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Apterodon intermedius, sp. nov., a new European Creodont Mammal from MP22 of Espenhain (Germany)

Apterodon intermedius, sp. nov., un nouveau mammifère créodonte européen de Espenhain (MP22, Allemagne)

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Abstract

A mandible fragment of a medium-sized creodont mammal representing a new species of *Apterodon, A. intermedius* has been discovered in a open cast mine near Leipzig (Germany), dated Late Ruppelian (MP22). For the first time an *Apterodon* species is well dated in Europe. The dental wear of molars is investigated under SEM. It looks like those described extant carnivores known as preferential flesh eaters. The new specimen together other mammal species questions possible migration ways from Africa to Europe, between the upper Eocene and lower Oligocene.

Résumé

Un fragment de mandibule appartenant à une nouvelle espèce d'*Apterodon*, *A. intermedius* sp. nov. (Mammifère, Créodonte), a été découvert dans une mine près de Leipzig (Allemagne) dans un

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niveau Oligocène (MP22) par l'ensemble de sa faune. Pour la première fois une espèce d'*Apterodon* est bien datée en Europe. L'usure des molaires étudiée au MEB est comparable à celle de carnivores actuels se nourrissant principalement de chair. La dispersion géographique des espèces d'*Apterodon* pose le problème des voies de migrations possibles entre l'Afrique et l'Europe entre l'Eocène supérieur et l'Oligocène.

Keywords: Mammalia; Creodont; *Apterodon*; Germany; Lower Oligocene; Migration way

Mots clés : Mammifères ; Créodontes ; *Apterodon* ; Allemagne ; Oligocène ; Migration

1. Introduction

Recently a new locality, Espenhain, rich in terrestrial fossil remains, has been discovered in the open cast mine near Leipzig (Germany). The fossil layer is embedded in a Ruppelian marine sequence. The fauna of the site is varied and has yielded: *Entelodon deguilhermi*, *Anthracotherium* ex gr. *illirycum/magnum/valdense*, *Ronzotherium filholi*, *Eggysodon* cf. *osborni*, *Protapirus bavaricus*, *Stenoplesictis cayluxi*, *Diplocynodon* sp., *Trionyx* sp., and vegetal remains (Böhme, 2001; Uhlig and Böhme, 2001). The fauna assemblage fits well with the reference mammal Palaeogene level MP22 (Lower Oligocene).

2. Systematics

Mammalia.
Order CREODONTA
Family HYAENODONTIDAE
Subfamily APTERODONTINAE

Genus ***Apterodon*** Fischer 1880
Type species: *Apterodon gaudryi* Fischer 1880.
This species is known only by two specimens:

- The holotype which is a part of the old collections from Phosphorites du Quercy. Its origin locality and its stratigraphical age are unknown. No new material of *A. gaudryi* has been collected during the recent field work in Quercy.
- *A. flonheimensis* (Andreae, 1887) the type of which is probably lost (M. Böhme, pers. com), synonym of *A. gaudryi* in Lange 1967. Three teeth P3, P4 and M1 (BM M55a) from Flonheim sands too are housed in the collections of the British Museum of Natural History (Lange-Badré, 1977).

Included species; *A. macrognathus* Andrews, 1906, *A. altidens* Schlosser, 1910, *A. saghensis* Simons and Gingerich, 1976, all of them from El Fayoum (Egypt).

Concerning *A. minutus* described by Schlosser (1910), the genus is misidentified and it is not *Apterodon* (Lange, 1967). This species differs clearly in having the two first molars with a very long talonid bearing two cups along the labial margin, and a low ridge surrounding a shallow depression, a short shearing-bladed paraconid and a vestigial metaconid. p4 has a compressed and cutting talonid.

Lavrov (1999) removes *minutus* from *Apterodon*. He does it the type of a new genus named unfortunately *Quasiapterodon*, without considering the species *Sinopa aethiopica* from the same site. It would have been better to adopt to *minutus*, a new generic denomination clearly not throwing into confusion. Concerning *S. aethiopica*, it is clearly not related to the North-American genus *Sinopa* (Lange, 1967).

Remarks: Szalay (1967) classified *Apterodon* in a new tribe "Apterodontini" as a subdivision of the Hyaenodontinae. Unfortunately the diagnosis of Apterodontini is based on dental characters the synapomorphic nature of which is debatable.

Van Valen (1967) comments Szalay's suggestion but he rejects the use of tribe subdivision in the Hyaenodontinae until their phylogenetic relations are elucided. At the present time, the systematic position and the relationship of *Apterodon* to other Hyaenodontinae remain uncertain.

Polly (1996) studying the basicranial and postcranial morphology establishes the diphylety of Hyaenodontinae as currently used. He proposes to distinguish two subfamilies, Hyaenodontinae s.s. and Pterodontinae in which are included genera *Pterodon*, *Hyainailouros*, *Megistotherium* and *Sivapterodon*. Maybe *Apterodon* should be referred to this group too. Consequently, the name Apterodontinae Szalay 1967 would have priority over Pterodontinae. Holroyd (1999) following Polly's suggestion uses Apterodontinae and she includes genera *Metapterodon* and *Akhatenatus*.

Lavrov (1999) keeps Hyaenodontinae and Proviverrinae as monophyletic taxa in the family of Hyaenodontidae. The Hyaenodontinae include 21 genera, five of which are gathered in two tribes, Hyaenodontini and Apterodontini for *Apterodon* and *Quasiapterodon*. The definition of this tribe details only symplesiomorphic character states.

Holroyd (1999) admits "by convenience" the tribe of Apterodontini like an outgroup for the Hyaenodontinae.

Although the relationships of many Hyaenodontinae genera are not related in detail by Polly, here we accept his conclusions based on a cladistic analysis and we adopt the subfamily Apterodontinae in waiting a better understanding of the relationship between taxa.

Distribution: Upper Eocene–Early Oligocene (El Fayoum, Egypt), Lower Oligocene (Germany), ?Upper Eocene–?Upper Oligocene (Phosphorites du Quercy, France).

3. *Apterodon intermedius* nov. sp.

Holotype: A fragment of right mandible with p4-m2 deposited at the Institute für Paläontologisches und historisches Geologie, Munich (Germany).

Type locality: Espenhain.

Etymology: From latin *intermedius*, allusive to the size and the morphologic characters between the African species and the European one.

Diagnosis: Medium-sized *Apterodon* differing from the species previously described in having m2 with a strong paraconid clearly separate from the protoconid by a broad valley, an enamel fold obliterated at the location of the metaconid, a crushing talonid with a voluminous rounded central cusp, filling partly a narrow lingual postfossid, a straight cingulid attenuated except on the mesiolabial corner of the paraconid.

Referred specimens: only holotype.

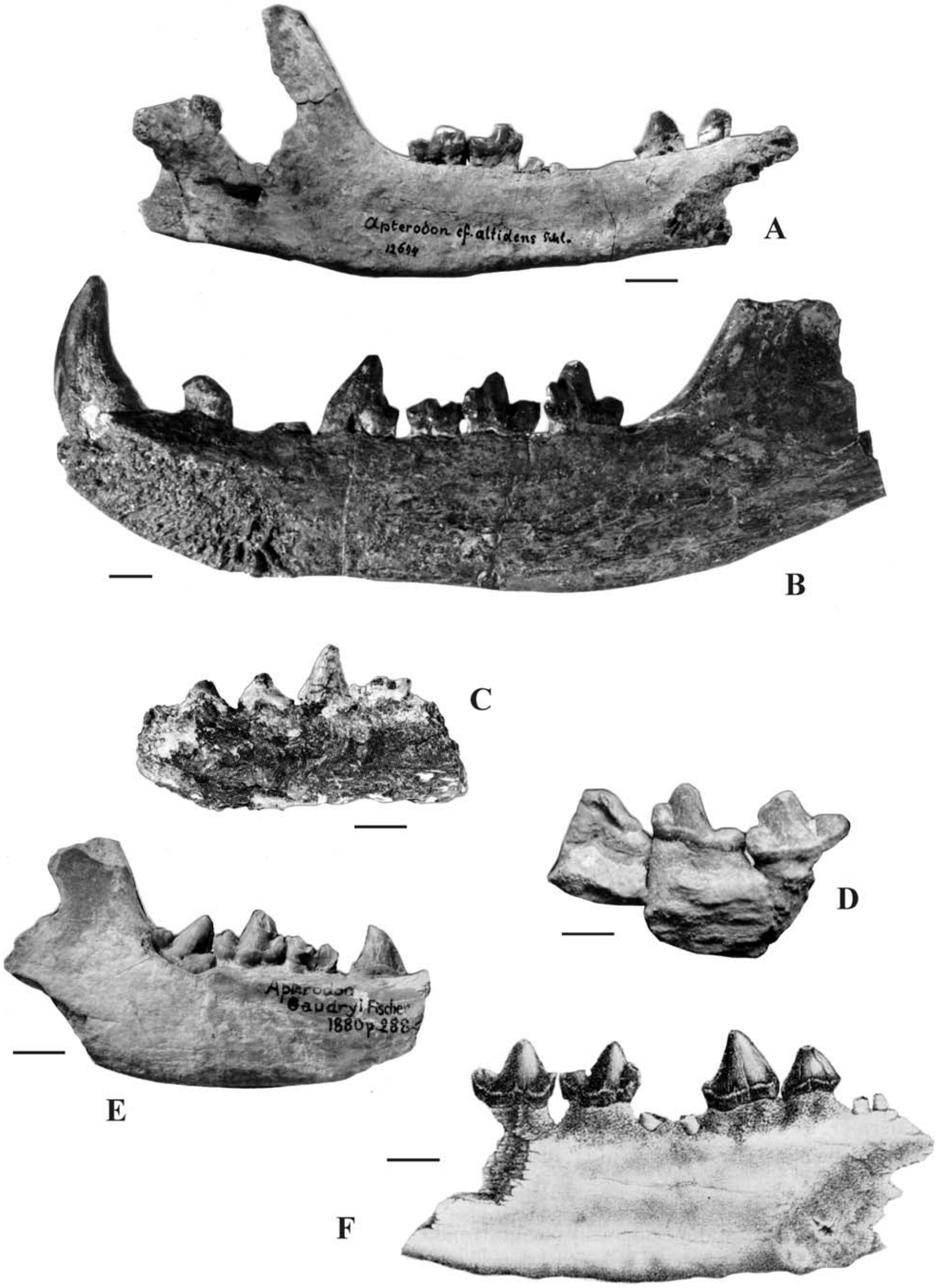


Fig. 1. Mandible of *Apterodon* species. **A**. *A*. cf. *altidens*, left mandible. Staatl. Mus. Naturk. Stuttgart. **B**. *A. macrognathus*, right mandible. Staatl. Mus. Naturk. Stuttgart. **C**. *A. saghensis*, fragment of left mandible, holotype. Cairo Geol. Mus. **D**. *A. intermedius*, fragment of right mandible, holotype. Staatl. Mus. Naturk. Stuttgart. **E**. *A. gaudryi*, left mandible, holotype, MNHN, Paris. **F**. *A. gaudryi* (ex-*flonheimensis*), right mandible. All specimens lingual views except *A. saghensis*.

3.1. Description

The specimen (Fig. 1D) is a badly preserved right mandible fragment with worn p4-m2, and corroded by post-mortem processes. The dentary is broken at the level of the root apex. There is a slight bone swelling under m1.

p4 is heavily damaged with an unusual appearance for a creodont tooth. The enamel has been removed from all the crown except a lingual scrap. The details of the crown structure have been lost and there is no possible meaningful measurements on it. The surviving dentine indicates that p4 consists of an asymmetric cone with the distal slope longer than the mesial one. It is implanted by two strong roots, the posterior much larger than the anterior.

m1 is considerably worn too, particularly the distal face of the protoconid where the apical wear is spread down from the top of the main cusp to the fully levelled talonid on which a conspicuous dentine band surrounds a very shallow central depression.

The wrinkled enamel is worn and it is missing on the buccal and lingual sides of the talonid. The paraconid, low and very reduced is a thick, conical cusp positioned mesiolingually relative to the protoconid, with a moderate apical wear. A weak blunted postparacristid joins the very short carnassial notch. The preprotocristid has not been observed. On the lingual face, the paraconid and the protoconid are well separated by a narrow valley.

The protoconid is a strong cone. The flat lingual face is twice longer than the paraconid one and both they are situated in the same anteroposterior vertical plane beyond the cingulid.

There is no metaconid: at its place a faint enamel fold stands up from the cingulid to the half height of the protoconid.

The ectocingulid is smooth, weakly developed, and partly obliterated by post mortem frictions. Straight, it stands up abruptly beneath the paraconid on the labial side. On the mesiobuccal corner, it is very thick, without forming an accessory cusp. The cingulid more conspicuous on the lingual face is missing on the mesial one.

m2, the best preserved tooth, is a little larger than m1 (Table 1). The two molars look morphologically much alike. The mesiobuccal cingulum of m2 is more developed, giving a rough outline to the crown base. The low and rounded paraconid, stronger and more lingual than the M/1 one, is well distinct on the labial view. It is separate from the high protoconid by a wide V-shaped valley open lingually above the entocingulid. A small crest, maybe the postparacristid, links the very short carnassial split to the paraconid top. The carnassial notch is shorter than that of M/1.

The apex of the conical protoconid is heavily worn and broken; its lingual base is very long and enlarged towards the talonid. There is a short postprotocristid only at the base of the distal face, down to the talonid.

The protoconid and the low paraconid are very thick and they do not form a shearing blade. There is no trace of the metaconid.

Fig. 1. Mandibules des différentes espèces d'*Apterodon*. **A**. *A*. cf. *altidens*, mandibule gauche. Staatl. Mus. Naturk. Stuttgart. **B**. *A. macrognathus*, mandibule droite. Staatl. Mus. Naturk. Stuttgart. **C**. *A. saghensis*, fragment de mandibule gauche. Holotype. Geol. Museum, Le Caire. **D**. *A. intermedius*, fragment de mandibule droite. Holotype. Staatl. Mus. Naturk. Stuttgart. **E**. *A. gaudryi*, mandibule gauche. Holotype, MNHN, Paris. **F**. *A. gaudryi* (ex-*flonheimensis*), fragment de mandibule droite. Tous les spécimens sont vus par la face linguale sauf *A. saghensis*.

Table 1
Measurements length/width (mm) of teeth of *Apterodon* species
Mesures longueur/largeur (en mm) des dents des différentes espèces d'*Apterodon*

	intermedius	*gaudryi*		*macrognathus*[b]	*altidens*
		Quercy	Flonheim		
p4	12.2[a]/6.0[a]	13/7.6	16.0/9.0	17.3/9.4	17/10
m1	13.2/7.3	11.0[a]/–	12[a]/–	12.5/6.5; 13.4/7.2	–/–
m2	14.0/8.2	14.0/9.0	16.5/8.7	17.0/9.0; 18.3/9.8	14.0/–
Talonid					
L	4.7	4.5	4.4	4.8	
Paraconid					
L	3.2 (buccal)	2.5	2.8	3.1	
	4.2 (lingual)	2.3			
H	5.2–5.4	5.8	6.0	8.0	
Protoconid					
labial base					
L.	7.3	7.9	7.4	7.1	

[a] Rough value/valeur approchée par défaut.

[b] Specimen from Institute für Paläontologie und historisches Geologie, Munich; values from Andrews (1906); Schlosser (1910).

The talonid voluminous and short is more longer and lower than the paraconid. It consists of only one very bulky cusp with the top blunted by the wear, filling the postfossid reduced to a buccolingual furrow well open lingually. The apex of the protoconid and the talonid cusp are aligned anteroposteriorly, the paraconid one is more lingual.

The ectocingulid is thick, rather crenulated, extending straight from the paraconid to the talonid ends, without encircling them. Beneath the carnassial split, the ectocingulum develops an oblique buttress less developed than the m1 one.

3.2. Comparison and discussion

Comparisons are exclusively limited to m2 because others teeth of *A. intermedius* are too poorly preserved. At the present time, five *Apterodon* species are recorded, included *A. intermedius*: two from West Europe, three from Africa, most of them are represented by very few specimens or only the holotype.

3.2.1. Comparison with European species

Table 1 shows m2 of *A. intermedius* has the same length as that of *A. gaudryi* and it is a little smaller than the specimen from Flonheim. It is less broad too. However nothing is known about intraspecific variations of *Apterodon* species and the differences could be insignificant.

The molars of *A. gaudryi* have the crown base encircled by a continuous, sinuous cingulum higher and thicker than the one of *A. intermedius*. It is smooth in *A. gaudryi*, the one of *A. intermedius* crenulated. The ectocingulid stands up abruptly beneath the paraconid, without forming a real mesiobuccal thickness. In *A. gaudryi*, the ecto- and the entocingulid meet on the posterior face of the tooth and both they form a tiny accessory cusp lined up with the other cusps of the talonid.

In *A. gaudryi* the paraconid is flattened and reduced to a very short, labiolingual and thick ridge closely appressed against the mediolingual part of the protoconid. Its lingual length is shorter (50%) than that of *A. intermedius* (Fig. 1D–F). The valley is not so widely and deeply open than in *A. intermedius*.

The paraconid of the specimen from Flonheim according to Andreae's figure (1887) is apparently similar to that of *A. intermedius* except it is a little higher. It is widely separated from the protoconid. The postparacristid is like this one of *A. gaudryi*.

The enamel fold, a vestigial metaconid, on the protoconid lingual face is more apparent in the specimen from Flonheim and a little less in the holotype. The pre- and postprotocristid are well marked in the two specimens.

The talonid of *A. gaudryi* is shorter than that of *A. intermedius*. It consists of two cups more and less fused: an anterior smaller and lower than the paraconid and a posterior, pyramidal larger one, followed by the tiny cusp from the posterior cingulum. They are joined up and form a straight shearing ridge, oblique labiolingually. There is no distinct cristid obliqua and no lingual rim. The basin is filled by the enlarged distal cusp. A deep notch cut away the talonid from the protoconid. The apex of the talonid main cusp is positioned more lingually relative to the protoconid one than in *A. intermedius*.

The talonid is shorter and consists of two small cusps united in a cutting ridge on the labial margin in *A. gaudryi*. The postprotocristid and the cristid obliqua join buccally, forming a slightly arcuated line. The postfossid is limited to the anterolingual part and widely open. The talonid of the specimen from Flonheim looks like that on *A. intermedius* but the unique cusp shearing and not grinding, stands in central position and the junction of the postprotocristid and the cristid obliqua very short and lined up with the anteroposterior axis of the protoconid.

The talonid of the same specimen looks like that of the *A. gaudryi* holotype with two cusps closely joined, which are aligned straight anteroposteriorly with the apex of the protoconid. Although they are thick, they form a crest cutting. On *A. intermedius* the two cusps are fused and there is only a voluminous one. The talonid basin is more widely open that one of *A. intermedius* and limited to the anterolingual part.

A transverse notch separates the postprotocristid from the thick and subhorizontal ridge of the talonid main cusp.

On the both European species, the enamel is finely wrinkled.

Generally speaking, *A. intermedius* is a little bit more grinding that *A. gaudryi*.

3.2.2. Comparison with the African species

Molars of *A. saghensis* are unknown except a broken m1 (Simons and Gingerich, 1976). Concerning *A. altidens*, the holotype is a maxillar. A mandible fragment (Fig. 1A) reported dubiously by Schlosser (1910) could belong to *A. macrognathus*. Consequently the comparison with the Egyptian species of *Apterodon* is limited to *A. macrognathus* (Fig. 1B).

A. macrognathus differs from the European species in having a larger size (Table 1). According to Andrews (1906) and Osborn (1909), m2 has a large talonid with a buccal blunt cutting edge and a strong cingulum developed on the lingual side. The talonid of m1 should be more plesiomorphic than on the other species. It consists of two or three distinct cusps surrounding a shallow depression. There is no posterior cingulid.

The strong paraconid is protruding relative to the protoconid on the lingual face. Andrews described it as being closely united to the anterolingual side of the protoconid. In fact, his Fig. 72 shows a broad lingual valley, which separates well the two cusps like on *A. inter-*

medius. The same pattern can be observed in Fig. 3 in Osborn (1909). There is a parastylid beneath the paraconid. The presence of a reduced metaconid is shortly discussed by the authors. Andrews said clearly "there is no trace of a posterolingual cusp in m2". Osborn did not said anything on the topic but in Fig. 3, m1 exhibits the same crista than the m2 figured by Andrews. For Schlosser (1910) the metaconid disappeared on the three molars. Simons and Gingerich considered the m1 of *A. saghensis* is too badly preserved to offer any positive evidence of a metaconid even reduced. Holroyd et al. (1997) are alone who mentioned a "very small metaconid" on the poorly preserved molars of a mandible which they did not assigned specifically. Moreover the figuration of the specimen represented on the buccal side is inaccurate.

From all over species of *Apterodon* previously reported, *A. macrognathus* seems more plesiomorphic than *A. intermedius* and *gaudryi*.

4. Occlusal pattern and dental microwear

Apterodon is an unusual and very distinctive Creodont. With the reduction of the paraconid and the loss of the metaconid on the lower molars, *Apterodon* has developed a peculiar occlusal pattern. The cheek teeth have not carnassial cutting blade. Consequently the feeding mechanism is unlike those of other Creodont and Carnivora. The lower molars of *Apterodon* species may be though as a series of premolars and they suggest similarities to the cheek teeth of some specialised mesonychids such as *Dissacus* or *Mesonyx* (Szalay, 1969; Van Valen, 1966). However it is evident that these pseudosimilar characters are not herited from a shared ancestor but they result from independent evolution. They are relevant to homoplasy. When strong environmental constraints are acting, identical dental morphologies can be obtained by parallel evolution (Muizon and Lange-Badré, 1997). There is no significant prevallid/postvallum shear in the *Apterodon* species and the transverse cutting is reduced on behalf of the increasing crushing forces of the molar tips.

It seems that the food was caught then hold between the apex of the opposite upper and lower teeth which were quickly worn. Fragments were teared and trapped between the buccodistal surface of the protoconid of m2 and the edge of the paracone of M2 and the short metastyle of M1 before being crushed between the talonid of m2 and the protocone of M2.

The special occlusal mode of *Apterodon* molars has suggested to investigate the dental wear surfaces of *A. intermedius* under SEM. Wear surfaces are well developed: some expose more and less widely dentine on the tip of the paraconid, the protoconid and the talonid.

We should consider only m2 wear surfaces because p4 and m1 are too damaged probably by taphonomic processes and post mortem transport. Epoxy cast of m2 was examinated under SEM at magnifications 50–450×.

An unexpected small wear surface is present on the mediolingual edge of the paraconid. It is characterised by short, broad, vertical and parallel grooves crossed by long and thin striae running subhorizontally near the mesial border (Pl. 1, Figs. 1–3). It was probably produced by contact with the distal lingual part of M1, and suggests few lateral motions of the lower jaw. No scratch has been observed.

The main attrition facet is situated on the distobuccal side of the protoconid and fitted with the paracone and the metacone of M2. The surface as a whole is crossed by numerous long, thin and parallel striae, sloping down the surface of the protoconid (Plate 1, Figs. 4 and 5). Some of them are wider and deeper, like furrows. There are rare, small and irregular pits too. This facet is also present on m2 of *A. gaudryi*.

Three small facets are present on the talonid: one buccal steeply inclined, which fits with the lingual side of the metacone of M2 and one lingual which comes into contact with the protocone of the same tooth. The third one, very small, is situated on the posteriormost edge of the talonid, suggesting the presence of m3. The second and third one have a frosted appearance with very few striations and pits. The first one has the same microwear pattern as the protoconid one. Only striae are thinner with a higher frequency of tiny and rounded pits (Plate 2, Figs. 1–4). There are no deep furrows.

The low variation in feature orientation shown by *A. intermedius* implies a restricted use of the cheek teeth for cutting preferentially to grinding. No crushing mark has been really observed except on the dentine of the apex of cusps. Scratches are small and rare. Striation requires ingestion of a harder item as a part of food such as bones or shells, or tiny sand particles. Compression is not sufficient to score enamel.

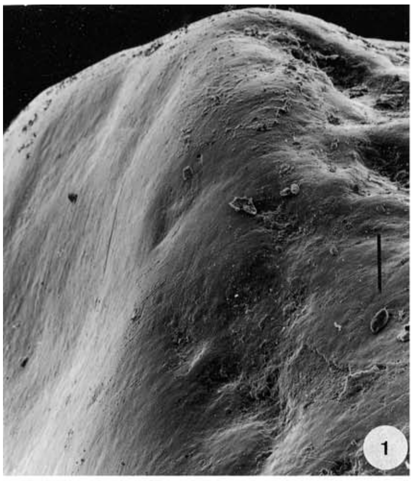
It seems the nature of *A. intermedius* diet cannot be precisely determinated from the dental microwear pattern. The disposition in *A. intermedius* looks like those described in extant carnivores such as genetta, ichneumon (Taylor and Hannam, 1987), cheetah (Van Valkenburgh et al., 1990) and in a Creodont *Hyaenodon exiguus* (Plate 2, Fig. 5). These species are known as preferential flesh eaters, which consume very little hard food items. However factors other than food may have abrasive effects on the enamel grit, mineral particles or dust on the food may contribute to realise dental abrasion although according to King et al (1999) “the dental microwear tends to be obliterated by taphonomic process.” On the other hand, striae are not specific of a diet neither a taxonomic group. Striations are present in Primates (Teaford, 1988a; 1988b), small herbivores and rodents (Rensberger, 1978) too.

5. *Apterodon* and transtethysian relations

The geographical distribution of *Apterodon* species on both sides of Tethys Sea and their temporal range between the Upper Eocene to Lower Oligocene questions about the ways of continental dispersal.

Simons and Gingerich (1976) suggested that *Apterodon* probably evolved in Africa with a limited migration toward the North and West of Europe in the Early Oligocene when terrestrial connections between Europe and North Africa are established. However according to later palaeogeographical maps (Dercourt et al., 1993; Rögl, 1999) there was no permanent terrestrial link between Eurasia and Africa, from Early Eocene to Miocene but all these documents are found on maxima transgressive periods or include too long a time in a strongly changing geographical environment.

In fact, faunal terrestrial assemblages document some punctual migrations between the Middle Eocene and the Lower Oligocene, the most famous one being from Asia to Western Europa named “Grande Coupure” (Stehlin, 1909) when the Turgai Strait vanished off shortly after the Eocene/Oligocene boundary. Further alternative palaeobiogeographic scenarios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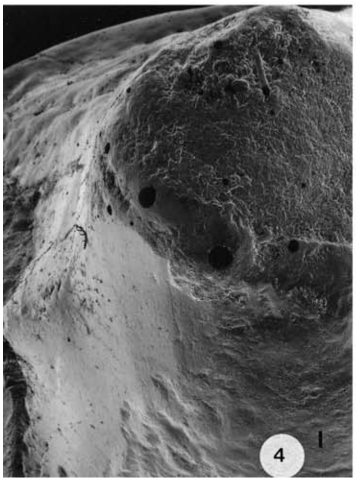
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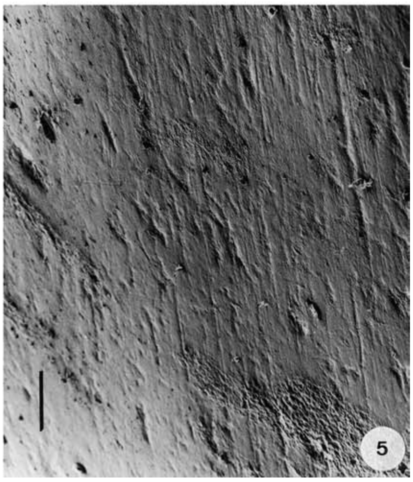
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have been investigated here. They take into account recent tectonic, climatic and faunal data (Thomas et al., 1989; Gheerbrant, 1990; Kappelman et al., 1992; Rasmussen et al., 1992).

The middle Eocene–early Oligocene interval was a significant period of severe climatic changes, which influenced the environmental conditions all around the world. The extensive development of polar cap in Antarctic, the opening of a seaway between Antarctic and Australia, the connection between the Arctic and Atlantic oceans produced a global cooling. Glaciation caused a lowered sea level of about 100 m, spreading merged areas, islands and land bridges between isolated continental regions. This event coincides with a faunal and floristic turn over at the middle – late Eocene boundary.

On the other hand, tectonic plate movements in Northern Hemisphere modified the configuration of continents and epicontinental seas. According to Akhmetiev (1996), the Turgaï sea has lost its polar connection at late Lutetian–Bartonian. A temporary land bridge is established between Siberia and Central Northern Europe.

Lastly, during the Upper Eocene (Ducrocq, 1995), maybe earlier — mid Eocene time (Sahni and Kumar, 1974; Jones and Simmons, 1996) — the Indian plate joined with the South-West of central Asia and made possible too, continental fauna migrations from Asia to Africa through the South of Eurasia.

Thus, from the Lower Eocene to Lower Oligocene the geographical and climatic conditions could make possible mammalian terrestrial dispersions. Three dispersal routes can be involved from West to East Tethys: (1) the Iberian way, (2) the Apulian plate way, (3) the Eastern way.

- Option 1 – The Iberian migration route.

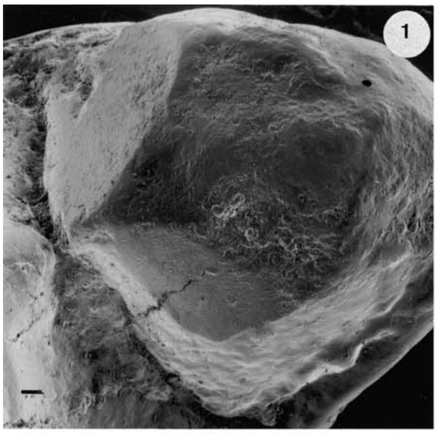
  The Iberian plate was a part of Africa from Late Cretaceous to the Middle Eocene (Srisvastava et al., 1990) and it was more and less isolated from the South of France by a seaway, at the emplacement of Pyrenees mountains, except at the eastern side.

  The Iberian faunal migration way has been involved during the Palaeocene and Lower Eocene (Gheerbrant, 1987, 2001). Several Moroccan mammal species, some of which are creodonts, shared affinities with North American and European taxa, indicating a significant S–N N–S interchange between the three areas at this time (Fig. 2).

  Later, the evolution of Iberian plate is poorly documented. It seems very complex (Sanz de Galdano, 2000). It has been greatly controlled by tectonic events: the North Atlantic opening, the Alpine and Pyrenean orogenies, the closure of the Tethys Sea and climatic variations. At the present time, there is no uncontroversial evidence of a postPalaeocene/Early Eocene migration route via Iberia. However some positive clues are provided recently by rodents from Middle or Upper Eocene of the Duero Basin, which are probably related to Africa or Asian species (Checa Soler, 1997; Hugueney and

Plate 1. SEM wear facet on *A. intermedius* trigonid. **1**. Lingual surface and the tip of the m2 paraconid. Scale bar = 100 µm. **2**. The same. Scale bar = 200 µm. **3**. Wear facet on the mesiolingual edge of the paraconid. Scale bar = 450 µm. **4**. Wear facets on the labiodistal face of the protoconid. Scale bar = 200 µm. **5**. Striae on the labial facet of the protoconid. Scale bar = 100 µm.

Planche 1. Facettes d'usure du trigonide de *A. intermedius*, observées au microscope électronique à balayage. **1**. Surface linguale et sommet du paraconide de m2. Échelle = 100 µm. **2**. La même. Échelle = 200 µm. **3**. Usure sur le bord mésio-lingual du paraconide. Échelle = 450 µm. **4**. Usure sur la face labio-distale du protoconide. Échelle = 200 µm. **5**. Stries sur la face labiale du protoconide. Échelle = 100 µm.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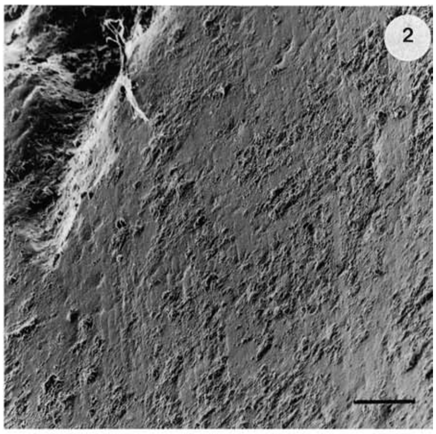
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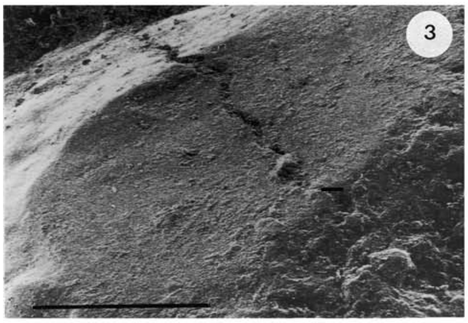
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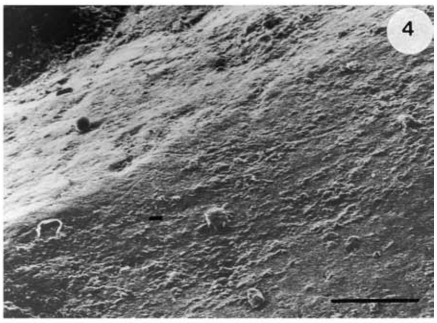
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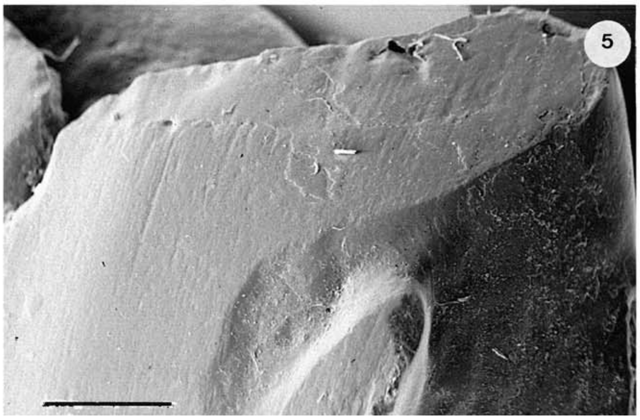
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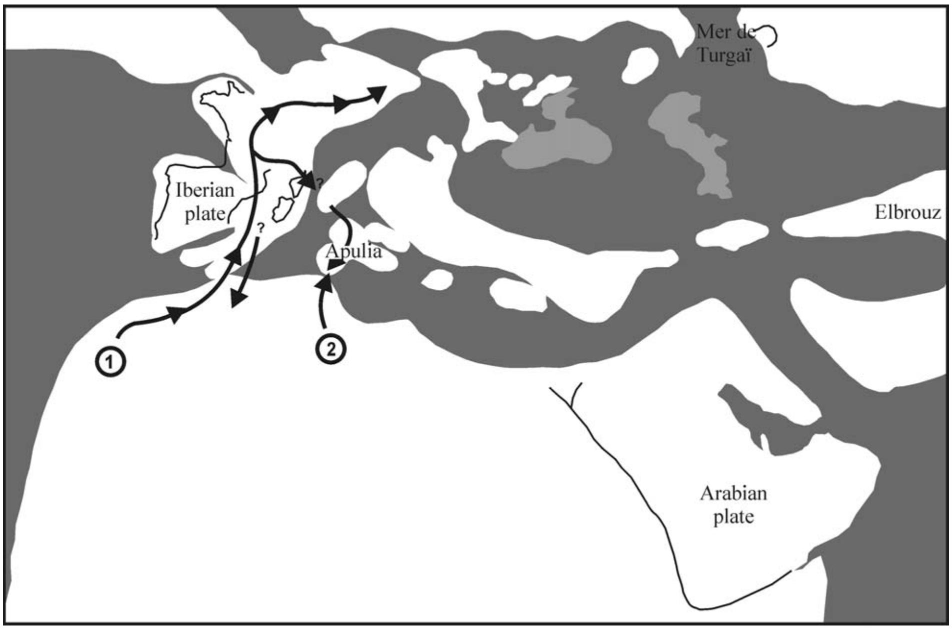

Fig. 2. Schematic palaeogeographical map of Western Eurasia and part of Africa, with hypothetical migration routes from South to North (from Rögl, 1999). **1**. Iberian route. **2**. Apulian route.

Fig. 2. Eventuelles voies de migration entre l'Europe occidentale et l'Afrique du Nord (d'après Rögl, 1999). **1**. Route ibérique. **2**. Route apulienne.

Adrover, 1991). An African origin of Perissodactyls Palaeotheriids has been suggested too (Hartenberger et al., 1985; Casanovas et al., 1991) a possible ancestor of which has been mentioned in the Lower Eocene of Morocco. Concerning creodonts, none hyaenodontine has yet been recorded before the Upper Eocene.

- Option 2 – The Apulian migration way.
  It is the poorliest documented way. The geographical extension of the Apulian plate situated between Tunisia and Liguria is not well known (Fig. 2). All this domain is strongly affected by processes of subduction and S–N compression in Eocene. However islands could provisionally play a part of relay and enable faunal migration the direction (S–N, N–S) of which cannot be precisely defined.

Plate 2. SEM wear facet on *A. intermedius* m2 talonid and *Hyaenodon exiguus* m3 paraconid. **1**. Talonid apical view. Scale bar = 200 µm. **2**. Hypoconid labial wear facet. Scale bar = 100 µm. **3**. Talonid mesiolingual wear facet. Scale bar = 45 µm. **4**. Talonid apical wear facet. Scale bar = 150 µm. **5**. *H. exiguus* m3 paraconid labial wear facet. Specimen from Garouillas, Quercy, France. Scale bar = 1 mm.

Planche 2. Facettes d'usure observées au MEB sur le talonide de m2 de *A. intermedius* et le paraconide de la m3 de *Hyaenodon exiguus*. **1**. Vue du sommet du talonide. Échelle = 200 µm. **2**. Usure sur la face labiale de l'hypoconide. Échelle = 100 µm. **3**. usure sur la face mésio-linguale du talonide. Échelle = 45 µm. **4**. Facette sur le sommet du talonide. Échelle = 150 µm. **5**. *H. exiguus*, M/3 usure sur la face labiale du paraconide. Garouillas, Quercy, France. Échelle = 1 mm.

Some Algerian localities (Crochet, 1988) and a Tunisian one (Hartenberger et al., 1997) dated from Late Lower Eocene or Early Middle Eocene provide the main palaeontological data. The mammal fauna includes Marsupials Peradectids, Rodents Ischyromyids, Primates, which have affinities with European taxa. Creodonts are represented only by proviverrines (Crochet, 1988). Presently, there is no hyaenodontines in Africa before the Upper Eocene (Holroyd et al., 1997; Holroyd, 1999). During the same time, they are present yet in Western Europe (Rich, 1972; Crochet et al., 1976; Lange-Badré and Haubold, 1990) and Asia (Lavrov, 1996, 1999).

- Option 3 – The East-West dispersal route.
  An alternative mammal dispersal route can be investigated from Asia across the Turgai Strait too. This way from Central Asia to Africa and Europe via Southern Eurasia, Irak, Iran, Arabo-Afro plate or Anatolia and Balkans was suggested by Heissig (1979) to explain the faunal renewal characteristic of Grande Coupure at Lower Oligocene. But more and more data (Iakoleva et al., 2001; Radionova et al., 2001) show Turgai Strait was not a barrier but probably like a filter bridge type, from the Late Palaeocene to the Early Eocene, between 55.3 and 54.5 Ma. The same scenario might be repeated several times, later during Middle–Upper Eocene, with selective and limited migrations following temporary terrestrial ways available from East to West, through West Siberia or Kazaksthan (Fig. 3).

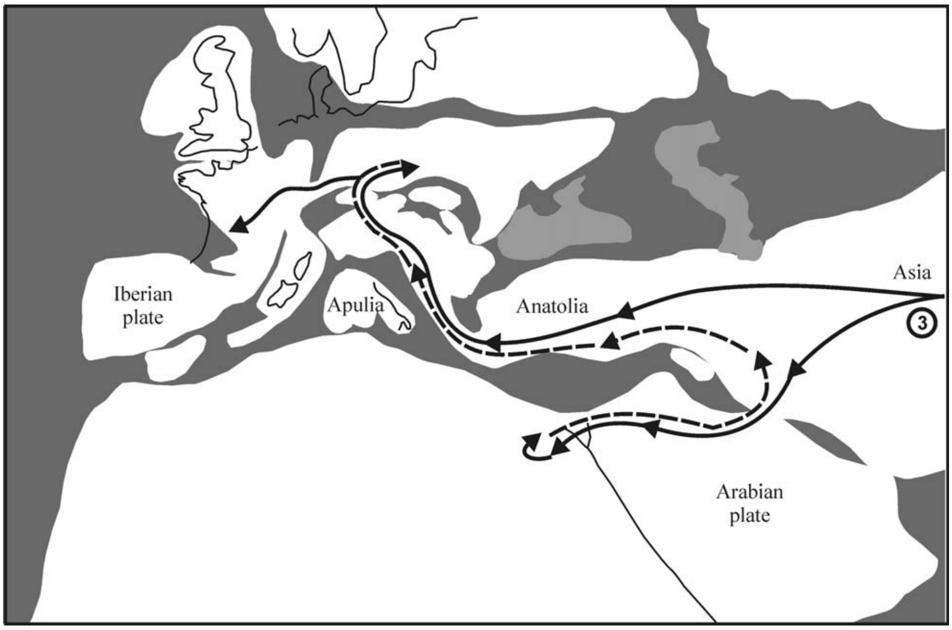

Fig. 3. Schematic palaeogeographical map of Western Eurasia and part of Africa, with hypothetical migration routes (3) from East to West (from Rögl, 1999).

Fig. 3. Voies de migration possibles entre l'Est et l'Ouest de l'Europe occidentale et le Moyen-Orient (d'après Rögl, 1999.

Although Creodonts seem presently have an African origin, the African origin of *Apterodon* is not clearly proved. Among the hyaenodontines from Fayoum, there are some species of *Pterodon* and *Hyaenodon*, two genera identified too in China (Qi Tao et al., 1996) and Mongolia (Dashzeveg, 1985) during the Middle Eocene although Lavrov disagrees with the determinations of the species and erects them as new genera (1996, 1998). In Europe *Hyaenodon minor* occurred to MP 17 (Salème, France; Hordle, UK). Maybe *Apterodon* or a form more and less related to it was yet differentiated in Asia, in spite of gaps in specimens and biostratigraphical record. All of these genus with some other taxa (Anthracotheriids, Traguloids, Entelodontids, Primates...), have taken the opportunity of emigrating to West where their presence is reported in Western Europe and Egypt. This suggests that faunal migrations were possible from Asia to Europe and Africa before the Early Oligocene and the important faunal turnover known as the "Grande Coupure, probably during the Middle Eocene (MP10-11) or the earlier Upper Eocene (MP17).

Apterodon could have reached Africa in Fayoum area at this time when a temporary marine regression has occurred. Then it could have joined Europe via Arabia, Anatolia and South of Europe, or through Apulian plate, at the Early Oligocene. But *Apterodon* species seem to be the only one mammal taxon that might have migrated in the South–North direction at a climatic cooling time with important floristic and faunal changes, which are unfavoured ecological conditions for a Creodont.

6. Conclusion

During the anteoligocene times, the Tethys Sea did not consist of an unovercome barrier. In spite of many obstacles, the palaeogeographic conditions made possible short, quick, terrestrial mammal migration between North and South continental areas on several times.

Among Creodonts, the transtethyan distribution of *Apterodon* species, during the Upper Eocene and Early Oligocene documents this hypothesis. However the African origin of European *Apterodon* species is not firmly demonstrated. It is possible the hyaenodontines like other taxons from Fayoum zone come in part from Asia by means of very temporary level sea fall about 40–37 Ma (Late Lutetian or Early Bartonian).

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