

# New multituberculate teeth from the Early Cretaceous of Morocco

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Three new multituberculate teeth are described from the Early Cretaceous of Morocco. *Denisodon moroccensis* gen. et sp. nov. is established for a second lower molar which differs from that of *Hahnodon taqueti*, from the same locality, by a preserved posterior buccal cusp, a smaller posterior lingual cusp and the less indented lingual wall of the crown. The second tooth is a posterior upper premolar. It is represented by the posterior portion of its crown on which is present only one row of cusps, similar to the conditions in *Kielanodon*, *Eobaatar*, *Bolodon*, and the Pinheirodontidae. The third tooth is a lower incisor, similar to that in *Kuehneodon*. Both teeth are grouped as „Hahnodontidae, gen. et sp. indet.” Paulchoffatioidea new superfamily is established for the Paulchoffatiidae, Hahnodontidae, and Pinheirodontidae. It is characterized by the following autapomorphies: premolarisation of I2-C, presence of a third row of cusps on the posterior upper premolars and the basin-like structure of the m2. Hahnodontidae and *Hahnodon* are redefined.

Key words: Mammalia, Multituberculata, Paulchoffatioidea, *Denisodon*, Early Cretaceous, Morocco.

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## Introduction

Remains of multituberculates are very rare fossils in the Gondwana area. *Staffia* Heinrich, 1999 from the Late Jurassic of Tanzania belongs to the Haramiyida. Gondwanatheria Mones, 1987 from the Late Cretaceous and Early Tertiary of South America and the Cretaceous of Madagascar, originally grouped with the Multituberculata, are now interpreted as an independent order of the Mammalia *incertae sedis* (Pascual et al. 1999). Thus, true multituberculates are confined to two regions, the Late Cretaceous of Madagascar (Krause and Grine 1996) and the Early Cretaceous (?Berriasian) of Morocco. Here, in the Anoual Syncline of the eastern High Atlas [= Moroccan High Atlas] (see map in Sigogneau-Russell et al. 1998: fig. 1, and lithological section in Sigogneau-Russell et al. 1988: fig. 3) a very remarkable mammalian fauna has been found and described since 1988 in several publications by Sigogneau-Russell and others (Sigogneau-Russell et al. 1988; Sigogneau-Russell 1989, 1991a, b, c, 1992, 1995; Sigogneau-Russell et al. 1990; Sigogneau-Russell et al. 1998). In the last of the quoted publications, a summary of the present knowledge on the locality is given. Accordingly, twelve genera of mammals are described, and six others said to be unpublished. Present are Triconodonta, Symmetrodonta, Pantotheria, Peramura, Tribosphenida and Multituberculata, the last confined to one genus and species, *Hahnodon taqueti* Sigogneau-Russell, 1991a, represented by a single specimen. Since then, three more multituberculate teeth have been found: one lower second molar, one anterior upper premolar and one lower incisor. They are described in the present paper. The rareness of multituberculates in the

Anoual fauna stands in stark contrast to their abundance in penecontemporaneous Laurasian faunas. Usually, remains of multituberculates are, as rodents today, abundant in the fossil record. The reasons for this rarity in Morocco are unknown.

*Storage.*—The teeth here described are stored in the Muséum national d'Histoire naturelle (MNHN) in Paris, France, with the catalogue numbers SA 97, SA 102 and SA 152.

*Nomenclature of cusps.*—The cusps of the buccal row are named from anterior to posterior “B1–B3” in the upper and “b1–b3” in the lower jaw. Accordingly, the lingual cusps are named “L1–L5” in the upper and “l1–l3” in the lower jaw.

## Systematic palaeontology

Order Multituberculata Cope, 1884  
Suborder Plagiaulacida McKenna, 1971  
[*pro* Plagiaulacoidea Ameghino, 1889]  
Superfamily Paulchoffatioidea nov.

Suborder Paulchoffatioidea; Kielan-Jaworowska and Ensom 1992: 99.  
Paulchoffatioidea; Kielan-Jaworowska and Hurum 2001: 392.  
Paulchoffatiid line Kielan-Jaworowska and Hurum 2001: 402, 412.

Kielan-Jaworowska and Hurum (2001) grouped the Plagiaulacida into three “lines”, the allodontid line, the paulchoffatiid line and the plagiaulacid line. The Arginbaataridae Hahn and Hahn, 1983 are excluded as “Suborder *incertae sedis*” (Kielan-Jaworowska and Hurum 2001: 403, 415). In our opinion, this family constitutes a fourth arginbaatarid

line. Each of these four lines represents its own evolutionary lineage, their common root still being unknown. We propose to stabilize these four lineages systematically as superfamilies, as is done here with the paulchoffatiid line.

**Families included.**—Paulchoffatiidae G. Hahn, 1969, Hahnodontidae Sigogneau-Russell, 1991a, and Pinheirodontidae Hahn and Hahn, 1999b.

**Distribution.**—?Late Rhaetic of France; ?Middle Jurassic (Bathonian) of England; Late Jurassic (Kimmeridgian) of Portugal; Early Cretaceous (~Berriasian) of Portugal, England and Morocco; Early Cretaceous (Barremian) of Spain.

**Diagnosis.**—A superfamily of the Plagiaulacida with the following characteristics: Tooth formula (known only in the Paulchoffatiidae): 3.1–0.5–4.2./1.0.4–3.2. I2 with one main cusp and 1 to 5 small additional cusps arranged transversely on the posterior portion of the crown in a line or in a semicircle. I3 enlarged, with an obliquely directed crest and 0 to 3 additional anterobuccally, and 0 to 3 posterolingually placed small cusps. C single-rooted, premolariform, with 2 to 5 cusps. Anterior upper premolars (P1–3/4) short, rounded to quadrangular, with 2 to 5 cusps. Posterior upper premolars (usually P4–5, rarely also P3) elongate, molariform, with 2 to 3 longitudinal rows of cusps. M1–2 with two rows of cusps. p3–4 with 3 to 6 serrations and mostly a labial row of small basal cusps. m1 with two rows of cusps. m2 with a central basin and the cusps more or less reduced in various ways. Skull known only in the Paulchoffatiidae, therefore excluded from the diagnosis.

**Discussion.**—The Paulchoffatioidea, especially the Paulchoffatiidae, are characterized by a peculiar combination of autapomorphic and plesiomorphic features (see also Kielan-Jaworowska and Hurum 2001: 402, 412–413). The following autapomorphies are diagnostic for the superfamily:

- Premolarisation of I2–C. The I2–3 are, in contrast to younger multituberculates, enlarged, multicuspoid, with a complicated structure of their crown (see diagnosis). A similarly enlarged I3 is present also in the plagiulacid line (*Bolodon crassidens*, see Simpson 1928: text-fig. 11a, b), but the oblique crest is less distinct. Moreover, in contrast to the Paulchoffatioidea, the canine is reduced in the plagiulacid line.
- Presence of three rows of cusps on the posterior upper premolars (P4–5). This feature is present in the Paulchoffatiinae and the Pinheirodontidae, but missing in the Kuehneodontinae; in the Hahnodontidae, the posterior upper premolars are unknown. In most genera of the Paulchoffatiinae the third row of cusps is present on P4 and P5, but in *Meketchoffatia* G. Hahn, 1993 and in the Pinheirodontidae it is confined to P5 only. This tendency to broaden the posterior upper premolars is unknown in all other evolutionary lineages of the Plagiaulacida as well as in all younger multituberculates.
- Presence of a central basin on m2. The evolution of this basin is combined with a reduction of cusps. In the Paulchoffatiidae and the Pinheirodontidae, the buccal row

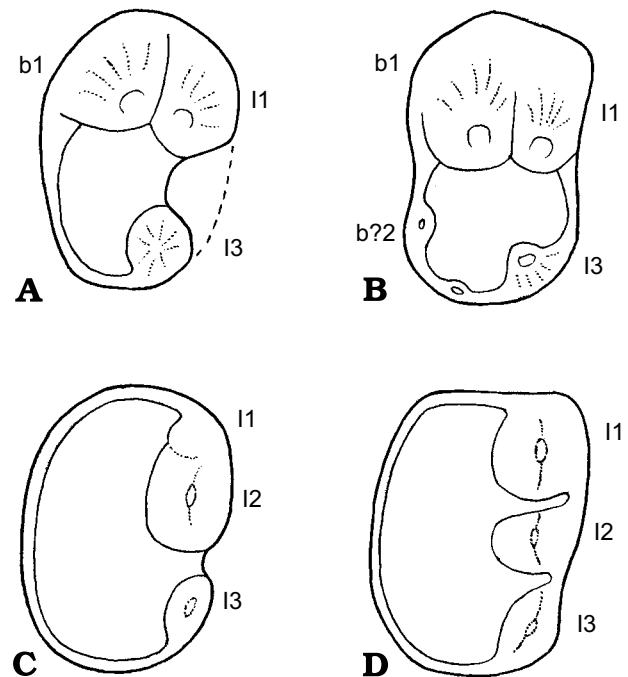


Fig. 1. Comparison of left lower m2 in Paulchoffatioidea superfam. nov. **A.** *Hahnodon taqueti* Sigogneau-Russell, 1991a; redrawn from Sigogneau-Russell, 1991a: fig. 2c. **B.** *Denisodon moroccensis* gen. et sp. nov. **C.** *Kuehneodon* sp.; redrawn from Hahn and Hahn 1998: fig. 39b. **D.** *Pinheirodon* sp.; redrawn from Hahn and Hahn 1999b: fig. 29c.

of cusps is completely reduced (Fig. 1C, D) with the exception of *Guimarotodon*, where cusp b2 is preserved (Hahn and Hahn 1998: fig. 39a). The lingual cusps are retained to a different degree (see Hahn and Hahn 1998: text-fig. 39a–f; Hahn and Hahn 1999b: text-fig. 1g). In the Hahnodontidae, the anterior buccal cusp is preserved, and the posterior cusps of both rows are more or less reduced, as discussed below under “Hahnodontidae” (Fig. 1A, B).

These autapomorphies definitely exclude the Paulchoffatioidea from the ancestry of younger multituberculates (“Cimolodonta”). The Paulchoffatioidea are thus the oldest known side branch on the multituberculate evolutionary tree.

These autapomorphies are combined with some very primitive structures in the skull (here excluded from discussion) and dentition, representing the most plesiomorphic conditions known among multituberculates. It must be emphasized that these plesiomorphies are confined at least partially to the Paulchoffatiidae, whereas the Pinheirodontidae represent an already more evolved and stratigraphically younger stage of evolution. The following plesiomorphic structures should be mentioned (see also the diagnosis of the Paulchoffatiidae in Kielan-Jaworowska and Hurum 2001: 412–413):

- The number of teeth in the upper jaw remains large; canine and five premolars are present.
- p4 is not or only slightly longer than p3 with only four serrations.
- A row of relatively large basal cusps is present on p3 as well as on p4.

- The function of the premolars is grinding, not cutting. The crowns of the lower premolars become completely eroded during the life of the animal.
- The angle between the longitudinal axis of the dentary and the tooth row is only 7 to 20°.
- The structure of the enamel is non-prismatic (studied only in Paulchoffatiidae; see Fosse et al. 1985).

### Family Hahnodontidae Sigogneau-Russell, 1991a

Hahnodontidae fam. nov.; Sigogneau-Russell 1991a: 123.

Hahnodontidae; Kielan-Jaworowska and Hurum: 2001: 413.

Sigogneau-Russell (1991a) described the genus *Hahnodon*, founded on an isolated m2, and established for it the family Hahnodontidae. Now, a second isolated m2 has been found, representing a new genus, *Denisodon*, as well as two other teeth that cannot be referred to a genus.

*Genera included.*—*Hahnodon* Sigogneau-Russell, 1991a and *Denisodon* gen. nov.

*Distribution.*—Early Cretaceous (?Berriasian) of Morocco.

*Revised diagnosis.*—A family of the Paulchoffatioidea, founded on m2 only, with the following characteristics: m2 with an anterior buccal cusp (b1) and an anterior lingual cusp (l1); b1 closely attached to l1, b1 larger than l1. Posterior lingual cusp (l3) present, posterior buccal cusps completely reduced or rudimentary. Posterior half of the crown occupied by a central basin surrounded by an elevated border. Enamel ridges weakly expressed. Apex of b1 and l1 far behind in position, posterior wall of both cusps sloping down nearly vertically.

*Discussion.*—The basin-like structure of the posterior portion of the crown of m2 confirms that the Hahnodontidae belong to the Paulchoffatioidea. The family differs from both other families, Paulchoffatiidae and Pinheirodontidae, in the following details:

- The anterior buccal cusp is preserved, whereas it is completely reduced in the other families.
- The anterior lingual cusp is a single, cohesive morphological unit, whereas it is composed of two confluent cusps, l1 and l2, in the Paulchoffatiidae (see Hahn and Hahn 1998: text-fig. 39 a–f).
- The enamel is nearly smooth. In both the other families the cusps have moderately to strongly developed enamel ridges, the border of the posterior basin is crenulated, and the bottom of this basin is covered with bars.
- The two anterior cusps are closely attached, whereas in both other families the lingual and buccal cusps are separated from one another by a broad longitudinal valley.
- The apex of b1 and l1 is located far posteriorly, whereas in the other family it is placed centrally. The presence of the anterobuccal cusp must be interpreted as a plesiomorphic character, as well as perhaps the smooth structure of the enamel. The evolutionary line leading to the Hahnodontidae must have separated from those leading to the two other families, before the anterior buccal cusp was reduced and the enamel had evolved ridges. So far the Hahnodontidae

are the most primitive family of the Paulchoffatioidea. On the other hand, the closeness of the anterior cusps to each other can be interpreted as an autapomorphy of this family.

Chronologically, the Hahnodontidae are contemporaries of the Pinheirodontidae, whereas the Paulchoffatiidae are distinctly older. In the structure of m2, the Hahnodontidae are more advanced than the Pinheirodontidae in the partial reduction of the lingual cusps (in the Pinheirodontidae all three lingual cusps are preserved, see Hahn and Hahn 1999b: fig. 1a), but more primitive in preservation of the anterobuccal cusp (which is reduced in the Pinheirodontidae). It would be very interesting to know something about the structure of the lower premolars (chewing as in the Paulchoffatiidae, cutting as in the Pinheirodontidae?), but, unfortunately, lower premolars have not yet been found.

The Hahnodontidae are isolated palaeogeographically. The two other families of the Paulchoffatioidea are known only from the Late Jurassic and the Early Cretaceous of Europe. The common ancestor of the Paulchoffatioidea and the geographical origin of this superfamily are unknown. The ancestral species has lived probably in the Middle Jurassic of Eurasia (as can be deduced from the distribution of the three attached families). Then, the Hahnodontidae must have been immigrated to Africa from Eurasia during the Late Jurassic. Also, descendants of the Hahnodontidae are not known. The only known younger Gondwana multituberculate from the Upper Cretaceous of Madagascar (Krause and Grine 1996) is a poor fragment of one tooth which has never been described sufficiently. Its systematical position is unclear. It is more probable that this tooth represents a member of the Cimolodonta than a descendant of the Hahnodontidae.

### Genus *Hahnodon* Sigogneau-Russell, 1991a

*Type species (monotypy):* *Hahnodon taqueti* Sigogneau-Russell, 1991a.

*Distribution.*—Early Cretaceous (?Berriasian) of Morocco (Anoual Syncline, eastern High Atlas).

*Revised diagnosis.*—The type genus of the Hahnodontidae has the following characteristics: Posterior lingual cusp (l3) of m2 large. Posterior buccal cusps completely reduced. Lingual wall of crown deeply indented between anterior and posterior cusp.

*Description.*—See Sigogneau-Russell 1991a: 120–122.

*Discussion.*—The holotype of *H. taqueti* (Sigogneau-Russell 1991a: figs. 1a, 2a, b) is a left m2, as correctly stated by the author. The tooth resembles, besides the presence of the anterobuccal cusp, the m2 of *Kuehneodon* (compare Fig. 1C). Both teeth show a relatively large anterior and a smaller posterior lingual cusp, separated one from the other by the indentation of the lingual wall.

In *Kuehneodon* (Fig. 1C), the anterolingual cusp is composed of originally two, now confluent cusps, the smaller l1 and the larger l2. Consequently, the posterolingual cusp is l3.

In *Hahnodon* (Figs. 1A, 2A) the anterolingual cusp is se-

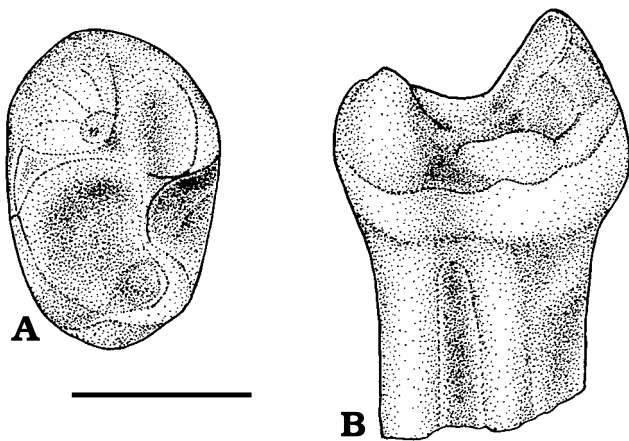


Fig. 2. *Hahnodon taqueti* Sigogneau-Russell, 1991a, holotype, left m2, MNHN SA 33, in occlusal (A) and lingual (B) views. Drawn after Sigogneau-Russell 1991a: fig. 2c, a, respectively. Scale bar 1 mm.

verely eroded. But the comparison with *Denisodon* (Figs. 1B, 3A–E) shows that this cusp is a morphological unit, not composed of two cusps. Nevertheless, the posterolingual cusp, in *Hahnodon*, is cusp I3, as is indicated by its position on the crown.

### Genus *Denisodon* gen. nov.

*Derivation of name:* After Dr. Denise Sigogneau-Russell, Paris, in honour of her contributions to our knowledge of Mesozoic mammals.

*Type species (monotypy):* *Denisodon moroccensis* sp. nov.

*Distribution.*—Early Cretaceous (?Berriasian) of Morocco.

*Diagnosis.*—A genus of the Hahnodontidae with the following characteristics: Posterolingual cusp (I3) of m2 small. Posterobuccal cusps (b?2, b?3) rudimentary. Lingual wall of crown only slightly indented.

*Discussion.*—*Denisodon* differs from *Hahnodon* by its more reduced posterolingual cusp, but better preserved posterobuccal cusps. Moreover the indentation of the lingual wall of the crown is missing. With that, *Denisodon* looks somewhat more primitive than *Hahnodon*. In comparison with the Paulchoffatiidae, *Denisodon* is similar to *Plesiochoffatia* (see Hahn and Hahn 1998: fig. 39e), where the posterolingual cusp is completely reduced.

### *Denisodon moroccensis* sp. nov.

Figs. 1B, 3A–E.

*Derivation of name:* After Morocco, where the species was found.

*Holotype (monotypy):* The isolated m2 MNHN SA 97.

*Type locality:* Anoual Syncline, eastern High Atlas, Morocco.

*Type stratum:* Early Cretaceous (?Berriasian).

*Diagnosis.*—As given for the genus.

### Description

*Measurements.*—Length = 1.0 mm; width = 1.2 mm; height of crown (at I1) = 1.2 mm.

*Preservation.*—Crown well preserved. The buccal cusp and

the central basin are distinctly eroded. Both roots are broken. Crown separated from the roots by a distinct furrow.

*Orientation.*—The tooth is a right m2 as is shown by comparison with the m2 of *Hahnodon* and the Paulchoffatiidae.

*Occlusal view* (Fig. 3A).—Crown somewhat hour-glass shaped, well rounded in front and behind. Lingual wall only slightly indented between the anterior and posterior cusps. Anterior half of the crown occupied by two large cusps, b1 and I1, closely attached to each other. Longitudinal valley between them narrowed to a slight furrow that fades on the anterior slope of the crown. Apex of both cusps placed posteriorly, with the anterior flank sloping down at 45°, but with the posterior flank sloping down nearly vertically. b1 larger than I1, slightly eroded only on its apex. I1 not composed of two confluent cusps, distinctly eroded at its apex and posterior wall. Both lateral flanks of I1 and anterior flank of b1 covered with some weakly indicated wrinkles of enamel, but without ridges as is characteristic of the Paulchoffatiidae. Posterior half of the crown occupied by a deep basin, surrounded by a raised border with three elevations. First elevation placed posterobuccally, interpreted here as the rudimental cusp b2. Second elevation placed in the posterobuccal corner of the crown, being only a very small peak of the border. It either is a last remnant of cusp b3 or only a slight bump of the border. Third elevation placed in the posterolingual corner of the crown, expressed as a relatively large, but low swelling, projecting somewhat into the central basin and having been partly demolished by erosion. It can, in comparison with *Hahnodon*, be interpreted as cusp I3. Flanks of b2 and I3 covered with some weakly expressed enamel ridges. Central basin flat, without cusps, cuspules or bars (as in Paulchoffatiidae), but with traces of erosion in its center.

*Buccal view* (Fig. 3B).—Cusp b1 high and pointed apically, marking the highest point of the crown. Anterior wall well rounded, posterior wall sloping down vertically. Cusp b2 low in comparison with b1, pointed, well defined. Buccal border of the crown again somewhat elevated close to its posterior corner, marking the position of cusp ?b3. Posterior border low, indistinct, ascending lingually to cusp I3. Wrinkling of the enamel on b1 distinct.

*Lingual view* (Fig. 3C).—Cusp I1 distinct, with eroded apex, less high than cusp b1. Anterior and posterior flank sloping down in the same degree as on cusp b1. Lingual border of the central basin low, raised again posteriorly to cusp I3, which is only 1/3 as high as cusp I1. Enamel of the buccal wall on I1 smooth, wrinkles confined to the anterior wall of this cusp.

*Anterior view* (Fig. 3D).—Both cusps, I1 and b1, steeply arising from the base of the crown. Apex of b1 somewhat rounded by wear, apex of I1 distinctly eroded, flat. Vertical furrow between I1 and b1 narrow and short, confined to the upper half of the crown. Wrinkling of the enamel visible on both flanks of b1 and on the outer flank of I1. Base of the crown ascending somewhat from the buccal side to the lingual side, with a blunt spur at the base of the lingual flank. No pressure mark visible on the anterior wall of the crown.

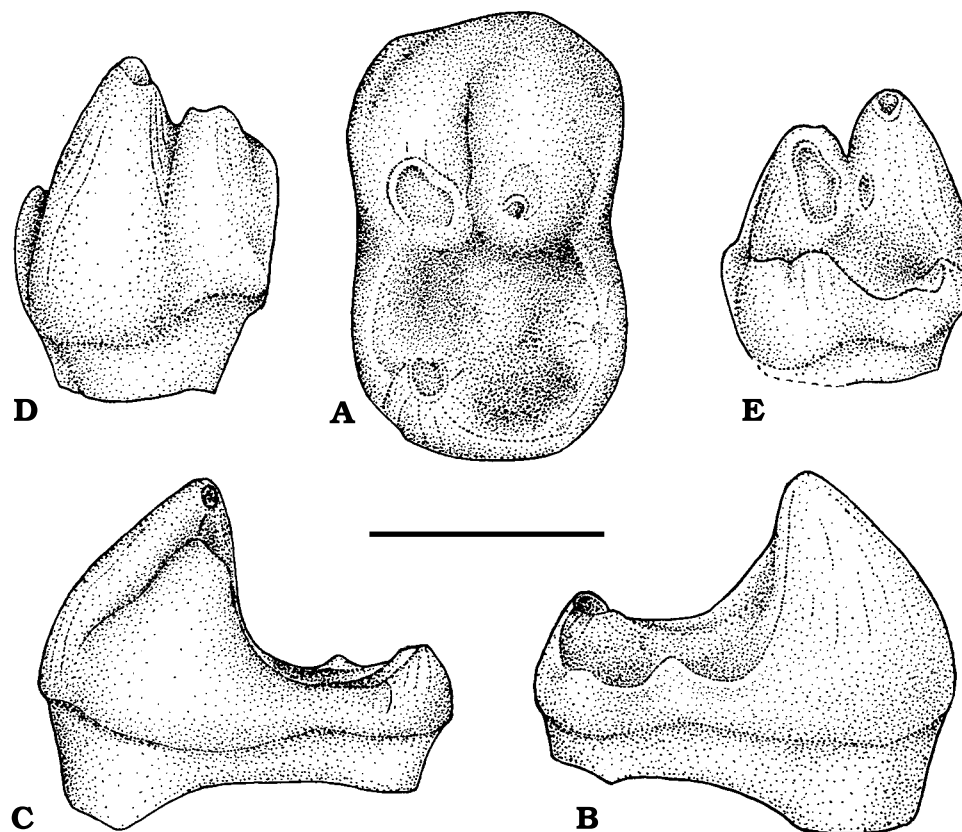


Fig. 3. *Denisodon moroccensis* gen. et sp. nov., right m2, holotype, MNHN SA 97, in occlusal (A), buccal (B), lingual (C), anterior (D), and posterior (E) views; in A anterior is up. Scale bar 1 mm.

**Posterior view** (Fig. 3E).—Apices high and well rounded, on b1 flat and deeper on l1. On b1 erosion confined to two small ovoid marks at the apex and on the posterior wall, on l1 posterior wall more strongly eroded with the dentine partly exposed. Furrow between l1 and b1 short and indistinct. Posterior border of the crown inclined somewhat to the buccal side, raised distinctly on the lingual side to cusp l3 which shows a small notch in its posterior wall. Cusp b2 very low, but distinct at the base of b1, cusp ?b3 marked as a gentle undulation of the buccal border. Distinct wrinkling of the enamel on the outer wall of b1. Posterior wall of the crown somewhat higher buccally than lingually. No pressure mark visible on the posterior wall of the crown.

#### Hahnodontidae, gen. et sp. indet.

Besides the holotype of *Denisodon moroccensis*, two other multituberculate teeth are present. It cannot be decided whether they belong to *Hahnodon* or *Denisodon*. Therefore, they are described here under open nomenclature.

Posterior upper premolar (P3 or P4), MNHN SA 152  
Figs. 4A–D, 5A.

#### Description

**Measurements.**—Length of fragment = 0.7 mm; width = 1.0 mm; height of crown = 0.9 mm.

**Preservation.**—Preserved is only the posterior portion of the tooth. Both roots are broken.

**Orientation.**—Present is the posterior portion of a left upper posterior premolar, as explained under “Discussion”.

**Occlusal view** (Fig. 4A).—Posterior border ovoid, with the lingual side somewhat more curved than the buccal side. Crown equipped with only one row of cusps which runs somewhat obliquely from the anterolingual to the postero-buccal side. Preserved portion of cusp row composed of three cusps, decreasing in size from front to behind. They are interpreted as cusps L3–L5 (see under “Discussion”). Cusps broader than long, with a broad, shelf-like area on both sides of the crown. All three cusps are connected by a longitudinally directed enamel ridge. The apex of the anterior cusp is broken. The apices of both other cusps are pointed and only slightly eroded. The enamel is damaged at both anterior corners of the crown and at the buccal flank of the first cusp.

**Lingual view** (Fig. 4B).—Preserved portion of the crown higher than long. Posterior wall curved convexly. Apex of anterior cusp broken. Apex of second cusp slightly rounded, as high as the anterior cusp, with some enamel ridges sloping up across the flank of the cusp. Third cusp distinctly smaller and lower than the other cusps, also with three enamel ridges. Posterior wall of the crown separated from the posterior cusp by a slight edge. Enamel damaged in a rounded area near to

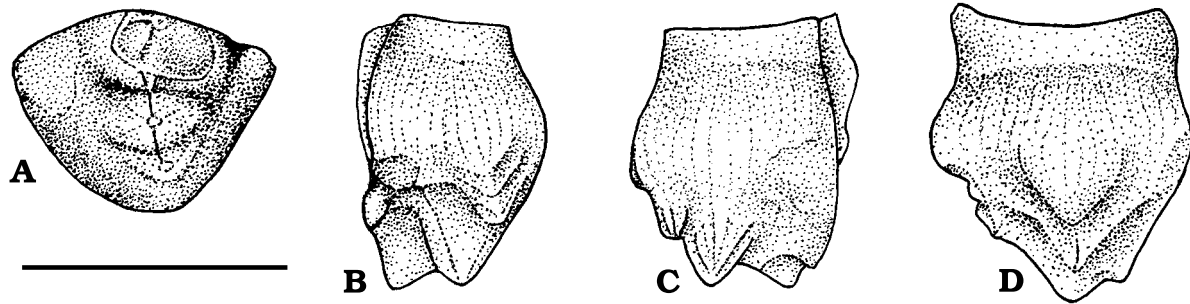


Fig. 4. Hahnodontidae, gen. et sp. indet., left upper posterior premolar (P3 or P4), MNHN SA 152 in occlusal (A), lingual (B), buccal (C), and posterior (D) views; in A anterior is up. Scale bar 1 mm.

the anterior wall. Enamel of the lingual, buccal and posterior walls of the crown slightly wrinkled.

**Buccal view** (Fig. 4C).—Proportions of the crown as in lingual view, also shape and height of the cusps. Second cusps with two distinct enamel ridges. Posterior cusp also with few enamel ridges which split into few branches that cover the postero-buccal region of the wall. At the base of the third cusp the enamel is damaged.

**Posterior view** (Fig. 4D): Shape of crown roughly triangular, with the buccal wall more arched than the lingual wall. The three cusps are visible one above the other. Crown somewhat narrowed on both sides at its base against the root. Posterior wall of the crown covered with some indistinct enamel ridges.

**Discussion.**—The most diagnostic feature of the tooth here described is the presence of only one row of cusps on the preserved portion of the crown. Upper premolars with only one row of cusps are unknown among the Plagiaulacida, but premolars with a shortened buccal row are known. Therefore, the present broken tooth can be interpreted best as the posterior portion of an upper premolar with only the posterior lingual cusps preserved. This interpretation is supported by the oblique course of the cusp row. A shortened buccal row of cusps is present in at least four families of the Plagiaulacida: Paulchoffatiidae, Pinheirodontidae, Eobaataridae and Plagiaulacidae. In all these families the lingual row has four cusps and covers the whole crown longitudinally, whereas the buccal row has only two cusps which are confined more or less to the anterior half of the crown. The following taxa must be mentioned:

- P3 of *Kielanodon hopsoni* G. Hahn, 1987 (see G. Hahn 1969: text-fig. 65; G. Hahn 1987: text-figs. 7, 8; here Fig. 5B). The P3 is relatively narrow and triangular in shape. Both the last lingual and buccal cusps are large. The second buccal cusp is located between the second and third lingual cusp. The fourth lingual cusp occupies the posterior portion of the crown alone. All cusps have coarse enamel ridges.
- P4 of the Pinheirodontidae (Hahn and Hahn 1999b: text-fig. 59a, c; here Fig. 5C). In contrast to *K. hopsoni*, the last lingual cusp is small, and the tooth is less narrowed posteriorly. The enamel ridges are less coarse than in *Kielanodon*.

- P4–5 of *Eobaatar magnus* Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987 (Kielan-Jaworowska et al. 1987: text-fig. 3b; here Fig. 5D). The last lingual cusp is the largest of the row. On P4, a very small third buccal cusp is present, placed beside the anterior half of the fourth lingual cusp. On P5, only two large buccal cusps are present, the second placed beside the valley between the second and third lingual cusps.
- ?P5 of *Eobaatar hispanicus* Hahn and Hahn, 1992 (Hahn and Hahn 1992: text-fig. 5a). The structure of the crown is similar to that in *E. magnus*.
- P5 of *Bolodon osborni* Simpson, 1928 (Kielan-Jaworow-

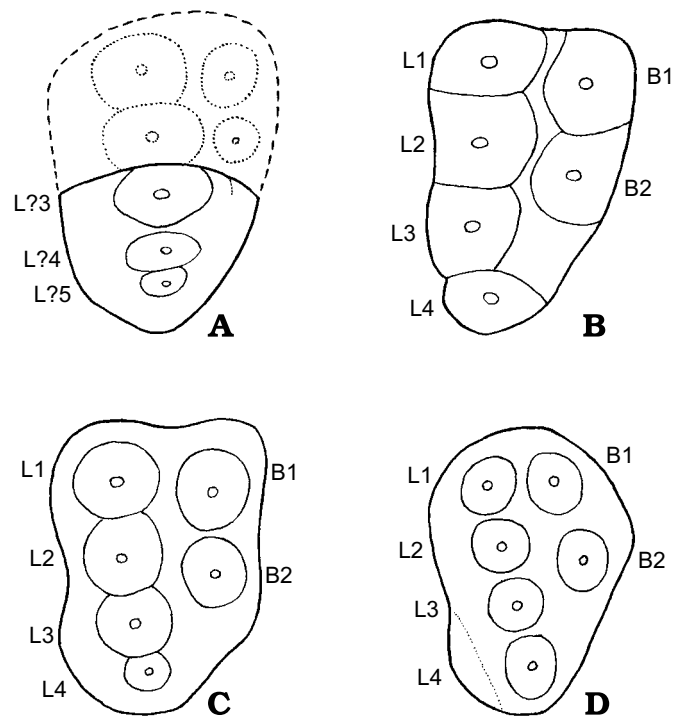


Fig. 5. Comparison of upper right premolars with a shortened buccal row of cusps. A. Hahnodontidae, gen. et sp. indet., P3 or P4, posterior portion of tooth with the preserved posterior lingual cusps, ?L3–5. B. *Kielanodon hopsoni* G. Hahn 1987, Paulchoffatiidae, P3. Redrawn from G. Hahn, 1987: text-fig. 8a. C. Pinheirodontidae, gen. et sp. indet., P4. Redrawn from Hahn and Hahn 1999b: fig. 59c. D. *Eobaatar magnus* Kielan-Jaworowska, Dashzeveg and Trofimov, 1987, Eobaataridae, P5. Redrawn from Kielan-Jaworowska et al. 1987: text-fig. 3B.

ska et al. 1987: text-fig. 3A). Structure is also similar to that in *Eobaatar*.

As is shown by this compilation, a shortened buccal cusp row can be present on the P3 of the Paulchoffatiidae, the P4 of the Pinheirodontidae, the P5 of the Plagiaulacidae and the P4–5 of the Eobaataridae. Consequently, the tooth described here is either a P3 (compared with the Paulchoffatiidae) or a P4 (compared with the Pinheirodontidae), but surely not a P5, because this tooth carries three rows of cusps in these two families.

Moreover, the new tooth differs from all the discussed teeth by two details: 1) the unusual width of its posterior portion and 2) the presence of two posterior lingual cusps without buccal antagonists (which may be explained by the presence of five instead of four lingual cusps on MNHN SA 152). A similarly small last lingual cusp is present again only in the Pinheirodontidae. Thus, the tooth described here of the Hahnodontidae is characterized by a combination of features unknown in the other families. It is not clear whether this tooth belongs to *Hahnodon* or to *Denisodon*; therefore it is grouped in open nomenclature.

#### Lower incisor, MNHN SA 102

Fig. 6A–D.

#### Description

**Measurements.**—Length of crown = 2.0 mm; height of crown ~1.2 mm.

**Preservation.**—Only crown preserved, corroded postmortem by several small pits. The dorsal face has been strongly eroded by wear. The crown was completely covered by enamel.

**Orientation.**—Present is a right incisor, as is demonstrated by comparison with the Paulchoffatiidae (see G. Hahn 1969: text-fig. 24). The inner face of the crown shows a longitudinal enamel ridge, and the outer face has a rounded upper edge as in the Paulchoffatiidae.

**Lateral view** (Fig. 6A).—Crown stout, with a broad base. Dorsal border gently concave, curving upward at the tip. Ventral border strongly convex. Upper edge of crown rounded. External wall strongly arched convex. Tip strongly eroded. Enamel smooth.

**Mesial view** (Fig. 6B).—Longitudinal enamel ridge confined to the anterior half of the crown, dividing it into a narrower upper and a wider lower portion. Tip more pointed than on lateral side. Upper edge not rounded. Otherwise shape as in lateral view.

**Dorsal view** (Fig. 6C).—Tongue-like shape, nearly symmetrical. Enamel of dorsal face completely eroded, dentine exposed.

**Anterior view** (Fig. 6D).—Crown somewhat higher than broad, ovoid in shape. External wall well rounded; internal wall less arched, longitudinal enamel ridge distinct. Tip rounded.

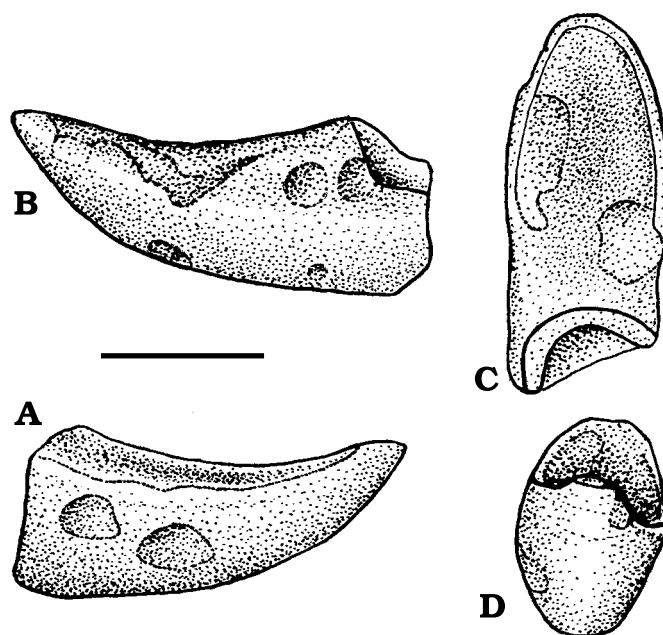


Fig. 6. Hahnodontidae, gen. et sp. indet., right lower incisor, MNHN SA 102, in lateral (A), mesial (B), dorsal (C), and anterior (D) views. Scale bar 1 mm.

**Discussion.**—The present incisor corresponds generally to those known from the Paulchoffatiidae (see under “orientation”). It is relatively short and stout with its crown distinctly bent upwards. In this it is most similar to some specimens of *Kuehneodon dietrichi* G. Hahn, 1969 (see G. Hahn 1978: pl. 3: 13a, b, pl. 4: 20a, b). But in *Kuehneodon* the internal wall of the crown is distinctly less arched as in the specimen described here (see G. Hahn 1978: pl. 2: 5c, pl. 4: 20a). In the Pinheirodontidae (Hahn and Hahn 1999b: fig. 14a, b) and other families of the Plagiaulacida the crown of the incisors is longer, more slender and also more curved than in this specimen. With that, the Hahnodontidae remain in the structure of their incisors, on a primitive level similar to that in the Paulchoffatiidae.

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