolated right P/2	Length	Width
Nr M8428	14.0	7.3

Mandible Nr M10351	Length	Width
right D/4	23.6	8.4
right M/1	17.7	10.5

Mandible Nr 8428	Length	Width
right M/2	18.1	12.4
right M/3	30.4	13.4

Mandible Nr 8505A	Length	Width
right P/4	18.3	9.9
right M/2	21.7	13.9
right M/3	34.5	15.8

Mandible Nr 8427	Length	Width
left P/3	16.4	10.9
left P/4	17.8	11.4
left M/1	17.8	–
left M/2	20.2	13.5

Mandible Nr 8428	Length	Width
left P/4	16.4	8.8
(badly preserved)		

Bothriogenys fraasi (SMNS)

Mandible Nr 11948	Length	Width
right D/2	12.8	6.6
right M/1	17.7	11.4
right M/2	23.2	14.7

Mandible Nr 44081	Length	Width
left M/1	16.8	11.3
left M/2	21.8	15.3
left M/3	34.7	17

Mandible Nr 44174	Length	Width
(very worn)	right P/4 21.2	
left P/2	–	8.6
left P/3	16.4	10.8
left P/4	20.0	12.5
left M/1	20.4	–
left M/2	>23.8	–
left M/3	32.0	–

Mandible Nr 44176	Length	Width
13.3		
right M/1	18.2	12.4
right M/2	22.9	>14.7
right M/3	38.0	>16.2

Mandible Nr 46509	Length	Width
right M/2	21.8	14.8
right M/3	31.6	17.4

Mandible Nr 46514	Length	Width
right M/1	17.5	9.4
right M/2	21.8	13.3
right M/3	–	15.0

Skull Nr 44175	Length	Width
right P1/	16.3	11.3
left P1/	15.2	10.0
right P2/	15.5	12.0
left P2/	15.8	13.2
right P3/	17.1	18.3
left P3/	18.1	17.7
right P4/	15.8	19.4
left P4/	16.3	19.1
right M1/	21.8	22.9
left M1/	22.4	22.7
right M2/	26.7	29.7
left M2/	27.4	29.3
right M3/	30.2	32.9
left M3/	31.3	34.3

Palate Nr 46513	Length	Width
right M1/	22.4	22.4
right M2/	25.8	27.5
left M2/	24.9	27.1

Bothriogenys fraasi (NHML)

Skull Nr M10186	Length	Width
left P1/	15.4	10.3
right P1/	15.8	10.2
left P2/	18.3	12.9
right P2/	17.7	14.6
left P3/	21.2	16.1
right P3/	20.8	16.5
left P4/	16.0	20.4
right P4/	16.3	19.8
left M1/	22.9	23.7
right M1/	23.9	23.0
left M2/	29.5	28.5
right M2/	28.8	28.9
left M3/	31.3	32.5
right M3/	30.8	32.8

Mandible Nr 9462	Length	Width
right P/3	18.0	9.6
right P/4	22.5	10.8
right M/1	18.5	11.5
right M/2	23.8	14.8
right M/3	35.0	15.9

Bothriogenys rugulosus (SMNS)

Mandible Nr 12636b	Length	Width
left P/3	12.5	7.8
left P/4	14.6	8.4
left M/1	11.3	–
left M/2	15.6	10.3
left M/3	26.7	12.7

Mandible Nr 12636a	Length	Width
left M/2	16.3	11.9
left M/3	25.9	13.3

Mandible Nr 46512	Length	Width
right M/3	27.8	13.1

Mandible Nr 44137	Length	Width
right M/2	16.8	11.7
right M/3	26.6	12.7

Palate Nr 44134	Length	Width
left P1/	11.6	6.9
left P2/	13.5	8.9

Mandible without Nr	Length	Width
right M/2	18.2	11.5

Isolated left M/3	Length	Width
	12.3	–

Palate Nr 44133	Length	Width
left P4/	11.5	15
left M1/	16.3	16.8
left M2/	20.4	20.7

Palate Nr 44136	Length	Width
left M1/	16.8	16.5
left M2/	19.2	18.1
left M3/	19.3	20.4

Bothriogenys rugulosus (NHML)

Maxilla Nr 9243	Length	Width
right M2/	16.3	16.0 (part of parastyle and mesostyle lack)
right M3/	18.3	19.8

Maxilla Nr 8425	Length	Width
right P3/	15.9	12.2
right P4/	12.8	16.4
right M1/	–	–
right M2/	20.5	–
right M3/	25.2	25.1 (min.)

Maxilla Nr 8423	Length	Width
right P3/	16.4	12.7
right P4/ (ling. broken)	13.1	14.3
right M1/	16.8	18.3
right M2/	21.8	22.5
right M3/	24.6	24.5

Maxilla Nr 8424	Length	Width
left P4/	12.3	14.3
right P4/ (broken)	12.4	14.1
left M1/	17.9	17.8
right M1/	16.7	17.6
left M2/	21.8	22.9
right M2/	21.7	21.5
right M3/	23.9	24.6

Maxilla Nr 8423	Length	Width
left M3/	24.4	24.9

Bothriogenys andrewsi (SMNS)

Isolated right D/4	Length	Width
Nr 44084	24.9	10.5

Isolated right M/3	Length	Width
Nr 44087	43.8	19.0

Isolated right M2/	Length	Width
Nr 44086	29.5	31.3

Isolated right M2/	Length	Width
	–	30.4

4. Comparisons with the Asian species of *Bothriogenys*

Outside North Africa, the genus *Bothriogenys* has also been described in the lower Oligocene of Xiaotun (Yunnan Province, south China) and of Baishuicun (Shanxi Province, northeast China) by Chow (1958) and Xu (1962), and from the late Eocene of Thailand (Ducrocq 1992, 1994a, in press). Chow previously described the fossils as *Hyoboops hui*, and later Xu referred this species to the genus *Brachyodus*. More recently, Dineur (1981) provisionally assigned this material to the genus *Bothriogenys* on the basis of its molar morphology. Chow & Chang (1960) also referred dental material from the lignite beds of Shiping (Gui-zhou Province) to an anthracothere close to *Brachyodus*. This material consists of a fragmentary upper molar and an isolated P^4. According to the illustrations, these teeth belong to two distinct species, and the upper premolar is probably a P^3 of an *Anthracotherium*-like mammal on the basis of its morphology, size and lack of well developed crests. The upper molar only preserves the lingual half, but reminds the corresponding upper teeth of *Bothriogenys*.

Xu (1962) referred to a fragmentary maxilla with the posterior part of M^2 and a complete M^3, and a fragmentary lower jaw preserving M_2-M_3 and an isolated M_3 from Lunan (Yunnan Province) to *Brachyodus hui*. I follow here the opinion of Dineur (1981) and refer the Chinese material figured by Xu to *Bothriogenys*. The Chinese anthracothere is about the size of *B. fraasi*, but the M^3 from Lunan (Vm 0028) differs from that of all species from the Fayum in its more lingually salient mesial lobe and in its metacone with more widely open mesial and distal arms. The Chinese lower molars (Vm 0050) also display the characteristic Y form of the prehypocristid, and the labially salient external cusps as in *B. fraasi*, but in a general way, these Asian molars have a weaker cingulid and a wider mesial part of the trigonid. In general, the molars described as *Brachyodus hui* strongly remind those of *Bothriogenys fraasi* by their dimensions and their structure.

The *Bothriogenys* species that has been found in the late Eocene lignite beds of south Thailand is known by its almost complete dentition and therefore deserves further consideration. Its complete description and illustrations are included in a monograph on anthracotheres from Thailand actually in press (Ducrocq in press). However, it is necessary, for the better understanding of this study, to give here the systematic paleontology of this species.

Bothriogenys orientalis n. sp.

Holotype: Almost complete skull with left P^1-M^3 and right P^2-M^3 (TF 2633), associated with two lower jaws preserving right and left P_1-M_3 (TF 2634 and TF 2635); Collections of the Department of Mineral Resources, Bangkok.

Formation: Bang Pu Dam lignite mine, Krabi basin, southern Thailand. Clay level underlying the main lignite seam (Formation B2), late Eocene (Bristow 1991).

Diagnosis. – Bothriodontine anthracothere about the size of *Bothriogenys fraasi* from the Fayum. *B. orientalis* differs from all Fayum species in its P^4 with less vertical labial wall of the paracone, its upper molars lacking a lingual cingulum, its caniniform P_1, and in its horizontal ramus lacking a downturned angular process under M_3. Differs from *Bothriogenys hui* from China in its upper molars with weaker parastyle and lacking a lingual cingulum. The astragalus of *B. orientalis* can be distinguished from that of the African species by its more slender outline.

Fig. 11. Comparison of lower tooth rows in different species of *Bothriogenys*. A: *Bothriogenys* from Krabi, B: *B. andrewsi*, C: *B. fraasi*, D: *B. gorringei*, E: *B. rugulosus*, F: *Qatraniodon parvus* (only known by M_1-M_2). Scale bar = about 10 mm.

For lower teeth, right lower tooth rows of *Bothriogenys* from Krabi: TF 2634; *B. andrewsi*: M_3 44087 (SMNS); *B. fraasi*: composite drawing with mandibles 44081 (SMNS) and 9462 (NHML); *B. gorringei*: cast of mandible 8881 (NHML); *B. rugulosus*: composite drawing from mandibles 12636a and 12636b (both inversed and SMNS); *Q. parvus*: C 8821.

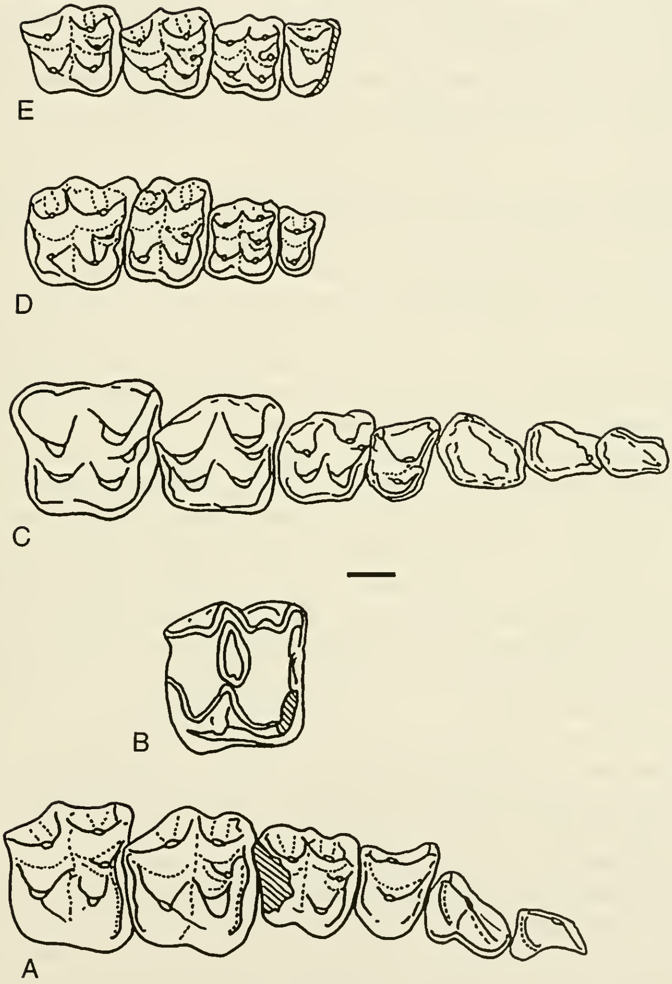


Fig. 11. (Continued). Comparison of upper tooth rows in different species of *Bothriogenys*. A–E: same as left side.

For upper teeth, right upper tooth rows of *Bothriogenys* from Krabi (A): TF 2633; *B. andrewsi* (B): M^2 Nr 46353 (SMNS); *B. fraasi* (C): skull 10186 (NHML); *B. gorringei* (D): composite drawing from maxillae 44079 (inversed) and 46352 (both SMNS); *B. rugulosus* (E): composite drawing from maxillae 44136 and 44133 (both SMNS).

The four recognized species of *Bothriogenys* from the Fayum fauna are morphologically very close to the Thai species described from the Krabi basin in southern Thailand (Ducrocq 1992, in press). As a whole, the Asian and African forms differ in relatively weak dental features: more slender and mesiodistally compressed parastyle and mesostyle, more developed lingual cingulum, lingual cusps somewhat more labially slanted and more laterally compressed paracone in the Fayum species.

More complete comparisons can be made with *B. fraasi* for which two almost complete skulls (Nr 44 175 and M 10 186) are housed in the Collections of the SMNS and of the NHML. The Asian and African species display about the same size, but several small differences can be pointed out. In ventral view, *Bothriogenys orientalis* possesses slightly lingually concave upper tooth rows when they are straight in *B. fraasi*. In addition, the anterior palatal foramina open in front of the distal wall of P^3 in *B. fraasi*, and these structures are almost not visible in the Asian species but it seems that they open in front of the mesial or distal wall of P^4. In dorsal view, the posterior zygomatic root arises somewhat behind the junction of the frontal crests in *B. fraasi*, and it begins at the level of the junction of these crests in the Thai species. In addition, the anterior rim of the orbite is above the mesial wall of M^2 in *B. orientalis*, and it is above the distal wall of the same tooth in *B. fraasi*.

Concerning the teeth, minor differences can be observed between the African and the Asian species (fig. 11). In general, the molar and premolar patterns of both taxa are very close and the main differences are the followings: in *B. fraasi*, the lingual cingulum is stronger and more complete on the upper molars, the parastyle is larger and more salient, and the lingual and labial cusps are slightly more vertical than in the Asian species. In the latter, the outer wall of the P^4 is more labially concave (it is straighter in *B. fraasi*), the lingual cingulum is more developed in the African species and there is a very slight crest that goes from the apex of the protocone down to the distolingual corner of the tooth that is absent in *B. orientalis*. The P^3 displays the same structure in both forms but the lingual wall of this tooth is straight in *B. fraasi* and concave in the Asian form. The same observations can be made for the P^2. The P^1 is weakly reduced with respect to P^2 but it displays the same morphology in *B. fraasi*. In the Thai *Bothriogenys*, this tooth is very simplified, it is not triangular in occlusal view and it is blade-shaped.

The mandible of *B. fraasi* is more curved under the tooth row and the symphysis only reaches the anterior wall of P_1 (the anterior wall of P_2 in the Thai species). The mesiolingual spur of P_2 is weaker in *B. fraasi*. In addition, the M_1 and M_2 are comparatively shorter in the Fayum species. Also, the premolar row is longer in *B. orientalis*, with a longer diastema between P_2 and P_1.

B. andrewsi is the largest species of *Bothriogenys*. It is slightly larger than the Thai species and differs from it in its better developed lingual cingulum, its more labially situated metastyle and its slightly more lingually slanted labial wall of the labial cusps on upper molars. The most noticeable feature of its P^4 is the much more developed mesiolabial corner of the tooth than in *B. orientalis*. The only known lower teeth of *B. andrewsi* are isolated D_4 and M_3. The M_3 is about the same size than that of the Thai species, but with a slightly more wrinkled enamel, and a more distolabially orientated hypoconulid. In addition, the trigonid is lingually slightly open in *B. andrewsi* while it is closed in *B. orientalis*, but this difference might likely be due to the difference of wear in the two teeth.

Schmidt (1913) noted that *B. rugulosus* can be distinguished from the other species by its strongly crenulated enamel and by its very steep labial cusps on the upper molars. These features also distinguish the African and the Asian forms. The P^2 of *B. rugulosus* (Nr 44 134) is more curved than that of the Thai *Bothriogenys* in occlusal view and its lingual and labial cinguli are better developed. In addition, the apex of the crown is situated above the anterior root whereas it is above the space between the two roots in *B. orientalis*. The same remarks can be made for the P^1 of the two species. The P^4 of the African form displays a stronger lingual cingulum and a straighter labial wall than in the Thai species. On the upper molars, the lingual cingulum is better developed, the metastyle on M^3 is more distolabially salient and the labial cusps are in a more vertical position in *B. rugulosus*.

B. rugulosus also displays a more curved mandible, a much more wrinkled enamel and a stronger labial cingulid on its lower molars than in the Thai *Bothriogenys*. Also, the lingual basal crest of the P_3-P_4 of *B. rugulosus* does not occur in the Asian form.

On the P^3 of *B. gorringei*, the distal crest labially curves, its apex is more mesially situated and its talon is slightly weaker than in *B. orientalis*. The P^4 of *B. gorringei* displays a much stronger distal cingulum, but its parastyle is more salient than its mesostyle thus resembling the corresponding tooth of the Thai species. In upper molars, the lingual cingulum is stronger and the labial styles are more labially salient in *B. gorringei*.

B. gorringei also displays a more dorsoventrally curved mandible with a longer retromolar space behind M_3. Its P_2 bears a strong lingual crest that joins the lingual cingulum and the apex of the tooth. Also, the P_3 of *B. orientalis* displays a double distal crest that remains on its posterior face; in *B. gorringei* the distal crest divides at mid-height of the distal face and its lingual part extends on the lingual face to join a strong enamel shelf that runs along the whole base of the crown. This lingual crest is oblique on the P_4 of *B. gorringei* and it is horizontal and parallel to the base of the crown in the Thai species.

Finally, a feature that distinguishes the four African species and the Asian form is the absence in the latter of a diastema between P_3 and P_2, although it can be very short in the Fayum forms (for example in the mandible Nr 44 174 of *B. fraasi* or in the mandible Nr M8881 of *B. gorringei*).

As a whole, the molar structure of the Fayum species is very similar with that of *B. orientalis*. The differences in the dental structure (lingual cingulum, styles, transversely compressed paracone and slope of the labial cusps on upper molars, lower molars with somewhat higher cusps, occurrence of a distinct diasteme between P_3 and P_2 and structure of the lower premolars) that can be pointed out in the African species suggest that they likely derive from the Thai form. An origin from the Chinese taxa listed above must also be considered, but the scarceness of the Chinese material does not allow to go further in this hypothesis. In addition, some of these differences are so tenuous that a short time might have separated *B. orientalis* and the species from Egypt. An independent parallel development of the Asian and African species is not likely because convergence cannot sufficiently explain the strinkingly close relations between the two groups.

5. Phylogenetic relationships

According to SCHMIDT (1913), *B. rugulosus* is the smallest and the most primitive species. It is also characterized by strong rugose sculptures of the enamel, and by the low but steep external cusps of upper molars. *B. gorringei* and *B. fraasi* can be distinguished mainly by the position and size of the diastema. *B. gorringei* displays a diastema before and behind the P_1, and between P_2 and P_3; *B. fraasi* has a diastema only before P_1.

The different species from North Africa are very close to that from Thailand. A South Asian origin of the Fayum anthracotheres seems now well established on the basis of the morphological and structural similarities observed on the dental material.

Nevertheless, it is difficult to propose a coherent set of characters for the species of *Bothriogenys* because the latters are very close each others. In addition, some features that could be used seem to reflect a more or less important degree of wear of the crown rather than a primitive or evolved state. That is the case, for example, of the preentocristid (the mesiolabial crest of the entoconid) on the lower molars. This crest can either join the cristid obliqua (the mesiolingual crest of the hypoconid) in the middle of the transverse valley, or it can join a small mesiolingual crest parallel to the cristid obliqua that descends from the apex of the hypoconid. In fact, the second situation only occurs in specimens of *Bothriogenys* which have fresh and unworn teeth, contrary to what is observed in the European species of *Elomeryx* (HELLMUND 1991).

However, I selected 14 dental characters that define four species of the Fayum anthracotheres (*B. gorringei*, *B. rugulosus*, *B. fraasi* and *B. andrewsi*) and the species from Thailand. The anthracotheres from China and the species *parvus* have not been included in the study because they are too poorly known, and/or because their generic status is not known with certainty. As outgroup, I chose the species *Siamotherium krabiense* from the late Eocene locality of Krabi, which is considered the most primitive anthracothere so far known (SUTEETHORN et al. 1988).

The computer processing of data was made with the PHYLIP program set (PHYLogeny Inference Package) by Joseph Felsenstein of the Department of Genetics, University of Washington, Seattle, Washington, U.S.A., using PENNY. PENNY is a programm which finds all the most parcimonious trees through the use of the 'branch and bound' search algorithm (GROVES & PATERSON 1991). The dental characters have been translated into derived (1) and primitive (0) features (Annex, table 2), and the characters have been considered irreversible.

On three trees out of six provided by the program PENNY, *B. rugulosus* is the sister-taxon of *Siamotherium*, the smallest and most conservative anthracothere from Thailand. Although *B. rugulosus* can be considered the most primitive species of *Bothriogenys*, it is not related to other African taxa on trees 1, 2, and 3 (fig. 12). To the contrary, trees 4, 5, and 6 indicate a direct relationship between *Siamotherium* and the Thai species of *Bothriogenys*, and the Fayum taxa form a monophyletic group. However, the relationships between *B. fraasi*, *B. andrewsi and B. gorringei* are identical on trees 1 and 4, 2 and 5, and on 3 and 6.

On all trees, characters 1 (length of symphysis) and 9 (development of premetacristid on lower molars) appear three times in the different phylogenies. These characters can therefore be regarded as homoplasies because they seem to be unreliable

CHARACTERS	*B. gorringei*	*B. rugulosus*	*B. fraasi*	*B. andrewsi*	*B.* Krabi	*Siamoth.*
1. Length of symphysis (1: reaches P/1; 0: shorter)	1	1	0	?	1	1
2. Diastema between P/3 and P/2 (1: yes; 0: no)	1	1	1	?	0	1
3. Diastema between C and P/1 >> diastema between P/1 and P/2 (1: yes; 0: no)	1	1	1	?	0	0
4. Metaconid on P/3 (1: yes; 0: no)	1	0	0	?	0	0
5. Metaconid on P/4 (1: yes; 0: no)	1	1	1	?	1	0
6. Y prehypocristid on lower molars (1: yes; 0: no)	0	1	1	0	0	0
7. Strong increase of size from M/1 to M/3 (1: yes; 0: no)	1	0	1	?	1	1
8. Marked labial cingulid on P/4 (1: yes; 0: no)	1	0	1	1	0	0
9. Premetacristid of lower molars well developed (1: yes; 0: no)	0	1	1	0	1	1
10. Cristid obliqua high (1) or low (0) on fresh lower molars	1	0	1	1	1	1
11. Upper molars wider than long (1: yes; 0: no)	1	0	1	1	1	1
12. Mesial crest of paracone and labial crest of metacone directed respectively mesiolabially and distolabially (1: yes; 0: mesially and distally)	1	0	1	1	1	0
13. Labial cingulum of upper molars continuous (1: yes; 0: no)	1	1	1	1	0	1
14. Parastyle of upper molars tends to be more salient than mesostyle (1: yes; 0: no)	1	0	0	0	0	0

Tab. 2. Dental characters used in the phylogenetical study of *Bothriogenys*, and their correspondance in apomorphy (1) and plesiomorphy (0).

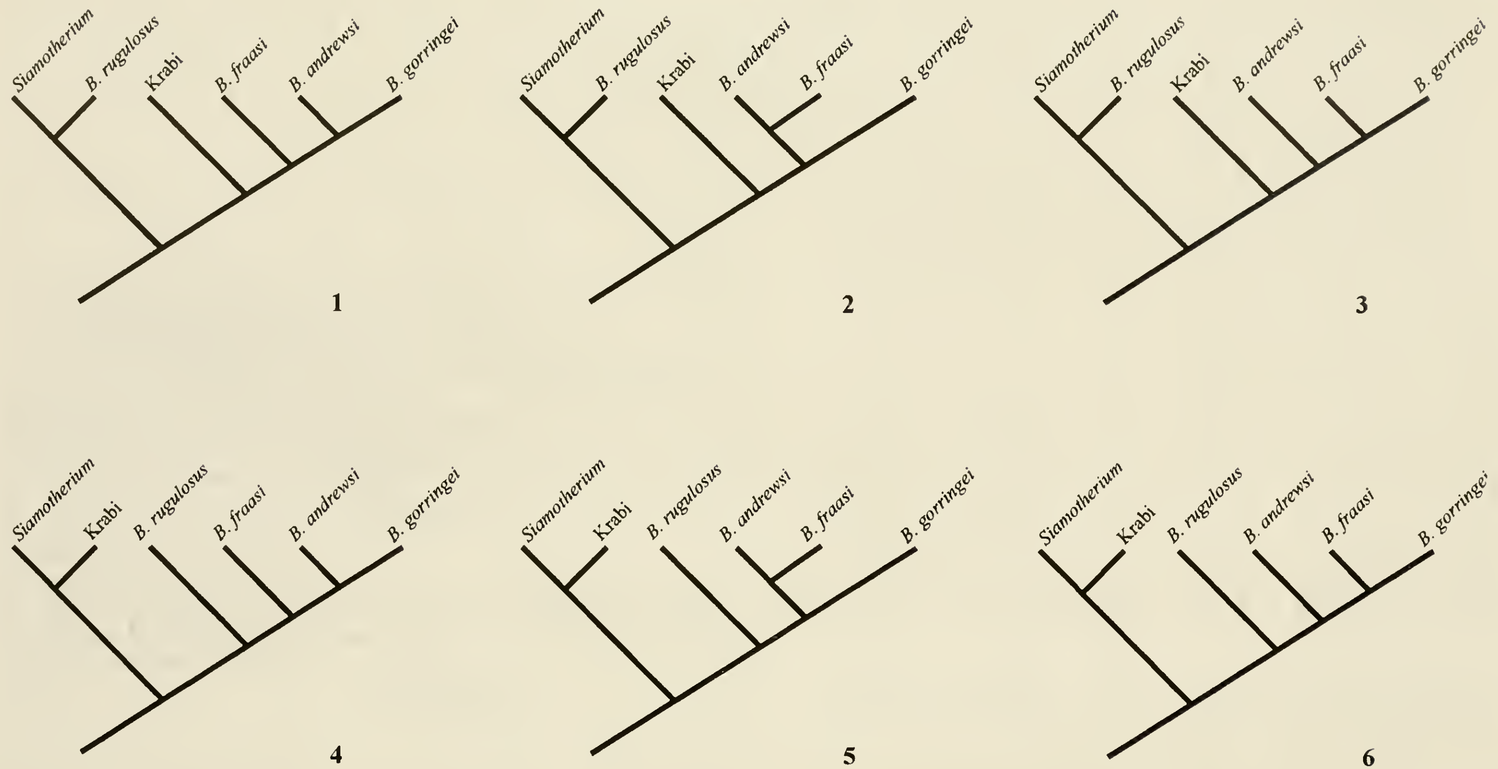


Fig. 12. Most parcimonious phylogenetical trees for the genus *Bothriogenys* (see explanations in text).

indicators for these phylogenies. On the other hand, characters 4 (metaconid on P_3), 8 (labial cingulid on P_4), 12 (orientation of crests on upper molars) and 14 (relative size of parastyle and mesostyle on upper molars) appear once only on trees 1 to 3, and thus are regarded by the program PENNY as the best and more reliable characters. Such characters on trees 4 to 6 are number 3 (diastema between C and P_1), 4, 8, and 14 which also occur once.

All trees presented in fig. 9 required 26 steps and thus are all the most parcimonious..In a general way, the trees 1 to 3 are not consistent with the paleobiogeographical distribution of the anthracotheres selected here. In a morphological point of view, *Siamotherium* is too much specialized to have given rise to the African species, and is more closely related to Asian taxa (Ducrocq 1994a). *B. rugulosus* is obviously closer to other species of *Bothriogenys* than to the Thai small form. For these reasons, trees 1, 2, and 3 are not representative of a phylogeny of the Fayum anthracotheres and should be eliminated.

Although it is known by very few dental material, *B. andrewsi* seems to be morphologically closer to *B. gorringei* than to the other species (the occlusal outline of its lower molars, its mesiodistally developed hypoconulid lobe, its orientation of cusps rather remind those of *B. gorringei*). This leads to suppose that the tree 5, in which *B. andrewsi* and *B. fraasi* are sister-taxa, does not reflect the relationships that could have linked both species. Trees 4 and 6 therefore appear to be the most reliable with the morphological arguments discussed above. As *B. andrewsi* and *B. gorringei* display a very similar tooth structure, it is more logical to consider both species more closely related, as discussed in chapter 3. Thus, I think that tree 4 is the most representative of the phylogenetical relationships that might have occurred between the different anthracothere species from the Fayum deposits.

It must be kept in mind that somewhat different results might be obtained if the characters and/or the computer program used in the study are changed; however, the conclusions discussed here are based on the dental material that is actually available in Stuttgart and London. When additional material is found for *B. andrewsi* for example, it is possible that the interpretation of the phylogenetical relationships can be modified.

6. Paleobiogeographical relationships between South Asia and the Arabo-african area during the Paleogene

The age of the Jebel Qatrani fossil beds has never been clearly established. This formation in the Fayum (Egypt) is alternatively regarded as lower Oligocene (Gingerich 1993; Pickford et al. 1994) or Upper Eocene (Van Couvering & Harris 1991), although some authors assume that the lower part of this formation is Upper Eocene in age and its upper part is lower Oligocene (Rasmussen et al. 1992).

If the African species of *Bothriogenys* derive from the Thai form, or from a closely related but yet unknown species, one must assume that a migration from South Asia to North Africa may have occurred during a relatively short time. In addition, it is reasonable to suppose that the Arabian area was a likely stage of this migration and that the anthracotheres might have begun to radiate before invading a more western region. As a matter of fact, mammalian exchanges between the Arabo-African continent and Asia are supported by several mammal groups such as primates (for example SIMONS & BOWN 1985; THOMAS et al. 1988), anthracotheres (present work), creodonts (for example CROCHET et al. 1990), marsupials (for example CROCHET et al. 1992), and even palaeoryctid insectivores (GHEERBRANT 1990).

The Fayum fauna also strongly suggests that other mammals might have entered quite far westwards in the late Eocene. As a matter of fact, the similarities displayed by the Anthracotheriidae of the Fayum fauna and those from Thailand suggest that *Bothriogenys*, as *Anthracotherium* (DUCROCQ 1994a), has an Asian origin. Such morphological similarities cannot be regarded as convergence because the anthracotheres from Thailand are somewhat more primitive than those from Egypt and they display too many common features to assume these resemblances as convergence. Therefore, one should conclude that intercontinental migrations from Asia to Africa were likely during the late Eocene and/or the lower Oligocene, and that these faunal exchanges occurred in a relatively short time given the evolutionary stage of the anthracotheres from both areas.

According to RASMUSSEN et al. (1992: Table 28.1), the genus *Bothriogenys* might be known in the Libyan site of Zella (cited in RASMUSSEN et al. 1992) which they regard as lower Oligocene in age. Indeterminate anthracotheres have also been recorded in the Algerian locality of Nementcha dated from the late Eocene by DE BONIS et al. (1988) and from the lower Oligocene by RASMUSSEN et al. (1992). The occurrence of *Bothriogenys* in the Fayum sediments and probably also in other parts of North Africa seems therefore to indicate that these mammals were able to reach North Africa in the late Eocene from South Asia, likely through the Afro-Arabian landmass.

However, additional discoveries of anthracothere remains (among others) should be expected in the Paleogene deposits of the Arabian Peninsula. Indeed, the rich mammalian faunas already discovered in the Sultanate of Oman (THOMAS et al. 1989; GHEERBRANT et al. 1993, 1995) tend to predict further discoveries of large mammals that could display important relationships with forms from South Asia.

7. Paleoenvironment of the Fayum fauna

Anthracotheres are classically considered to have had a hippopotamid mode of life. As a matter of fact, fossil remains of these animals are often found in lignite deposits, and thus suggest that they were common in areas with swamps or lakes. Indeed, the limb bones of anthracotheres are massive and relatively short with extremities adapted for soft ground. Also, the dentition of older animals often displays a very strong degree of wear, thus indicating a diet of very abrasive vegetation. BLACK (1978: 424) moreover pointed out that the pattern of tooth wear of some anthracotheres is similar with that of the extant *Hippopotamus amphibius* (LAWS 1968).

Nevertheless, the localities from which the anthracotheres from the Fayum Depression originate are not characterized by lignite or even by coal levels. The matrix that coats and fills the fossils of the older collections from the SMNS and the NHML mainly consists of more or less consolidated fluviatile gravels and sands. RASMUSSEN & SIMONS (1992: 499) stated that the reconstructions based on geological informations and on fossil birds, invertebrates, and plants of the quarries L-41 and E (= lower part of the Jebel Qatrani Formation, Fayum Faunal Zones 1 and 2) indicated '... a tropical, swampy, near-shore environment, at least partially forested by large trees', Bown et al. (1982) and Olson & Rasmussen (1986) had previously reached similar conclusions in studying the geology and the fossil record of the formation.

Rasmussen et al. (1992) further stressed that the Eocene-Oligocene boundary is located between the Fayum Faunal Zone 2 and 3 and that the climate conditions remained relatively stable across the Eocene-Oligocene boundary with no significant changes in the fauna.

A paleoenvironmental study has been conducted by means of the cenogram method. The cenogram method developed by Legendre (1989) displays the relation between the body mass distribution for all mammal species in a community and their environment. Indeed, the vegetation density of the area occupied by a mammalian fauna seems to have an impact on the species of intermediate weight in the fauna. Thus, the structure of the cenogram is related to the general environment (structure of vegetation cover and climate) of a faunal community. The cenogram that has been constructed for the entire fauna of the Jebel Qatrani Formation is presented in fig. 13A and includes 58 mammal species (Annex, table 3). The carnivorous taxa and bats have not been included in the study (see Legendre 1989 for explanations). The hyracoids included in the faunal list used here have been selected on the basis of their recent revisions (Rasmussen & Simons 1988; Rasmussen 1989; Rasmussen & Simons 1991).

Tab. 3. List of taxa for the entire Jebel Qatrani fauna.

Rank	Log Weight	Taxa	Rank	Log Weight	Taxa
1	16.1	*Arsinoitherium andrewsi* (LP)	30	8.1	*Propliopithecus haeckeli* (UP)
2	15.7	*Palaeomastodon wintoni* (LP)	31	7.9	*Parapithecus grangeri* (UP)
3	15.2	*Arsinoitherium zitteli* (LP)	32	7.3	*Parapithecus fraasi* (UP)
4	15.0	*Palaeomastodon beadnelli* (LP)	33	7.2	*Apidium phiomense* (UP)
5	13.6	*Moeritherium lyonsi* (LP)	34	7.2	*Afromonius dieides* (LP)
6	12.7	*Bunohyrax major* (LP)	35	7.1	*Oligopithecus savagei* (LP)
7	12.2	*Bothriogenys andrewsi* (LP, UP)	36	6.9	*Metoldobotes stromeri* (UP)
8	12.1	*Megalohyrax eocaenus* (LP, UP)	37	6.8	*Serapia eocaena* (LP)
9	12.0	*Bunohyrax fajumensis* (LP, UP)	38	6.6	*Plesiopithecus teras* (LP)
10	12.0	*Pachyhyrax crassidentatus* (UP)	39	6.5	*Apidium moustafai* (UP)
11	11.9	*Titanohyrax angustidens* (UP)	40	6.5	*Catopithecus browni* (LP)
12	11.7	*Bothriogenys fraasi* (LP, UP)	41	6.2	*Paraphiomys simonsi* (UP)
13	11.4	*Bothriogenys gorringei* (LP, UP)	42	6.0	*Proteopithecus sylviae* (LP)
14	11.3	*Mixtotherium mezi* (LP)	43	6.0	Lorisid indet. (UP)
15	11.2	*Geniohyus mirus* (LP)	44	6.0	Omomyid indet. (LP)
16	10.6	*Bothriogenys rugulosus* (LP, UP)	45	6.0	*Qatrania fleaglei* (UP)
17	10.4	*Qatraniodon parvum* (LP, UP)	46	5.7	*Afrotarsius chatrathi* (UP)
18	10.3	*Selenohyrax chatrathi* (UP)	47	5.6	*Herodotius pattersoni* (LP)
19	10.3	*Ragatherium aegyptiacum* (LP)	48	5.6	*Arsinoea kallimos* (LP)
20	9.7	*Thyrohyrax litholagus* (LP)	49	5.4	*Metaphiomys beadnelli* (UP)
21	9.6	*Saghatherium antiquum* (LP)	50	5.3	*Qatrania wingi* (LP)
22	9.3	*Saghatherium humarum* (UP)	51	5.0	*Metaphiomys schaubi* (LP)
23	9.0	*Thyrohyrax domorictus* (UP)	52	4.3	*Gaudeamus aegyptius* (LP)
24	8.9	*Aegyptopithecus zeuxis* (UP)	54	3.8	*Phiomys* aff.*paraphiomyoides* (UP)
26	8.6	*Thyrohyrax meyeri* (LP)	55	3.8	*Phiomys andrewsi* (UP)
27	8.5	*Ptolemaia lyonsi* (LP)	56	3.2	*Phiomys paraphiomyoides* (UP)
28	8.2	*Propliopithecus chirobates* (UP)	57	2.6	*Phiocricetomys minutus* (UP)
29	8.1	*Moeripithecus markgrafi* (UP)	58	2.6	*Phiomys lavocati* (LP)

In the cenogram of the entire Jebel Qatrani fauna (fig. 13 A), the microfauna (weight < 500 g) is well represented, and the large mammals (weight > about 6 kg) are abundant. In addition, the middle sized taxa (weight comprised between 500 g and 5–6 kg) are also well represented. This structure suggests a forested environment submitted to wet and hot climatic conditions, thus a tropical environment. Also, the structure of the cenogram of the Jebel Qatrani mammalian community is similar to that of the cenograms constructed for extant fauna living in tropical forests of Asia and of South America (LEGENDRE 1989).

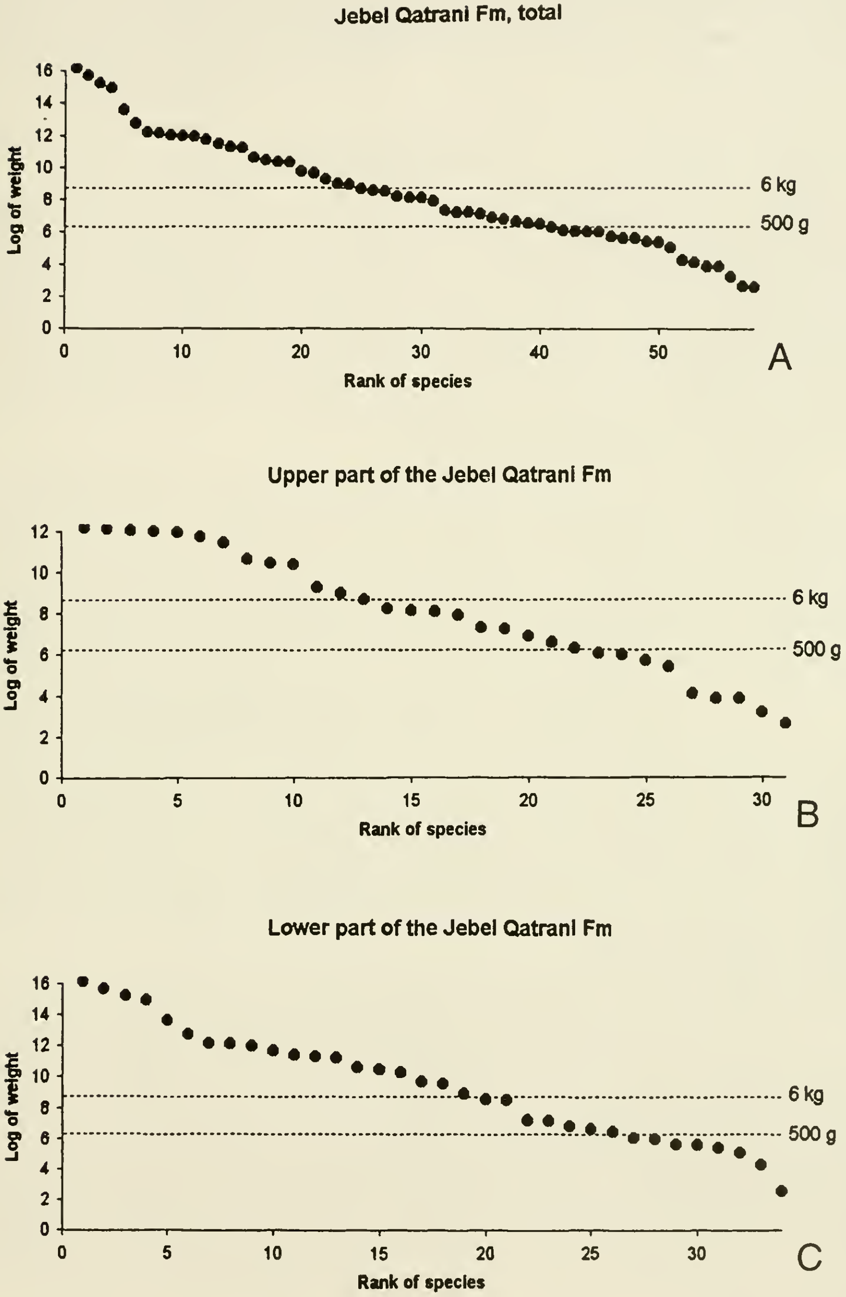
RASMUSSEN et al. (1992) suppose that the barite sandstone bed situated between the Fayum Faunal Zones 2 and 3 indicates the Eocene-Oligocene boundary in the

Tab. 4. List of taxa of the lower part of the Jebel Qatrani Formation.

Rank	Log Weight	Taxa	Rank	Log Weight	Taxa
1	16.1	*Arsinoitherium andrewsi*	18	9.6	*Saghatherium antiquum*
2	15.7	*Palaeomastodon wintoni*	19	8.9	*Saghatherium bowni*
3	15.2	*Arsinoitherium zittelli*	20	8.6	*Thyrohyrax meyeri*
4	14.9	*Palaeomastodon beadnelli*	21	8.5	*Ptolemayïa lyonsi*
5	13.6	*Moeritherium lyonsi*	22	7.2	*Afromonius dieides*
6	12.7	*Bunohyrax major*	23	7.1	*Oligopithecus savagei*
7	12.2	*Bothriogenys andrewsi*	24	6.8	*Serapia eocaena*
8	12.1	*Megalohyrax eocaenus*	25	6.6	*Plesiopithecus teras*
9	12.0	*Bunohyrax fajumensis*	26	6.5	*Catopithecus browni*
10	11.7	*Bothriogenys fraasi*	27	6.0	*Proteopithecus sylviae*
11	11.4	*Bothriogenys gorringei*	28	6.0	Omomyid indet.
12	11.3	*Mixtotherium mezi*	29	5.6	*Herodotius pattersoni*
13	11.2	*Geniohyus mirus*	30	5.5	*Arsinoea kallimos*
14	10.6	*Bothriogenys rugulosus*	31	5.3	*Qatrania wingi*
15	10.4	*Qatraniodon parvum*	32	5.0	*Metaphiomys schaubi*
16	10.3	*Ragatherium aegyptiacum*	33	4.3	*Gaudeamus aegyptius*
17	9.7	*Thyrohyrax litholagus*	34	2.6	*Phiomys lavocati*

Tab. 5. List of taxa of the upper part of the Jebel Qatrani Formation.

Rank	Log Weight	Taxa	Rank	Log Weight	Taxa
1	12.2	*Bothriogenys andrewsi*	17	7.9	*Parapithecus grangeri*
2	12.1	*Megalohyrax eocaenus*	18	7.3	*Parapithecus fraasi*
3	12.0	*Bunohyrax fajumensis*	19	7.2	*Apidium phiomense*
4	12.0	*Pachyhyrax crassidentatus*	20	6.9	*Metoldobotes stromeri*
5	11.9	*Titanohyrax angustidens*	21	6.5	*Apidium moustafai*
6	11.7	*Bothriogenys fraasi*	22	6.2	*Paraphiomys simonsi*
7	11.4	*Bothriogenys gorringei*	23	6.0	Lorisid indet.
8	10.6	*Bothriogenys rugulosus*	24	6.0	*Qatrania fleaglei*
9	10.4	*Qatraniodon parvum*	25	5.7	*Afrotarsius chatrathi*
10	10.3	*Selenohyrax chatrathi*	26	5.3	*Metaphiomys beadnelli*
11	9.3	*Saghatherium humarum*	27	4.1	*Peratherium africanus*
12	9.0	*Thyrohyrax domorictus*	28	3.8	*Phiomys* aff. *paraphiomyoides*
13	8.7	*Aegyptopithecus zeuxis*	29	3.8	*Phiomys andrewsi*
14	8.2	*Propliopithecus chirobates*	30	3.2	*Phiomys paraphiomyoides*
15	8.1	*Moeripithecus markgrafi*	31	2.6	*Phiocricetomys minutus*
16	8.1	*Propliopithecus haeckeli*			



Jebel Qatrani Fm, total

Upper part of the Jebel Qatrani Fm

Lower part of the Jebel Qatrani Fm

Fig. 13. Cenograms of the Jebel Qatrani Formation fauna. A: total; B: upper part; C: lower part. For explanations see text.

Jebel Qatrani Formation. I therefore have constructed two additional cenograms. The first one includes all species which occur in the Fayum Faunal Zones 1 and 2 (for example in quarries L-41, A, B, E), under the hypothetical Eocene-Oligocene boundary (Annexe, table 4), and the second one comprises the species known in the Fayum Faunal Zones 3 and 4 (for example in quarries G, I, M, V) above the barite sandstone level (Annexe, table 5). The occurrence of mammalian taxa has been inferred from recent contributions about Fayum mammals (SIMONS & RASMUSSEN 1990, RASMUSSEN et al. 1992for a general review, SIMONS et al. 1986, 1994, 1995for the primates, RASMUSSEN & SIMONS 1988, RASMUSSEN 1989 and RASMUSSEN & SIMONS 1991for the hyracoids, WOOD 1968for the rodents). Several taxa occur in both lower and upper Fayum Faunal Zones. The two cenograms presented in fig. 13B and C display the same structure with that of the cenogram constructed for the whole Jebel Qatrani Formation, with an abundance of small, middle sized and large mammals. The lower and upper part of the Jebel Qatrani Formation therefore indicate a tropical environment (pattern of vegetation and of annual rainfall and temperature). This situation leads to two distinct interpretations:

1. – RASMUSSEN et al. (1992: 563) stressed that the climate in North Africa remained relatively stable across the Eocene-Oligocene boundary, and that there were no dramatic faunal changes during this period. RASMUSSEN et al. (1992) further argued that the stable climate during the Paleogene of North Africa allowed for the maintenance of mammals, birds and plants. However, this situation seems to be rather common in tropical environments (see for example DUCROCQ et al. 1992, 1993, in press). Moreover, the climatic changes (cooling and increased aridity) associated with the extinctions of floras and both land and marine faunas at the Eocene-Oligocene boundary are known to have had a global extension (BERGGREN & PROTHERO 1992). In that case, why would have Africa contrasted with other continental areas in maintaining a stable tropical climate across the Eocene-Oligocene boundary? Nevertheless, it could be suggested that the barite sandstone does not represent the Eocene-Oligocene boundary. In addition, the anthracotheres studied here do not display any changes in their dental evolutionary stage that could reflect a change in their diet or in their environment, as is the case in Europe or North America at the Eocene-Oligocene boundary.

2. – If one follows the opinion of GINGERICH (1993) according to which the entire Jebel Qatrani Formation is Oligocene in age, both cenograms presented in fig. 13B and C correspond to a tropical environment that occurred during the Oligocene, and would suggest that a rather closed habitat submitted to a tropical climate occurred in North Africa during the Oligocene. This is in opposition to the classical view of an Oligocene gradual cooling admitted by the scientific community (see BERGGREN & PROTHERO 1992). However, it must be stressed that the climatic changes at the Eocene-Oligocene are seen to have been a gradually cooling primarily at high latitudes. During the Eocene-Oligocene, the Fayum region was situated slightly closer to the Equator than it is actually. As a consequence of this more southern position of North Africa, a delay in the establishment of the climatic events could have been induced.

A third solution is to consider that the entire Jebel Qatrani Formation would have been late Eocene in age, as suggested by VAN COUVERING & HARRIS (1991). The similarities of the two cenograms therefore could indicate that the mammalian faunas listed in tables 4 and 5 lived in warm and wet tropical to subtropical conditions that characterized the late Eocene. However, the derived evolutionary stage of anthracotheres and of several anthropoid primates (for example *Aegyptopithecus* and *Propliopithecus*) rather suggest that an Oligocene age is more likely for these mammals and thus for the Jebel Qatrani Formation.

8. Conclusions

The revision of the Fayum anthracothere dental material housed in Stuttgart and London led to consider only four species of the genus *Bothriogenys* out of the five described by Andrews & Beadnell (1902), Andrews (1906), and Schmidt (1913). The fragmentary mandible attributed to *B. parvus* can no longer be referred to that genus on the basis of its dental structure and morphology, and is assigned to a new genus, *Qatraniodon*. No precise indications about the place of find of the fossil material can be given, but according to the geological studies it is assumed that they come mainly from the lower part of the Jebel Qatrani Formation, and that these species also occurred in the upper part, although they were less common there.

Comparisons of the Fayum material with that of a species of *Bothriogenys* known from the late Eocene of Thailand revealed close morphological and likely phylogenetical relationships between taxa of both landmasses. The phylogenetical study of the Fayum anthracotheres has demonstrated that several dental characters chosen to construct parcimonious trees likely correspond to homoplasies because they seem to have occurred several times in the evolution of the genus *Bothriogenys*. On the other hand, *B. rugulosus* appears to be the most primitive species (as stated by Schmidt, 1913), and *B. andrewsi* and *B. gorringei* are very closely related.

Paleobiogeographical relationships between South Asia and North Africa are likely during the late Eocene and perhaps the early Oligocene on the basis of the fossil record of both regions (anthracotheres and primates), and the Afro-Arabian landmass might have been a stage during the faunal exchanges between Asia and Africa. The paleoenvironmental investigations of the Jebel Qatrani Formation allowed to construct several cenograms that display informations about the environment in which a mammal community lived. The Fayum fauna appears to have been characterized by a forested habitat submitted to a hot and wet (tropical) climate. In addition, an early Oligocene age is proposed for the Jebel Qatrani Formation, which seems to be confirmed by the evolutive stage of the anthracotheres.

With the exception of the paleoenvironmental study, these conclusions have been assumed on the basis of the Fayum anthracotheres. In addition, I tried to take into account the data displayed by the literature available when proposing the conclusions developed here. Nevertheless, when more informations are known about the different quarries that have yielded anthracothere remains in the Jebel Qatrani Formation, it is possible that some of the results and consequences reported here can be modified.

9. References

Andrews, C.W. (1906): A descriptive catalogue of the Tertiary vertebrata of the Fayûm, Egypt. Based on the collection of the Egyptian Government in the Geological Museum, Cairo, and on the collection in the British Museum (Natural History). 324 pp; London (British Museum – Natural History).

ANDREWS, C.W. & BEADNELL, H.J.L. (1902): A preliminary note of some new mammals from the Upper Eocene of Egypt. – Egypt Survey Dept., **1**: 1–9; Cairo.

BERGGREN, W.A. & PROTHERO, D.R. (1992): Eocene-Oligocene climatic and biotic evolution: an overview. – *In*: PROTHERO, D.R. & BERGGREN, W.A. (Eds.): Eocene-Oligocene climatic and biotic evolution: 1–28; Princeton (University Press).

BLACK, C.C. (1978): Anthracotheriidae. – *In*: MAGLIO, V.J. & COOKE, H.B.S. (Eds.): Evolution of African mammals: 423–434; Cambridge & London (Harvard University Press).

BOWN, T.M. & KRAUS, M.J. (1988): Geology and paleoenvironment of the Oligocene Jebel Qatrani Formation and adjacent rocks, Fayum Depression, Egypt. – U. S. Geol. Surv. Professional Papers, **1452**: 1–64; Washington.

BOWN, T.M., KRAUS, M.J., WING, S.L., FLEAGLE, J.G., TIFFNEY, B.H., SIMONS, E.L. & VONDRA, C.F. (1982): The Fayum primate forest revisited. – J. Human Evol., **11**: 603–632; London.

BRISTOW, C.S. (1991): Sedimentology of the Tertiary Krabi basin, Thailand. – Seventh Regional Conference on Geology, Mineral and Energy Resources of Southeast Asia (GEOSEA VII), Bangkok, 5–8 November 1991: 22–23 (Abstract).

CHOW, M. (1958): Some Oligocene mammals from Lunan, Yunnan. – Vert. PalAsiatica, **2/4**: 263–267; Beijing.

CHOW, M. & CHANG, Y. (1960): Discovery of the Tertiary mammal in Kweichow. – Vert. PalAsiatica, **2/2**: 177–178; Beijing.

COIFFAIT, P.-E., COIFFAIT, B., JAEGER, J.-J. & MAHBOUBI, M. (1984): Un nouveau gisement à mammifères fossiles d'âge Eocène supérieur sur le versant sud des Nementcha (Algérie orientale): découverte des plus anciens rongeurs d'Afrique. – C. R. Acad. Sci., Paris, **299**: 893–898; Paris.

COLBERT, E.H. (1935): Distributional and phylogenetics studies on Indian fossil mammals. Part IV: Suidae and Hippopotamidae. – Am. Mus. Nov., **799**: 1–11; New York.

– (1938): Fossil mammals from Burma in the American Museum of Natural History. – Bull. Am. Mus. nat. Hist., **74**: 255–436; New York.

CROCHET, J.-Y., THOMAS, H., ROGER, J., SEN., S. & AL-SULAIMANI, Z. (1990): Première découverte d'un créodonte dans la péninsule arabique: *Masrasector ligabuei* nov. sp. (Oligocène inférieur de Taqah, Formation d'Ashawq, Sultanat d'Oman). – C. R. Acad. Sci. Paris, **311**: 1455–1460; Paris.

CROCHET, J.-Y., THOMAS, H., SEN., S., ROGER, J., GHEERBRANT, E. & AL-SULAIMANI, Z. (1992): Découverte d'un Péradectidé (Marsupialia) dans l'Oligocène inférieur du Sultanat d'Oman: nouvelles données sur la paléobiogéographie des Marsupiaux de la plaque arabo-africaine. – C. R. Acad. Sci. Paris, **314**: 539–545; Paris.

COURT, N. & HARTENBERGER, J.-L. (1992): A new species of the hyracoid mammal *Titanohyrax* from the Eocene of Tunisia. – Palaeontology, **35**: 309–317; London.

DE BONIS, L., JAEGER, J.-J., COIFFAIT, B. & COIFFAIT, P.-E. (1988): Découverte du plus ancien primate catarrhinien connu dans l'Eocène supérieur d'Afrique du Nord. – C. R. Acad. Sci., Paris, **306**: 929–934; Paris.

DINEUR, H. (1981): Le genre *Brachyodus*, Anthracotheriidae (Artiodactyla, Mammalia) du Miocène inférieur d'Europe et d'Afrique. – Thèse de 3° cycle, Université Paris VI, 180 pp.

DUCROCQ, S. (1992): Etude biochronologique des bassins continentaux tertiaires du Sud-Est asiatique: contribution des faunes de mammifères. – Thèse de 3° cycle, 245 pp.; Université Montpellier II.

– (1994): Les anthracothères paléogènes de Thaïlande: paléogéographie et phylogénie. – C. R. Acad. Sci., Paris, **318**: 549–554; Paris. – [1994a]

– (1994): An Eocene peccary from Thailand and the biogeographical origins of the Artiodactyl family Tayassuidae. – Palaeontology, **37/4**: 765–779; London. – [1994b]

– (1995): The contribution of Paleogene anthracotheriid artiodactyls in the paleobiogeographical history of southern Europe. – N. Jb. Geol. Paläont. Mh., **6**: 355–362; Stuttgart.

– (In press): The Anthracotheriidae from the Upper Eocene of Thailand. – Palaeontographica; Stuttgart.

DUCROCQ, S., BUFFETAUT, E., BUFFETAUT-TONG, H., JAEGER, J.-J., JONGKANJANASOONTORN, Y. & SUTEETHORN, V. (1992): First fossil flying lemur: a dermopteran from the late Eocene of Thailand. – Palaeontology, **35/2**: 373–380; London.

Ducrocq, S., Jaeger, J.-J. & Sigé, B. (1993): Un mégachiroptère dans l'Eocène supérieur de Thaïlande. Incidence dans la discussion phylogénique du groupe. – N. Jb. Geol. Paläont. Mh., **9**: 561–575; Stuttgart.

Ducrocq, S., Chaimanee, Y., Suteethorn, V. & Jaeger, J.-J. (1995): New primate from the Paleogene of Thailand and the biogeographical origin of anthropoids. – J. Human Evol., **28**/5: 477–485; London. – [1995a]

– (1995): Mammalian faunas and the ages of the continental Tertiary fossiliferous localities from Thailand. – J. South East Asian Earth Sci., **12**/1–2: 65–78; Oxford. – [1995b]

Gentry, A.W. & Hooker, J.J. (1988): The phylogeny of the Artiodactyla. – *In*: Benton, M.J. (Ed.): The phylogeny and classification of the tetrapods. Vol. 2: Mammals: 235–272; Oxford (Clarendon Press).

Gheerbrant, E. (1990): On the early biogeographical history of the African placentals. – Histor. Biol., **4**: 107–16; Cambridge.

Gheerbrant, E., Thomas, H., Roger, J., Sen, S. & Al-Sulaimani, Z. (1993): Deux nouveaux primates dans l'Oligocène inférieur de Taqah (Sultanat d'Oman): premiers adapiformes (? Anchomomyini) de la péninsule arabique. – Palaeovertebrata, **22**: 141–196; Montpellier.

Gheerbrant, E., Thomas, H., Sen, S. & Al-Sulaimani, Z. (1995): Nouveau primate Oligopithecinae (Simiiformes) de l'Oligocène inférieur de Taqah, Sultanat d'Oman. – C. R. Acad. Sci. Paris, **321**: 425–432; Paris.

Gingerich, P.D. (1993): Oligocene age of the Gebel Qatrani Formation, Fayum, Egypt. – J. Human Evol., **24**: 207–218; London.

Godinot, M. & Mahboubi, M. (1992): Earliest known simian primate found in Algeria. – Nature, **357**: 324–326; London.

Groves, C.P. & Paterson, J.D. (1991): Testing hominoid phylogeny with the PHYLIP programs. – J. Human Evol., **20**: 167–183; London.

Hartenberger, J.-L. & Marandat, B. (1992): A new genus and species of an early Eocene primate from North Africa. – Human Evol., **7**: 9–16; Firenze.

Heller, F. (1930): Die Säugetierfauna der mitteleozänen Braunkohle des Geiseltales bei Halle a. S. – Jb. Hallescher Verb., **9**: 13–41; Halle.

Hellmund, M. (1991): Revision der europäischen Species der Gattung *Elomeryx* Marsh, 1894 (Anthracotheriidae, Artiodactyla, Mammalia) – Odontologische Untersuchungen. – Palaeontographica, A, **220**: 1–101; Stuttgart.

Laws, R.M. (1968): Dentition and ageing of the hippopotamus. – E. Afr. Wildl. J., **6**: 19–52; Nairobi.

Legendre, S. (1989): Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe occidentale: structures, milieux et évolution. – Münch. geowiss. Abh., **16**: 1–110; München.

Macdonald, J.R. (1956): The North American anthracotheres. – J. Paleontol., 30/3: 615–645; Tulsa.

Mahboubi, M., Ameur, R., Crochet, J.-Y. & Jaeger, J.-J. (1986): El Kohol (Saharan Atlas, Algeria), a new Eocene mammal locality in northwestern Africa: stratigraphic, phylogenetic and paleobiogeographical data. – Palaeontographica, A, **192**: 15–49; Stuttgart.

Olson, S.L. & Rasmussen, D.T. (1986): Paleoenvironment of the earliest hominoids: evidence from the Oligocene avifauna of Egypt. – Science, **233**: 1202–1204; Washington.

Pickford, M. (1993): Old World suoid systematics, phylogeny, biogeography and biostratigraphy. – Paleontologia i Evolució, **26–27**: 237–269; Barcelona.

Pickford, M., Thomas, H., Sen, S., Roger, J., Gheerbrant, E. & Al-Sulaimani, Z. (1994): Early Oligocene Hyracoidea (Mammalia) from Thaytiniti and Taqah, Dhofar Province, Sultanate of Oman. – C. R. Acad. Sci. Paris, **318**: 1395–1400; Paris.

Rasmussen, D.T. (1989): The evolution of the Hyracoidea: a review of the fossil evidence. – *In*: Prothero, D.R. & Schoch, R.M. (Eds.): The evolution of perissodactyls. – Oxford Monographs on Geology and Geophysics **15**: 57–78; New York (Oxford University Press).

Rasmussen, D.T. & Simons, E.L. (1988): New Oligocene hyracoids from Egypt. – J. Vert. Paleont., **8**/1: 67–83; San Diego.

– & – (1991): The oldest Egyptian hyracoids (Mammalia: Pliohyracidae): new species of *Saghatherium* and *Thyrohyrax* from the Fayum. – N. Jb. Geol. Paläont. Abh., **182**/2: 187–209; Stuttgart.

– & – (1992): Paleobiology of the oligopithecines, the earliest known anthropoid primates. – Int. J. Primatol., 13/5: 477–508; New York.

Rasmussen, D.T., Bown, T.M. & Simons, E.L. (1992): The Eocene-Oligocene transition in continental Africa. – *In*: Prothero, D.R. & Berggren, W.A. (Eds.): Eocene-Oligocene climatic and biotic evolution: 548–566; Princeton (University Press).

Said, R. (1962): The geology of Egypt. 377 pp; Amsterdam (Elsevier).

Savage, R.J.G. (1971): Review of the fossil mammals of Libya. – *In*: Gray, C. (Ed.): Symposium on the Geology of Libya: 215–226; Tripoli (Univ. of Libya).

Schmidt, M. (1913): Über Paarhufer der fluviomarinen Schichten des Fajum. – Geol. Paläont. Abh., **11**: 155–263; Jena.

Simons, E.L. (1968): Early Cenozoic mammalian faunas, Fayum Province, Egypt. Part I. African Oligocene mammals: introduction, history of study, and faunal succession. – Bull. Peabody Mus. nat. Hist., **28**: 1–21; New Haven.

Simons, E.L. & Bown, T.M. (1985): *Afrotarsius chatrathi*, first tarsiiform primate (?Tarsiidae) from Africa. – Nature, **313**: 475–477; London.

Simons, E.L., Bown, T.M. & Rasmussen, D.T. (1986): Discovery of two additional prosimian primate families (Omomyidae, Lorisidae) in the African Oligocene. – J. Human Evol., **15**: 431–437; London.

Simons, E.L. & Rasmussen, D.T. (1990): Vertebrate paleontology of Fayum: history of research, faunal review and future prospects. – *In*: Said, R. (Ed.): The geology of Egypt: 627–638; Rotterdam (A.A. Balkema).

Simons, E.L., Rasmussen, D.T., Bown, T.M. & Chatrath, P. (1994): The Eocene origin of anthropoid primates. Adaptation, evolution, and diversity. – *In*: Fleagle, J.G. & Kay, R.F. (Eds.): Anthropoid origins: 179–201; New York (Plenum Press).

Simons, E.L., Rasmussen, D.T. & Gingerich, P.D. (1995): New cercamoniine adapid from Fayum, Egypt. – J. Human Evol., **29**: 577–589; London.

Stucky, R.K. (1992): Mammalian faunas in North America of Bridgerian to early Arikareean 'Ages' (Eocene and Oligocene). – *In*: Prothero, D.R. & Berggren, W.A. (Eds): Eocene-Oligocene climatic and biotic evolution: 464–493; Princeton (University Press).

Sudre, J. (1977): Les artiodactyles de l'Eocène moyen et supérieur d'Europe occidentale; systématique et évolution. – Thèse d'Etat, 257 pp.; Université Montpellier II.

Suteethorn, V., Buffetaut, E., Helmcke-Ingavat, R., Jaeger, J.-J. & Jongkanjanasoontorn, Y. (1988): Oldest known Tertiary mammals from South-East Asia: middle Eocene primate and anthracotheres from Thailand. – N. Jb. Geol. Paläont. Mh., **9**: 563–570; Stuttgart.

Thomas, H., Roger, J., Sen, S. & Al-Sulaimani, Z. (1988): Découverte des plus anciens 'Anthropoïdes' du continent arabo-africain et d'un primate tarsiiforme dans l'Oligocene du Sultanat d'Oman. – C. R. Acad. Sci. Paris, **306**: 823–829; Paris.

Thomas, H., Roger, J., Sen, S., Bourdillon-de-Grissac, C. & Al-Sulaimani, Z. (1989): Découverte de vertébrés fossiles dans l'Oligocène inférieur du Dhofar (Sultanat d'Oman). – Géobios, **22**: 101–120; Lyon.

Van Couvering, J.A. & Harris, J.A. (1991): Late Eocene age of Fayum mammal faunas. – J. Human Evol., **21**: 241–260; London.

Wight, A.W.R. (1980): Paleogene vertebrate fauna and regressive sediments of Dur at Talhah, southern Sirt, Libya. – *In*: Salem, M.J. & Busrewil, M.T. (Eds.): The geology of Libya, Vol. I: 309–325; London (Academic Press).

Wood, A.E. (1968): The African Oligocene Rodentia. – Bull. Peabody Mus. nat. Hist., **28**: 23–105; New Haven.

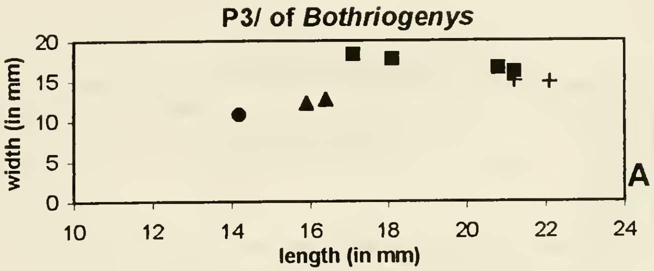
Xu, Y. (1962): Some new anthracotheres from Shansi and Yunnan. – Vert. PalAsiatica, **6/3**: 243–250; Beijing.

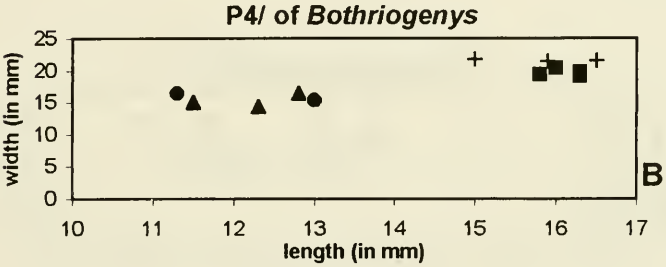
Address of the author:
Dr Stéphane Ducrocq, Institut des Sciences de l'Evolution, UMR 5554 C.N.R.S., Case 064,
Université Montpellier II, Place E. Bataillon, F-34095 Montpellier cedex 5, France.

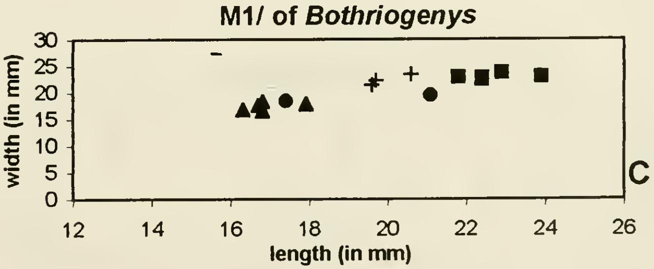
Annex

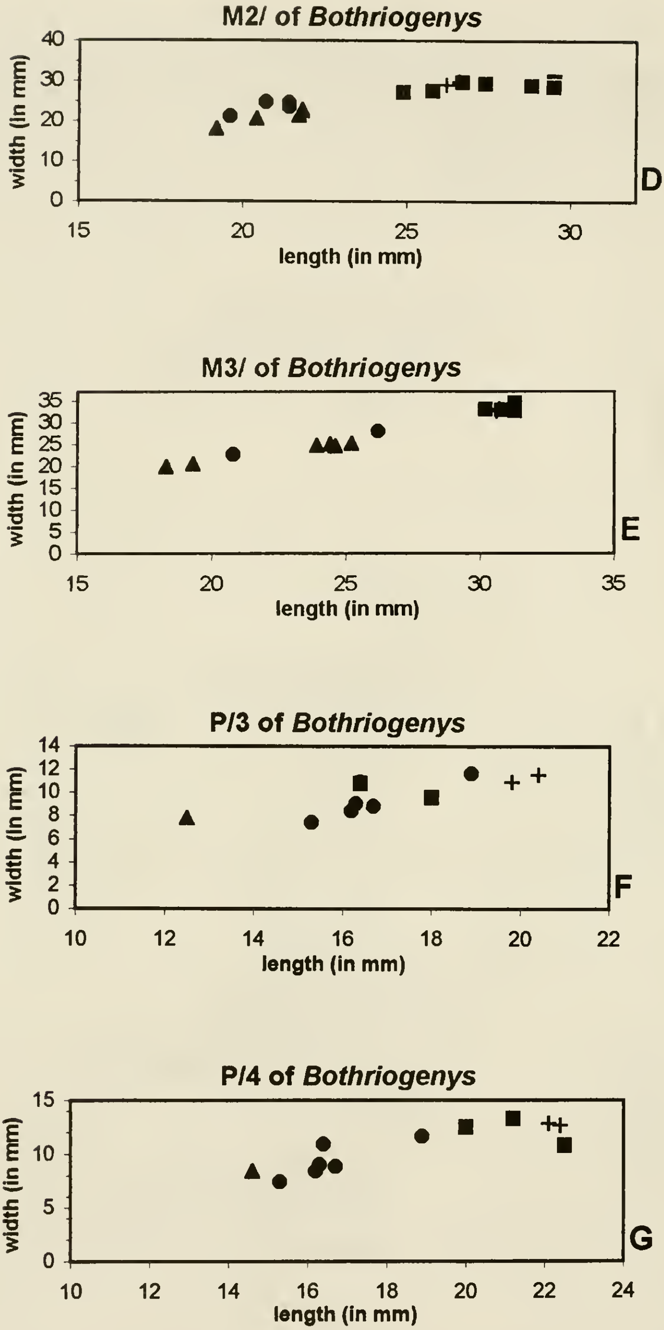
Scatter diagrams for P^3 (A), P^4 (B), M^1 (C), M^2 (D), M^3 (E), P_3 (F), P_4 (G), M_1 (H), M_2 (I), M_3 (J), upper teeth (length: K, width: L), lower teeth (length: M, width: N) of *Bothriogenys*.
Conventional signs for all diagrams:

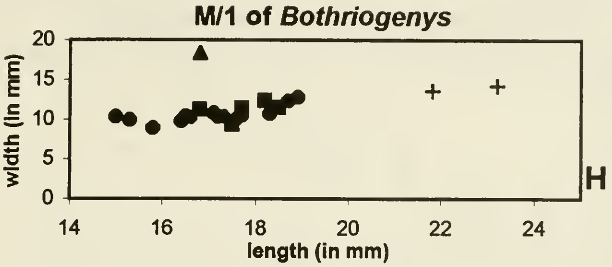
● *B. gorringei*
■ *B. fraasi*
▲ *B. rugulosus*
− *B. andrewsi*
+ *B.* from Krabi

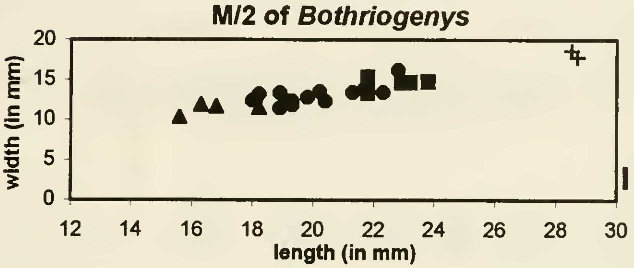


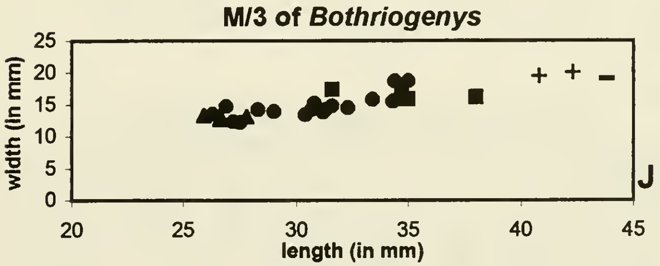


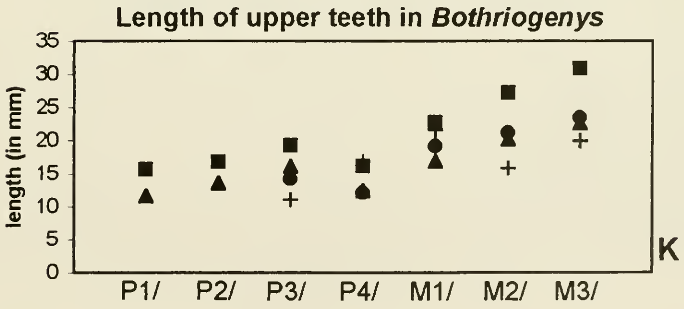


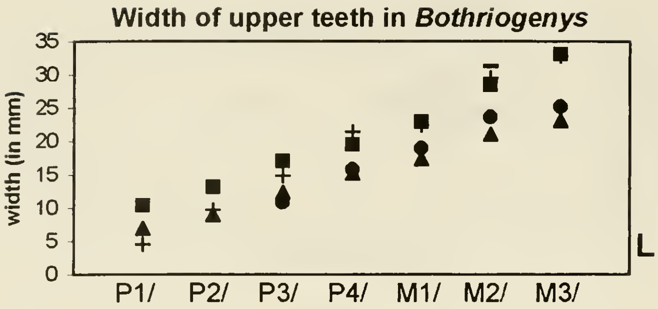

M2/ of *Bothriogenys*
width (in mm)
40
30
20
10
0
15
20
25
30
length (in mm)
D
M3/ of *Bothriogenys*
width (in mm)
35
30
25
20
15
10
5
0
15
20
25
30
35
length (in mm)
E
P/3 of *Bothriogenys*
width (in mm)
14
12
10
8
6
4
2
0
10
12
14
16
18
20
22
length (in mm)
F
P/4 of *Bothriogenys*
width (in mm)
15
10
5
0
10
12
14
16
18
20
22
24
length (in mm)
G

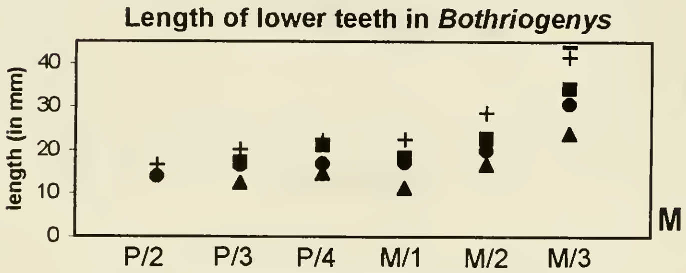

M/1 of *Bothriogenys*
width (in mm)
20
15
10
5
0
14
16
18
20
22
24
length (in mm)
H

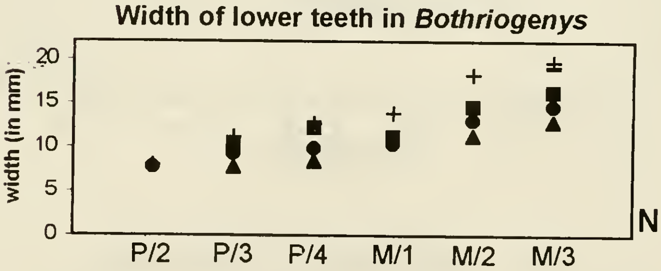

M/2 of *Bothriogenys*
width (in mm)
20
15
10
5
0
12
14
16
18
20
22
24
26
28
30
length (in mm)
I


M/3 of *Bothriogenys*
width (in mm)
25
20
15
10
5
0
20
25
30
35
40
45
length (in mm)
J


Length of upper teeth in *Bothriogenys*
length (in mm)
35
30
25
20
15
10
5
0
P1/
P2/
P3/
P4/
M1/
M2/
M3/
K







ISSN 0341-0153

Schriftleitung: Dr. Gert Bloos, Rosenstein 1, D-70191 Stuttgart
Gesamtherstellung: Gulde-Druck GmbH, D-72070 Tübingen

Zeitschrift/Journal: Stuttgarter Beiträge Naturkunde Serie B [Paläontologie]

Jahr/Year: 1997

Band/Volume: 250_B

Autor(en)/Author(s): Ducrocq Stephane

Artikel/Article: The anthracotheriid genus Bothriogenys (Mammalia, Artiodactyla) in Africa and Asia during the Paleogene: phylogenetical and paleobiogeographical relationships 1-44