

Cricetidae (Rodentia) from the type-Aragonian; the genera *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia* nov. gen., and *Renzimys*

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This paper deals with four cricetid genera that were formerly assembled under the genus names *Democricetodon* and *Fahlbuschia*. Four new species are described, *Fahlbuschia decipiens*, *Fahlbuschia corcolesi*, *Renzimys lacombai*, and *Pseudofahlbuschia jordensi* gen. nov., sp. nov. The material studied is placed in its stratigraphic context, and appears to be most valuable for a stratigraphic subdivision of the Aragonian. The evolution and paleoecology are discussed.

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Introduction

From 1976 through 1981 the authors have been carrying out yearly field campaigns of two months in the type area of the Aragonian in the southern part of the province of Zaragoza (Spain), and the adjoining northern part of the province of Teruel. During these campaigns we were assisted by many Spanish and Dutch friends, to all of whom we wish to express our sincere thanks. Several of these campaigns were made financially possible by the Netherlands Organization for pure-scientific research (Z.W.O.). We are very grateful for this support. Without this personal and financial aid it would never have been possible to do the kind of work we did.

The subject of the present paper will be the genera *Democricetodon*, *Fahlbuschia*, *Renzimys*, and the new genus *Pseudofahlbuschia*. The reason for this combination of genera is, that it is often quite difficult to distinguish them at first sight. After selecting from the total cricetid material the genera *Megacricetodon*, *Cricetodon* and *Eumyarion*, which are easily recognizable, the remaining cricetid material was taken as the subject for this study. The other genera will be treated in separate publications. For more details on the field work see the synopsis published in this volume.

METHODS AND MATERIAL

The statistical work, histograms and scatter diagrams were calculated and drawn by means of computer programs developed by the first author, and run on the mainframe computer of the Leiden University.

Measuring equipment and technique are as described by Freudenthal, 1966. It seems appropriate to stress here once more, that in this measuring scheme the length taken need not be the greatest length of the molar, nor need the width be perpendicular to the length. This may sound unnatural, but it gives representative, reliable, and reproducible results. This scheme seems not to have been generally adopted, which means that one must be careful in comparing measurements in other publications with ours, the more so since in many publications the way of measuring is not even mentioned.

The terminology used in the description of the molars is the one proposed by Mein & Freudenthal, 1971b. However, during the study of the material it was realized that this

terminology, though fully adequate for all the lower molars and for M^1 and M^2 , failed as an instrument for the description of the M^3 . For this reason in the next chapter a fundamental approach of the morphology of the cricetid third upper molar is presented, trying to homologate M^3 with M^2 . This led to the introduction of several new descriptive terms, aimed at the facilitation of the description.

Apart from the material collected during our field campaigns (which is kept in the collections of the Rijksmuseum van Geologie en Mineralogie, Leiden), part of the material studied by Freudenthal (1963, 1967) and Daams & Freudenthal (1974) was reexamined. This material, characterized by a registration number containing two or three leading letters is kept in the Instituut voor Aardwetenschappen (IVA), University of Utrecht. Furthermore the material from Córcoles, belonging to the Universidad Complutense, Madrid, has been studied.

In the descriptions of the material, more precisely of the M_1 , two ratios are used, that seem to give good diagnostic results. The first one is the length/width ratio of M_1 , which helps to separate our *Democricetodon* material from *Fahlbuschia*, and which also serves to distinguish the various species of *Fahlbuschia*.

The second one is the prelobe ratio of M_1 : it represents the percentage of the total length of the molar occupied by the anteroconid. The length of the anteroconid (prelobe) is measured from the foremost point of the molar to the junction point of metalophulid and anterolophulid, and this length is divided by the total molar length.

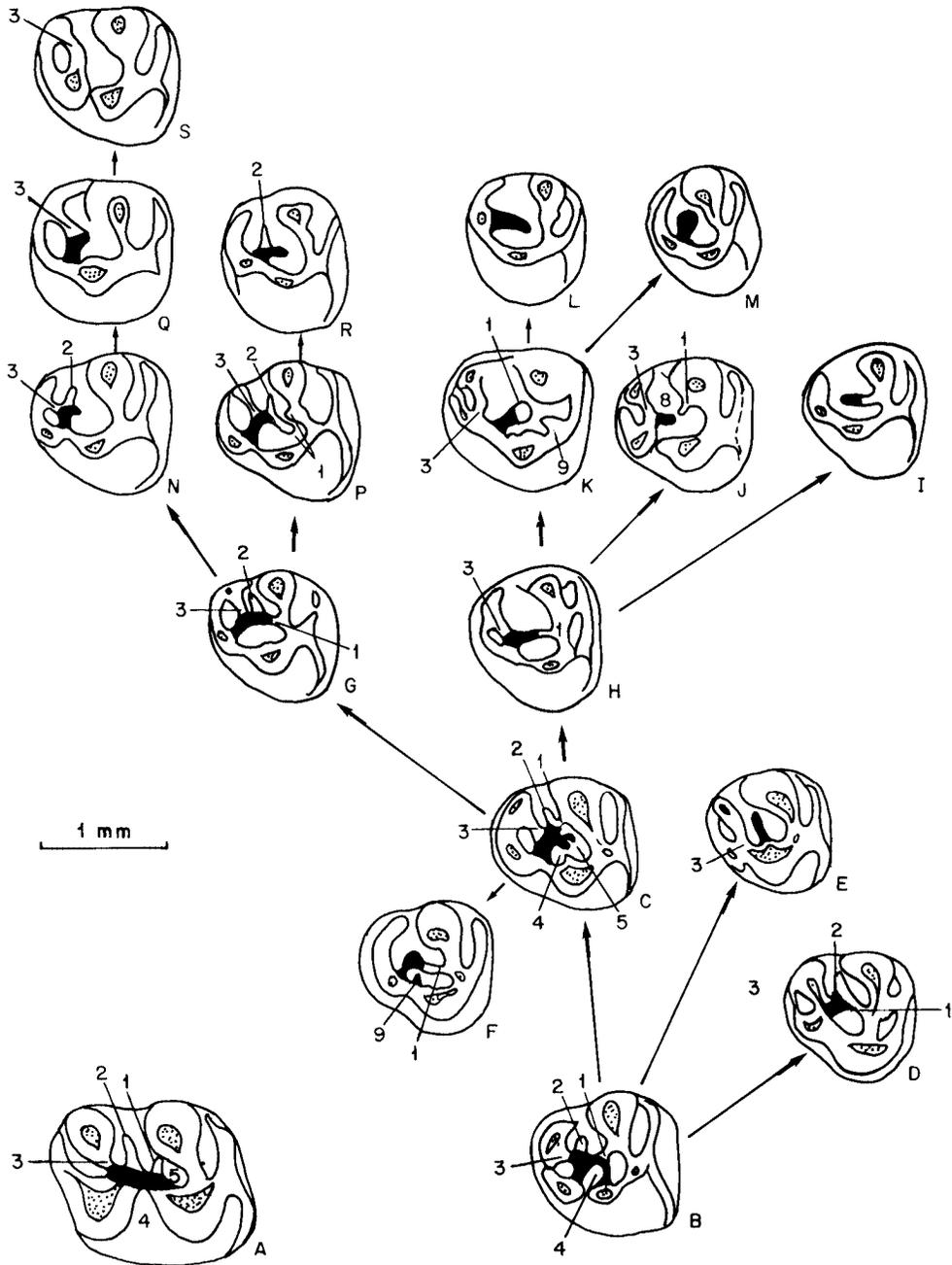
The length/width ratio is generally calculated as mean length/mean width for an entire population. The prelobe ratio is the mean of ratios of up to five randomly chosen specimens. The prelobe ratio appears to be a good tool, that should be calculated over the complete populations. This has not yet been done, since no reliable measuring method has been found so far.

The cricetid M^3

In all Miocene European cricetids M^3 is a moderately to highly reduced element. This often makes its interpretation and description difficult. In this paragraph it will be tried to give a solution for this problem.

In Fig. 1 an M^2 dext. and a number of M^3 dext. (or sin., drawn reversed) of *Fahlbuschia koenigswaldi* from Vargas 1A are shown. The drawings are not exact replicas of the original teeth, but have been stylized, in order to make comparisons easier. Especially the wear facets of the cusps have been enlarged.

Fig. 1A is an M^2 , Fig. 1B is one of the most complex M^3 found. Homologies in this case are comparatively easy: 1 is the posterior protolophule, 2 is the mesoloph, and 3 is the anterior metalophule. The dentine areas are diagonally hatched. The dark shaded area is the entoloph. 4 is the sinus. From this interpretation it appears, that the entoloph which is more or less straight in M^2 , is curved into an almost complete circle in M^3 . Furthermore the protocone has rotated clockwise (in an M^3 dext., anti-clockwise in an M^3 sin., always in occlusal view), so that the posterior corner of the protocone is now the middle of the labial wall. The originally most labial point of the protocone is now in contact with the anterior end of the hypocone. The sinus is closed by what we propose to call the **neo-entoloph**.



In Fig. 1C the originally anterior part of the entoloph is interrupted between '4' and '5'; 4 is again the sinus, and 5 is the valley that lies between the two branches of the protolophule and the protocone.

In Fig. 1D the anterior branch of the protolophule has disappeared, the valley no. 5 has shifted antero-lingually, the 'anterior' part of the entoloph and the mesoloph are strongly developed. The sinus (no. 4) is completely closed.

Fig. 1. *Fahlbuschia koenigswaldi* (Freudenthal, 1963) from Vargas 1A. Morphotypes of M³ compared with M².

A: M² dext.; B: based on M³ sin., RGM 301 442; C: based on M³ dext., RGM 302 714; D: based on M³ dext., RGM 302 173; E: based on M³ dext., RGM 301 466; F: based on M³ sin., RGM 302 696; G: based on M³ dext., RGM 301 481; H: based on M³ dext., RGM 302 169; I: based on M³ dext., RGM 302 163; J: based on M³ dext., RGM 301 470; K: based on M³ dext., RGM 301 174; L: based on M³ dext., RGM 301 482; M: based on M³ dext., RGM 302 715; N: based on M³ dext., RGM 301 472; P: based on M³ sin., RGM 302 698; Q: based on M³ sin., RGM 301 444; R: based on M³ dext., RGM 302 716; S: based on M³ dext., RGM 302 162.

The cyphers in the drawings have the following meaning: 1: posterior protolophule; 2: mesoloph; 3: anterior metalophule; 4: sinus; 5: valley between the two branches of the protolophule and the protocone; 6: mesosinus; 7: 'anterior' part of the entoloph; 8: posterior part of the entoloph; 9: a ridge of unknown homology; 10: centrocone.

In Fig. 1E no. 7 is the anterior part of the entoloph, strongly developed and directed labially. The posterior part of the entoloph and the mesoloph have disappeared. The sinus is closed by the neo-entoloph, but lingually open.

In Fig. 1J the 'anterior' part of the entoloph has disappeared. 8 is the remaining posterior part, pointing towards the posterior protolophule (1). There is no mesoloph.

In Fig. 1K the paracone is shifted towards the anterior border of the molar, obliterating the anterosinus. 9 can be interpreted as a remnant of the anterior protolophule.

In Fig. 1L the posterior part of the molar is extremely reduced; 8 is the posterior part of the entoloph.

In Fig. 1I the central longitudinal crest may be composed of the posterior protolophule (1) and the posterior part of the entoloph (8). 3 is the anterior metalophule, which has fused with the posteroloph.

In Fig. 1G the mesoloph is rather well developed (2).

In Fig. 1H the posterior protolophule (1) and the posterior part of the entoloph have fused to form a continuous long ridge.

In Fig. 1F 9 represents a crest that can difficultly be explained. It cannot be homologized with any feature in M².

In Fig. 1M, 1N, 1R, and 1P a feature is seen, that is quite common in the M³ of a wide variety of genera of cricetids: 10 is a small cusp in the centre of the molar, which we propose to call **centrocone**. It is probably homologous with the mesocone of M², that is the place where the mesoloph arises from the entoloph. Once this homology is accepted there is little difficulty in interpreting the morphology of this kind of molars.

Finally Fig. 1S represents another common type of cricetid M³: an either transverse or anteriorly curved ridge, connecting the hypocone with the postero-labial border of the molar, which may receive the name **centroloph**, in order to facilitate descriptions. Fundamentally its labial half is the anterior metalophule, its lingual part is the posterior part of the entoloph. The centrocone, if present, marks the separation between these two original components.

So, three new terms have been introduced for the description of the M³: the neo-entoloph, which is a short-cut between the hypocone and the rotated protocone; the centrocone, which is homologous with the mesocone of M²; and the centroloph, which is interpreted as a combination of the anterior metalophule and the posterior part of the (ancient) entoloph. In order to facilitate descriptions even more it seems appropriate to introduce a fourth term: **axioloph**. The axioloph is an axial connection between paracone

and hypocone, fundamentally composed of the posterior protolophule and the posterior part of the (ancient) entoloph.

The arrows in Fig. 1 indicate possible relationships between the various morphotypes; it must be stressed, however, that other interpretations and relationships are possible as well. E.g. morphotype M may be derived from S, N may be derived from P, etc. Nevertheless it seems probable that the morphotypes in the lower part of the figure are phylogenetically primitive, and those in the upper part more advanced, assuming a general tendency towards a simplification of the molar pattern. The evolutionary features are:

- closing of the neo-entoloph,
- reduction of the external part of the sinus,
- reduction of the ancient entoloph (= axioloph p.p),
- reduction of the mesoloph,
- reduction of the metalophule,
- reduction of the entire posterior part of the molar.

The theory laid out above is strongly supported by the shape of the sinus and the protocone in the M³ of *Cricetodon* (e.g. *Cricetodon meini* Freudenthal, 1963, from Vieux-Collonges). The same shape of the sinus is frequently found in the M² of *Cricetodon* and *Megacricetodon*. It is, however, not found in the M² of *Fahlbuschia* and *Democricetodon*, but morphotype B in Fig. 1 is clear evidence that it occurs in the M³ of *Fahlbuschia*.

So far the neo-entoloph has not been found in the M² of Neogene Cricetidae. However, several Oligocene cricetids show that it may occur in M²: some specimens of *Eucricetodon atavus* (Misonne, 1957) from Hoogbutsel (Belgium) and of *Pseudocricetodon montalbanensis* Thaler, 1969 from Montalbán (Spain) show the ancient entoloph rooted on the centre of the labial wall of the rotated protocone, and the more or less well-developed neo-entoloph running from the posterior corner of the protocone towards the hypocone. We wish to state this fact, without implying any phylogenetic consequences.

It cannot be decided, whether all M³ of *Fahlbuschia* are derived from morphotypes with curved entoloph. Morphotypes like K and M may easily be interpreted as being derived from a normal *Fahlbuschia* M² with transverse sinus and a posterior protolophule running from the paracone to the posterior branch of the protocone.

Fig. 2A and B are based on M³ of *Democricetodon gaillardi* (Schaub, 1925) from Sansan. 2A can easily be interpreted without assuming an ancestral phase with curved sinus. However, a very small funnel is visible at the base of the mesoloph; such a funnel is better developed in the specimen of Fig. 2B; it gives the impression, that the ancient entoloph is curved into a complete circle around this little funnel, and that the direct connection between protocone and hypocone is the neo-entoloph. Contrary to the situation described before in the M³ of *Fahlbuschia*, however, in this case the protocone is not rotated, and the ancient entoloph arises from the posterior corner of the protocone.

Fig. 2C and 2D are based on M³ of *Fahlbuschia koenigswaldi* (Freudenthal, 1963) from Casetón 2B. Fig. 2D may be interpreted without assuming an ancestral phase with curved sinus; Fig. 2C however, gives the impression that the dark shaded area is the lingual part of the ancient entoloph, and that the posterior part of this entoloph is interrupted; this means that two specimens that are morphologically almost identical may have quite a different origin. For the moment the best guess seems to be that the advanced morphotypes of Fig. 1 can be achieved along various ways.

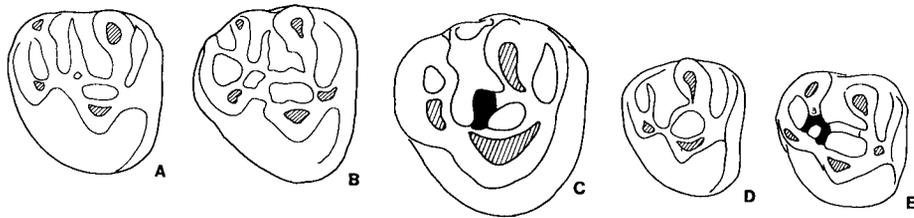


Fig. 2. Various morphotypes of M³. *Democricetodon gaillardii* (Schaub, 1925) from Sansan: A: based on M³ sin., RGM 262 896; B: based on M³ sin., RGM 262 898; *Fahlbuschia koenigswaldi* (Freudenthal, 1963) from Caseton 2B: C: based on M³ dext., RGM 301 839; D: based on M³ dext., RGM 301 850; *Fahlbuschia* or *Democricetodon* from Caseton 1A: E: based on M³ dext., RGM 301 672.

Fig. 2E is an M³ from Casetón 1A. There seems to be hardly any doubt that the dark area is the ancient entoloph, surrounding a funnel that is lingually closed by the neo-entoloph. Apart from the missing mesoloph this specimen shows a remarkable similarity with Fig. 2B, *Democricetodon gaillardii* from Sansan. The typical features of *Fahlbuschia* are less developed in Casetón 1A than they are in other occurrences of *F. koenigswaldi*. At least a part of the material from Casetón 1A is suspected to belong to *Democricetodon*.

So far M³ had been a hardly understood element of the cricetid dentition, and for that reason it has not been used to distinguish taxa. We have now managed to find several discriminating features in M³, that make it possible to distinguish *Fahlbuschia* populations from each other. It is not yet clear whether the morphology of M³ will serve for the distinction of *Fahlbuschia* and *Democricetodon*, partly because we did not have sufficient material of M³ of *Democricetodon*.

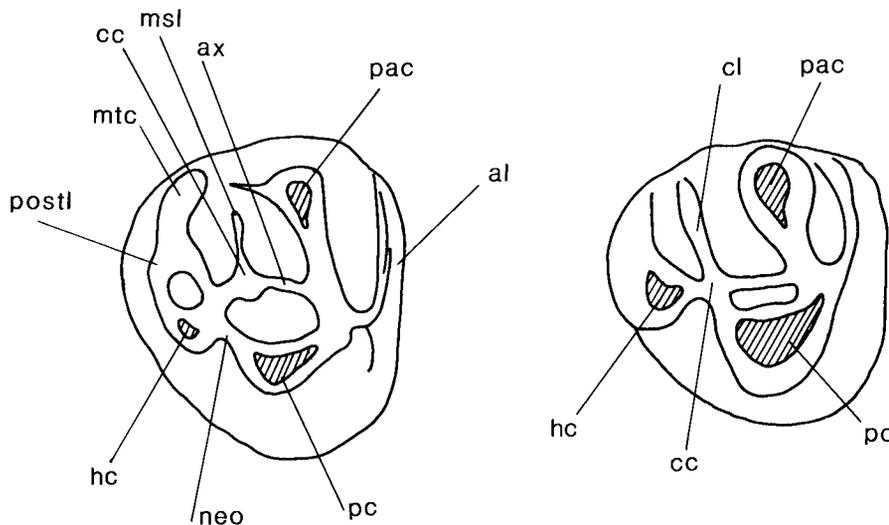


Fig. 3. Terminology of the parts of M³. al = anteroloph; ax = axioloph; cc = centrocone; cl = centroloph; hc = hypocone; msl = mesoloph; mtc = metacone; neo = neo-entoloph; pac = paracone; postl = posteroloph; pc = protocone; s = sinus.

Distinction between *Fahlbuschia* and *Democricetodon*

There is certainly no difficulty in distinguishing *Fahlbuschia larteti* (Schaub, 1925), genotype of the genus *Fahlbuschia*, from *Democricetodon crassus* Freudenthal, 1969, genotype of the genus *Democricetodon*. The size of the molars and the complexity of the dental pattern leave hardly any doubt, that we are dealing with two species belonging to different genera. Mein & Freudenthal (1971a) placed *Democricetodon* in the Cricetinae, and *Fahlbuschia* in the Cricetodontinae, mainly on the basis of the position of the foramen incisivum. The characters of the mandible and the humerus of *Fahlbuschia*, however, are more like those of the Cricetinae. The material described in this paper does not give any further arguments concerning the taxonomic position of the genus *Fahlbuschia*. It can neither be excluded nor proven that *Fahlbuschia* might be a descendant of *Democricetodon* or vice versa. The recognition of two different genera, however, is beyond doubt when one compares the type-species.

The real difficulties in the distinction of *Democricetodon* and *Fahlbuschia* are presented by the oldest representatives of *Fahlbuschia*, *F. koenigswaldi* from Valdemoros 1A and several newly discovered localities like Vargas 1A, Caseton, etc., and *F. decipiens* sp. nov. from Buñol. *F. koenigswaldi* is larger than *D. hispanicus*, and falls within the size limits of *D. affinis*, *D. mutilus*, etc. It is extremely difficult to distinguish a small specimen of *F. koenigswaldi* from a large one of *D. hispanicus*, and if *F. koenigswaldi* and *D. affinis* occur together in the same locality it may be impossible to distinguish them on the basis of their isolated teeth. In the following we will give some arguments why we preferred to keep *F. koenigswaldi* in *Fahlbuschia* and not to place it in *Democricetodon*:

Maxilla — The foramen incisivum ends behind the anterior end of the M^1 (seen only in a few specimens from Valdemoros 1A and Casetón 2B).

M_1 — In many specimens there exists a more or less well-developed crest pointing from the centre of the anterior wall of the metaconid towards the anteroconid. This crest divides the anterosingulid into two parts, or at least reduces the size of this valley considerably. We consider this feature to be different from an anterolophid that descends from the anteroconid, and forms a connection along the border of the molar. The latter feature is common in both *Fahlbuschia* and *Democricetodon*, but the crest protruding forward from the centre of the metaconid is a common feature in *Fahlbuschia*, and rare, if present at all, in *Democricetodon*. It is true that some specimens of *Democricetodon* figured by Fahlbusch (1964) present such a connection, but one must keep in mind, that it was never investigated whether e.g. *D. gracilis* Fahlbusch, 1964 is a *Democricetodon* or a *Fahlbuschia*.

M_3 — In the youngest representatives of *Fahlbuschia* M_3 is very much reduced; in the youngest *Democricetodon* this reduction is never so extreme. In the oldest representatives of both genera, however, M_3 may have the same degree of reduction. In several *Democricetodon* species the mesolophid continues to exist, whereas in *Fahlbuschia* it is never present. But even if the mesolophid in a *Democricetodon* has disappeared, a difference with *Fahlbuschia* appears to be that the sinusid in *Democricetodon* is comparatively short and wide, leaving some space for a short, but often distinct hypolophulid. In *Fahlbuschia* the sinusid is generally narrow, and it carves very far into the molar, reducing entoconid and hypolophulid to almost nothing.

M^1 — In *Democricetodon* the double protolophule is frequently present, in *Fahlbuschia* it is rare or absent. However, precisely the oldest *Democricetodon*, *D. hispanicus*, known from localities like Olmo Redondo 3 and 5, San Roque 1 and 2 and

Villafeliche 2A does not fit well in this definition. In San Roque 1 the anterior proto-lophule (or some kind of spur on the anterolophule) is extremely rare; in Villafeliche 2A it is present in 20 % (3 out of 16) of the specimens. On the other hand the double proto-lophule in M^1 is fairly frequent in some of the youngest populations of *Fahlbuschia* (*F. cf. crusafonti* from Solera).

M^2 — In *Fahlbuschia* the anterior proto-lophule tends to disappear, whereas it seems to be more persistent in *Democricetodon*. This feature is not useful for distinguishing the oldest populations.

M^3 — The development of the axioph and mesoph may present a difference between the two genera. Unfortunately, only limited numbers of M^3 of *D. hispanicus* are available.

The prelobe ratio may present a possibility to distinguish *Democricetodon* and *Fahlbuschia*; it is the length of the prelobe part of the M_1 divided by the total length of M_1 . We have not yet managed to find a reliable method for measuring the prelobe. For the moment we have defined the length of the prelobe as the distance from the foremost point of the tooth to the junction of metalophulid and protoconid, or to the foremost point of the protoconid. The difficulty is that the value may be influenced by the degree of wear of the tooth and by accidental details of the morphology; if, however, a good way is found to define the length of the prelobe, the prelobe ratio may prove to be a useful tool. Even now, despite of the insufficient definition and the small number of specimens measured, it seems to be clear that the prelobe ratio in *Democricetodon* is always over 0.20, whereas in *Fahlbuschia* it is always under 0.20, which means that in *Fahlbuschia* the prelobe is relatively shorter than it is in *Democricetodon*. Values for the prelobe ratio are given in Table 1.

Another method to distinguish *Democricetodon* and *Fahlbuschia* may be found in the length/width ratio of M_1 (mean length/mean width). Values of this ratio for a large number of populations are given in Table 1.

In *Fahlbuschia* there appears to be a relation between the length/width ratio and the absolute size: in the smallest species, *F. decipiens* sp. nov., this ratio is 1.42; in the small species *F. koenigswaldi* this ratio varies between 1.41 and 1.47, in the larger *F. darocensis* it varies between 1.47 and 1.51, and in the very large *F. (cf.) crusafonti* it is between 1.52 and 1.58.

In this respect the value of 1.47 for the small species *F. corcolesi* sp. nov. from Córcoles is high, and the values for *F. freudenthali* (1.42 – 1.43) are relatively low with respect to its absolute size.

In *Democricetodon* the ratio is less related to size: it varies between 1.31 for the small *D. crassus* to 1.50 for the equally small *D. sulcatus*, and the values for the large *D. gaillardi* vary between 1.42 and 1.48. There may be a relation between the ratio and the stratigraphic position of the population: the oldest species *hispanicus* and *franconicus* have values from 1.38 to 1.43, the youngest species, *sulcatus*, has 1.50, but here again, the picture is not very clear since the lowest value (1.31) is found in the material from Sansan which has an intermediate stratigraphic position.

Evidently the inconsistent figures for *Democricetodon* are due to the fact that the known material represents at least two, and probably more than two, evolutionary lineages. The few inconsistent figures for *Fahlbuschia* probably have the same explanation (see the chapter on evolution and biostratigraphy).

One fact, however, is quite clear: *D. hispanicus* can be distinguished from *F. koenigswaldi* by its lower length/width ratio. The lowest value for *koenigswaldi* is 1.41,

the highest value for *hispanicus* is 1.42. *D. hispanicus* ranges from 1.38 to 1.42, and the only *Fahlbuschia* species within this range is *F. decipiens* sp. nov. with 1.415. A problem is encountered in the locality Olmo Redondo 5. In this locality *D. hispanicus* and *F. koenigswaldi* are found together, and for both species the length/width ratio is too high: 1.45 for *hispanicus* and 1.51 for *koenigswaldi*. In both cases the number of specimens is small.

Table 1. Length/width ratios (mean length/mean width), and prelobe ratios (P/L) of M_1 . The number of specimens (N) is given for the calculation of the length/width ratio. The prelobe ratio is based on a small number of specimens (generally not more than 5), because no reliable way of measuring this ratio has been found yet.

Taxon	Locality	N	\bar{L}	\bar{W}	L/W	P/L
<i>Rezimys</i>	Escobosa	21	23.2	15.0	1.547	0.25
	Regajo 2	9	22.24	14.31	1.554	0.26
<i>Pseudofahlbuschia</i>	Villafeliche 4A	37	18.26	11.54	1.582	0.23
	Valdemoros 3D	6	19.67	12.36	1.591	0.21
	Vieux-Collonges?	122	20.05	12.63	1.587	0.23
	Valdemoros 3B	14	19.0	12.2	1.557	0.23
	Casetón 1A	2	20.00	12.30	1.626	0.22
<i>F. cf. crusafonti</i>	Carrilanga	3	23.90	15.57	1.535	0.23
	Nombrevilla	5	22.34	14.74	1.516	0.24
	Solera ¹⁾	8	21.84	14.16	1.542	0.22
	Toril 1	1	22.5	14.7	1.531	0.24
	Las Planas 5H	2	22.45	14.3	1.570	0.20
	Sant Quirze	4	24.8	16.2	1.531	—
	Hostalets	1	24.3	15.4	1.578	—
<i>F. darocensis</i>	Solera ¹⁾	4	20.28	13.95	1.454	0.20
	Toril 1	15	19.71	13.41	1.470	0.19
	Borjas	37	20.41	13.55	1.506	0.20
	Manchones 1	108	20.1	13.6	1.478	0.18
	Valalto 2C	10	20.27	13.71	1.478	0.18
	Las Planas 4A+B	11	20.0	13.6	1.471	0.19
<i>F. freudenthali</i>	Regajo 2	87	19.16	13.48	1.421	0.17
	Valdemoros 3E	26	18.00	12.61	1.427	0.19
<i>F. koenigswaldi</i>	Casetón 2B	41	17.02	11.59	1.469	0.18
	Casetón 1A	52	16.75	11.37	1.473	0.18
	Valdemoros 1A	26	17.12	12.04	1.422	0.19
	Olmo Redondo 9	23	17.23	11.87	1.452	0.18
	Olmo Redondo 8	3	16.57	11.77	1.408	0.17
	Vargas 1A	90	16.65	11.51	1.447	0.16
	Olmo Redondo 5	5	17.20	11.36	1.514	0.17
<i>F. decipiens</i>	Buñol	19	14.98	10.58	1.416	0.21
<i>F. corcolesi</i>	Córcoles	17	15.28	10.45	1.462	0.19
miscellaneous <i>Fahlbuschia</i>						
<i>F. larteti</i>	La Grive M	50	20.90	14.27	1.465	0.18
<i>F. sp.</i>	La Grive L3	6	22.57	14.55	1.551	0.20

<i>D. hispanicus</i>	Olmo Redondo 5	2	13.60	9.40	1.447	0.24
	Villafeliche 2A	13	14.1	10.1	1.396	0.23
	San Roque 2	19	13.67	9.90	1.381	0.19
	San Roque 1	14	14.21	10.15	1.400	0.23
	Olmo Redondo 3	2	12.85	9.50	1.353	0.22
	Olmo Redondo 2	6	14.08	9.94	1.416	0.21
	Olmo Redondo 1	3	13.50	9.63	1.402	0.24
miscellaneous <i>Democricetodon</i>						
<i>D. franconicus</i>	Erkertshofen	200	14.4	10.1	1.426	0.21
<i>D. romieviensis</i>	La Romieu	22	14.6	10.4	1.404	0.19
<i>D. crassus</i>	Sansan	60	13.6	10.4	1.308	0.24
<i>D. gracilis</i>	Sandelzhausen	1	13.1	9.3	1.409	—
<i>D. brevis</i>	La Grive	1	16.0	11.1	1.441	—
<i>D. brevis</i>	Anwil	55	14.85	10.54	1.408	—
<i>D. gaillardi</i>	Sansan	50	17.3	12.1	1.430	0.22
<i>D. gaillardi</i>	Las Planas 5K	1	16.4	11.7	1.402	0.26
<i>D. cf. gaillardi</i>	La Grive L3	5	16.47	11.66	1.412	0.24
<i>D. aff. gaillardi</i>	Borjas	1	17.3	11.5	1.504	0.24
<i>D. sp.</i>	La Grive L7	37	16.62	11.46	1.450	0.24
<i>D. mutilus</i>	Langenmoosen	1	17.0	11.5	1.478	—
<i>D. cf. mutilus</i>	Giggenhausen	2	17.6	12.05	1.461	—
<i>D. affinis</i>	La Grive M	19	17.62	11.91	1.479	0.25
<i>D. cf. affinis</i>	Valdemoros 3B	2	15.85	10.93	1.450	0.24
<i>D. sulcatus</i>	Pedregueras 2C	11	15.2	10.1	1.505	—
Gen. indet.	Villafeliche 4A	1	18.3	10.5	1.743	0.26
Gen. indet.	Manchones 1	1	20.9	15.4	1.357	0.25

1): the separation of two species of *Fahlbuschia* in Solera is arbitrary; however, splitting this material into two groups yields quite different values for the smaller and the larger specimens.

The question-mark after Vieux-Collonges means that the attribution of this material to *Pseudofahlbuschia* is not certain.

Democricetodon Fahlbusch, 1964

The type species of *Democricetodon* is *D. minor* (Lartet, 1851), sensu Fahlbusch, 1964. Freudenthal in Fahlbusch & Freudenthal (1969) did not agree with Fahlbusch's interpretation of the name *Cricetodon minus* Lartet, 1851, and named this species from Sansan *Democricetodon crassus*. According to Opinion 1419 of the International Commission on Zoological Nomenclature (Tubbs, 1986), *D. crassus* is the valid name for the type species of *Democricetodon*.

Democricetodon hispanicus Freudenthal, 1967

Pls 1, 2, 3.

Type-locality — Villafeliche 2A, Zaragoza, Spain.

Holotype — M₁ dext., Museo de Paleontología, Sabadell, figured in Freudenthal, 1963, pl. 1, fig. 16.

Distribution — Dominant in the Aragonian Zone B; also present in Zone C, and in the lower part of Zone D1.

Democricetodon hispanicus was first described by Freudenthal (1963) under the name *Cricetodon* cf. *vindoboniensis*. This description is still valid. In Freudenthal (1967) it was recognized as a new species and placed in the genus *Democricetodon*. In 1974 Daams & Freudenthal described *D.* aff. *hispanicus* from Buñol (Valencia, Spain). Until our recent campaigns these were the only occurrences of *D. hispanicus* known. We found this species in the localities of Olmo Redondo 1, 2, and 3, San Roque 1 and 2, Olmo Redondo 5, Vargas 1A, and Olmo Redondo 9. In the latter three localities it concurs with *F. koenigswaldi*. All these localities are situated in a restricted area with a diameter of less than a kilometre. This is most certainly not a geographic limitation of the species, but it is due to the fact that beds of similar age have not been found in any other place of the area under study. We assume that *D. hispanicus* must have had a wider geographic range, as proven by the occurrence in Buñol (in this paper the larger part of the Buñol material is attributed to *Fahlbuschia decipiens* sp. nov.).

Recently Aguilar (1981) described *D. hispanicus* from Chelas 1 (Portugal). However, this material should be ascribed to *Fahlbuschia koenigswaldi*.

Locality Villafeliche 2A (code VL 2A, Zone B)

Though the original description still holds good, some additional remarks may be made.

In the maxilla the foramen incisivum is short, it ends before the anterior end of M¹. The mandible is inclined, the foramen mentale being hidden in occlusal view.

M₁ — Length/width ratio 1.40, prelobe ratio 0.23. The mesolophid is short (1), of medium length (3), or long (10). The posterosinusid may remain open, but generally it is closed by the posterolophid.

M₂ — The mesolophid is short (4), of medium length (4), or long (2). The posterosinusid is often open.

M₃ — At least one of the specimens is quite long, with a little reduced posterior part.

M¹ — The mesoloph is short (3), of medium length (4), or long (12).

M² — The mesoloph is of medium length (2), or long (11).

M³ — One specimen has axioloph, mesoloph and centroloph, 2 specimens have axioloph and mesoloph, and 1 specimen has centroloph and mesoloph.

Plate 1

All figures approx. 25 ×.

Democricetodon hispanicus Freudenthal, 1967

Olmo Redondo 1

- Fig. 1. M₁ sin., RGM 303 005.
- Fig. 2. M₂ dext., RGM 303 010.
- Fig. 3. M₃ dext., RGM 303 013.
- Fig. 4. M¹ dext., RGM 303 016.
- Fig. 5. M² dext., RGM 303 019.
- Fig. 6. M³ dext., RGM 303 021.

Olmo Redondo 2

- Fig. 7. M₁ sin., RGM 303 028.
- Fig. 8. M₂ dext., RGM 303 032.
- Fig. 9. M¹ dext., RGM 303 040.
- Fig. 10. M² dext., RGM 303 047.
- Fig. 11. M³ dext., RGM 303 052.

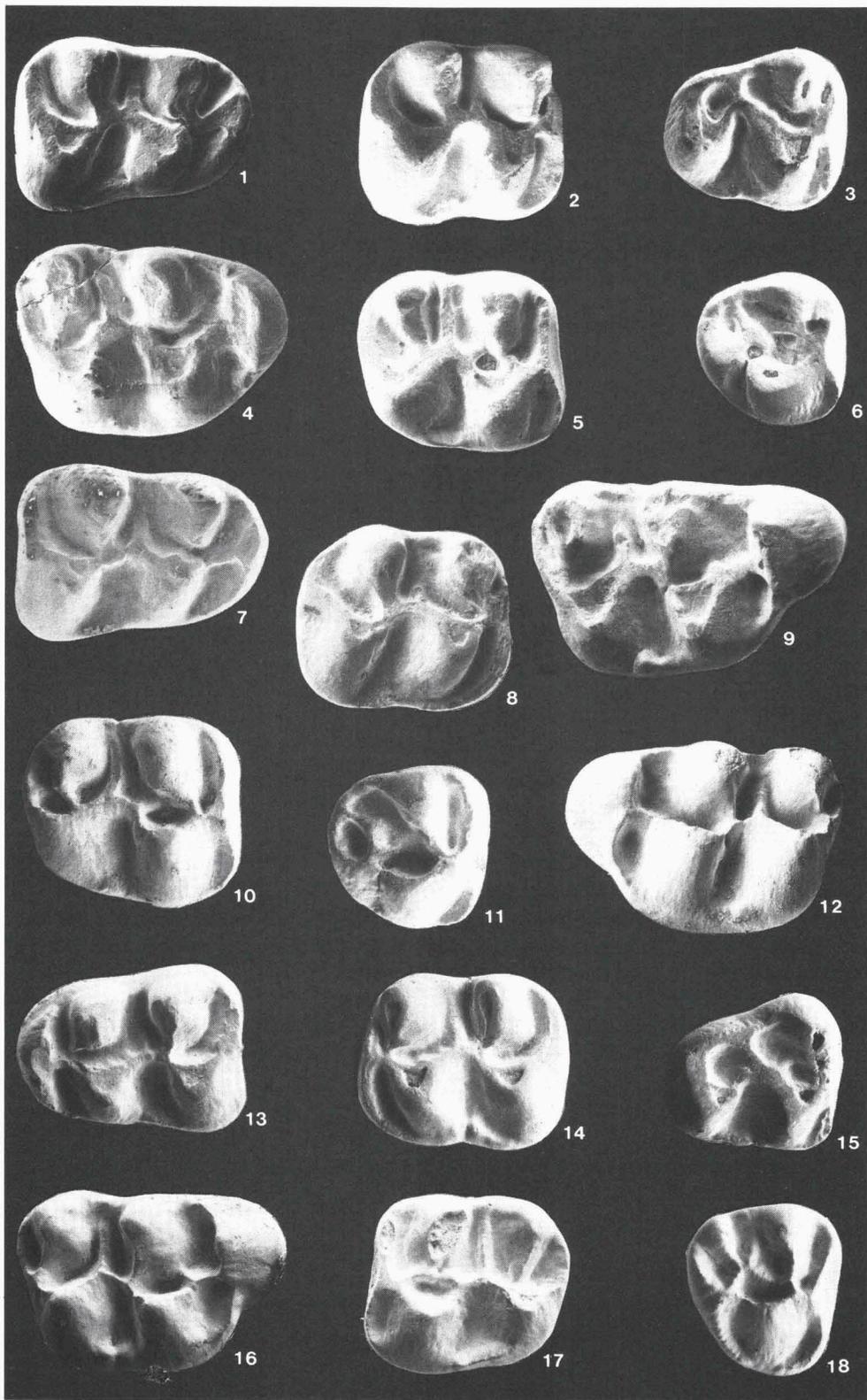
Olmo Redondo 3

- Fig. 12. M¹ sin., RGM 301 496.

Olmo Redondo 5

- Fig. 13. M₁ sin., RGM 302 641.
- Fig. 14. M₂ sin., RGM 302 644.
- Fig. 15. M₃ dext., RGM 302 650.
- Fig. 16. M¹ dext., RGM 302 653.
- Fig. 17. M² sin., RGM 302 658.
- Fig. 18. M³ dext., RGM 302 661.

Plate 1



Locality Olmo Redondo 1 (code OR 1, Zone B)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	3	13.3	13.50	13.6	0.173	3	9.0	9.63	10.0	0.551
M ₂	4	11.0	11.58	11.8	0.386	4	10.3	10.40	10.5	0.082
M ₃	5	9.8	10.24	10.5	0.288	5	8.0	8.62	9.3	0.522
M ¹	1	—	16.30	—	—	1	—	10.70	—	—
M ²	3	11.6	11.90	12.2	0.300	3	10.3	10.43	10.5	0.115
M ³	2	8.4	8.55	8.7	0.212	2	8.8	8.95	9.1	0.212

Description

M₁ — Length/width ratio 1.40, prelobe ratio 0.24. The anteroconid is triangular, with cingulum ridges descending along the sides of the molar towards protoconid and metaconid. The protosinusid and anterosinusid are deep and narrow, and not dammed by these cingulum ridges. The anteroconid lies slightly lingually of the axis of the molar, or on the axis. The anterolophulid is short and runs anterolingually towards the top of the anteroconid. In the two broad specimens the metaconid is transversely connected to the posterior end of the anterolophulid, and there is no connection to the protoconid. In the third, more slender, specimen the metalophulid points obliquely forward, towards the middle of the anterolophulid. In the broad specimens the mesolophid is of medium length, in the slender one it reaches the edge of the molar. The sinusid points obliquely forwards. The hypolophulid is either straight (2), or curved (1), and it points forward. The posterolophid closes the posterosinusid slightly.

M₂ — The lingual anterolophid remains visible, and it may be separated from the metaconid by a tiny valley. The labial anterolophid reaches the basis of the protoconid. The metalophulid and hypolophulid point obliquely forward, and they are settled in front of the labial cusps. The mesolophid is short, touching the base of the metaconid. The sinusid is oblique or transverse.

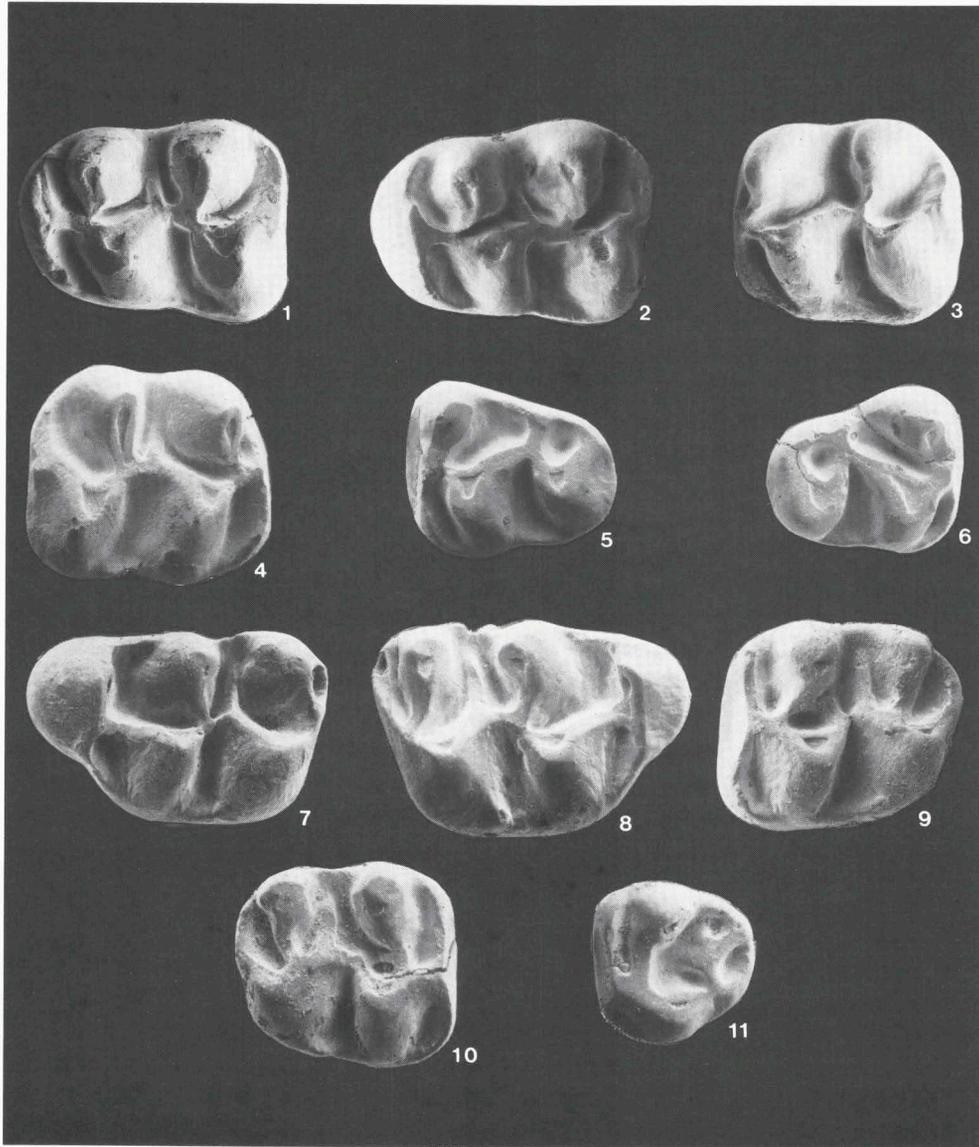
M₃ — The lingual anterolophid is present, and may be separated from the metaconid by a small valley. The mesolophid is missing. The sinusid is transverse or backward. The curve of the ectolophid remains at a distance from the lingual border of the molar, so that a hypolophulid of some length may be distinguished.

M¹ — The anteroloph is broad, with a vague connection to the protocone. The protolophule is obliquely backward, connected to the entoloph which curves very deeply into the molar. The mesoloph is long. The sinus is transverse and long. The metalophule is almost transverse, placed on the posteroloph, leaving a shallow, transverse posterosinus.

M² — The protolophule is symmetrically double (2), or obliquely backwards (1). The sinus is transverse, the mesoloph is long, reaching the edge of the molar in 1 specimen. The metalophule is forward, transverse, or backward.

M³ — In 1 specimen there is no neo-entoloph. The ancient entoloph is very curved, with a well-developed centrocone, no mesoloph, and both the anterior and posterior protolophule are present; the protocone is not rotated. In the other specimen the neo-entoloph is complete, the centroloph bears a centrocone, with some remnants of the entoloph and the mesoloph; there is no axiolph.

Plate 2



All figures approx. 25 ×.

Democricetodon hispanicus Freudenthal, 1967

San Roque 1

- Fig. 1. M₁ sin., RGM 302 777.
- Fig. 2. M₁ sin., RGM 301 525.
- Fig. 3. M₂ sin., RGM 302 785.
- Fig. 4. M₂ dext., RGM 302 790.
- Fig. 5. M₃ sin., RGM 302 792.
- Fig. 6. M₃ dext., RGM 302 798.
- Fig. 7. M¹ sin., RGM 302 809.
- Fig. 8. M¹ dext., RGM 302 818.
- Fig. 9. M² sin., RGM 302 826.
- Fig. 10. M² dext., RGM 302 831.
- Fig. 11. M³ sin., RGM 302 834.

Locality Olmo Redondo 2 (code OR 2, Zone B)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	6	13.2	14.08	15.4	0.906	5	9.2	9.94	10.7	0.550
M ₂	4	11.4	12.18	12.7	0.556	2	10.3	10.45	10.6	0.212
M ₃	3	9.8	10.17	10.5	0.351	3	8.7	8.90	9.1	0.200
M ¹	2	17.1	17.70	18.3	0.849	2	11.3	11.40	11.5	0.141
M ²	9	11.7	12.38	13.3	0.499	7	10.3	10.96	11.7	0.522
M ³	2	7.8	8.35	8.9	0.778	2	8.4	8.80	9.2	0.566

Description

M₁ — Length/width ratio: 1.42, prelobe ratio: 0.21. The anteroconid is triangular, bean-shaped, or round. Labial and lingual cingulum ridges descend from the anteroconid. The anterossinusid is deep or shallow, the protossinusid is always deep; the cingulum ridges never block the entrances to these valleys completely. The anteroconid lies slightly lingually of the axis of the molar. The anterolophulid is short and runs antero-lingually towards the top of the anteroconid. The metalophulid is transverse (3), obliquely forward (2), curved forward (1), or interrupted (1). It is generally connected to the anterolophulid, only in one case to the protoconid. The sinusid is directed obliquely forward, either open or slightly dammed by a very low cingulum ridge. The mesolophid is of medium length and well developed. The hypolophulid is transverse in 3 specimens, oblique in 3, and curved forward in 1. At the point of contact with the ectolophid the hypolophulid is often very broad. The posterolophid is a low, fairly broad ridge, descending from the hypoconid, in most cases reaching the basis of the entoconid, thus closing the posterossinusid.

M₂ — The anterossinusid has disappeared, but the metaconid may be separated from the anterior border of the molar by a flat spot in which the metalophulid and the anterior branch of the protoconid meet. The labial anterolophid meets the base of the protoconid, and in one case it continues almost to the sinusid. The metalophulid and hypolophulid are directed obliquely forward, ending in front of the labial cusps. The mesolophid is long, short, or absent. The sinusid is transverse or it points obliquely forward, not dammed by a cingulum ridge. The posterossinusid is rather deep, and closed by the broad posterolophid that reaches the base of the entoconid.

M₃ — The lingual anterolophid remains visible, the labial anterolophid reaches the base of the protoconid. The mesolophid is missing. The sinusid is transverse or curved backward, cutting halfway into the molar, thus leaving space for a relatively well-developed hypolophulid. There is no entoconid cusp. The shape of the molar is a short triangle, not the elongated shape that often occurs in other *Democricetodon* species.

M¹ — The anterocone is a broad, transverse ridge, with some crenulations at the base of its anterior wall. In 1 specimen the protolophule is double, in the others the anterior protolophule is missing. The mesoloph is long (2 specimens). The sinus is transverse. The metalophule is transverse, connected to the posteroloph. The posterossinus is small.

M² — The protolophule is forward (2), or double (7). The posterior protolophule is always weaker than the anterior one, being sometimes very low, or interrupted. The mesoloph is long, often reaching the border of the molar and forming a small mesostyl.

The sinus is transverse. The metalophule is curved forward (5), or transverse (3). A very weak trace of a longitudinal connection towards the posteroloph is present in 2 specimens. The posterosinus is relatively wide and deep, closed by the posteroloph. The general shape of the molar is rather rectangular, the width of the molar at the level of the hypocone is not much less than it is at the level of the protocone.

M³ — The neo-entoloph is present, the protolophule is the anterior one. In 1 specimen there is a normal centroloph, with a slight indication of the centrocone; the centroloph is curved. In the other specimen a crest comparable to a centroloph is connected to the middle of the protocone. It may be interpreted as a combination of the 'anterior' part of the ancient entoloph with the metalophule. This means that the protocone is rotated. The hypocone has almost completely disappeared.

Remark — The M¹ no. RGM 303 040 is larger than any other M¹ of *D. hispanicus* (18.3 × 11.5) in the Villafeliche area. It might represent another species of *Democricetodon* (cf. *affinis*) or *Fahlbuschia koenigswaldi*; the latter is improbable because the protolophule is double. On the other hand the M¹ of *F. decipiens* sp. nov. from Buñol frequently has an anterior protolophule. For this reason, and by its size, specimen RGM 303 040 may well belong to *F. decipiens* sp. nov. If this is true it is not impossible that the above-mentioned M³ with rotated protocone belongs to *Fahlbuschia* as well.

Locality Olmo Redondo 3 (code OR 3, Zone B)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	2	12.8	12.85	12.9	0.071	1	—	9.50	—	—
M ₂	4	11.7	12.33	12.8	0.519	4	9.6	10.20	10.8	0.516
M ₃	2	11.6	11.75	11.9	0.212	2	9.5	9.60	9.7	0.141
M ¹	3	16.0	16.80	17.9	0.985	3	10.5	10.83	11.4	0.493
M ²	3	11.6	12.47	13.3	0.850	2	10.6	11.55	12.5	1.344
M ³	2	9.0	9.10	9.2	0.141	2	8.6	9.30	10.1	1.061

Description

M₁ — Length/width ratio: 1.35, prelobe ratio: in one (very worn) specimen 0.16, in the other one 0.22. The material is too bad to allow a description. The mesolophid is short.

M₂ — The anterosinusid has disappeared, or it is very small. The labial anterolophid meets the base of the protoconid. The metalophulid and hypolophulid are directed obliquely forward. The mesolophid is of medium length, or short. The sinusid is transverse, open, or partially closed by a low cingulum ridge descending from the protoconid. The posterosinusid is deep, generally closed by the posterolophid.

M₃ — The lingual anterolophid remains visible, the labial branch reaches the base of the protoconid. The mesolophid is absent. The sinusid is transverse or curved backwards, the hypolophulid is relatively well developed. The general shape of the molar is somewhat elongated.

M¹ — The anterocone is part of a broad transverse anteroloph; the cusp lies labially of the axis of the molar, and may be slightly separated from the lingual part which

continues as a descending cingulum ridge; the anterior slope is smooth. Only the posterior protolophule is present. The mesoloph is long (1), or of medium length (3). The sinus is transverse and rather long. The metalophule is curved backwards, towards the posteroloph; the posterosinus is small.

M² — The protolophule is double (4), or posterior (1). The sinus is transverse. The metalophule is curved forwards (3), directed obliquely backwards (1), or absent (1). The posterosinus is relatively large, except in the specimen with the backward metalophule. The postero-lingual corner of the molar is somewhat rounded.

M³ — The protolophule is anterior, the external part of the sinus is relatively well developed, the neo-entoloph is complete. In 1 specimen the axioloph is well developed, bearing a broad centroloph, which seems to be a fusion of metalophule and mesoloph. The other specimen only has a slightly curved centroloph, broad in its lingual part, bifurcated into a metalophule and a remnant of the mesoloph.

Locality Olmo Redondo 5 (code OR 5, Zone C)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	2	13.5	13.60	13.7	0.141	2	9.4	9.40	9.4	0.0
M ₂	4	12.4	12.73	13.1	0.287	4	9.7	10.25	10.8	0.532
M ₃	3	10.4	10.87	11.4	0.503	3	8.8	8.90	9.0	0.100
M ¹	6	15.6	16.23	17.1	0.501	6	10.3	10.62	11.1	0.337
M ²	1	—	12.20	—	—	2	10.6	10.65	10.7	0.071
M ³	2	8.6	8.70	8.8	0.141	2	9.2	9.40	9.6	0.283

Description

M₁ — Length/width ratio 1.45, prelobe ratio 0.24. The anteroconid is triangular or bean-shaped with descending labial and lingual cingulum ridges. The anterosinusid is deep and relatively wide, and remains open, nor is the protosinusid blocked by a cingulum ridge. The anteroconid lies lingually of the axis of the molar. The anterolophulid is short and does not ascend to the top of the anteroconid. The metalophulid is directed obliquely forward, and it is connected to the anterolophulid. The sinusid is transverse, wide and dammed by a low cingulum ridge. In 1 specimen a very low ridge runs from the cingulum ridge towards the middle of the base of the anterior wall of the hypoconid (this feature is reminiscent of the typical 'gaillardi-ridge', though much weaker). The mesolophid is short, of medium length, or long. The hypolophulid points obliquely forward (2), or it is transverse (1), and it is always connected to the ectolophid. The posterolophid is swollen at the centre of the posterior border of the molar. It reaches the base of the entoconid, closing the fairly wide and deep posterosinusid.

M₂ — The anterosinusid is small but clearly visible (1), very small (1), or it has completely disappeared (2). In the specimen with anterosinusid the metalophulid is connected to the short anterolophulid. In the others it reaches the centre of the anterior border of the molar, tending to form a small anteroconid. The labial anterolophid meets the base of the protoconid. The metalophulid is directed obliquely forward. The hypolophulid is oblique (3), or transverse (1); in this latter case a very low but well discernable posterior hypolophulid is present as well. The mesolophid is of medium length, or long. The sinusid is transverse or directed obliquely forward, blocked by a fairly well-devel-

oped cingulum ridge which does not descend from the protoconid. This cingulum ridge may form a small ectostylid, from which a very low ridge enters into the sinusid. The posterosinusid is deep and wide, closed by the posterolophid. The swelling of the posterolophid (like in M_1) is present in the specimen with posterior hypolophulid.

M_3 — The anterosinusid is small or very small, the labial anterolophid reaches the base of the protoconid. The metalophulid points obliquely forward, and a trace of a posterior metalophulid may be present as well (1). There is no mesolophid. The sinusid is transverse and of medium length, leaving space for a well-developed, transverse or oblique hypolophulid; it is blocked by a low cingulum ridge. The entoconid is very small.

M^1 — The anteroloph is a broad transverse ridge, with a cusp labially of the axis of the molar. Protosinus and anterosinus may be open or blocked by cingulum ridges. The protolophule is posterior (3), or double (3), the anterior connection being low and weak. The mesoloph is long, generally reaching the border of the molar. The sinus is transverse and not very long. The metalophule is transverse or directed obliquely forward, toward the posteroloph; the posterosinus is small.

M^2 — The protolophule is symmetrically double, the mesoloph reaches the border of the molar, the sinus is transverse, the metalophule is anterior or transverse.

M^3 — The neo-entoloph is complete, the external part of the sinus has disappeared or it is relatively well developed. The metacone is recognizable or even relatively large. Axioloph and mesoloph are well developed. The centroloph is well developed (1), or its labial part is very weak (1).

Locality San Roque 1 (code SR 1, Zone B)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	14	13.2	14.21	15.2	0.713	16	9.3	10.15	10.7	0.416
M_2	14	11.4	12.37	13.3	0.508	14	9.9	10.56	11.1	0.320
M_3	20	9.2	10.55	11.8	0.597	20	7.9	8.89	9.8	0.588
M^1	14	15.2	16.34	17.3	0.549	19	9.5	10.62	11.4	0.573
M^2	18	10.4	11.99	13.1	0.697	19	9.2	10.64	11.5	0.576
M^3	12	8.4	8.83	9.4	0.311	12	8.6	9.08	9.7	0.282

Description

M_1 — Length/width ratio 1.40, prelobe ratio 0.23. The anteroconid is triangular or bean-shaped, with cingulum ridges descending labially and lingually. The protosinusid and anterosinusid are deep, generally not closed by these cingulum ridges. The anteroconid lies slightly lingually of the axis of the molar, or on the axis. The anterolophulid is relatively long, either longitudinal, or directed antero-lingually. In the single unworn specimen it does not rise to the top of the anteroconid. The metaconid is directed obliquely forward, towards the anterior corner of the protoconid (2), or towards the anterolophulid (9). There is no spur on the anterior wall of the metaconid. The mesolophid is short (1), of medium length (6), or long (8), sometimes reaching the border of the molar. The sinusid points obliquely forward. The hypolophulid is directed obliquely forward or transverse, towards the ectolophid. The posterolophid is a rather broad ridge, closing the posterosinusid, or leaving it somewhat open.

M_2 — In most unworn specimens either a labial anterolophid or even a small anterosinusid is visible. The labial anterolophid does not always close the protosinusid.

The metalophulid and hypolophulid point obliquely forward. The mesolophid is absent (2), short (5), or of medium length (5). The sinusid is transverse or directed obliquely forward; its entrance remains open, or it is blocked by a low cingulum ridge. The posterolophid closes the posterosinusid or leaves its entrance open; it is a fairly broad ridge, in a few cases somewhat inflated at its labial beginning.

M_3 — Generally the lingual anterolophid exists. There is no mesolophid. The sinusid is transverse or directed backwards, in most cases not very long. The hypolophulid is in most cases well developed, sometimes short. There is no entoconid. The general shape of the molar is triangular, not elongated.

M^1 — The anteroloph is a broad transverse ridge, with a labial cusp. The anterolophule reaches the lingual end of the cusp. There is no anterior protolophule, except for one case. The posterior one points obliquely backwards or — rarely — it is transverse, connected to the entoloph. The mesoloph is short (2), of medium length (4), or long (14). The sinus is transverse or directed obliquely backwards, not very long. The metalophule is transverse towards the middle of the hypocone (2), pointing obliquely backwards towards the hypocone (1), or towards the posteroloph (16). The posterosinus is always present, of variable size.

M^2 — The protolophule is symmetrically double (11), anterior (2), or the posterior branch is weaker than the anterior one (3). The mesoloph is of medium length (1), long (9), or it reaches the border of the molar (7). The sinus is transverse, generally blocked by a low cingulum ridge. The metalophule is directed forward, towards the hypocone (3), towards the entoloph (9), or backwards towards the posteroloph (1). The general shape of the molar is rectangular or the postero-lingual corner is rounded.

M^3 — The neo-entoloph is complete (6), or interrupted (2). The external part of the sinus may be visible. A centrocone is developed in all cases. It may have two branches (centroloph: 2), three branches (centroloph and axiolooph: 4), or four branches (centroloph, axiolooph and mesoloph: 3). The axiolooph is not or weakly connected to the paracone.

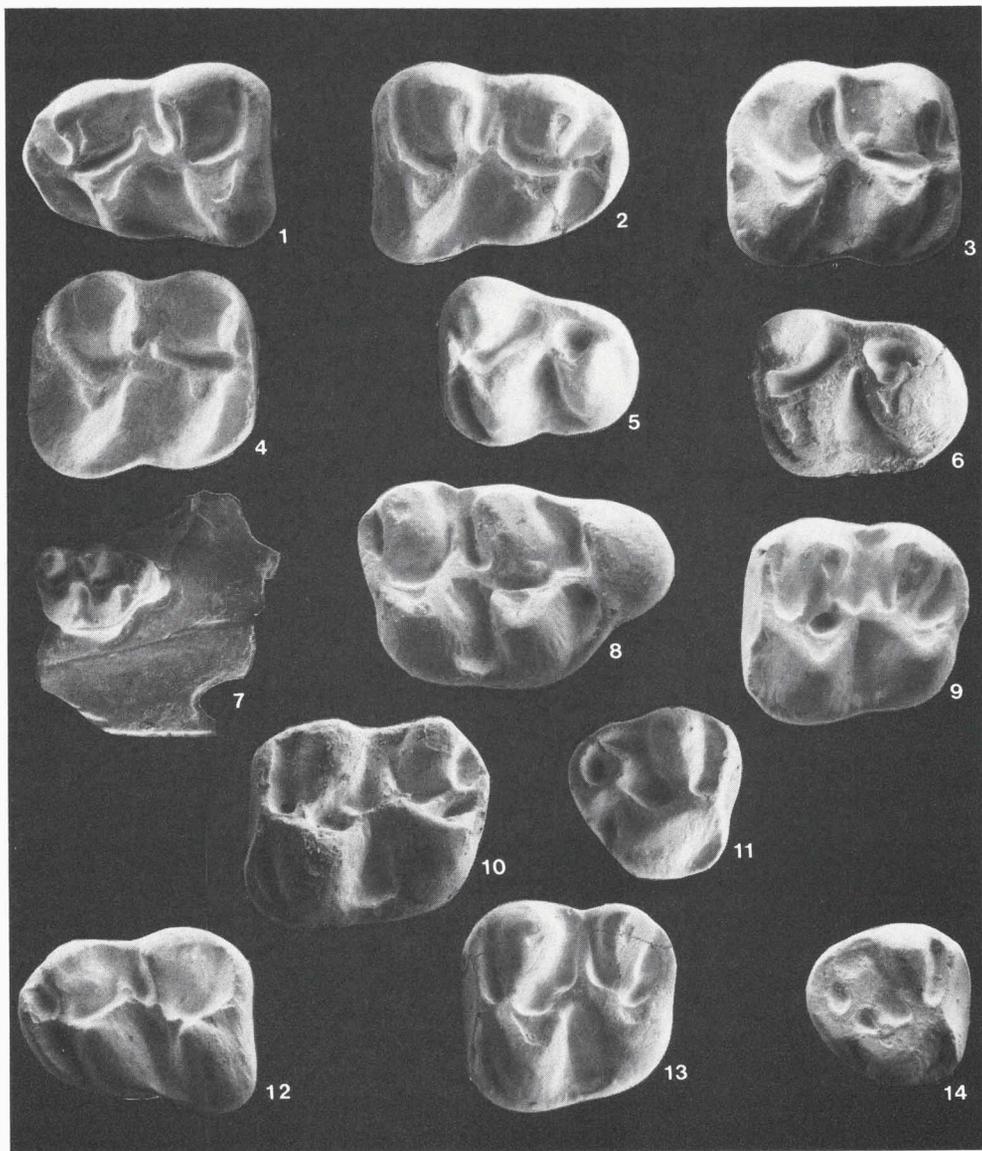
Locality San Roque 2 (code SR 2, Zone B)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	19	12.8	13.67	14.6	0.523	23	9.3	9.90	10.7	0.329
M_2	22	10.5	11.91	13.0	0.586	22	9.4	10.13	10.7	0.351
M_3	14	9.6	10.44	11.2	0.462	15	8.3	8.75	9.3	0.354
M^1	14	15.3	16.71	17.7	0.643	17	10.3	10.79	11.5	0.404
M^2	10	10.8	12.00	12.9	0.643	10	9.9	10.55	11.1	0.395
M^3	19	7.8	8.44	9.0	0.379	20	8.2	8.71	9.5	0.336

Description

M_1 — Length/width ratio 1.38, prelobe ratio 0.19. The anteroconid is triangular or bean-shaped, with labial and lingual descending cingulum ridges, which may or may not close the entrances of the anterosinusid and protosinusid. The protosinusid is deep, the anterosinusid may be equally deep (10), or rather shallow (5). This is especially the case in an M_1 sin., RGM 302 844. This specimen also has a lingual connection between anteroconid and metaconid, and a low prelobe ratio (0.16). For these reasons one would



All figures approx. 25 ×.

Democricetodon hispanicus Freudenthal, 1967

San Roque 2

- Fig. 1. M₁ sin., RGM 302 851.
- Fig. 2. M₁ dext., RGM 302 853.
- Fig. 3. M₂ dext., RGM 302 871.
- Fig. 4. M₂ dext., RGM 302 879.
- Fig. 5. M₃ sin., RGM 302 889.
- Fig. 6. M₃ sin., RGM 301 562.
- Fig. 7. M¹ dext., RGM 302 908.
- Fig. 8. M¹ dext., RGM 302 909.
- Fig. 9. M² sin., RGM 302 919.
- Fig. 10. M² sin., RGM 302 920.
- Fig. 11. M³ dext., RGM 302 935.

Democricetodon hispanicus or *Fahlbuschia* sp.

San Roque 2

- Fig. 12. M₁ sin., RGM 302 844.
- Fig. 13. M² sin., RGM 302 924.
- Fig. 14. M³ dext., RGM 301 566.

be inclined to ascribe it to *Fahlbuschia*. However, its small dimensions (12.8×9.9) and its length/width ratio of 1.29 make this improbable. The metalophulid is obliquely forward (14), or interrupted (4), always directed towards the anterolophulid. In one case the protoconid is not connected to the anterolophulid. The mesolophid is short (1), of medium length (9), or long (9), sometimes reaching the border of the molar. The sinusid is directed obliquely forward, with an open or slightly closed entrance. In 1 specimen a weak ectomesolophid descends from the anterior corner of the hypoconid towards the labial border. The hypolophulid is directed obliquely forward. The posterolophid may or may not close the entrance of the posterosinusid. The hypoconid passes gradually into the posterolophid without a swelling or a cuspid of some kind.

M_2 — The anterosinusid is fairly well developed, or at least a lingual anterolophid is present. The labial anterolophid may or may not close the protosinusid. The metalophulid and hypolophulid are obliquely forward. In one case there is a posterior metalophulid, which is probably identical with the mesolophid that has taken a longitudinal position. In another case the connection between protoconid and anterolophid is interrupted. The mesolophid is short (6), of medium length (13), or long (2). The sinusid is transverse or it points obliquely forward; it is open or closed by a cingulum ridge. Postero-lingually of the hypoconid there is often a cusp-like swelling at the beginning of the posterolophid. The posterolophid is fairly broad, and generally closes the entrance of the posterosinusid.

M_3 — The lingual anterolophid is always present, and there often is an anterosinusid. There is no mesolophid. The sinusid is transverse or curved backwards, either long (2), or of medium length (12). Consequently the hypolophulid is generally well developed. In 1 specimen the hypoconid sends a lingual spur into the posterosinusid. In 1 specimen the posterior wall bears a descending crest. The general shape of the molar is triangular.

Maxilla — A maxilla fragment with M^1 dext., RGM 302 908, shows that the foramen incisivum ends before the anterior border of the M^1 .

M^1 — The anteroloph is a broad transverse ridge with a labial cusp. The anterolophule runs longitudinally or antero-labially towards the lingual part of the anterocone. In two or three specimens an incomplete anterior protolophule is present. Generally only the posterior branch is present, which is directed obliquely backwards. In several cases the entoloph is constricted between protocone and protolophule. The mesoloph is of medium length (4), long (10), or it reaches the border of the molar (2). The sinus is transverse or directed obliquely backwards, generally open, sometimes closed by a low cingulum ridge which may form a tiny cusp. The metalophule is directed backwards towards the posteroloph. The posterosinus is small but well-developed, except in one case where it has disappeared.

M^2 — The protolophule is symmetrically double (5), anterior only (2), or anterior plus a weak or interrupted posterior branch (3). The mesoloph is of medium length (2), or long (8). The sinus is transverse, generally closed by a cingulum ridge. The metalophule is anterior (7), posterior (1), or double (1). The postero-lingual corner of the molar is somewhat rounded.

M^3 — The neo-entoloph is complete. The hypocone is set off from the protocone by the external part of the sinus. A more or less curved centroloph is present in most cases; its labial end often doesn't reach the border of the molar. In 2 specimens it lies so far backward, that it fuses with the posteroloph. Apart from the centroloph, the centrocone may bear an incomplete axioloph (8), traces of axioloph and mesoloph (1), or a fairly complete axioloph (2). In RGM 301 566 the ancient entoloph is complete, connecting the centrocone with the middle of the labial wall of the protocone.

Remark — It cannot be excluded, that some of this material belongs to a very primitive *Fahlbuschia*. *F. corcolesi* from Córcoles, mentioned by Díaz & López (1979) and Alférez et al. (1982) as *F. cf. koenigswaldi*, is such a *Fahlbuschia* species, characterized among other things by a predominance of anterior and frequent lack of posterior protolophules in M². Two M² described above also have the anterior connection only, a feature that is certainly not common, neither in *Democricetodon* nor in any known *Fahlbuschia*. These specimens and the M₁ no. RGM 302 844, and the M³ no. RGM 301 566 may belong to *Fahlbuschia corcolesi* sp. nov.

Locality Vargas 1A (code VR 1A, Zone C)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₃	1	—	10.70	—	—	1	—	9.70	—	—
M ¹	3	16.0	16.67	17.4	0.702	3	10.9	11.43	12.0	0.551
M ²	1	—	11.90	—	—	1	—	10.50	—	—
M ³	3	8.6	8.73	8.9	0.153	3	9.2	9.43	9.6	0.208

Description

M₃ — The lingual and labial anterolophid have disappeared. There is no mesolophid. The sinusid is strongly curved backwards. The hypolophulid is fairly well developed. There is a small ectostylid.

M¹ — The protolophule and metalophule are posterior. The mesoloph is long, the sinus is transverse.

M² — The protolophule is double, the posterior branch being the weaker one. The mesoloph is long. The metalophule is anterior.

M³ — The neo-entoloph is complete, the external part of the sinus is present (1), or absent (1). The centroloph is strongly curved. In one specimen a complete axioloph is present, in the other one a trace of the anterior part of the ancient entoloph is visible on the labial wall of the paracone.

Locality Olmo Redondo 9 (code OR 9, Zone D1)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	1	—	14.10	—	—	1	—	9.6	—	—
M ₂	4	12.5	12.82	13.5	0.472	4	10.4	10.82	11.2	0.330
M ₃	2	11.2	11.20	11.2	0.000	2	9.2	9.45	9.7	0.354
M ¹	0	—	—	—	—	2	10.5	10.95	11.4	0.636
M ²	1	—	12.90	—	—	1	—	10.40	—	—

Description

M₁ — This specimen is too badly preserved to allow a full description. The mesolophid is broad and of medium length.

M_2 — The anterosinusid is relatively well developed (3), or absent (1). A tiny anteroconid exists at the junction of anterolophid, metalophulid and anterolophulid. Metalophulid and hypolophulid are directed obliquely forward. The mesolophid is short or medium. The sinusid is transverse, open, or closed by a cingulum ridge. The posterosinusid is deep and wide, closed by the posterolophid. The posterolophid may be slightly swollen at the centre of the posterior border of the molar.

M_3 — The anterosinusid or a lingual branch of the anterolophid are present. The sinusid is curved backwards, either long or of medium length. The metalophulid is well developed or rather short. There is no mesolophid nor an entoconid. The general shape of the molar is a short triangle, or it is somewhat elongated.

M^1 — Protolophule and metalophule point obliquely backwards. The anterolophule bears a low labial spur. The mesoloph is long. The sinus is transverse, blocked by a low cingulum ridge. In the second specimen the protolophule is double. The metalophule is posterior, and there is a connection towards the mesoloph.

M^2 — The protolophule is symmetrically double. The metalophule is obliquely forward. Sinus and mesoloph are as in M^1 .

Locality Valdemoros 1A (code VA 1A, Zone D1)

Freudenthal (1963) mentioned a badly preserved M_1 of a *Democricetodon* from this locality as *Cricetodon* cf. *affinis*. It cannot be decided whether this specimen represents *D. hispanicus* or *D. affinis*.

Democricetodon gaillardi (Schaub, 1925)
Pl. 4, figs. 1-4.

Locality Las Planas 5K (code LP 5K, Zone G)

Material and measurements

M_1 sin., – \times 10.9; M_1 dext., 16.4 \times 11.7; M_2 dext., 15.5 \times 12.1; M_2 sin., – \times 13.3; M_3 dext., 13.7 \times 11.3; M^1 dext., 17.2 \times 12.3; M^2 dext., 14.2 \times 12.1.

The M_1 , M_2 and M_3 probably belong to one individual; the M^1 might be from this same individual as well.

Description

M_1 — Length/width ratio 1.40, prelobe ratio 0.20. The anteroconid is bean-shaped; the anterolophulid is bifurcated anteriorly. The mesolophid is long and very thick and there is an equally well-developed ectomesolophid, descending from the hypolophulid towards the ectostylid.

M_2 has a small anterosinusid. Mesolophid and ectomesolophid are as in M_1 .

M_3 — Mesolophid and hypolophulid are well developed. The sinusid is transverse and long.

M^1 — The protolophule is posterior. The mesoloph is long and thick, and there is an equally well-developed spur in the anterosinus.

M^2 — The protolophule is double, the metalophule is anterior, the mesoloph is long.

Locality Las Planas 5B (code LP 5B, Zone G)

One fragmentary M² with very long and strongly developed mesoloph may be attributed to *D. gaillardi*. An M¹, RGM 301 573, 18.9 × 11.7, also belongs to this species. Unfortunately the specimen has been lost.

Democricetodon aff. *gaillardi* (Schaub, 1925)
Pl. 4, figs. 5-7.

Locality Borjas (code BOR, Zone G)

Material and measurements

M₁: 17.3 × 11.5; M¹: 16.8 × 10.4.

Description

M₁ — Length/width ratio 1.50, prelobe ratio 0.24. The anteroconid is broad; the cingulum ridge descending at the labial side does not close the protosinusid; a high cingulum ridge along the lingual border of the molar fuses with the metaconid and transforms the anterosinusid into a deep and narrow funnel. In front of the metalophulid the anterolophulid is bifurcated into a longitudinal and an antero-lingual branch, separated by a small valley. The mesolophid is long and thick. An ectomesolophid descends from the hypolophulid towards the ectostylid.

M¹ — The anterolophule is longitudinal, and meets the anteroloph in a very lingual position. A broad spur of medium length extends from the anterolophule into the anterosinus. Protolophule and metalophule point obliquely backwards. The mesoloph is long. The sinus is transverse. The posterosinus is small.

Morphologically this material is very much like *D. gaillardi*. M₁ fits well in the size distribution of *D. gaillardi* from Sansan, M¹ is too small for that species, but it cannot be measured exactly because the specimen is damaged.

Locality Solera (code SOL, Zone G)

Material and measurements

M¹: 18.6 × 12.0, 18.7 × 12.0; M²: 13.6 × 10.9.

Description

M¹ — In 1 specimen the anteroloph is badly worn, in the other one the anterior wall of the anteroloph is smooth, the posterior wall is carved-in, so that a labial and a lingual cusp on the anteroloph are separated. The anterolophule is bifurcated, sending a branch to each one of these cusps. The labial branch sends a long spur into the anterosinus, which forms a small cusp on the border of the molar. There is a very weak trace of an anterior protolophule. Protolophule and metalophule are backwards. The mesoloph is long. The sinus is transverse. The posterosinus is small.

M² — The protolophule is double, the mesoloph is long, the metalophule is posterior, the posterosinus is small. The sinus is transverse.

Morphologically these specimens are much like *D. gaillardi*. However the widths are considerably smaller, so that we assume we are dealing with a different, probably new species.

Locality Valalto 1 (code VT 1, Zone G)

One badly preserved M^1 is attributed to *Democricetodon*. It has an interrupted anterior protolophule; the mesoloph is absent. Measurements: 19.5×13.4 .

Democricetodon cf. affinis (Schaub, 1925)

Pl. 4, figs. 8-10.

Locality Valdemoros 3B (code VA 3B, Zone D2)

Freudenthal (1963) mentioned 1 M_3 , 3 M^2 and 2 M^3 from this locality. In our new material we have a number of additional specimens. Measurements for the entire collection (RGM and GIU) are:

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	2	15.3	15.85	16.4	0.778	3	10.8	10.93	11.1	0.153
M_2	1	—	15.00	—	—	1	—	11.20	—	—
M_3	1	—	11.00	—	—	1	—	10.10	—	—
M^1	1	—	19.40	—	—	1	—	13.20	—	—
M^2	8	13.5	14.11	14.7	0.436	8	12.0	12.40	12.8	0.273
M^3	4	8.6	9.25	10.1	0.635	4	9.8	10.00	10.3	0.216

Plate 4

All figures approx. $20 \times$.

Democricetodon gaillardi (Schaub, 1925)

Las Planas 5K

- Fig. 1. M_1 dext., RGM 252 466.
 Fig. 2. M_2 dext., RGM 252 467.
 Fig. 3. M_3 dext., RGM 252 468.
 Fig. 4. M^1 dext., RGM 256 937.

Democricetodon aff. gaillardi (Schaub, 1925)

Borjas

- Fig. 5. M_1 dext., RGM 268 208.

Solera

- Fig. 6. M^1 sin., RGM 255 439.
 Fig. 7. M^2 sin., RGM 255 441.

Democricetodon cf. affinis (Schaub, 1925)

Valdemoros 3B

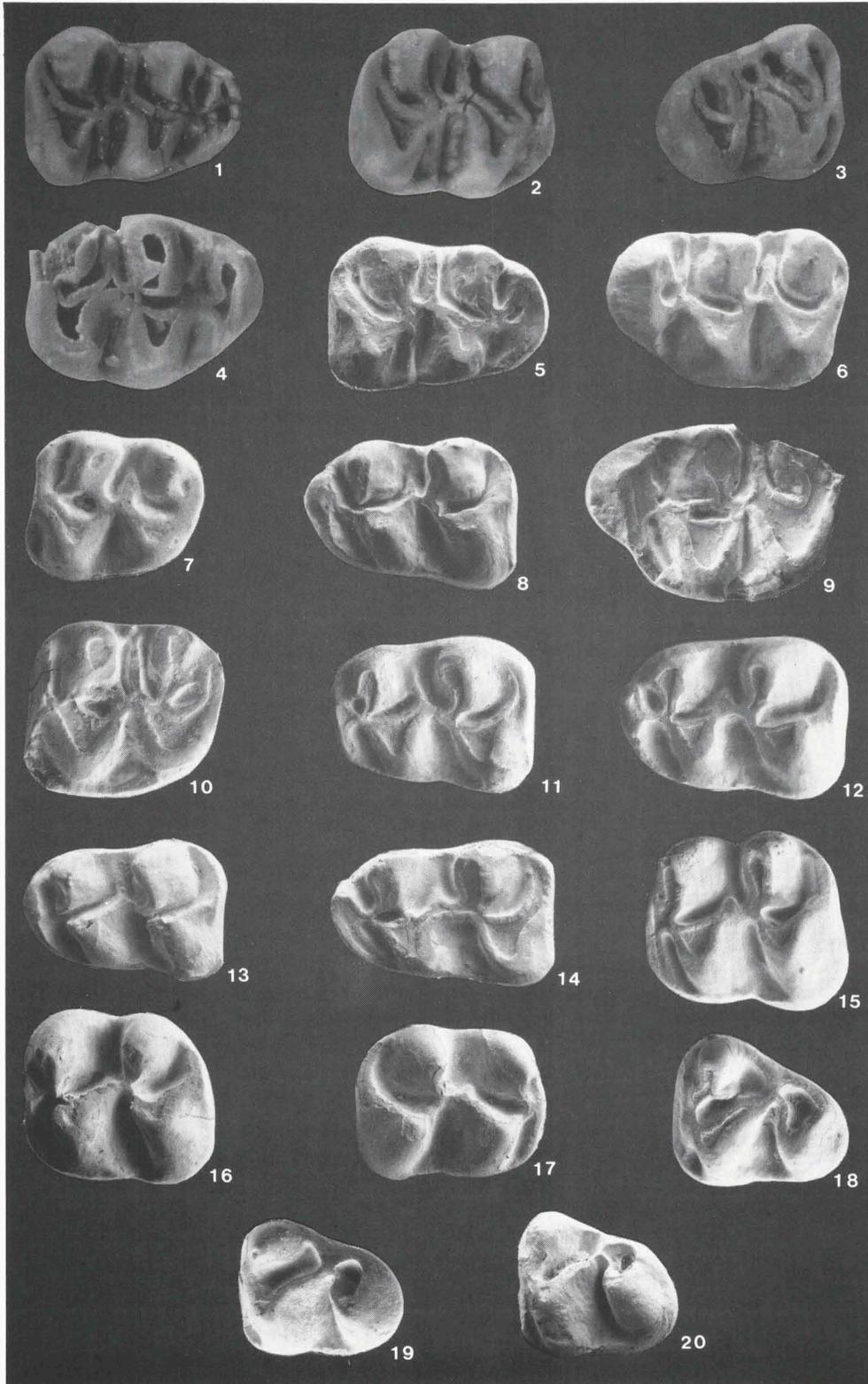
- Fig. 8. M_1 sin., RGM 268 358.
 Fig. 9. M^1 sin., RGM 268 361.
 Fig. 10. M^2 sin., RGM 268 362.

Fahlbuschia koenigswaldi (Freudenthal, 1963)

Vargas 1A

- Fig. 11. M_1 sin., RGM 301 252.
 Fig. 12. M_1 sin., RGM 301 930.
 Fig. 13. M_1 sin., RGM 302 676.
 Fig. 14. M_1 sin., RGM 301 917.
 Fig. 15. M_2 sin., RGM 301 284.
 Fig. 16. M_2 sin., RGM 301 300.
 Fig. 17. M_2 dext., RGM 301 994.
 Fig. 18. M_3 sin., RGM 301 327.
 Fig. 19. M_3 sin., RGM 301 329.
 Fig. 20. M_3 sin., RGM 301 331.

Plate 4



Description

M_1 — Length/width ratio 1.45. The anterosinusid is narrow and open. The mesolophid is long.

M_2 — The lingual anterolophid and the anterosinusid are small but present. The mesolophid is long.

M_3 — The outline of the molar is a very short triangle. There is a small anterosinusid, and no mesolophid. The sinusid is curved backwards.

M^1 — The protolophule is double, the mesoloph is long.

M^2 — The protolophule is double, the metalophule forward. The mesoloph is long.

M^3 — The axioloph is complete. There is a centroloph, which in 2 specimens may be interpreted as the mesoloph, and in 2 others as the metalophule.

Discussion

This material is not sufficient to allow a specific determination. By its size it agrees fairly well with *D. affinis*, but there are some morphological differences. In *D. affinis* from La Grive the metalophule of M^2 is posterior in all specimens we have seen, whereas in all specimens from Valdemoros 3B the metalophule is curved forwards. M^3 in Valdemoros 3B seems to be more reduced.

In *D. cf. affinis* from Vieux-Collonges a forward metalophule in M^2 is rather frequent. Mesolophs are more reduced than they are in Valdemoros 3B.

Morphologically the M^2 from Valdemoros agree pretty well with the M^2 of *D. mutilus*. We prefer, however, not to use this name, because part of the *mutilus*-material (including the holotype) might belong to *Fahlbuschia*.

Genus *Fahlbuschia* Mein & Freudenthal, 1971

Fahlbuschia koenigswaldi (Freudenthal, 1963)

Pl. 4, figs. 11-20; Pls 5, 6.

Type-locality — Valdemoros 1A, Zaragoza, Spain.

Holotype — M^1 sin., Museo de Paleontología, Sabadell, figured in Freudenthal, 1963, pl. 1, fig. 8.

Distribution — Aragonian Zones C and D1.

Fahlbuschia koenigswaldi was first described by Freudenthal (1963) under the name *Cricetodon koenigswaldi*. Freudenthal (1965) placed it – hesitantly – in the genus *Democricetodon*. Mein & Freudenthal (1971a) created the genus *Fahlbuschia* (genotype *C. larteti* Schaub, 1925), and placed *Fahlbuschia koenigswaldi* in this genus.

Originally *F. koenigswaldi* was known only by a small collection from the type-locality, and a few badly preserved specimens from Valtorres, a locality in the same sedimentary basin as Valdemoros. Subsequently it was described from the localities Buñol (Daams & Freudenthal, 1974), Navarrete 5 (Adrover et al., 1978), Córcoles (Díaz & López, 1979; Alférez et al., 1982), and Chelas 2 (Aguilar, 1981).

In our opinion *Democricetodon hispanicus*, described by Aguilar (1981) also belongs to *F. koenigswaldi*. Bulot (1981) described a *Democricetodon* sp. from Le Chêne-de-Navère. The description of M_1 and the specimen figured (op. cit., fig. 4) suggest, that this in fact is a *Fahlbuschia*. Because of its size it may be *F. koenigswaldi*.

The populations described by Freudenthal (1963) as a transitional form between *F. koenigswaldi* and *F. darocensis* are proven to belong to a different species, which is not a descendant of *F. koenigswaldi* and does not even belong to the genus *Fahlbuschia*.

In our recent campaigns we found material of *F. koenigswaldi* in the localities of Olmo Redondo 5, Olmo Redondo 8, Olmo Redondo 9, Vargas 1A, Vargas 1E, Casetón 1A, Casetón 1B and Casetón 2B.

The population from Buñol does not belong to *F. koenigswaldi*, but represents a new species, *F. decipiens*, described below.

The population from from Córcoles represents a new species, that probably is the most primitive *Fahlbuschia* known so far. It will be described below.

Locality Olmo Redondo 5 (code OR 5, Zone C)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	5	15.7	17.20	18.0	0.943	8	10.0	11.36	12.3	0.802
M ₂	2	15.0	15.20	15.4	0.283	3	12.8	13.47	14.3	0.764
M ₃	4	12.9	13.43	14.3	0.640	6	11.0	11.33	11.9	0.446
M ¹	1	—	20.20	—	—	2	12.5	12.85	13.2	0.495
M ²	5	14.0	15.04	15.9	0.709	3	12.2	12.67	13.5	0.723
M ³	6	10.4	11.25	12.8	0.869	7	10.7	11.36	12.1	0.571

Description

M₁ — Length/width ratio 1.51, prelobe ratio 0.17. The anteroconid is triangular. A connection from the metaconid towards the anteroconid through the middle of the anterosinusid is indicated (6), or absent (1). The metalophulid points obliquely forward or it is transverse. The mesolophid is short (2), of medium length (2), or long (4). The sinusid is obliquely forward. The hypolophulid points obliquely forward. The posterosinusid is closed by the posterolophid.

M₂ — The mesolophid is short or absent. The sinusid is curved backwards. The hypolophulid points obliquely forward. The posterosinusid is closed by the posterolophid.

M₃ — The lingual anterolophid is absent (3), or present (2). Only 1 specimen has an anterosinusid. The anterior metalophulid is transverse. A posterior metalophulid is indicated in 1 specimen by a bulge of the lingual wall of the protoconid. The sinusid is curved backwards, either long (3), or short (2); 2 specimens have the triangular shape and short hypolophulid that are typical of *Fahlbuschia*.

M¹ — There is no anterior protolophule, the mesoloph is short or of medium length, the posterosinus is fairly well developed, though small.

M² — The protolophule is anterior (2), double (2), or posterior (2). The mesoloph is absent (1), short (1), or of medium length (4). The metalophule is anterior (4), or transverse (2). The sinus points obliquely backwards or it is transverse.

M³ — The outer part of the sinus is absent, or it is moderately developed. The axioloph is present, the mesoloph is present (4), or absent (2). The anterior metalophule (centroloph) is present (4), or absent (2).

Locality Olmo Redondo 8 (code OR 8, Zone C)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	3	15.7	16.57	17.2	0.777	3	10.9	11.77	12.5	0.808
M ₂	1	—	15.90	—	—	1	—	12.50	—	—
M ₃	4	12.8	13.55	14.3	0.645	4	10.5	11.13	11.8	0.532
M ¹	2	18.5	19.85	21.2	1.909	2	12.5	12.75	13.0	0.354

Description

M₁ — Length/width ratio 1.41, prelobe ratio 0.17. In the 2 unworn specimens the anteroconid is very close to the metaconid, and connected through the small and shallow anterosinusid. In 1 specimen the anteroconid is split by a narrow, deep groove. The metalophulid is anterior. The mesolophid is short or absent. The sinusid is directed obliquely forward. In 1 specimen the anterior branch of the hypoconid is constricted.

M₂ — The anterosinusid is fairly well developed. The mesolophid is absent.

M₃ — Three out of five specimens have a trace of a posterior metalophulid on the lingual wall of the protoconid. The sinusid is long and narrow and the hypolophulid is short (4), or the sinusid is short and broad and the hypolophulid is long (1).

M¹ — The anterolophule is a smooth ridge (2), or it shows a tendency to split up (1). There is no anterior protolophule. The mesoloph is absent or short. The posterosinusid is present.

Locality Olmo Redondo 9 (code OR 9, Zone D1)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	23	15.7	17.23	18.5	0.695	25	10.8	11.87	12.9	0.537
M ₂	12	15.0	15.66	16.4	0.423	14	12.4	12.99	13.8	0.457
M ₃	15	12.5	13.40	15.2	0.744	14	9.9	11.01	12.2	0.718
M ¹	12	18.9	20.43	22.1	0.827	15	12.1	13.31	14.2	0.526
M ²	18	13.5	15.11	16.4	0.647	19	11.8	12.94	14.1	0.590
M ³	25	9.7	10.96	12.9	0.823	27	9.7	11.14	13.0	0.798

Description

M₁ — Length/width ratio 1.45, prelobe ratio 0.18. In several specimens the anterosinusid is somewhat wider and deeper than it normally is in this species. In 13 specimens there is no connection between metaconid and anteroconid through the anterosinusid. In 3 specimens there is a connection along the border of the molar. In 6 other specimens the metaconid bulges forward. By these features the material does not look very much like a *Fahlbuschia*. It is attributed to this genus on the basis of its size, its high length/width ratio and low prelobe ratio. The mesolophid is absent (10), short (8), of medium length (6), or long (2). The hypolophulid is directed obliquely forward or

transverse; in 1 specimen there is a trace of a posterior hypolophulid as well. The posterolophid closes the posterosinusid lingually.

M₂ — The lingual anterolophid is present and may enclose a tiny valley. The mesolophid is short (5), or absent (8). The metalophulid points obliquely forward. The sinusid is directed obliquely forward, transverse or curved backwards. The posterolophid closes the posterosinusid. In 1 specimen both the metalophulid and the hypolophulid are double: a weak posterior connection exists along with the normal anterior connection.

M₃ — The lingual anterolophid is relatively well developed and may enclose a small anterosinusid. The metalophulid points obliquely forward or it is transverse. In 2 specimens a spur on the lingual wall of the protoconid indicates a posterior metalophulid. The sinusid is curved backwards, narrow and long, generally leaving little space for a hypolophulid. One specimen is so much reduced in its posterior part that the posterosinusid has vanished.

M¹ — The anterior protolophule is absent (14), or indicated by a very weak trace (2). The posterior one is oblique. In 1 specimen the posterior wall of the paracone bears a backward spur. The mesoloph is absent (3), short (10), or of medium length (4). The metalophule is posterior, the posterosinus is always present, either small or relatively well developed. In 1 specimen there is no metalophule. The sinus is directed obliquely backwards, transverse or slightly curved forwards.

M² — The protolophule is anterior (6), double (11), or posterior (2). The mesoloph is absent (1), short (6), of medium length (3), or long (7). The metalophule is directed forward or transverse. The sinus is transverse, rarely backward.

M³ — In 8 specimens the curved ancient entoloph is present and complete, in 3 more specimens its anterior part presents itself as a spur on the labial wall of the protocone. Such a high percentage of 'primitive' M³ is not found in any other population of *Fahlbuschia*. The axioloph is absent (7), interrupted (5), or complete (14). The mesoloph is absent (18), or present (7). The metalophule is absent (1), or present (25). In many cases the external part of the sinus forms a clear separation between protocone and hypocone, and in one case the neo-entoloph is not even closed, so that the sinus continues until the ancient entoloph in the centre of the molar (RGM 301 906).

Locality Vargas 1A (code VR 1A, Zone C)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	90	15.1	16.65	18.2	0.683	97	10.0	11.51	12.8	0.582
M ₂	101	13.4	14.95	16.6	0.668	98	10.5	12.13	13.2	0.575
M ₃	90	11.2	13.11	14.5	0.720	91	9.0	10.59	12.3	0.563
M ¹	68	18.0	19.72	21.7	0.916	84	11.4	12.87	14.4	0.633
M ²	97	13.0	14.83	16.3	0.775	96	10.9	12.69	14.0	0.647
M ³	95	9.2	10.57	12.4	0.700	95	9.8	10.82	12.8	0.586

Description

M₁ — Length/width ratio 1.45, prelobe ratio 0.16. The anteroconid is triangular or bean-shaped, with descending cingulum ridges on both sides. The anterosinusid is generally shallow. It is closed by a ridge along the border of the molar (13), a ridge connects anteroconid and metaconid through the middle of the anterosinusid (13), such a

connection is merely indicated (14), or there is no connection at all (46). The protosinusid is either closed by a cingulum ridge or it remains open. The metalophulid always points obliquely forward, towards the anterolophulid (76); a weak posterior metalophulid may be present in addition (2); seldom the metalophulid is transversely directed towards the protoconid (6). The metalophulid may be interrupted (11), the anterolophulid may be interrupted (11), or both connections may be missing (3). Even if there is no connection between metaconid and anteroconid through the anterosinusid, the metaconid and metalophulid are sharply curved, comma-shaped, the anterior point of the metaconid lying as far forward as the point of connection of metalophulid and anterolophulid, the anterior wall of the metaconid being concave. The mesolophid is absent (13), short (52), of medium length (29), or long (13). The sinusid is generally directed obliquely forward, open, or closed by a cingulum ridge. In 1 specimen this ridge does not descend from the protoconid, but it runs all the way from the anteroconid backwards, separating the protoconid from the border of the molar. The hypolophulid is directed obliquely forward or – seldom – transverse. In 1 specimen a relatively well-developed posterior hypolophulid is present as well. The ectolophid may be somewhat constricted or even interrupted, just in front of the hypoconid. The posterosinusid is either open, or closed by the posterolophid. On the average the crests are not very thick.

M_2 — The anterosinusid is very small or relatively well developed, rarely absent. At least a trace of the lingual anterolophid is always present, and often there is a fairly well-developed anteroconid. The labial anterolophid closes the protosinusid, or leaves it open. In 1 specimen it continues until the sinusid, separating the base of the protoconid from the border of the tooth. The metalophulid is directed obliquely forward, either towards the anteroconid, or – less frequently – towards the anterolophid. In 2 specimens the metalophulid is interrupted. In one case it is transverse towards the anterolophulid, while the anterosinusid is curved backwards, and the anterolophulid starts from the middle of the lingual wall of the protoconid. The mesolophid is absent (35), short (42), of medium length (16), long (4), or it reaches the border of the molar (1). It has a tendency to fuse with the posterior wall of the metaconid, and often it is a low, thin, weakly developed crest. The sinusid points obliquely forward or it is transverse, sometimes slightly curved backwards, generally closed by a cingulum ridge descending from the protoconid. The hypolophulid is directed obliquely forward, and in a few specimens a weak posterior connection exists as well. The posterolophid may or may not close the

Plate 5

Fig. 17 approx. 7.5 ×, other figures approx. 20 ×.

Fahlbuschia koenigswaldi (Freudenthal, 1963)

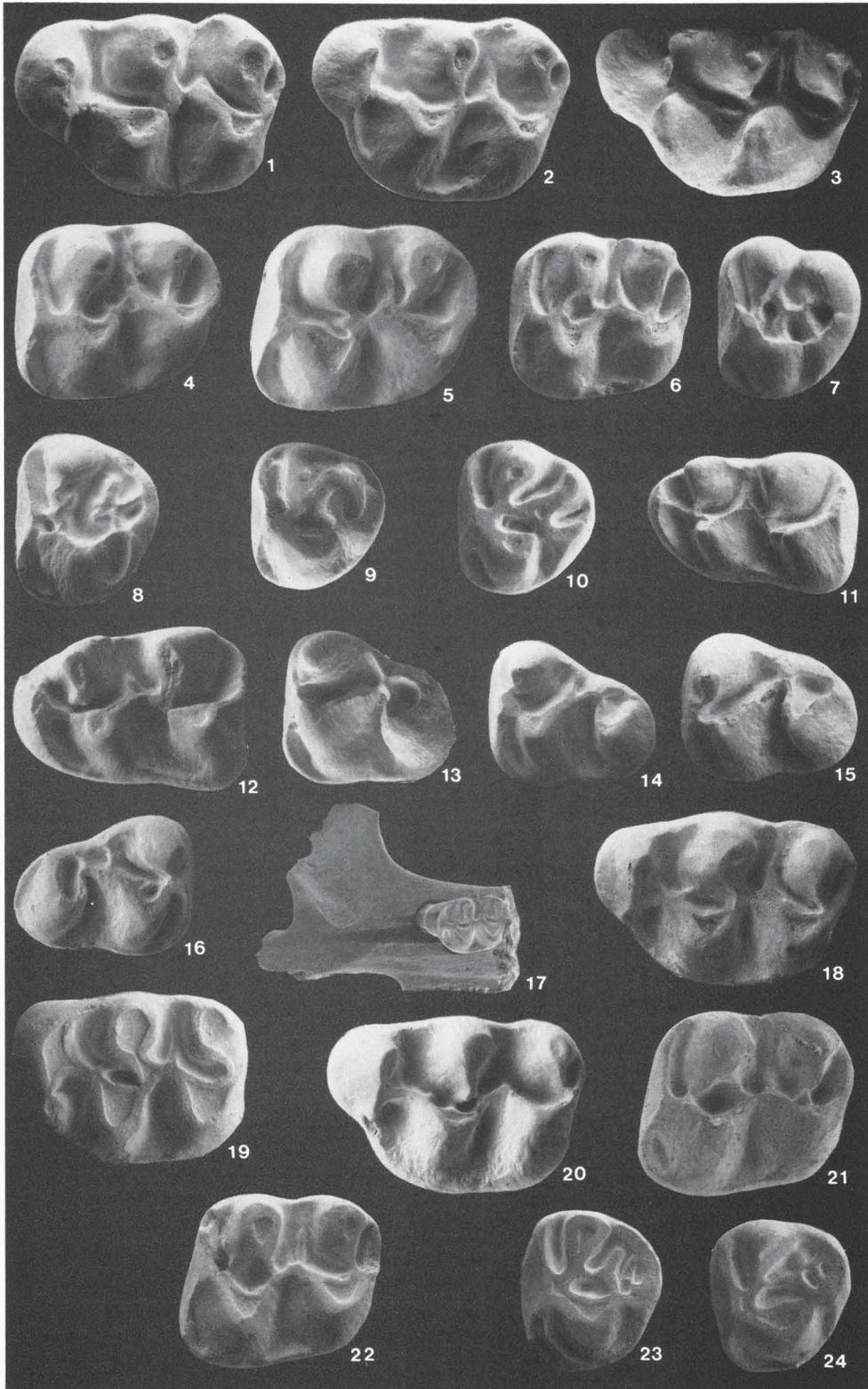
Vargas 1A

- Fig. 1. M^1 sin., RGM 301 364.
- Fig. 2. M^1 sin., RGM 301 373.
- Fig. 3. M^1 sin., RGM 302 070.
- Fig. 4. M^2 sin., RGM 301 403.
- Fig. 5. M^2 sin., RGM 301 404.
- Fig. 6. M^2 sin., RGM 302 112.
- Fig. 7. M^3 sin., RGM 301 442.
- Fig. 8. M^3 sin., RGM 301 441.
- Fig. 9. M^3 sin., RGM 301 447.
- Fig. 10. M^3 sin., RGM 301 449.

Caseton 1A

- Fig. 11. M_1 sin., RGM 301 609.
- Fig. 12. M_1 sin., RGM 302 506.
- Fig. 13. M_3 sin., RGM 301 627.
- Fig. 14. M_3 sin., RGM 301 631.
- Fig. 15. M_3 sin., RGM 302 289.
- Fig. 16. M_3 dext., RGM 302 327.
- Fig. 17. Max. fragm. with M^1 sin., RGM 302 340.
- Fig. 18. M^1 sin., RGM 302 346.
- Fig. 19. M^1 sin., RGM 302 348.
- Fig. 20. M^1 sin., RGM 302 353.
- Fig. 21. M^2 sin., RGM 302 402.
- Fig. 22. M^2 sin., RGM 302 401.
- Fig. 23. M^3 sin., RGM 301 666.
- Fig. 24. M^3 sin., RGM 301 669.

Plate 5



posterosinusid. The anterior and the posterior widths are almost equal, giving the molar a quadrangular outline. The ectolophid may be constricted or rather low between hypoconid and hypolophulid.

M₃ — The lingual anterolophid is missing (13), or – at least a trace of – it is present. (58). The anterosinusid is small (12), or relatively well developed (10) (the 58 specimens with anterolophid include the specimens with anterosinusid). The metalophulid is directed obliquely forward, and a posterior connection may be indicated: no posterior connection (65), weakly developed (4), strongly developed (4), the lingual wall of the protoconid bulges towards the metaconid (15), or the metaconid bulges towards the protoconid (2). Only in one case the spur on the protoconid could be taken for a mesolophid. The sinusid is curved backwards, narrow, not very long (40), or carving far into the molar (50). Consequently the hypolophulid is either fairly well developed or rather reduced. About 25 specimens have the very reduced hypolophulid and the short triangular shape which often are typical of *Fahlbuschia*. Several other specimens, however, might well be attributed to *Democricetodon* (see the remarks at the end of the description).

M¹ — The anteroloph consists of a labial cusp (the anterocone) and a descending labial loph, which is often somewhat separated from the anterocone. This descending cingulum ridge may close the protosinus, or may leave it slightly open. The anterosinus is almost always closed by a fairly well-developed cingulum ridge, which does not descend from the anterocone. The anterolophule is oblique towards antero-labiad, less frequently longitudinal, connected to the lingual tip of the anterocone, or to the lingual loph. The anterolophule may bear a weak labial spur (2). A complete, though weak anterior protolophule may be present (2), or a trace of this connection may be present (3), but mostly only the posterior protolophule exists. The latter is directed obliquely backwards, less frequently transverse, connected to the entoloph, immediately behind the protocone, or at some distance behind this cusp. The posterior wall of the paracone is straight or smoothly convex (70), or it is angular, protruding posteriorly slightly (20). This reminds one of the posterior spur on the paracone which is frequently found in *Cricetodon* and *Megacricetodon*. The mesoloph is absent (9), short (28), of medium length (32), long (16), or it reaches the border of the molar (5). The metalophule is generally posterior, but there may be no connection at all between metacone and hypocone (6). The posterosinus is almost always small, and may be completely absent (7).

M² — The protolophule is absent (1), anterior (19), anterior plus a trace of a posterior connection (12), double (45), posterior (5), or posterior with a trace of an anterior connection (5). When the protolophule is double the anterior branch tends to be slightly better developed than the posterior one. The mesoloph is absent (5), short (14), of medium length (37), long (29), or it reaches the border of the molar (3). The metalophule is absent (3), anterior (44), transverse (14), posterior (17), or double (4). The sinus is generally open and transverse. The postero-lingal corner of the molar is not much rounded.

M³ — The anterior part of the ancient entoloph – or a trace of it – is present in 14 specimens; it may be rather well developed (see Figs. 1B, 1E), or it presents itself as a slight bulging of the labial wall of the protocone. The outer part of the sinus has vanished (23), it is moderately developed (42), or well developed (25). In a few specimens there is no anterior protolophule. Specimens without axioloph, with interrupted axioloph and with complete axioloph are about equally frequent. A mesoloph is more or less well developed in 18 specimens (about 16 %). In 18 specimens the anterior metalophule (centroloph) is missing.

Remarks — This material is treated as a homogeneous population. It is, however, not impossible that a few specimens belong in reality to a *Democricetodon* species. E.g. the M₁ RGM 301 262 has a fairly long anterior part (prelobe ratio 0.21), and the general aspect of *D. affinis*. If this population is a mixture of *Democricetodon* and *Fahlbuschia* it must be admitted that the separation of these two species is impossible. The same holds for all localities where *F. koenigswaldi* might concur with a *Democricetodon* of equal size. Vargas 1A also contains material of *Democricetodon hispanicus* and of *Pseudofahlbuschia jordensi* gen. et sp. nov., but these two species are easily distinguished from *F. koenigswaldi* on the basis of size.

Locality Casetón 1A (code CS 1A, Zone D1)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	52	15.4	16.75	18.3	0.628	50	9.6	11.37	12.5	0.537
M ₂	52	13.8	15.05	16.4	0.650	50	11.0	12.40	13.7	0.592
M ₃	61	11.5	13.03	14.3	0.614	59	10.0	11.01	11.9	0.499
M ¹	55	17.3	19.61	21.5	0.899	61	11.1	12.94	14.0	0.545
M ²	67	13.7	15.15	17.0	0.673	67	11.1	12.89	14.0	0.573
M ³	69	9.4	10.74	12.2	0.644	67	9.9	11.21	12.2	0.487

Description

M₁ — Length/width ratio 1.47, prelobe ratio 0.18. The anteroconid is small, triangular, with descending cingulum ridges. The anterosinusid may be small and shallow, but often it is better developed than it is e.g. in Vargas 1A. It is closed by a cingulum ridge along the border of the molar (10), a ridge connects metaconid and anteroconid through the middle of the valley (3), such a connection is indicated (15), or the anterior wall of the metaconid is straight (14). This means that on the whole the typical *Fahlbuschia*-morphology of M₁ is less developed in this material than it is in the population from Vargas 1A. The metalophulid is directed obliquely forward, towards the anterolophulid, rarely transverse towards the anterolophulid. Metaconid and metalophulid are often comma-shaped. The metalophulid may be interrupted (3). The anterolophulid may also be interrupted (7), either before or behind the metalophulid. The mesolophid is absent (1), short (21), of medium length (17), or long (11). The sinusid is obliquely forward, open or closed by a ridge descending from the protoconid. The hypolophulid points obliquely forward, or – rarely – it is transverse. In a few specimens the ectolophid is somewhat constricted behind the hypolophulid.

M₂ — The lingual anterolophid is absent (13), or present (27); if present it is generally very short, forming an anterosinusid or an anteroconid in a few cases only. The labial anterolophid closes the protosinusid or leaves it open. The metalophulid is directed obliquely forward, in a few cases curved forward, or transverse, towards the middle of the anterior border of the molar. The mesolophid is absent (12), short (31), of medium length (4), or long (2). It often is a vague bulge of the ectolophid that fuses with the posterior wall of the metaconid. The sinusid is directed obliquely forward or transverse, often closed by a cingulum ridge descending from the protoconid. The hypolophulid points obliquely forward, 2 specimens have a very weak trace of a posterior hypolophulid. The posterolophid often closes the posterosinusid.

M₃ — The lingual anterolophid is almost always present (40), though very small, rarely better developed, less frequently absent (7). There is no anterosinusid. The metalophulid is directed obliquely or transversely forward. The posterior metalophulid is absent (47), indicated by a spur on the lingual wall of the protoconid (6), or by a bulging of this wall (4). Only 1 specimen has a mesolophid. The sinusid is narrow, long, curved backwards; the hypolophulid is very short. The posterosinusid is often very small, in 3 specimens it has vanished.

M¹ — The anteroloph consists of a smooth curved ridge, in which a labial cusp may be marked; lingually it descends towards the protocone, generally closing the posterosinus; the anterosinus too is frequently closed by a ridge along the border of the molar, but this ridge often does not descend from the anterocone. The anterior protolophule is absent (28), merely indicated (4), or present (28). It is always less developed than the posterior connection. The posterior wall of the paracone is straight or smoothly convex (45), or somewhat angular, indicating a very small spur (8). The mesoloph is absent (6), short (10), of medium length (28), or long (16). The metalophule is posterior, the posterosinus is small to very small (44), or absent (3). In one case the metalophule is transverse, in another one it is interrupted. The sinus is directed obliquely backwards or transverse, generally closed by a ridge along the border of the molar.

M² — The protolophule is absent (1), anterior (3), anterior with a trace of a posterior connection (1), posterior with a trace of an anterior connection (1), or symmetrically double (60). When the protolophule is double, both connections are equally well developed. The mesoloph is absent (5), short (22), of medium length (25), long (13), or it reaches the border of the molar (2). In about half the number of specimens the posterior wall of the paracone is smooth, in the other half it shows an angular protrusion. The metalophule is anterior (26), transverse (16), posterior (11), or double (10). Many of the specimens with transverse connection are worn specimens that might have been attributed to another category, had they been fresh. The postero-lingual corner of the molar is rounded more frequently than it is in the population from Vargas 1A. The sinus is transverse and closed by a ridge along the border of the molar. Only in a few cases the sinus is very slightly curved forwards.

M³ — The axioloph is absent (2), incomplete (7), or complete (56). The mesoloph is present (29), or absent (36). The metalophule (centroloph) is present in all but 3 specimens. In 1 specimen (RGM 302 480) the anterior part of the ancient entoloph connects the incomplete axioloph to the middle of the labial wall of the protocone. Seven specimens show a morphology as seen in Fig. 2E: a small funnel exists antero-labially of the hypocone. The lingual border of this funnel is the neo-entoloph or the anterior branch of the hypocone. The other borders may represent the strongly curved ancient entoloph. In that case these teeth resemble very much the picture of M³ of *Democricetodon gaillardii* in Fig. 2B. It is also possible that the other borders are formed by a double metalophule. The external part of the sinus is in most cases moderately or fairly well developed, seldom vanished. The posterior part of the tooth is extremely reduced in 9 specimens.

Remark — Among the M₁ and M³ from this locality we find a relatively high number of specimens that may be attributed to *Democricetodon* instead of *Fahlbuschia*; at least the percentage is higher than it is in other populations of *F. koenigswaldi*. It is suspected, that in fact this material is a mixture of *Democricetodon* and *Fahlbuschia*. We have not managed to separate two different species.

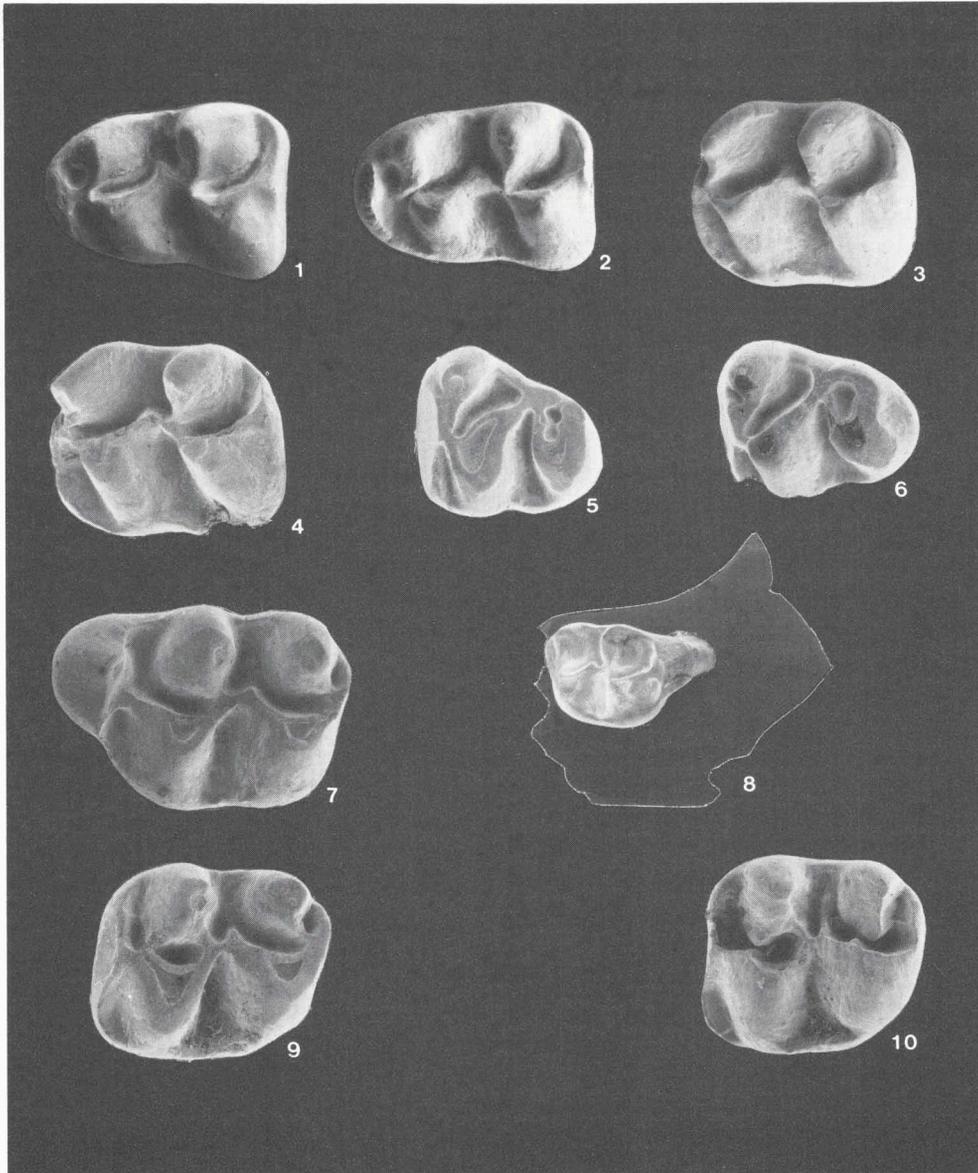


Fig. 8 approx. 7.5 ×, other figures approx. 20 ×.

Fahlbuschia koenigswaldi (Freudenthal, 1963)

Caseton 2B

Fig. 1. M_1 sin., RGM 301 699.

Fig. 2. M_1 sin., RGM 302 176.

Fig. 3. M_2 dext., RGM 301 715.

Fig. 4. M_2 dext., RGM 301 718.

Fig. 5. M_3 sin., RGM 301 748.

Fig. 6. M_3 sin., RGM 301 749.

Fig. 7. M^1 sin., RGM 301 759.

Fig. 8. Maxilla fragment with M^1 dext., RGM 301 777.

Fig. 9. M^2 sin., RGM 301 795.

Fig. 10. M^2 sin., RGM 301 793.

Locality Casetón 1B (code CS 1B, Zone D1)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	1	—	16.40	—	—	1	—	11.50	—	—
M ₂	1	—	14.80	—	—	1	—	12.00	—	—
M ₃	1	—	14.70	—	—	1	—	12.20	—	—
M ¹	3	18.5	19.23	20.2	0.874	3	12.4	12.67	13.1	0.379
M ³	3	10.7	11.03	11.6	0.493	3	10.6	10.83	11.1	0.252

Description

M₁ — Length/width ratio 1.43, prelobe ratio 0.21. The anteroconid is small, triangular. The metaconid is comma-shaped. The mesolophid is very short.

M₂ — The lingual anterolophid is very small. The labial anterolophid closes the protosinusid, encircles the protoconid, and continues to the hypoconid. The mesolophid is short.

M₃ — There is no lingual anterolophid. The sinusid is curved backwards. The hypolophulid is not very short.

M¹ — The anteroloph is a smooth ridge. The anterolophule is longitudinal. The anterior protolophule is weak or absent. The mesoloph is of medium length. The metalophule is posterior. There is a posterosinusid.

M³ — There is an axioph. The mesoloph is present or absent. The metalophule is present or absent.

Locality Casetón 2B (code CS 2B, Zone D1)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	41	15.7	17.02	18.5	0.627	39	10.1	11.59	12.6	0.571
M ₂	46	14.1	15.48	17.2	0.695	40	11.6	12.55	14.2	0.607
M ₃	30	12.0	13.18	14.1	0.593	28	10.2	10.96	12.0	0.503
M ¹	47	18.1	20.15	21.7	0.792	52	12.0	13.39	14.1	0.521
M ²	47	14.3	15.36	16.5	0.530	48	12.2	13.24	14.0	0.441
M ³	37	9.2	10.81	12.1	0.644	38	9.9	11.05	11.9	0.508

Description

M₁ — Length/width ratio 1.47, prelobe ratio 0.18. The anteroconid is triangular, with a ridge descending towards the protoconid, that may close the posterosinusid. The anterosinusid is often small and shallow. The anteroconid is connected to the metaconid along the border of the molar (7), there is a connection through the middle of the anterosinusid (4), such a connection is indicated (16), or the metaconid-metalophulid is comma-shaped (5). Only in 3 specimens the metaconid has a straight anterior wall. The foremost point of the metaconid lies generally as far forward as, or farther forward than the junction of metalophulid and anterolophulid. The anterolophulid is frequently

interrupted before the metalophulid, and in many of these cases the metalophulid is interrupted too, just before it reaches the anterolophulid. The metalophulid is posterior in one case. The mesolophid is absent (10), short (24), of medium length (7), or long (2). The sinusid is directed obliquely forward, either open or closed by a ridge along the border of the molar. The hypolophulid is directed obliquely or transversely forward. The posterolophid generally closes the posterosinusid.

M₂ — The lingual anterolophid is generally small, but present, there is no anterosinusid or a very small one. The labial anterolophid closes the posterosinusid. The metalophulid is pointing obliquely forward. The mesolophid is absent (18), short (23), or of medium length (4), often in contact with the base of the metaconid. The sinusid is directed obliquely forward or transverse, generally closed at its labial border. The hypolophulid is directed obliquely forward. The posterolophid closes the posterosinusid.

M₃ — About half the number of specimens have a tiny lingual anterolophid, in the other half it is missing. There is an anterosinusid. One specimen has a mesolophid, and 1 has a crest that may either be the posterior metalophulid or a mesolophid. In a few specimens there is a very small thickening of the posterior branch of the protoconid, at the place where one would expect a posterior metalophulid. In all other specimens there is no posterior metalophulid nor a trace of such a connection. The sinusid is curved backwards, narrow, cut far into the molar, leaving hardly any place for a hypolophulid. The posterosinusid is variable in size, never absent.

M¹ — The anteroloph is a smooth ridge, often somewhat concave anteriorly, in which a labial cusp may be marked. It descends lingually to close the posterosinus. The ridge closing the anterosinus does not descend from the anterocone. An anterior protolophule is absent (49), or present (7). The posterior wall of the paracone is smooth (33), or it shows a tiny angular protrusion (15). The mesoloph is absent (10), short (34), of medium length (11), or long(1). The sinus is transverse or directed obliquely backwards. The posterosinus is always present, small or relatively well developed.

M² — The protolophule is anterior (1), posterior (1), or double (48). In 1 specimen with double protolophule the posterior one is interrupted, in 2 specimens the anterior one is interrupted. In all other specimens the two connections are equally well developed. In a fair minority of the specimens the posterior wall of the paracone is somewhat angular. The mesoloph is absent (8), short (19), of medium length (10), or long (13). The metalophule is absent (3), anterior (11), transverse (2), double (11), or posterior (21). The sinus is transverse or slightly curved forward. The postero-lingual corner of the molar is like in Casetón 1A.

M³ — The mesoloph is always absent, the centroloph is always present. The axiolooph is incomplete (7), or complete (24). In 2 specimens the axiolooph bears a lingual spur that may be a remnant of the ancient entoloph, in another one the ancient entoloph is complete, forming an almost complete circle between the labial wall of the protocone and the hypocone; in this specimen the neo-entoloph is not closed. There is another specimen with open neo-entoloph, in which the sinus continues forward as far as the anterior protolophule. In 3 specimens the axiolooph is curved towards the posterior corner of the protocone; in these cases it cannot be decided whether its posterior part is the ancient entoloph. The external part of the sinus is often fairly well developed.

Locality Valdemoros 1A (code VA 1A, Zone D1)

This material contains a number of specimens that were collected after Freudenthal's 1963 paper was published. Excluded are some specimens that have been transferred to *Pseudofahlbuschia* (see the next chapter).

For a description the reader is referred to Freudenthal, 1963. Only the M² have been remeasured, because Freudenthal at the time used a different measuring method than we do now. We will give a new description of the M³ because in 1963 this element was not well understood, and the old description is poor.

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	26	16.1	17.12	18.3	0.568	25	10.9	12.04	13.3	0.510
M ₂	30	14.6	15.89	16.9	0.647	31	12.3	13.24	14.6	0.582
M ₃	16	12.0	13.41	14.7	0.714	16	9.8	11.61	12.8	0.734
M ¹	23	19.7	20.58	22.1	0.595	24	12.6	13.57	14.6	0.469
M ²	24	14.6	15.51	16.5	0.516	24	12.1	13.50	14.3	0.510
M ³	19	10.3	11.10	11.9	0.489	19	10.3	11.50	12.3	0.462

M³ — Generally (15 specimens) both axiolph and centroloph are present. Of these, in 1 specimen the labial wall of the protocone bulges towards the axiolph; in 2 others the ancient entoloph persists between protocone and axiolph; in 1 other specimen the neo-entoloph is not closed. In 1 specimen the axiolph is present and the centroloph is missing. In 2 specimens both axiolph and centroloph are absent; in these specimens the protolophule is double: one branch forward, and one branch transversely towards the middle of the protocone.

Locality Vargas 1E (code VR 1E, Zone D1)

This locality has yielded about 20 specimens of *F. koenigswaldi*. It will not be described in detail, because the material is very poor. There is not a single complete specimen of M₁, so that the length/width ratio cannot be measured. Several M¹ have a labial spur on the anterolophule, which may enclose a funnel on the posterior wall of the anterocone, a feature generally absent in this species, but present in *F. freudenthali* and *darocensis*. Both these species are larger than the Vargas 1E material, which may represent an evolved stage of *F. koenigswaldi*.

Comparison of some morphological features of *F. koenigswaldi* from Vargas 1A, Casetón 1A and Casetón 2B

There are some remarkable differences between the populations of Casetón 1A and Casetón 2B, though they are almost identical in their measurements. A number of features found in the populations of Vargas 1A, Casetón 1A and Casetón 2B are tabulated below in percentages. The number of specimens in each of the populations is sufficiently high to permit the use of percentages instead of actual numbers.

		VR1A	CS1A	CS2B
M ₁	anteroconid-metaconid connection present or indicated	47	66	77
	mesolophid absent + short	61	44	79
	metalophid or anterolophid interrupted	26	20	??
M ₂	mesolophid absent + short	79	88	91
M ₃	mesolophid present	1	2	2

M ¹	anterior protolophule present	7	53	13
	mesoloph short + absent	41	28	79
M ²	anterior protolophule	87	97	98
	posterior protolophule	63	92	98
	anterior metalophule	71	77	48
	posterior metalophule	31	45	70
	mesoloph absent + short	22	40	54
M ³	axioloph present	66	97	100
	mesoloph present	16	45	0
	ancient entoloph present	12	12	16

A further difference is, that the two available maxillae and a number of toothless fragments from Casetón 1A have a short foramen incisivum, whereas the single specimen from Casetón 2B has a foramen incisivum that continues backwards in between the first molars.

Fahlbuschia freudenthali Antunes & Mein, 1981
Pl. 7; Pl. 8, figs. 1-11.

Type-locality — Amor (Leiria), Portugal.

Holotype — M¹ sin., Antunes & Mein, 1981, pl. 2, fig. 16.

Distribution in the Calatayud-Teruel Basin — Aragonian Zone D3.

The diagnosis of this species (translated into English) is: 'larger than *F. koenigswaldi* and smaller than *F. darocensis* with mesoloph(id)s of short or of medium length in the first two molars'.

The original description states that the protolophule is double in the holotype, backwards in the other 2 specimens. Inspection of the figure of the original, and of some of the casts Mr Mein kindly put at our disposal, shows that at least one of the other specimens has an interrupted anterior protolophule too. The metalophule of the holotype is anterior, in the other specimens posterior. The mesoloph of M¹ is of medium length or short. In M² the protolophule is posterior, the mesoloph short, and the metalophule transverse. The figured M³, in the terminology used in this paper, has an axioloph, a mesoloph, and a metalophule. The other specimen has only the posterior half of the axioloph, no mesoloph and no metalophule. M₁ has a short mesolophid. There appears to be a direct connection between metaconid and anteroconid through the anterosinusid in 2 specimens. The metalophulid is more or less transverse toward the protoconid, and not forward towards the anterolophulid. In 1 of the M₃ the posterosinusid is slightly subdivided into two depressions by a longitudinal spur arising from the anterior branch of the hypoconid.

According to the diagnosis *F. freudenthali* is smaller than *F. darocensis*. In fact this is true for M¹ only. The M₁ fall within the distribution field of the Manchones material. Most of the other teeth are similar in length to the smaller specimens from Manchones 1; their widths are somewhat smaller indeed. This means that the M¹ from Amor are small in relation to the other teeth. Of course this may be a coincidence, since the collection from Amor is rather poor. Another problem is the length/width ratio of M₁. While most specimens are relatively slender, the M₁ are fairly broad (length/width ratio 1.36 and 1.46, mean value 1.41, among the lowest values found in *Fahlbuschia*). Again, this may be a coincidence, but it cannot be excluded that the *Fahlbuschia* material from Amor is not a homogeneous population.

The most striking feature of *F. freudenthali* is possibly the double protolophule of M^1 , present in 2 of the 3 specimens. In *F. decipiens* n. sp. from Buñol the anterior connection is present in 15 %, and indicated in another 15 % of over 30 specimens; in *F. koenigswaldi* from Valdemoros 1 A it is present in 5 % (1 out of 19 specimens), and in *F. darocensis* from Manchones 1 only in a few percent of almost 100 specimens. It appears to be very frequent in *F. freudenthali* from Amor.

Only in the populations from Casetón 1A (over 50 % of 60 specimens), Solera and Carrilanga the anterior protolophule of M^1 is frequent. Maybe there is a phylogenetic relationship between them. The very high frequency of anterior protolophules in the M^1 from Casetón 1A may be due to the presence of *Democricetodon* in that sample.

A remarkable fact is the absence of an anterior protolophule in the M^2 from Amor. Generally in *Fahlbuschia* (and in all other Miocene cricetids) the anterior protolophule in M^2 is more persistent than it is in M^1 . In *F. freudenthali* (though the material is scarce) the situation seems to be reversed. This, combined with the relative slenderness of the teeth, may mean that the M^2 , and possibly also the M_3 and M^3 do not belong to *F. freudenthali*, but to a *Pseudofahlbuschia*, e.g. *P. jordensi* sp. nov. The M_1 cannot belong to *Pseudofahlbuschia* because of their low length/width ratio of 1.41, whereas the length/width ratio of *Pseudofahlbuschia* varies between 1.59 and 1.62, higher values than ever encountered in a *Fahlbuschia*. In the present paper we describe *F. freudenthali* from the localities of Regajo 2, and Valdemoros 3 E. It was also found in the unpublished localities of Valhondo 4 B, 4C, and 4E, which are geographically and stratigraphically close to Regajo 2.

Amended diagnosis

Larger than *F. koenigswaldi*, smaller than *F. darocensis*. Length/width ratio of M_1 very low: 1.40 – 1.42. Anterior protolophule in M^1 frequent.

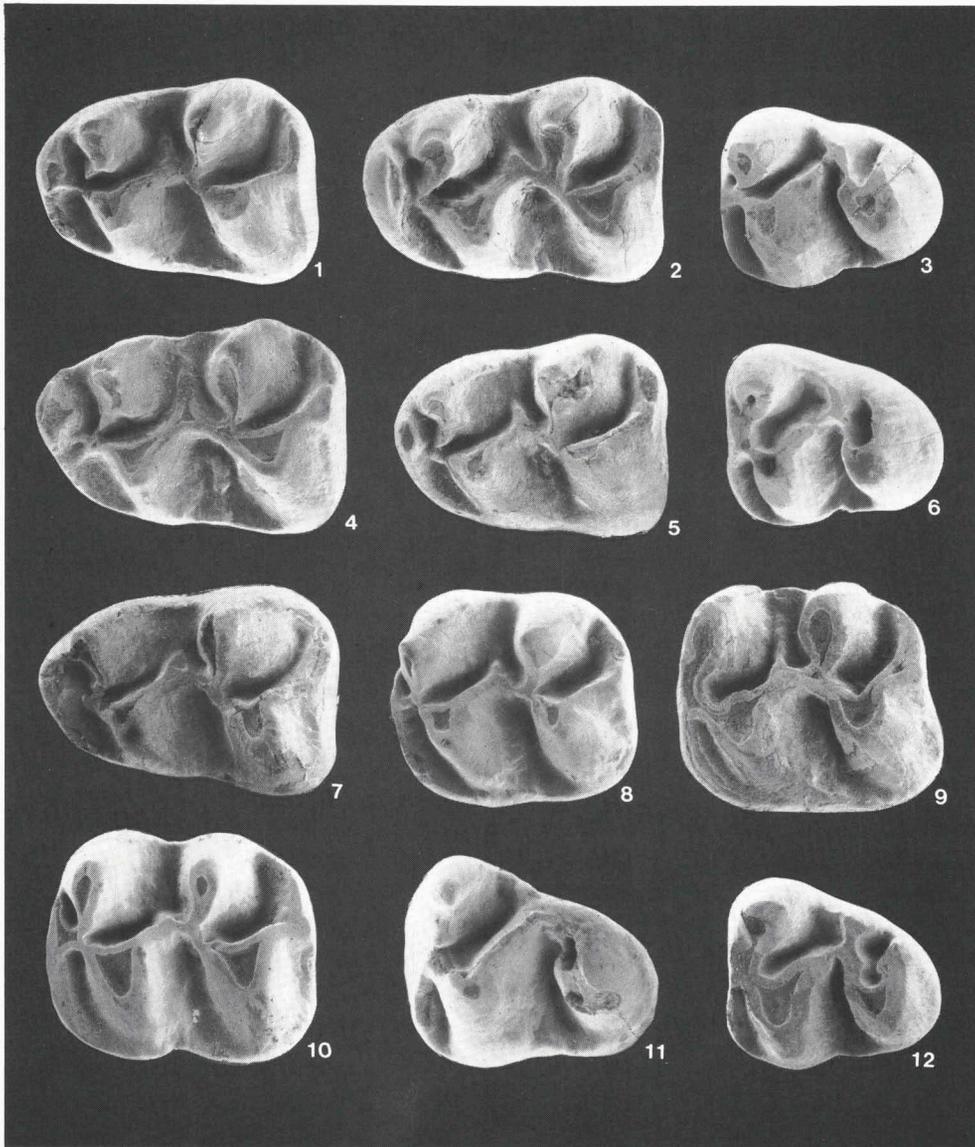
Locality Regajo 2 (code REG 2, Zone D3)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	87	17.3	19.16	21.4	0.846	86	11.5	13.48	14.6	0.570
M_2	97	15.1	17.54	19.0	0.689	97	12.5	14.40	16.2	0.596
M_3	87	13.3	15.14	17.6	0.799	87	11.6	12.75	14.7	0.660
M^1	64	21.1	23.19	25.2	0.977	75	13.1	14.96	16.3	0.576
M^2	78	15.5	17.19	18.6	0.629	79	13.7	14.90	16.6	0.555
M^3	80	10.9	12.07	13.6	0.663	79	11.5	12.72	14.0	0.592

Description

M_1 — Length/width ratio 1.42, prelobe ratio 0.17. The anteroconid is small, triangular, or it forms a curved ridge. In most cases there is only a labial anterolophid. The anterosinusid is narrow and shallow. The anterior wall of the metaconid is smooth (15), protruding forward with a more or less well-developed spur (42), or there is a direct connection from metaconid to anteroconid through the anterosinusid (20). The metalophulid is directed forward, either straight or bent (63), transverse towards the anterior tip of the protoconid (10), or towards the middle of the protoconid (1). In one case there is a trace of a second, posterior metalophulid, and in two cases this posterior connection



All figures approx. 20 ×.

Fahlbuschia freudenthali Antunes & Mein, 1981

Regajo 2

- Fig. 1. M_1 sin., RGM 385 115.
- Fig. 2. M_1 sin., RGM 385 116.
- Fig. 3. M_3 sin., RGM 385 260.
- Fig. 4. M_1 sin., RGM 385 118.
- Fig. 5. M_1 sin., RGM 385 121.
- Fig. 6. M_3 sin., RGM 385 265.
- Fig. 7. M_1 sin., RGM 385 095.
- Fig. 8. M_2 sin., RGM 385 164.
- Fig. 9. M_2 sin., RGM 385 165.
- Fig. 10. M_2 sin., RGM 385 171.
- Fig. 11. M_3 sin., RGM 385 263.
- Fig. 12. M_3 sin., RGM 385 264.

is complete. The connection of the protoconid with the metalophulid may be interrupted (16). In many other cases the anterolophulid is rather low. In eight cases the anterolophulid is forked or double, and the posterior wall of the anteroconid may show a beginning of subdivision. The mesolophid is absent (7), short (46), of medium length (18), or long (9). One specimen has a well-developed ectomesolophid. The sinusid points obliquely forward. The hypolophulid is either transversely or obliquely directed forward. The posterolophid is low, and closes the posterosinusid.

M_2 — The lingual anterolophid is present, and frequently there is even a tiny anterosinusid. The labial anterolophid descends towards the protoconid, but does not really close the protosinusid. One specimen has a very small trace of a posterior metalophulid on the posterior corner of the protoconid. The mesolophid is absent (11), short (57), of medium length (20), or long (8). The sinusid is generally directed obliquely forward. The posterolophid closes the posterosinusid.

M_3 — In most cases the lingual anterolophid is present, and frequently there is an anterosinusid. The sinusid is narrow, backward or transverse. Four specimens have an ectomesolophid. In four specimens there is a crest that may either be a remainder of the posterior metalophulid, or the mesolophid. The posterosinusid is closed (83), open (2), or absent (1). In 2 specimens the posterosinusid is divided into two valleys by a more or less longitudinal crest.

M^1 — The anteroloph is a smooth ridge with a slightly concave anterior wall. There may be a small antero-lingual cingulum at the base of the anteroloph. In 2 specimens the anteroloph is slightly subdivided into two cones. The anterolophule is forked in two cases, but generally it is a simple ridge towards the lingual part of the anteroloph. Shortly behind the anteroloph this ridge may be sharply bent, and the posterior wall of the anterocone may show a tiny protrusion towards the anterolophule, indicating a tendency towards the development of a forked anterolophule. There is a lingual spur on the anterolophule in two cases. The posterior protolophule is always present. In addition an anterior connection may be present, either complete (15), or interrupted (3). In 55 cases it is absent. The sinus is transverse, blocked by a low cingulum ridge. The mesoloph is absent (12), short (45), of medium length (13), or long (1). The entoloph is frequently constricted or even interrupted between protocone and protolophule. The posterosinusid is absent in a few cases.

Plate 8

All figures approx. 20 ×.

Fahlbuschia freudenthali Antunes & Mein, 1981

Regajo 2

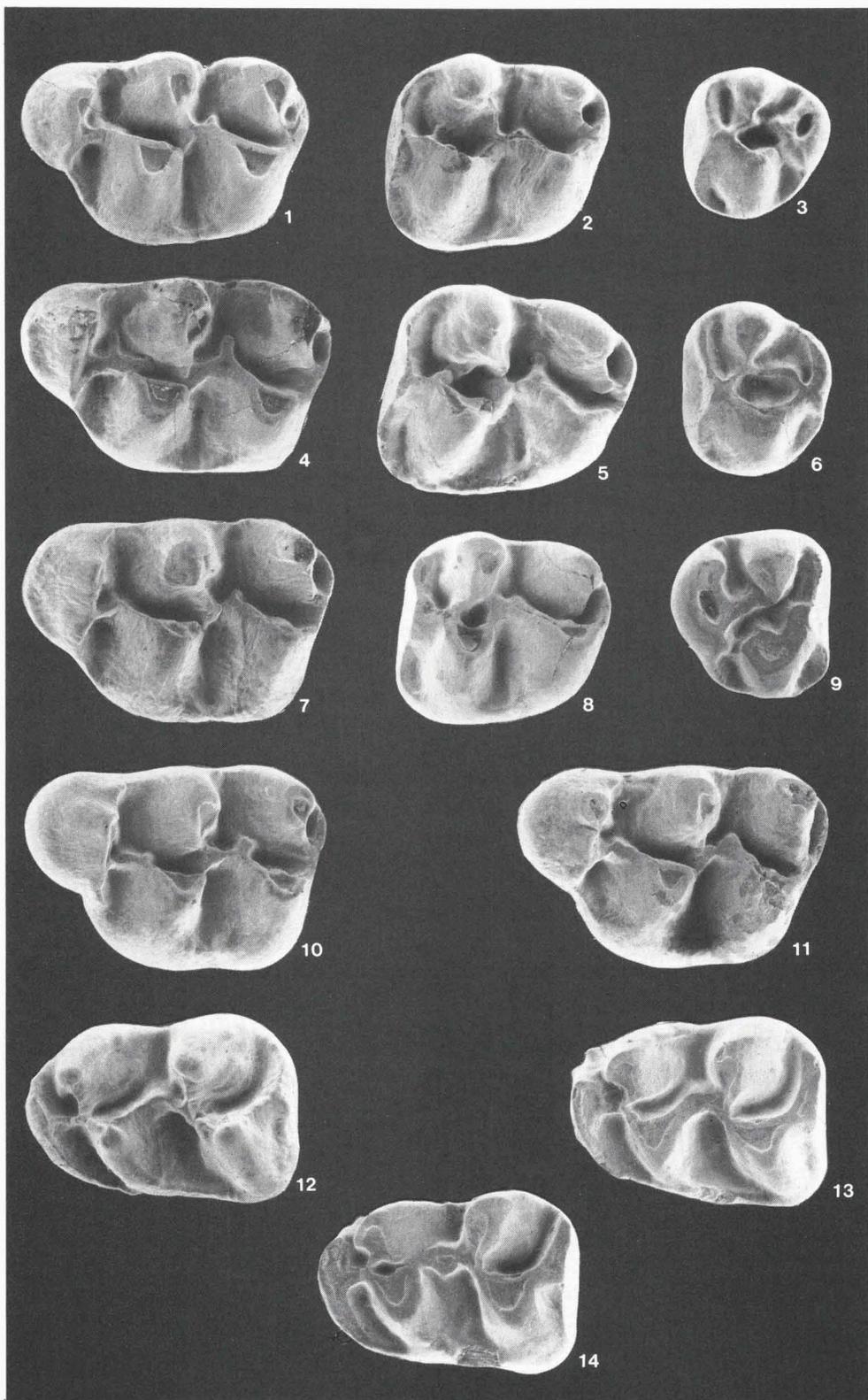
- Fig. 1. M^1 sin., RGM 385 340.
- Fig. 2. M^2 sin., RGM 385 418.
- Fig. 3. M^3 sin., RGM 385 497.
- Fig. 4. M^1 sin., RGM 385 342.
- Fig. 5. M^2 sin., RGM 385 422.
- Fig. 6. M^3 sin., RGM 385 498.
- Fig. 7. M^1 sin., RGM 385 350.
- Fig. 8. M^2 sin., RGM 385 417.
- Fig. 9. M^3 dext., RGM 385 540.
- Fig. 10. M^1 sin., RGM 385 361.
- Fig. 11. M^1 sin., RGM 385 372.

Fahlbuschia darocensis (Freudenthal, 1963)

Borjas

- Fig. 12. M_1 sin., RGM 268 026.
- Fig. 13. M_1 sin., RGM 268 033.
- Fig. 14. M_1 sin., RGM 268 035.

Plate 8



M² — The protolophule is mostly double (55), but it may be anterior with a weak posterior connection (1), posterior with a weak or interrupted anterior connection (11), or only the posterior connection is present (12). Like in M¹, but less frequently, the entoloph may be interrupted or constricted. The mesoloph is absent (15), short (38), of medium length (18), or long (8). The metalophule is anterior (11), double (9), transverse (4), posterior (43), or absent (7).

M³ — In about 10 cases the neo-entoloph is somewhat interrupted, and in 2 specimens protocone and hypocone are separated by a deep furrow. These specimens (RGM 385 540 and 385 668) may belong to the same individual. They have a well-developed spur on the lingual wall of the protocone, indicating the anterior part of the ancient entoloph. Some other specimen have such a spur too, but much less developed. Most specimens have axioloph and centroloph (68); no axioloph (5), no centroloph (5). Only 1 specimen has a mesoloph.

Discussion

As explained before the homogeneity of the type-population of *F. freudenthali* from Amor is doubtful, and the collection is very small. For these reasons it will always be difficult to attribute another population to this species.

As far as M₁ and M¹ are concerned both populations seem to coincide. The length/width ratio of M₁ is identical (1.41 in Amor, 1.42 in Regajo 2; both very low values for *Fahlbuschia*). In the Amor population 2 of the 3 specimens of M¹ have an anterior protolophule, in Regajo 2 25 % of the specimens show this feature. In most other *Fahlbuschia* populations of similar size this feature is much less frequent. So, the M₁ and M¹ from Regajo cannot be distinguished from *F. freudenthali* and must be attributed to this species. This does not apply to M² and M³: in the overwhelming majority of M² from Regajo 2 the protolophule is double, in the specimens from Amor only the posterior connection is present. In the M³ from Regajo 2 most specimens have axioloph and centroloph, and no mesoloph; in the M³ from Amor, on the other hand, the axioloph is absent or incomplete, 1 specimen has a mesoloph, and in the other the centroloph is missing. Though these morphotypes do occur in the Regajo 2 material their frequency is so low, that it is improbable that they represent the same species. These facts agree with the supposition stated above, that the M² and M³ from Amor do not belong to *F. freudenthali*.

Locality Valdemoros 3E (code VA 3E, Zone D3)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	26	17.1	18.00	19.7	0.687	31	11.4	12.61	13.5	0.552
M ₂	26	14.8	16.27	18.1	0.690	30	11.8	13.39	14.8	0.687
M ₃	15	13.2	13.93	14.7	0.472	17	11.3	11.92	12.7	0.375
M ¹	15	20.3	21.00	22.4	0.692	16	13.4	14.11	14.8	0.433
M ²	17	15.2	16.16	17.2	0.587	21	12.3	13.81	15.1	0.659
M ³	16	10.3	11.69	13.1	0.840	16	11.2	12.14	13.5	0.543

Description

M_1 — Length/width ratio 1.43, prelobe ratio 0.19. The anteroconid is triangular with a long ridge descending labially, closing the protosinusid. In about half the number of specimens this ridge is not a smooth continuation of the anteroconid, but it is slightly set off from that cusp by a little constriction. The anterosinusid is mostly small, shallow, rarely deep. The anterior wall of the metaconid is smooth (4), provided with a protruding spur (9), or there is a connection between metaconid and anteroconid through the middle of the valley (10), or along the border of the molar (1). The metalophulid is directed forward, either obliquely or curved, towards the middle of the anterolophulid. The anterolophulid is complete (18), or interrupted in front of the junction with the metalophulid (6). The mesolophid is absent (2), short (21), or of medium length (3). The sinusid is directed obliquely forward.

M_2 — The lingual anterolophid is small, but generally present. Together with the metalophulid it tends to form a very small anteroconid and anterosinusid. The labial anterolophid descends to close the protosinusid. The mesolophid is absent (10), short (10), or of medium length (1). The sinusid is generally directed obliquely forward, less frequently slightly curved backwards.

M_3 — The lingual anterolophid is absent (3), or visible (4). There is no mesolophid, but the posterior branch of the protoconid may be slightly curved. There is hardly an entoconid, or no entoconid at all. The hypolophulid is very short or almost absent (7), or somewhat longer (3); in the latter case the sinusid is wider and less deeply cut into the molar than it is in the other ones. The posterosinusid is small.

M^1 — The anteroloph is a smooth ridge, often slightly concave anteriorly. The anterior protolophule is absent (10), or present (6). In 2 out of 14 specimens a cingulum on the antero-lingual corner of the anteroloph is weakly indicated. The mesoloph is short (8), or of medium length (7). In a few specimens the posterior wall of the paracone has a small protrusion. The sinus is transverse or directed obliquely backward, dammed by a ridge along the border of the molar. The metalophule is absent (1), or posterior (15), the posterosinus has disappeared in 1 specimen.

M^2 — The protolophule is always double; both branches are equally developed. The mesoloph is short (8), of medium length (5), or long (4). The metalophule is anterior (2), anterior plus a trace of a posterior connection (1), double (4), posterior (4), or posterior with a trace of an anterior connection (3). The sinus is transverse or directed obliquely backward, closed by a cingulum ridge. The postero-internal corner of the molar is generally rounded and reduced. The posterosinus has vanished in 2 specimens.

M^3 — Axioloph and centroloph are always present, the mesoloph is always absent. Two specimens out of 10 have a remnant of the ancient entoloph, whereas in 1 specimen the curved entoloph is complete. The axioloph is interrupted in one case. The neo-entoloph is always closed, but the exterior part of the sinus is always visible and may be fairly large.

Fahlbuschia darocensis (Freudenthal, 1963)

Pl. 8, figs. 12-14; Pls 9, 10.

Type-locality — Manchones 1, Zaragoza, Spain.

Holotype — Mandible with M_1 - M_3 dext., Museo de Paleontología, Sabadell, figured in Freudenthal, 1963, pl. 1, fig. 11.

Distribution — Aragonian Zones E, F and G.

Fahlbuschia darocensis was first described by Freudenthal (1963) under the name *Cricetodon darocensis*. Mein & Freudenthal (1971a) placed it in the new genus *Fahlbuschia*. Until now *F. darocensis* was known from the localities Manchones 1, Las Planas 4A, Las Planas 4B, Arroyo del Val 6, and Armantes 3 (Freudenthal, 1963). Antunes & Mein (1977) described it from Póvoa de Santarém (Portugal).

Fahlbuschia cf. *darocensis* has been described from Armantes 4 (Freudenthal, 1963), Armantes 7 (Freudenthal, 1967), Vieux-Collonges (Guérin & Mein, 1971), Pero Filho (Antunes & Mein, 1977), Libros corte 2 (Adrover et al., 1978) and Pont d'Aiguines (Gigot et al., 1976).

In our recent campaigns we encountered *F. darocensis* in the localities of Valalto 1, Valalto 2B, Valalto 2C, Las Planas 4C, Las Planas 5B, Borjas, Villafeliche 9, Alcocer 2, Toril 1, Las Planas 5H, and Solera.

Locality Las Planas 4C (code LP 4C, Zone E)

A fragmentary M_1 , M_2 and M^2 prove the occurrence of this species at a level several metres above Las Planas 4B.

Locality Valalto 1 (code VT 1, Zone G)

Two M_1 , a M_2 and a M^3 from this locality belong to *F. darocensis*.

Locality Valalto 2B (code VT 2B, Zone F)

The few available specimens do not differ from the material from Valalto 2C.

Locality Valalto 2C (code VT 2C, Zone F)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	10	18.9	20.27	21.1	0.785	14	12.7	13.71	14.8	0.649
M_2	4	16.9	17.58	18.1	0.512	4	13.7	14.40	14.8	0.497
M_3	4	14.1	15.15	16.2	0.904	3	11.0	11.93	12.6	0.833
M^1	9	22.4	23.72	25.4	1.043	10	14.7	15.50	17.0	0.709
M^2	10	16.5	17.71	18.5	0.664	9	13.9	15.31	16.7	0.816
M^3	12	11.5	12.37	13.2	0.647	12	12.6	13.46	14.2	0.545

Description

M_1 — Length/width ratio 1.48, prelobe ratio 0.18. The anteroconid is small, triangular, with a descending labial ridge. The anterosinusid is small and shallow. The anterior wall of the metaconid is smooth (3), slightly protruding (2), bearing a forward spur (1), or connected to the anteroconid through the middle of the anterosinusid (5). In RGM 252 713 the anterosinusid is not so shallow, and the anteroconid has a symmetrical aspect because of its labially and lingually descending ridges. A direct connection between the metaconid and the anteroconid lies close to the axis of the molar (RGM 252 713), and appears to form a second anterolophulid. RGM 252 707 has two anterolophulids: one from the metalophulid towards the anteroconid and one from the

protoconid towards the labial anterolophid; in addition there is a strong forward spur on the anterior wall of the metaconid. The metalophulid is absent (3), directed obliquely forward towards the middle of the anterolophulid (8), or towards the anterior corner of the protoconid (2). The mesolophid is absent (5), or short (8). The sinusid is directed obliquely forward, generally closed along the border. The posterosinusid is not closed by the posterolophid. Often the posterior wall of the hypoconid-posterolophid is concave.

M₂ — The scarce material hardly allows a description. In 2 specimens there is a small anteroconid, lingual anterolophid and anterosinusid; in the others these are not visible. The mesolophid is absent (1), or short (4). The posterosinusid remains open. The posterior wall of hypoconid-posterolophid is concave.

M₃ — The lingual anterolophid is small but present. There is no mesolophid. The entoconid has disappeared. The sinusid is curved backwards, entering deeply into the molar. There is no hypolophulid. The posterosinusid remains present.

Cranium — RGM 268 315 is a fragmentary cranium, partly preserved as a natural cast, that allows the study of some features of *Fahlbuschia* that were unknown so far. The incisor probably is proodont or orthodont. The foramen incisivum extends as far backwards as the posterior wall of the anterocone of M¹. The distance between the protocones of the first molars is about 1.6 times the length of M¹. The suture between maxillary and palatal bone lies at the level of the anterior part of M². The palate bone probably extended as far backward as the posterior border of M³, or farther. The foramen incisivum is about three times as long as the length of M¹. The distance from the incisor to the anterior border of the foramen incisivum is somewhat larger than the length of M¹. The lower border of the foramen infraorbitale lies very low. The internal wall of this foramen appears to be almost vertical, the maxillary bone being practically flat. Only the lower part of the ramus inferior of the processus zygomaticus is preserved; it makes an angle of c. 30° with the vertical axis. Consequently the lower part of the foramen infraorbitale appears to be rather widely open. The entire snout is curved downwards, relative to the tooth rows, but this may be due to postmortal deformation. There is no prominent crest on the intermaxillary. Supraorbital constriction and ridges are less prominent than they are for example in *Cricetus*.

M¹ has no anterior protolophule, no mesoloph, an extremely posterior metalophule and no posterosinus. M² has no anterior protolophule, the smallest possible trace of a mesoloph, and the metalophule is transversely anterior. M³ has an axioph, no mesoloph, and a centroloph of which the labial part is interrupted, or no centroloph at all.

M¹ — The anterior wall of the anteroloph is convex or slightly concave. The anterolophule is longitudinal, either simple (5), or bifurcated shortly behind the anterocone (3). There is no anterior protolophule. The mesoloph is absent (4), or very short (4). The metalophule is posterior; in 1 specimen the posterosinus has disappeared.

M² — The protolophule is double (3), posterior (3), or posterior with a trace of the anterior connection (2). The mesoloph is absent (5), or short (3). The metalophule is anterior (2), interrupted (2), or posterior (4). The postero-lingual corner of the molar is quite reduced in some cases.

M³ — The axioph is absent (1), interrupted (3), or complete (4). The centroloph is absent (1), or present (8), often interrupted. There is no mesoloph. The sinus may be absent (1), but generally its external part is recognizable (7). One of these specimens is extremely reduced: apart from the anteroloph and posteroloph the tooth exists of nothing else but a protocone, a paracone, and a transverse protolophule, connected to the posterior part of the protocone.

Locality Manchones 1 (code MA or MA 1, Zone G)

The type-collection of *F. darocensis* has been reexamined in order to make the description comparable to the descriptions of other populations given in this paper. All features not mentioned are as described by Freudenthal, 1963.

Description

The mandible and the maxilla show the characteristic features of *Fahlbuschia*.

M₁ — The metaconid-anteroconid connection through the anterosinusid is absent (43), interrupted (12), or complete (20). The mesolophid is absent (36), or short (41). The specimen MA 2107 with mesolophid of medium length, mentioned by Freudenthal (1963) is certainly not a *Fahlbuschia*. It will be treated afterwards. The metalophid is forward in most cases, transversely posterior in 1, and absent in 3 specimens. In some cases the anterolophid is interrupted. The posterior hypolophid is present in one case. The posterior wall of the hypoconid is concave. The posterosinusid is generally not closed by the posterolophid.

M₂ — The mesolophid is absent (35), short (27), of medium length (5), or long (1). There often is a small anterosinusid, the lingual anterolophid is often present, not always. The posterolophid tends to close the posterosinusid a little bit more than it does in M₁. The posterior wall of the hypoconid is concave.

M₃ — The mesosinusid and posterosinusid are often not closed by cingulum ridges along the border. In many cases there is no hypolophid and the entoconid (or what is left of it) is no longer on the lingual border of the molar, but it has moved inward, towards the ectolophid. The most frequent morphotype is one that has a moderately long hypolophid, directed from the curve of the ectolophid slightly forward, and that shows no trace of an entoconid cusp at all. In a few specimens the flat area that represents the entoconid has a concave lingual wall, and in 1 specimen this area is split up into two diagonal crests.

M¹ — A cingulum at the base of the anteroloph is present (64), or absent (17); it is often well developed. In fresh or little-worn specimens the anterolophule is simple in 11 specimens; in 29 specimens there is either a backward spur on the anterocone, or the anterolophule is forked, often forming a small funnel with the anterocone. The anterior protolophule is present in 2 specimens only.

M² — The protolophule is double (21), posterior (25), or posterior with a trace of the anterior connection (9). The metalophule is posterior (40), double (12), posterior with a trace of the anterior connection (1), or anterior (1). The posterior connection is often almost longitudinal, but the posterosinusid remains visible in all specimens except 1.

M³ — In most specimens axioph and centroloph are present (27), there may be an additional trace of the mesoloph (2); there is a centroloph and no axioph (3), axioph and no centroloph (1), or both these crests are absent (1). The neo-entoloph is generally complete, sometimes interrupted (4), or completely open (1).

Locality Las Planas 5B (code LP 5B, Zone G)

A few specimens from this locality fully agree in size and morphology with the material from other, richer, localities.

Locality Borjas (code BOR, Zone G)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	37	18.6	20.41	22.4	0.800	39	12.5	13.55	15.3	0.648
M ₂	29	17.2	18.09	19.1	0.532	29	13.9	14.78	15.5	0.387
M ₃	22	13.4	15.00	16.5	0.825	23	11.9	12.91	13.6	0.432
M ¹	30	23.3	24.71	26.3	0.713	34	14.5	15.48	16.4	0.409
M ²	41	16.2	17.78	19.0	0.707	39	13.9	15.15	16.4	0.560
M ³	24	11.5	12.22	13.8	0.580	24	12.2	13.16	13.8	0.418

Description

M₁ — Length/width ratio 1.51, prelobe ratio 0.20. The anteroconid is a small triangle. Two types may be distinguished: either the asymmetrical one with a descending labial cingulum ridge (12), or a more symmetrical one with both a labial and a lingual ridge (20). In the latter case the anterosinusid tends to be more open, wider and deeper than it is in the specimens with asymmetrical anteroconid, where the direct connection between metaconid and anteroconid tends to be present, or at least indicated. The specimens with symmetrical anteroconid are on the average longer and relatively narrower than the other ones. A clear distinction between the two types cannot be made, however. The forward protrusion of the metaconid may be present in the specimens with symmetrical anteroconid as well. The anterior wall of the metaconid is smooth (13), there is an anterior protrusion or spur (9), or there is a direct connection with the anteroconid through the anterosinusid (9). The metalophulid is generally directed obliquely forward (24), sometimes interrupted (3), transversely towards the middle of the protoconid (3), or double (3); in the latter case one branch points obliquely forward, the other one is transverse (2), or backward (1). In several cases the posterior wall of the metaconid is angular, indicating a vestige of a posterior metalophulid. The mesolophid is absent (21), or short (14). The posterolophid generally does not close the posterosinusid. The sinusid is directed obliquely forward, closed by a ridge along the border, which descends from the protoconid. The posterolophid often makes a sharp angle at the middle of the posterior border of the molar, causing the posterior wall of the hypoconid to be concave.

M₂ — Lingual anterolophid and anterosinusid have practically disappeared, but there often is a small anteroconid at the junction of anterolophid and metalophulid. The metalophulid is anterior, and in one case a spur on the hind corner of the protoconid indicates a posterior metalophulid. The mesolophid is absent (8), short (16), or of medium length (3), better developed than in M₁. The sinusid is transverse or curved backwards, closed by a cingulum ridge descending from the protoconid. The posterolophid closes the posterosinusid (at a low level). The posterior wall of the hypoconid is concave. Hypoconid and posterolophid often form a 90° angle.

M₃ — The lingual anterolophid has practically disappeared. A mesolophid is present in 1 specimen. The sinusid is transverse or curved backwards. The entoconid may be reduced to zero, but often it forms a flat, broad area. The posterosinusid is closed (3), lingually open (10), or absent (6).

Maxilla — In the single maxilla fragment available the foramen incisivum ends a little behind the anterior border of the first alveolus. The distance between the protocone of M¹ and the cranial axis is c. 0.6 times the length of M¹.

M¹ — The anterior wall of the anteroloph is smoothly convex or – less frequently – somewhat concave. There may be a cingulum at the antero-lingual base of the anteroloph: absent (20), present (11), or fairly well developed (1). The anterolophule is longitudinal towards the lingual part of the anteroloph, either simple (10), or bifurcated shortly behind the anteroloph (17). In reality the percentage of specimens with forked anterolophule may be higher still, but this feature disappears easily by wear. There is a trace of an anterior protolophule in 1 specimen, and in 1 specimen the posterior protolophule is curved sharply forward, towards the middle of the protocone; in all other specimens the protolophule is connected to the posterior branch of the protocone. The mesoloph is absent (20), or short (13). The metalophule is always posterior, in one case interrupted. The posterosinus is present (21), or absent (1). The sinus is transverse, blocked by ridges descending from protocone and hypocone in most cases.

M² — The protolophule is anterior plus a trace of a posterior connection (1), double (19), posterior (9), or posterior with a trace of an anterior connection (8). The mesoloph is absent (24), short (12), or of medium length (1). The metalophule is anterior (3), double (15), or posterior (17), in one case interrupted. The sinus is transverse or curved forward, blocked by a ridge descending from the hypocone. The postero-lingual corner of the molar is rounded.

M³ — The axioloph is complete (18), or interrupted (1). The centroloph is present (18), or absent (1). The mesoloph is absent (17), or indicated (2). The hypocone has shifted labially and is reduced in most cases; the external part of the sinus remains generally visible, and may be fairly well developed. In 1 specimen (RGM 268 203) the hypocone is relatively large, not shifted labially, and a small funnel exists lingually of the neo-entoloph. This gives the tooth an aspect like seen in Fig. 2E. Maybe it does not belong to *F. darocensis* but to a *Democricetodon* species of similar size.

Two specimens of *Democricetodon* cf. *gaillardi* have been found in Borjas, and are described in this paper. It is hardly probable, that the M³ mentioned above belongs to *D. gaillardi* since it has no trace of a mesoloph, whereas in *D. gaillardi* from Sansan the mesoloph in M³ is a dominant feature.

Locality Villafeliche 9 (code VL 9, Zone G)

Nine specimens from Villafeliche 9 agree with *F. darocensis*, morphologically and by their size.

Plate 9

All figures approx. 20 ×.

Fahlbuschia darocensis (Freudenthal, 1963)

Borjas

Fig. 1. M₂ sin., RGM 268 065.

Fig. 2. M₃ sin., RGM 268 094.

Fig. 3. M₃ sin., RGM 268 096.

Fig. 4. M₃ sin., RGM 268 107.

Fig. 5. M₃ sin., RGM 268 108.

Fig. 6. M¹ sin., RGM 268 121.

Fig. 7. M¹ sin., RGM 268 116.

Fig. 8. M¹ sin., RGM 268 122.

Fig. 9. M¹ dext., RGM 268 138.

Fig. 10. M² sin., RGM 268 154.

Fig. 11. M³ sin., RGM 268 198.

Fig. 12. M² sin., RGM 268 157.

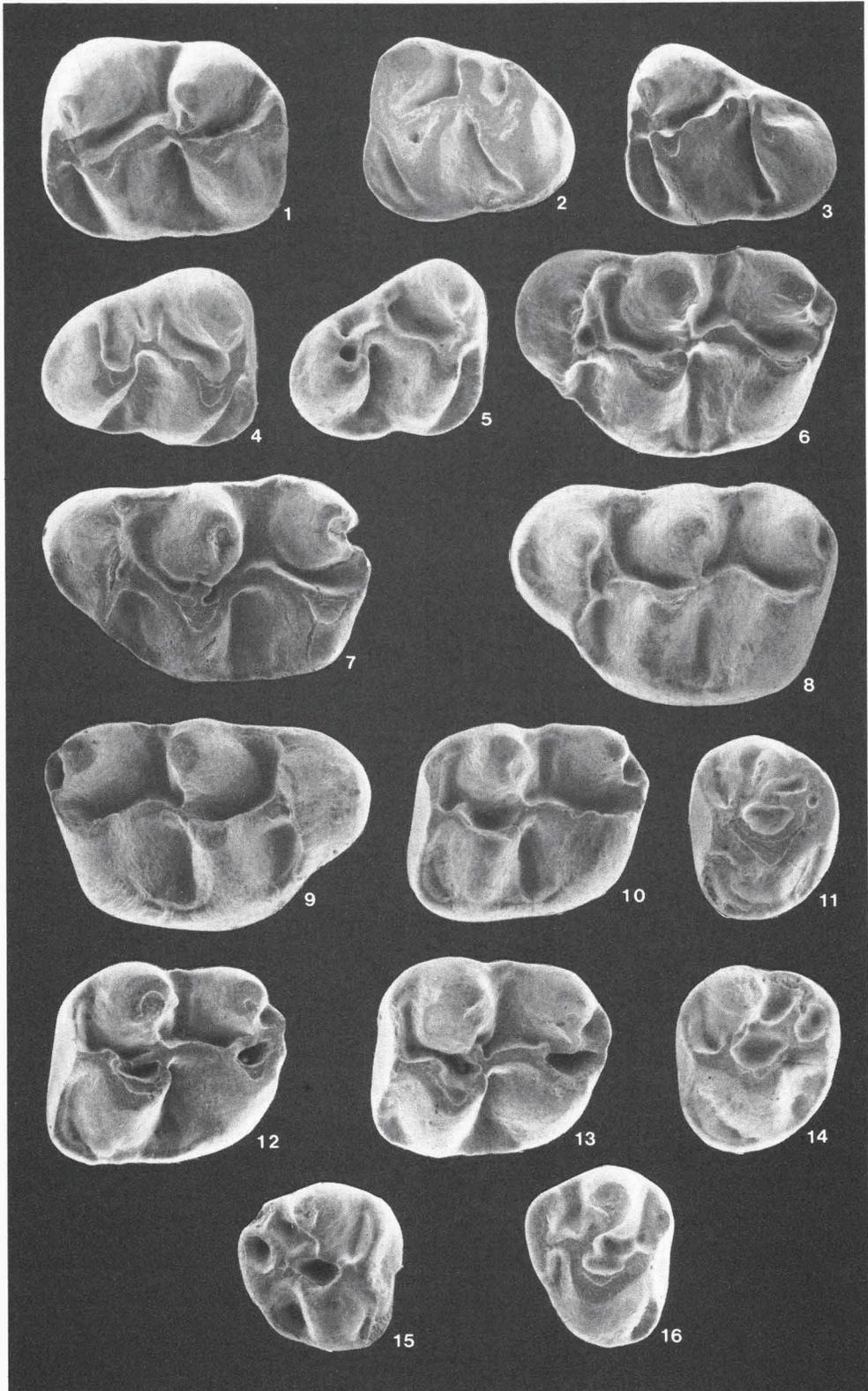
Fig. 13. M² sin., RGM 268 162.

Fig. 14. M³ sin., RGM 268 200.

Fig. 15. M³ dext., RGM 268 203.

Fig. 16. M³ dext., RGM 256 523.

Plate 9



Locality Alcocer 2 (code AC 2, Zone G)

A few specimens from this locality are ascribed to *F. darocensis*. However, the mesolophid of M_2 is fairly well developed, and in M^1 both the protolophule and metalophule are double. Such features may occur in *F. darocensis* but are not characteristic of that species. As far as the measurements are concerned this material may belong to *F. cf. crusafonti* from Solera where an anterior protolophule in M^1 is not uncommon.

Locality Toril 1 (code TOR, Zone G)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	15	18.4	19.71	21.2	0.764	19	12.1	13.41	14.2	0.559
M_2	22	17.1	18.01	19.1	0.619	24	13.5	14.80	15.8	0.652
M_3	12	13.1	14.68	15.3	0.611	13	11.5	12.59	13.7	0.565
M^1	12	22.9	24.66	25.9	0.869	13	14.0	15.74	16.4	0.671
M^2	13	17.0	18.30	19.2	0.677	15	14.2	15.34	16.4	0.599
M^3	7	11.1	11.96	12.6	0.547	7	12.8	13.34	14.5	0.586

Description

M_1 — Length/width ratio 1.47, prelobe ratio 0.19. Some specimens make a stretched impression and have a more or less symmetrical anteroconid; others have a more robust shape and an asymmetrical anteroconid. It is, however, not possible to separate them. Generally the anterosinusid is small and narrow, but in 1 specimen it is almost as deep and wide as the protosinusid (RGM 252 547). The anterior wall of the metaconid is smooth, protruding towards the anteroconid (2), or solidly connected by a crest through the anterosinusid (4). The metalophulid is directed obliquely forward (11), or interrupted (3). The mesolophid is absent (5), short (6), or of medium length (1). The sinusid is directed obliquely forward, blocked by a cingulum ridge descending from the protoconid. The posterior wall of the hypoconid is concave. The posterolophid may or may not close the posterosinusid.

M_2 — The lingual anterolophid is small, but – in not too much worn specimens – almost always visible, and it may enclose a tiny anterosinusid. The mesolophid is absent

Plate 10

All figures approx. 20 ×.

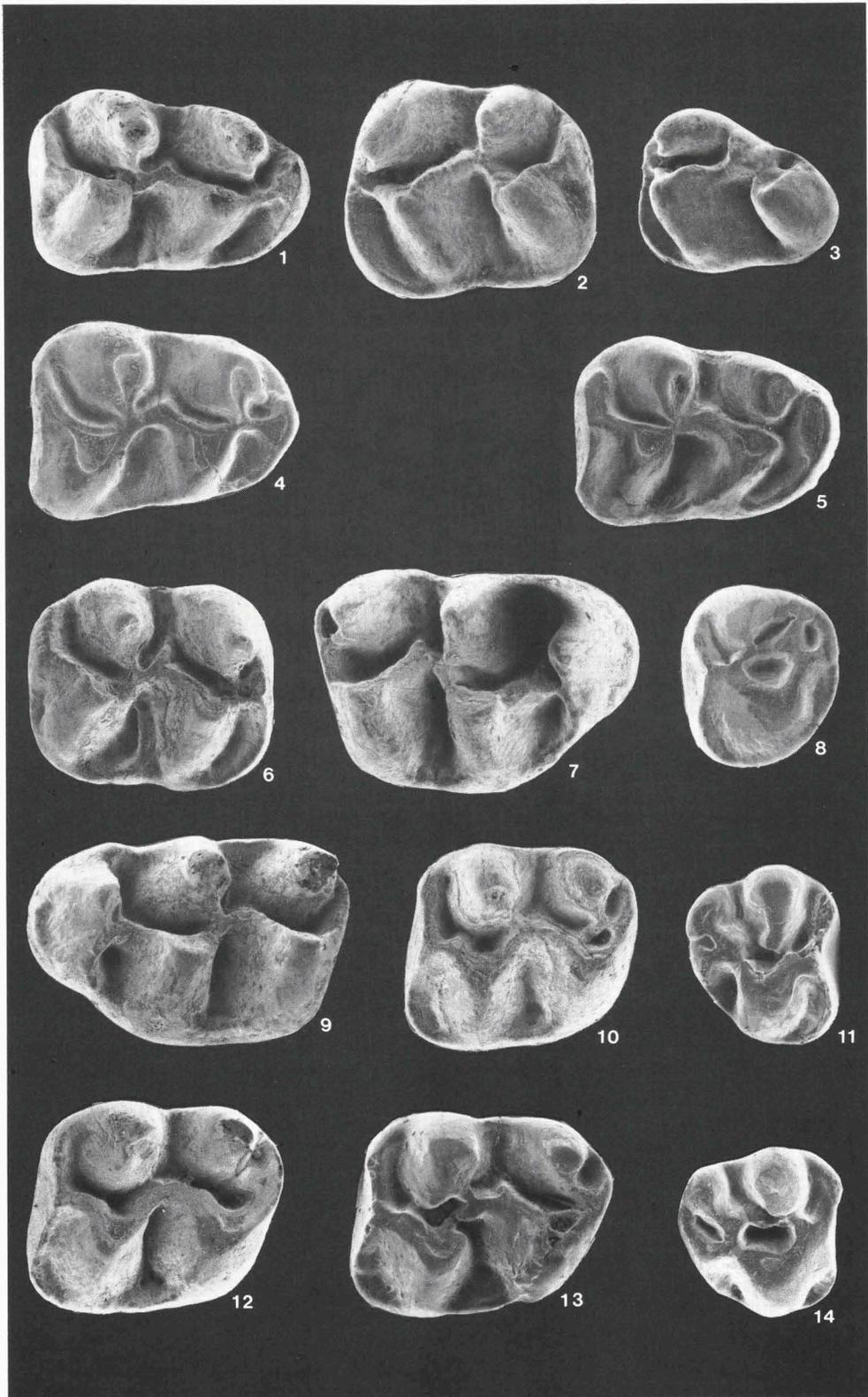
Fahlbuschia darocensis (Freudenthal, 1963)

Toril 1

- Fig. 1. M_1 sin., RGM 252 553.
 Fig. 2. M_2 sin., RGM 252 556.
 Fig. 3. M_3 sin., RGM 267 633.
 Fig. 4. M_1 dext., RGM 252 552.
 Fig. 5. M_1 dext., RGM 252 551.
 Fig. 6. M_2 dext., RGM 252 561.
 Fig. 7. M^1 dext., RGM 252 506.

- Fig. 8. M^3 sin., RGM 267 628.
 Fig. 9. M^1 sin., RGM 252 519.
 Fig. 10. M^2 sin., RGM 252 527.
 Fig. 11. M^3 dext., RGM 267 629.
 Fig. 12. M^2 sin., RGM 252 524.
 Fig. 13. M^2 sin., RGM 252 532.
 Fig. 14. M^3 dext., RGM 267 630.

Plate 10



(13), or short (9). The sinusid is directed obliquely forward, closed by a cingulum ridge descending from the protoconid. Two specimens have an ectomesolophid. The posterior wall of the hypoconid is concave. The posterolophid closes the posterosinusid, or leaves this valley open.

M_3 — The anterolophid is like in M_2 . The sinusid is curved backwards. The posterosinusid is closed or lingually open.

M^1 — The anterior wall of the anterocone is smoothly convex or slightly concave, indicating a beginning of subdivision. There often is a small cingulum visible at the base of the antero-lingual wall of the anterocone. In almost all sufficiently fresh specimens the anterolophule is bifurcated shortly behind the anterocone, sending a longitudinal branch towards the lingual anteroloph and a transverse labial branch towards the labial end of the anterocone. In addition to the always present posterior protolophule, 2 specimens out of 12 have a low anterior protolophule. The mesoloph is absent (6), or short (8), the short mesoloph often being nothing else but the labial curve of the entoloph. The sinus is often blocked by a low cingulum ridge, and such a ridge, much higher and better developed, is frequently found at the entrance of the anterosinus. The metalophule is directed backwards, the posterosinus remains present, but may disappear through wear.

M^2 — The protolophule is double (5), posterior (6), or posterior with a trace of an anterior connection (3). The mesoloph is absent (6), or short (8), like in M^1 . The sinus is transverse, or directed obliquely backward, generally blocked by a fairly high cingulum ridge descending from the hypocone. In RGM 252 532 the sinus is curved forward strongly, and the entoloph begins at the middle of the labial wall of the protocone, a position that reminds one of the theory on the rotation of the protocone of M^3 , as explained before. The metalophule is generally posterior, rarely double. The posterosinus is as in M^1 .

M^3 — The axioloph is complete (6), or interrupted (1). There is always a centroloph, only 1 specimen has a mesoloph. The degree of development of the external part of the sinus is variable.

Locality Las Planas 5H (code LP 5H, Zone G)

Twelve specimens from this locality belong to *Fahlbuschia*. Most specimens are rather large, and are therefore attributed to *F. cf. crusafonti*. A single M_1 (19.6×13.8) is considerably smaller, falls within the size range of *F. darocensis* and is attributed to that species.

It is a typical *Fahlbuschia* with a smoothly curved anterolophid, lying close to the metaconid. The metaconid sends a well-developed spur towards the anteroconid. The mesolophid is short and broad.

Fahlbuschia larteti (Schaub, 1925)

Type-locality — La Grive, France.

Lectotype — Maxilla sin., with M^1 - M^3 , no. La Gr 145, Mus. Sci. Nat. Lyon, figured in Schaub, 1925, pl. 3, fig. 3.

Distribution — Upper Aragonian.

Freudenthal (1963) distinguished *F. darocensis* from *F. larteti* by its slightly smaller dimensions, the better developed connection between anteroconid and metaconid, better developed mesolophids and mesolophs, less reduced third molars, and the better developed anterior protolophule in M^2 .

Schaub (1925) cited *F. larteti* from La Grive-St. Alban and Vieux-Collonges. The form from Vieux-Collonges is certainly not *F. larteti*, nor is it *F. darocensis*. Its M_1 has a relatively wide anterosinusid, no spur on the anterior wall of the metaconid, and a rather high length/width ratio (1.58) in M_1 . In M^2 the anterior protolophule is frequently absent. For these reasons the form from Vieux-Collonges may be a *Pseudofahlbuschia*.

All other citations of *F. larteti* (see chapter on literature citations) refer to very small populations and/or they have been transferred to other species of *Fahlbuschia* (mainly *F. crusafonti*) subsequently. This leaves us with the original citation from La Grive-St. Alban and the one from Armantes 7, that will be treated later.

Guérin & Mein (1971) state that three different faunal niveaus are present in the La Grive quarries, the middle one being the one containing the classical La Grive fauna (carrière M and L7). We may assume, that the holotype of *F. larteti* originates from this niveau. The upper level (L3) contains a large, elongated *Fahlbuschia*, cited as *Fahlbuschia* sp. by Guérin & Mein.

A revision of the La Grive *Fahlbuschia* is being undertaken by Freudenthal & Mein (in press), but it seems appropriate to analyze *F. larteti* shortly in this place, because *F. larteti* is only known by the original description of Schaub, which was quite good at the time, but is outdated now.

F. larteti indeed is somewhat larger than *F. darocensis* (mean length M_1 21.05, mean length M^1 25.15), but the difference is not so large that it would warrant a specific separation by itself. In this respect it is important to know that the upper size limit of both species is almost identical, and that the differences in the mean lengths are caused by the fact that the lower size limit is smaller in *F. darocensis* than it is in *F. larteti*. The length/width ratio of M_1 in both populations is identical.

In *F. larteti* the anteroconid-metaconid connection through the anterosinusid in M_1 is frequent, and often strongly developed. The mesolophid is short and broad, seldom absent or of medium length. In M_2 the lingual anterolophid is very small or absent. The mesolophid is absent, or seldom of medium length. In M_3 the entoconid is very much reduced, as well as the entire posterior part of the molar. The posterolophid is low, the sinusid strongly curved backwards.

In M^1 the anterocone is simple or – rarely – it shows a beginning of subdivision. The anterolophule may possess a labial spur, but this spur never reaches the anterocone. There is no cingulum ridge on the anterior wall of the anteroloph. There is no anterior protolophule. The mesoloph is short or of medium length. In M^2 the anterior protolophule is absent or present. The mesoloph is absent.

F. larteti may be distinguished from *F. darocensis* by:
 its better developed anteroconid-metaconid connection in M_1 ;
 more reduced lingual anterolophid in M_2 ;
 more reduced M_3 ;
 absence of a cingulum on the anterior wall of the anteroloph of M^1 ;
 more reduced anterior protolophule in M^2 .

Furthermore in *F. larteti* the mesoloph(id)s of the second molars seem to be more reduced than they are in the first molars, whereas in *F. darocensis* this is the opposite.

Fahlbuschia sp.

The population from Armantes 7 (Zone F), first described by Freudenthal (1963), remains problematic. After the revision by Freudenthal (1967) again some new material was collected. In Fig. 4 the histograms of the lengths of M_1 and M^1 of the entire collection

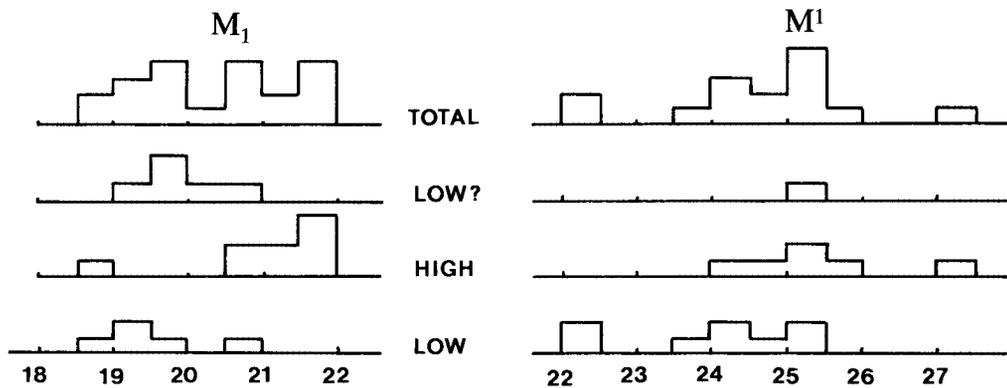


Fig. 4. Histograms of lengths of M_1 and M^1 from Armantes 7.

are given. Since the locality of Armantes 7 contains two different beds, the exact provenance of the specimens is indicated too. It is clear that there are significant differences between the size distributions of the populations from these two levels. The material from the lower level (especially the M_1) is smaller than the material from the upper level. But furthermore, the distribution of the population from the lower level appears not to be homogeneous: 1 M_1 is considerably smaller, and 1 M^1 seems to be larger than the rest of the material. Nevertheless the entire material falls within the size limits of *F. darocensis* and *F. larteti*.

It cannot belong to *F. larteti* because in M_1 the anteroconid-metaconid connection is less developed, and the anteroconid is farther apart from the metaconid, and in M^1 there often is an ingulum ridge in front of the anteroloph.

The material is best treated as belonging to *F. darocensis*, though this does not explain the irregularities in the size distributions. One specimen, M^1 no. 58-128, has an anterior protolophule. This feature is rather frequent in the *Fahlbuschia* from Solera (cf. *crusafonti*), but it may occur, though rarely, in the type population of *darocensis*. It cannot be excluded that the Armantes 7 material is a mixture of *F. darocensis* and *F. cf. crusafonti*.

Plate 11

All figures approx. 20 ×.

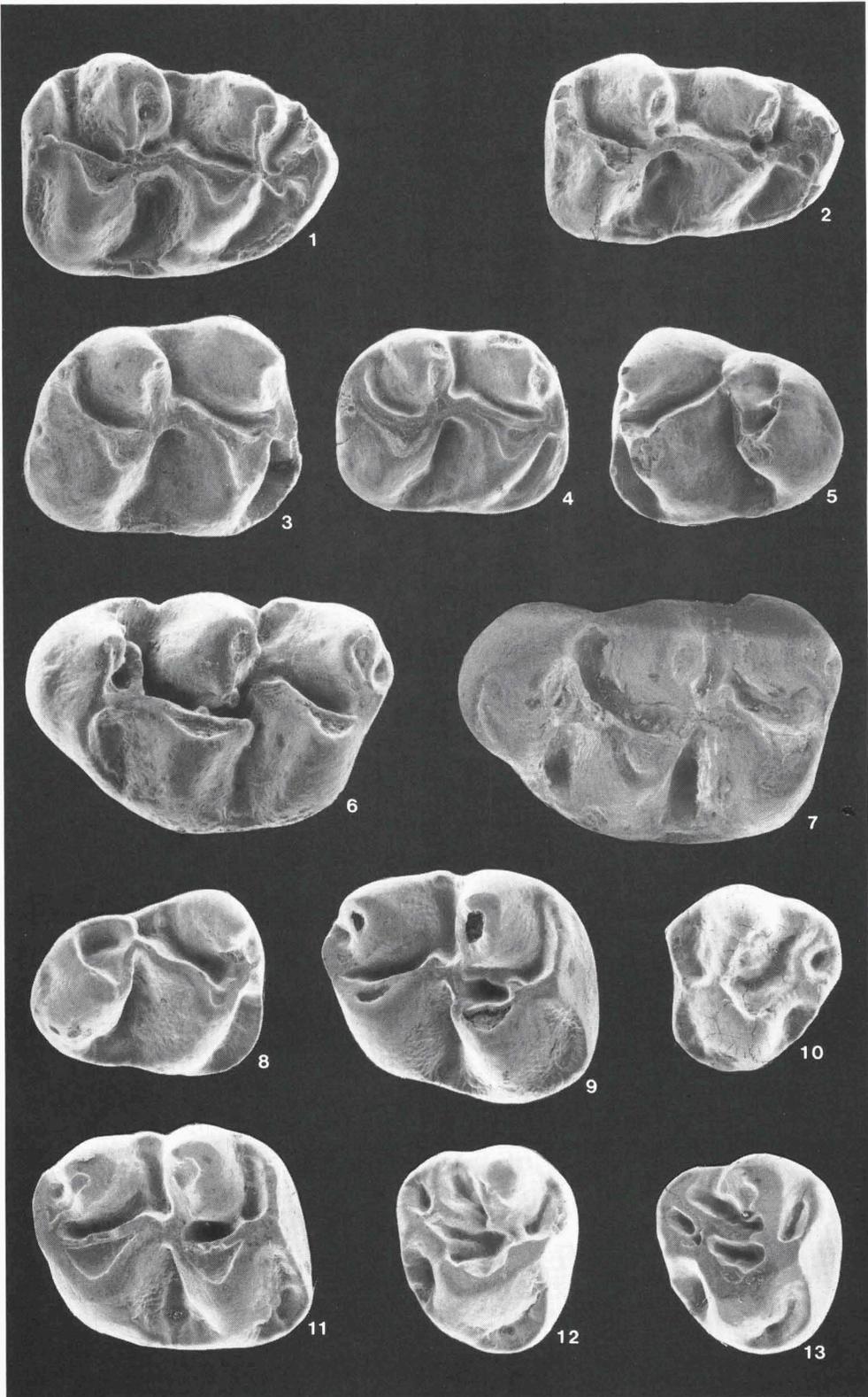
Fahlbuschia cf. *crusafonti* Agustí, 1978

Solera

- Fig. 1. M_1 dext., RGM 255 802.
- Fig. 2. M_1 dext., RGM 255 809.
- Fig. 3. M_2 dext., RGM 255 814.
- Fig. 4. M_2 dext., RGM 255 815.
- Fig. 5. M_3 sin., RGM 255 832.
- Fig. 6. M^1 sin., RGM 255 768.
- Fig. 7. M^1 sin., RGM 268 408.

- Fig. 8. M_3 dext., RGM 255 841.
- Fig. 9. M^2 dext., RGM 255 776.
- Fig. 10. M^3 dext., RGM 255 788.
- Fig. 11. M^2 dext., RGM 255 777.
- Fig. 12. M^3 dext., RGM 255 785.
- Fig. 13. M^3 dext., RGM 255 795.

Plate 11



Fahlbuschia crusafonti Agustí, 1978

Type-locality — Sant Quirze, Trinxera (Barcelona, Spain).

Holotype — Mandibula sin., with M_1 - M_3 , VP 570, Museo de Paleontología, Sabadell, figured in Schaub, 1947, fig. 4.

Distribution — Aragonian Zone G and Vallesian Zone H.

In several localities from the Upper Aragonian and Lower Vallesian of our area a very large *Fahlbuschia* is found, that may well represent a new species. Unfortunately none of these localities has yielded a collection sufficiently large to allow a valid and useful description of such a new species.

The problem is greater still, because the two species that should be taken into account for comparison (*F. crusafonti* and *F. ultima* Antunes et al., 1983) are even less well-documented.

Worst of all, our study has shown that as a rule Upper Aragonian and Lower Vallesian localities contain more than one species pertaining to, or resembling *Fahlbuschia*.

In our localities Toril 1, Las Planas 5H and Solera *F. darocensis* and *F. sp. nov. cf. crusafonti* occur together. In Nombrevilla only one species has been found (*F. cf. crusafonti*), and in Carrilanga there seem to be two species.

This complication is certainly not restricted to the Upper Aragonian. In the Middle Aragonian we see the co-occurrence of *F. koenigswaldi* with *Pseudofahlbuschia jordensi*, or *F. freudenthali* with *Renzimys lacombai*, and in the Vallesian locality Molina de Aragón *Renzimys bilobatus* may be based on a heterogeneous material that contains a few specimens of a large *Fahlbuschia*.

A similar situation may be present in Hostalets de Pierola and Sant Quirze. There is a great discrepancy between the sizes of M_1 and M^1 . Normally in *Fahlbuschia* M^1 is about 1.20 times the size of M_1 . On this basis one would expect the M^1 of *F. crusafonti* to reach a length of about 31.1, whereas the maximum length found by Agustí is 27.2. Equally the lower limit of M_1 can be calculated at about 21.8, whereas the minimum actually found is 24.1. On the basis of these extrapolated values the variability coefficient as defined by Freudenthal & Cuenca (1984) would reach values of 18.25 and 17.20, values that are very high in respect to the small number of specimens. It is therefore probable that the type-material of *F. crusafonti* contains two different species. The smaller one of

Plate 12

All figures approx. 20 ×.

Fahlbuschia cf. crusafonti Agustí, 1978

Carrilanga

Fig. 1. M_1 sin., RGM 301 513.

Fig. 2. M_1 dext., RGM 301 514.

Fig. 3. M_2 sin., RGM 267 196.

Fig. 4. M_2 dext., RGM 267 197.

Fig. 5. M_3 dext., RGM 301 515.

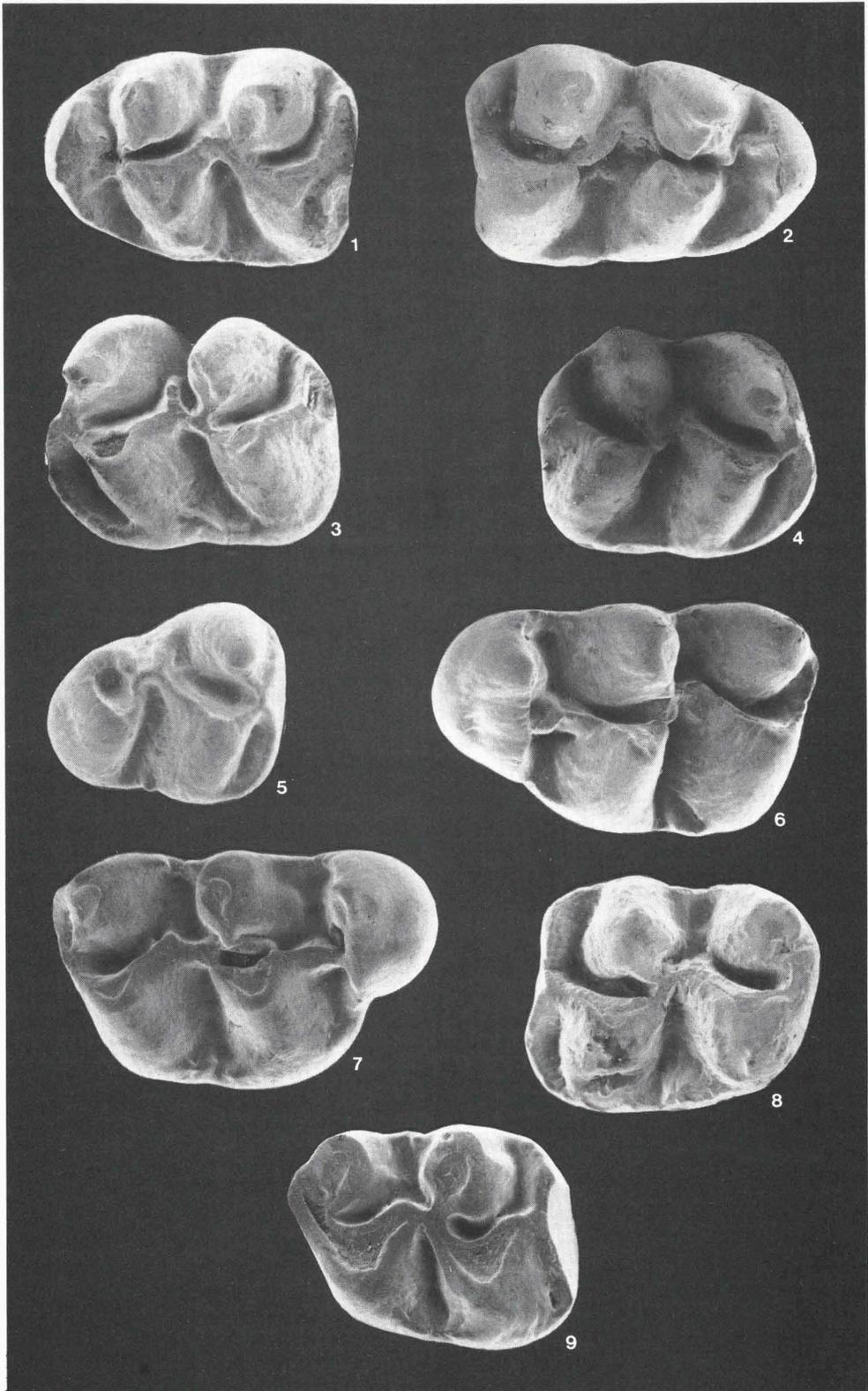
Fig. 6. M^1 sin., RGM 301 517.

Fig. 7. M^1 dext., RGM 301 519.

Fig. 8. M^2 sin., RGM 301 520.

Fig. 9. M^2 dext., RGM 301 523.

Plate 12



these would more or less cover the size distribution of *Renzimys bilobatus* and of *F. sp. nov. cf. crusafonti* from Aragón, the larger one coincides with the dimensions of *F. ultima* from Portugal and with the larger specimens of *Fahlbuschia* from Carrilanga. It is not clear to which one the holotype of *F. crusafonti* belongs.

Schaub (1947) already recognized the existence of two species of different size in the Vallés-Penedés material, calling the smaller one *Cricetodon larteti* and the larger one *Cricetodon cf. larteti*. Our *F. sp. nov. cf. crusafonti* partly agrees in size with *F. larteti* from La Grive, but on the average our form is somewhat larger. Morphologically our new form differs sufficiently from *F. larteti* to exclude the possibility that it belongs to that species.

F. ultima from Azambujeira (Portugal) presents yet another difficulty. Apart from the fact that there is very little material, there is not even a single complete specimen of M_1 . On the basis of its M^1 with split anterocone it may be a very large species of *Renzimys*. It seems best to refrain from creating any new species of large *Fahlbuschia* until statistically reliable populations are found.

Finally, the following descriptions will show that there are considerable morphological differences between the various populations assembled under the name *F. sp. nov. cf. crusafonti*. It is not impossible, that these populations represent more than one species, but, again, the scarcity of the material does not permit to solve this problem.

Through the kind co-operation of Mr Agustí we have been able to reexamine the type material of *F. crusafonti*. We will now give a description of this material using our standardized terminology:

M_1 — The anteroconid is simple and asymmetrical. The labial anterolophid descends towards the protoconid. The lingual anterolophid descends almost vertically; it may be set off from the anteroconid as a sort of stylid. A small stylid may be present at the bottom of the anterosinusid. The mesolophid is short or absent. Metalophid and hypolophid are short and broad: the entoconid may be fused to the ectolophid directly. The valleys between the labial and the lingual cusps are very narrow. Cingulum ridges are not much developed, and in 2 of the 3 specimens the posterosinusid remains completely open.

M_2 — There is no lingual anterolophid. The mesolophid is absent or very short. The valley between protoconid and metaconid is very narrow, the one between hypoconid and entoconid somewhat wider. The sinusid may be blocked by a very low cingulum ridge, the other valleys are open.

M_3 — A very small lingual anterolophid remains. There is no mesolophid. The sinusid is transverse or strongly curved backwards. The entoconid is larger than it normally is in *Fahlbuschia*, and it points forward, partly closing the mesosinusid; it is more a flat area than a cusp; its lingual wall is concave or grooved. The sinusid is open or blocked by a low cingulum ridge. The posterosinusid is closed or lingually open.

M^1 — The anterocone is simple, asymmetrical, without a cingulum at the base of the antero-lingual border. The anterior wall may be concave. Protosinus and sinus are open, anterosinus and mesosinus may be blocked by a low cingulum ridge. An anterior protolophule may be vaguely indicated, the posterior protolophule is the normal one. The valleys between the labial and lingual cusps are narrow. There is a short mesoloph. The posterosinus is small, but present.

M^2 — The protolophule is double. The mesoloph is short. The valleys are hardly, or not at all, blocked by cingulum ridges. The shape of the hind part of the molar is rectangular or rounded.

Length/width ratios of M_1 of some upper Aragonian and Lower Vallesian cricetids.

<i>F. crusafonti</i> Sant Quirze (Agusti, 1981)	1.53
<i>F. crusafonti</i> Sant Quirze (Agusti, 1981, pl. 1, fig. 10)	1.60
<i>F. crusafonti</i> Hostalets (Agusti, 1981)	1.58
<i>F. cf. crusafonti</i> Solera (total fauna)	1.52
<i>F.</i> from Solera (small specimens = <i>darocensis</i> ?)	1.45
<i>F.</i> from Solera (large specimens = <i>crusafonti</i> ?)	1.54
<i>F. cf. crusafonti</i> Carrilanga	1.54
<i>F. cf. crusafonti</i> Las Planas 5H	1.57
<i>F. cf. crusafonti</i> Toril 1	1.53
<i>F. cf. crusafonti</i> Nombrevilla	1.52
<i>F. darocensis</i> Manchones 1	1.48
<i>Renzimys bilobatus</i> Molina de Aragón	1.55

The length/width ratios of *F. darocensis* in well-documented cases vary between 1.47 and 1.51. The highest value found is 1.52, based on 2 specimens from Valalto 1, one of which is damaged. So, the length/width ratio of *F. darocensis* is consistently smaller than it is in *F. crusafonti*, and possibly the ranges of values for these two species do not even overlap. The length/width ratio for *R. bilobatus* equals the highest values found for *F. crusafonti*.

Fahlbuschia sp. nov. cf. *crusafonti*
Pls 11, 12.

Locality Toril 1 (code TOR, Zone G)

An M_1 (22.5×14.7) and an M^1 (27.0×16.1) fall outside the distribution limits of the *F. darocensis* population from this locality. This discrepancy is more due to the length than to the width. The teeth make a more slender impression. Morphologically the differences are not great. The anteroconid of M_1 is triangular and lies not so close to the protoconid-metaconid as is generally the case in *Fahlbuschia*, and the anterosinusid is relatively wide and deep. A similar disposition is encountered in one of the specimens from Toril 1 attributed to *F. darocensis*. Differences with respect to that specimen are a styloid in the entrance of the anterosinusid, and a mesolophid of medium length. The value of such features is limited when no statistically reliable numbers are available.

The M^1 has an anterocone with a tendency to split, forked anterolophule, and a short mesoloph. There is a cingulum at the base of the antero-lingual wall of the anterocone. None of these features distinguishes this specimen from the *darocensis* population from the same locality.

If these 2 specimens indeed belong to *F. cf. crusafonti* they can only be distinguished from *F. darocensis* by their larger size and larger length/width ratio.

Locality Las Planas 5H (code LP 5H, Zone G)

Material and measurements

M_1 : 22.2×14.2 , 22.7×14.4	M^2 : 20.2×16.7 , 19.5×16.7
M_2 : 18.9×15.9 , 19.7×15.3	M^3 : 13.7×15.0 .
M_3 : 15.7×13.8 , 16.3×14.5 , – $\times 14.6$	

Description

M_1 — The anteroconid is relatively large, triangular, with a labially descending cingulum ridge. The anterosinusid is small. In 1 specimen the anterior wall of the metaconid sends a spur towards the anteroconid. In this specimen the metalophulid is longitudinal towards the anteroconid and the anterolophulid is interrupted. The mesolophid is short and broad. The sinusid is obliquely forward, blocked by a low cingulum ridge. The posterolophid closes the posterosinusid. The posterior wall of the hypoconid is concave in 1 specimen.

M_2 — The mesolophid is short or of medium length. Sinusid and posterosinusid are as in M_1 . The posterior wall of the hypoconid is concave. In the single fresh specimen there is no trace of a lingual anterolophid.

M_3 — There may be a trace of a lingual anterolophid. The sinusid is curved backwards. The lingual border of the posterosinusid is lower than the entoconid.

M^2 — The protolophule is double. The posterior branch of the protocone is reduced in 1 specimen. The mesoloph is short. The metalophule is double, the anterior connection being complete or interrupted. The posterosinusid remains visible. The sinusid is blocked by a cingulum ridge connecting protocone and hypocone.

M^3 — Axioleph, centroleph and the external part of the sinus are present. There is no mesoloph.

Locality Solera (code SOL, Zone G)

The homogeneity of this material is not certain. The histograms Figs. 5 and 6 suggest a separation into two species. There are, however, no consistent morphological differences to warrant a reliable separation. In the scattergrams the Solera material appears to be homogeneous (not taking into account the specimens of *Democricetodon* that are much smaller).

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	12	19.7	21.29	22.7	0.941	18	13.5	14.12	15.5	0.524
M_2	15	17.9	19.32	20.7	0.918	16	13.6	15.77	17.0	0.939
M_3	13	14.8	16.51	17.8	0.935	13	12.8	13.71	14.4	0.542
M^1	11	24.5	26.89	29.2	1.335	15	15.9	16.89	17.8	0.622
M^2	12	17.9	19.57	21.0	0.927	14	15.2	16.44	17.4	0.678
M^3	16	12.0	13.44	14.1	0.514	16	13.6	14.57	15.4	0.529

Description

M_1 — Length/width ratio 1.51, prelobe ratio 0.20. Some specimens are rather elongated, others have the typical compact outline of *Fahlbuschia*. The anteroconid is simple, triangular in 4 specimens. In 4 others the anterolophulid is forked, just behind the anteroconid, and two crests are seen on the posterior wall of the anteroconid. This feature is bound to disappear rapidly with wear, and at least 2 of the 4 specimens with simple anteroconid may have had a similar complication. The anterosinusid is relatively deep and wide. Only in 1 specimen the anteroconid and metaconid are connected by a crest through the anterosinusid. Protosinusid and sinusid are blocked by fairly well developed cingulum ridges. The metalophulid is directed forward, sometimes interrupt-

ed. The mesolophid is absent (6), or short (7). The posterolophid often leaves the posterosinusid open. The posterior wall of the hypoconid is straight or – less frequently – concave.

M₂ — The lingual anterolophid is either absent or very small. The mesolophid is absent (9), short (6), or of medium length (2). The sinusid is directed obliquely forward, generally blocked by a well-developed cingulum ridge. The posterolophid generally closes the posterosinusid. The posterior wall of the hypoconid is generally somewhat concave.

M₃ — There is a trace of the lingual anterolophid. The metalophulid is normally directed towards the anterolophid, but in 1 specimen it is curved backwards towards the middle of the protoconid, and the anterior branch of the protoconid is missing. The sinusid is narrow or wide, curved backwards, often blocked by a well-developed cingulum ridge. The posterosinusid is lingually open (6), or closed (2). In 1 specimen a longitudinal ridge separates a central funnel from the open exterior part of the posterosinusid, in another one such a ridge is indicated.

M¹ — The anterior wall of the anterocone may be slightly concave. In 9 out of 13 specimens there is a cingulum ridge at the base of the antero-lingual wall of the anterocone, and this ridge may be so well developed, that it encircles a small valley. The anterolophule is forked (6) or simple (4), but the specimens with simple anterolophule may have lost this feature through wear. Cingulum ridges closing the valleys are generally well developed. The protolophule is double (5), or posterior (13). The mesoloph is absent (3), or short (9). In 3 specimens the entoloph is more or less interrupted behind the protocone. The sinus is transverse. The posterosinus is small.

M² — The protolophule is posterior with a trace of an anterior connection (3), or double (11). The mesoloph is absent (4), or short (9). The metalophule is double (6), or posterior (6). The postero-lingual corner of the molar is often much rounded.

M³ — The axioph is present (14), or absent (1). The metalophule is present (14), or absent (1). There is no mesoloph. In 6 specimens a spur from the neo-entoloph inward, may be interpreted as a part of the ancient entoloph. It may form a small funnel (see the M³ of *Democricetodon gaillardi*, Fig. 2A and 2B). The external part of the sinus is fairly well developed in most cases; in 2 specimens only the basal cingulum ridge remains.

The histogram of M₁, Fig. 5, suggests that two species are present in this locality. The length/width ratio of the smallest 4 specimens is 1.45, the rest of the specimens yields 1.54. These values are normal for *F. darocensis* and *F. sp. nov. cf. crusafonti*, respectively. So it is quite possible that both these species are represented in Solera.

A remarkable feature in the Solera material is the frequent presence of an anterior protolophule in M¹. One of the 3 specimens from Carrilanga shows this feature too. It has not been found in Toril 1, Las Planas 5H and Nombrevilla, but the material from these localities is very poor. Nor is it found in the type material of *F. crusafonti* and *R. ultima*, but these species also are hardly known. It has been found in 1 specimen (out of 14) from Armantes 7, which may be an argument to attribute (part of) the material from Armantes 7 to *F. sp. nov. cf. crusafonti*.

Locality Carrilanga (code CAR, Zone H)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	3	22.3	23.90	25.7	1.709	3	14.4	15.57	16.2	1.012
M ₂	2	21.1	21.65	22.2	0.778	2	16.8	17.10	17.4	0.424
M ₃	2	14.5	16.20	17.9	2.404	2	12.5	13.90	15.3	1.980
M ¹	2	29.8	29.80	29.8	0.000	3	15.4	17.00	17.9	1.389
M ²	5	19.8	21.74	24.1	1.795	5	14.9	16.74	18.1	1.346
M ³	1	—	13.90	—	—	0	—	—	—	—

Description

M₁ — Length/width ratio 1.54, prelobe ratio 0.23. In 1 specimen the anteroconid has a longitudinal backward spur towards the metaconid. In another one this spur forms a complete connection, and the anterolophulid is absent. In this -unworn- specimen the anteroconid shows a slight trace of subdivision. The metalophulid is forward (2), or interrupted (1). The anterosinusid is fairly wide. There is no mesolophid. The hypolophulid is hardly recognizable: the entoconid is fused to the ectolophid over almost its entire width. The posterosinusid and sinusid are blocked by well-developed cingulum ridges. The posterosinusid is open. The posterior wall of the hypoconid is almost straight.

M₂ — There is no lingual anterolophid. The mesolophid is absent or of medium length. Protosinusid and sinusid are blocked by well-developed cingulum ridges. The hypolophulid is normally developed. The posterosinusid is lingually open or closed. The sinusid is narrow, transverse, or curved backwards.

M¹ — The anterior wall of the anterocone is convex, smooth in 1 specimen, provided with a very weak cingulum in the other. The anterolophule is longitudinal, directed towards the lingual anteroloph, not forked. The posterior wall of the anterocone bulges somewhat backwards. The labial valleys are closed by cingulum ridges, the lingual ones are open. The protolophule is posterior (2), or double (1). The mesoloph is short, the metalophule is posterior. The posterosinus is small (2), or absent (1).

M² — The protolophule is posterior (4), or posterior with a trace of an anterior connection (1). The mesoloph is short (4), or absent (1). The valleys are open or blocked by cingulum ridges. The metalophule is posterior. The posterosinus is present or absent.

M³ — There is an axiolph, and no mesoloph or centroloph.

Locality Nombrevilla (code NO, Zone H)

The material is the same as described by Freudenthal, 1967. No additional material is available.

Description

M₁ — Length/width ratio 1.52, prelobe ratio 0.24. The anteroconid is round or triangular, with or without descending cingulum ridges. The anterosinusid is fairly wide in 1 specimen, narrower in the other ones. In 1 specimen the anterolophulid is forked, just behind the anteroconid, forming a small crest that encircles the posterior wall at the top of that cusp. In another specimen the anterolophulid seems to be replaced by a crest from the metaconid towards the lingual end of the anteroconid. The mesolophid is absent

(4), or short (1). In fresh specimens the hypoconid descends steeply to the relatively low posterolophid. The posterosinusid is slightly closed (1), or it remains open (4). In 1 specimen there is a small ectomesolophid, running from the border of the molar inward.

M_2 — The lingual anterolophid is absent or small. The mesolophid is absent or short. One specimen has a long ectomesolophid at the bottom of the sinusid. The posterior part of the molar is as in M_1 .

M_3 — There is no lingual anterolophid. The posterosinusid is open. The hypoconid and posterosinusid are much reduced in 2 of the 3 specimens.

M^1 — The anterolophule is forked, directly before the protocone. There is no anterior protolophule. The mesoloph is short. The posterosinusid is small.

M^2 — The protolophule is posterior with a trace of the anterior connection. The mesoloph is absent. The metalophule is directed backward towards the posteroloph.

Fahlbuschia decipiens sp. nov.

Pl. 16, fig. 13.

Holotype — M_1 dext., BU 1564, kept in the Instituut van Aardwetenschappen, Utrecht, figured in Daams & Freudenthal, 1974, pl. 1, fig. 11.

Type-locality — Buñol, Valencia, Spain.

Type-level — Middle Aragonian, Zone B-C.

Derivatio nominis — Latin *decipiens* = deceiving. We chose this name, because in our 1974 publication we were deceived and mistook this species for a *Democricetodon*.

The *Fahlbuschia* and *Democricetodon* material from Buñol, published by Daams & Freudenthal (1974) has been reexamined, because several errors appear to occur in that publication. The M_1 figured on pl. 1, fig. 7 is no. BU 2005, not BU 1801. The M_3 on pl. 1, fig. 8 is no. BU 2001. The measurements of this M_1 are 15.5×11.2 . Fig. 11 on pl. 1 is not a good representation of the specimen. In reality it has a very small anterosinusid, closed by a ridge along the lingual border of the molar.

Comparison of the Buñol material of *Democricetodon* aff. *hispanicus* Freudenthal, 1967 with the new *Democricetodon* and *Fahlbuschia* material from the Calatayud-Teruel Basin has shown, that in fact it is not a *Democricetodon* but a *Fahlbuschia*, in view of the connection between anteroconid and metaconid of M_1 , and the deeply carved-in sinusid in M_3 . The M_1 mentioned above fits well in this population. The M_3 may be somewhat too large.

The Buñol material has smaller dimensions than *F. koenigswaldi*: the mean value of the length of M_1 is 15.0, identical to the lower length limit of M_1 of *F. koenigswaldi* from Vargas 1A; the M_1 of the type-population of *F. koenigswaldi* from Valdemoros 1A has a lower limit of 16.4 and a mean of 17.2. 50 % of the specimens from Buñol are smaller than the smallest M_1 from Vargas 1A, and all specimens from Buñol are smaller than the smallest one from Valdemoros 1A. This is sufficient evidence that we are dealing with a new species.

So, most of the material previously ascribed to *Democricetodon* is now considered to be *Fahlbuschia*. A few small specimens, like for example M^2 BU 1936, are kept in *Democricetodon* aff. *hispanicus*.

Diagnosis

Very small *Fahlbuschia*. In almost all M_1 the anterosinusid is small and shallow, and there is a connection between anteroconid and metaconid, either along the border of the molar or through the middle of the anterosinusid. The sinusid of M_3 carves far into the

molar, and leaves little space for the hypolophulid. A relatively large percentage of the M^3 has conserved a trace of the anterior part of the entoloph/posterior branch of the protocone.

Differential diagnosis

Smaller than *Fahlbuschia koenigswaldi*, larger than the contemporaneous *Democricetodon hispanicus*. Over 25 % of the M^3 show a trace of the anterior part of the entoloph, in Vargas 1A this feature occurs in less than 12 % of the M^3 of *F. koenigswaldi*. An anterior protolophule (or a labial spur on the anterolophule) of M^1 is more frequent in Buñol (over 20 %) than it is in Vargas 1A (7 %) or Valdemoros (less than 5 %).

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	19	13.9	14.98	16.0	0.614	20	9.7	10.58	11.6	0.479
M_2	30	12.8	13.80	15.1	0.650	33	10.3	11.61	13.0	0.663
M_3	26	10.7	11.99	13.4	0.681	25	9.0	10.00	12.4	0.742
M^1	26	16.7	17.98	19.7	0.805	28	11.0	11.96	13.2	0.595
M^2	18	13.2	13.77	14.6	0.483	16	11.4	11.92	13.3	0.542
M^3	22	8.8	9.83	11.0	0.597	22	8.9	10.17	12.0	0.763

For a description of the material the reader is referred to Daams & Freudenthal, 1974.

F. decipiens sp. nov. may be the ancestor of *F. koenigswaldi*. It is smaller and morphological characters considered to be primitive are more frequent in Buñol than they are in Vargas 1A or Valdemoros 1A. The stratigraphic position of Buñol between Villafeliche 2A and Valdemoros 1A, as supposed by Daams & Freudenthal (1974) is confirmed by these facts. Buñol seems to represent a stratigraphic level hitherto unknown in the Calatayud-Teruel Basin.

However, the evolution of *Fahlbuschia* appears to be a very complicated matter, and the ancestry of *F. koenigswaldi* is not certain. The evolution of *Fahlbuschia* will be discussed in relation with the biostratigraphic results.

Fahlbuschia corcolesi sp. nov.

Pl. 13.

Holotype — M_1 sin., COR 2, kept in the Universidad Complutense, Madrid.

Type-locality — Córcoles, Cuenca, Spain. The material from this locality was kindly put at our disposal by Dr N. López Martínez, Madrid.

Type-level — Lower Aragonian, Zone B-C

Derivatio nominis — after the type-locality Córcoles.

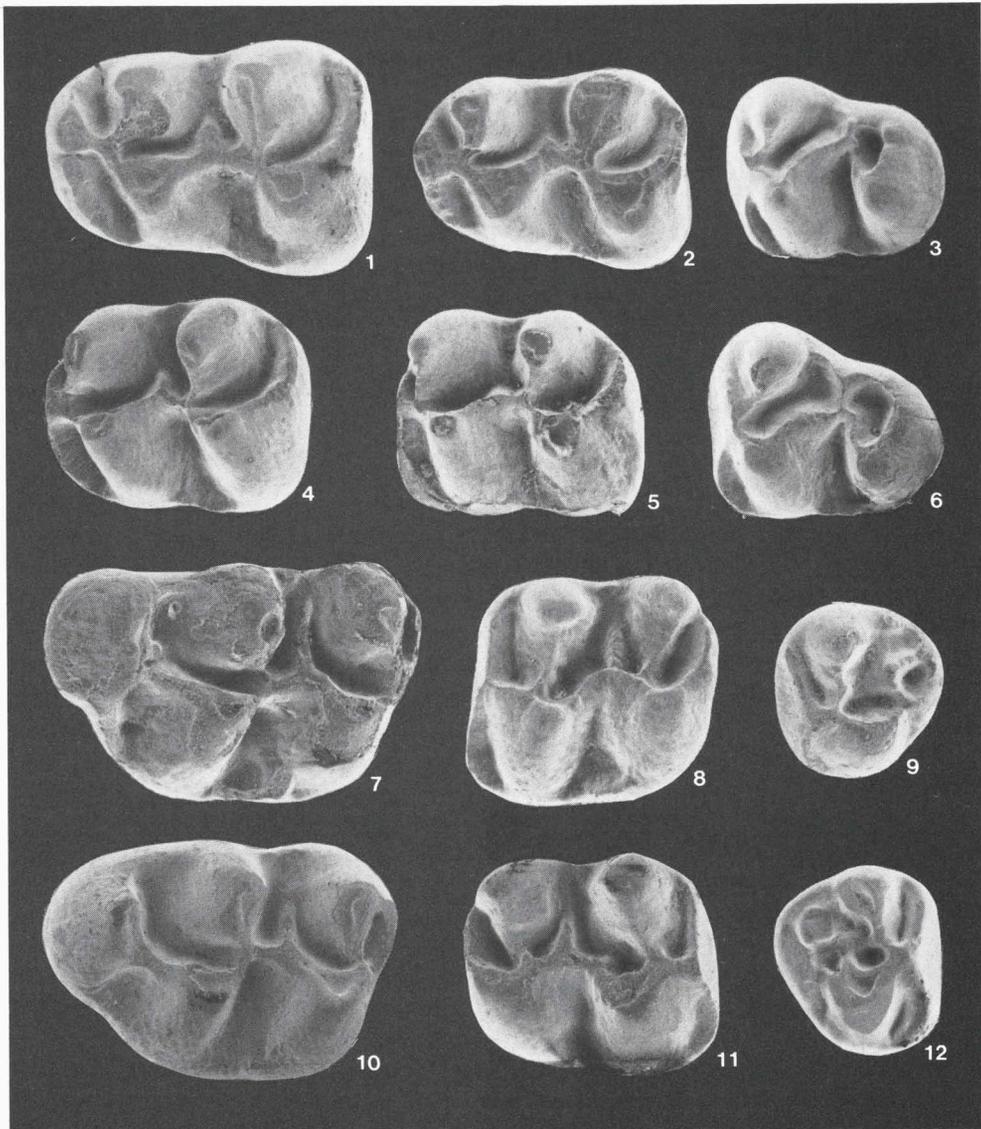
Synonymy

F. cf. koenigswaldi in Díaz & López, 1979.

F. cf. koenigswaldi in Alférez et al., 1982.

Diagnosis

Smallest *Fahlbuschia* known so far. In M_1 the direct connection between metaconid and anteroconid is not very well developed. The mesolophids of the lower molars are little developed. The most striking feature is, that in M^2 the protolophule is predominantly anterior, whereas in M^1 there is no anterior protolophule.



All figures approx. 25 ×.

Fahlbuschia corcolesi sp. nov.
Córcoles

- Fig. 1. Holotype, M₁ sin., COR 2.
- Fig. 2. M₁ sin., COR 1.
- Fig. 3. M₃ sin., COR 45.
- Fig. 4. M₂ sin., COR 23.
- Fig. 5. M₂ sin., COR 27.
- Fig. 6. M₃ sin., COR 42.
- Fig. 7. M¹ sin., COR 69.
- Fig. 8. M² sin., COR 83.
- Fig. 9. M³ sin., COR 102.
- Fig. 10. M¹ sin., COR 63.
- Fig. 11. M² dext., COR 94.
- Fig. 12. M³ dext., COR 106.

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	17	13.6	15.28	16.0	0.647	17	9.9	10.45	11.6	0.496
M ₂	21	13.0	13.72	14.6	0.404	21	10.5	11.22	12.2	0.480
M ₃	15	10.6	11.95	13.3	0.646	16	8.9	9.92	10.7	0.451
M ¹	16	17.0	18.50	19.8	0.863	15	11.6	12.14	12.6	0.316
M ²	18	12.6	13.41	14.4	0.515	18	11.0	11.73	12.4	0.380
M ³	7	8.6	9.39	10.3	0.604	7	9.2	9.81	10.4	0.445

Description

M₁ — Length/width ratio 1.47, prelobe ratio 0.19. The anteroconid is small, triangular, either symmetrical or slightly asymmetrical. Generally there are labial and lingual cingulum ridges descending from the anteroconid; the labial ridge is often very thick. The anterosinusid is smaller than the protosinusid. The anterior wall of the metaconid is either smooth or bulging forward; only in 3 specimens there is a direct connection from the metaconid towards the anteroconid through the middle of the anterosinusid. The metalophulid points transversely or obliquely forward towards the anterolophulid; in 1 specimen it is directed transversely towards the middle of the protoconid, in another one it is interrupted. The mesolophid is absent (3), short (8), of medium length (9), or long (1). The sinusid is transverse, or directed obliquely forward, rarely blocked by a low cingulum ridge along the border of the molar. The posterosinusid is generally not closed by the posterolophid.

M₂ — In unworn specimens the lingual anterolophid and a small anterosinusid are present. The mesolophid is absent (7), short (7), or of medium length (8). In 1 specimen there is a small mesostylid. The sinusid is oblique, generally open. The posterolophid rarely closes the posterosinusid.

M₃ — Lingual anterolophid and anterosinusid are present. The sinusid is curved backwards. There is no mesolophid. The hypolophulid is fairly long, transverse, connected to the ectolophid in front of the curve. The posterosinusid is fairly large. The shape of the molar is generally a long triangle.

M¹ — The anterior wall of the anteroloph is often slightly concave. There is a cingulum at the antero-lingual base of the anteroloph (7), or such a cingulum is absent (10). In 1 specimen the anterocone bears a backward spur. There is no anterior protolophule, except in 1 specimen where a trace of it is present on the anterior corner of the protocone. The mesoloph is absent (1), short (4), of medium length (7), or long (6). In 1 specimen the paracone bears a backward spur. The sinus is transverse, sometimes slightly blocked. The metalophule is posterior towards the posteroloph, or – in one case – towards the posterior corner of the hypocone.

M² — The protolophule is anterior (10), anterior with a trace of a posterior connection (5), posterior with a trace of an anterior connection (1), or interrupted (1). The metalophule is anterior (16), or posterior (3). The mesoloph is absent (1), short (3), of medium length (9), or long (6).

M³ — There is a centroloph and no axioloph or mesoloph (2), axioloph plus centroloph (1), axioloph, centroloph and mesoloph (1), axioloph plus a trace of a mesoloph (1). In specimen COR 106 the ancient entoloph is complete and the rotation of the protocone is clearly visible.

Discussion

Since no mandibles or maxillae have been found, and the anteroconid-metaconid connection in M_1 is not well developed we cannot be certain, that this is a *Fahlbuschia* and not a *Democricetodon*. However, the length/width ratio, the prelobe ratio and the general aspect of the molars make it probable that we are dealing with a *Fahlbuschia*. By the structure of the protolophule of M^2 it seems to be the most primitive *Fahlbuschia* known. However, the cingulum in front of the anteroloph of M_1 and the reduction of the mesolophids seem to be modernized characters.

Pseudofahlbuschia gen. nov.

Type-species — *Pseudofahlbuschia jordensi* sp. nov.

Derivatio nominis — *Pseudo-Fahlbuschia*, because of its great resemblance with *Fahlbuschia*.

Diagnosis

Cricetidae of medium size, morphology of cheek teeth close to *Fahlbuschia*. Mesolophids and mesoloph strongly reduced. Anterior protolophule in M^1 always absent, in M^2 nearly always. Teeth more slender than in *Fahlbuschia*. All M_2 shorter than the shortest specimen of M_1 . The foramen incisivum, as seen in 1 specimen from Villafeliche 4A, is long like it is in *Fahlbuschia*, ending between the M^1 . Some details on the mandible are given in the descriptions of Villafeliche 4A and Casetón 1A. They may be characteristic for *Pseudofahlbuschia*, but the material is very poor.

Differential diagnosis

The populations of *Pseudofahlbuschia* known so far fill the size gap between *Fahlbuschia koenigswaldi* and *Fahlbuschia darocensis*, partly overlapping the distribution areas of the measurements of these species. They are roughly of the same size as *F. freudenthali*. When *Pseudofahlbuschia* concurs with *Fahlbuschia koenigswaldi* in one locality it can be distinguished by its larger size. *Pseudofahlbuschia* may be distinguished from *Fahlbuschia* by its relatively elongated teeth, and by the strong reduction of the anterior protolophule in M^2 . In *Fahlbuschia* and *Democricetodon* there is a size overlap between M_1 and M_2 ; in *Pseudofahlbuschia* all M_2 are shorter than the shortest specimen of M_1 .

Freudenthal (1963) recognized these differences, but didn't consider them sufficiently important to separate the material from Villafeliche 4A from the other cricetids of the 'larteti group' (after all, at the time the subdivision of the genus *Cricetodon* into the genera *Cricetodon*, *Megacricetodon*, *Democricetodon*, *Fahlbuschia*, *Eumyarion*, etc. had not yet taken place). He interpreted the population from Villafeliche 4 as a transitional form between *Fahlbuschia koenigswaldi* and *Fahlbuschia darocensis*. For reasons explained in the chapter on evolution and biostratigraphy, this theory cannot be maintained. The Villafeliche population must belong to a different evolutionary lineage.

It is difficult to assess the taxonomic rank of these differences. One may simply attribute them specific value, and recognize two evolutionary lineages of *Fahlbuschia* in the Aragonian. We prefer, however, to give them generic value and place the Villafeliche 4 population in the new genus *Pseudofahlbuschia*.

Pseudofahlbuschia has been found in the following localities: Villafeliche 4, Villafeliche 4A, Valdemoros 3B, Casetón 1A, Casetón 2B, Valdemoros 1A, Valdemoros 3D, Vargas 1A, Vargas 1E, and possibly in Borjas.

Further occurrences are Armantes 1 (*Cricetodon* Übergang *koenigswaldi-darocensis* in Freudenthal, 1963) and the unpublished locality of Torralba 2B. The material from Torralba 1, published by Freudenthal (1963) is too poor to allow a determination. It may belong to *F. freudenthali*.

Not all the material from Armantes 1 can be ascribed to *Pseudofahlbuschia*. Some of it may belong to *Eumyarion* and *F. freudenthali* or *darocensis*.

Fahlbuschia cf. *darocensis* from Vieux-Collonges (Guérin & Mein, 1971) is probably a *Pseudofahlbuschia*, somewhat larger than the type-species.

Pseudofahlbuschia jordensi sp. nov.

Pl. 14.

Holotype — M₁ dext., RGM 253 932, measurements 19.1 × 11.9.

Type-locality — Villafeliche 4A.

Distribution — Dominant in the Aragonian Zone D2, present in D1.

Derivatio nominis — In honour of Mr F. Jordens, who participated many times in our field campaigns.

Diagnosis — The same as for the genus.

Synonymy

Cricetodon Übergang *koenigswaldi-darocensis* in Freudenthal, 1963.

Locality Villafeliche 4A (Code VL 4A, Zone D2)

Material and measurements (RGM collection only)

There is additional material in the Utrecht collections, that has been used in the morphological descriptions, but not in the table of measurements.

Plate 14

All figures approx. 20 ×.

Pseudofahlbuschia jordensi sp. nov.

Villafeliche 4A

Fig. 1. Holotype, M₁ dext., RGM 253 932.

Fig. 2. M₁ sin., RGM 253 923.

Fig. 3. M₁ sin., RGM 302 945.

Fig. 4. M₂ sin., RGM 253 951.

Fig. 5. M₂ sin., RGM 253 940.

Fig. 6. M₂ sin., RGM 253 943.

Fig. 7. M₃ sin., RGM 253 970.

Fig. 8. M₃ sin., RGM 253 967.

Fig. 9. M₃ sin., RGM 253 975.

Fig. 10. M³ dext., RGM 254 045.

Fig. 11. M¹ sin., RGM 253 986.

Fig. 12. M¹ sin., RGM 253 987.

Fig. 13. M² sin., RGM 254 007.

Fig. 14. M¹ sin., RGM 253 990.

Fig. 15. M¹ sin., RGM 253 992.

Fig. 16. M³ sin., RGM 254 030.

Fig. 17. M³ dext., RGM 254 046.

Fig. 18. M³ sin., RGM 254 032.

Fig. 19. M² sin., RGM 302 986.

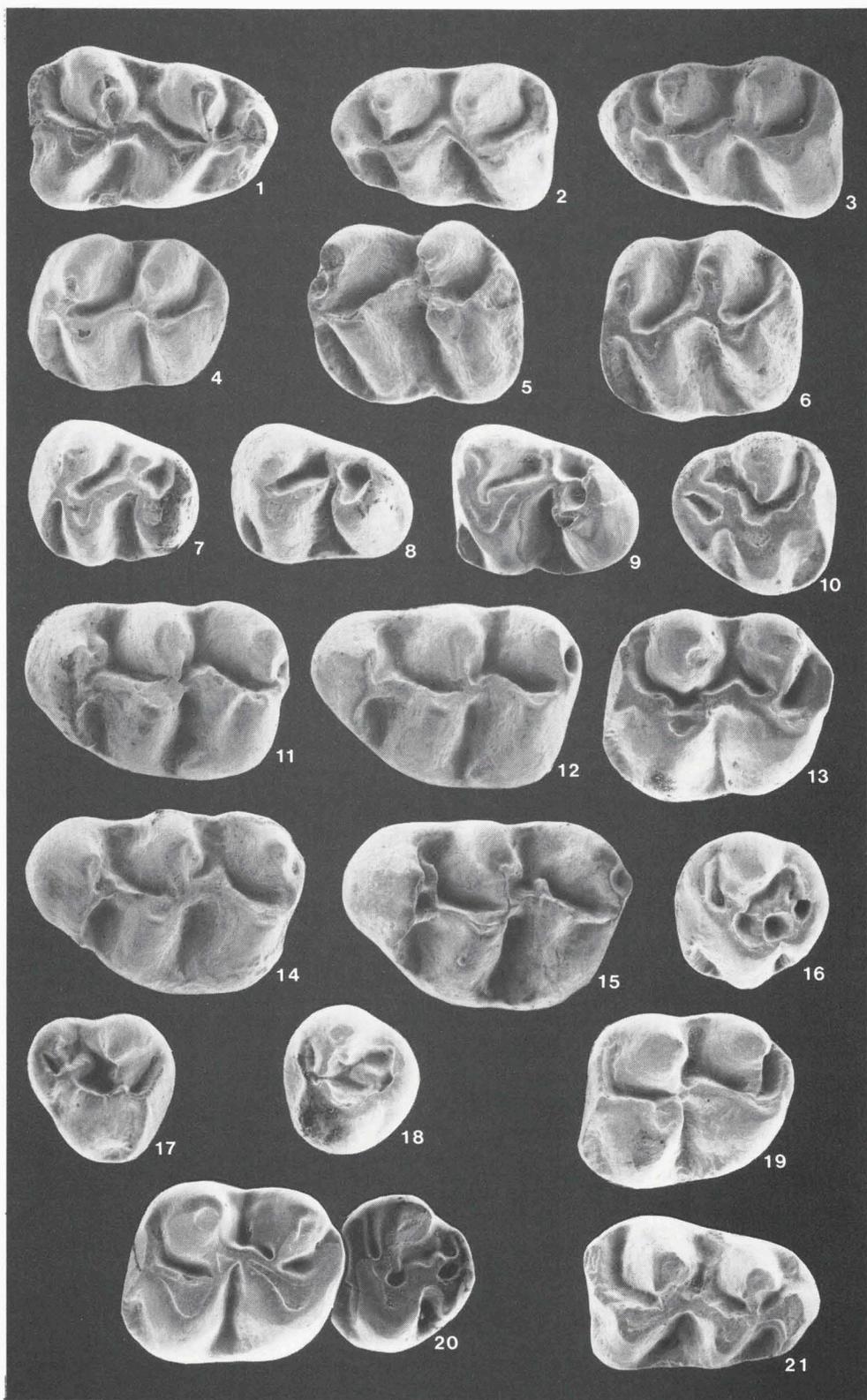
Fig. 20. M², M³ sin., RGM 254 006.

Pseudofahlbuschia jordensi sp. nov., or *Fahlbuschia* sp.

Villafeliche 4A

Fig. 21. M₁ dext., RGM 302 957.

Plate 14



	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	37	16.7	18.26	19.9	0.740	40	10.4	11.54	13.0	0.525
M ₂	38	13.9	15.57	16.6	0.659	39	11.2	12.61	14.2	0.657
M ₃	22	12.1	13.57	15.3	0.812	21	10.1	11.11	12.5	0.600
M ¹	28	19.5	21.10	23.1	0.966	30	12.4	13.41	14.2	0.488
M ²	35	14.2	15.58	17.4	0.813	37	11.4	13.14	14.5	0.712
M ³	25	9.9	11.10	12.7	0.714	25	10.3	11.27	12.1	0.524

Description

The mandible is a little inclined in occlusal view, hiding the foramen mentale. In lateral view only a small part of the M₃ is hidden by the ramus ascendens. The upper masseter crest is very weak, the lower one is sharp and well developed. The lower incisor is like in *Fahlbuschia*.

M₁ — Length/width ratio 1.58, prelobe ratio 0.23. Both these ratios are considerably higher than the values found in *Fahlbuschia*, which indicates that the teeth are more elongated than they are in *Fahlbuschia*, an elongation, that takes – mainly – place in the area of the anteroconid. The anteroconid is small, triangular and generally symmetrical, far away from the metaconid. In most cases there are a labial and a lingual cingulum ridge descending from the anteroconid. The labial one reaches the protoconid, the lingual one ends before the metaconid, leaving the anterosingid open. The lingual ridge may be absent, giving the lingual end of the anteroconid a rounded shape. In 6 out of 39 specimens there is a spur on the anterior wall of the metaconid, pointing towards the anteroconid. The anterosingid is wider than it is in *Fahlbuschia*. The anterolophulid has an axial position and it is connected to the centre of the anteroconid. The metalophulid is directed obliquely forward towards the anterolophulid, or – less frequently – towards the anterior corner of the protoconid. The mesolophid is absent (34) or very short (6), only in one case it is of medium length. It cannot be excluded that this specimen (RGM 302 957), which also has a spur on the metaconid, is a *Fahlbuschia*. The sinusid is directed obliquely forward. The posterosingid is closed by the posterolophid or it remains open. The posterior wall of the hypoconid is straight, or slightly concave. There are two roots, without an accessory root in between them.

M₂ — The lingual anterolophid may have disappeared, but in most sufficiently fresh specimens it is present, small, or even fairly well developed. The mesolophid is absent (34), or short (8). The sinusid is obliquely forward, or less frequently curved backwards. The posterosingid is generally closed by the posterolophid.

M₃ — The lingual anterolophid is present or absent, sometimes fairly well developed. The labial anterolophid normally descends from the anteroconid, along the border of the molar, towards the basis of the protoconid. However, in 9 out of 21 specimens it is only a low ridge at the antero-labial basis of the molar, without contact with the anteroconid. The sinusid is directed obliquely forward, transverse or curved backwards. Frequently the entoconid is fairly well developed, and the hypolophulid is rather long and more or less transverse. The posterosingid is absent in one case, very small and lingually open in another. In 2 specimens a longitudinal crest, lingually of the hypoconid, divides the posterosingid, and in one of these (RGM 253 975) a spur on the posterior branch of the protoconid indicates a similar feature in the anterior part of the molar.

M¹ — The anteroloph is a broad transverse crest, with a convex or slightly concave anterior wall. The anterocone lies labially of the anterolophule. There may be a backward spur on the labial part of the posterior wall of the anteroloph; in other specimens the

anterolophule is forked shortly behind the anteroloph, but most specimens are too much worn to assess a reliable frequency figure for these features. The anterolophule is generally longitudinal, towards the lingual part of the anteroloph. There is no anterior protolophule. There often is a backward protrusion on the posterior wall of the paracone. The mesoloph is absent (14), short (13), or of medium length (2). The sinus is transverse. The metalophule points backwards. The posterosinus may be small, but in sufficiently fresh specimens it does not disappear.

M² — The protolophule is double in 1 specimen only; in 2 others both the anterior and the posterior connection are interruptedly present. In the remaining specimens the protolophule is posterior (30), or posterior with a trace of an anterior connection (5). The mesoloph is absent (15), or short (21). There is frequently a backward protrusion on the posterior wall of the paracone. The sinus is transverse or curved forward. The metalophule is anterior (21), posterior (4), transverse (3), or double (1). The anterior connection is frequently not straight, but curved forward. The postero-internal corner of the molar is well rounded.

M³ — In 2 specimens the ancient entoloph is preserved as an almost complete circle (RGM 254 030, Pl. 14, fig. 16). In 2 other specimens the anterior part of the ancient entoloph is visible as a spur on the middle of the labial wall of the protocone. The axioloph is complete (4), absent (4), or its posterior part is present (12). The mesoloph is present (6), or absent (16). The centroloph is present (18), or absent (3).

Locality Casetón 1A (code CS 1A, Zone D1)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	2	19.7	20.00	20.3	0.424	3	12.2	12.30	12.5	0.173
M ₂	1	—	16.90	—	—	2	12.8	13.25	13.7	0.636
M ₃	1	—	15.00	—	—	2	12.2	12.25	12.3	0.071
M ¹	3	22.8	23.37	24.2	0.737	3	14.2	14.77	15.2	0.513
M ²	3	16.0	17.10	17.8	0.964	3	13.5	14.23	14.8	0.666
M ³	1	—	12.20	—	—	1	—	11.90	—	—

Description

There is a mandibula fragment without teeth. In occlusal view it is almost vertical, not inclined, the foramen mentale being visible. In lateral view the M₃ is only partly hidden by the ramus ascendens. The lower masseter crest is stronger than the upper one. At their junction the crests form a fairly large flat surface, inclined downward at a 45° angle with the mandibula.

M₁ — Length/width ratio 1.63, prelobe ratio 0.22. The anteroconid is symmetrical, with labial and lingual cingulum ridges. In 1 out of 3 specimens the metaconid points forward towards the anteroconid. The mesolophid is absent (3), or short (1). One specimen has an ectomesolophid, running from the border of the molar into the sinusid. The posterosinusid is closed by the posterolophid (3), or open (1).

M₂ — The mesolophid is short or of medium length. Two specimens have an ectomesolophid.

M₃ — The lingual anterolophid is present. The sinusid is narrow, curved backwards. The posterosinusid is fairly large, lingually closed.

M¹ — The anterocone has a clear tendency to subdivision, and in 1 specimen it is actually split at its top. Two specimens out of 6 have a small cingulum ridge at the antero-lingual base of the anteroloph. The labial part of the anteroloph has a backward spur (3), the anterolophule is forked (3), or the construction is simple (1). There is no anterior protolophule (6). The mesoloph is short (3), or absent (2). One specimen has a backward spur on the posterior wall of the paracone. The posterosinus is present.

M² — The anterior protolophule is weaker than the posterior one. One specimen has a spur on the paracone. The mesoloph is short. The metalophule is curved forward.

M³ — The axiolph is interrupted. There is a mesoloph and a centroloph.

Locality Casetón 2B (code CS 2B, Zone D1)

Material and measurements

M₁: – × 12.3

M¹: 23.1 × 14.9, 24.1 × 15.3

M²: 17.3 × 14.9, 17.7 × 15.2.

Description

M¹ — The anterolophule is forked. There is no anterior protolophule and no mesoloph.

M² — The protolophule is double or posterior. There is no mesoloph. The metalophule is transversely forward.

Locality Valdemoros 1A (code VA 1A, Zone D1)

Material

IVA, Utrecht: VA 313, 314, 319, 329, 132, 128, 309, 159, 308.

Measurements

M¹: 23.5 × 14.2, 23.9 × 15.1, – × 16.3

M²: 18.3 × 14.2, 18.1 × 14.7, 17.7 × 14.2, 18.1 × 15.2

M³: 13.3 × 12.6

These specimens, attributed to *F. koenigswaldi* by Freudenthal (1963) appear to belong to *Pseudofahlbuschia*. An additional M², VA 308, 18.4 × 15.0, was found after completion of Freudenthal's study.

Description

M¹ — In 1 specimen the anterolophule is forked. There is no anterior protolophule. The mesoloph is short or absent.

M² — The protolophule is posterior (2), posterior with a trace of the anterior connection (1), double (1). The mesoloph is absent (2), or short (2). The metalophule is probably curved forward in all specimens, and there is an additional posterior connection in 2 of them. A backward spur on the posterior wall of the paracone is present or at least indicated.

M³ — The hypocone-metacone part of the tooth is fairly large. The posterior part of the axiolph is well developed; there is a mesoloph and a centroloph.

Locality Valdemoros 3D (code VA 3D, Zone D2)

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M ₁	6	18.0	19.67	20.4	0.898	7	11.6	12.36	13.0	0.435
M ₂	6	14.0	16.43	18.4	1.465	6	11.6	13.38	14.7	1.248
M ₃	9	13.1	14.30	16.3	1.141	9	10.3	11.62	12.9	0.965
M ¹	7	22.5	23.39	24.1	0.729	10	13.2	14.40	15.5	0.773
M ²	11	14.9	16.89	18.9	1.252	11	12.6	14.07	15.0	0.746
M ³	5	11.4	11.80	12.9	0.620	6	11.0	11.90	12.4	0.473

Description

M₁ — Length/width ratio 1.59, prelobe ratio 0.21. The teeth make a slender impression, and the anteroconid lies relatively far away from the metaconid. The anterosinusid is deep or shallow. The anterior wall of the metaconid is either smooth, or bulging forward, or connected to the anteroconid. The mesolophid is short (4), or absent (6). The posterosinusid is open, or closed by the posterolophid at a low level. The posterior wall of the hypoconid is generally concave.

M₂ — In unworn specimens the labial anterolophid and the anterosinusid exist. The mesolophid is absent (6), or short (1). The posterosinusid is closed at a low level. The posterior wall of the hypoconid is concave.

M₃ — The anterosinusid exists in unworn teeth. The sinusid is transverse or directed backwards. There is no mesolophid. The posterior part of the tooth may be very much reduced. One very big specimen (16.3 × 12.9) possibly belongs to another species (e.g. *F. freudenthali* ?).

M¹ — The anterior wall of the anterocone is concave in well-preserved specimens, except one which has a small, round anterocone. The protolophule is posterior. The anterolophule is forked just behind the anterocone, or the anterocone bears a backward spur on the labial part of its posterior wall; most specimens are too much worn to see this detail. There often is a backward spur on the paracone. The mesoloph is absent (9), or short (3). The metalophule is posterior. The posterosinusid remains visible in all but 1 specimen.

M² — The protolophule is double (4), or posterior (9). The mesoloph is absent (7), short (5), or of medium length (1). The metalophule is posterior (3), double (1), transverse/anterior (5), or absent (3). In about half the number of specimens the paracone bears a well-developed backward spur.

M³ — The axioloph is complete (3), incomplete (1), or absent (2). The centroloph is present (4), or absent (2). Three specimens have a trace of the ancient entoloph on the labial wall of the protocone.

Locality Borjas (code BOR, Zone G)

A rather worn M¹ sin., measurements 22.8 × 13.0 may belong to this species. There is no anterior protolophule, the mesoloph is of medium length. By its length this specimen falls within the size limits of *F. darocensis*, but its width is much too small. It has the same slender appearance as the M¹ from Villafeliche 4A, and lies at the upper size limit of *P. jordensi*.

Discussion

The most important occurrences of *P. jordensi* are contemporaneous with *Renzimys lacombai* sp. nov. *P. jordensi* is distinguished by its smaller size, its sinus and sinusid which are wide and transverse or oblique, not curved, its thinner enamel, and the normal crest-like hypophulids. In M_1 the anteroconid is symmetrical and small, and the antero-phulid has an axial position, pointing towards the centre of the anteroconid.

There are considerable size differences between the various occurrences of *Pseudofahlbuschia*, indicating that we are possibly dealing with more than one species. However, only Villafeliche 4A has yielded a sufficiently rich collection. The other populations are too poor to allow the description of yet another species.

The population of *F. cf. darocensis* from Vieux-Collonges is probably a *Pseudofahlbuschia*. It certainly represents a species different from *P. jordensi*.

Genus *Renzimys* Lacomba, 1983

Type-species — *Renzimys bilobatus* Lacomba, 1983 from Molina de Aragón, Guadalajara, Spain.

Attributed species

Fahlbuschia ultima Antunes, Ginsburg & Mein, 1983

Renzimys lacombai sp. nov.

Renzimys was created by Lacomba in 1983. In this volume an English translation of his paper will appear (Lacomba, 1988).

Renzimys bilobatus Lacomba, 1983

Renzimys bilobatus Lacomba, 1983 by its size and general morphology, looks very much like *F. crusafonti* Agustí, 1978. The most striking difference is the subdivision of the anterocone of M^1 , as described by Lacomba. Before we proceed with the description of a new species of *Renzimys* we wish to make some remarks on the type-material of *Renzimys bilobatus*.

One specimen from Molina de Aragón, RGM 336 915, a fragmentary mandible, permits to study some additional details. In *Fahlbuschia*, e.g. *F. larteti* from La Grive-St. Alban the diasteme slopes gently downward from the M_1 . The bone is about equally thick over the entire diasteme. The lingual edge of the anterior part of the diasteme is sharply angular. The foramen mentale lies under the first root of M_1 , and enters longitudinally and horizontally into the mandible. The lower border of the foramen mentale is flat and does not protrude from the surface of the bone. In *R. bilobatus* the posterior limit of the diasteme is almost vertical. The bone is constricted above the foramen mentale. The foramen lies far forward, shortly behind the middle of the diasteme, and enters the bone in a more downward and transversal direction. Its lower border is a very well marked crest. The lingual edge of the anterior part of the diasteme seems to be less angular. Another specimen (RGM 336 942) shows that the mandible is almost vertical with respect to the tooth row, and that the masseter crests are weakly developed.

The type collection of *R. bilobatus* contains 18 M^1 . Of these, 6 specimens have a well-divided anterocone, and in 4 specimens it is weakly split. In 2 specimens the subdivision is hardly indicated, and 6 specimens are too much worn. The latter 6 specimens do not differ from *Fahlbuschia crusafonti*. The specimens with moderately

divided anterocone resemble *F. crusafonti* closely, since in that species too the anterior wall of the anterocone may be concave or slightly grooved. Only the remaining 6 specimens with deeply split anterocone are decisive for the genus *Renzimys*. One or several specimens may indeed belong to *F. crusafonti*, but we prefer to consider the population as homogeneous, and attribute all the specimens to *R. bilobatus*.

In the lower molars a distinctive character for *Renzimys* may be, that the bottom of the mesosinusid is not horizontal, but descends steeply from the ectolophid to the molar border.

On the whole, *Renzimys* is easily distinguished from *Fahlbuschia* by its relatively thick enamel and inflated cusps, reminding one of the general aspect of *Cricetodon* teeth.

Through the kind cooperation of Dr P. Mein (Lyon) we have been able to study casts of *Fahlbuschia ultima* Antunes, Ginsburg & Mein, 1983 from Azambujeira (Portugal). Unfortunately no M_1 of this species are known. The 2 available specimens of M^1 show a well-divided anterocone, which makes it probable that this species belongs to the genus *Renzimys*. *Renzimys ultima* is considerably larger than *R. bilobatus*.

Renzimys lacombai sp. nov.
Pl. 15; Pl. 16, figs. 1-8.

Holotype — M^1 sin., RGM 385 623, measurements 27.4×16.8 .

Type-locality — Regajo 2, Teruel, Spain, code REG 2.

Type-level — Aragonian Zone D3.

Derivatio nominis — In honour of Mr J.I. Lacomba Andueza, who first described the genus *Renzimys*, and who participated many times in our field campaigns.

Diagnosis

M_1 and M_2 on the average somewhat smaller than in *R. bilobatus*, M_3 somewhat larger and less reduced morphologically. Upper molars with a tendency to form ectolophs on the posterior walls of the paracones.

Material and measurements

	Length					Width				
	n	min.	mean	max.	σ	n	min.	mean	max.	σ
M_1	9	21.1	22.24	23.5	0.847	11	13.2	14.31	15.1	0.601
M_2	10	19.0	19.65	20.1	0.417	10	15.4	16.24	17.0	0.502
M_3	10	17.0	17.84	18.9	0.560	10	13.9	14.51	15.3	0.532
M^1	11	25.4	26.63	27.7	0.811	19	15.4	16.30	17.7	0.570
M^2	18	18.0	19.44	20.3	0.684	20	15.4	16.17	17.0	0.451
M^3	17	13.0	13.85	14.6	0.493	17	13.6	14.28	14.8	0.386

Description

M_1 — Length/width ratio 1.55, prelobe ratio 0.26. The anteroconid is symmetrical or somewhat asymmetrical, with descending cingulum ridges on both sides, which may or may not close the valleys. The anterosinusid is smaller and shallower than the protosinusid. The anterolophulid is simple (4), or it bears a labial spur (3). It lies labially of the axis of the molar and is connected to the labial corner of the anteroconid. The metalophulid is directed obliquely forward or transverse, meeting the anterolophulid just in front of the protoconid. The valley between protoconid and metaconid is narrow and shallow.

There is a mesolophid. The ectolophid may be constricted before or behind the hypolophid. The hypolophid is often very broad. The posterosinusid remains open or it is closed at a very low level by the posterolophid. In the specimens with preserved roots there is a small accessory root in between the main roots.

M_2 — The labial anterolophid is well developed and the anterosinusid remains visible, sometimes it is even fairly large. The protosinusid is open. The valley between protoconid and metaconid is narrow. The mesolophid is absent or short, often nothing more than a mere bulge on the ectolophid. The ectolophid may be constricted. The sinusid is directed obliquely forward and often curved backwards, closed by a low cingulum ridge. The hypolophid is often very broad. The posterosinusid is like in M_1 .

M_3 — The lingual anterolophid is very small and disappears rapidly with wear. The protosinusid is open or closed. There is no mesolophid, but in several cases the lingual wall of the protoconid shows some irregularities. The entoconid is well marked, because the mesosinusid and – to a lesser extent – the posterosinusid are not closed. The sinusid is transverse or curved backwards. In 2 specimens the posterosinusid is divided by a more or less longitudinal crest.

M^1 — The anterolophule is superficially divided into two cusps. The anterolophule is forked in all but 1 specimen. The cingula descending from the anterocones are not very important and leave the valleys open. The protolophule is posterior, and in 1 specimen there is also a weak anterior connection. The paracone shows almost always a beginning of a posterior ectoloph. The mesoloph is absent (14), short (4), or of medium length (1). The mesosinus is dammed by a low cingulum ridge. The sinus is transverse or somewhat curved forward, often very narrow, open. In many cases there is not even a trace of a cingulum ridge descending from the hypocone. The metalophule is posterior, the posterosinus present.

M^2 — The posterior protolophule is always present, either directed obliquely backward, or transverse. Besides, an anterior connection may exist (2), be indicated (3), or a small funnel in the labial part of the protocone is a vestige of its existence (2). A beginning of an ectoloph on the paracone is present (19), or absent (2). The mesoloph is absent (12), or short (7). The sinus is seldom transverse, mostly curved forward, often narrow, open, or closed at a low level. The metalophule is posterior (8), double (5), anterior (5), or absent (1).

M^3 — The posterior ectoloph is always indicated; in 2 specimens an anterior ectoloph is present as well. The centroloph is always present. The axioloph may be complete (4), interrupted (6), or absent (2). One specimen has a little mesoloph. In 2 specimens the neo-entoloph is only weakly developed, in the others it is well developed.

Plate 15

All figures approx. 20 ×.

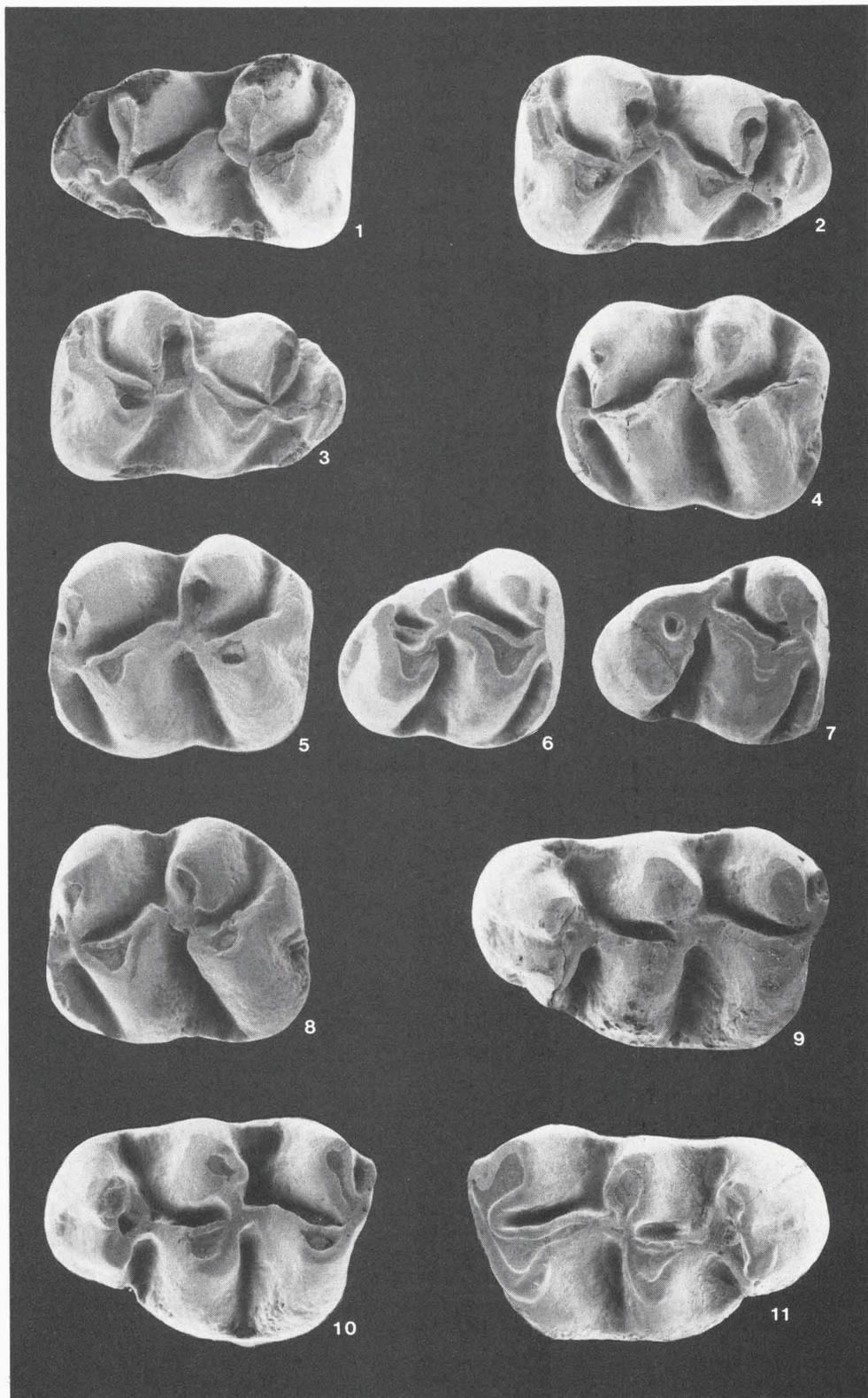
Renzimys lacombai sp. nov.

Regajo 2

- Fig. 1. M_1 sin., RGM 385 584.
 Fig. 2. M_1 dext., RGM 385 588.
 Fig. 3. M_1 dext., RGM 385 591.
 Fig. 4. M_2 sin., RGM 385 595.
 Fig. 5. M_2 sin., RGM 385 599.
 Fig. 6. M_3 dext., RGM 385 608.

- Fig. 7. M_3 dext., RGM 385 616.
 Fig. 8. M_2 sin., RGM 385 600.
 Fig. 9. Holotype, M^1 sin., RGM 385 623.
 Fig. 10. M^1 sin., RGM 385 625.
 Fig. 11. M^1 dext., RGM 385 628.

Plate 15



Discussion

M_1 — In *R. bilobatus* the anterolophulid seems to be more complicated than in *R. lacombai*. The morphotype with two complete branches, both reaching the anteroconid is quite frequent in *bilobatus* and absent in *lacombai*. Short mesolophids exist in *bilobatus* and are absent in *lacombai*.

M_2 — The labial anterolophid and the anterosinusid exist in *lacombai*, and lack completely, or are very reduced, in *bilobatus*.

M_3 — The posterosinusid is fairly well developed and mostly closed in *lacombai*, much reduced and lingually open in *bilobatus*.

M^1 — On the average the subdivision of the anterocone is much more pronounced in *bilobatus* than it is in *lacombai*. In the latter species the ectolophs on the paracones are much more prominent.

M^2 — In *R. bilobatus* only the posterior metalophule exists, and the paracone bears no trace of an ectoloph. In *R. lacombai* the metalophule is variable and an ectoloph-spur is always present.

M^3 — In *bilobatus*, contrary to *lacombai*, axioph and centroloph are often absent, and there is no ectoloph-spur.

Some specimens of *R. lacombai* may be mistaken for *Pseudofahlbuschia jordensi* sp. nov., which is almost contemporaneous. *R. lacombai* is larger, the enamel is thicker, the sinusid is narrower and often curved, the sinus may even be strongly curved. The hypolophulids are very broad. In M_1 the anteroconid is more asymmetrical, and the anterolophulid lies labially of the molar axis.

Nothing can be said about the phylogeny of *Renzimys*, because the known species show a mixture of 'primitive' and 'modern' characters. E. g. the subdivision of the anterocone of M^1 is more pronounced in *R. bilobatus*, the ectolophs in the upper molars are better developed in *R. lacombai*. In the future it may appear necessary to assign them to different genera.

Apart from the type-locality *R. lacombai* has been found in the localities Valhondo 4B and 4C, in association with *F. freudenthali*.

Plate 16

Fig. 13 approx. 25 ×, other figures approx. 20 ×.

Cricetidae gen. et sp. indet., cf. *Lartetomys*

Renzimys lacombai sp. nov.

Manchones 1

Fig. 12. M_1 dext., MA 2107.

Regajo 2

Fig. 1. M^2 dext., RGM 385 643.

Fig. 2. M^2 dext., RGM 385 644.

Fig. 3. M^3 sin., RGM 385 662.

Fig. 4. M^2 dext., RGM 385 646.

Fig. 5. M^2 dext., RGM 385 647.

Fig. 6. M^3 sin., RGM 385 663.

Fig. 7. M^3 dext., RGM 385 680.

Fig. 8. M^3 sin., RGM 385 669.

Fahlbuschia decipiens sp. nov.

Buñol

Fig. 13. Holotype, M_1 dext., BU 1564.

Cricetidae gen. et sp. indet.

Villafeliche 4A

Fig. 9. M_1 sin., RGM 254 050.

Fig. 10. M^1 sin., RGM 254 051.

Fig. 11. M^2 dext., RGM 254 052.

Plate 16



Cricetidae gen. et sp. indet.

Locality Villafeliche 4A (code VL 4A, Zone D2)

Pl. 16, figs. 9-11.

Three specimens from Villafeliche 4A draw the attention by their very slender appearance: M_1 : 18.3×10.5 ; M^1 : 24.3×13.9 ; M^2 : 17.6×13.8 .

The length/width ratio of M_1 , 1.74, is very high, even higher than in most *Megacricetodon* species, and its prelobe ratio of 0.26 shows that the prelobe part makes a considerable contribution to the length of the molar. Nevertheless, the rounded lingual end of the anteroconid reminds one more of *Fahlbuschia* than of *Megacricetodon*. The anterolophulid is long. The metalophulid is transverse towards the anterior corner of the protoconid. There is a mesolophid. The posterosinusid is open. The valleys are wide, the cusps relatively small. If this is not an aberrant specimen of *Pseudofahlbuschia jordensi*, it probably represents an unknown genus.

The very long and slender M^1 falls outside the size distribution of *P. jordensi*. It is not certain that it belongs to the same species as the M_1 described above, but is not impossible either. Morphologically it is not different from *P. jordensi*. The anterolophule is concave anteriorly, indicating a slight subdivision. Its labial part has a backward spur. There is no anterior protolophule. The mesoloph is short.

A single M^2 without anterior protolophule, with a mesoloph of medium length, and an anterior metalophule may go with this M^1 .

Locality Manchones 1 (code MA or MA 1, Zone G)

Pl. 16, fig. 12.

The M_1 MA 2107 from Manchones 1, mentioned by Freudenthal (1963) is certainly not a *Fahlbuschia darocensis*, and it does not even belong to the genus *Fahlbuschia*. Its measurements, 20.9×15.4 , length/width ratio 1.36, make it improbable that it belongs to *Democricetodon*. Morphologically it seems to be close to *Lartetomys*, but the few known *Lartetomys* specimens (Vieux-Collonges, Biorosse, Neudorf, Thenay) are all larger than the specimen from Manchones 1. It is not clear to what genus this specimen belongs.

Biostratigraphy and evolution

In the Calatayud-Teruel Basin *Democricetodon*, *Fahlbuschia*, *Renzimys*, and the new genus *Pseudofahlbuschia* are good stratigraphic markers. Whether the sequence found is valid also for other basins in Spain, or even outside Spain, cannot be judged, because of insufficient documentation.

Fig. 5. Histograms of lengths of M_1 .



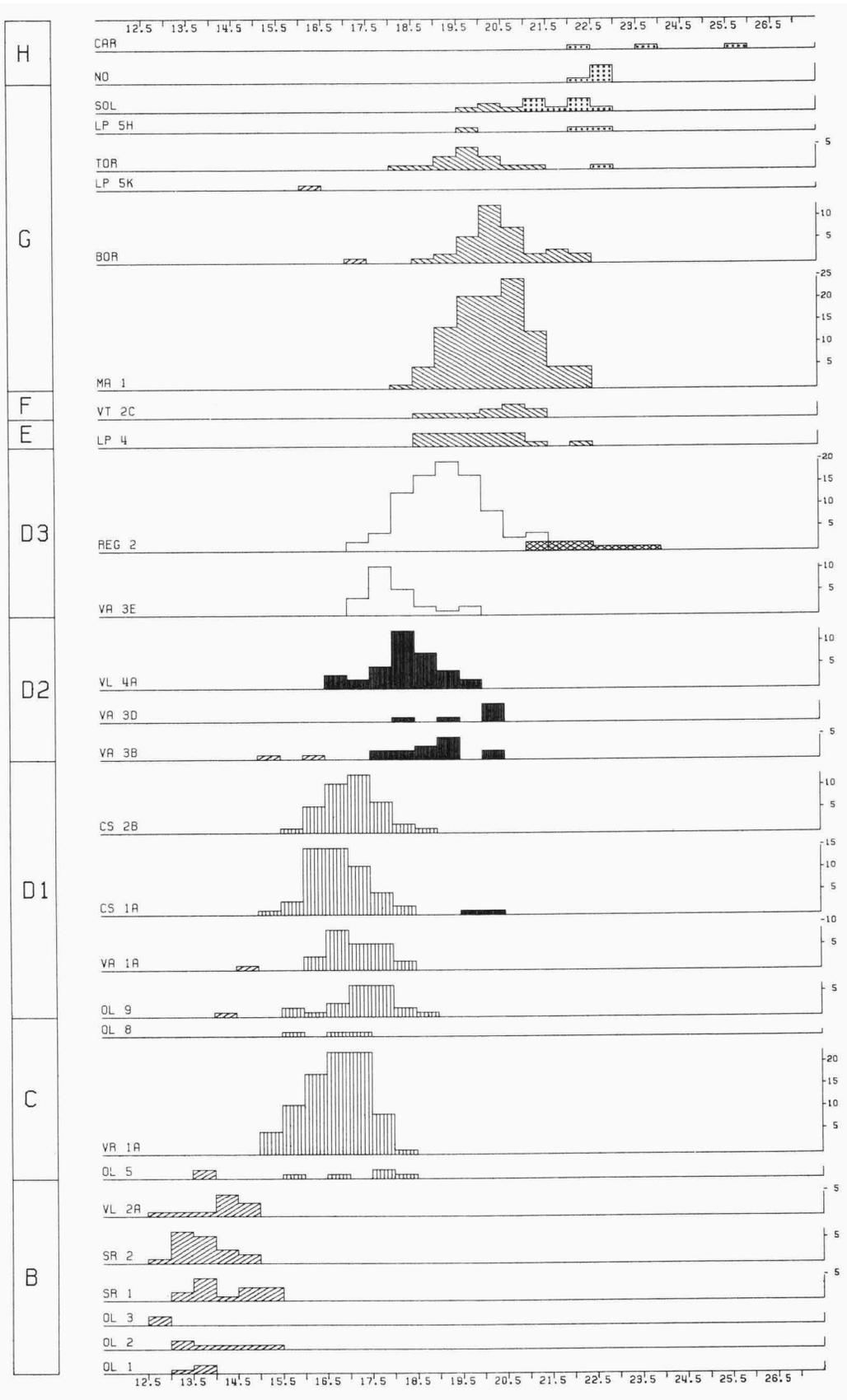


Fig. 5 gives the histograms of the lengths of M_1 of the mentioned genera. A few very poor localities have been left out because they didn't add anything extra to the overall picture. Fig. 6 represents the same histograms for M^1 .

The sequence of the localities in these figures is partly based on sedimentary superposition observed in the field, partly on the faunal composition of these localities. In the latter case the degree of evolution of the *Megacricetodon* species has been used as a primary criterion for the adopted sequence.

Though the vertical sequence of the localities is the one considered most likely, the vertical scale of these figures is certainly not a time scale. E.g. the space taken by the localities Vargas 1A through Casetón 2B is relatively large, due to the fact that these localities have yielded an abundant material, resulting in histograms with high peaks. In fact, the time elapsed between Vargas 1A and Casetón 2B may be relatively short.

Possibly the most striking feature in the histograms is the gradual increase in size throughout time. Without taking into account generic and specific determinations it is evident, that the specimens in the oldest localities are small, and that size increases gradually towards the largest specimens in the youngest localities. It is almost possible to decide the stratigraphic position of a locality on the basis of the size of the specimens found, without bothering to what genus or species they belong.

Freudenthal (1963, p. 97) attempted to reconstruct the evolution of the '*larteti* group'. This attempt, based on a small number of localities in the area of Daroca-Calatayud, has to be rejected, now that more and better material is available. It is now evident, that the so-called '*Übergang koenigswaldi - darocensis*' represents a separate lineage, which is transferred to the new genus *Pseudofahlbuschia*.

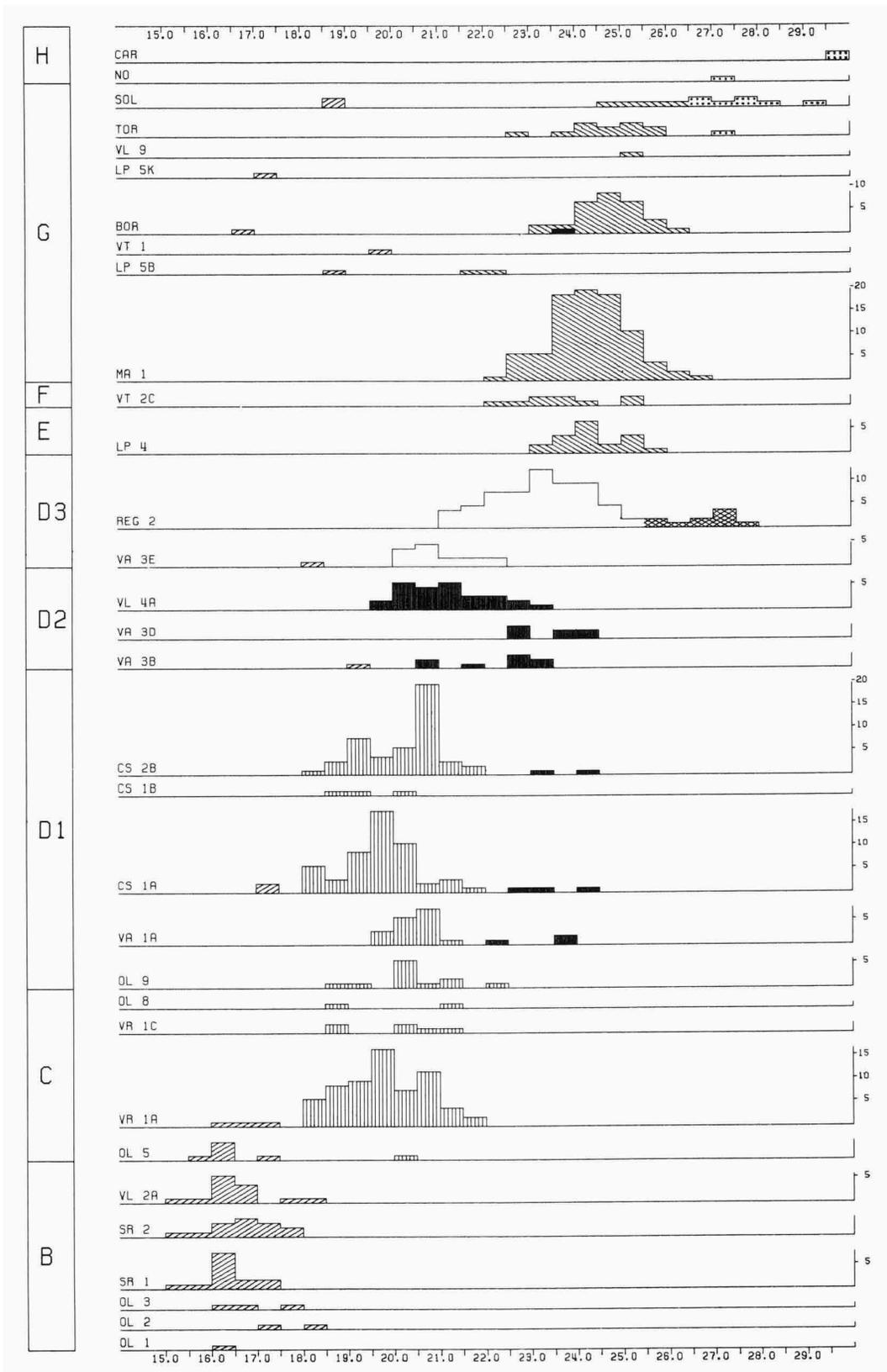
Essential in the idea of *Fahlbuschia* evolution was – in the 1963 paper – that *F. koenigswaldi* is characterized by short, broad molars; in the transitional phase *koenigswaldi - darocensis* the teeth become longer, but keep the same width, thus changing essentially the length/width ratio. *F. darocensis* and its successor *larteti* were larger than the transitional form, but were considered to retain the same length/width ratio.

Our new material has shown that this is not the case. The length/width ratio of M_1 in *F. koenigswaldi* from Valdemoros 1A, and from a number of new localities like Vargas 1A, Casetón 1A, Casetón 2B, etc. varies around 1.45. In the so-called transitional form from Villafeliche 4A it is 1.60, in Valdemoros 3B it is somewhat less at 1.56. In the *darocensis* samples from Manchones 1 and the newly discovered localities of Borjas, Toril 1, etc. it varies between 1.47 and 1.51. So the *darocensis* molars are somewhat more elongated than the *koenigswaldi* specimens, but the transitional form is the most slender of all. Data of length/width ratios are given in Table 1.

This makes it already rather improbable that we are dealing with a single evolutionary lineage, and several other discrepancies discard this possibility altogether. Among these, the most important one is the morphology of M^2 . In Valdemoros 1A, and other comparable localities, the protolophule of M^2 is predominantly double: an anterior protolophule from the paracone to the anterior corner of the protocone, and a posterior branch towards the posterior corner. The same situation is found in our samples of *darocensis*. So, if *darocensis* is a descendant of *koenigswaldi* there is no reduction of the anterior protolophule of M^2 in this lineage. In Villafeliche 4A and Valdemoros 3B the

Fig. 6. Histograms of lengths of M^1 .





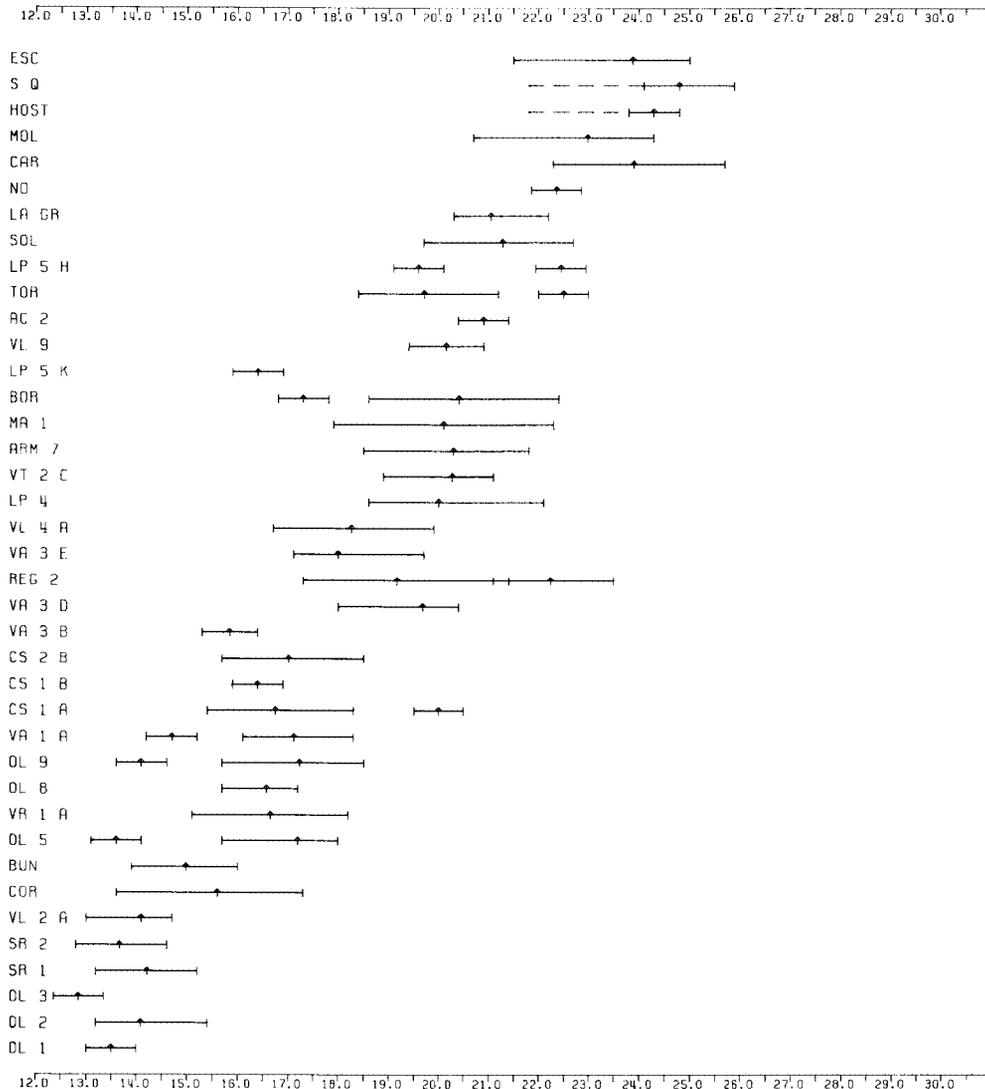


Fig. 7. Distribution of lengths of M_1 .

anterior protolophule is absent in most specimens; only in a few cases a trace of it is present, always being less developed than the posterior protolophule.

This fact eliminates the form from Villafeliche 4A and Valdemoros 3B from the stock of *F. koenigswaldi*. The anterior protolophule is considered a primitive feature, that tends to disappear; for this reason there might be an evolutionary lineage from the Valdemoros 1A population towards the one from Villafeliche 4A, but, so far, we know not a single example of an almost 100 % change of a character of a cricetid molar in such a short time as is assumed to have elapsed between the deposition of these two localities. If there were an evolutionary connection the anterior protolophule might be absent or interrupted in e.g. 20 or 30 % of the Villafeliche specimens, but certainly not in over 90 % as is actually the case.

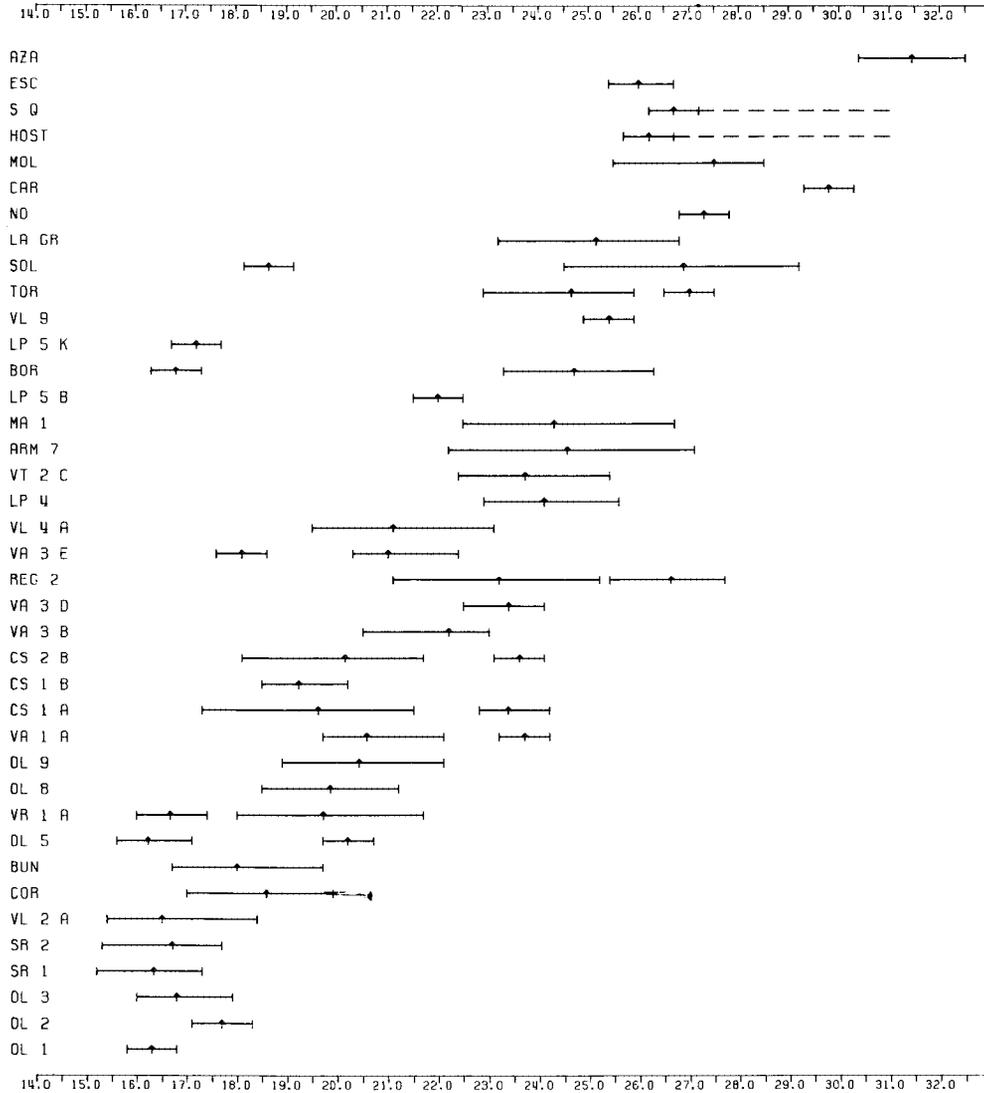


Fig. 8. Distribution of lengths of M¹.

Nor can the Villafeliche 4A population be the ancestor of *F. darocensis*. In this case the same arguments apply as in the previous lines: a 100 % change is highly improbable. Furthermore it is not likely that the anterior protolophule would reappear in *darocensis*, once it had disappeared in the form from Villafeliche 4.

Hence it follows that the material from Villafeliche 4A and Valdemoros 3B represents a separate lineage, which we place in the new genus *Pseudofahlbuschia*.

Looking at Figs. 5 and 6 we see a small cricetid in the lowermost localities Olmo Redondo 1 through Olmo Redondo 5. This is a small *Democricetodon*, the first of the 'modern' cricetids to arrive in our area, and possibly the oldest one known in the whole of Europe. Nothing is known of its origin or provenance, though a small form of comparable age is known from Erkertshofen (Fahlbusch, 1966). There is no doubt that *Democricetodon* is an immigrant, and did not evolve in our area.

In Olmo Redondo 5 *Fahlbuschia koenigswaldi* appears, and in all later localities *Democricetodon* is absent or very rare. *Fahlbuschia* continues to be, after *Megacricetodon*, the dominant cricetid in almost all localities in our area until the end of the Aragonian. From Olmo Redondo 5 through Casetón 2B hardly anything happens. There are some slight variations in dental morphology between the populations from these localities, the size variations remain well within the limits of statistical significance. Then, all of a sudden, at the level of Valdemoros 3B *F. koenigswaldi* disappears, and is replaced by *Pseudofahlbuschia jordensi*. As explained before, *jordensi* cannot be a descendant of *koenigswaldi*, so it must be an immigrant in our area, that existed before elsewhere. This is proven by the fact that a few specimens from Valdemoros 1A and Casetón belong to the *jordensi* lineage. The most plausible explanation for such a sudden change may be a change in climate and biotope.

Within the range Valdemoros 1A through Villafeliche 4A *Pseudofahlbuschia jordensi* is present, at first in small numbers, then dominating in Valdemoros 3B, Valdemoros 3D and Villafeliche 4 and 4A. In Valdemoros 3E *Pseudofahlbuschia* has disappeared, and *Fahlbuschia* is back again. But this is a new form of *Fahlbuschia*, *Fahlbuschia freudenthali*, somewhat larger than *koenigswaldi* and smaller than *darocensis*. In view of its length *F. freudenthali* might be an intermediate step between *koenigswaldi* and *darocensis*, but this is not probable: in both *koenigswaldi* and *darocensis* the anterior protolophule in M¹ is rare, in *freudenthali* from Regajo 2 it is more frequent. Also, in Regajo the mesoloph of the upper molars seem to be better developed. Another difference is the very low length/width ratio in *freudenthali*. For these reasons we think that *F. freudenthali* cannot be an intermediate stage between *koenigswaldi* and *darocensis*, but that it is a representative of a separate lineage, and may be related to *F. cf. crusafonti* from the Upper Aragonian. *F. freudenthali* is accompanied by *Renzimys lacombai* in Regajo 2 and in several unpublished localities at Valhondo. This association is not restricted to the Calatayud-Teruel Basin. A similar association appears to be present in the Madrid Basin (unpublished data, kindly put at our disposal by Miss E. Herraéz, Madrid).

Though the sequence of most localities in Figs. 5 and 6 is pretty sure, the sequence of the range Valdemoros 3B through Regajo 2 is not certain at all. Regajo is some 30 km away from the other localities, and the position of Villafeliche 4A within the Valdemoros 3 section cannot be ascertained due to tectonic movements. So, the sequence of these localities is entirely based on a logical grouping of the occurrences of *F. freudenthali* and *Pseudofahlbuschia jordensi*. It is possible that in reality the sequence is different, and that the occurrences of *freudenthali* and *jordensi* alternate. However, since we know that the same association of *F. freudenthali* and *Renzimys lacombai* has been found in another basin too, we think these associations have chronological and stratigraphical value (probably based on climate), and that the *freudenthali* – *lacombai* association is actually younger than the *Pseudofahlbuschia* fauna.

After Regajo 2 *F. freudenthali* disappears, making place for *F. darocensis*, larger than, and morphologically quite comparable with *F. koenigswaldi*. *F. darocensis* may be an immigrant in our area, taking over from *F. freudenthali* after a supposed change of biotope; another immigrant at the same level of Las Planas 4A is *Cricetodon*. On the other hand, *F. darocensis* may be a descendant of *F. koenigswaldi*.

From Las Planas 4A through Toril 1 *F. darocensis* persists, showing only minor variations in size and morphology. It should be stressed, however, that Manchones 1, Borjas and Toril 1 are considered to be of almost the same age.

From Toril 1 onwards *F. darocensis* disappears and yields to another form of *Fahlbuschia*, which is considerably larger. Unfortunately this large form is badly repre-

sented, and cannot be determined with certainty. We call it – provisionally – *F. nov. sp. cf. crusafonti*, but we are not even sure that it is only one species. Some features of this material, like the anterior protolophule in M^1 , remind one of *F. freudenthali*.

Daams & Freudenthal (1981) subdivided the Miocene of the Daroca area in Zone A through I, G being the Upper Aragonian, and H and I belonging to the Vallesian. As far as *Democracetodon*, *Fahlbuschia*, *Pseudofahlbuschia*, and *Renzimys* are concerned the definition of these Zones is as follows:

Aragonian A — No *Democracetodon* and *Fahlbuschia*.

Aragonian B — *Democracetodon hispanicus*, no *Fahlbuschia*.

Aragonian C — *Democracetodon hispanicus* persists. The bulk of the material belongs to *Fahlbuschia koenigswaldi*.

Aragonian D — *Democracetodon hispanicus* still persists in the lower part of Zone D, though very rare; *Fahlbuschia koenigswaldi* is frequent. Besides, a few specimens of *Pseudofahlbuschia* may be present. In the middle part of Zone D *Pseudofahlbuschia* replaces *Fahlbuschia*. In the upper part of Zone D *Fahlbuschia freudenthali* is present. *Democracetodon hispanicus* has disappeared, but a larger *Democracetodon* may be present from time to time in very small numbers.

Aragonian E and F — *Fahlbuschia darocensis* and some rare specimens of *Democracetodon*.

Aragonian G — like E and F; in the upper part *F. cf. crusafonti* appears; the presence of *Pseudofahlbuschia* is doubtful.

Vallesian H — *F. darocensis* has disappeared; *F. cf. crusafonti* persists.

So, the oldest *Fahlbuschia* in our area is *F. koenigswaldi*. This is, however, not the most primitive *Fahlbuschia* known. *F. decipiens* sp. nov. from Buñol may be the ancestor of *F. koenigswaldi*. An even more primitive species is *F. corcolesi* from Córcoles. This species is even smaller than *decipiens*, and the majority of the M^2 only have the anterior protolophule. We don't think this is the ancestor of *F. decipiens*, because it has lost already some primitive features that persist in Buñol. So it is probable that even in the oldest levels two different lineages of *Fahlbuschia* are present.

Córcoles and Buñol are supposed to represent a span of time anterior to Vargas 1A and posterior to Villafeliche 2A, that has left no fossil documentation in the Calatayud-Teruel Basin. This may be linked to the fact that at about this time the type area of the Aragonian is subject to important tectonic movements: in Villafeliche 2A and lower localities the beds are subhorizontal; in Vargas 1A and Valdemoros 1A they are steeply inclined, due to the upthrust of the Paleozoic block of Daroca-Murero. Another possibility is that Buñol and Córcoles are time-equivalent with Villafeliche 2A or Vargas 1A, but that they simply contain a different fauna.

On the basis of size one might construe the sequence *F. decipiens* – *F. koenigswaldi* – *F. freudenthali* – *F. darocensis* – *F. cf. crusafonti*. This does, however, not agree with the morphology. In Córcoles the anterior protolophule of M^1 is absent, in Buñol (*decipiens*) it is frequent, in *koenigswaldi* it is rare, in *freudenthali* it is rather frequent, in *darocensis* it is very rare, and in *cf. crusafonti* it is fairly frequent. These fluctuations plead against the theory of one single evolutionary lineage. At least two lineages should be present, one with fairly well-developed anterior protolophule in M^1 (*freudenthali* – *cf. crusafonti*) and one with reduced anterior protolophule (*decipiens* – *koenigswaldi* – *darocensis*). The position of *F. corcolesi* is unclear. By various features (morphology of M_1 , length/width ratio, antero-lingual cingulum of M^1 , etc.) it may be placed in the *freudenthali* – *crusafonti* lineage; however, this would mean a progressive development of the anterior protolophule in M^1 , which is contrary to the generally accepted trend. The

reason for the alternating occurrences of these two lineages in the Aragonian type area may be a number of changes in biotope. It would be very interesting to see whether a similar picture is found in other areas.

The most complex part of our sequence is Zone D, which we propose to subdivide into D1, D2, and D3.

D1 is characterized by the absence of *Democricetodon hispanicus*, the dominance of *Fahlbuschia koenigswaldi*, and some incidental finds of *Pseudofahlbuschia*.

D2 is defined by the absence of *Fahlbuschia*; its place is taken by *Pseudofahlbuschia* (of course an incidental occurrence of *Fahlbuschia* cannot be excluded).

D3 is characterized by the association *Fahlbuschia freudenthali* and *Renzimys lacombai*.

As explained before the superposition of D1, D2 and D3 is not (yet) certain. The radical change of fauna in the reach D1 – D3 may be due to changes in biotope, linked to the end of the tectonic phase. In this part of the type-section the beds are subhorizontal again. It is strange that the faunal change is not reflected in *Megacricetodon*, nor in other groups of rodents.

Literature citations of *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia*, and *Renzimys* (including this paper)

The following list contains mere citations, without any interpretation on our part. Type-localities are marked with an *.

Locality	source	cited as
<i>Democricetodon affinis</i> (Schaub, 1925)		
Sansan	Schaub, 1925	<i>C. affinis</i>
La Grive-St. Alban *	Schaub, 1925	<i>C. affinis</i>
Vieux-Collonges	Schaub, 1925	<i>C. affinis</i>
Spornegg	Schaub, 1925	<i>C. affinis</i>
Rümikon	Schaub, 1925	<i>C. affinis</i>
Schwamendingen	Schaub, 1925	<i>C. affinis</i>
Steinheim	Schaub, 1925	<i>C. affinis</i>
Hostalets de Pierola	Bataller, 1938	<i>C. affinis</i>
Sant Quirze	Bataller, 1938	<i>C. affinis</i>
Langenmoosen	Dehm, 1952	<i>C. affinis</i>
La Grive-St. Alban	Freudenthal, 1963	<i>C. affinis</i>
Veyran	Thaler, 1966	<i>D. cf. affinis</i>
Mala Miliva	Petronijevic', 1967	<i>C. affinis</i>
La Grive-St. Alban	Guérin & Mein, 1971	<i>D. affinis</i>
Cases-de-Pènes	Mein & Cornet, 1973	<i>D. affinis</i>
La Grive-St. Alban	Vianey-Liaud, 1974	<i>D. affinis</i>
Pont d'Aiguines	Gigot, Mein & Truc 1976	<i>D. affinis</i>
Luc-sur-Orbieu	Aguilar, 1980	<i>D. aff. affinis</i>
Veyran	Aguilar, 1980	<i>D. aff. affinis</i>
Leucate Butte 1	Aguilar, 1980	<i>D. aff. affinis</i>
Valdemoros 3B	this paper	<i>D. cf. affinis</i>

<i>Democricetodon brevis</i> (Schaub, 1925)		
La Grive-St. Alban *	Schaub, 1925	<i>C. brevis</i>
Sansan	Schaub, 1925	<i>C. brevis</i>
Rümikon	Schaub, 1925	<i>C. brevis</i>
Hostalets inf.	Schaub, 1947	<i>C. cf. brevis</i>
Viladecabals	Schaub, 1947	<i>C. brevis</i>
Langenmoosen	Dehm, 1952	<i>C. brevis</i>
Vieux-Collonges	Mein, 1958	<i>C. brevis</i> or <i>affinis</i>
Neudorf	Čtyroký & Fejfar, 1962	<i>C. brevis</i>
Sansan	Freudenthal, 1963	<i>C. brevis</i>
La Grive-St. Alban	Freudenthal, 1963	<i>C. brevis</i>
Giggenhausen	Fahlbusch, 1964	<i>D. brevis</i>
Markt	Fahlbusch, 1964	<i>D. brevis</i>
La Grive-St. Alban	Fahlbusch, 1964	<i>D. brevis</i>
Serre de Lobrieu	Mein & Truc, 1966	<i>D. cf. brevis</i>
Mollon	Mein & Truc, 1966	<i>D. cf. brevis</i>
Sibnica	Petronijevic', 1967	<i>C. brevis</i>
La Grive-St. Alban	Guérin & Mein, 1971	<i>D. brevis</i>
L'Isle d'Abeau	Guérin & Mein, 1971	<i>D. cf. brevis</i>
Anwil	Engesser, 1972	<i>D. minor brevis</i>
Hammerschmiede	Mayr & Fahlbusch, 1975	<i>D. minor brevis</i>
Collet-Redon	Jullien, et al., 1979	<i>D. brevis</i>
Castell Barbera	Aguilar et al., 1979	<i>D. cf. brevis</i>
Port-la-Nouvelle	Aguilar, 1980	<i>D. brevis</i>
Martinsbrünneli	Bürgisser et al., 1983	<i>D. brevis</i>
Songlinzhuhang	Li Chuankuei et al., 1983	<i>D. cf. brevis</i>
Shuanggou	Li Chuankuei et al., 1983	<i>D. cf. brevis</i>
<i>Democricetodon crassus</i> Freudenthal, in Freudenthal & Fahlbusch, 1969		
Sansan *	Freudenthal, 1969	<i>D. crassus</i>
Sansan	Baudelot, 1972	<i>D. crassus</i>
Liet	Baudelot & Collier, 1978	<i>D. crassus</i>
La Condoue	Baudelot & Collier, 1978	<i>D. crassus</i>
<i>Democricetodon cretensis</i> de Bruijn & Meulenkamp, 1972		
Plakia *	de Bruijn & Meul., 1972	<i>D. affinis cretensis</i>
<i>Democricetodon franconicus</i> Fahlbusch, 1966		
Erkertshofen *	Fahlbusch, 1966	<i>D. minor franconicus</i>
Orechov	Cicha et al., 1972	<i>D. minor franconicus</i>
Orechov	Fejfar, 1974	<i>D. franconicus</i>
Dolnice 1	Fejfar, 1974	<i>D. franconicus</i>
Dolnice 2	Fejfar, 1974	<i>D. franconicus</i>
Dolnice 3	Fejfar, 1974	<i>D. franconicus</i>
Dolnice	Fejfar, 1974	<i>D. franconicus</i>
Aliveri	Benda & de Bruijn, 1982	<i>D. franconicus</i>
Petersbuch	Ziegler & Fahlbusch, 1986	<i>D. franconicus</i>
Erkertshofen	Ziegler & Fahlbusch, 1986	<i>D. franconicus</i>
Rauscheröd 1b	Ziegler & Fahlbusch, 1986	<i>D. franconicus</i>
Rauscheröd 1c	Ziegler & Fahlbusch, 1986	<i>D. franconicus</i>
Rembach	Ziegler & Fahlbusch, 1986	<i>D. franconicus</i>
Forsthart	Ziegler & Fahlbusch, 1986	<i>D. franconicus</i>
<i>Democricetodon freisingensis</i> Fahlbusch, 1964		
Giggenhausen *	Fahlbusch, 1964	<i>D. gaillardi freisingensis</i>
Anwil	Engesser, 1972	<i>D. gaillardi freisingensis</i>
Hammerschmiede	Mayr & Fahlbusch, 1975	<i>D. gaillardi freisingensis</i>
Santiga	Agustí & Gibert, 1979	<i>D. cf. freisingensis</i>
Collet-Redon	Jullien et al., 1979	<i>D. freisingensis</i>
Santiga	Agustí, 1981	<i>D. freisingensis</i>
Vermes 2	Engesser et al., 1981	<i>D. freisingensis</i>

<i>Democricetodon gaillardi</i> (Schaub, 1925)		
Sansan *	Schaub, 1925	<i>C. gaillardi</i>
Steinheim	Schaub, 1925	<i>C. gaillardi</i>
Vieux-Collonges	Mein, 1958	<i>C. ? gaillardi</i>
Aumeister	Stromer, 1928	<i>C. cf. gaillardi</i>
Appertshofen	Dehm, 1961	<i>C. aff. gaillardi</i>
Armantes 9	Freudenthal, 1963	<i>C. cf. gaillardi</i>
Aumeister	Fahlbusch, 1964	<i>D. cf. gaillardi</i>
Opole	Kowalski, 1967	<i>D. gaillardi</i>
Armantes 9	Freudenthal, 1967	<i>D. cf. gaillardi</i>
Pedregueras 1A	Freudenthal, 1967	<i>D. cf. gaillardi</i>
La Grive-St. Alban	Guérin & Mein, 1971	<i>D. gaillardi</i>
Sansan	Baudelot, 1972	<i>D. gaillardi</i>
Birosse	Baudelot & Collier, 1978	<i>D. cf. gaillardi</i>
Liet	Baudelot & Collier, 1978	<i>D. gaillardi</i>
Taut	Feru et al., 1979	<i>D. group gaillardi</i>
Comanesti 1	Feru et al., 1980	<i>D. group gaillardi</i>
Jalalpur	Cheema et al., 1983	<i>D. cf. gaillardi</i>
Rudabánya	Kordos, 1987	<i>D. gaillardi</i>
Las Planas 5K	this paper	<i>D. gaillardi</i>
Las Planas 5E	this paper	<i>D. gaillardi</i>
Las Planas 5B	this paper	<i>D. gaillardi</i>
Borjas	this paper	<i>D. aff. gaillardi</i>
Solera	this paper	<i>D. aff. gaillardi</i>
Valalto 1	this paper	<i>D. aff. gaillardi</i>
 <i>Democricetodon gracilis</i> Fahlbusch, 1964		
Langenmoosen	Fahlbusch, 1964	<i>D. gracilis</i>
Sandelzhausen *	Fahlbusch, 1964	<i>D. gracilis</i>
Gündlkofen	Fahlbusch, 1964	<i>D. gracilis</i>
Pöttmes	Fahlbusch, 1964	<i>D. gracilis</i>
Rosshaupten	Fahlbusch, 1964	<i>D. gracilis</i>
Jettingen	Fahlbusch, 1964	<i>D. gracilis</i>
Oggenhof	Fahlbusch, 1964	<i>D. gracilis</i>
Vermes	Engesser, 1972	<i>D. minor gracilis</i>
Franzensbad	Fejfar, 1974	<i>D. gracilis</i>
Strakonice	Fejfar, 1974	<i>D. gracilis</i>
Sant Mamet	Agustí, 1981	<i>D. cf. gracilis</i>
Chêne-de-Navère	Bulot, 1981	<i>D. cf. gracilis</i>
Vermes 1	Engesser et al., 1981	<i>D. gracilis</i>
Puttenhamen	Wu Wenyu, 1982	<i>D. gracilis</i>
Maszendorf	Schötz, 1983	<i>D. gracilis</i>
Forsthart	Ziegler & Fahlbusch, 1986	<i>D. gracilis</i>
 <i>Democricetodon hasznosensis</i> Kordos, 1986		
Hasznos *	Kordos, 1986	<i>D. hasznosensis</i>
 <i>Democricetodon hispanicus</i> Freudenthal, 1967		
Villafeliche 2A *	Freudenthal, 1967	<i>D. minor hispanicus</i>
Buñol	Daams & Freudenthal, 1974	<i>D. aff. hispanicus</i>
Chelas 1	Aguilar, 1981	<i>D. aff. hispanicus</i>
Can Martivell 1	Agustí, 1981	<i>D. aff. hispanicus</i>
Can Martivell 2	Agustí, 1981	<i>D. aff. hispanicus</i>
El Canyet	Agustí, 1981	<i>D. aff. hispanicus</i>
St. Mamet	Agustí, 1981	<i>D. aff. hispanicus</i>
Can Martivell 1	Agustí, 1983	<i>D. aff. hispanicus</i>
Can Martivell 2	Agustí, 1983	<i>D. aff. hispanicus</i>
Buñol	this paper	<i>D. aff. hispanicus</i>
Olmo Redondo 1	this paper	<i>D. hispanicus</i>

Olmo Redondo 2	this paper	<i>D. hispanicus</i>
Olmo Redondo 3	this paper	<i>D. hispanicus</i>
Olmo Redondo 5	this paper	<i>D. hispanicus</i>
Olmo Redondo 9	this paper	<i>D. hispanicus</i>
San Roque 1	this paper	<i>D. hispanicus</i>
San Roque 2	this paper	<i>D. hispanicus</i>
Vargas 1A	this paper	<i>D. hispanicus</i>
Valdemoros 1A	this paper	<i>D. hispanicus</i>
<i>Copemys (Democricetodon) kohatensis</i> Wessels, de Bruijn, Hussain & Leinders, 1982		
Banda Daud Shah *	Wessels et al., 1982	<i>Copemys (D.) kohatensis</i>
Jalalpur	Cheema et al., 1983	<i>D. cf. kohatensis</i>
<i>Democricetodon minor</i> Fahlbusch, 1964		
Sansan *	Fahlbusch, 1964	<i>D. minor</i>
Rümikon	Fahlbusch, 1964	<i>D. minor</i>
Villafeliche 2A	Fahlbusch, 1964	<i>D. minor</i>
Rosshaupten	Fahlbusch, 1964	<i>D. cf. minor</i>
Mandlach	Fahlbusch, 1964	<i>D. cf. minor</i>
Oggenhof	Fahlbusch, 1964	<i>D. cf. minor</i>
Veyran	Thaler, 1966	<i>D. cf. minor</i>
Rothenstein 1	Heissig, 1978	<i>D. cf. minor</i>
Hasznos	Kordos, 1981	<i>D. cf. minor</i>
Götzendorf	Bachmayer & Wilson, 1984	<i>D. minor?</i>
<i>Democricetodon mutilus</i> Fahlbusch, 1964		
Langenmoosen *	Fahlbusch, 1964	<i>D. affinis mutilus</i>
Sandelzhausen	Fahlbusch, 1964	<i>D. affinis mutilus</i>
Undorf	Fahlbusch, 1964	<i>D. affinis mutilus</i>
Oggenhof	Fahlbusch, 1964	<i>D. affinis mutilus</i>
Pöttmes	Fahlbusch, 1964	<i>D. affinis mutilus</i>
Altbach	Fahlbusch, 1964	<i>D. affinis mutilus</i>
Appertshofen	Fahlbusch, 1964	<i>D. affinis mutilus</i>
Giggenhausen	Fahlbusch, 1964	<i>D. affinis cf. mutilus</i>
Dechbetten	Fahlbusch, 1964	<i>D. cf. affinis mutilus</i>
Vieux-Collonges	Fahlbusch, 1964	<i>D. mutilus</i>
Vieux-Collonges	Guérin & Mein, 1971	<i>D. cf. mutilus</i>
Collet-Redon	Aguilar & Clauzon, 1979	<i>D. affinis mutilus</i>
Rothenstein 1	Heissig, 1978	<i>D. cf. affinis mutilus</i>
Port-la-Nouvelle	Aguilar, 1980	<i>D. aff. mutilus</i>
Veyran	Aguilar, 1980	<i>D. aff. mutilus</i>
Leucate Butte 1	Aguilar, 1980	<i>D. aff. mutilus</i>
Beaumont 2	Aguilar, 1981	<i>D. mutilus</i>
Beaumont 3	Aguilar, 1981	<i>D. mutilus</i>
Vermes 1	Engesser et al., 1981	<i>D. mutilus</i>
Vermes 2	Engesser et al., 1981	<i>D. mutilus</i>
Puttenhausen	Wu Wenyu, 1982	<i>D. mutilus</i>
Maszendorf	Schötz, 1983	<i>D. mutilus</i>
Steinberg	Heizmann & Fahlbusch, 1983	<i>D. mutilus</i>
Thenay	Sen & Makinsky, 1983	<i>D. cf. mutilus</i>
Soucaret	Bulot, 1986	<i>D. mutilus</i>
<i>Democricetodon nemoralis</i> Agustí, 1981		
Castell Barbera *	Aguilar et al., 1979	<i>D. cf. brevis</i>
Castell Barbera	Agustí, 1981	<i>D. brevis nemoralis</i>
Hostalets inf.	Agustí, 1981	<i>D. brevis nemoralis</i>
<i>Democricetodon romieviensis</i> (Freudenthal, 1963)		
La Romieu *	Freudenthal, 1963	<i>C. romieviensis</i>
La Romieu	Baudelot, 1969	<i>D. romieviensis</i>

Bézian	Bulot, 1972	<i>D. romieviensis</i>
Pellecahus	Baudelot & Collier, 1978	<i>D. romieviensis</i>
Soucaret	Baudelot & Collier, 1978	<i>D. romieviensis</i>
Serido	Baudelot & Collier, 1978	<i>D. cf. romieviensis</i>
La Romieu sup.	Bulot, 1986	<i>D. romieviensis</i>
Soucaret	Bulot, 1986	<i>D. aff. romieviensis</i>
<i>Democricetodon</i> sp.		
Valdemoros 1A	Freudenthal, 1963	<i>Cricetodon</i>
Armantes 1	Freudenthal, 1963	<i>Cricetodon</i>
Valdemoros 3B	Freudenthal, 1963	<i>Cricetodon</i>
Weže	Fahlbusch, 1969	<i>Copemys</i>
Sořca	Tobien, 1975	<i>Democricetodon</i>
Masia del Barbo	van de Weerd, 1976	<i>Democricetodon</i>
Soucaret	Baudelot & Collier, 1978	<i>Democricetodon</i>
Serido	Baudelot & Collier, 1978	<i>Democricetodon</i>
Erkertshofen 2	Heissig, 1978	<i>Democricetodon</i>
Petersbuch 2	Heissig, 1978	<i>Democricetodon</i>
Rothenstein 2	Heissig, 1978	<i>Democricetodon</i>
Hürth 1	Heissig, 1978	<i>Democricetodon</i>
Córcoles	Díaz & López, 1979	<i>Democricetodon</i>
Doué-la-Fontaine	Aguilar, 1981	<i>Democricetodon</i>
Chêne-de-Navère	Bulot, 1981	<i>Democricetodon</i>
Soucaret	Bulot, 1986	<i>Democricetodon</i> small
Soucaret	Bulot, 1986	<i>Democricetodon</i> large
<i>Democricetodon sulcatus</i> Freudenthal, 1967		
Pedregueras 2C *	Freudenthal, 1967	<i>D. minor sulcatus</i>
Nombrevilla	Freudenthal, 1967	<i>D. minor sulcatus</i>
Casas Altas	Adrover et al., 1978	<i>D. sulcatus</i>
Molina de Aragón	Lacomba, 1987	<i>D. sulcatus</i>
<i>Democricetodon vindoboniensis</i> (Schaub & Zapfe, 1953)		
Neudorf a.d. March *	Schaub & Zapfe, 1953	<i>C. brevis vindoboniensis</i>
Franzensbad	Fejfar et al., 1959	<i>C. brevis vindoboniensis</i>
Neudorf a.d. March	Čtyrky & Fejfar, 1962	<i>C. vindoboniensis</i>
Villafeliche 2A	Freudenthal, 1963	<i>C. cf. vindoboniensis</i>
Neudorf a.d. March	Cicha et al., 1972	<i>D. minor vindoboniensis</i>
Neudorf 1	Fejfar, 1974	<i>D. vindoboniensis</i>
Neudorf 2	Fejfar, 1974	<i>D. vindoboniensis</i>
<i>Fahlbuschia corcolesi</i> sp. nov.		
Córcoles *	this paper	<i>F. corcolesi</i>
<i>Fahlbuschia crusafonti</i> Agustí, 1978		
St. Quirze Trinxera *	Agustí, 1978b	<i>F. crusafonti</i>
Hostalets inf.	Agustí, 1978b	<i>F. crusafonti</i>
Can Feliu	Agustí & Gibert, 1979	<i>F. crusafonti</i>
St. Quirze Trinxera	Agustí, 1981	<i>F. crusafonti</i>
Can Feliu	Agustí, 1981	<i>F. crusafonti</i>
Hostalets inf.	Agustí, 1981	<i>F. crusafonti</i>
Hostalets	Agustí & Gibert, 1982	<i>F. crusafonti</i>
Can Almirall	Agustí et al., 1984	<i>F. crusafonti</i>
Hostalets sup.	Agustí et al., 1984	<i>F. crusafonti</i>
Toril 1	this paper	<i>F. cf. crusafonti</i>
Las Planas 5H	this paper	<i>F. cf. crusafonti</i>
Solera	this paper	<i>F. cf. crusafonti</i>
Carrilanga	this paper	<i>F. cf. crusafonti</i>
Nombrevilla	this paper	<i>F. cf. crusafonti</i>

Fahlbuschia darocensis (Freudenthal, 1963)

Manchones 1 *	Freudenthal, 1963	<i>C. darocensis</i>
Las Planas 4A	Freudenthal, 1963	<i>C. darocensis</i>
Las Planas 4B	Freudenthal, 1963	<i>C. darocensis</i>
Arroyo del Val 6	Freudenthal, 1963	<i>C. darocensis</i>
Armantes 3	Freudenthal, 1963	<i>C. darocensis</i>
Armantes 4	Freudenthal, 1963	<i>C. cf. darocensis</i>
Armantes 7	Freudenthal, 1967	<i>D. cf. darocensis</i>
Vieux-Collonges	Guérin & Mein, 1971	<i>F. cf. darocensis</i>
Pont d'Aiguines	Gigot et al., 1976	<i>F. larteti</i> or <i>darocensis</i>
Pero Filho	Antunes & Mein, 1977	<i>F. cf. darocensis</i>
Póvoa de Santarém	Antunes & Mein, 1977	<i>F. darocensis</i>
Libros (corte 2)	Adrover et al., 1978	<i>F. cf. darocensis</i>
Mira	Agustí et al., 1984	<i>F. cf. darocensis</i>
Henares 1	Alberdi et al., 1984	<i>F. cf. darocensis</i>
Paracuellos 3	Alberdi et al., 1984	<i>F. cf. darocensis</i>
Henares 1	Sesé et al., 1985	<i>F. darocensis</i>
Paracuellos 3	Sesé et al., 1985	<i>F. darocensis</i>
Valalto 1	this paper	<i>F. darocensis</i>
Valalto 2B	this paper	<i>F. darocensis</i>
Valalto 2C	this paper	<i>F. darocensis</i>
Manchones 1	this paper	<i>F. darocensis</i>
Borjas	this paper	<i>F. darocensis</i>
Villafeliche 9	this paper	<i>F. darocensis</i>
Toril 1	this paper	<i>F. darocensis</i>
Las Planas 5H	this paper	<i>F. darocensis</i>

Fahlbuschia decipiens sp. nov.

Buñol *	this paper	<i>F. decipiens</i>
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Fahlbuschia freudenthali Antunes & Mein, 1981

Amor *	Antunes & Mein, 1981	<i>F. freudenthali</i>
Regajo 2	this paper	<i>F. freudenthali</i>
Valdemoros 3E	this paper	<i>F. freudenthali</i>
Valhondo 4B	this paper	<i>F. freudenthali</i>
Valhondo 4C	this paper	<i>F. freudenthali</i>
Valhondo 4E	this paper	<i>F. freudenthali</i>

Fahlbuschia koenigswaldi (Freudenthal, 1963)

Valdemoros 1A *	Freudenthal, 1963	<i>C. koenigswaldi</i>
Valtorres	Freudenthal, 1963	<i>C. koenigswaldi</i>
Valdemoros 3B	Freudenthal, 1963	<i>C. koenigswaldi-darocensis</i>
Villafeliche 4	Freudenthal, 1963	<i>C. koenigswaldi-darocensis</i>
Armantes 1	Freudenthal, 1963	<i>C. koenigswaldi-darocensis</i>
Torralba 1	Freudenthal, 1963	<i>C. koenigswaldi-darocensis</i>
Buñol	Daams & Freudenthal, 1974	<i>F. cf. koenigswaldi</i>
Navarrete 5	Adrover et al., 1978	<i>F. koenigswaldi</i>
Córcoles	Díaz & López, 1979	<i>F. cf. koenigswaldi</i>
Chelas 2	Aguilar, 1981	<i>D. ou F. koenigswaldi</i>
Córcoles	Alfárez et al., 1982	<i>F. cf. koenigswaldi</i>
Tarazona de Aragón	Astibia et al., 1984	<i>F. koenigswaldi</i>
O'Donell	Alberdi et al., 1984	<i>F. cf. koenigswaldi</i>
O'Donell	Sesé et al., 1985	<i>F. koenigswaldi</i>
Tarazona de Aragón	Valdés et al., 1986	<i>F. koenigswaldi</i>
Valdemoros 1A	this paper	<i>F. koenigswaldi</i>
Olmo Redondo 5	this paper	<i>F. koenigswaldi</i>
Olmo Redondo 8	this paper	<i>F. koenigswaldi</i>
Olmo Redondo 9	this paper	<i>F. koenigswaldi</i>
Vargas 1A	this paper	<i>F. koenigswaldi</i>
Vargas 1E	this paper	<i>F. koenigswaldi</i>
Casetón 1A	this paper	<i>F. koenigswaldi</i>

Casetón 1B	this paper	<i>F. koenigswaldi</i>
Casetón 2B	this paper	<i>F. koenigswaldi</i>
<i>Fahlbuschia larteti</i> (Schaub, 1925)		
La Grive-St. Alban *	Schaub, 1925	<i>C. larteti</i>
Hostalets inf.	Schaub, 1947	<i>C. cf. larteti</i>
Can Flaque	Schaub, 1947	<i>C. cf. larteti</i>
Sant Quirze	Schaub, 1947	<i>C. cf. larteti</i>
Vieux-Collonges	Mein, 1958	<i>C. aff. larteti</i>
Armantes 7	Freudenthal, 1963	<i>C. larteti</i>
Armantes 8	Freudenthal, 1963	<i>C. larteti</i>
Armantes 3	Freudenthal, 1963	<i>C. cf. larteti</i>
Nombrevilla	Freudenthal & Sondaar, 1964	<i>C. cf. larteti</i>
Nombrevilla	Freudenthal, 1967	<i>D. cf. larteti</i>
Armantes 7	Freudenthal, 1967	<i>D. cf. larteti</i>
Póvoa de Santarém	Antunes & Zbyszewski, 1973	<i>D. larteti</i>
Quinta do Marmelal	Antunes & Zbyszewski, 1973	<i>D. sp. larteti ?</i>
Pont d'Aiguines	Gigot et al., 1976	<i>F. larteti</i> ou <i>darocensis</i>
Mourel de l'Oreille	Aguilar & Magné, 1978	<i>F. larteti</i>
Hostalets	Agustí, 1978a	<i>F. larteti</i>
La Grenatière	Aguilar, 1980	<i>F. larteti</i>
Can Almirall	Aguilar, 1981	<i>D.</i> ou <i>F. larteti</i>
<i>Fahlbuschia</i> sp.		
Escobosa	López & Sanz, 1977	<i>Fahlbuschia</i>
Escobosa	Sesé, 1977	<i>Fahlbuschia</i>
Henares 2	Alberdi et al., 1984	<i>Fahlbuschia</i>
Arroyo del Olivar	Alberdi et al., 1984	<i>Fahlbuschia</i>
O'Donell	Alberdi et al., 1984	<i>Fahlbuschia</i>
Henares 2	Sesé et al., 1985	<i>Fahlbuschia</i>
O'Donnel	Sesé et al., 1985	<i>Fahlbuschia</i>
Tarazona de Aragón	Valdés et al., 1986	<i>Fahlbuschia</i>
<i>Fahlbuschia ultima</i> Antunes, Ginsburg & Mein, 1983		
Azambujeira inf. *	Antunes et al., 1983	<i>F. ultima</i>
<i>Pseudofahlbuschia jordensi</i> sp. nov.		
Villafeliche 4A *	this paper	<i>P. jordensi</i>
Casetón 1A	this paper	<i>P. jordensi</i>
Casetón 2B	this paper	<i>P. jordensi</i>
Valdemoros 1A	this paper	<i>P. jordensi</i>
Valdemoros 3D	this paper	<i>P. jordensi</i>
Borjas ?	this paper	<i>P. jordensi</i>
<i>Renzimys bilobatus</i> Lacomba, 1983		
Molina de Aragón *	Lacomba, 1983	<i>R. bilobatus</i>
<i>Renzimys lacombai</i> sp. nov.		
Regajo 2 *	this paper	<i>R. lacombai</i>
Valhondo 4B	this paper	<i>R. lacombai</i>
Valhondo 4C	this paper	<i>R. lacombai</i>

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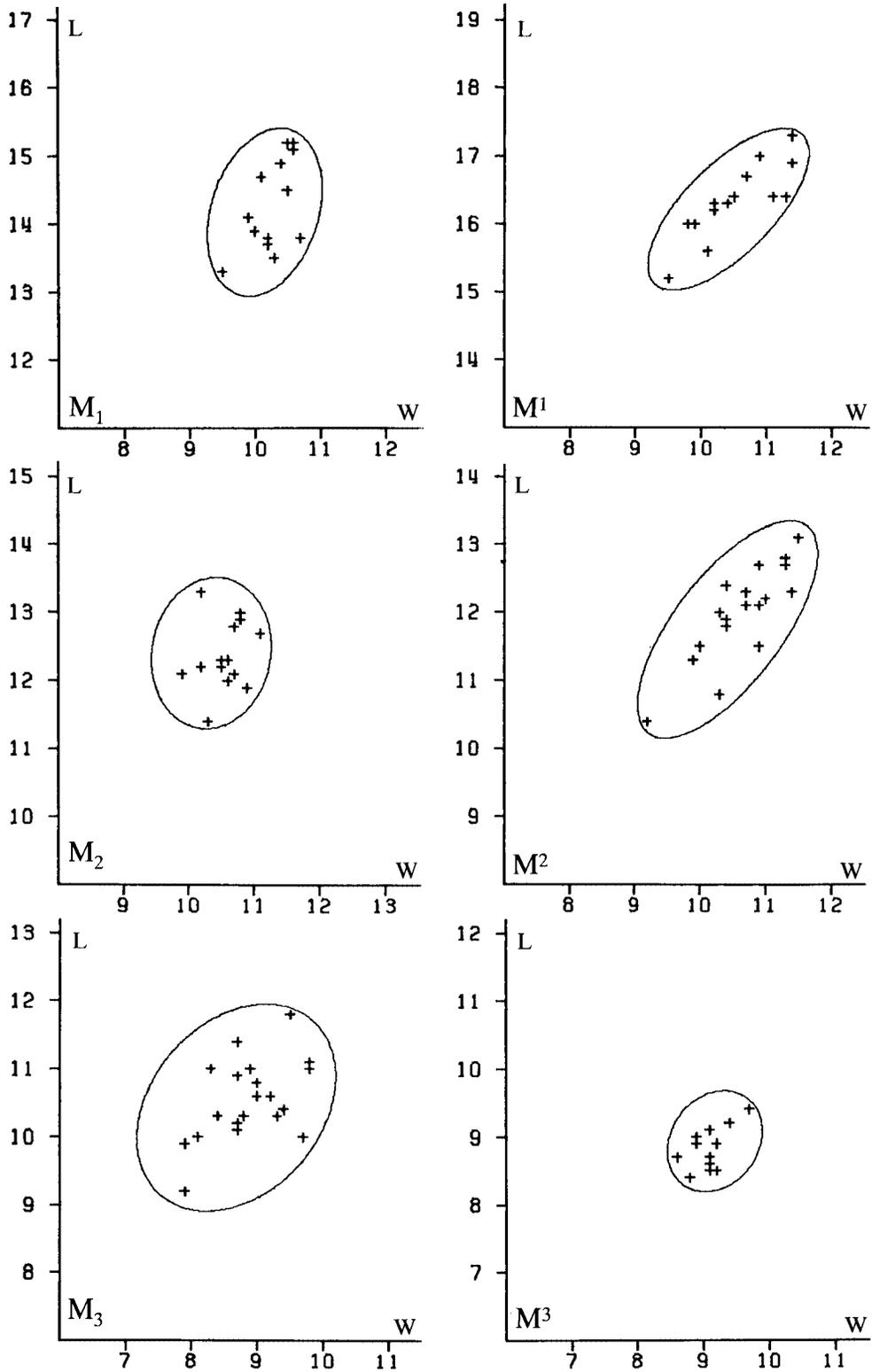


Fig. 9. Length-width diagrams for San Roque 1. + *D. hispanicus*.

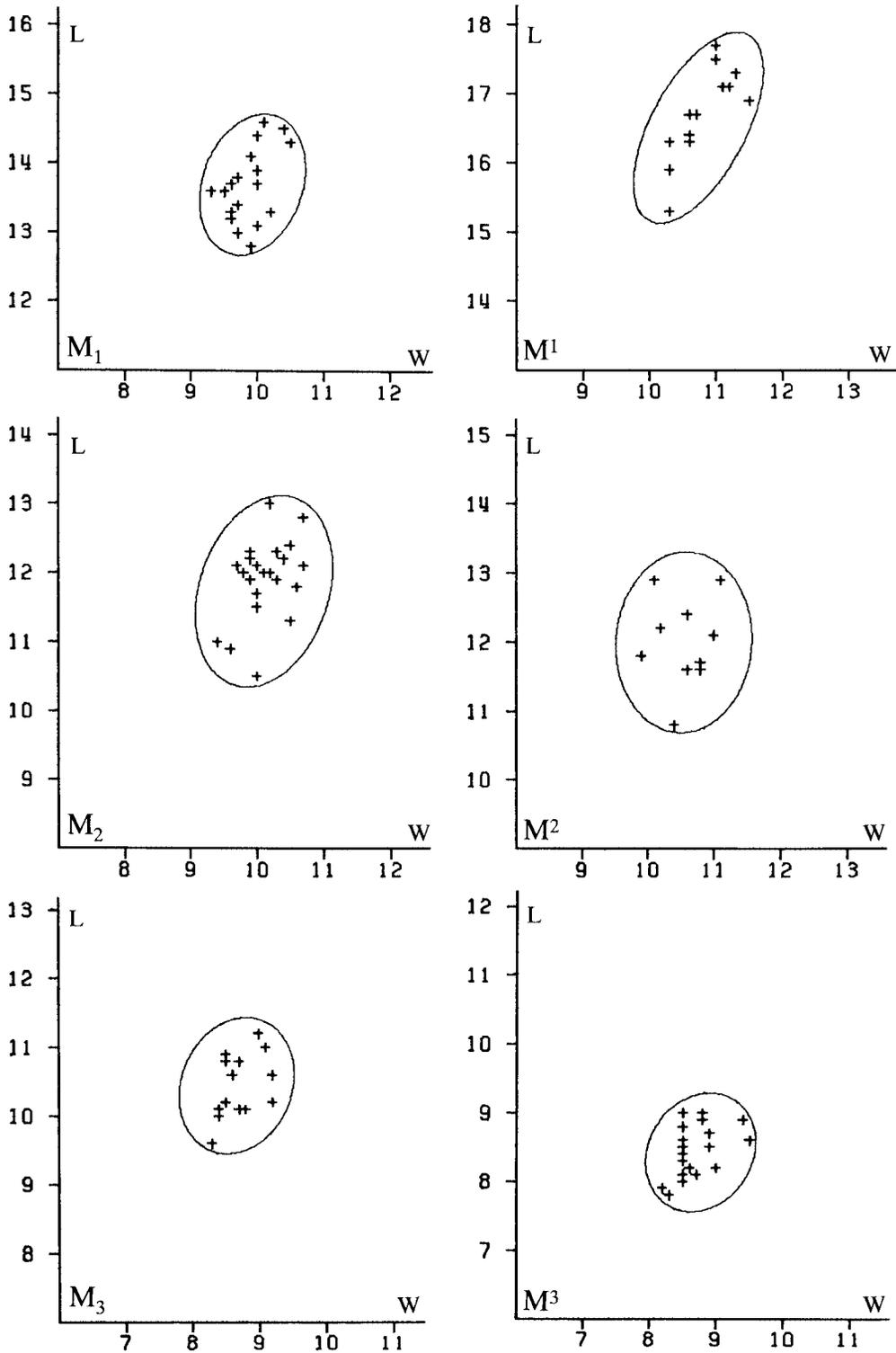


Fig. 10. Length-width diagrams for San Roque 2. + *D. hispanicus*.

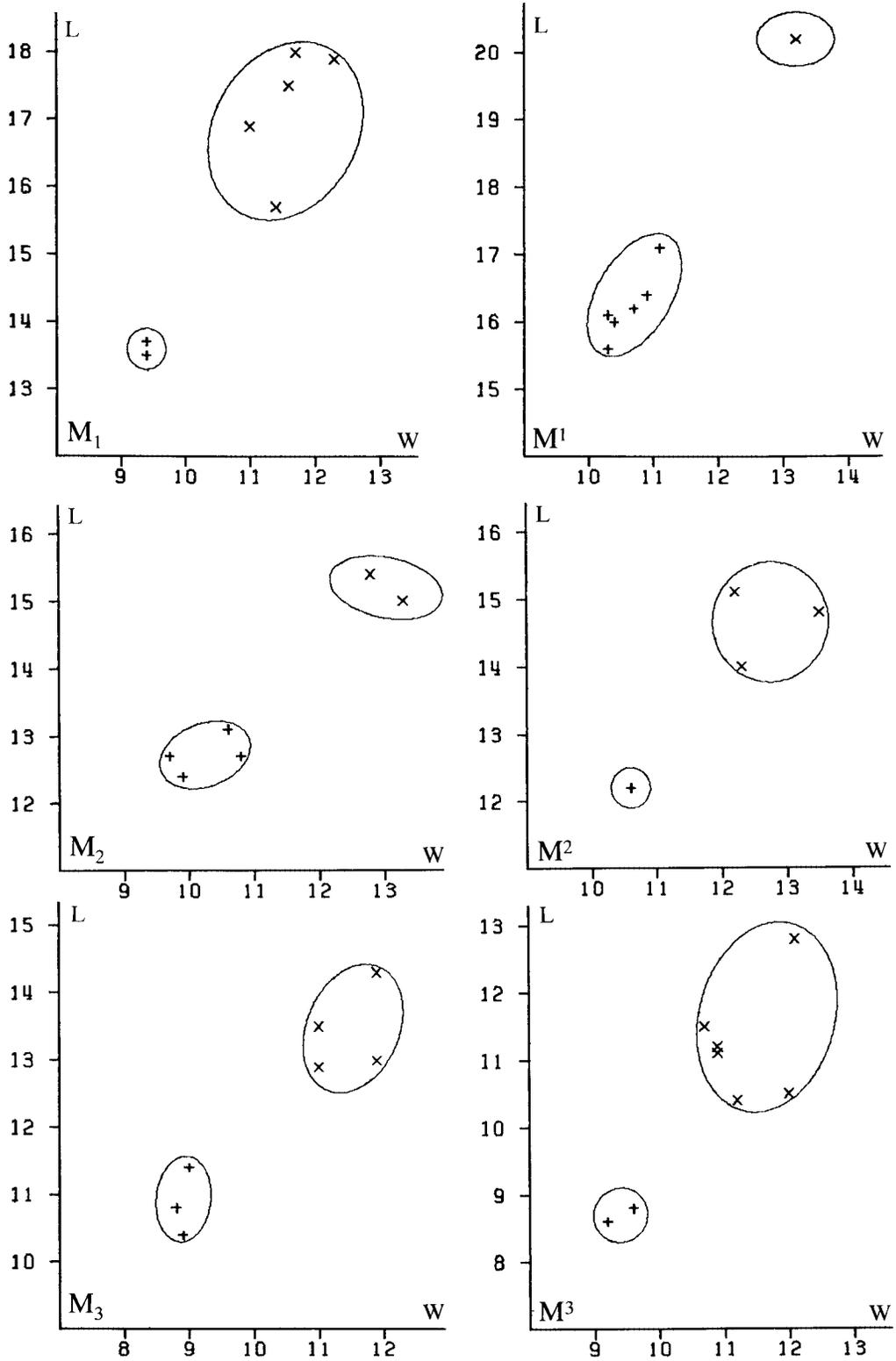


Fig. 11. Length-width diagrams for Olmo Redondo 5. + *D. hispanicus*; x *F. koenigswaldi*.

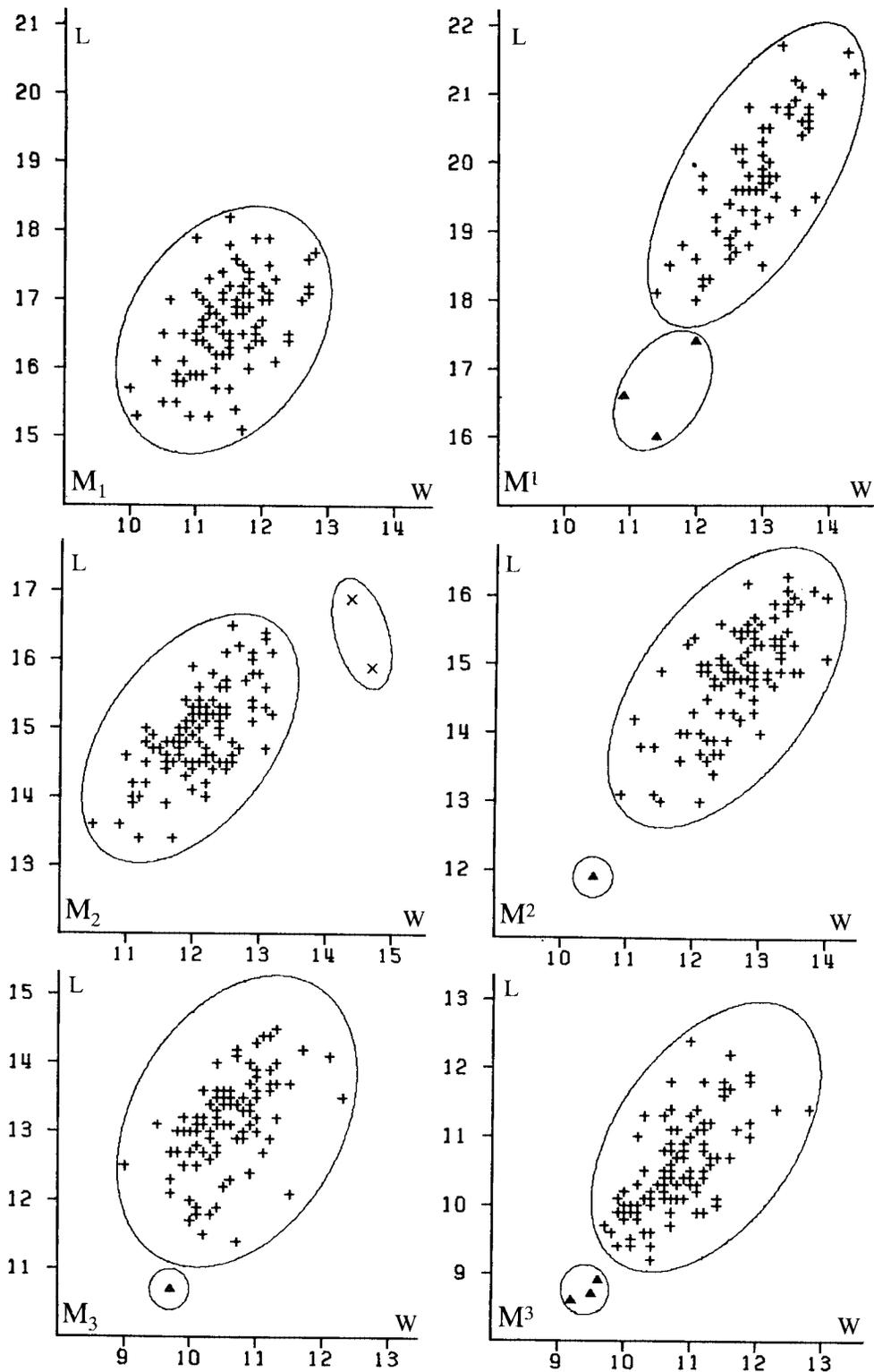


Fig. 12. Length-width diagrams for Vargas 1A. \blacktriangle *D. hispanicus*; $+$ *F. koenigswaldi*; \times *P. jordensi*.

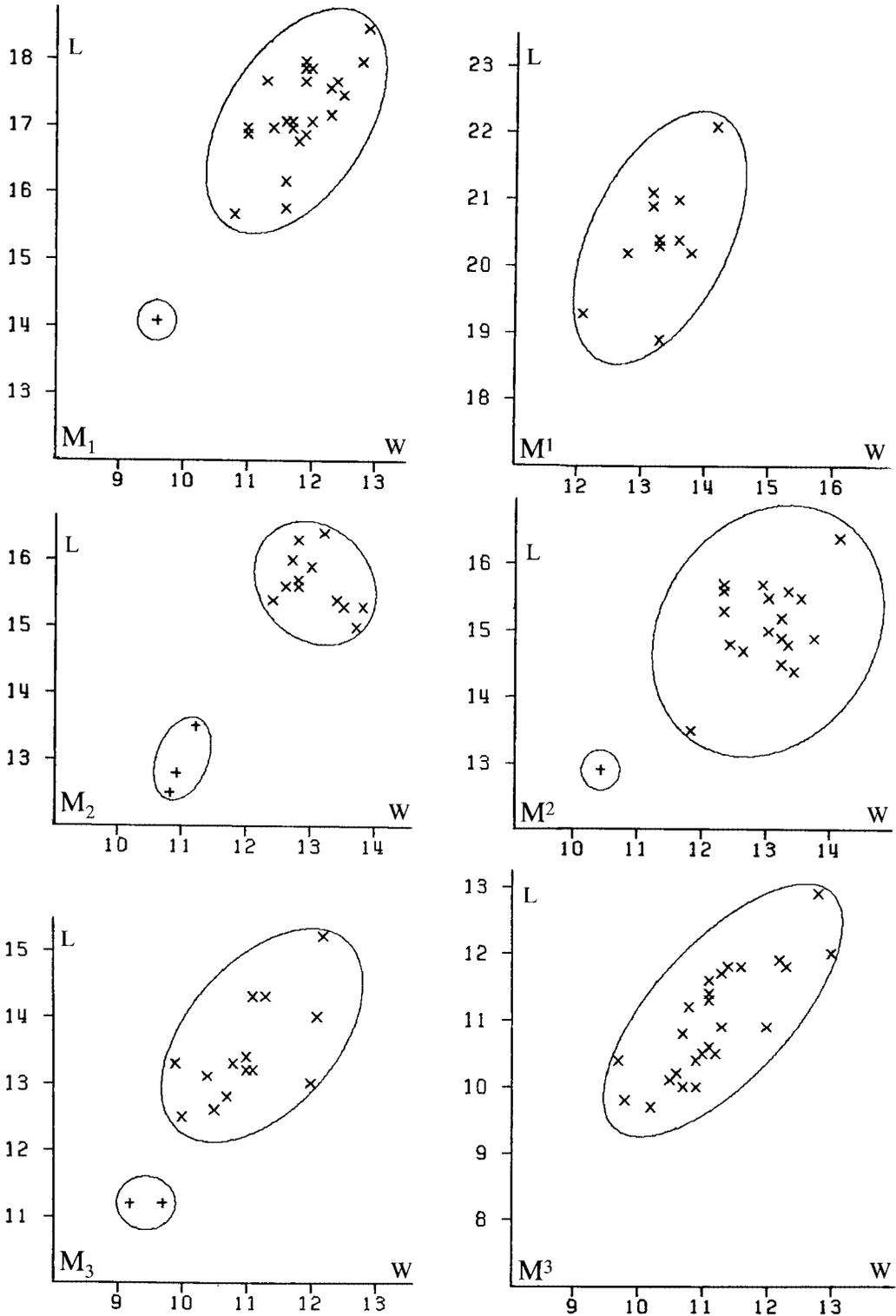


Fig. 13. Length-width diagrams for Olmo Redondo 9. + *D. hispanicus*; × *F. koenigswaldi*.

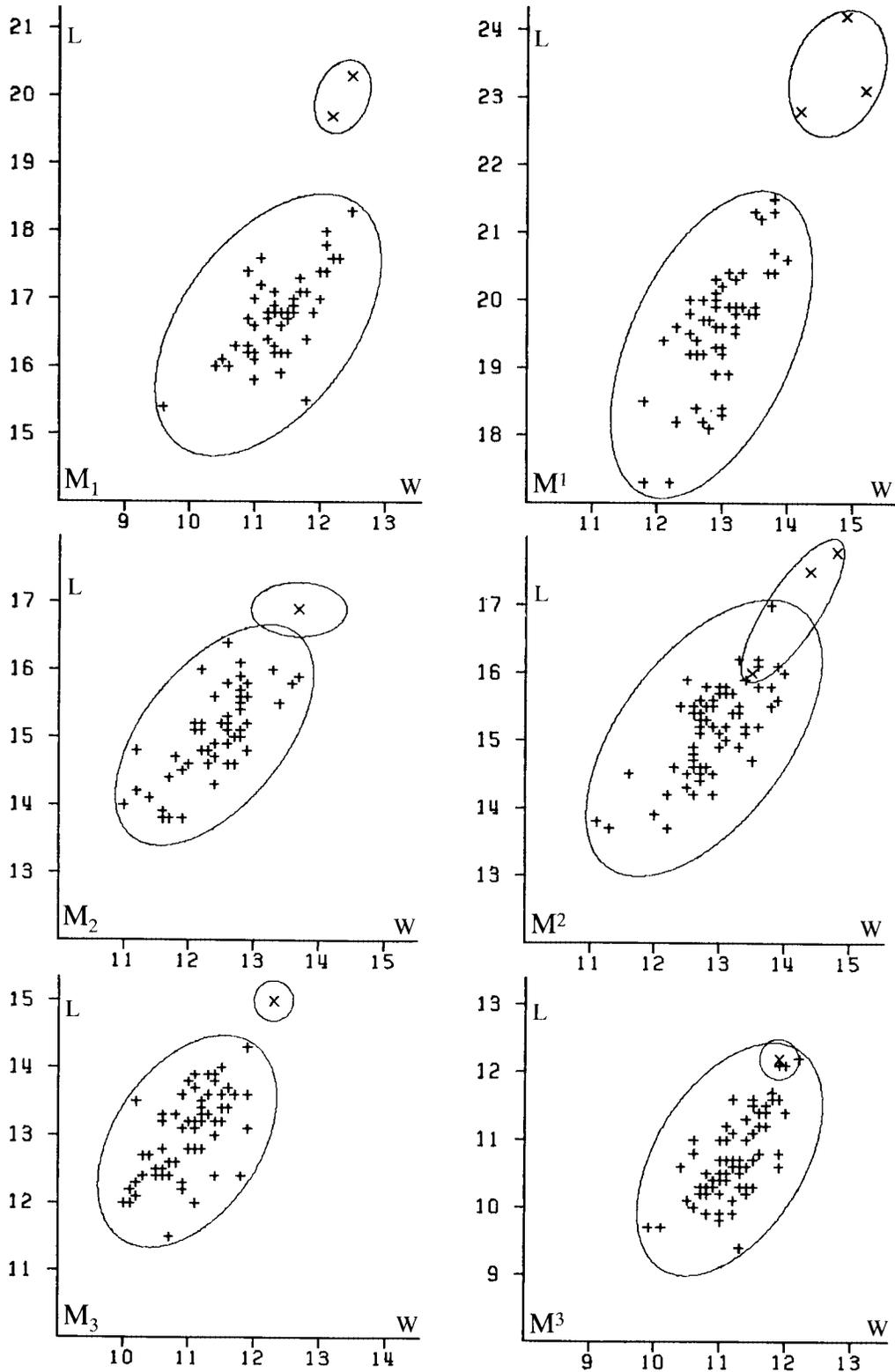


Fig. 14. Length-width diagrams for Casetón 1A. + *F. koenigswaldi*; x *P. jordensi*.

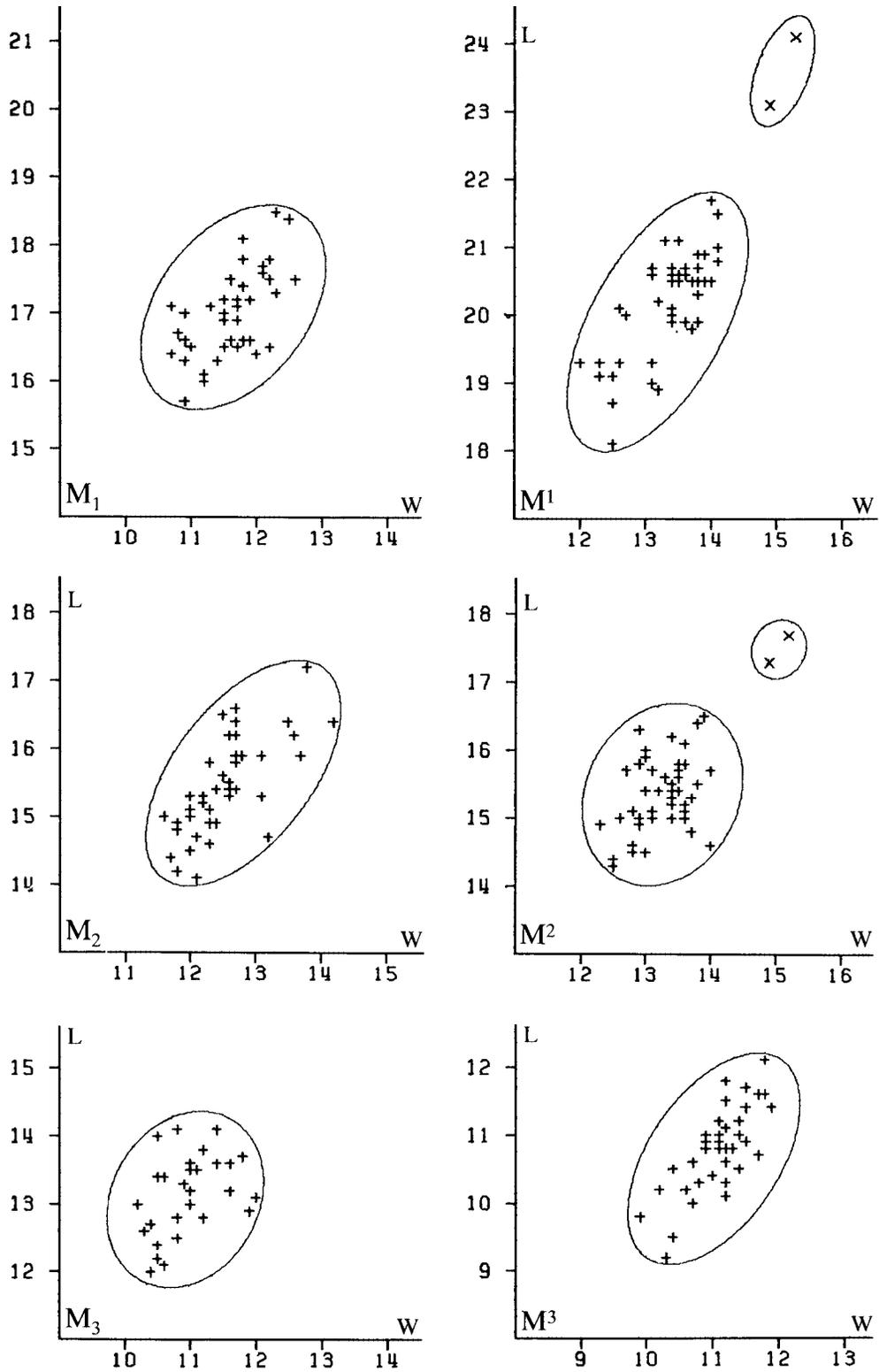


Fig. 15. Length-width diagrams for Casetón 2B. + *F. koenigswaldi*; x *P. jordensi*.

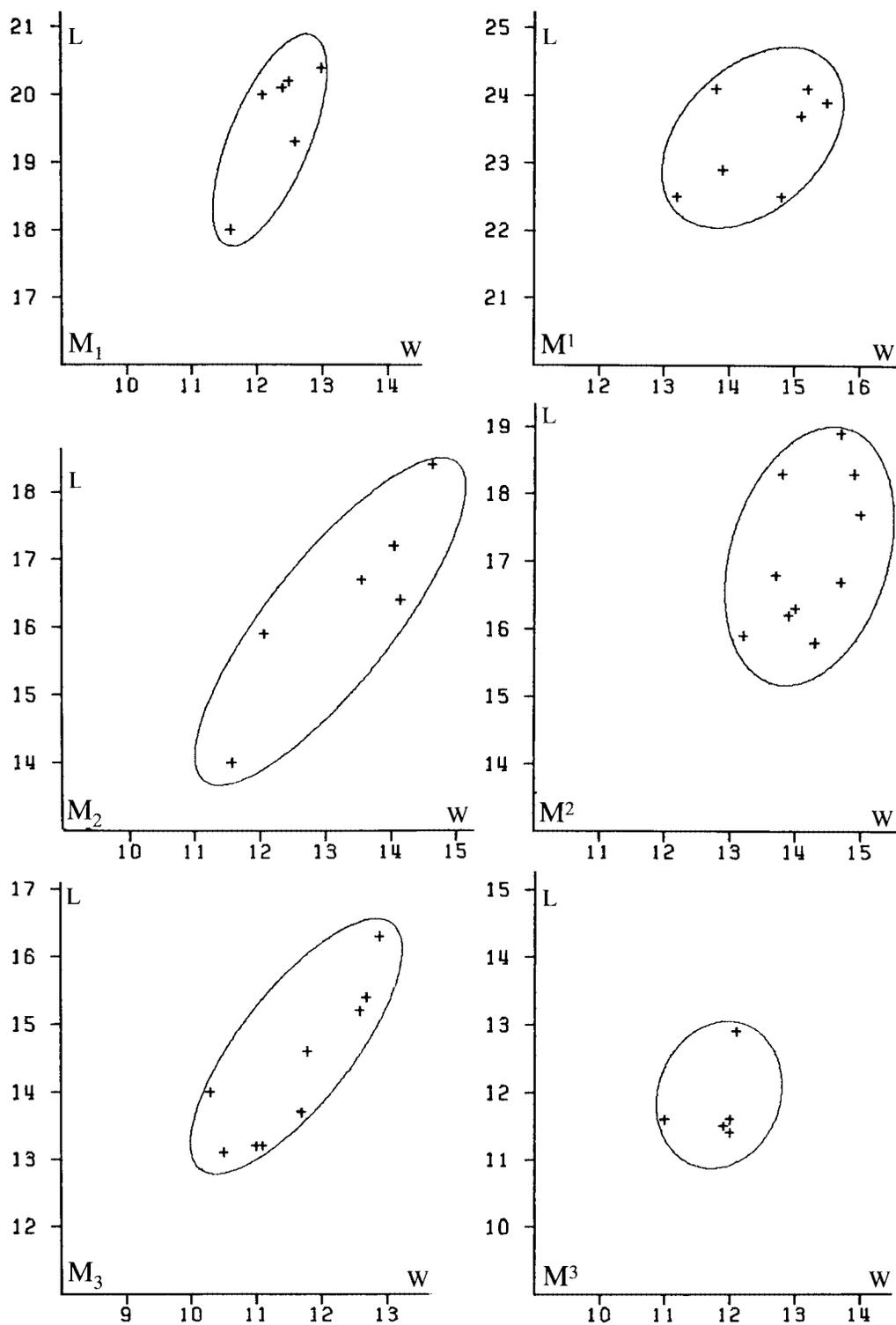


Fig. 16. Length-width diagrams for Valdemosos 3D. + *P. jordensi*.

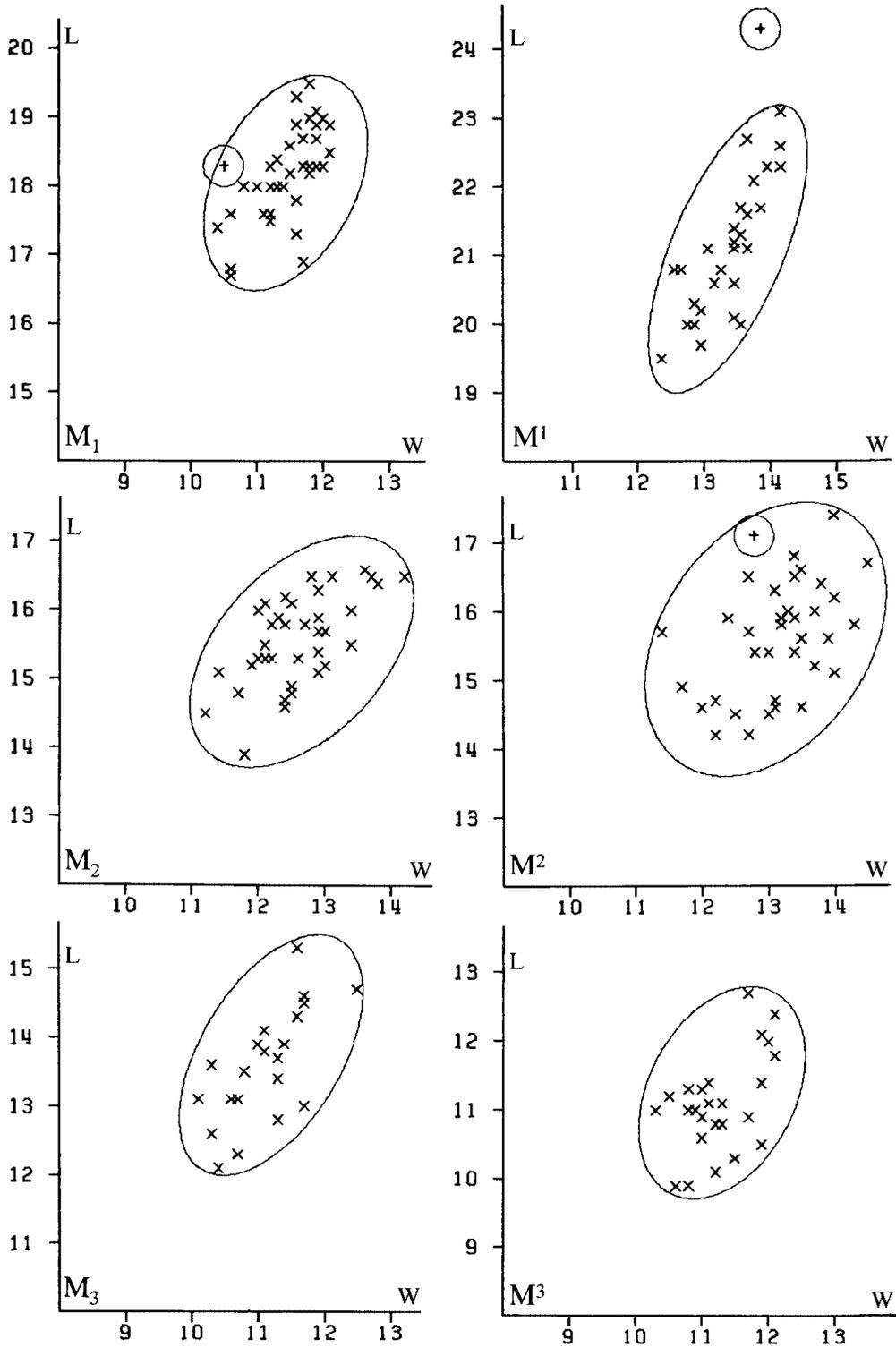


Fig. 17. Length-width diagrams for Villafeliche 4A. × *P. jordensi*; + Gen. indet. sp. indet.

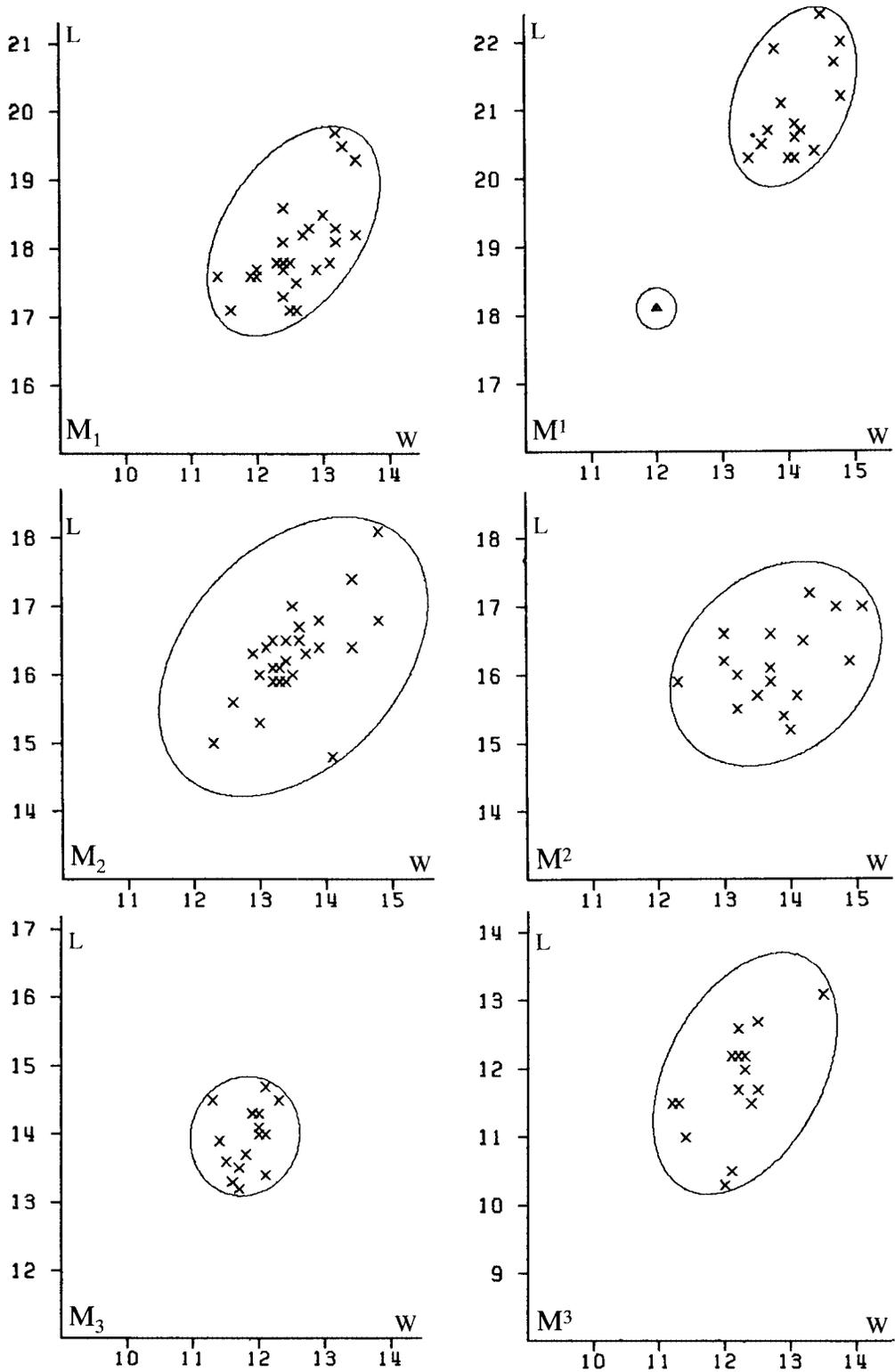


Fig. 18. Length-width diagrams for Valdemosos 3E. ▲ *Democricetodon* sp.; × *F. freudenthali*.

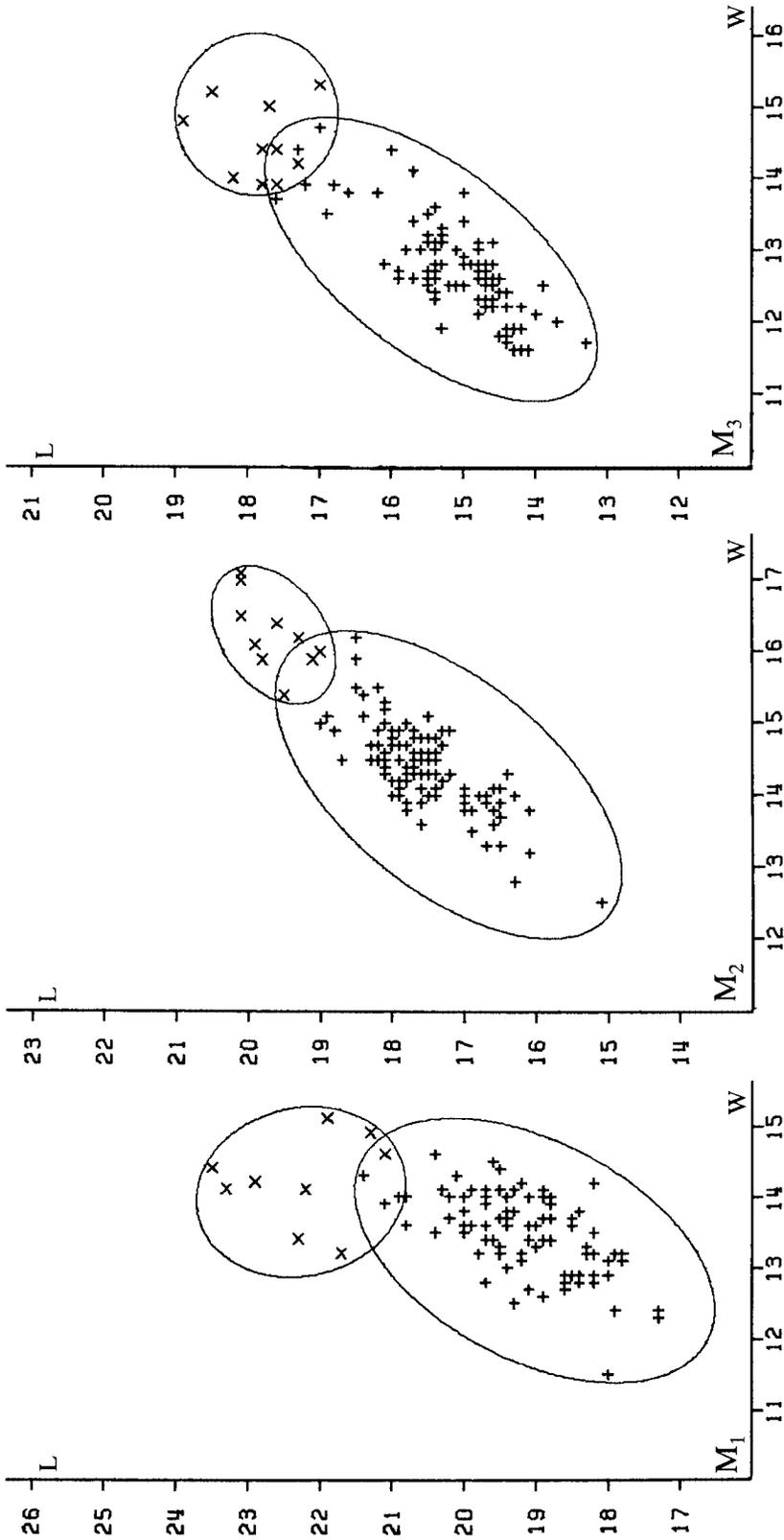


Fig. 19. Length-width diagrams for lower molars from Regajo 2. + *F. freudenthali*; × *R. lacombai*.

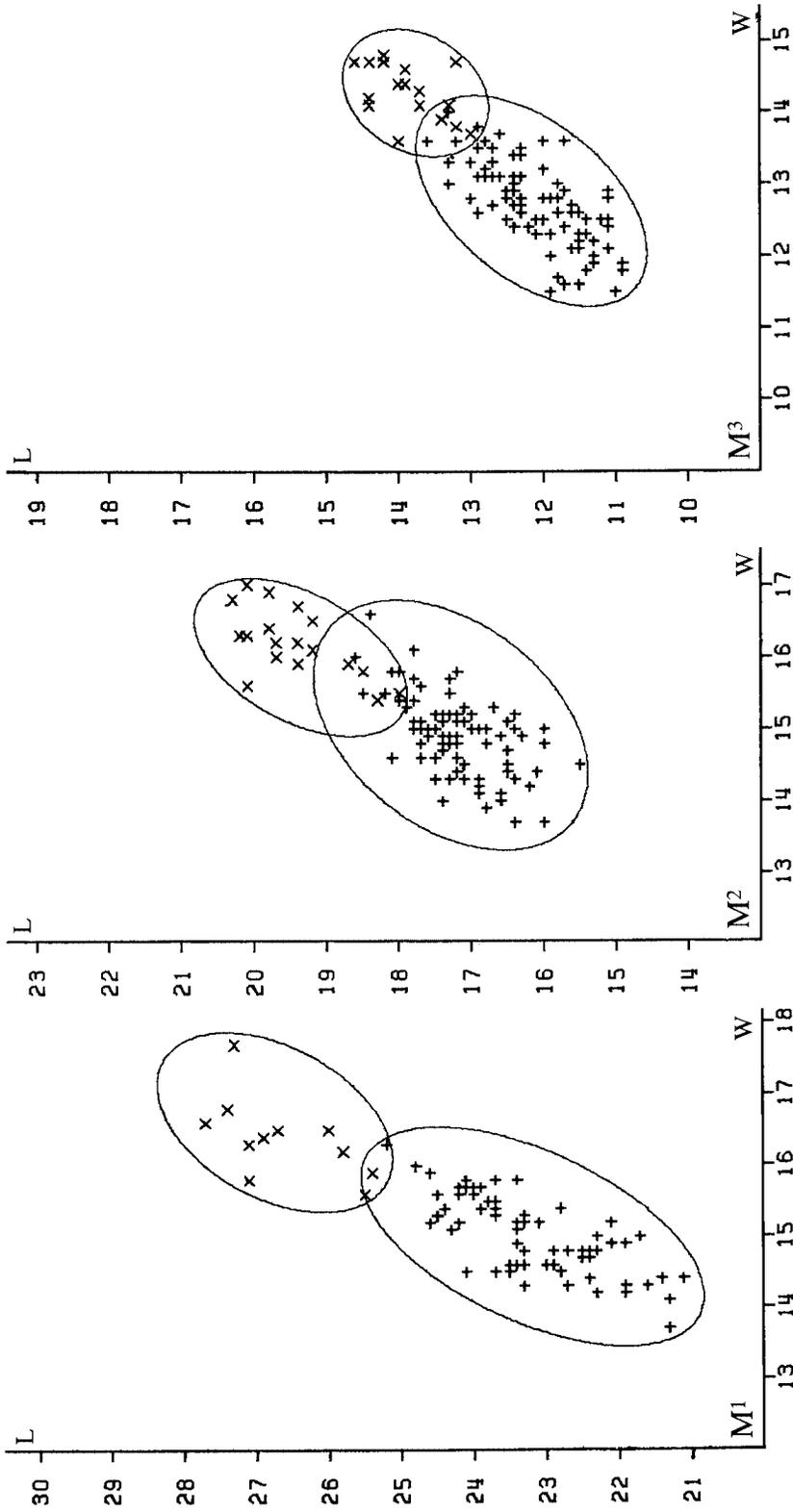


Fig. 20. Length-width diagrams for upper molars from Regajo 2. + *F. freudenthali*; x *R. lacombai*.

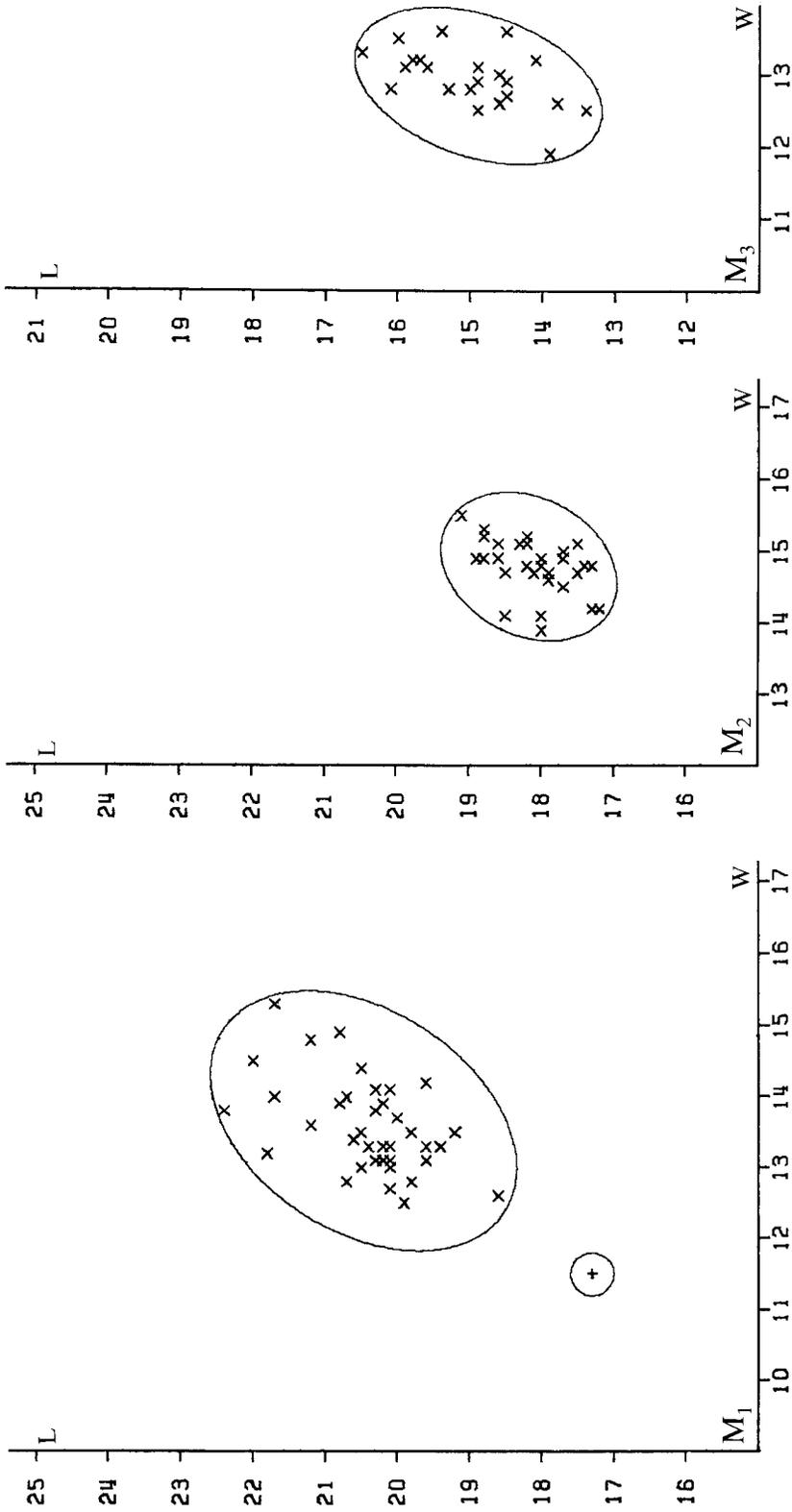


Fig. 21. Length-width diagrams for lower molars from Borjas. + *D. aff. gaillardii*; x *F. darocensis*.

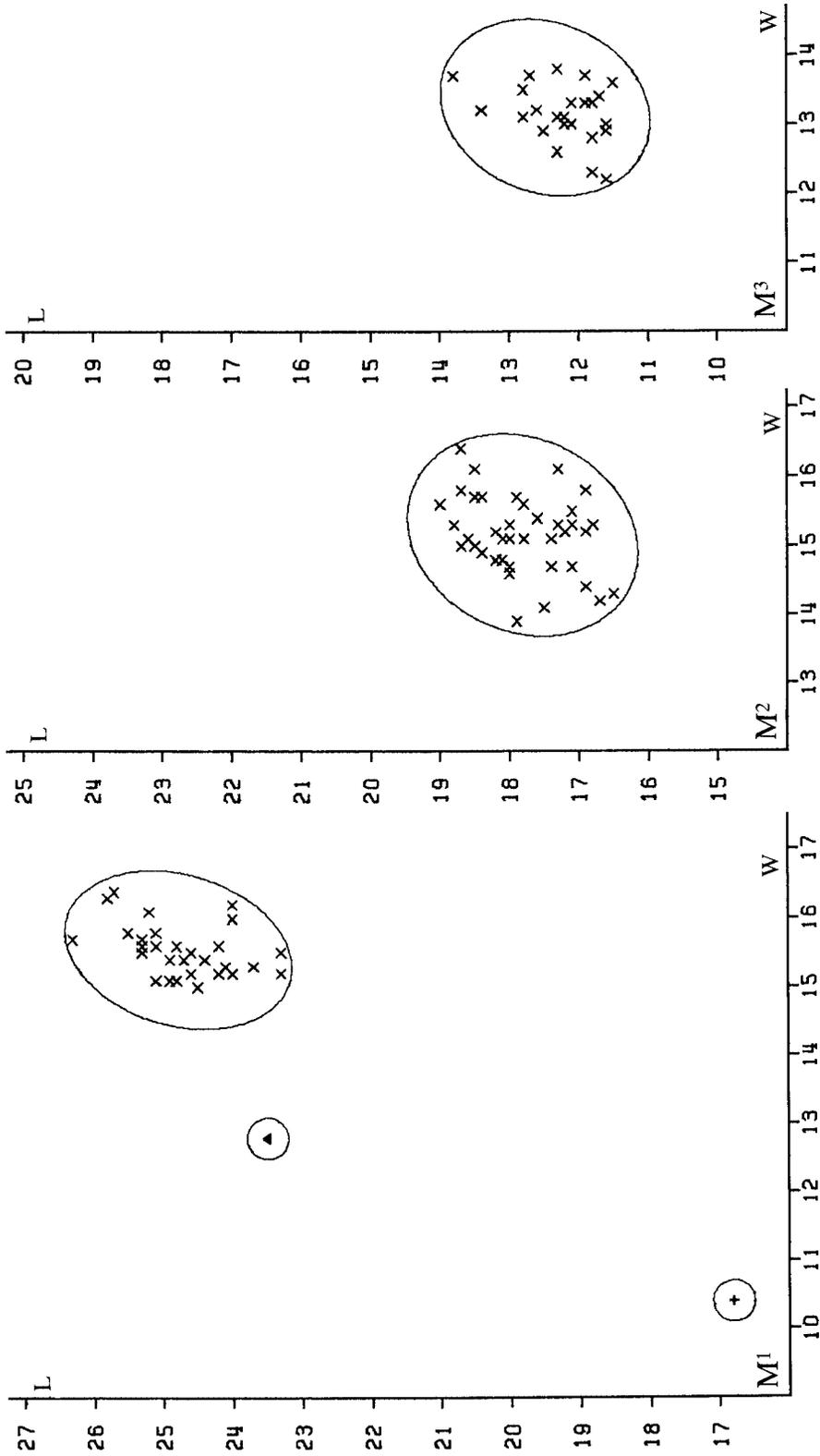


Fig. 22. Length-width diagrams for upper molars from Borjas. + *D. aff. gaillardi*; ▲ *F. darocensis*; × *Pseudofahlbuschia?*

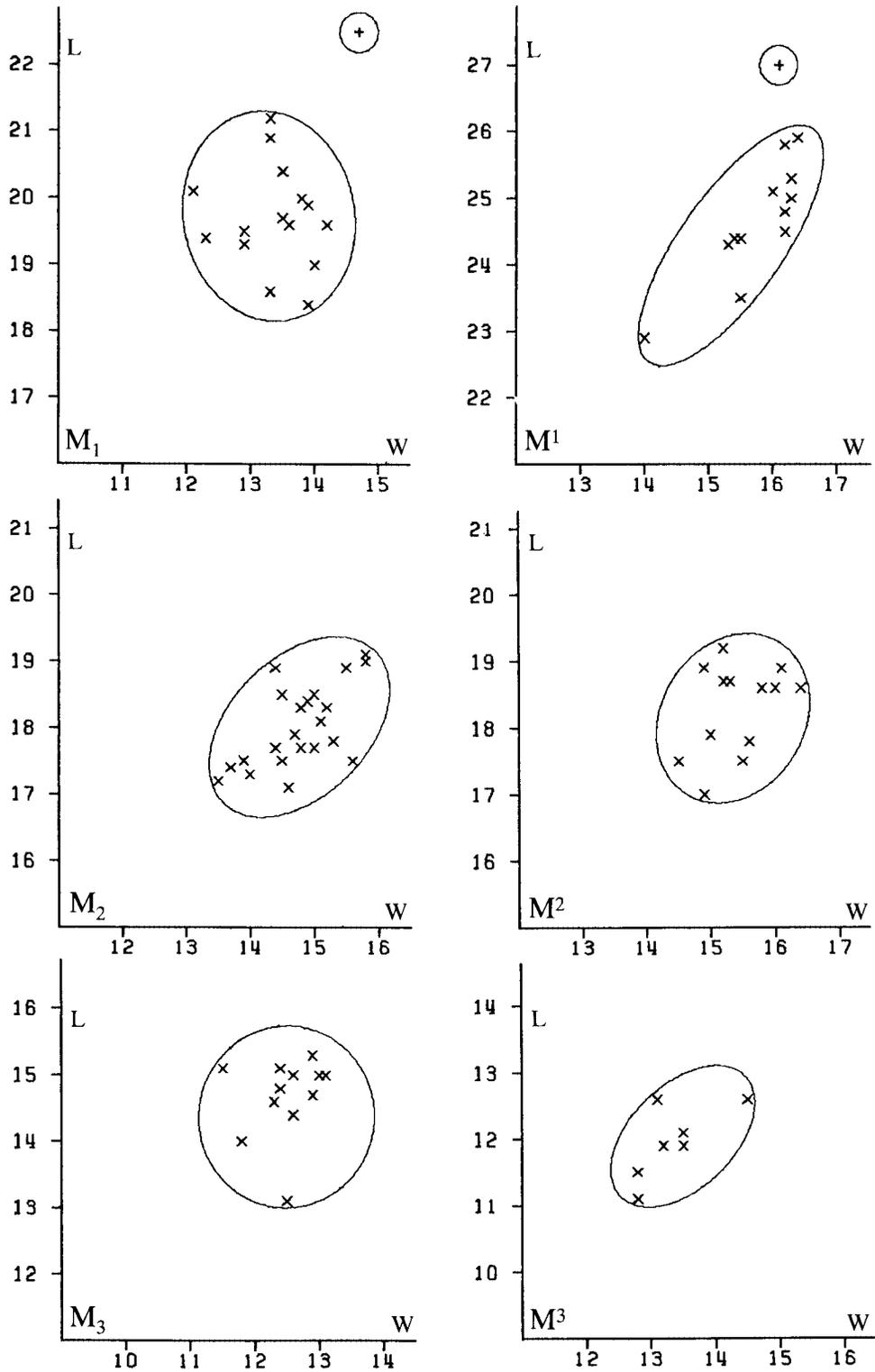


Fig. 23. Length-width diagrams for Toril 1. x *F. darocensis*; + *F. aff. crusafonti*.

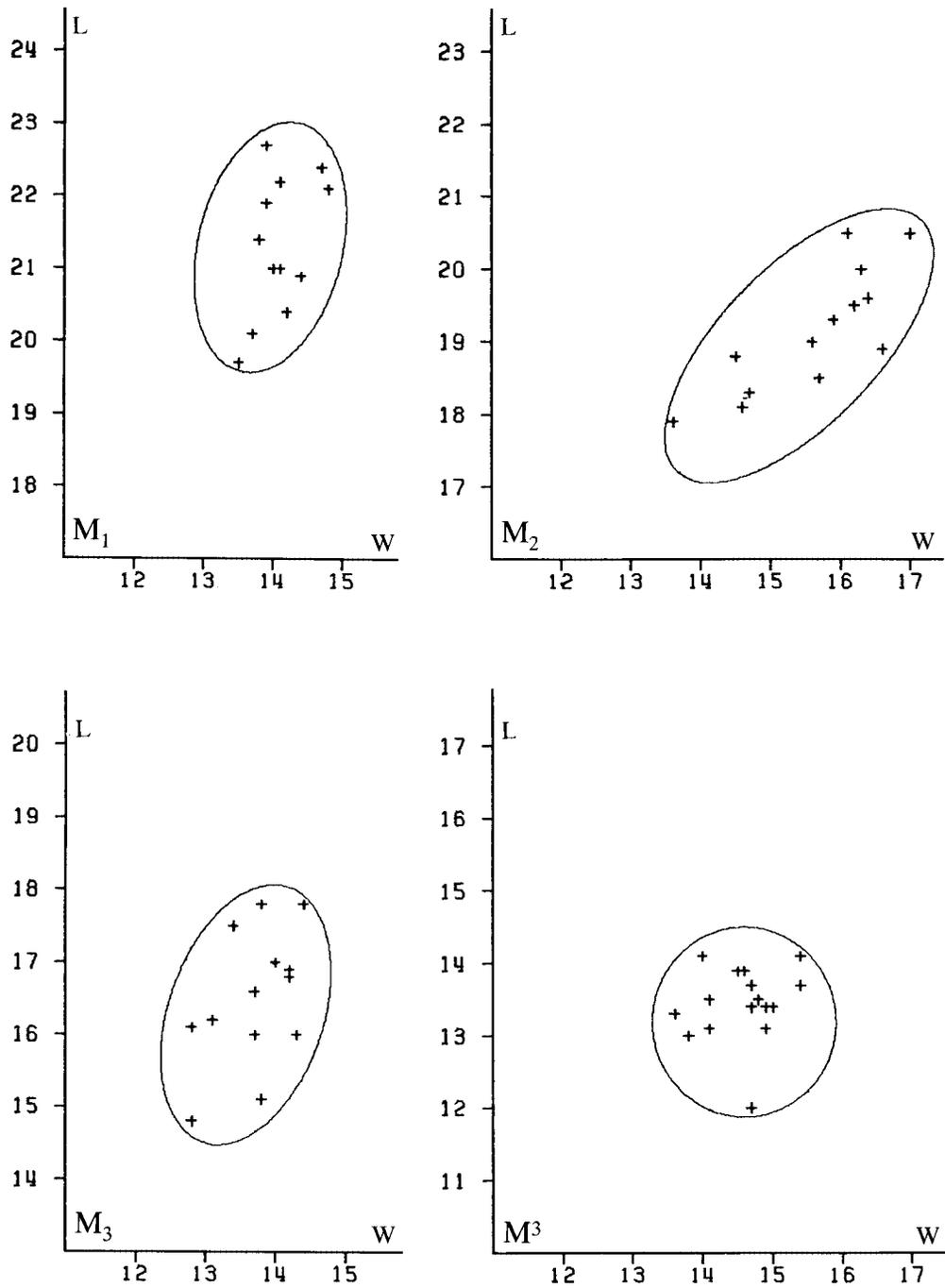


Fig. 24. Length-width diagrams for M₁, M₂, M₃ and M₃ from Solera. + *F. aff. crusafonti*.

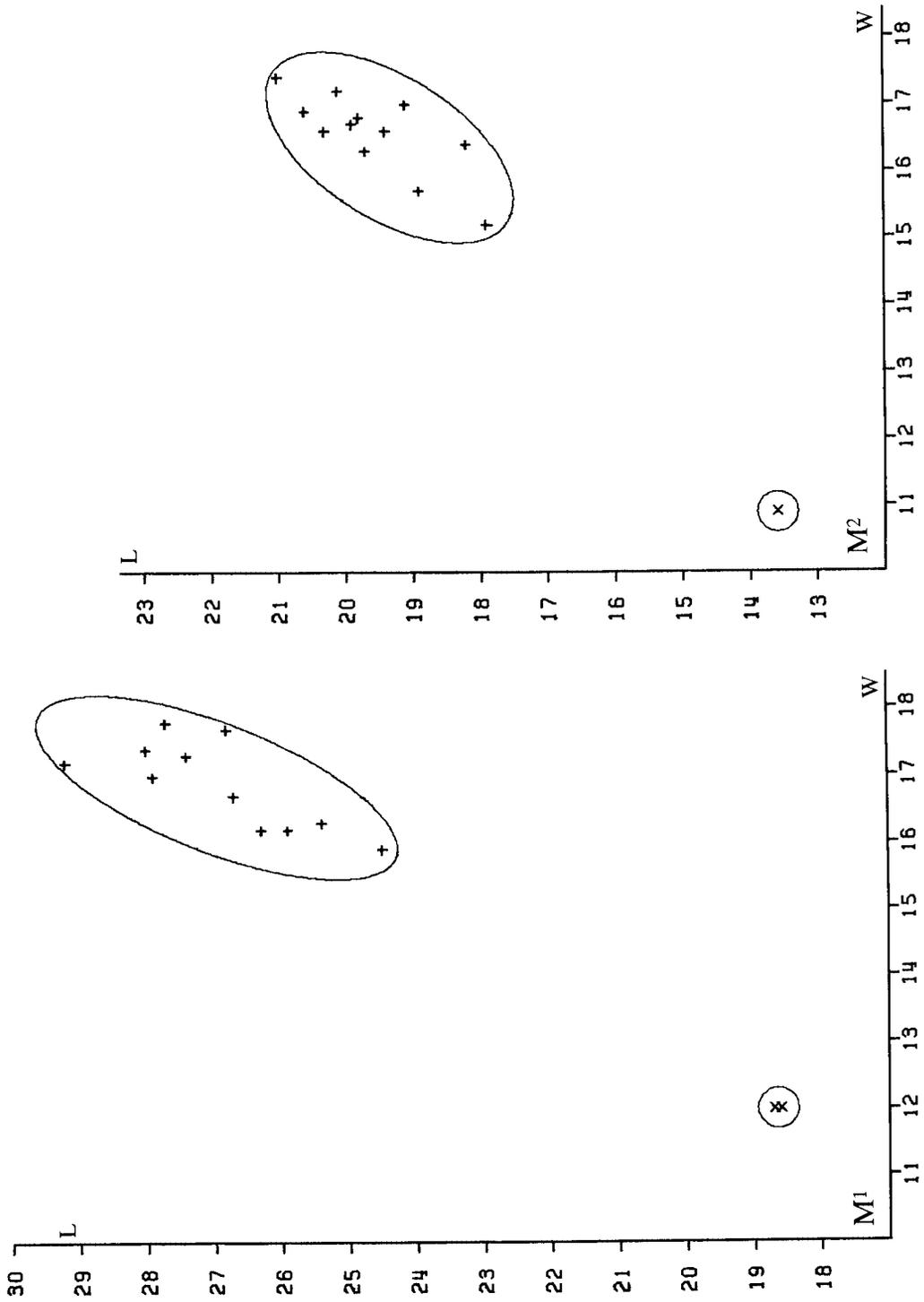


Fig. 25. Length-width diagrams for M¹ and M² from Solera. × *D. aff. gaillardi*; + *F. aff. crusafonti*.

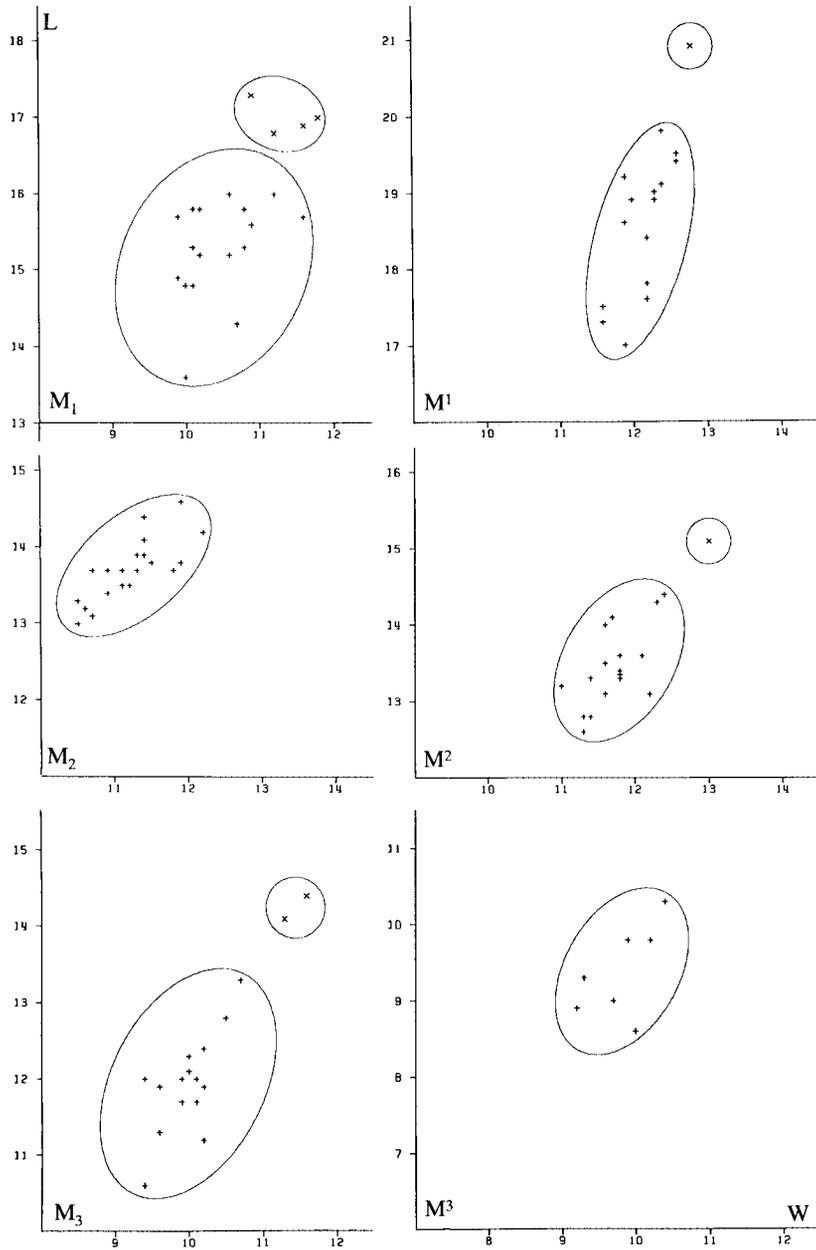


Fig. 26. Length-width diagrams for *Córcoles*.