THE EARLIEST MAMMAL OF THE EUROPEAN PALEOCENE: THE MULTITUBERCULATE *HAININA*

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ABSTRACT—A new species of multituberculate mammal, *Hainina pyrenaica* n. sp. is described from Fontllonga-3 (Tremp Basin, Southern Pyrenees, Spain), correlated to the later part of chron C29r just above the K/T boundary. This taxon represents the earliest European Tertiary mammal recovered so far, and is related to other *Hainina* species from the European Paleocene. A revision of the species of *Hainina* allows recognition of a new species, *H. vianeyae* n. sp. from the Late Paleocene of Cernay (France). The genus is included in the family Kogaionidae Rãdulescu and Samson, 1996 from the Late Cretaceous of Romania on the basis of unique dental characters. The Kogaionidae had a peculiar masticatory system with a large, blade-like lower p4, similar to that of advanced Ptilodontoidea, but occluding against two small upper premolars, interpreted as P4 and P5, instead of a large upper P4. The endemic European Kogaionidae derive from an Early Cretaceous group with five premolars, and evolved during the Late Cretaceous and Paleocene. The genus *Hainina* represents a European multituberculate family that survived the K/T boundary mass extinction event.

INTRODUCTION

THE IMPACT of the Cretaceous-Tertiary (K/T) mass extinction on European mammals is unknown because of the complete absence of data for about the first four millions years of the Tertiary. Hitherto the fossil mammals from Hainin (Belgium) comprised the only mammalian record for the Early Paleocene of Europe (Godfriaux and Thaler, 1972; Thaler, 1977). This assemblage may be correlated to the later part of chron C27 (approximately 61 Ma; Sigé and Marandat, 1997), whereas the K/T boundary is situated in the later part of chron C29r (approximately 65 Ma). Consequently, there is a gap of about four million years in the earliest Tertiary record of mammals in Europe.

A recently discovered locality, Fontllonga-3, just above the K/T boundary in the continental sediments of the Tremp Formation (Southern Pyrenees, Lleida, Spain; Alvarez-Sierra et al., 1994; López-Martinez et al., 1996) has yielded some mammalian remains which partly fill the gap in this critical period in mammalian history.

We describe here a new multituberculate mammal from this locality and discuss its affinities. We include this species in the early Paleocene genus *Hainina* Vianey-Liaud, 1979. A reinterpretation of this taxon allows its inclusion in the family Kogaionidae, known from the Late Cretaceous of Romania (Rãdulescu and Samson, 1996). Therefore, the genus *Hainina* was a descendent from European Late Cretaceous multituberculates that survived the K/T boundary mass extinction event.

GEOLOGICAL SETTING

The Tremp Formation represents the top of a transgressive-regressive sedimentary cycle of Late Cretaceous-early Tertiary age, filling the first stage of the Pyrenean foreland basin. In the Ager syncline, the Tremp Formation is well exposed at the Fontllonga section (Fig. 1), comprised of up to 1,000 m of peritidal and lacustrine limestones, reddish claystones and sandstones (Mey et al., 1968; Nagtegaal et al., 1983). The biostratigraphy of this section, based on pollen, charophytes, dinosaurs and other vertebrates, has been calibrated with paleomagnetism and stable isotopes (Galbrun et al., 1993; López-Martínez et al., 1998). The Fontllonga paleomagnetic section is the longest and the most continuous succession across the K/T transition in continental deposits from Europe.

The Fontllonga-3 mammal site is a lenticular clay bed intercalated within a sandstone channel fill from the lower part of the Tremp Formation. This level is situated in the uppermost part of a thickening-upward sequence of channel sandstone bodies, up to 15 m thick, which can be correlated across the 30 km wide Ager syncline. The complete sandstone sequence has a Late Maastrichtian age and is correlated to chron C29r (Galbrun et al., 1993). The sandstones contain marine bioclasts and sigmoidal cross-bedding, typical for an upper estuarine environment (López-Martínez et al., 1998).

Several localities with dinosaur footprints from the same area are correlated to the top of the sandstone channel fill situated approximately three meters below Fontllonga-3 (López-Martínez et al., 1998). A Danian flora just above Fontllonga-3 has been correlated to the latest part of chron C29r (Galbrun et al., 1993; Médus et al., 1992). Consequently, Fontllonga-3 is situated in a 3 m thick interval which contains the K/T boundary.

After exhaustive sampling and screening of nearly 10 tons of marls from Fontllonga-3, no dinosaur remains, either bones or eggshell fragments, were found. Bony fishes are abundant, such as the pycnodont *Coelodus laurenti* known in the Paleocene of the Paris basin (Soler and De la Peña, 1995). Palynological analysis indicates the presence of the Normapolles taxon *Pseudoromeinipollenites paleocenicus* Kedves, 1982 similar to that described from a Late Paleocene (Thanetian) site at Menat (France, López-Martinez et al., 1997). The absence of dinosaurs, common in lower levels, and the presence of Paleocene fishes and pollen indicate an earliest Tertiary age for Fontllonga-3. Therefore, the Fontllonga-3 site represents the earliest Tertiary vertebrate fauna from the Old World.

The mammal assemblage contains two taxa. A therian mammal is represented by a single tooth, the majority of the material belonging to the new multituberculate *Hainina pyrenaica* n. sp. described below.

SYSTEMATIC PALEONTOLOGY

Order MULTITUBERCULATA Cope, 1884
Suborder incertae sedis
Family KOGAIONIDAE Rãdulescu and Samson, 1996

Type genus.—*Kogaionon* Rãdulescu and Samson, 1996

Occurrence.—Upper Cretaceous of Romania and Paleocene of Spain, Belgium, and France.

Genus HAININA Vianey-Liaud, 1979

Type species.—*Hainina belgica* Vianey-Liaud, 1979

Other species.—Two other *Hainina* species are known: *H.*

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[3]Dr. R. Daams passed away during the editing of this work.

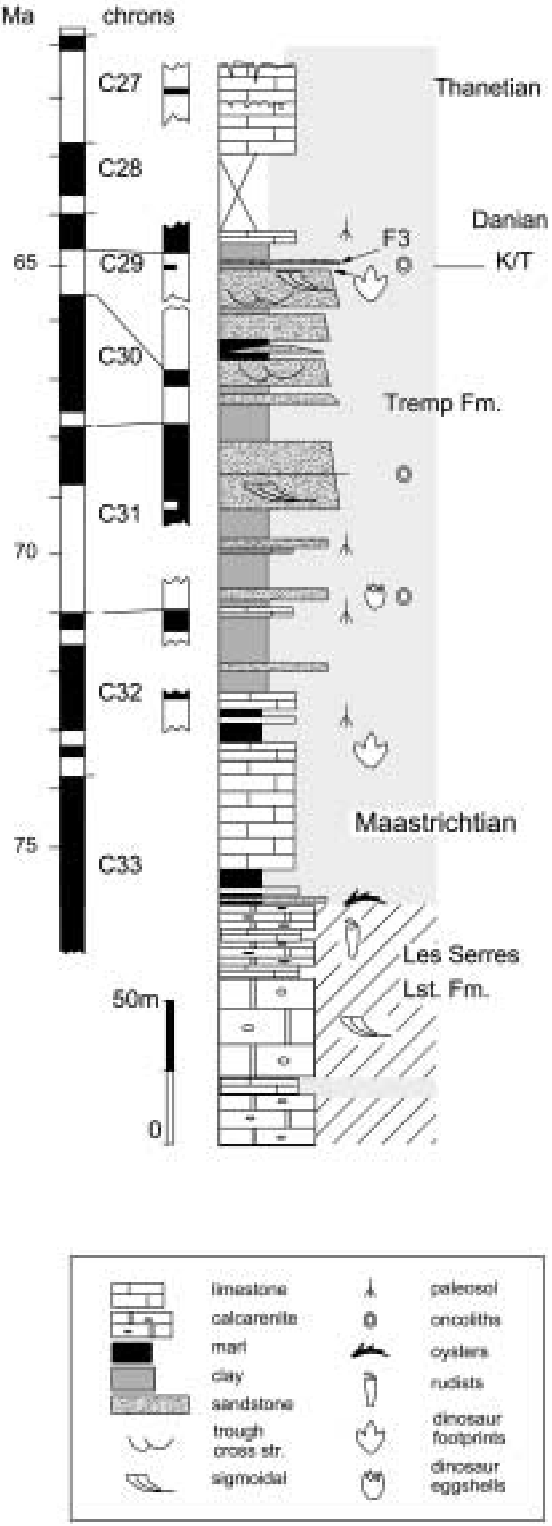

FIGURE *1*—Map and lithological log of the Fontllonga section. The stratigraphic data are from López-Martinez et al., 1998, and the paleomagnetic data are from Galbrun et al., 1993.

belgica Vianey-Liaud, 1979 represented by nine teeth from the Lower Paleocene of its type locality Hainin (Belgium) and *H. godfriauxi* Vianey-Liaud, 1979 represented by five teeth from the same type locality. The emended diagnosis of the latter species is partly based on 24 specimens from the younger fauna of Cernay (Late Paleocene, France). The Cernay material included in this species by Vianey-Liaud (1979, 1986) differs significantly in size and has a distinct cusp formula in m1, allowing its recognition as a different species described herein as *Hainina vianeyae* n. sp.

Emended diagnosis.—Multituberculates with four upper premolars (P2-P5) having two roots each. P4 with one to three labial cusps. P5 with a labial crest, which decreases in height backwards, and a postero-lingual cingulum. M1 with a well-developed, postero-lingual ridge, usually reaching the anterior margin of the tooth. Upper and lower molars with less than eight cusps per row. The p4 is about twice as long as the P4.

HAININA VIANEYAE new species

1964 Ptilodontiné, n. gen. et n. sp.; RUSSELL, p. 40, pl. I, figs. 8a–8b
p.1979 *Hainina godfriauxi* nov. sp.; VIANEY-LIAUD, p.126, fig. 5 M1/, pl. 3, fig. 7; non figs 4, 5a and 5 M2/
p.1986 *Hainina godfriauxi* VIANEY-LIAUD, p. 144, texte-fig. 15 a–b and f–p, texte-fig. 19 a–l; non texte-fig. 15 c–e

Diagnosis.—A large-sized *Hainina* species with P4 having two labial cusps, M1 with cusp formula 3–4:4:4–7, and m1 cusp formula 3:4. Hainina *vianeyae* n. sp. differs from *H. belgica* in having much larger teeth. It differs from *H. godfriauxi* by its smaller and slender teeth and by its more complicated m1 with cusp formula 3:4.

Etymology.—In honour to Mme. Monique Vianey-Liaud from the University of Montpellier, the first author who studied this material.

Type.—An isolated right M1 (cat. nr. CR 1043, Text-Fig 19e In Vianey-Liaud, 1986).

Other material examined.–4 m1, 1 m2, 1 P2, 2 P3, 4 P4, 2 P5, 7 M1 and 3 M2 from Cernay. See Vianey-Liaud, 1986.

Description.—See Vianey-Liaud, 1986.

Occurrence.—Late Paleocene (MP6) of France.

Discussion.—The type M1 of *H. vianeyae* n. sp was assigned to *H. godfriauxi* by Vianey-Liaud, 1979. There is no measurable M1 of *H. godfriauxi* from Hainin ; the only M1 from *H. godfriauxi* from Hainin is a fragment that is significantly larger in size (Vianey-Liaud, 1979; pl. 3, fig. 8). Comparing the measurements between both assemblages, it is clear that the teeth of *H. godfriauxi* from Hainin are wider than those of *H. vianeyae* of Cernay. The measure of the lower m2 of *H. godfriauxi* in Vianey-Liaud (1979) is not correct; its width is close to 1.9 mm. This tooth is almost as long as wide, as can be seen clearly in the two figures from Vianey-Liaud (1979, fig. 4b and pl. 3, fig. 10). Furthermore, the length/width ratio is significantly lower in *H. godfriauxi* than in *H. vianeyae* for all the dental elements represented in both samples.

Morphologically, these assemblages can be differentiated on the basis of m1 with cusp formula 3:3 in *H. godfriauxi* and 3:4 in *H. vianeyae.* It is significant that the latter formula is absent in early Paleocene *Hainina.* Therefore, based on the differences in morphology as well as in length/width proportions, the material from Cernay can be separated as a distinct new species, despite the scarcity of material.

HAININA PYRENAICA new species

Figures 2.1–2.7, 3.1–3.5, 4.2, 4.4

Diagnosis.—A small *Hainina* species with P4 having three labial cusps, a simple M1 with cusp formula 3:4:4 and m1 with cusp formula 3:3. *Hainina pyrenaica n. sp.* differs from *H. belgica* in its more complex P4 with three external cusps instead of one, a wider and more simple M1 with four cusps instead of seven in the internal row which is also shorter, and a longer m1. *Hainina pyrenaica* n. sp. differs from *H. godfriauxi* in its smaller size. It differs from *Hainina vianeyae* n. sp. from Cernay in having a better developed posterior labial cusp on P4 and by its much smaller size.

Description.—P2. (0.77 × 0.64 mm; 0.80 × 0.62 mm). The simple dental pattern consists of two conical cusps of the same height, separated by a shallow valley. Two roots are present.

P4. (1.64 × 0.95 mm; 1.66 × 0.92 mm). Two cusp rows are present; the lingual one consists of 5 cusps of which the four anterior ones are of similar size, and the fifth one is the smallest. The labial row has three well-developed cusps. Two roots are present.

P5. (1.63 × 1.02 mm). This tooth has a subrectangular outline. The labial border is higher than the lingual one. An incomplete, centrally situated ridge, is present. Two antero-labially situated cusps form part of a longitudinal ridge running along the labial border of the tooth. The lingual wall of these two cusps form a steep cutting edge. Two well-developed roots are present.

M1. (2.00 × 1.52 mm). This tooth has a subrectangular-shaped crown with two longitudinal valleys separating three cusp rows of which the cusp formula is 3:4:4. The central row is obliquely oriented, with four well-individualised cusps, separated by transverse valleys. At either side of the central row there is a cusp row of similar length, with three and four badly individualised cusps respectively. The lingual longitudinal valley is deeper and more intensively affected by wear than the shallower labial valley. The wear facets are particularly well developed at each end of the lingual valley. The facets are strongly affected by wear striae showing *hertzian cones* allowing the direction of occlusal movements to be oriented (see below, Figs. 1–3). Accordingly, the higher cusps of the lingual row form the posterior end. Two roots are present, the anterior one being narrower than the posterior one.

m1. (2.13 × —). This tooth has a cusp formula 3:3; the enamel in the only specimen is severely damaged, but permits distinguishing a longitudinal valley only and transverse valleys at either side of the tooth separating the alternating cusps. Two roots are present.

m2. (1.42 × 1.65 mm). Two large and well-individualised cusps are present at the labial side of the molar. The lingual row has a distinct anterior cusp, followed by a crenulated wall. This wall is connected to the anterior labial cusp by means of a low, obliquely running, ridge.

Etymology.—pyrenaica—after the Pyrenees where the type locality is situated.

Type.—An isolated left M1 (cat. nr. FTN3-1, Fig. 2.6; Department of Paleontology, Complutense University of Madrid, Spain).

Other material examined.—2P2, 2P4, 1P5, 1m1, 1m2. FNT3-2 to FNT3-4 and FNT3-7 to FNT3-10.

Occurrence.—Fontllonga-3, a grey marl intercalated in reddish sandstones of a channel fill at the eastern side of the main road from Tremp to Lleida, some 30 km south of Tremp, Lleida province, Spain. Early Paleocene, late part of chron C29r.

Discussion.—The new Pyrenean species shares with the other European multituberculates included in the genus *Hainina* the symmetrical shape of M1, the pattern of P4 and the peculiar P5.

Hainina pyrenaica n. sp. is similar in size to *H. belgica* and much smaller than *H. godfriauxi* and *Hainina vianeyae* n. sp. The P4 of *H. pyrenaica* is the most complex of the genus, since it has three external cusps instead of one (*H. belgica*) or two (*Hainina vianeyae*). In contrast, the M1 of *H. pyrenaica* is the most simple of the genus, with four cusps in the internal row instead of seven. The m1 is relatively longer in *H. pyrenaica* than in *H. belgica.*

Dental formula of Hainina.—Since only isolated teeth are available, the dental formula of *Hainina* is not known and must be inferred. P4 and M1 coincide in shape and relative dimensions in the three localities where they have been recovered. The P4 and M1 width ratio varies between 0.60 and 0.76, similar to the Asiatic multituberculates Djadochtatheria (*Sloanbaatar, Kryptobaatar* and *Kamptobaatar*) and the European *Kogaionon* (see Kielan-Jaworowska, 1969; Rãdulescu and Samson, 1996; Kielan-Jaworowska and Hurum, 1997). Moreover, in two localities another premolar type appears, here interpreted as a P5 (see below).

The correct orientation of M1 in *Hainina* may be controversial. The criteria used for orientation in all multituberculate M1's are: 1) the lingual valley is always the deepest; 2) in the lingual cusp row, the posterior cusps are the highest ones, and 3) the anterior root is generally smaller and narrower than the posterior one (see Clemens, 1963 p. 65 and Sahni, 1972 p. 373). Additionally we have observed two other criteria: the orientation of the hertzian cones in the wear striae, and the wear pattern of the dentine.

The hertzian cones are triangular gaps in the enamel (Fig. 3.1, 3.2) produced by the abrasive effect of food particles (Gordon, 1984). The base of the cones are oriented following the direction of the movement (Fig. 3.2). According to Krause (1982), the multituberculate lower jaw moved backwards when pressing during the masticatory movements, and forwards when relaxing (palinal direction). Therefore, the base of the hertzian cones (the shortest side of the triangular notch) indicates the posterior side of the upper teeth.

The wear pattern of the dentine indicates the orientation of the tooth (Krause, 1982). There is a sharp step between the enamel and the dentine in the trailing edge of the cusps, vs. an even slope in the leading edge. The trailing edge is oriented backwards in the upper teeth. According to these five criteria, the holotype of *Hainina pyrenaica* is a left M1, oriented as shown in Figure 4.2. The lingual cusp row has more cusps than the labial one, which is unusual for multituberculates (Fig. 2.6, anterior side upwards).

A main problem of *Hainina* is the interpretation of the upper premolars. *Hainina* is supposed to have four upper premolars and an extra element, tentatively interpreted as a milk tooth (Vianey-Liaud, 1986). According to this interpretation, the upper tooth row is relatively too short comparing with other multituberculates having a long, blade-like p4. The nearly complete skull of *Kogaionon ungureauni* Rãdulescu and Samson, 1996 with preserved tooth rows, assigned by these authors to the new multituberculate family Kogaionidae, may serve for interpretation of the arrangement and homologies of the dental elements of *Hainina,* and sheds new light on its evolutionary relationships.

Premolar nomenclature in multituberculates.—In the multituberculate literature, there are two different nomenclatural schemes for the upper premolars. On one hand, some authors designate the five premolars of Jurassic multituberculates as P1 to P5, and the four premolars of Cretaceous and Tertiary multituberculates as P1 to P4. Some of these authors do not consider this nomenclature to reflect homology (Clemens and Kielan-Jaworowska, 1979; Kielan-Jaworowska and Ensom, 1992), while Hahn (1977, 1993) does. On the other hand, other authors designate the Jurassic multituberculate premolars as P0 to P4 and the Cretaceous and Tertiary multituberculates as P1 to P4 ; they use this nomenclature as an implicit homology (Fig. 5),and it is used that way in cladistic analyses (Simmons, 1993; Rougier et


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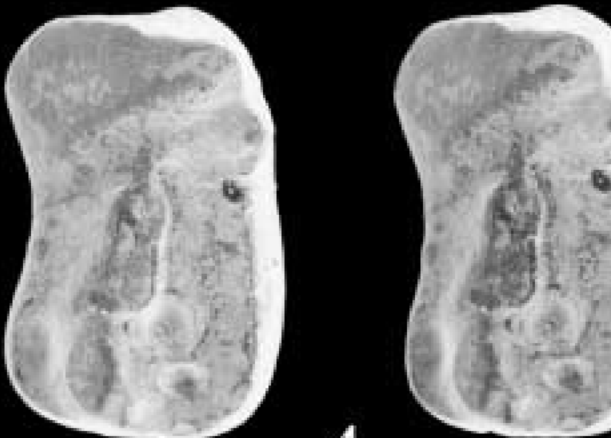
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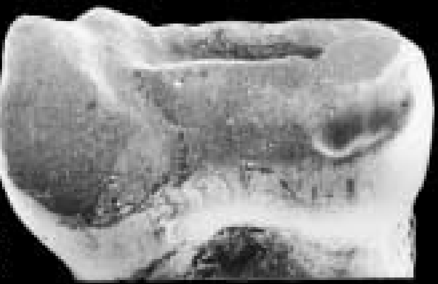
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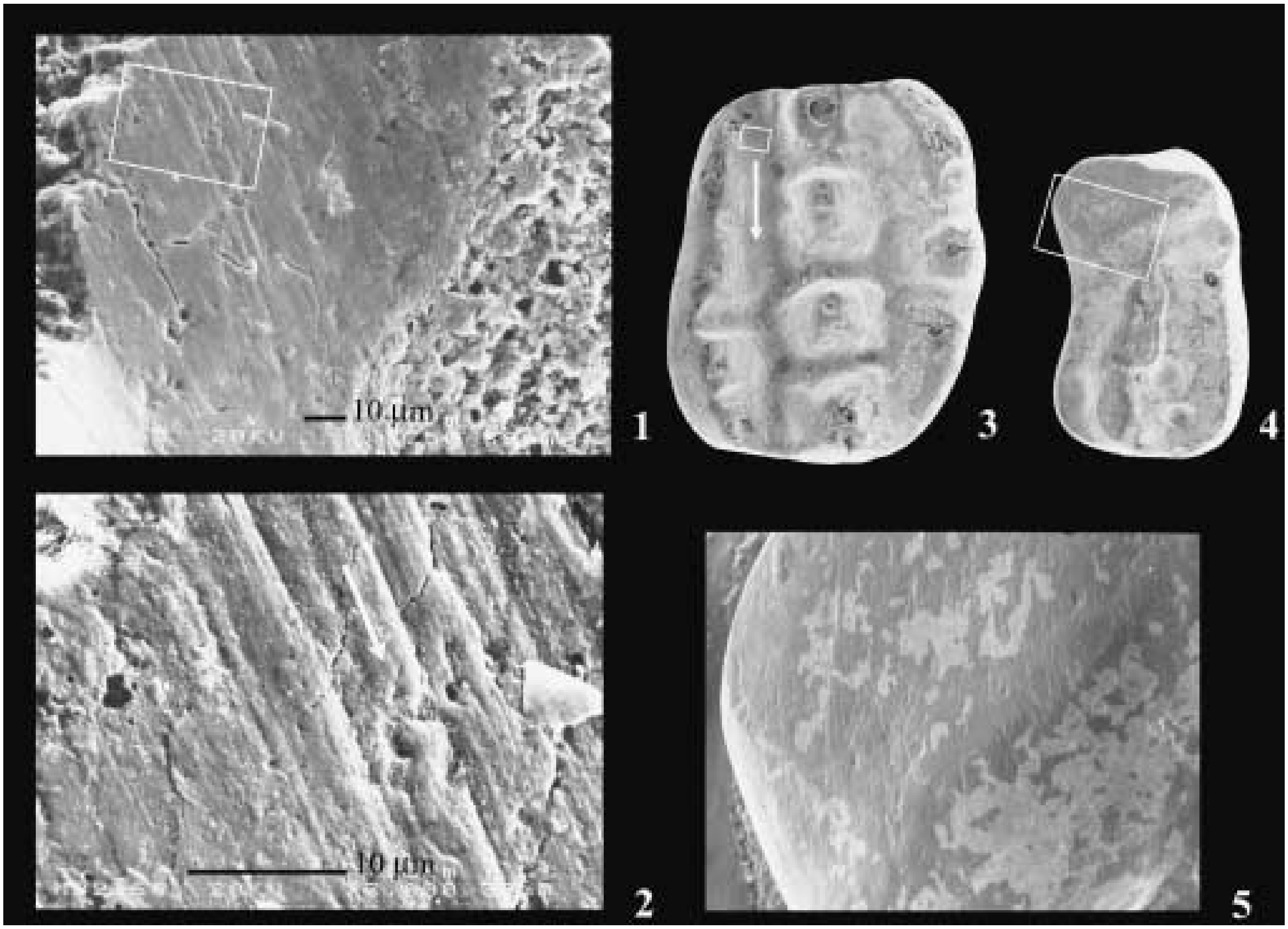

FIGURE 3—Wear marks on the enamel surface of the teeth from *Hainina pyrenaica* sp. nov. *1, 2,* Hertzian cones in the deepest valley of M1; *1,* ×750, *2,* ×3,000, The shortest side of the hertzian cones indicates the direction of the masticatory strength (Gordon, 1984), marked by an arrow; *3,* Left M1 (FNT3-1), the arrow indicates the direction of the masticatory strength; squares on *1* and *3* indicate the magnified areas in *2* and *1* respectively; *4.* Left P5 (FNT3-2), square indicates the magnified area of *5*; *5,* Wear striae longitudinally and obliquely oriented in the antero-lingual facet of the P5 (×125).

al, 1997). Nevertheless, none of these authors have discussed the reasons to propose this homology between the upper premolar of multituberculates.

The results of our study on *Hainina* and *Kogaionon* indicate to us the necessity of using the former nomenclature for upper premolars with an explicit homology (Fig. 5), as will be discussed below.

Premolar homologies in Hainina.—We have established the homologies of the different upper premolars in *Hainina* on the basis of four criteria: 1) morphology, 2) topological relations between the different premolars, 3) relative size, and 4) functional analogy in relation to other multituberculates.

Morphology.—Five upper premolar types can be recognized among the available material of the genus *Hainina,* here described as types *a* to *e* (Fig. 6). Types *a* and *b* have not been found in the same locality. Type *a* appears in *H. pyrenaica* (Fontllonga-3) and *Hainina vianeyae* (Cernay), and type *b* in *H. belgica* (Hainin). Three hypotheses can be proposed for their homologies. Either 1) the genus *Hainina* has five upper premolars, type *a* representing P1 and type *b* the P2; or 2) the genus *Hainina* has four upper premolars, and one of the types *a* or *b* would represent the deciduous tooth. Since the deciduous teeth are generally more complicated than the permanent ones, the deciduous tooth would probably be type *b*; or 3) the two types represent the variability of the permanent premolars of the genus. We consider the first hypothesis as less probable, since the five types have never been found together in the same sample. Moreover, all known Late Cretaceous and early Tertiary multituberculates have only four upper premolars, of which the anterior one is similar to type *b*. Therefore, until more complete

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FIGURE 2—*Hainina pyrenaica* n. sp. *1,* FNT3-10 occlusal view of left P4, stereo pair; *2,* FNT3-9, lingual view of right P4; *3,* FNT3-4 occlusal view of right m2.; *4, 5,* FNT3-2 left P5, *4,* occlusal view, stereo pairs; *5,* lingual view; *6,* FNT3-1 left M1 (holotype), occlusal view, stereo pairs; *7,* FNT3-7, anterior view of left P2. All specimens from the Earliest Danian, Fontllonga-3, Tremp Formation (Lleida, Spain). Material stored in the Department of Paleontology, Complutense University of Madrid. Graphic scale represents 1 mm.

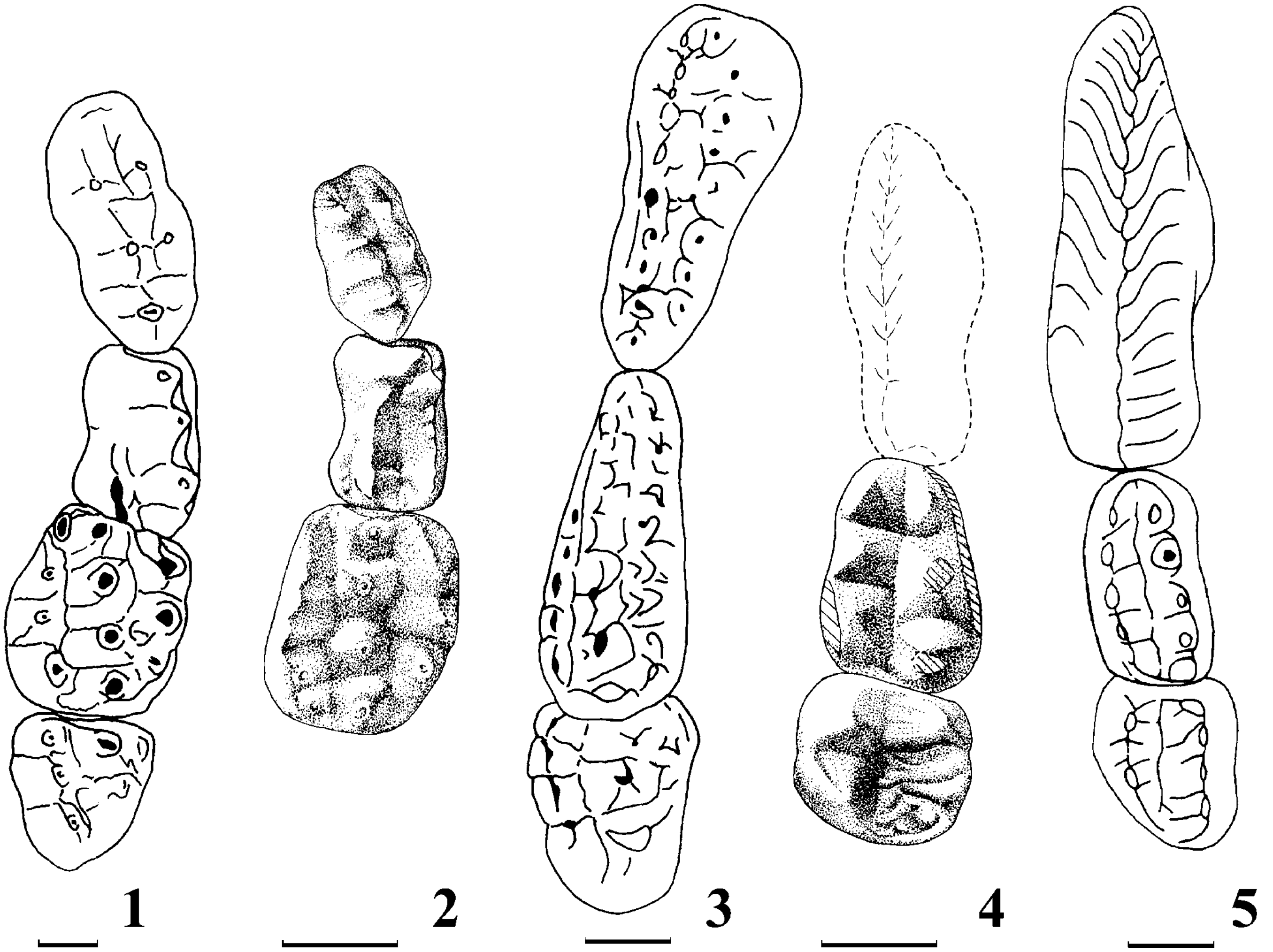

FIGURE *4*—Left dental tooth rows: *1, Kogaionon ungureanui* Rãdulescu and Samson (after Rãdulescu and Samson, 1996); *2* and *4, Hainina pyrenaica* n. sp. (reconstruction after *H. belgica*); *3* and *5, Ptilodus montanus* Douglass (after Simpson, 1937a). *1, 2* and *3,* upper tooth rows; *4* and *5,* lower tooth rows. The lower tooth row of *Kogaionon ungureanui* is unknown. Graphic scales represent 1 mm.

material is available, we suggest that *Hainina* probably had four upper premolars, types a and b being the expression of the variability of the anterior premolar, either being both permanent or one of them being decidual. Since the morphology of types *a* and *b* is relatively simple (see Fig. 6), the anterior premolar in *Hainina* may correspond either to P1, P2 or P3 (comparing with *Arginbaatar,* Kielan-Jaworowska et al., 1987 and *Nemegtbaatar,* Kielan-Jaworowska, 1974).

Type *c* of *Hainina,* represented in *H. belgica* and *H. vianeyae,* is similar to the second premolar of *Kogaionon.* It has a subrectangular outline, 4 or 5 cusps arranged in two parallel rows, and a slightly concave posterior slope. Most of Late Cretaceous-Paleocene multituberculates show this advanced morphology in the P3 (e.g. *Neoplagiaulax* and *Liotomus*; see Vianey-Liaud, 1986); however, *Kogaionon* shows this type in the second locus (Rãdulescu and Samson, 1996).

Type *d* of *Hainina* has been interpreted as a P4 (Vianey-Liaud, 1979, 1986), since it shows the general pattern of most multituberculate's P4 with cutting edges. The main row is the lingual one and its cusps increase in size backwards, with the penultimate cusp being the highest one. The buccal row presents some isolated cusps of uniform size. This arrangement of cusps can be observed in P4 and P5 of primitive multituberculates, such as *Eobaatar* and *Arginbaatar* (Kielan-Jaworowska et al., 1987). Advanced genera, such as *Neoplagiaulax* (Vianey-Liaud, 1986), *Bulganbaatar* and *Nemegbaatar* (Kielan-Jaworowska, 1974) have a similar structure in the P4, with a higher number of cusps. Here again *Kogaionon* differs in having a tooth with this arrangement of cusps in the third locus instead of the fourth one.

Type *e* is a peculiar tooth with an unique morphology. Characteristic features of this element are the presence of a buccal cusp row decreasing in size backwards. This row is longer than the postero-lingual cusp row, which is obliquely directed towards the anterior cusp of the buccal one. This unique morphology made Vianey-Liaud (1986) doubt the correct interpretation of this element, hitherto only known in *Hainina vianeyae.* The two specimens from Cernay show the posterior buccal cusps either distinct or integrated in a ridge (Vianey-Liaud, 1986, texte-figs. 15 l-p). Vianey-Liaud (1986) finally considered them to represent D4. The presence of this type in *Hainina pyrenaica* confirms that it belongs to this genus. Moreover, this element in *H. pyrenaica* fits perfectly with the M1, suggesting that both belong to a single individual. Therefore, it can be interpreted as the last premolar of *Hainina.* This peculiar dental morphology

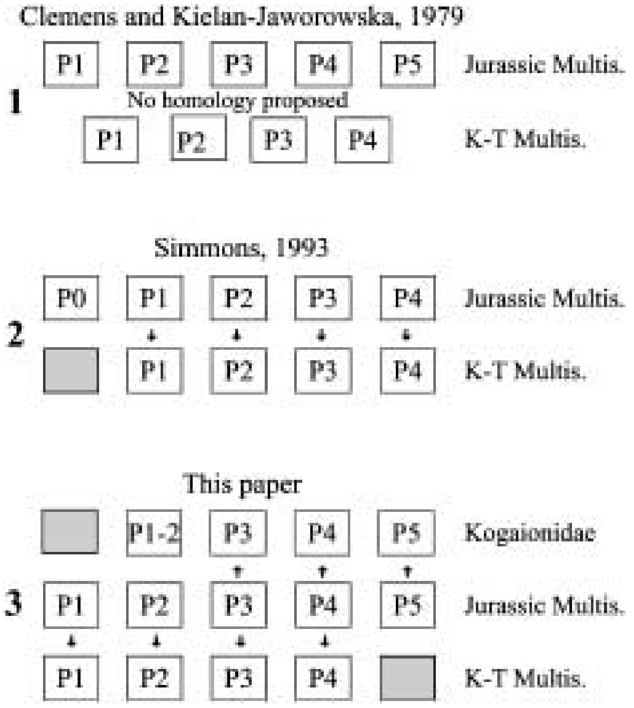

FIGURE 5—Nomenclature used by different authors for upper premolars of multituberculates. *1,* Nomenclature used by Clemens and Kielan-Jaworowska, 1979; *2,* Nomenclature used as homology by Simmons, 1993 without discussion; *3,* nomenclature used in this paper. Arrows indicate homologies between elements of Kogaionidae, Jurassic, and Cretaceous-Tertiary (K-T) multituberculates. Grey squares represent lost dental elements.

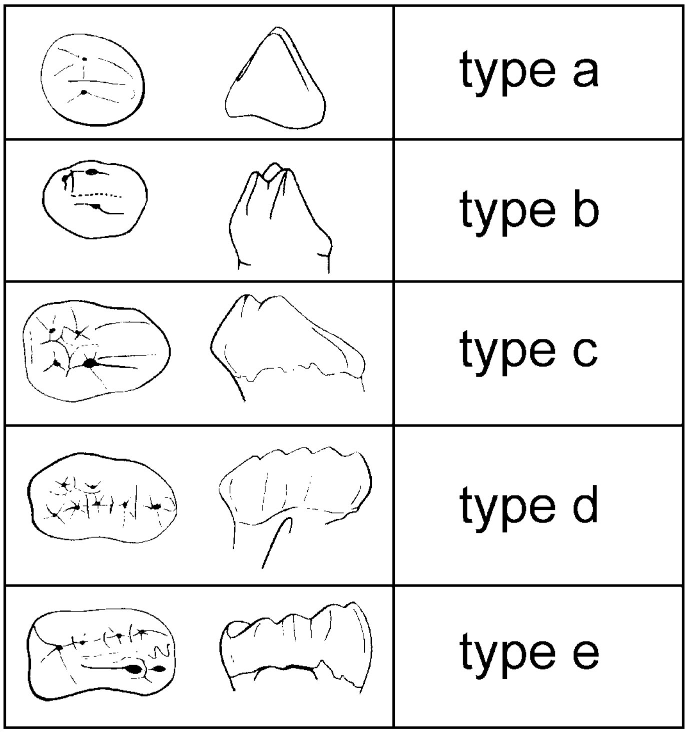

FIGURE 6—Types of upper premolar present in the genus *Hainina.* Type a.—Circular outline with 2 cusps (Fig. 2.7; Vianey-Liaud, 1986, texte-figs. 15 a–b). Type b.—Circular outline with 3 cusps (Vianey-Liaud, 1979, texte-figs. 3 c–d). Type c.—Rectangular outline with 4–5 cusps (Vianey-Liaud, 1986, texte-figs. 15 c–h). Type d.—Elongated tooth with 1–3:5 cusps formula (Fig. 2.1, 2.2; Vianey-Liaud, 1986, texte-figs. 15 i–k). Type e.—Elongated tooth with 4:2 cusp formula (Fig. 2.4, 2.5; Vianey-Liaud, 1986, texte-figs. 15 l–p) . Drawings are after Vianey-Liaud, 1979 and 1986. All lateral views represented from their lingual side, except type e that is represented from the buccal one.

is similar to that shown by the last permanent premolar of *Kogaionon.* The position in front of the M1 would coincide in both genera. Therefore, we consider the type *e* of *Hainina* homologous to the last premolar of *Kogaionon.*

This cusp arrangement in the last premolar of *Hainina* and *Kogaionon* is unknown in any other multituberculate. The main cusp row decreasing in size backwards, and the lingual posterior accessory cusps appear only in P5 of the Early Cretaceous genera *Kuehnodon* Hahn, 1969 and *Lavocatia* Canudo and Cuenca, 1996, although the latter have 3 cusp rows instead of two. All other multituberculates have a structurally different P4 (and P5 when present), with the main cusp row in lingual position increasing in size backwards, and an accessory row in anterobuccal position (Kielan-Jaworowska et al., 1987; Kielan-Jaworowska and Ensom, 1992). According to these comparisons, type *e* can only be morphologically related with P5 of some primitive European multituberculates.

Concluding, we may consider types *c, d* and *e* homologous to the three last premolars of *Kogaionon.* Accordingly, the *Hainina* upper tooth row can be reconstructed as shown in Figure 4.2. The morphological criterion suggests that these three types correspond to premolars P3-P4-P5 respectively. We discuss this hypothesis below on the basis of the two other criteria.

Dental relations.—The spatial relations of the dental elements and their relative size is an important criterion for dental homologies. The primitive multituberculates with P5, such as *Bolodon, Eobaatar, Arginbaatar* or *Kuehneodon,* have two relatively large premolars, P4 and P5, which are of similar size (Kielan-Jaworowska and Ensom, 1992; Kielan-Jaworowska et al., 1987; Hahn, 1977). The advanced multituberculates with four premolars (Taeniolabidoidea, Djadochtatheria and Ptilodontoidea) have different premolar size ratios, in which the third one is smaller than the last one (Clemens and Kielan-Jaworowska, 1979). As shown in Figure 4, the genera *Kogaionon* and *Hainina* have the two later upper premolars of similar size. Their premolar ratio is thus similar to the primitive multituberculates with five premolars (Fig. 7). This indicates that the four premolars in *Kogaionon* and *Hainina* are P2, P3, P4 and P5 instead of P1, P2, P3 and P4 as in their contemporaneous multituberculates.

Moreover, in *Kogaionon* the premolar in the third position overlaps the two other neighboring premolars, as is the case in the multituberculates with five upper premolars (e.g., *Bolodon*; Kielan-Jaworowska and Ensom, 1992). In the advanced multituberculates Taeniolabidoidea, Djadochtatheria and Ptilodontoidea, the premolar which overlaps the two other neighbouring elements is situated in the fourth position (P4). The imbrication pattern thus confirms that the premolar in the third position in *Kogaionon* is P4. In *Hainina* the pattern would be similar to that of *Kogaionon,* according to the anterior facet of contact observed in the last premolar of *H. pyrenaica.* Therefore, the premolar relations shown by *Kogaionon* and *Hainina* are similar to that in primitive multituberculates, supposing that one of the first premolars has been lost.

Functional analogies.—The wear facets on the teeth of *H. pyrenaica* make it possible to infer its masticatory function. This genus is compared with *Ptilodus* (Fig. 4.3, 4.5; masticatory

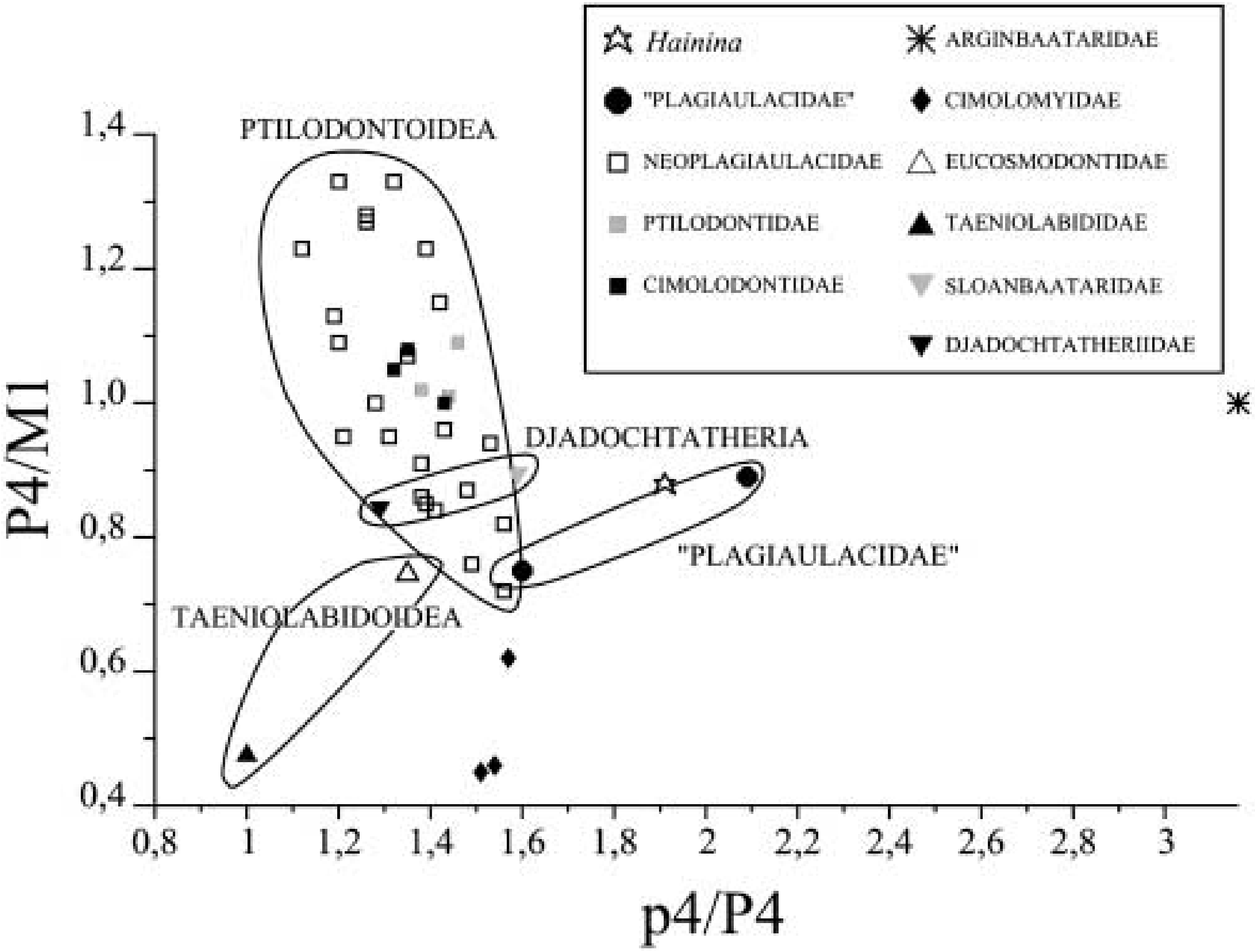

FIGURE 7—Scatter diagram showing the p4/P4 against the P4/M1 length ratios in multituberculate mammals (data from Archibald, 1982; Clemens, 1963; Kielan-Jaworowska, 1969, 1974; Kielan-Jaworowska et al., 1987; Kielan-Jaworowska and Ensom, 1992; Krause, 1977; Simpson, 1937b; Sloan, 1987; Storer, 1991 and Vianey-Liaud, 1986).

movements studied in detail by Krause, 1982, and Wall and Krause, 1992), because it presents a large, blade-like p4 similar to that of *H. belgica* (Vianey-Liaud, 1979).

The penultimate premolar (P4) of *H. pyrenaica* shows only slight wear on the penultimate, largest cusp. This facet is situated on the top of the cusp and dips about 45 degrees towards the lingual side. There is no sign of wear on the remaining cusps of this element.

The ultimate premolar (P5) of *H. pyrenaica* shows wear facets in three main regions of the tooth. The lingual part of the large, anterior cusp has a large facet that almost reaches the base of the crown. This facet shows wear striae, most of them longitudinally oriented, and some of them inclined towards the apex of the cusp (see Fig. 3.4, 3.5). On the lingual cusp row, two other wear facets are present. The one near the base is in the same plane as the anterior cusp, and the other near the top of the cusps is situated in a horizontally oriented plane. Both have longitudinally oriented striae.

The M1 of *H. pyrenaica* shows wear facets on both sides of the lingual valley and on the lingual side of the labial valley. Moreover, the middle cusp row shows horizontal wear at the apices of the cusps. There is also a conspicuous concave wear facet at the bottom of the anterior opening of the lingual valley. All facets show longitudinal wear striation, although these are more abundant and deeper on the buccal side of the lingual valley.

In *Kogaionon* the wear facets have not been described by Rãdulescu and Samson (1996), but from the figures it is possible to observe a conspicuous wear facet situated in the opening of the lingual valley of the M1 (Fig. 4.1), similar to the one described in *H. pyrenaica.*

According to Krause (1982), the three anterior premolars in *Ptilodus* show horizontal wear facets affecting mainly the apices of the cusps. The P4 has a distinct postero-lingual facet which shows curved wear striations. The striae were formed during the palinal grinding cycle. Their trajectory starts obliquely antero-ventrally and continues horizontally postero-dorsally (Krause, 1982). The M1 of *Ptilodus* show striations at the antero-lingual side of the middle cusp row, starting longitudinally and continuing obliquely from an antero-dorsal towards a postero-ventral direction. The middle and posterior part of the M1 of *Ptilodus* show mainly longitudinal wear striations (Krause, 1982).

Comparing these wear facets with those observed in *H. pyrenaica*, the facets of the two elements, P5 and M1 from *Hainina* are similar to those of M1 of *Ptilodus.* The wear striae in the anterior part of the M1 of *Ptilodus* are similar to those from the anterior part of the last upper premolar of *H. pyrenaica*, and those from the posterior part of the M1 of *Ptilodus* are similar to that of the M1 of *Hainina.* The function developed by the single first upper molar of *Ptilodus* grinding against the large, blade-like p4, was thus performed by both, the last premolar and the M1 of *H. pyrenaica*, as a composite functional structure (compare Fig. 4.2 and 4.3). Thus, the short and symmetrical M1 in *Hainina* is a functional equivalent of the posterior half of the large, asymmetrical M1 in *Ptilodus.*

According to these conclusions, the penultimate premolar of *H. pyrenaica*, and probably *Kogaionon* as well, functioned as the anterior part of the P4 in Ptilodontoidea, based on the position and inclination of the wear facet in this element. It supports the hypothesis of the two last premolars in these genera being the P4 and the P5.

Therefore, according to the four criteria (morphology, topology, size and function), the following dental homologies for the upper premolars of *Hainina* and *Kogaionon* are proposed:

Type *a* and *b* of *Hainina* correspond to the 1st locus of *Kogaionon* representing P1 or P2.

Type *c* of *Hainina* corresponds to the 2nd locus of *Kogaionon* representing P3.

Type *d* of *Hainina* corresponds to the 3rd locus of *Kogaionon* representing P4.

Type *e* of *Hainina* corresponds to the 4th locus of *Kogaionon* representing P5.

Relationships with other multituberculates.—The relationships of *Hainina* with other multituberculates are controversial. *Hainina* shows a peculiar set of dental characters that differentiate it from any other multituberculate, and it presents a unique combination of primitive and derived features:

1) The M1 of *Hainina* presents a small number of cusps (a maximum of seven in the longest row) which is a primitive feature. However, this element has three complete cusp rows, which is a very derived feature. Moreover, the lingual row is the longest one, which is a uniquely derived feature.

2) The two last upper premolars are of similar size, which is a very primitive feature, elsewhere known in Early Cretaceous multituberculates. However, they present two cusp rows, which is a derived condition.

3) The last upper premolar has a buccal cusp row decreasing in size backwards and a lingual one extending only along the posterior two thirds of the tooth. Both are unique features.

4) The p4 is a relatively large, blade-like tooth, which is a derived feature. However it is almost twice as long as the P4, which is a primitive characteristic.

5) The lower molars present few cusps per row, which is a primitive feature.

Hainina has been previously assigned to the family Cimolomyidae (Vianey-Liaud, 1986) on the basis of the three complete cusp rows in M1. Afterwards it has been related to the Cimolodonta, without giving any lower rank assignation (Simmons, 1993; McKenna and Bell, 1998) and to the Ptilodontoidea, mainly on the basis of its relatively large p4 (Rougier et al., 1997). The family Kogaionidae, defined on the basis of *Kogaionon ungureanui* Rãdulescu and Samson, 1996 sheds new light on the evolutionary relationships of *Hainina.*

The addition of a lingual cusp row in M1 is a derived feature of advanced multituberculates and thus it is usually the shortest row. In *Hainina* the opposite occurs, the lingual cusp row is even longer than the labial one. This unique feature shows similarities only with representatives of the families Cimolomyidae and Kogaionidae. Both families have a symmetrical M1, with lingual and labial cusp rows having a similar number of cusps. However, the family Cimolomyidae differs from *Hainina* in its much larger M1 and the P4 : M1 ratio close to 0.5 instead of 1 (Fig. 7). Moreover, the p4 of *Hainina* is a relatively large, blade-like tooth, while in Cimolomyidae it is relatively small (Archibald, 1982). Therefore, a relationship between *Hainina* and the Cimolomyidae can be excluded on the basis of the differences in the dental pattern.

Kogaionon Rãdulescu and Samson, 1996, the type genus of the family Kogaionidae, shares with *Hainina* the long lingual cusp row of M1. Moreover this element has a similar cusp formula in both genera, with 4 cusps in the central cusp row and 3–7 in the lateral rows. Furthermore, the last upper premolar of *Kogaionon* shows close similarities to the upper tooth of *Hainina* here described as a P5. Both show a general pattern with two main cusp rows. The buccal row decreases in height from front to rear and the lingual one is placed at the back of the crown. In *Kogaionon* and *H. vianeyae* the P5 cusp formula is 4: 2. The only difference between these genera is the more lophodont pattern of P5 in *Hainina.* The lophodonty precludes observation of the P5 cusp formula in *H. pyrenaica.*

The strong dental similarities between *Hainina* and *Kogaionon* and the presence of a unique P5 allow us to suggest a close relationship between them, and therefore to propose the assignment of *Hainina* to the family Kogaionidae. The peculiar four upper premolars of the family Kogaionidae would correspond to P2, P3, P4 and P5 as discussed above (Fig. 5). This dental formula distinguishes the Kogaionidae from Late Jurassic-Early Cretaceous primitive multituberculates and from other Late Cretaceous–early Tertiary advanced multituberculates.

Hainina shows a unique combination of a large, blade-like p4 and a short P4 that differentiates it from all derived multituberculates (Fig. 7). This feature is only known in two Early Cretaceous genera from Mongolia, the Bolodontidae *Eobaatar* and the peculiar *Arginbaatar*, both with five upper premolars (Kielan-Jaworowska et al., 1987; Simmons, 1993). This latter genus shows a specialised p4. The blade-like p4 was independently acquired by Late Cretaceous advanced Ptilodontoidea. Probably such a feature was independently acquired by the family Kogaionidae as well, since no indication for a common origin of *Arginbaatar,* Kogaionidae and Ptilodontoidea can be found.

Therefore, the family Kogaionidae cannot be related to any of the described Late Cretaceous and Paleocene multituberculates included in the Cimolodonta (McKenna and Bell, 1998). Its closer relatives must be found among the Early Cretaceous Plagiaulacidae (sensu McKenna and Bell, 1998). Kogaionidae differs from most of these Plagiaulacidae in having an internal cusp row increasing in height backwards in the P5 (Kielan-Jaworowska et al., 1987; Kielan-Jaworowska and Ensom, 1992). However, it is similar to some genera arranged in that group, such as *Kuehneodon* and *Lavocatia,* because they present the same peculiar P5 pattern with an external cusp row decreasing in height backwards (Hahn, 1969, 1977; Canudo and Cuenca 1996). In addition, *Kuehneodon* has a dental formula similar to Kogaionidae, since it lost the P1 (Hahn, 1993), as we infer for Kogaionidae. Accordingly, the peculiar dental morphology of the Kogaionidae seems to be evolved from some Early Cretaceous primitive multituberculates included in the paraphyletic family Plagiaulacidae (McKenna and Bell, 1998), recorded in Europe.

CONCLUSIONS

The phylogenetic affinities of the new species *Hainina pyrenaica* from the Early Danian of the Tremp basin (Spain) lead us to assign the genus *Hainina* to the family Kogaionidae. Furthermore, we propose for this family a dental formula with four upper premolars P1–2, P3, P4 and P5, on the basis of dental morphology, dental relations and functional analogy. Therefore the reduction of the upper tooth row from five to four premolars occurred in the proximal premolar in Europe, instead of in the distal one as was the case in America and Asia (Fig. 5).

The premolar size ratio, the unique morphology of the last upper premolar, unknown in any other multituberculate, and the symmetrical shape of M1 indicate that the family Kogaionidae evolved independently from other upper Cretaceous and Paleocene multituberculates. Only some European Early Cretaceous Plagiaulacidae can be related to Kogaionidae because of their last upper premolar with a similar arrangement of cusps. Therefore, the family Kogaionidae represents a group of multituberculates that survived the K/T mass extinction event and reached its maximum diversity in Western Europe during the Paleocene. Thus, the earliest Tertiary mammal recorded in Europe, *Hainina pyrenaica,* represents a relict of the Late Cretaceous mammalian fauna from this continent.

ACKNOWLEDGMENTS

We acknowledge the field assistance of L. Ardévol (Geoprep, Tremp), M.E. Arribas, A. de la Peña, R. Soler Gijón and P. Sevilla (UCM, Madrid), J. Civis and J.A. González-Delgado (Univ.Salamanca), A. Lacasa (I.E.I., Lleida) and B. Marandat, B. Sigé and M.Vianey-Liaud (U.S.T.L., Montpellier). Antonio de la Peña identified the bony fish remains and J. J. Moratalla (Iberdrola-UAM), the dinosaur footprints. We thank Z. Kielan-Jaworowska for her critical reading and improvement of earlier versions of the manuscript, although we do not necessarily agree in our conclusions. We also thank the constructive comments of the reviewers M. Vianey-Liaud and G. W. Rougier, and T. M. Lehman for technical assistance. Funds were provided by the DGICYT, Ministerio de Educación y Cultura, (project PB95–0398).

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