

Early African hyaenodontid mammals and their bearing on the origin of the Creodonta

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Abstract – We report a new proviverrine hyaenodontid creodont mammal, *Boualitomus marocanensis*, n.g., n.sp., from the earliest Eocene of Morocco, and provide new comments on *Tinerhodon* from the late Paleocene of Morocco. Aside from the autapomorphic loss of P/1, *Boualitomus* is characterized by a primitive morphology (e.g. M/3 subequal to M/2, short molar trigonid, narrow talonid, metaconid comparable to paraconid) which resembles most closely the proviverrine *Prototomus*. *Boualitomus* is more primitive than *Prototomus*, especially in its small size and the talonid of P/4 not being fully simplified, bearing at least two accessory cusps including a bulbous protostylid. These primitive features are remarkably reminiscent of *Tinerhodon*. The morphological relationship of *Boualitomus* and *Tinerhodon* supports the proviverrine affinity of the latter. Significant basal hyaenodontid synapomorphies of *Boualitomus* and *Tinerhodon* are the paraconid and paracristid development in M/1–3, anterior premolar morphology and occurrence of diastemata. *Boualitomus* and *Tinerhodon* throw new light upon the question of the origin of the Creodonta. *Tinerhodon* further fills the structural gap between Hyaenodontidae and primitive insectivore-like eutherians, and it provides additional data for the hypothesis of a didelphodontan origin for the Creodonta. The presence of cimolestids (as the stem-group of hyaenodontids) in the late Paleocene of Morocco, and the identification of *Boualitomus* and *Tinerhodon* as the most primitive and earliest known Hyaenodontidae, support an African origin of the family and its order.

Keywords: Africa, Morocco, Creodonta, Hyaenodontidae, new taxon, Early Eocene.

1. Introduction

The Creodonta is an important extinct Palaeogene and Miocene order of primitive carnivorous placentals. Its origin and basal phylogeny remain poorly resolved. This is especially true for the supra-ordinal relationships (e.g. relationships with Carnivora) and the relationships between the Hyaenodontidae and Oxyaenidae (e.g. Gingerich, 1980; Gunnell, 1998). The family Oxyaenidae probably originated in North America, where *Tythaena* from the late Paleocene (middle Tiffanian; Gingerich, 1980) represents its earliest record. North America is also the main centre of radiation of this family. Oxyaenids are known in much smaller numbers in Europe since the early Eocene, and in Asia since the middle or possibly early Eocene. Although more primitive, the family Hyaenodontidae is recorded later than the Oxyaenidae. The Hyaenodontidae makes an abrupt appearance as a diverse group in Laurasia in the early Eocene of both North America

and Europe, and in the latest Paleocene of Asia (Fig. 1), probably as the result of an immigration from an unspecified continental province, possibly from Africa (e.g. Gingerich, 1986). In Laurasia, creodonts coexisted with modern carnivorous placentals of the extant order Carnivora.

In Africa, creodonts are the dominant carnivorous placentals during the Palaeogene period, in the near-absence of carnivorans (two uncertain occurrences are reported by Gheerbrant, 1995 and Crochet, Peigne, & Mahboubi, 2001) as the result of the isolation of the continent. African creodonts are represented by the hyaenodontid subfamilies Proviverrinae, Koholiinae, Apterodontinae and Hyainailourinae (= Pterodontinae). Early Oligocene localities, and especially the Fayum sites, provide the best picture of the creodont radiation in Africa, with more than twenty species reported (Savage & Russell, 1983; P. Holroyd, unpub. Ph.D. thesis, Duke Univ. 1995; Holroyd, 1999). However, the Palaeogene radiation and the origin of creodonts in Africa are still poorly known. Early African creodonts are poorly documented by scarce

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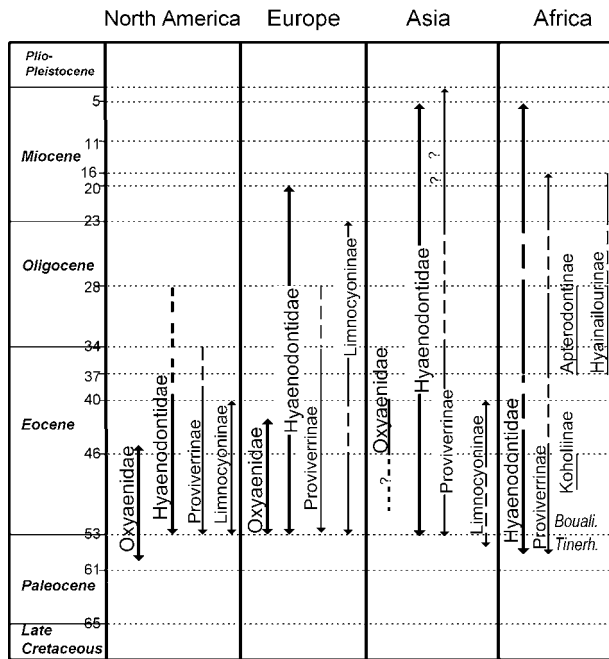


Figure 1. Known stratigraphic and geographic distribution of the main lineages of creodonts. Only primitive lineages are figured here, with the exception of the case of Africa where the known subfamilies are detailed. It should be noted that the systematics of the creodonts is confused and in need of a thorough review, which may have implications especially in the definition and distribution of subfamilies reported here.

Eocene fossils. The earliest known and best characterized example (although poorly known) is *Koholia atlasense* from the late early Eocene of El Kohol, Algeria (Crochet, 1988). Earlier African occurrences have been tentatively reported from the late Paleocene of Morocco (Ouarzazate Basin: Gheerbrant, 1995; Gheerbrant *et al.* 1998), especially *Tinerhodon disputatum* of uncertain systematic position. Here we report a new hyaenodontid from the early Eocene (Ypresian) of the Ouled Abdoun Basin, Morocco, which permits a new look at the relationships of *Tinerhodon disputatum* and at the origin of the order Creodonta in Africa. This new early African creodont is the smallest mammal discovered in the phosphatic deposits of the Ouled Abdoun Basin (see Gheerbrant *et al.* 2003).

2. Material and methods

Abbreviations. OCP DEK/GE – Palaeontological collections of the Office Chérifien des Phosphates, Khouribga, Morocco; OCP – Office Chérifien des Phosphates, Morocco; MNHN – collections of the Muséum national d'Histoire naturelle de Paris; PM – Ouled Abdoun Basin (Morocco); THR, NTG – material from Adrar Mgorn 1 and N'Tagourt 2 localities, Thanetian and Ypresian of the Ouarzazate basin, Morocco, collections of the University of Montpellier II (USTL).

The material reported here is of unknown exact locality from the Ouled Abdoun Basin, Morocco. It was collected in 1997 by local people from the village of the Ouled Bou Ali in the quarries of the Grand Daoui area, eastern part of the Ouled Abdoun Basin (see Gheerbrant *et al.* 2003), and was recovered and kindly donated for study by F. Escuillié from the Rhinopolis Association.

Measurements follow Gheerbrant (1992): L, W, H – length, width, height; tri, tal – trigonid, talonid. Dental nomenclature is that of Van Valen (1966).

3. Systematic study

Order CREODONTA Cope, 1875
 Family HYAENODONTIDAE Leidy, 1869
 Subfamily PROVIVERINAE Schlosser, 1886
Boualitomus n.g. Gheerbrant

Type species and only known species. *Boualitomus maroccanensis* n.sp.

Diagnosis and distribution. As for the type species, only known species.

Etymology. From the name of the village Ouled Bou Ali located close to the quarries of Sidi Daoui, Ouled Abdoun, and tomus, tomeus (Gr.) = blade, knife, in reference to the carnassial morphology of the teeth of the species.

Boualitomus maroccanensis n.sp. Gheerbrant
 Figures 2–4, 6b, 7b, 8a–b, 9b

Etymology. From Morocco, where the type locality is situated.

Holotype. OCP DEK/GE 306, right dentary with M/3–1, P/4–2 and C/1 (broken).

Hypodigm. The holotype, only known specimen.

Type locality and age. Ouled Abdoun Basin, area of Grand Daoui (quarries of Sidi Daoui and Recette 4); probably basal Eocene (earliest Ypresian), lowermost bed I of the mining lithostratigraphic terminology, as for most other mammal specimens collected in the Ouled Abdoun Basin, including those of *Phosphatherium* (Gheerbrant *et al.* 2003). The exact level and locality remain unknown.

Diagnosis. Dental morphology close to that of proviverine hyaenodontids (M/1 smaller than M/2–3, M/2 and M/3 similar in size, large paraconid and sharp paracristid, protoconid high and pointed, metaconid not reduced, trigonid moderately compressed, talonid narrow with weak cusps, entoconid distal, premolars sharp and elongated, P/2–3 asymmetric, diastemata

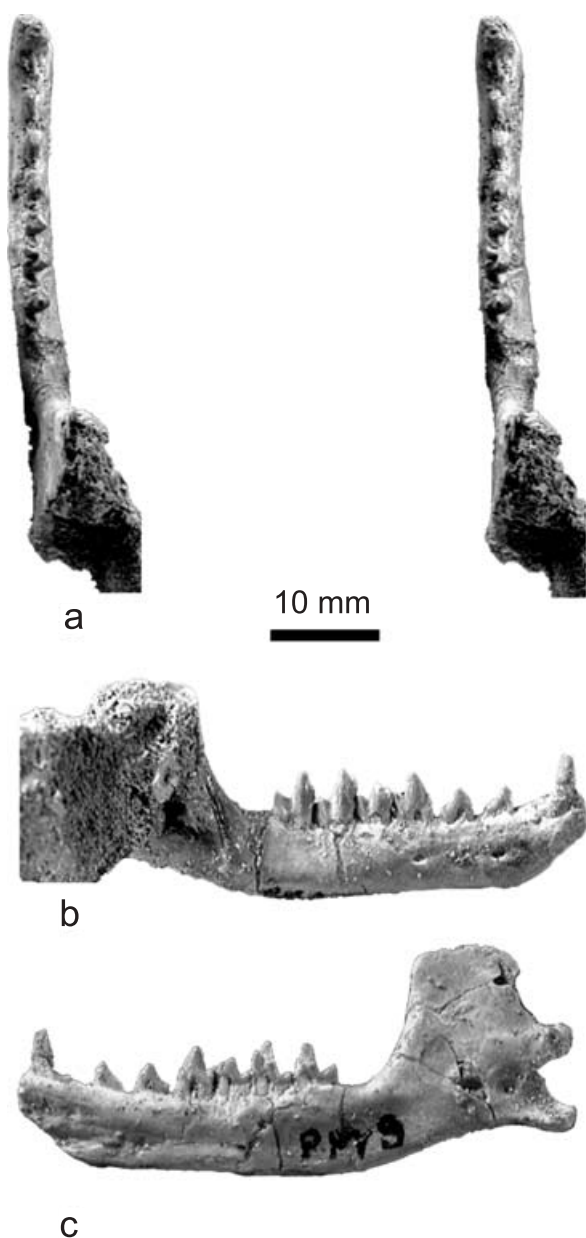


Figure 2. *Boualitomus maroccanensis* n.g., n.sp. General views of the holotype OCP DEK/GE 306, right lower jaw bearing M/3–1, P/4–2, C/1. (a) Occlusal view; stereo pair; (b) labial view; (c) lingual view. Scale bar: 10 mm.

between anterior premolars). Dental morphology closest to *Prototomus* among proviverrines, but differs in the absence of P/1. Small size, close to that of *Prototomus minimus*. Differs from *P. minimus* in having M/3 unreduced with respect to M/2, the cusps less differentiated on the talonid of the molars, the P/4 and molars slightly narrower, and the talonid narrower in M/1. The talonid of P/4 bears at least two accessory cusps.

3.a. Description of *Boualitomus maroccanensis*

The dentition of OCP DEK/GE 306 is characterized by high cusps (especially the protoconid) and sharp crests

(especially the paracristid), indicating that it belongs to a carnivorous species. The trigonid is large and tall with respect to the talonid, at least in M/2–3 (in M/1 the protoconid is worn off).

Dental formula. I/?, C/1, P/2–4, M/1–3.

Lower molars. M/1 is significantly smaller than M/2 and M/3 that represent the carnassial teeth. The trigonid of M/1 is especially smaller than that of M/2. M/2 and M/3 are comparable in size, except for the talonid which is wider in M/2. The trigonid of the molars is sharp and tall (more than twice as tall as the talonid). It is much wider than the talonid. The occlusal outline of the trigonid is moderately compressed mesio-distally, and more so on M/2–3 than on M/1. The paraconid, preserved only in M/2, is well mesial to the protoconid, and it is lingually located, at the level of the metaconid. It is strong, tall and large, probably as voluminous as the metaconid. In lingual view, its mesio-lingual angle appears to be sharp, nearly crested and projects noticeably mesially above the anterior root. Although the metaconid is broken or worn off in OCP DEK/GE 306, it was clearly well developed. There is a distinct carnassial notch on the paracristid (not preserved on the protocristid). The protocristid is more transverse than the paracristid, but the metaconid is slightly distal to the protoconid. The precingulid is very thin and extends labially as a very slight labial inflation of the crown below the protoconid. The protoconid is noticeably taller than the paraconid and very sharp. There is no postmetacristid.

The talonid and its postfossid are narrow and elongated. They are slightly oblique (mesio-lingual to disto-labial) with respect to the longitudinal axis of the tooth row. The postfossid is shallow. All talonid cusps are crestiform and weak. The hypoconulid is the smallest, except in M/3, on which it is salient distally. The entoconid is located distally, close to the hypoconulid. The hypoconulid is distal, approximately median between the entoconid and the hypoconid. The hypoconid is located more lingually than the protoconid apex, in keeping with the narrow talonid width. The entocristid is well developed, and joins the base of the metaconid (postfossid not opened lingually). The cristid obliqua crest joins the trigonid in its lingual half (lingually with respect to the protocristid notch). It is nearly parallel to the entocristid which is oblique. It does not rise on the trigonid. It seems that the carnassial notch on the cristid obliqua was absent (M/3, M/1) or very reduced (M/2). However, this must be checked on unworn specimens. The hypoflexid is deep in its higher part. There is no ectocingulid, nor postcingulid, although the labial base of the talonid at the hypoflexid level is inflated and angular. The posterior root is larger in diameter than the anterior one.

Wear facets are especially distinct on the mesial flank of the trigonid (facet 2, prevallid shearing) and on the



Figure 3. *Boualitomus maroccanensis* n.g., n.sp. Detailed s.e.m. views of the lower dentition M/3–1, P/4–2, C/1, holotype OCP DEK/GE 306. (a) Labial view; (b) occlusal view, stereo pair; (c) lingual view. Scale bar: 10 mm.

labial flank of the cristid obliqua (facet 3) of M/2 and M/3. Both of these facets are in about the same plane and they bear subvertical wear striae. The presence of the facet 2 indicates in upper molars a strong postmetacrista, and facet 3 indicates a tall paracone bearing a well-developed postparacrista (shearing with the cristid obliqua).

Lower premolars. All premolars are two-rooted and simplified (at least the trigonid); the crown is compressed laterally and it is dominated by the high and sharp protoconid, the metaconid is absent, and the paraconid when present is small and low. There are diastemata of increasing length between P/4 and P/3, P/3 and P/2, and P/2 and C/1.

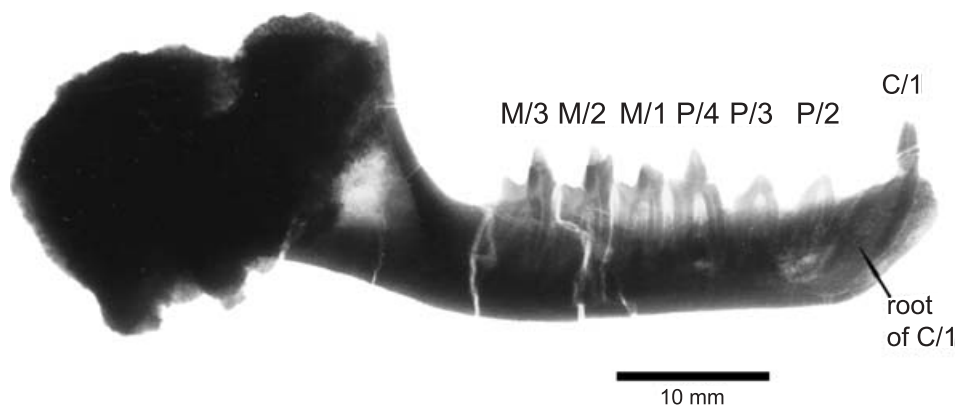


Figure 4. *Boualitomus marocanensis* n.g., n.sp. Radiographic view of the holotype OCP DEK/GE 306, right lower jaw bearing M/3–1, P/4–2, C/1. Labial view. Note the absence of P/1, the diastemata between the anterior premolars, and the large size of the root of the lower canine. Scale bar: 10 mm.

P/4: The crown is tall and narrow. Its occlusal outline is slightly inflated labially and wider behind the protoconid, at the level of the hypoflexid. The protoconid is centrally located on the length of the crown and bears mesial and distal crests. Its labial and lingual flanks are slightly inflated. The paraconid is very small, low and mesio-lingual, and there is no metaconid. A well-differentiated but shallow hypoflexid separates the trigonid and the talonid labially. The talonid is small and it bears two accessory cusps. One cusp is distal (hypoconid), pointed and tall, and the other cusp is more mesial and lingual (protostylid), and is separated from the protoconid by a notch. This mesial accessory cusp (protostylid) is low and bulbous (not crested). Below it, there is a very slight and short vertical cingular ridge (vestigial entoconid?; see comparisons).

P/3 and P/2: The anterior premolars are smaller than P/4, and have no paraconid, metaconid, or talonid. They are elongated and narrow. With respect to P/4, the protoconid is more mesial on the crown, and more markedly so on P/2, resulting in a more asymmetric lateral profile. Both P/3 and P/2 share the presence of a long and mesially inclined distal crest on the protoconid, whereas the mesial crest is weaker and more vertically raised. P/3 and P/2 probably have a small distal cusp (broken). No cingulids are distinct on P/3 and P/2. The roots of P/2 are slightly inclined mesially (Fig. 4). P/3 is larger than P/2.

P/1: P/1 is absent. This is supported by the radiographic view (Fig. 4) which shows no trace of an alveolus or root, but rather dense bone at the level of the short diastema between P/2 and C/1. The absence of P/1 is probably linked to a shortening of the anterior part of the dentary (see below).

C/1 and anterior teeth. C/1 is large. Its root is very large and stout, extending below P/2 (radiographic view: Fig. 4). It has an oval cross-section. The crown bears a distal crest. The incisors are unknown, but were probably small.

Dentary. The horizontal ramus is narrow in lateral view. Its height is nearly constant from its distal part to the level of P/2 where it narrows abruptly, in contrast to many other proviverrines. The abrupt narrowing of the dentary is probably correlated with the loss of P/1, both features indicating a shortening of the dentary in its anterior part. The base of the horizontal ramus is slightly inflated. There are three well-developed mental foramina: under P/4, P/2 and C/1. The symphysis extends below P/2. The vertical ramus and the coronoid process are not tall. Their anterior margin is slightly inclined distally, forming an angle of 117° with respect to the alveolar border. The masseteric fossa is very deep and limited mesially by a sharp crest. The angular process is narrow (height about 2.5 mm) and salient posteriorly. It is isolated from the articular condyle by a distal notch. The condyle is more or less cylindrical and located at the level of the tooth row (above the alveolar border). The mandibular foramen opens as a small pit anterior to the notch between the angular process and the condyle.

Dimensions of the holotype OCP DEK/GE 306 of Boualitomus marocanensis. See Table 1.

3.b. Comparisons and discussion of *Boualitomus marocanensis*

Boualitomus marocanensis n.g., n.sp. from the Ouled Abdoun is characterized by a carnassial dental morphology. The absence of a 'true' specialized carnassial lower molar and the reduced size of M/1 in OCP DEK/GE 306 exclude the species from the order Carnivora. Other features which differ from carnivorans are the unreduced M/3, the molars with a tall and pointed protoconid, the small hypoconid, the elongated talonid and the P/4 with a short talonid.

The entire molar row was specialized for shearing, which is a key feature of the Creodonta, according

Table 1. Dimensions of the holotype OCP DEK/GE 306 of *Boualitomus maroccanensis* (in mm)

Locus	Teeth						
	L	Ltri	Ltal	Wtri	Wtal	Htri	Htal
M/3	4	2.3	1.7	2.65	1.7	*4.7	2.6
M/2	3.9	2.4	1.4	2.6	2.1	*5	2.3
M/1	3.4	2.1	1.4	2.1	1.6	?	2.3
P/4	3.8	–	–	1.9	–	*3.6	–
P/3	3.	–	–	1.4	–	*2.7	–
P/2	2.4	–	–	1.1	–	2.1	–
C/1	≥4	–	–	*2.4	–	–	–

Tooth row	
Length of tooth row	Length of diastemata
C/1–M/3: 28	P/3–P/4: 1
P/2–M/3: 22	P/2–P/3: 1.4
P/4–M/3: 14	C/1–P/2: 2
M/1–M/3: 10.5	–

Dentary	
Height of the horizontal ramus below M/1:	7.5
Length from the condyle to the mesial border:	~ 50
Estimated height of the vertical ramus, from the coronoid apex:	17

* – estimated measurement; L, W, H: length, width, height; tri, tal: trigonid, talonid.

to Flynn, Neff & Tedford (1988, p. 76). The carnassial specialization is particularly marked by the enlargement of the paraconid and paracristid, which is derived with respect to primitive eutherians such as ‘insectivores’. The retention of a well-developed M/3 departs from the family Oxyaenidae, and it indicates that the Ouled Abdoun species belongs to the family Hyaenodontidae. Diagnostic features shared with hyaenodontids are particularly the M/1 being smaller than M/2 and M/3 and the carnassialization of both M/2 and M/3 (e.g. Polly, 1996). This pattern might be representative of the ancestral morphotype of hyaenodontids or of creodonts.

Within the Hyaenodontidae, *Boualitomus* shows several primitive features that are typical of the subfamily ‘Proviverrinae’ (e.g. Barry, 1988; Polly, 1996; Gunnell, 1998): (1) there are three molars, and M/3 is unreduced (and not enlarged as in hyaenodontinae) and similar in size to M/2; (2) the shearing specialization of the molars is poorly advanced: the molar pattern is tuberculo-sectorial, which departs from the more strictly sectorial pattern of advanced taxa such as Hyaenodontinae; (3) there is no true specialized carnassial tooth; (4) the metaconid is weakly reduced with respect to the paraconid, if at all; (5) the paraconid is not shifted mesially; (6) the hypoconulid is enlarged distally on M/3; (7) the dentary is shallow; (8) the size is small.

Following Gunnell (1998), the derived features of *Boualitomus* shared with ‘Proviverrinae’ are the tall and pointed protoconid (much taller than the paraconid and metaconid), and the elongate and laterally compressed premolars (especially P/2–3).

All these features clearly exclude *Boualitomus* from other hyaenodontid subfamilies (Limnocyoninae, Hyaenodontinae, Apterodontinae, Hyainailourinae and Teratodontinae). However, it should be noted that *Koholia* (late early Eocene of Algeria), of the monotypic Koholiinae, cannot be compared with *Boualitomus* because only P4/–M1/ are known (Crochet, 1988).

The subfamily ‘Proviverrinae’ is admittedly paraphyletic (Barry, 1988; Polly, 1996; Morlo & Habersetzer, 1999) and is the probable stem group of several other hyaenodontid subfamilies (e.g. Limnocyoninae). Following the cladistic study of Barry (1988), Morlo & Gunnell (2003, p. 47) distinguished two groups within ‘Proviverrinae’ in its classical concept: (1) ‘true’ Proviverrinae or Proviverrinae s.s. (roughly equivalent to ‘Old World Proviverrines’ of Barry, 1988) which are characterized by molars with a tricuspid talonid bearing a broad postfossid, and a two-rooted P/1; (2) other ‘Proviverrinae’ (North American European, and Asian genera: *Acarictis*, *Arfia*, *Galecyon*, *Gazinocyon*, *Prototomus*, *Proviverroides*, *Pyrocyon*, *Sinopa*, *Tritemnodon*, *Paratritemnodon*), which are characterized by molars with reduced entoconid, elongated postfossid and primitively single-rooted P/1. Here, in the absence of formal systematic revision and diagnosis of these two groups, we will refer to the classical sense of the subfamily ‘Proviverrinae’, the quotation marks underlining its paraphyletic status, and we informally distinguish the unnamed group (2) as the ‘*Prototomus*-group’. *Boualitomus* is clearly related to this *Prototomus*-group, although it lacks a P/1. However, the absence of P/1 is a derived feature, which is closer to the single-rooted P/1 of the *Prototomus*-group than to the double rooted P/1 of ‘true’ Proviverrinae. The loss of P/1 is actually a striking autapomorphic feature of *Boualitomus*. It is also known in the later African ‘true’ proviverrine *Metasinopa*, as a probable parallelism.

The small size of *Boualitomus* is a remarkable primitive feature within proviverrines (Fig. 5). Using the size classes of Morlo & Habersetzer (1999), the size of *Boualitomus* is that of the ‘very small species’ of proviverrines, with an estimated body mass ranging from 300 to 570 g. Other comparable proviverrines are mostly taxa from the early–middle Eocene of Europe such as *Prototomus minimus* (Smith & Smith, 2001), *Proviverra eisenmanni* (Godinot, 1981) and *Parvagula palulae* (Godinot *et al.* 1987). *Acarictis* from the early Eocene of North America (Gingerich & Deutsch, 1989) is the only similarly small-sized proviverrine from the early Eocene of North America. *Acarictis* is, however, slightly larger than *Boualitomus*.

Within ‘Proviverrinae’, *Boualitomus* most closely resembles *Prototomus*, which is the most primitive described genus in the subfamily (‘stem hyaenodontid’ in Van Valen, 1965). *Boualitomus* shares with *Prototomus* the well-developed metaconid, the anterior premolars separated by diastemata, the M/3 comparable in size to

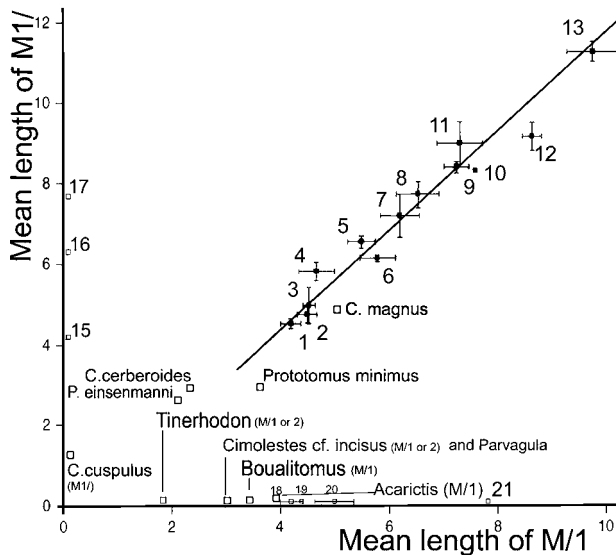


Figure 5. Comparison of the size of *Boualitomus marocanensis* n.g., n.sp. and *Tinerhodon disputatum* with middle Eocene European Proviverrinae (taxa 1–22), some of the smallest other proviverrines (*P. minimus* Smith & Smith, 2001; *Proviverra einseimanni* Godinot, 1981; *Acarictis ryani* Gingerich & Deutsch, 1989; *Parvagula palulæ* Godinot *et al.* 1987) and selected cimolestids from North America and Africa (*Cimolestes cerberoides* Lillegraven, 1969; *Cimolestes magnus* Clemens & Russell, 1965; *Cimolestes cusculus* Gheerbrant, 1992; *Cimolestes cf. incisus* (Gheerbrant, 1992)). Modified from figure 16 of Morlo & Habersetzer (1999); see these authors for identification of proviverrine taxa 1–22. Measurements (in millimetres) are based on the mean length of M/1–2 for *Tinerhodon* and on the holotype for *Boualitomus*.

M/2, the narrow talonid and postfossid of the molars, the very oblique cristid obliqua and the relatively mesio-distally compressed trigonid (Van Valen, 1965; Gingerich & Deutsch, 1989; Gunnell, 1998). Other shared features are the weak entoconid, the protoconid height at least comparable to the trigonid length, the relative length of the trigonid and talonid (2/3, 1/3 of total length) and the simple P/4. The smallest species, *Prototomus minimus* from Dormaal (Smith & Smith, 2001), approaches the size of *Boualitomus* (Fig. 5), and shares the unusual occurrence of two accessory cusps on the talonid. *P. minimus* differs from *Boualitomus* in its slightly reduced M/3 (a diagnostic feature of the species), the more differentiated talonid cusps of the molars, the wider talonid, especially on M/1, and the slightly narrower teeth (P/4 and molars). Additionally, the trigonid of M/3 is larger (wider) with respect to M/2 and the P/4 is shorter than M/1. Most of these differences seen in *P. minimus* can be interpreted as derived features with respect to *Boualitomus* which, in these respects, recalls primitive eutherians such as cimolestids.

The genus *Proviverra*, considered as a ‘true’ proviverrine (see above), is poorly characterized with respect to *Prototomus* (e.g. Van Valen, 1965). However,

recent cladistic analyses suggest that it is more primitive than *Prototomus*, being the sister group of all other hyaenodontids (Polly, 1996), and therefore it is interesting to compare with *Boualitomus*. Its small size and narrow talonid recall *Boualitomus*. However, *Proviverra* differs in important features: the double-rooted P/1, the paraconid probably larger, the P/2 longer and taller than P/3, the P/3 more symmetric in lateral view, the labial cingulid more developed on the molars and the entoconid larger in the molars. Other proviverrine genera are more distinctive from *Boualitomus*, having a more specialized sectorial morphology.

As a whole, *Boualitomus* is characterized by a primitive morphology with respect to proviverrines, including *Prototomus* and *Proviverra*. Its only derived feature is the autapomorphic loss of P/1 and the probably related anterior shortening of the dentary. Notable primitive features (for most, known in cimolestids) include the small size, unreduced M/3, well-developed metaconid, trigonid moderately mesio-distally compressed, and P/4 talonid not fully simplified and sectorial, bearing at least two accessory cusps (protostylid, hypoconid). The protostylid of P/4, known in few hyaenodontids (some species of *Prototomus* and *Galecyon*), is bulbous. We assume here that this is the protostylid that is lost in hyaenodontids (on the basis of the relative position of the cusps), but this homology is uncertain; the important point is that *Boualitomus* is primitive in the retention of additional cusps on the talonid of P/4.

These primitive features especially recall *Tinerhodon disputatum*, a late Paleocene species from Ouarzazate Basin, Morocco, which was described as a carnivorous form possibly related to the creodonts (Gheerbrant, 1995). The morphology of the talonid of P/4 is remarkably reminiscent, with the occurrence of two labial accessory cusps, the protostylid and the hypoconid, and even an additional lingual accessory cusp (Fig. 6). The resemblance of the protostylid is especially notable: it shares the same general topographic relations on the talonid and it has a similar distinctive bulbous morphology. The lingual accessory cusp on the talonid of P/4 of *Tinerhodon* is also suggestive. In *Boualitomus*, this cusp is seen in a vestigial state in the small vertical ridge with similar position between the two labial accessory cusps (Fig. 6). Moreover, the two taxa share the occurrence of sizeable diastemata between the anterior premolars (between P/4 and P/3, and between P/3 and P/2) (Fig. 7), and a similar position and development of mental foramina (below P/4 and P/2). We also stress the resemblance of the anterior premolars, which have a similar asymmetric lateral profile, resulting especially from the mesial position of the protoconid on the crown (Fig. 7). Other resemblances are noted: (1) premolars (Figs 6, 7)—no metaconid, paraconid small or absent; P/2–3 simple, laterally compressed and elongated; presence of a small distal cusp on P/3;

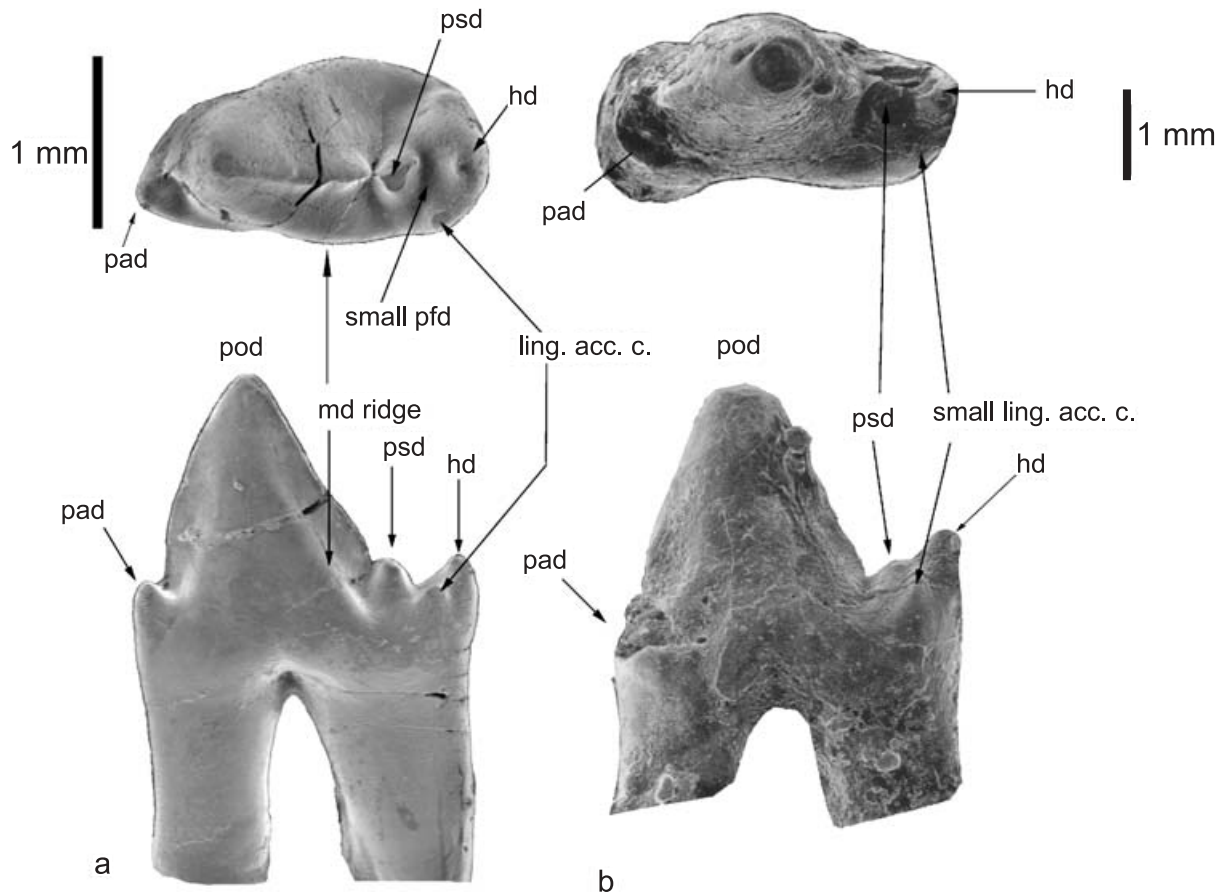


Figure 6. Comparison of the P/4 of *Tinerhodon disputatum* (a), and *Boulditimus maroccanensis* n.g., n.sp. (b) in occlusal (upper pair) and lingual (lower pair) views. Scale bar: 1 mm. Abbreviations: hd—hypoconid; ling. acc. c.—lingual accessory cusp; md—metaconid; pad—paraconid; pfd—postfossid; pod—protoconid; psd—protostylid.

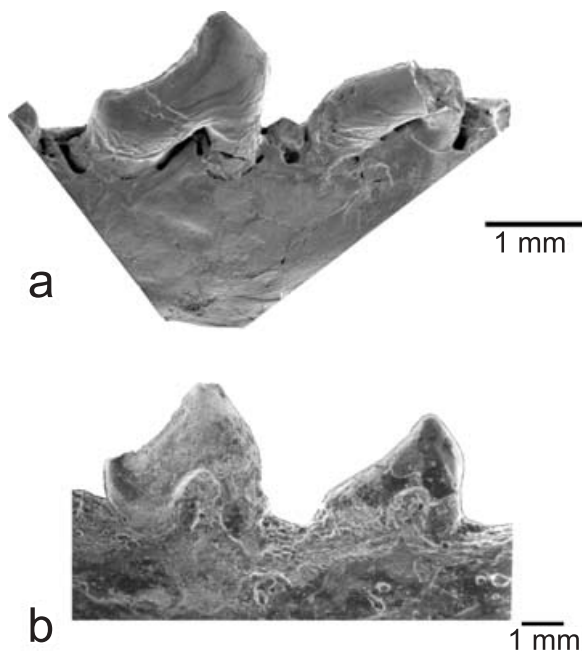


Figure 7. Comparison of the P/3–2 of *Tinerhodon disputatum* (a) and *Boulditimus maroccanensis* n.g., n.sp. (b) in labial view. Scale bar: 1 mm.

trigonid of P/4 simple, sharp and high and with the paraconid in a similar position; (2) molars (Fig. 8)—paraconid enlarged and lingual; paracristid sharp with carnassial notch; protoconid tall and pointed; entocristid well developed, not deepened by a talonid notch; cristid obliqua noticeably oblique (hypoflexid deep); talonid elongated and oblique with respect to the longitudinal axis; entoconid distal and close to the hypoconulid. Although most of these features are symplesiomorphic within the Hyaenodontidae, several are derived with respect to the generalized eutherian construction such as that of the cimolestids *Cimolestes* and *Procerberus*. This is especially true for the development of the paraconid and paracristid, the tall and pointed protoconid and the premolar morphology (e.g. premolars laterally compressed, elongate, and P/2–3 asymmetric). This comparison supports the familial and subfamilial affinity of *Tinerhodon* and *Boulditimus*, both of which are identified as proviverrine hyaenodontids. Based on the shared proviverrine features of *Tinerhodon* and *Boulditimus*, an M/1 smaller than M/2–3 can be inferred as an additional probable important shared feature of the two genera (feature unknown in *Tinerhodon*).

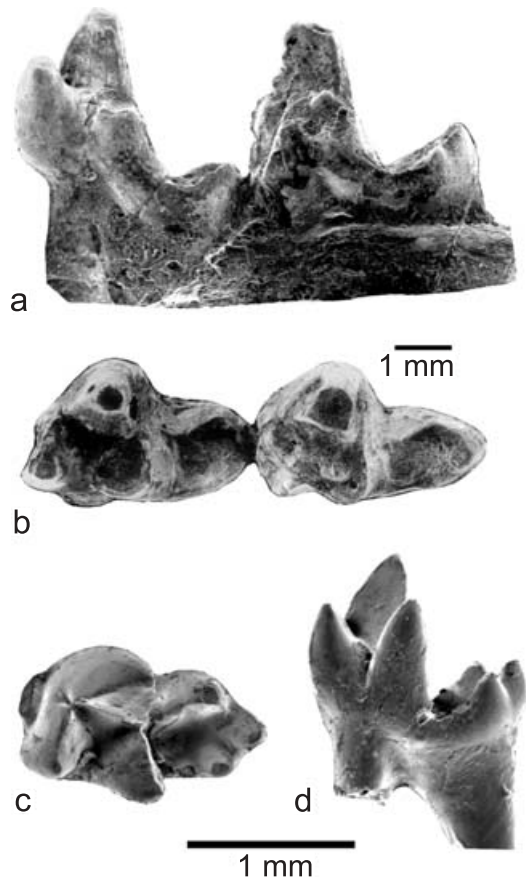


Figure 8. Comparison of the M3–2 of *Boualitomus marocanensis* n.g., n.sp. (a, b) and *Tinerhodon disputatum* (c, d), in occlusal and lingual views. Scale bar: 1 mm. Note shared features such as high and sharp paraconid and paracristid, lingual paraconid, high protoconid, carnassial notches, moderate trigonid mesio-distal extension, cristid obliqua oblique, elongated talonid and talonid cusp location (e.g. entoconid distal). Significant differences are the size, the relative width of the talonid, the development of the talonid cusps, and in *T. disputatum*, the trigonid cusps distally recurved, the presence of mesoconid and entoconulid, and the strong precingulid.

However, some of the resemblances of *Tinerhodon* and *Boualitomus* are probable symplesiomorphic features that were previously undescribed in hyaenodontids. This is especially true for the construction of the talonid of P/4, which retains molarized features reminiscent of a former puncturing and crushing function, and which departs from the (derived) sectorial talonid of creodonts. This is more obvious in *Tinerhodon*: the talonid is more developed and molarized (bearing three well-developed accessory cusps, a small postfossid and a hypoflexid), corresponding to a more puncture–crushing morphology (Gheerbrant, 1995). *Tinerhodon* indeed shows many other distinctive features that are primitive with respect to *Boualitomus*, the most remarkable being its very small size (about half the size of *Boualitomus*), close to that of the cimolestids, which has very few equivalents in previously described hyaenodontids (some species of *Proviverra*, *Paravagula*;

see Fig. 5 and above). Other (primitive) differences of *Tinerhodon* distinguishing it from *Boualitomus* are the following:

- (1) Molars: talonid cusps more cuspidate and less reduced, and presence of accessory cusps (mesoconid and entoconulid; these are variable in *T. disputatum*, but their occurrence is unlikely in *Boualitomus*, because other major talonid cusps are significantly reduced compared to *Tinerhodon*); hypoconulid noticeably larger, conical and distally salient in *Tinerhodon disputatum*; talonid significantly wider with respect to the trigonid; precingulid stronger and shorter; ectocingulid more differentiated at the base of the hypoflexid; hypoconulid more widely separated from the hypoconid by a more developed notch on the postcristid; crown slightly more exodaenodont above the roots; two other possible differences must be checked on unworn specimens of *Boualitomus*: in OCP DEK/GE 306 the molar trigonid (protoconid) seems to be slightly taller with respect to the talonid, and the carnassial notch seems reduced or absent on the cristid obliqua.
- (2) P/4: crown more inflated transversely (especially labially below the hypoflexid); distinct lingual accessory cusp; in *Boualitomus* it is vestigial, reduced to a slight and short vertical ridge, and has lost its connection with the hypoconid; postfossid more individualized and hypoflexid deeper labially; protostylid more inflated and closer to the protoconid (from which it is separated by a more pronounced carnassial notch); a trace of metaconid is retained in the form of a smooth ridge bordered by a groove on the disto-lingual flank of the protoconid.

Boualitomus is clearly more specialized in the carnassial function than *Tinerhodon*, as illustrated by the narrower talonid, the talonid cusps more reduced on the molars and the P/4 more compressed and simplified (no trace of metaconid, talonid less molarized), all features closer to *Prototomus* and other more derived proviverrines.

3.c. Systematic and phylogenetic conclusions on *Boualitomus marocanensis*

Boualitomus shows clear affinities with the Hyaenodontidae, and among them with the ‘Proviverrinae’. Within ‘Proviverrinae’, *Boualitomus* is characterized by many primitive features. It also has some remarkable autapomorphic derived features with respect to the proviverrines, such as the loss of the P/1, and the related shortening of the dentary. Comparison of *Boualitomus* with *Tinerhodon* supports their close relationship, and it confirms the proviverrine hyaenodontid status

of *Tinerhodon*. It is notable that the latter is much more primitive than *Boualitomus* and that there is no evidence in the available material of divergent specialized features of both genera. However, we still lack synapomorphies to support the idea that *Boualitomus* and *Tinerhodon* belong to a single African proviverrine lineage. Their notable differences in size and morphology might in fact agree with distinct lineages.

The discovery and comparison of *Boualitomus* leads to a revision of the systematic status and diagnosis of *Tinerhodon*.

Tinerhodon disputatum Gheerbrant, 1995
Figures 6a, 7a, 8c, d, 9a, 10

Holotype. THR 192, left M/3 (Figs 8c, d; 10s–u).

Hypodigm. Lower molars: see Gheerbrant (1995); lower premolars: P/4: THR 292 (right); P/3: THR 294 (right), THR 313 (left); P/2: THR 294 (right).

Localities and age. Adrar Mgorn 1 (type locality), Ihadjamene (Gheerbrant, 1995), Adrar Mgorn 1bis (Gheerbrant *et al.* 1998), Ouarzazate Basin, Morocco; Jbel Guersif Fm, Thanetian.

Emended diagnosis. Dentition showing affinities with the proviverrine hyaenodontids, and especially with *Boualitomus*: M/3 not reduced; paraconid lingual and enlarged, only slightly smaller than metaconid; paracristid and protocristid sharp; carnassial notches on paracristid, protocristid and cristid obliqua; trigonid moderately compressed mesio-distally; talonid narrower than trigonid and bearing cusps of similar height; talonid elongated and oblique with respect to the longitudinal axis; entoconid distal and close to the hypoconulid; premolars simple and sharp; P/2–3 laterally compressed, elongated and with asymmetric lateral profile; diastemata between anterior premolars; large mental foramina below P/4 and P/2. *Tinerhodon* especially resembles *Boualitomus* in the morphology of the talonid of P/4 which bears several accessory cusps, including a bulbous protostylid. *Tinerhodon* differs from *Boualitomus* and other proviverrines in some unusual primitive features: (1) smaller size (half size of *Boualitomus*); (2) molars with wider talonid, with more cuspidate talonid cusps (hypoconulid especially larger) and with variable accessory cusps; (3) P/4 with occlusal outline more inflated transversely and with talonid more molarized (lingual accessory cusp more developed, protostylid more inflated, postfossid distinct, and hypoflexid more developed). It also differs from *Boualitomus* in having the protostylid closer to the protoconid and the presence of a metaconid ridge on P/4, and the distally more recurved protoconid on the molars.

Comments. Our comparisons of *Boualitomus* support the proviverrine affinities of *Tinerhodon disputatum*,



Figure 9. Composite reconstruction of the lower dentition M/3–1, P/4–2, of *Tinerhodon disputatum* (a) and its comparison with *Boualitomus maroccanensis* n.g., n.sp. (b) Occlusal views. *Tinerhodon disputatum*: P/2 and P/3: THR 294; P/4: THR 292; M/2?: THR 193, M/3: THR 192, holotype (reversed view). Scale bar: 1 mm.

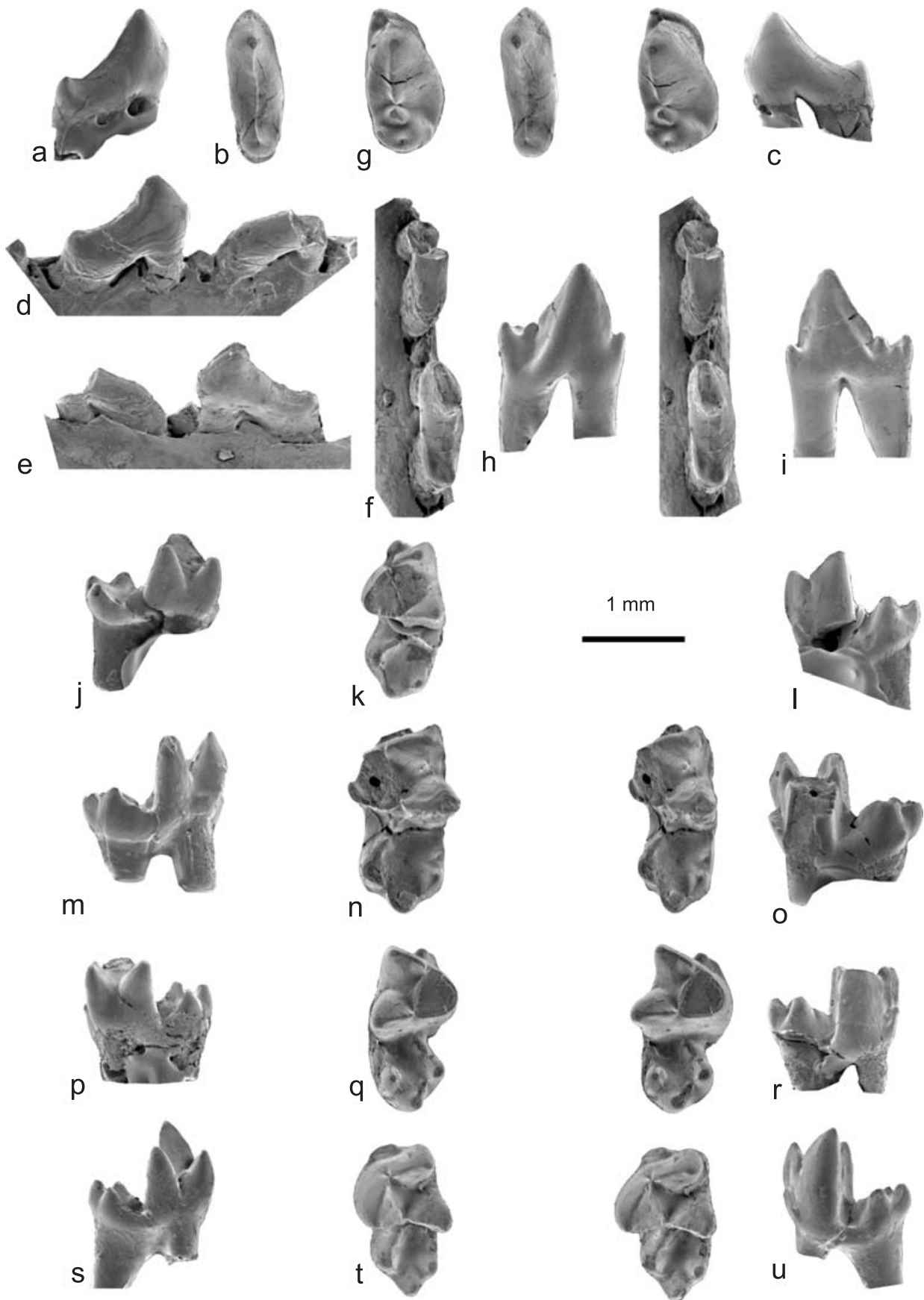


Figure 10. *Tinerhodon disputatum*. S.e.m. views of the lower teeth. (a–c) THR 313, right P/3, in labial, occlusal (stereoview) and lingual views. (d–f) THR 294, right P/3–2, in labial, lingual and occlusal (stereo pair) views. (g–i) THR 292, right P/4, in occlusal (stereo pair), labial and lingual views. (j–l) IDJ 1, left M/1 or M/2 in lingual, occlusal and labial views. (m–o) THR 111, left M/1 or M/2 in lingual, occlusal (stereo pair) and labial views. (p–r) THR 193, right M/1 or M/2 in lingual, occlusal (stereo pair) and labial views. (s–u) THR 192, holotype, left M/3 in lingual, occlusal (stereo pair) and labial views. Scale bar: 1 mm.

which appears to be the oldest and most primitive known hyaenodontid. The relationships of *Tinerhodon* and *Boualitomus* have several implications. They support the specific identification of the isolated P/4 and P/3 (THR 192, THR 294, THR 313), initially described as cf. *Tinerhodon disputatum* by Gheerbrant (1995). These premolars are consequently formally identified as *Tinerhodon disputatum* and associated with the hypodigm of the species. The diagnosis of *Tinerhodon disputatum* is amended to account for this identification and its relationships with *Boualitomus* and proviverrines. The upper dentition of *Tinerhodon disputatum* is still unknown, as it is for *Boualitomus*. The identification of *Tinerhodon* as a proviverrine would support it having an M1/ smaller than M2/, in contrast especially with *Aboletylestes robustus* Gheerbrant, 1992 from the same locality (see comparison in Gheerbrant, 1995). Gheerbrant (1995) noted resemblances of *Tinerhodon* with a species from the early Eocene of Mongolia, known by a lower molar (specimen PSS 20-128) described as an undetermined pantolestid by Russell & Dashzeveg (1986). This species, characterized by a large paraconid, a large trigonid and the occurrence of carnassial notches, is a probable hyaenodontid (proviverrine?). It differs from *Tinerhodon* in having a longer prefossid, the protoconid not being recurved distally, the absence of accessory cusps, the smaller entoconid and shorter talonid and the larger size. It is more derived than *Tinerhodon*.

Besides their hyaenodontid affinities, *Boualitomus* and *Tinerhodon* share several remarkable primitive features (e.g. talonid morphology of P/4), which were previously unknown in hyaenodontids. *Tinerhodon* is more primitive than *Boualitomus*, with more striking cimolestid-like features (small size, P/4 less simplified and more inflated transversely, talonid of molars wider and bearing more developed cusps). *Tinerhodon* further fills the structural gap between hyaenodontids and generalized insectivore-like eutherians. It is the most compelling fossil evidence for a didelphodontan origin of the family Hyaenodontidae.

4. Palaeobiogeographic and phylogenetic implications for Hyaenodontidae and Creodonta

Tinerhodon and *Boualitomus* are the earliest and most primitive known hyaenodontids. They clearly support an African origin of the Hyaenodontidae and its order, the Creodonta following the current taxonomy, a hypothesis which was initially proposed by Gingerich (1980, 1986, 1989; Gingerich & Deutsch, 1989), mainly on the basis of the diversity and dominance of the hyaenodontids in the early Oligocene faunas of the Fayum. There are scarce dental remains probably belonging to other taxa of hyaenodontids in the

Paleocene and early Eocene of the Ouarzazate Basin (Gheerbrant, 1995; Gheerbrant *et al.* 1998), which are suggestive of some early African diversity of the family even if the fossil evidence obviously remains very poor. This is at least in agreement with the antiquity of the order in Africa.

The hyaenodontids make their first appearance in Laurasia at the base of the Eocene (Wasatchian Wa0 in North America; MP7 (Dormaal, Le Quesnoy) in Europe; Gashatan-Bumbanian in Asia). A precocious late Paleocene Asiatic occurrence is *Prolimnocyon* from the Gashatan of Bayan Ulan, China (Meng, Zhai & Wyss, 1998; Bowen *et al.* 2002). However, the early Asiatic hyaenodontid from Bayan Ulan belongs to the derived subfamily Limnocyoninae, which is characterized by a reduced M/3. The Gashatan limnocyonine does not provide direct evidence for an Asiatic origin of the creodonts, but it supports the antiquity of the radiation of the hyaenodontids from a proviverrine stem, which is in accordance with an old age and origin of the Hyaenodontidae in Africa. *Tinerhodon* and *Boualitomus* do not show special relationships with the early Asiatic limnocyonines, but the diversity of early African creodonts remains largely unknown. Interestingly, Gingerich & Deutsch (1989, p. 364) note that M/1 and M/2 of *Prolimnocyon* are characterized by a 'talonid more angled labially relative to the trigonid' with respect to *Prototomus*, which is also a feature of the two Moroccan genera. It should also be noted that *Boualitomus* is more closely related to the proviverrine 'Prototomus-group', which is discussed as the possible sister-group of the Limnocyoninae (Morlo & Gunnell, 2003; but see the phylogeny of Polly, 1996). The Bayan Ulan limnocyonine lineage emphasizes an early trans-Tethyan dispersal between Africa (from stem proviverrines) and Asia, that is consistent with a subsequent rapid expansion of the involved immigrants from Asia into the rest of Laurasia at the base of the Eocene (e.g. Gingerich, 1989; 'East of Eden' scenario of Beard, 1998; Bowen *et al.* 2002). However, this is probably not the single trans-Tethyan dispersal event that occurred for the family Hyaenodontidae and led to their colonization of Laurasia; there are several other hyaenodontid lineages implying several other later Palaeogene trans-Tethyan dispersal events between Africa and Asia (including India) and between Africa and Europe (e.g. Gheerbrant, 1990, 1995; P. Holroyd, unpub. Ph.D. thesis, Duke Univ. 1995; Egi *et al.* 2004). *Tinerhodon* and *Boualitomus* support the trans-Tethyan dispersal of early hyaenodontids between Africa and Europe, especially for the stem group of *Prototomus*. The subsequent rapid colonization of North America from Europe is supported by the primitive features of the European hyaenodontid lineages, as emphasized by Godinot & Lapparent de Broin (2003).

Tinerhodon and *Boualitomus* fill the gap in structural pattern, time, and even place, for the primitive eutherian

origin of the hyaenodontid creodonts. *Tinerhodon* especially supports a derivation from cimolestid-like eutherians, as illustrated for instance by its referral to the Cimolestidae by McKenna & Bell (1997). The cimolestid origin of the Creodonta was initially suggested by Van Valen (1966), Lillegraven (1969) and also Gingerich (1980). Such an ancestral cimolestid relationship was also suggested for the Carnivora, and was based on comparisons with North American material (Van Valen, 1966; Lillegraven, 1969). For the Carnivora, an origin from the North American 'Cimolestes' seems supported by the diversity and early age of the Viverravidae in North America (e.g. Lillegraven, 1969; Flynn, Neff & Tedford, 1988; but see Fox & Youzwyshyn, 1995). However, the presence of cimolestids in the late Paleocene of Africa, such as *Cimolestes cusculus* and *C. cf. incisus* (Gheerbrant, 1992; Gheerbrant *et al.* 1998), and the identification of *Boualitomus* and *Tinerhodon* as the most primitive and earliest known Hyaenodontidae, suggest that the place of origin of the Hyaenodontidae and its order was Africa, from an autochthonous cimolestid, instead of from a North American cimolestid. Such an implicit independent origin of the two major carnivorous orders is in agreement with Fox & Youzwyshyn's (1995) dental study that refutes the close relationship of Creodonta and Carnivora, and also with the possible sister-group relationship of Carnivora and Lipotyphla (Wyss & Flynn, 1993; Polly, 1996). No known primitive insectivore-like eutherians from the late Cretaceous and Paleocene of North America, including *Cimolestes magnus* (Lillegraven, 1969), indeed show any peculiar relationship with *Tinerhodon*. They differ especially in the morphology of the talonid of P/4, which is so striking in *Tinerhodon*. On the other hand, it is still not possible to identify a precise relationship between hyaenodontids and known African cimolestid-like eutherians because of the inadequate available material (Gheerbrant, 1992, 1995; Gheerbrant *et al.* 1998). However, in the light of our comparisons, we suggest that additional discoveries in the late Cretaceous and early Palaeogene of Africa will provide important data for the question of the primitive 'insectivore' origin of the hyaenodontids and the creodonts. Key features that should be checked in the possible African cimolestid ancestors (in contrast to North American cimolestids) of the hyaenodontids, are P/4 morphology (e.g. molarization of the talonid), the reduction of M/1 (in contrast to the P4/M/1 carnassial specialization of Carnivora), and the development of the paraconid and paracristid related to that of the postmetacrista in the upper molars. The development of the paraconid, paracristid and postmetacrista, that is, the enhancement of prevallid/postvallum shearing, is an important feature of the ancestral morphotype of the Creodonta. According to Fox & Youzwyshyn (1995), the paraconid and paracristid were relatively low on M/1 in the

ancestral morphotype of the Carnivora. The difference from the Creodonta is probably even stronger for the M/2–3, which are typically well developed in the latter order.

It should be noted that an African origin of the Hyaenodontidae does not solve the debated question of the monophyly of the order Creodonta (see Gingerich, 1980; Polly, 1996; Gunnell, 1998). A common ancestor of the Hyaenodontidae and Oxyaenidae, which should be older than the late Paleocene *Tytthaena*, cannot be excluded in the light of the morphology of *Tinerhodon* and *Boualitomus*. These African genera are consistent with possible basal creodont synapomorphies such as the enlargement of the paraconid, paracristid and metacrista. However, the known distribution of Oxyaenidae favours a North American centre of origin of this family (see Introduction), in contrast to the Hyaenodontidae as analysed here. This would support a possible convergence of oxyaenids and hyaenodontids (Polly, 1996) and the diphyly of the Creodonta (e.g. Gunnell, 1998). The development of the paracristid–metacrista shearing couple is an adaptive carnassial feature certainly subject to independent evolution (e.g. Muizon & Lange-Badre, 1997). Further fossil data are, however, needed to reconcile our current conflicting views of the palaeobiogeography and phylogeny of the Oxyaenidae and the Hyaenodontidae, which make the creodonts still enigmatic.

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