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(Island of Evia, Greece)**

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and its relationships**

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I. SUMMARY

A new ochotonid lagomorph, named *Albertona balkanica*, from the Early Miocene lignites of Aliveri (Greece) is described. It is compared with related European and Asiatic lagomorphs, and a phylogeny of the Old World ochotonids is proposed. *Albertona* shows the closest phylogenetic relationships with *Alloptox* Dawson from the Middle Miocene of Asia, which may be its descendant. Both have closer affinities with European ochotonids such as *Marcuinomys* and *Lagopsis* than with Asiatic genera. *Albertona* seems to be associated with a humid biotope. Its mode of life may be compared to that of the recent riparian leporids.

II. INTRODUCTION

The Lower Miocene lignites of Aliveri on the island of Evia (Greece) contain an important fossil assemblage of micromammals (see De Bruijn and Van Der Meulen, 1979; De Bruijn, Van Der Meulen and Katsikatsos, 1980; Van Der Meulen and De Bruijn, 1982), carnivores (Schmidt-Kittler, 1983) and pollen (Benda and De Bruijn, 1982). Among the micromammals there is a lagomorph which is represented by a great number of isolated teeth, a lower jaw and several postcranial remains. The examination of this material has revealed that we are dealing with a new genus and species of Ochotonidae, which we propose to call *Albertona balkanica*. It shows some similarity with *Alloptox* Dawson, 1961, *Marcuinomys* Croizet, 1939, *Lagopsis* Schlosser, 1884 and *Kenyalagomys* Mc Innes, 1953, in the morphology of the upper molars and the third upper premolar. The other cheek-teeth of *Albertona* are, however, different.

Albertona will be compared with Late Oligocene and Early-Middle Miocene European, Asiatic and African ochotonid lagomorphs. A search for its affinities will be of particular interest because of its unique features and the biogeographic location of the site where it was found.

The European Oligo-Miocene ochotonids have been studied by Tobien (1963, 1975), Lopez-Martinez (1974, 1977, 1978, 1984), Ringeade (1979), Bucher (1982) and Agadjanian and Erbaeva (1983); various reconstructions of their phylogenetic relationships have been made. Asiatic Oligo-Miocene ochotonids have been described by Dawson (1961), De Muizon (1977), Unay and Sen (1976), Li (1978), Li and Qiu (1980), Qiu, Li and Wang (1981) and Erbaeva (1981); African Miocene ochotonids have been described by Stromer (1926), McInnes (1953) and Janvier and De Muizon (1976), but phylogenetic models were not proposed. Recently, McKenna (1982) has published a lagomorph phylogeny, including some European and Asiatic, but no African ochotonids. Therefore a phylogenetic analysis of the Old World ochotonids will be necessary to interpret the relationships of *Albertona*.

III. ACKNOWLEDGEMENTS

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E. Garcia-Moreno processed the data on a VM 370 IBM computer at the Centro de Cálculo, Universidad Complutense de Madrid. Photographs were made by E. Martin. The manuscript was typed by M. de Andrés, I. Corchón, R. Palomo and Mrs. A. Pouw-van den Dolder. The figures were drawn by the author.

IV. METHODS

The dental terminology of the upper teeth of Lagomorpha has been under discussion since the last century (see Major, 1899; Ehik, 1926; Burke, 1936; Hürzeler, 1936; Wood, 1949; Bohlin, 1942; Russell, 1958; Van Valen, 1964; Tobien, 1974b; McKenna, 1982; Lopez-Martinez, 1985). The tribosphenic model cannot easily be applied because no primitive lagomorph with a clear intermediate dental pattern has yet been recorded. Descriptive terminologies have been used (Tobien, 1974a, 1975; Lopez-Martinez, 1974; Lopez and Thaler, 1975) to avoid confusion. Recently Lopez-Martinez (1985) proposed an interpretation of the dental pattern of the lagomorphs, based on the wear facets. The cusp homologies have been deduced from the wear facet homologies. This model agrees with the interpretations of Wood (1949, 1957) and Bohlin (1940),

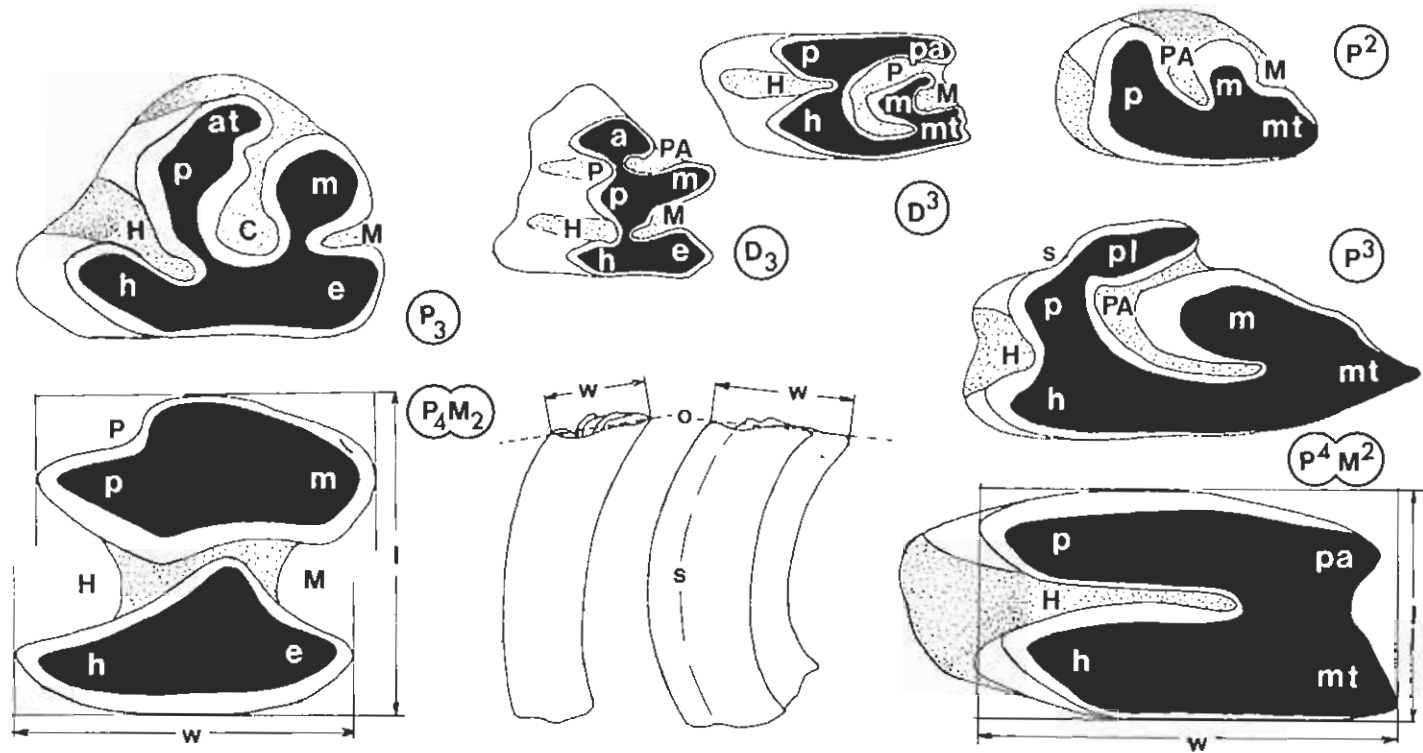


Fig. 1. Dental terminology and the method of measuring the cheek-teeth in Lagomorphs, according to Lopez-Martinez (1985). *Anticlinal*s: *a* - anteroconid; *at* - anterostylid; *e* - entoconid; *h* - hypocone (-id); *m* - metacone (-id); *mt* - metastyle; *p* - protocone (-id); *pa* - paracone; *pl* - protoloph. *Synclinal*s: *C* - centroflexid; *H* - hipoflexus (-id); *M* - metaflexus (-id); *P* - protoflexid; *PA* - paraflexus (-id); *s* - stria. *o* - occlusal surface. *l* - length. *w* - width. Black - ivory. White - enamel. Dots - cement.

but contradicts the other authors mentioned. The nomenclature for the anticlines (cusp-lophs) and synclines (flexa-fossets) and the scheme for taking measurements are given in Fig. 1. The nomenclature used for the molars has also been applied to the premolars (premolar analogy).

Contrary to other mammals, the size of lagomorphs cannot be estimated by the mean size (length or width) of their teeth, because the teeth size in lagomorphs is a function of individual age. If one assumes that fossil lagomorph assemblages generally contain a majority of adult specimens, the modal lengths of the bones and the teeth provide a better estimate of the size of lagomorphs than does the mean length (Lopez-Martinez, 1974).

In order to evaluate the evolutionary polarity of the dental characters, Eocene-Oligocene lagomorphs are here considered as the outgroup of the Oligo-Miocene Old World ochotonids. Furthermore, the polarity of morphotypes is evaluated on the basis of comparative, ontogenetic, functional, biogeographic and paleontologic criteria (Hecht et al., 1977).

V. SYSTEMATICS

Order: Lagomorpha Brandt, 1855

Family: Ochotonidae Thomas, 1897

Genus: *Albertona* n. gen.

Table 1. Dental measurements of *Albertona balkanica* in mm.

	N	Length		Width	
		Range	Mode	Range	Mode
P ²	24	0.56 - 0.96	0.70	1.00 - 1.36	1.16
P ³	60	1.06 - 1.49	1.39	1.88 - 2.84	2.34
P ⁴	24	1.10 - 1.50	1.36	1.80 - 3.00	2.50
M ¹	63	1.18 - 1.52	1.36	2.20 - 2.48	2.40
M ²	33	1.06 - 1.40	1.32	1.80 - 2.22	2.15
P ₃	45	0.96 - 1.44	1.33	0.98 - 1.84	1.63
P ₄ -M ₂	56	1.28 - 1.80	1.65	1.16 - 1.97	1.83
D ₃	10	1.22 - 1.62	1.35	0.98 - 1.34	1.01
D ₄	7	1.22 - 1.38	1.30	0.96 - 1.36	1.17
D ³ -D ⁴	4	0.97 - 1.03	1.01	1.42 - 2.08	1.70
I ^{sup}	4	1.48 - 1.56	1.50	1.36 - 1.40	1.37
I _{inf}	5	1.40 - 1.50	1.43	1.48 - 1.52	1.49

Derivatio nominis: After Dr. Albert van der Meulen, Instituut voor Aardwetenschappen, Utrecht, The Netherlands.

Type species: *Albertona balkanica* n. sp.

Diagnosis: Small Ochotonidae with dental formula 2, 0, 3, 2, / 1, 0, 2, 3, rootless teeth and molariform P^4 ; P^2 with two flexa; the posterior and lingual faces meet at right angles; P^3 without mesoflexus and with an antero-lingual constriction in the protoloph (stria); P_3 without anteroconid, with a small lobe (anterostylid) in some specimens, fused to the protoconid; centroflexid and mesoflexid present, but no protoflexid. Lower molariform teeth with a protoflexid. D_3 with small anteroconid. A very thick cement layer on all the premolars.

Differential diagnosis : *Albertona* differs from other Neogene and younger Ochotonidae by being less hypsodont and by the absence of an anteroconid in P_3 . It differs from *Titanomys* and *Marcuinomys* in having rootless teeth, in lacking labial flexa in $P^4 - M^2$, in the presence of a centroflexid in P_3 , and in having a wide talonid in $P_4 - M_2$ with a wear facet. *Kenyalagomys* differs from *Albertona* in having a relatively smaller P^2 with one flexus only, in the absence of a mesoflexid in adult P_3 , and in its very shallow centroflexid. *Alloptox* differs from *Albertona* in having a large anteroconid and generally lacking a mesoflexid in the P_3 , and in having a hypoflexus in P^2 . *Lagopsis* differs in having a large anteroconid and lacking a centroflexid in the P_3 .

Species: *Albertona balkanica* n. sp.

Derivatio nominis: After the Balkan region

Type locality: Aliveri (Island of Evia, Greece)

Type level: Early Aragonian

Holotype: Left lower jaw with P_{3-4} and M_2 , no. 1 (Plate 1, Fig. 1a, 1b).

Diagnosis: The same as for the genus

Material and measurements: 325 isolated cheek-teeth and 59 fragments of incisors. Measurements in Table 1.

VI. COMPARATIVE DESCRIPTION

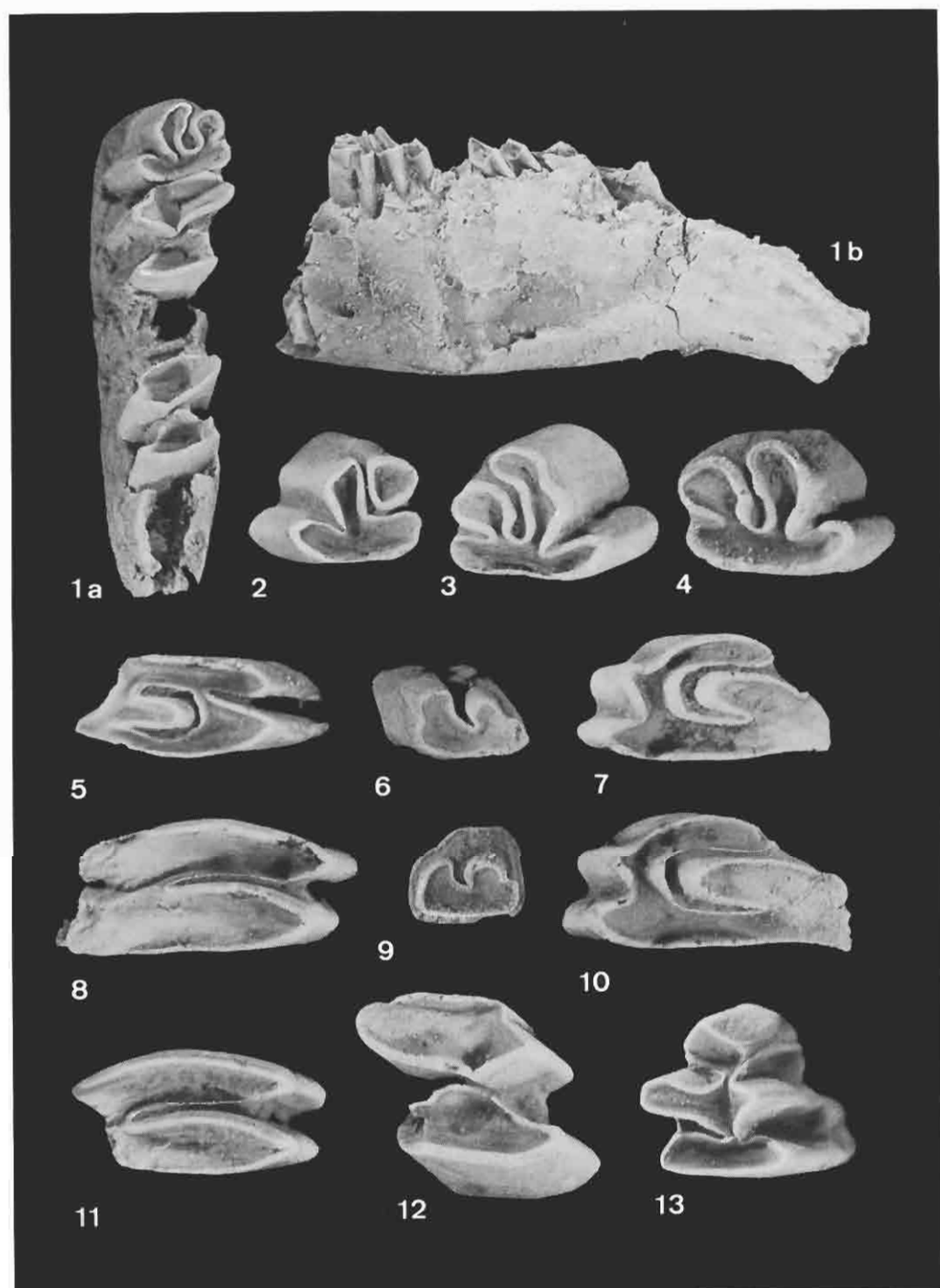
Lower jaw

The only known specimen is the holotype (Plate 1, Fig. 1a, 1b). The lower incisor begins lingually of the talonid of M_1 .

Two indistinct mental foramina are present on the lateral face of the mandible. The anterior one is under the P_3 and surrounded by a pitted area. The posterior one is situated below the trigonid of M_2 . These positions seem to be apomorphic since these foramina are situated more anteriorly in older Ochotonidae. The lack of the tubercle in the anterior part of the masseteric fossa in *Albertona* is also an apomorphic feature (pl. 1, fig. 1b).

Dentition

All the permanent teeth of *Albertona* lack roots and were therefore ever-



growing. The dental formula is 2, 0, 3, 2, / 1, 0, 2, 3, as in the majority of the Ochotonidae.

Incisors. – The incisors of *Albertona* are similar to those of other ochotonids; the lower one has a flat anterior face, and the first upper one is divided by an anterior longitudinal furrow. The enamel is thin and there is no cement. Medial wear facets on the anterior tips of the incisors prove that some movement occurred between them.

As far as can be seen from the height and curvature of the upper teeth, the degree of hypsodonty of the cheek teeth of the Aliveri lagomorph seems less than in *Alloptox* and *Lagopsis*, and about the same as in *Prolagus schnaitheimensis* (see Tobien, 1975, figs. 80–83). The length of the circle radius of the curve does not provide a good estimate of hypsodonty because it is size-dependent. The degree of torsion of the labial root ridges is a much better indicator (pl. 2, fig. 9).

P². – The P² is strongly convex on the anterior side. It has three cusps decreasing in size labially, the protocone being the most prominent one. One aberrant P² has an isolated accessory anterolabial cusp. The paraflexus is the most important of the two valleys. It is directed towards the posterolabial corner of the tooth. A shallow mesoflexus separating the metacone from the metastyle is always present. The lingual and posterior walls meet at right angles at the protocone. A very thick cement layer covers the metacone entirely.

The P² of *Albertona* differs from that of *Prolagus* and *Lagopsis* in having a relatively small mesoflexus and mesastyle; moreover the posterior and lingual walls meet at right angles instead of at an acute angle (pl. 1, figs. 6, 9; pl. 2, fig. 1).

P³. – The shaft of this tooth is slightly curved, with a lingual convexity. The occlusal outline is triangular in specimens with a small protoloph, and trapezium-like in specimens with a well-developed protoloph, extending to the

Plate 1. *Albertona balkanica* n. gen. n. sp. Lower Miocene of Aliveri (Greece)

1 – Holotype - left mandible with P₃, P₄, M₂ and alveolus of M₁ and M₃

a – occlusal view, b – lateral view no. 1

2 – left P₃ occlusal no. 38

3 – right P₃ occlusal no. 27

4 – right P₃ occlusal no. 29

5 – right D³ occlusal no. 344

6 – left P² occlusal no. 54

7 – left P³ occlusal no. 90

8 – right P⁴ occlusal no. 155

9 – left P² occlusal no. 52

10 – left P³ occlusal no. 82

11 – right M² occlusal no. 92

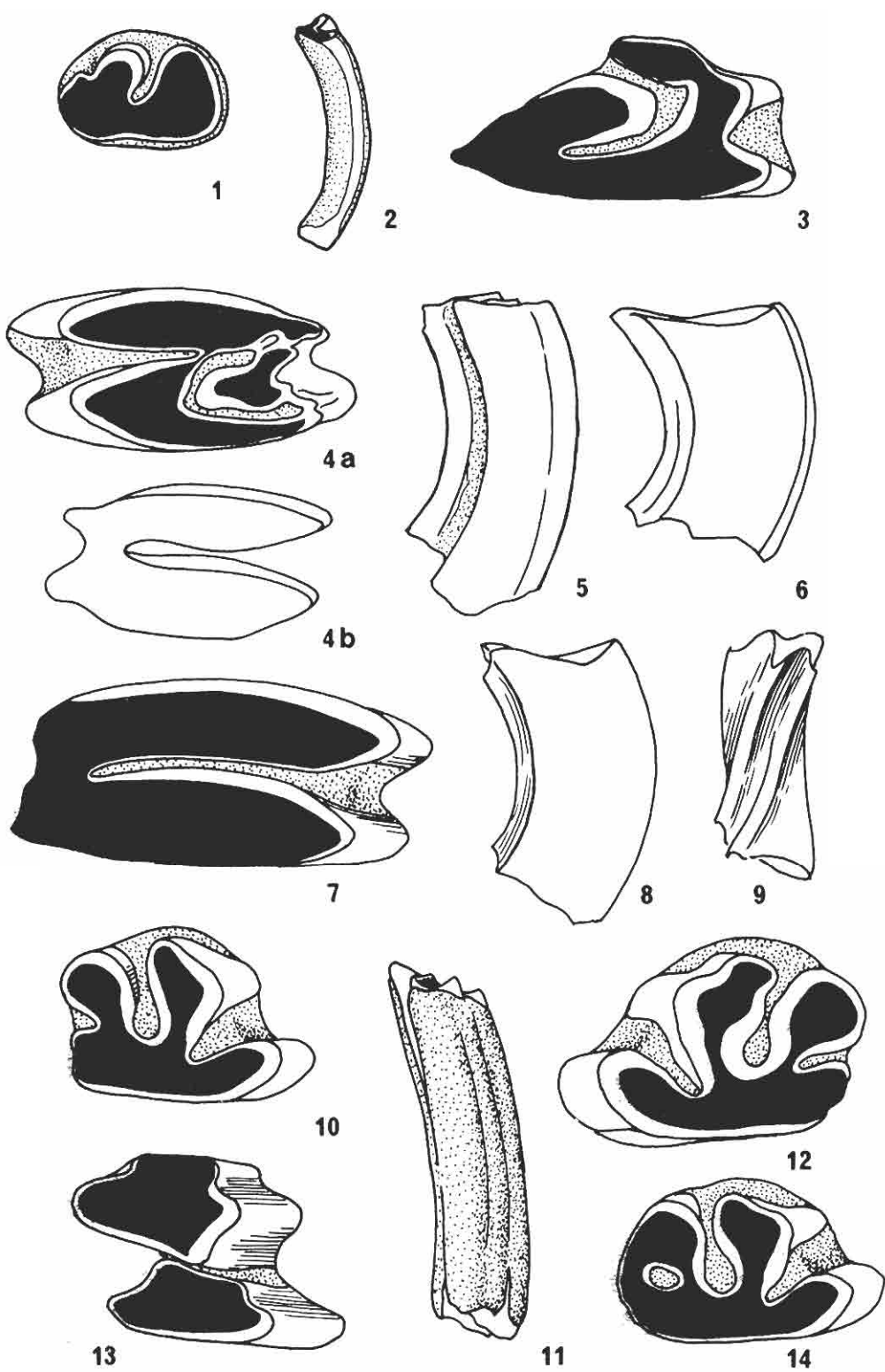
12 – right P₄ occlusal no. 282

13 – right D₃ occlusal no. 346

Fig. 1 × 8.5

rest × 14

Collection of the Rijksuniversiteit, Utrecht.



end of the paraflexus. The latter shows a deep lingual convexity, characteristic of the P^3 of Ochotonidae. A shallow hypoflexus separates the unequal protocone and hypocone. The protoloph is compressed by an anterolabial stria, which in one specimen splits the protoloph completely. The labial end of the protoloph is slender and may occasionally show a small interruption of the enamel (the *hiatus*, see pl. 2, fig. 3). A thick layer of cement fills the hypostria and overlies both protocone and hypocone (pl. 1, figs. 7, 10).

The P^3 of *Albertona* differs from that of *Lagopsis* in the absence of the mesoflexus. This can be considered to be an apomorphic feature. The P^3 looks very much like the P^3 of *Alloptox*, *Bellatona*, *Ochotona* and *Kenyalagomys*, but there are differences. These four genera lack the constriction (stria) on the protoloph and *Alloptox* has a rare shallow mesoflexus. All these genera show an apomorphic development of the protoloph.

P^4 . - The P^4 of *Albertona* is molariform because of the loss of the anterolabial flexa and fossets and the presence of a deep hypoflexus. This syncline reaches half-way along the crown width, and shows a thickened posterior enamel band. The younger individuals have a deeper hypoflexus than the older ones, but it is never as deep as in *Alloptox*, *Bellatona* and the later representatives of *Lagopsis*. The youngest individual has a U-shaped paraforeset in the labial half of the crown, which disappears with wear (pl. 2, fig. 4). The degree of molarisation of the P^4 of *Albertona* is similar to that of *Kenyalagomys russingae* (pl. 1, fig. 8).

M^1 - M^2 . - These teeth have lost the flexa and fossets except for the hypoflexus, which penetrates transversally, nearly reaching the labial wall of the crown. Protocone and hypocone are similarly sharp and prominent. The thickened enamel band on the posterior border of the hypoflexus indicates the presence of a second wear facet, typical of modern ochotonids (pl. 1, fig. 11; pl. 2, fig. 7).

Plate 2. *Albertona balkanica* n. gen. n. sp. Lower Miocene. Aliveri (Greece)

- 1 - right P^2 occlusal no. 67
 - 2 - right P^2 lingual no. 59
 - 3 - right P^3 occlusal no. 138
 - 4a - left P^4 occlusal, young - 4b - root face of the same, no. 148
 - 5 - left P^3 anterior no. 90
 - 6 - right P^4 posterior no. 145
 - 7 - right M^1 occlusal no. 171
 - 8 - right M^1 posterior no. 223
 - 9 - right P^4 labial no. 145
 - 10 - right P_3 occlusal no. 5
 - 11 - left P_3 anterior no. 2
 - 12 - left P_3 occlusal no. 42
 - 13 - right D_4 occlusal no. 257
 - 14 - right P_3 occlusal no. 19
- occlusal view $\times 21.5$
lateral $\times 8.5$

Collection of the Rijksuniversiteit, Utrecht

Table 2. Size distribution in Oligo/Miocene Ochotonids. Number of specimens is placed in the modal size class. (★) Measurements after McInnes, 1953; Dawson, 1961; Unay & Sen, 1976; Li, 1978; Li & Qiu, 1980 and Erbaeva, 1981.

Taxa	P ₃ length	P ⁴ or M ¹ length	Mandibular ramus length	Mandibular ramus height
★ <i>Kenyalagomys rusingae</i>	18	36	25	11.5
★ <i>Bellatona forsythmajori</i>	4	6	—	—
★ <i>Sinolagomys pachygnathus</i>	1	2	—	—
<i>Bohlinotona pusilla</i>	1	2	13	6.3
★ <i>Alloptox minor</i>	1	—	—	—
★ <i>Alloptox anatoliensis</i>	5	6	—	—
★ <i>Alloptox gobiensis</i>	73	29	23	10
<i>Albertona balkanica</i>	45	87	ca. 16	6.8
<i>Lagopsis peñai</i>	83	36	18	7.5
<i>Marcuinomys roquesi</i>	7	10	18	7
<i>Prolagus oeningensis</i>	81	42	18	7
<i>Prolagus vasconiensis</i>	20	15	18	7
	0.8 1.2 1.6 2.0 2.4 0.8	1.2 1.6 2.0 2.4	mm.	

P₃. - The shaft of the third lower premolar is gently curved with a lingual convexity. A very thick layer of cement covers the anterior, labial and lingual faces of the shaft (Pl. 2, fig. 11).

The occlusal surface of this tooth shows a morphology that is unique among the Ochotonidae. The trigonid is divided by a longitudinal centrofloxid and separated from the talonid by two flexids, the labial hypoflexid and the lingual mesoflexid. The protoconid may be short and triangular (pl. 1, fig. 2), or lengthened by a rounded, anterior lobe named anterostylid (pl. 1, fig. 1). This anterostylid is well-developed only in two cases (4%, pl. 1, fig. 3) and never covers the metaconid. It can be interpreted as an incipient anteroconid.

The protoconid, retracted relative to the hypoconid, shows a shallow concavity which separates it from the anterostylid. The rounded, well-developed metaconid is as large as the protoconid, a derived feature. It may be isolated (4% of the cases), but normally it is fused to the talonid by one or two connections (pl. 2, fig. 14). It never joins the protoconid. The talonid has a long and narrow hypoconid, curving antero-labially and making a wide angle with the entoconid. There is no hypoconulid.

The centrofloxid is an antero-posteriorly directed valley. Its anterior part may be deflected lingually by the anterostylid. The posterior end of the centrofloxid may be inflated or slender, but is always smooth, without a "crochet". There is no protoflexid, but only a shallow concavity in the anterior wall of the protoconid. The hypoflexid is the main labial valley; it is short and triangular in

shape, and runs straight towards the posterior wall of the talonid. The lingual mesoflexid is always present, even as a closed fosset (one specimen, pl. 2, fig. 14); it joins the centroflexid when the metaconid is isolated (pl. 1, fig. 2).

The morphology of the P_3 of *Albertona* is unlike that of any other ochotonid. A centroflexid is sometimes found in the P_3 of *Prolagus* and *Alloptox*, but these have an anteroconid and protoflexid also, whereas in *Albertona* these features are always absent. The presence of a mesoflexid in the P_3 is a distinctive feature of European ochotonids (*Titanomys*, *Marcuinomys*, *Lagopsis*, *Piezodus*, *Prolagus*, *Eurolagus*).

$P_4 - M_1 - M_2$. - The lower molariform teeth are morphologically very similar. They differ in the convexity of the shaft only. The crown consists of two rhomboid lobes, the trigonid and talonid, joined by cement. The trigonid has a sharp protoconid and a rounded metaconid. The anterior face of the protoconid shows a conspicuous groove: the protoflexid. This feature has not been observed in any other lagomorph. The posterior face of the trigonid, the main wear facet, is inclined anteriorly. The talonid is as wide as the trigonid. Its posterior face has a thickened enamel band and the corresponding wear facet. The amount of cement decreases from P_4 through M_2 , as is the case in the upper tooth row (pl. 1, figs. 1a, 12).

A small, rounded alveolus behind the M_2 in the holotype shows that an M_3 was present, but no specimens of this tooth have been found. The presence of an unilobed M_3 corresponds in lagomorphs to the absence of an M^3 in the upper dentition.

Diciduous teeth - The D^2 is not represented in the Aliveri material. The D^3 and D^4 are very similar, having a U-shaped paraflexus. A mesoflexus can be seen in one unworn specimen. The protocone is smaller than the hypocone and there is no enamel on the labial face of the teeth (pl. 1, fig. 5).

D_3 has three lobes connected by two central enamel bands. The enamel is interrupted at the labial corner of the small, rhomb-shaped, anteroconid. The morphology is similar to the D_3 of *Ochotona* as described by Gureev and Erbaeva (1975), and more simple than the D_3 of *Prolagus* and *Lagopsis*. The latter always have an anteroflexid as well as one or two labial cusps added to the anteroconid. In *Albertona* there is no centroflexid or hypoconulid. The two-lobed D_4 is similar to the adult P_4 , but it has a paraflexid, and roots (pl. 1, fig. 13; pl. 2, fig. 13).

Size

The jaw size and the lengths of P^4 or M^1 and of P_3 have been chosen to estimate the size of *Albertona*. In table 2 the size distributions of several ochotonid genera are summarized.

Bohlinotona pusilla (Teilhard, 1926) is the smallest lagomorph known, but its teeth are relatively large. *Alloptox* and *Kenyalagomys* are clearly larger. The size of *Albertona* is very close to that of the other European ochotonids, but its P_3 is relatively small because of the lack of the anteroconid. The P_3 length is a poor size indicator because of its morphological variability.

VII. PHYLOGENETIC RELATIONSHIPS

The characteristics of *Albertona balkanica* can be grouped into three categories: A) plesiomorphies (primitive characters), B) apomorphies (derived characters shared with other taxa) and C) autapomorphies (unique derived characters). In the search for the phylogenetic relationships of *Albertona*, the second group of characters should be emphasized. Table 3 summarizes the selected features.

The evolutionary polarity of most of the characters has already been indicated in the comparative description. Nevertheless, two characters deserve discussion since several interpretations are possible.

In young individuals of some taxa, such as *Piezodus* and *Marcuinomys*, a third flexus (metaflexus) may be present labially of the metastyle in the P². This feature was considered to be primitive on the basis of the ontogeny (Lopez-Martinez, 1978). *Albertona* and many other ochotonids (*Prolagus*, *Lagopsis*, *Amphilagus*) show two flexa in the P². The same is true for the primitive Lagomorpha (*Mytonolagus*, *Megalagus*). Consequently it is probable that the

Table 3. Features of *Albertona balkanica* distributed according to the inferred polarity.

n°	A. Plesiomorphies	B. Apomorphies	C. Autapomorphies
1	Only two flexa (paraflexus and mesoflexus) in P ²	Mental foramina in backward position	very thick cement layer on the premolars
2	Anteroconid in P ₃ missing	Masseter tubercle missing	Antero-lingual stria in P ³
3	Protoconulid in P ₃ missing	Two main wear facets on molariform teeth	Anterostylid in P ₃ variable
4	Mesoflexid in P ₃ always present	Teeth ever growing	Protoconid in P ₃ retracted
5		Dental formula 2032/1023	Protoflexid in P ₄ -M ₁ -M ₂ present
6		Mesoflexus in P ³ missing	
7		Proximal hyperloph in P ³ developed	
8		Molarized P ⁴	
9		Centroflexid in P ₃	
10		Metaconid in P ₃ developed	
11		Hypoconulid in P ₃ -M ₁ missing	

morphotype with two flexa is the more primitive one. *Paludotona* and *Ochotona* show only one flexus (the paraflexus) a configuration which is considered derived. The morphology of the P^2 of *Alloptox* is derived, but differs in having also an hypoflexus.

The presence of a mesoflexid in the P_3 has usually been interpreted as a primitive feature (Dice, 1929; Dawson, 1958; Lopez-Martinez, 1978). The mesoflexid of the rooted P_3 disappears with wear and does not occur in the rootless P_3 such as are found in the majority of lagomorphs. The presence of a permanent mesoflexid in the rootless P_3 , a characteristic of the European ochotonids, is unusual, and might be interpreted as a derived feature in this family. However, a small mesoflexid sometimes occurs in Asiatic genera such as *Ochotona* (Erbaeva, 1970, fig. 7; Agadjanian and Erbaeva, 1983, fig. 20) and *Alloptox* (AMNH 26758, pers. obs.), as well as in the rootless primitive Leporinae (*Alilepus*). Consequently, the presence of a mesoflexid can be interpreted as a plesiomorphy for Lagomorpha.

Fifteen mandibular and dental features of the 12 ochotonid genera included in the phylogenetic analysis are shown in table 4. The coded characters are ex-

Table 4. Distribution of character states according to table 3. Polarity is indicated at the bottom. Dashes mean information is not available.

characters taxa	A1	A2	A3	A4	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11
<u>Albertona</u>	0	0	0	0	1	1	1	1	1	1	1	1	2	1	1
<u>Piezodus</u>	1	1	0	0	0	0	0	0	2	0	1	0	0	1	0
<u>Prolagus</u>	0	1	1	0	1	1	1	1	2	0	1	0	2	1	1
<u>Amphilagus</u>	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
<u>Titanomys</u>	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0
<u>Marcuinomys</u>	1	0	0	0	1	1	0	0	1	1	1	0	0	1	0
<u>Lagopsis</u>	0	1	0	0	1	1	1	1	1	1	1	1	0	1	1
<u>Bohlinotona</u>	-	0	0	1	0	0	0	1	0	1	0	0	0	0	1
<u>Sinolagomys</u>	-	0	0	2	1	-	0	1	1	1	0	1	1	0	1
<u>Alloptox</u>	2	1	0	1	1	1	1	1	1	1	1	1	2	1	1
<u>Bellatona</u>	3	0	0	1	-	1	1	1	1	1	1	1	0	0	1
<u>Kenyalagomys</u>	3	0	0	2	1	1	1	1	1	1	1	1	1	0	1
Polarity	$\begin{smallmatrix} 1 \\ 0 \end{smallmatrix} \begin{smallmatrix} 2 \\ 3 \end{smallmatrix}$	0→1		$\begin{smallmatrix} 0 \\ 1 \end{smallmatrix} \begin{smallmatrix} 1 \\ 2 \end{smallmatrix}$	0→1								$\begin{smallmatrix} 0 \\ 1 \end{smallmatrix} \begin{smallmatrix} 1 \\ 2 \end{smallmatrix}$	0→1	

plained in table 3. For each character, "O" means plesiomorphy, and "1", "2" and "3" denote different apomorphies.

More than half of the characters combine in every possible arrangement, indicating a high number of convergences (Lequesne, 1969; Lopez-Martinez, 1978). A calculation minimizing the convergences leads to more than one cladogram, never containing less than 22 convergences.

The chronological succession of apomorphies is different in Asia and Europe. In Asia the ever-growing teeth (B4), the loss of the hypoconulid (B10) and molarized P⁴ have existed since the Oligocene; in Europe these features do not appear until the late Early Miocene. The Asiatic genera have relatively smaller premolars than the European ones, and they are more precocious in their evolution towards complete hypsodonty. The character B3 (two main wear facets on molariform teeth, which results in a wide talonid and a deep hypoflexus) must have been achieved in the three continents at about the same time. On the other hand, the anteroconid on the P₃ (character A2) does not appear in Asia before the Middle Miocene, whereas in Europe this feature is present from the Oligocene onwards. Also, the dental formula is modified earlier in Europe than in Asia. For these reasons, a separate cladogram should be made for each region. Both are shown in fig. 2.

Alloptox, in spite of being an Asiatic genus, appears to be closely related to the European cluster. A close group of the three genera, *Alloptox*, *Albertona* and *Lagopsis*, based on its synapomorphies B3, B4, B8 and B11, seems to be related to *Marcuinomys* by the synapomorphies B6, B7 and B10. An *Alloptox-Albertona* sister-group may be proposed on the basis of its synapomorphy B9 (centroflexid). Although the anteroconid (A2) relates *Alloptox* to *Lagopsis*, the

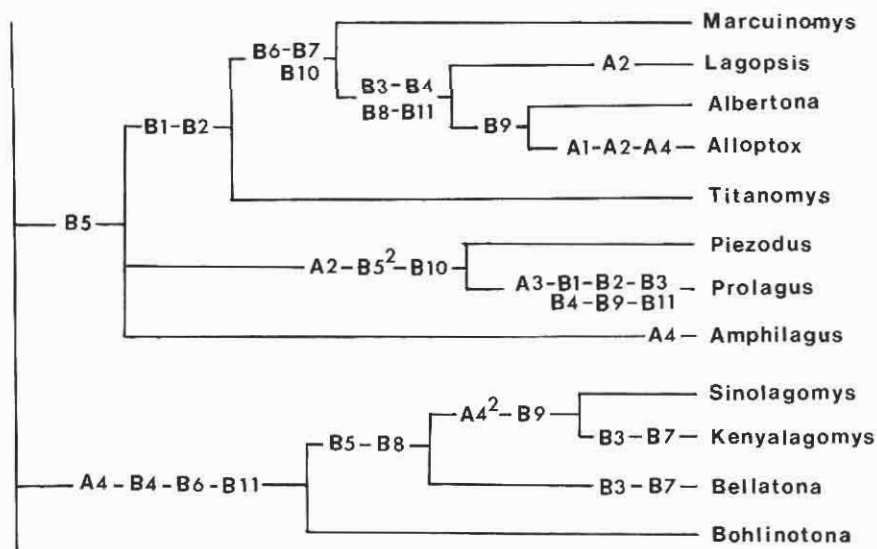


Fig. 2. Cladograms of the Oligo-Miocene Old World ochotonids. Only derived characters are shown. See code of characters in tables 3 and 4.

first alternative has been preferred because the *Albertona* anterostylid is a plausible precursor of the *Alloptox* anteroconid. A sister-group relationship is consistent with an ancestor-descendant hypothesis (Szalay, 1977; Lopez-Martinez, 1978), therefore *Albertona* can be assumed to be a possible ancestor of *Alloptox*. The biostratigraphic distribution should serve to test this hypothesis.

VIII. RESULTS

In fig. 3, the results of the phylogenetic analysis are placed in the chronological and geographical framework. During Oligo-Miocene times, the most diversified ochotonid fauna is found in Europe. The Asiatic genus *Alloptox* has closer affinities with the European ochotonids than with the other

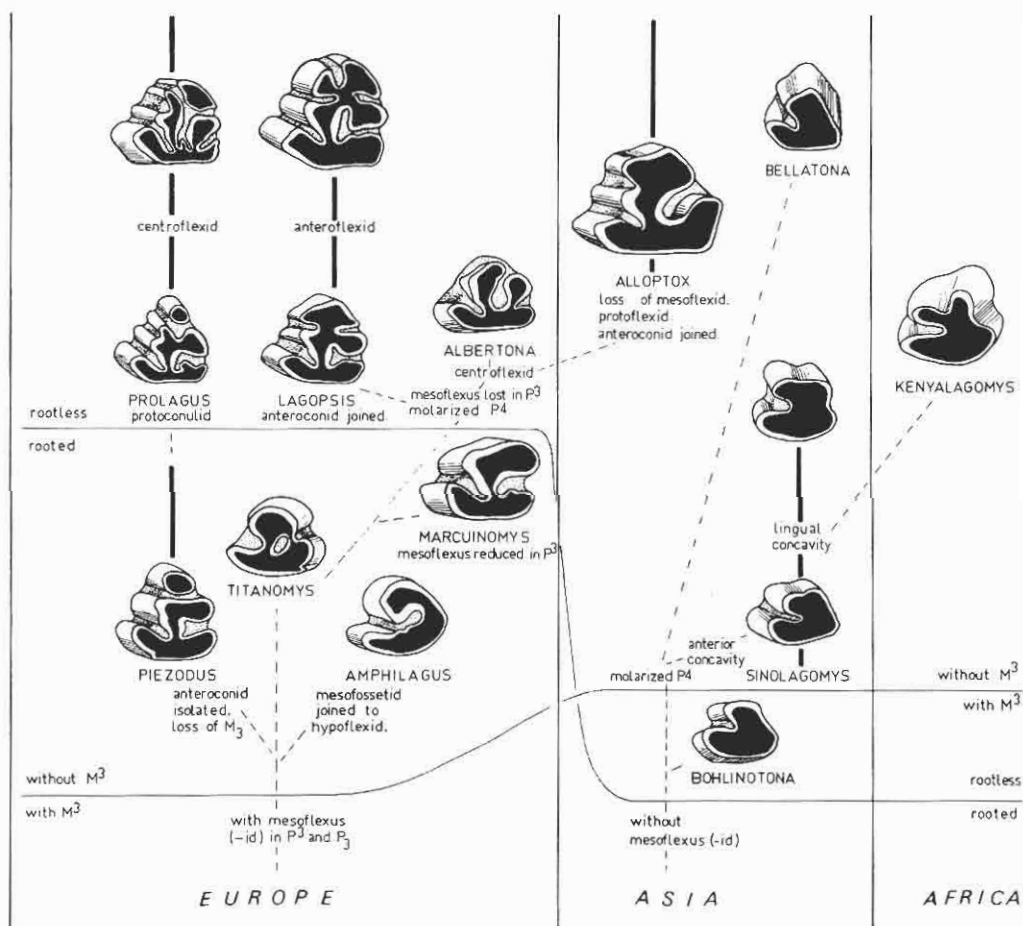


Fig. 3. Phylogenetic, chronologic and geographic relationships of the Old World ochotonid genera through the Upper Oligocene and Middle Miocene. Known occurrence, in thick lines. Postulated phylogenetic relationships, according to the cladograms, in dashed lines. Inferred derived characters unite the proposed sister-groups.

Asiatic genera, and therefore may be considered the vicar of *Lagopsis*. The African *Kenyalagomys*, on the other hand, seems a vicar of the Asiatic *Sinolagomys*.

According to the phylogenetic hypothesis, *Albertona* might be dated between the first appearance of *Lagopsis* (with which it shares a common ancestor) and the first record of *Alloptox* (that would be the descendant of *Albertona*).

Lagopsis lived from the Late Aagenian to the Late Aragonian (MN 2b to MN 8 units). *Alloptox* has been recorded from the Shanwangian to the Tungurian; these faunas have been correlated with the MN 5 to MN 8 units (Li *et al.*, 1981; Li *et al.*, 1984). To be consistent with the phylogenetic model, the time span of *Albertona* record would be from MN 2b to MN 4b.

The age of the Aliveri fauna, assigned by De Bruijn and Van der Meulen (1979) to Early Miocene (MN 3 unit, Early Aragonian), has been recently revised by Fejfar and Schmidt-Kittler (1984) and moved to MN 4b unit (Middle Aragonian). The lack of a faunal sequence from the Lower Miocene of the Balkans means that correlations cannot be accurate, but either age would agree with the phylogenetic hypothesis.

Albertona has an intermediate geographical distribution between the vicarious genera *Lagopsis* and *Alloptox*. *Lagopsis* is a western form which never reached farther East than the Italian Peninsula (its insular descendant *Paludotona* Dawson, 1959, is found in the Late Miocene from Tuscany). *Alloptox* is an eastern genus that extends from Anatolia towards China. The fossil record of the Lower Miocene in Eastern Europe and Western Asia is still too incomplete to allow biogeographical statements to be made.

The paleoenvironment inferred is not the same for the three genera. *Lagopsis* and *Alloptox* are found associated with arid-type faunas such as the *Hispanotherium* assemblages, and are thought to have lived in open-land savanna. They probably inhabited open country as the majority of lagomorph taxa. *Albertona* however, occurs associated with a very special assemblage of mammals and pollen, indicating a forest environment (Benda and De Bruijn, 1982). No extant ochotonid has this peculiar way of life. Its habitat possibly resembled that of some recent forest leporids, such as the Brazilian *Sylvilagus*, which is more or less riparian amphibious in its habits and which eats roots and bark, as do castorids. The very thick cement layer on the premolars of *Albertona* is probably a functional feature, since the presence of rich dental cement is generally associated with a diet consisting of tough plants.

BIBLIOGRAPHY

- Agadjanian, A.K. and M.A. Erbaeva - Late Cenozoic Rodents and Lagomorphs of the USSR. XI Congr. INQUA - Nauka, Moscou, 1-190 (1983).
- Benda, L. and H. de Bruijn - Biostratigraphic correlations in the Eastern Mediterranean Neogene. Calibration of sporomorph - and rodent - associations in the Aliveri - Kymi basin/Island of Euboea (Greece). Newsl. Stratigr., 11 (3), 128-135 (1982).
- Bohlin, B. - The fossil Mammals from the Tertiary Deposits of Taben-Buluk, Western Kansu. Part. 1: Insectivora and Lagomorpha. Paleont. Sinica N.S.C., 8 (123), 1-113 (1942).
- Bruijn, H. de and J. van der Meulen - A review of the Neogene rodent succession in Greece. Ann. Géol. Pays Hellen. h.s., 1, 207-217 (1979).

- Bruijn, H. de, A. van der Meulen and G. Katsikatos – The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part. 1: The Sciuridae. Proc. Kon. Ned. Akad. Wetensch. (B) **83** (3), 241–262 (1980).
- Bucher, H. – Etude des genres *Marcuinomys* Lavocat et *Lagopsis* Schlosser (Lagomorpha, Mammalia) du Miocène inférieur et moyen de France. Implications biostratigraphiques et phylogénétiques. Bull. Mus. nat. Hist. nat. Paris 4^e sér. **4** (1–2), 43–47 (1982).
- Burke, J.J. – *Ardynomys* and *Desmatolagus* in the North American Oligocene. Ann. Car. Mus., **25**, 135–154 (1936).
- Dawson, M.R. – Late Tertiary Leporidae of North America. Univ. Kansas Paleont. Contrib., **22** (6), 1–79 (1958).
- Dawson, M.R. – *Paludotona etruria*, a new ochotonid from the Pontian of Tuscany. Verh. Naturf. Ges. Basel., **70** (2), 157–166 (1959).
- Dawson, M.R. – On two Ochotonids (Mammalia, Lagomorpha) from the later Tertiary of Inner Mongolia. Amer. Mus. Novitates **2061**, 1–15 (1961).
- Dice, L.R. – The Phylogeny of the Leporidae, with description of a new genus. Journ. Mammal., **10** (4), 340–344 (1929).
- Ehik, J. – The right interpretation of the cheek-teeth tubercles of *Titanomys*. Annal. Mus. Nat. Hungarici, **23**, 178–186 (1926).
- Erbaeva, M.A. – Historiya Antropogennoi fauni zaiceobrazidh (Lagomorpha) i grizunov (Rodentia) selenginskogo srednogoriya. izdatelstvo Nauka, Moskva. 132 p. (1970).
- Erbaeva, M.A. – Miotsenovye pizhuji Mongolii. Iskopaemye pozvonochnye Mongolii (Trudi, vip. 15). Nauka, Moskva (1981).
- Fejfar, O. and N. Schmidt-Kittler – *Sivanasua* und *Eubiocetus* n. gen. – zwei pflanzenfressende Schleichkatzenvorläufer (Viverridae, Carnivora, Mammalia) im europäischen Untermiozän. Mainzer geowiss. Mitt., **13**, 49–72 (1984).
- Hecht, M.K. and J.L. Edwards – The methodology of Phylogenetic inference above the species level. In: Hecht, M.K.; Goody, P.C. and B.M. Hecht (Eds.) Major Patterns in Vertebrate Evolution. NATO Adv. Sc. Inst. Plenum Press (A) **14**, 3–52 (1977).
- Hürzeler, J. – Osteologie und Odontologie der Caenotheriden. Abh. Schweiz. Paleont. Gesell., **58/59**, 1–111 (1936).
- Janvier, P. and C. de Muizon – Les lagomorphes du Miocene de Beni Mellal, Maroc. Geol. Medit., **3** (2), 87–90 (1976).
- Lequesne, W.J. – A method of selection of characters in numerical taxonomy. Syst. Zool. **18** (2), 201–205 (1969).
- Li, C.K. – Two New Lagomorphs from the Miocene of Lantian (Shensi). Prof. Pap. of Stratigr. and Paleont., **7**, 143–148 (1978).
- Li, C.K. and Z.D. Qiu – Early Miocene mammalian fossils of Xining basin, Qinghai. Vertebrata Palasiatica, **18** (3), 198–215 (1980).
- Li, C.K., Z.D. Qiu and Sh. Wang – Discussion on Miocene stratigraphy and mammals from Xining basin, Qinghai. Vertebrata Palasiatica, **19** (4), 313–320 (1981).
- Li, C.K., W.Y. Wu and Z.D. Qiu – Chinese Neogene subdivision and correlation. Vertebrata Palasiatica, **22** (3), 163–178 (1984).
- Lopez-Martinez, N. – Evolution de la lignée *Piezodus-Prolagus* (Lagomorpha, Ochotonidae) dans le Cénozoïque d'Europe sud-occidentale. Thèse Univ. Sci. Tech. Languedoc. Acad. Montpellier, 165 p. (1974).
- Lopez-Martinez, N. – Nuevos Lagomorfos (Mammalia) del Neógeno y Cuaternario Español. Trabajos Neógeno-Cuaternario, **8**, 7–45 (1977).
- Lopez-Martinez, N. – Cladistique et paléontologie. Application à la phylogénie des Ochotonidés européens (Lagomorpha, Mammalia). Bull. Soc. Géol. France, **20** (6), 821–830 (1978).
- Lopez-Martinez, N. – Los Lagomorfos (Mammalia) de la sucesión del Mioceno Inferior de Calamocha (prov. de Teruel). Col-pa, **39**, 27–44 (1984).
- Lopez-Martinez, N. – Reconstruction of the ancestral cranioskeletal features in the Order Lagomorpha. In: Luckett, P. and Hartenberger, J.L. (Eds.). – Evolutionary relationships among rodents. A multidisciplinary analysis. NATO Adv. Sc. Inst. Plenum Press (A) **92**, 151–189 (1985).

- Lopez-Martinez, N. and L. Thaler – Biogéographie, évolution et compléments à la systématique du groupe d'Ochotonidés *Piezodus-Prolagus* (Mammalia, Lagomorpha). Bull. Soc. Géol. France, 7 (7) 5, 850–866 (1975).
- McInnes, D.G. – The Miocene and Pleistocene Lagomorpha of East Africa. Fossil Mammals of Africa. Brit. Mus. Nat. Hist., 6, 1–30 (1953).
- McKenna, M.C. – Lagomorph interrelationships. Géobios, Mém. spec., 6, 213–223 (1982).
- Major, C.I.F. – On fossil and recent Lagomorpha. Trans. Linn. Soc. London, 2^a ser. Zool. 7 (9), 433–520 (1899).
- Meulen, A. v.d. and H. de Bruijn – The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). part. 2. The Gliridae. Proc. Koninkl. Ned. Akad. v. Wetensch., 85 (4), 485–524 (1982).
- Muizon, C. de – Révision des Lagomorphes des couches à *Baluchitherium* (Oligocene supérieur) de San-tao-lo (Ordos, Chine). Bull. Mus. Nat. Hist. Nat., 488, 265–292 (1977).
- Qiu, Z.D., C.K. Li and S.J. Wang – Miocene mammalian fossils from Xining basin, Qinghai. Vertebrata Palasiatica, 19 (2), 157–170 (1982).
- Ringeade, M. – Découverte de nouveaux Lagomorphes dans le Miocène inférieur d'Aquitaine et implications biostratigraphiques. Bull. Inst. Géol. Bassin d'Aquitaine, Bordeaux, 26, 111–157 (1979).
- Russell, L.S. – The dentition of rabbits and the origin of the Lagomorpha. Nat. Mus. of Canada, 166, 41–45 (1958).
- Schmidt-Kittler, N. – The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece) III. On a new species of *Sivanasua* Pilgrim 1931 (Feliformia, Carnivora) and the phylogenetic position of this genus. Proc. Koninkl. Ned. Akad. Wetensch. 86 (3), 301–318 (1983).
- Stromer, E. – Reste Land- und Süßwasser-Bewohnender Wirbeltiere aus den diamantfeldern Deutsch-Südwestafrikas. Kaiser, E. – Die diamanten Wüste Südwest Afrikas, II, 2, 107–153 (1926).
- Szalay, F.S. – Ancestors, Descendants, Sister Groups and testing of Phylogenetic Hypotheses. Syst. Zool. 26 (1), 12–18 (1977).
- Theilard de Chardin, P. – Mammifères tertiaires de Chine et de Mongolie. Ann. Paléont., 15, 1–51 (1926).
- Tobien, H. – Zur Gebiss-Entwicklung Tertiärer Lagomorphen (Mamm.) Europas. Notizbl. Hess. L.-Amt. Bodenforsch., 91, 16–35 (1963).
- Tobien, H. – Zur Gebißstruktur, Systematik und Evolution der Genera *Amphilagus* and *Titanomys* (Lagomorpha, Mammalia) aus einigen Vorkommen jüngerer Tertiär Mittel- und Westeuropas. Mainzer geowiss. Mitt. 3, 202–214 (1974a).
- Tobien, H. – The structure of the Lagomorphous molar and the origin of the Lagomorpha. 1th Int. Theriolog. Congress. Moscow., 2, 238 (1974b).
- Tobien, H. – Zur Gebißstruktur, Systematik und Evolution der Genera *Piezodus*, *Prolagus* und *Ptychoprolagus* (Lagomorpha, Mammalia) aus einigen Vorkommen in jüngerer Tertiär Mittel- und Westeuropas. Notizbl. Hess. L.-Amt. Bodenforsch. 103, 103–186 (1975).
- Unay, E. and S. Sen – Une nouvelle espèce d'*Alloptox* (Lagomorpha, Mammalia) dans le Tortonien de l'Anatolie. Bull. Min. Res. Inst. Turkey, 85, 145–149 (1976).
- Van Valen L. – A possible origin for rabbits. Evolution, 18 (3), 484–491 (1964).
- Wood, A.E. – The Mammalian fauna of the White River Oligocene. Part. III: Lagomorpha. Trans. Amer. Phil. Soc. Philadelphia. N.S., 28 (3), 271–362 (1940).
- Wood, A.E. – What, if anything is a rabbit? Evolution 6 (4), 417–425 (1957).