Cricetidae (Rodentia) from the type-Aragonian; the genus *Megacricetodon*

R. Daams & M. Freudenthal

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This paper is a detailed study of 10 000 *Megacricetodon* teeth from 35 localities of Aragonian and early Vallesian age. One new species is described: *M. rafaeli* sp. nov. from Armantes 7. Evolutionary trends of this group are discussed and a comparison with French and Central European material is made.

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Introduction

Until 1964 most Oligocene and Miocene European Cricetidae were referred to as *Cricetodon* (Lartet, 1851; Schaub, 1925, 1944; Freudenthal, 1963, etc.). In that year Fahlbusch introduced the genus name *Democricetodon* and within the genus *Democricetodon* he created the subgenus *Megacricetodon*. Most subsequent authors have assigned genus level to *Megacricetodon*. It stands for a group of Cricetidae in which the most characteristic features are the well-split anterocone of M^1, and the long anteroconid of M_1. During the larger part of the Aragonian and the early Vallesian representatives of *Megacricetodon* constitute the major part of the Spanish micromammal faunas, and they are common in France and Central Europe as well.

Freudenthal (1963, 1965) was the first to recognize the various evolutionary stages of the *M. primitivus – ibericus* lineage as a valuable stratigraphic tool. This was made possible by the excellent exposures and the stratigraphic superposition of the fossiliferous sediments in the Calatayud-Teruel Basin.

The material studied in this paper was collected by a team of Dutch and Spanish students, led by the present authors, in the type area of the Aragonian. The localities are located in a number of sections that have been correlated in the field. On the basis of these correlations our ideal 'composite section' has been constructed.

The large amount of rich faunas collected during the field campaigns of the Aragonian project, gave us the opportunity to make a more detailed study of this genus and to evaluate its evolution. There are two hypotheses to explain the evolution of *M. primitivus* to *M. ibericus*: either a continuous evolution with some – stepwise – changes, or an evolution that is interrupted by an immigrant with similar dental pattern by the close of the Middle Aragonian.

Megacricetodon presents a very good standard for the correlation of Miocene vertebrate faunas within Spain. Correlation of non-Spanish faunas with this standard is hazardous due to the less complete fossil record in France and Central Europe, but an effort has been made. This resulted in the distinction of a Central European 'province' on the one hand and a Southern French-Spanish 'province' on the other.

METHODS

In this paper 16 morphological features have been studied, described and tabulated for approximately 10 000 *Megacricetodon* molars. In each set of standard morphotypes intermediate specimens may be present, that are arbitrarily assigned to one of the standard stages. Such arbitrary decisions depend on one's personal interpretation and may vary from student to student. But even if the same author repeats the analysis of the variability of a certain character discrepancies of up to 20 % may occur, especially so, when a considerable span of time has elapsed between the first and the second analysis. Apparently one's appraisal of these morphological features may change with time.

In this study this possible error has been taken into account, when drawing conclusions. On the other hand it has been attempted to reduce this kind of errors as much as possible by counting the variability of each character within a limited space of time.

Furthermore it is evident that the error level depends on the kind of feature studied. For discontinuous features like the position of the protolophule and the metalophule in M^2 interpretative errors are limited. In continuous features, like the length of

the mesoloph(id) and in features that are highly influenced by the degree of wear of the specimen individual interpretation and its related errors play a larger role. As a rule too much worn specimens have not been counted.

Freudenthal (1976) calculated morphology values for the teeth of *Microtia* from Gargano (Italy) in the following way: each specimen is assigned a value, coinciding with its number of crests. These values are added up and the result is divided by the number of specimens. We applied the same method to various morphological characters that appear to show an evolutionary trend and that are not numeric in themselves, like e.g. the length of the mesoloph(id): specimens with a long mesolophid (the supposedly primitive stage) are assigned the value 1, specimens in which the mesolophid is absent (the most evolved stage) are assigned value 4, and the intermediate stages medium and short are counted as 2 and 3. For each assemblage these values are added up and divided by the number of specimens, and the resulting morphology value (MV) is a measure for the degree of evolution of the specified character in each assemblage: the higher MV, the more evolved the assemblage with respect to that character. MV is quite significant if the distribution is not bimodal.

These morphology values have been listed in the figures of the character distribution for the *Megacricetodon* lineage of large size.

Example of the calculation of MV
Locality: Borjas; feature: shape of anteroconid of M_1.

stage	value	frequency	subtotal
simple	1	5	5
slightly divided	2	28	56
8-shaped	3	67	201
deeply split	4	12	48
Total		112	310

MV = 310/112 = 2.77

All teeth have been measured as proposed by Freudenthal, 1963 (Fig. 1). The lengths and widths are given in 0.1 mm units. Measurements have been taken using a Leitz Orthoplan microscope (objective 4 ×, ocular 10 ×) with mechanical stage and measuring clocks. Previously published material has not been remeasured, but these data have been taken from Freudenthal (1963, 1968).

The measurements have been used to calculate length/width ratios.

The nomenclature of the parts of the cheek teeth is after Mein & Freudenthal, 1971 (Fig. 2).

STORAGE OF THE MATERIAL

Most of the material is stored in the collections of the Rijksmuseum van Geologie en Mineralogie, Leiden, The Netherlands and is registered in the RGM data base. The following collections are kept at the Instituut voor Aardwetenschappen, Utrecht, the Netherlands: Valtorres, Valdemoros 1A, Valdemoros 3B, part of the collection of Villafeliche 4A, Villafeliche 4B, part of the collection of Las Planas 4A, Las Planas 4B, part of the collection of Las Planas 4C, Armantes 7, Arroyo del Val 6, Manchones, Nombrevilla, and Pedregueras 2C.

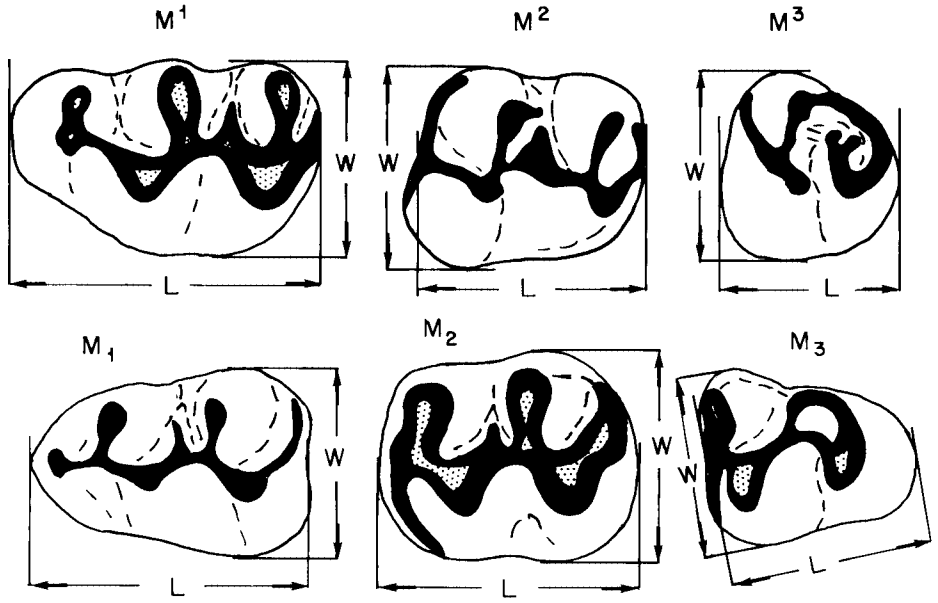


Fig. 1. Method of taking measurements of cricetid molars.

Review of the genus *Megacricetodon*

Megacricetodon Fahlbusch, 1964 is a common element of the rodent faunas of the Aragonian and Lower Vallesian of Spain. It may constitute up to 95 % of the rodent fauna. In the Middle Aragonian localities the *Megacricetodon* associations are monospecific, in most Upper Aragonian and Lower Vallesian localities two – and sometimes three – species are present, whereas in the two uppermost localities of our composite section the associations are monospecific again. In this paper we distinguish two evolutionary lines: *M. primitivus – ibericus* and *M. minor – debruijni*. A separate group, that of *M. rafaeli*, occurs in a short interval, and hitherto no ancestors or descendants are known.

In the following paragraphs a compilation of the genus *Megacricetodon* and its Spanish representatives will be given. As far as original descriptions and diagnoses are provided, they are translated into English and re-written in present-day terminology.

The original diagnosis of *Megacricetodon* Fahlbusch, 1964 (translated and re-written) is as follows:

The ectolophid and entoloph are short, curved or straight; generally the sinusid is slightly curved backwards; the sinus is sometimes curved forward; the anteroconid of M_1 is long, simple, or split; the anterocone of M^1 is always split; the protolophule and metalophule are generally single, transverse, or pointing backwards; the paracones of M^1 and M^2 generally are provided with a backward spur.

Nine species of *Megacricetodon* are found in the Spanish Miocene:

M. primitivus (Freudenthal, 1963), type locality Valtorres

M. collongensis (Mein, 1958), type locality Vieux-Collonges

M. rafaeli sp. nov., type locality Armantes 7

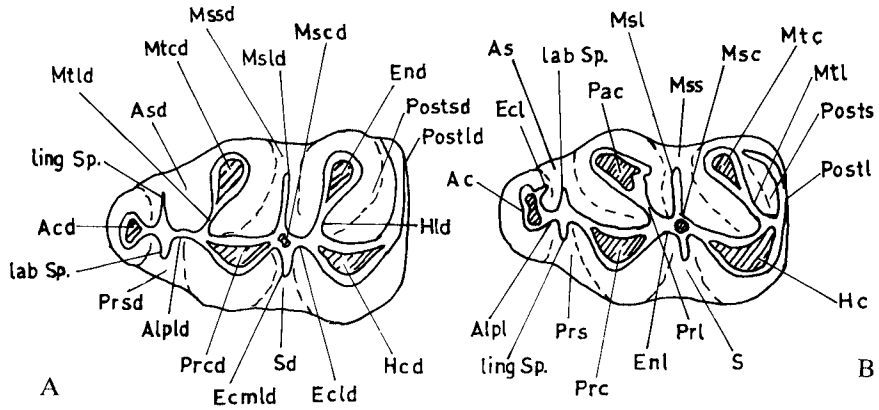


Fig. 2. Nomenclature of parts of the cheek teeth of the Cricetidae (after Mein & Freudenthal, 1971).
A: lower molars: Acd = Anteroconid; Alpld = Anterolophulid; Asd = Anterosinusid; Ecld = Ectolophid; Ecmld = Ectomesolophid; End = Entoconid; Hcd = Hypoconid; Hld = Hypolophulid; lab. Sp. = Labial spur of the anterolophulid; ling. Sp. = Lingual spur of the anterolophulid; Mscd = Mesoconid; Msld = Mesolophid; Mssd = Mesosinusid; Mtcd = Metaconid; Mtld = Metalophulid; Postld = Posterolophid; Postsd = Posterosinusid; Prcd = Protoconid; Prsd = Protosinusid; Sd = Sinusid.
B: Upper molars: Ac = Anterocone; Alpl = Anterolophule; As = Anterosinus; Ecl = Ectoloph; Enl = Entoloph; Hc = Hypocone; Hld = Hypolophulid; lab. Sp. = Labial spur of the anterolophule; ling. Sp. = Lingual spur of the anterolophule; Msc = Mesocone; Msl = Mesoloph; Mss = Mesosinus; Mtc = Metacone; Mtl = Metalophule; Pac = Paracone; Postl = Posteroloph; Posts = Posterosinus; Prc = Protocone; Prl = Protolophule; Prs = Protosinus; S = Sinus.

M. minor (Lartet, 1851), type locality Sansan
M. debruijni Freudenthal, 1968, type locality Pedregueras 2C
M. crusafonti (Freudenthal, 1963), type locality Manchones 1
M. ibericus (Schaub, 1944), type locality Hostalets de Pierola
M. lopezae García Moreno, 1986, type locality Simancas 2
M. freudenthali García Moreno, 1986, type locality Ampudia 9.

M. primitivus — Freudenthal (1963, p. 70) characterized this species as follows: 3 out of 36 M_1 have an ectomesolophid. In 5 out of 15 M_3 a weak mesolophid or a remnant of the posterior metalophulid is present. In other respects this species agrees with *M. minor*.

M. collongensis — Has been described in detail by Freudenthal (1963, p. 77). A summary of this description is as follows: the M_1 has a simple anteroconid (77 %), slightly split (20 %), or 8-shaped (3 %). In 20 % of the M_1 the anterolophulid has a labial spur. The mesolophid is of medium length. M_2 has a well-developed lingual anterolophid and a medium-sized mesolophid. M^1 has a symmetrically split anterocone; the anterolophule is connected to the lingual cusp of the anterocone. In some specimens remains of a double protolophule or a double metalophule are present. The mesoloph is long and some specimens have a posterior spur on the paracone. The sinus points obliquely backwards, or it is transverse, or it is curved forwards. In M^2 the protolophule is generally double, and the sinus is transverse. The metalophule is anterior or double.The mesoloph is long and a posterior spur on the paracone may be present.

M. rafaeli — This new species from Armantes 7 is characterized as a *Megacricetodon* species of medium size with a slightly split anterocone, a simple anteroconid, relatively long mesoloph(id)s, and a wide posterosinus in M^1 and M^2.

M. minor — Schaub (1925, p. 15) characterized this species as follows: M_1 is long and narrow with a simple anteroconid. M_3 has four cusps, a not much narrowed posterior part and a reduced entoconid. The metalophulid points forward in all three lower teeth. The mesolophid is of variable length. In M^1 the protolophule and metalophule point backwards, in M^2 and M^3 forwards. In M^2 there are traces of the posterior protolophule. The mesoloph is variable. Anterocone of M^1 asymmetrically split, set off from the protocone. M^3 very short and rounded.

This definition must be treated with care, since it is not exclusively based on material from the type-locality Sansan. The Sansan material was first described in detail by Baudelot (1964, 1972). Some important elements of her description are:
Slender molars. M_1 has a simple, high and rounded anteroconid, 4 specimens seem to present a slightly constricted anteroconid. In 10 out of 64 specimens a small cingulum or metastylid is present at the border of the anterosinusid. 19 % of the M_1 has a long mesolophid, 57 % a mesolophid of medium length and 24 % has a short one. M_2 has a reduced lingual anterolophid, and the rest of the dental pattern resembles that of M_1. The anterocone is well-split in 70 % of the M^1, and in the remaining 30 % it is a constricted cusp without a deep furow. In 36 % of the M^1 a trace of an anterior protolophule is present. The mesoloph is short (8 %), of medium length (65 %), or long (27 %). The posterosinus is very reduced. In M^2 63 % has a double protolophule. The metalophule is transverse in 81 %. A double metalophule is rare, and the sinus is generally transverse. The mesoloph tends to be a little longer than in M^1.
Remark — Since 1969 (see Freudenthal & Fahlbusch) a discussion has been going on about the correct interpretation of the name *Cricetodon minor* Lartet, 1851. In 1987 the International Commission on Zoological Nomenclature accepted Freudenthal's proposal to follow Schaub's interpretation:

> '(a) *minor* Lartet, 1851, as published in the binomen *Cricetodon minus* [sic], as defined by reference to the neotype designated by Freudenthal, 1969' is placed on the Official List of Specific Names in Zoology (Tubbs, 1986, p. 328).

So, *Cricetodon minor* Lartet, 1851 is the small *Megacricetodon* from Sansan, and not the small *Democricetodon*.

M. debruijni — The original diagnosis (Freudenthal, 1968, p. 61) reads as follows: '*Megacricetodon* species of small size, with subdivided anteroconid in M_1. Mesolophids are on the average short or absent; mesolophs are short or medium in M^1, medium or long in M^2. The internal valley of M^2 is sharply curved forward.'

M. debruijni is of the same size as *M. minor*; it differs from this species by its split anteroconid in M_1. The known species of *Megacricetodon* with subdivided anteroconid are generally considerably larger than *M. debruijni*.

M. crusafonti — Translation of the original diagnosis by Freudenthal (1963, p. 88): On the average smaller than *M. gregarius* and larger than *M. minor*. The anteroconid is slightly or deeply split in more than half of the specimens. The mesolophid in M_1 is short or absent, rarely longer. M^1 always has a split anterocone, and almost always protolophule and metalophule point backwards. Generally there is a spur on the posterior wall of the paracone.

M. ibericus — As Schaub's (1944, 1947) characterization of this species is not very extensive we prefer to refer to the description of *M. ibericus* from the levels with *Hipparion*, given by Agustí (1980, p. 35). Translated and summarized it reads as follows: The anteroconid of M_1 is deeply split, forming an X-pattern with the metaconid and protoconid. Mesoloph(id)s are absent in all molars. The M_2 and M_3 have a well-developed labial anterolophid, reaching the base of the protoconid. M^1 has a deeply split anterocone with small cingulum ridges or cusps at its anterior border. A small posteroloph is present in M^1. In M^2 the sinus is straight, and the paracone has a small ectoloph.

Schaub described this species in 1944 without assigning a holotype, and without figuring any element. In 1947 Schaub figures a mandibular and a maxillary tooth row of *M. ibericus*, but unfortunately the legend of the figures was mixed up (see also Freudenthal, 1968 and Agustí, 1980) and again no type was assigned. Freudenthal (1968) suggests the mandible from the upper levels of Hostalets de Pierola to be the holotype of *M. ibericus*. This mandible with M_{1-3}, figured in Schaub (1947, fig. 1, with erroneous explanation) is stored in the collections of the Museo de Paleontología 'Miquel Crusafont' at Sabadell under number IPS 2916. The label bears the indication 12-VII-1943, and the word 'tipo', presumably in Schaub's handwriting (pers. comm. J. Agustí, Sabadell). This specimen must be considered to be the holotype of *M. ibericus*.

M. lopezae — The original diagnosis (García, in Alvarez & García, 1986, p. 164) reads as follows: '*Megacricetodon* larger than *M. minor* and smaller than *M. crusafonti*. The anteroconid is simple in 50 % of the molars, it [is] divided into two cusps in 25 % of the cases, and it is slightly split in 25 % of the cases.

The anterocone is divided in 70 % of the specimens, being slightly split in the rest of the cases. The mesolophid is frequently absent, but a short mesolophid may be present. There is often a short mesoloph, but in some cases it may be long or it may be absent. In the M^2, the internal valley is frequently directed forwards, and rarely it may be transverse. The posterolophid is always long. In the M^1, there is often a short posteroloph, but long and absent posterolophs may appear with a significative frequency. In the M^2 the posteroloph is long.'

M. freudenthali — The original diagnosis (García, in Alvarez & García, 1986, p. 169) reads as follows: 'Small sized *Megacricetodon*. The anteroconid is simple. The M_1 and M_2 almost always have an mesolophid, which often is long. The anterocone is simple or bilobulated, and the anterior furrow is very slight or absent. The M^1 and M^2 almost always have a mesoloph. The external valley in the M^2 is generally directed forwards. In the M^1 and M_1 the posteroloph('id) is always long, as well as in the M^2.'

Morphological descriptions

THE *M. PRIMITIVUS – IBERICUS* LINEAGE

Anteroconid of M_1 (Fig. 3)

Four morphotypes are distinguished. The first one is the simple round or bean-shaped anteroconid. Lingually and/or labially ridges may descend to enclose the anterosinusid and the protosinusid. The second morphotype is slightly subdivided, but this can only be seen in fresh or slightly worn specimens, as the furrow is shallow. Therefore much-worn

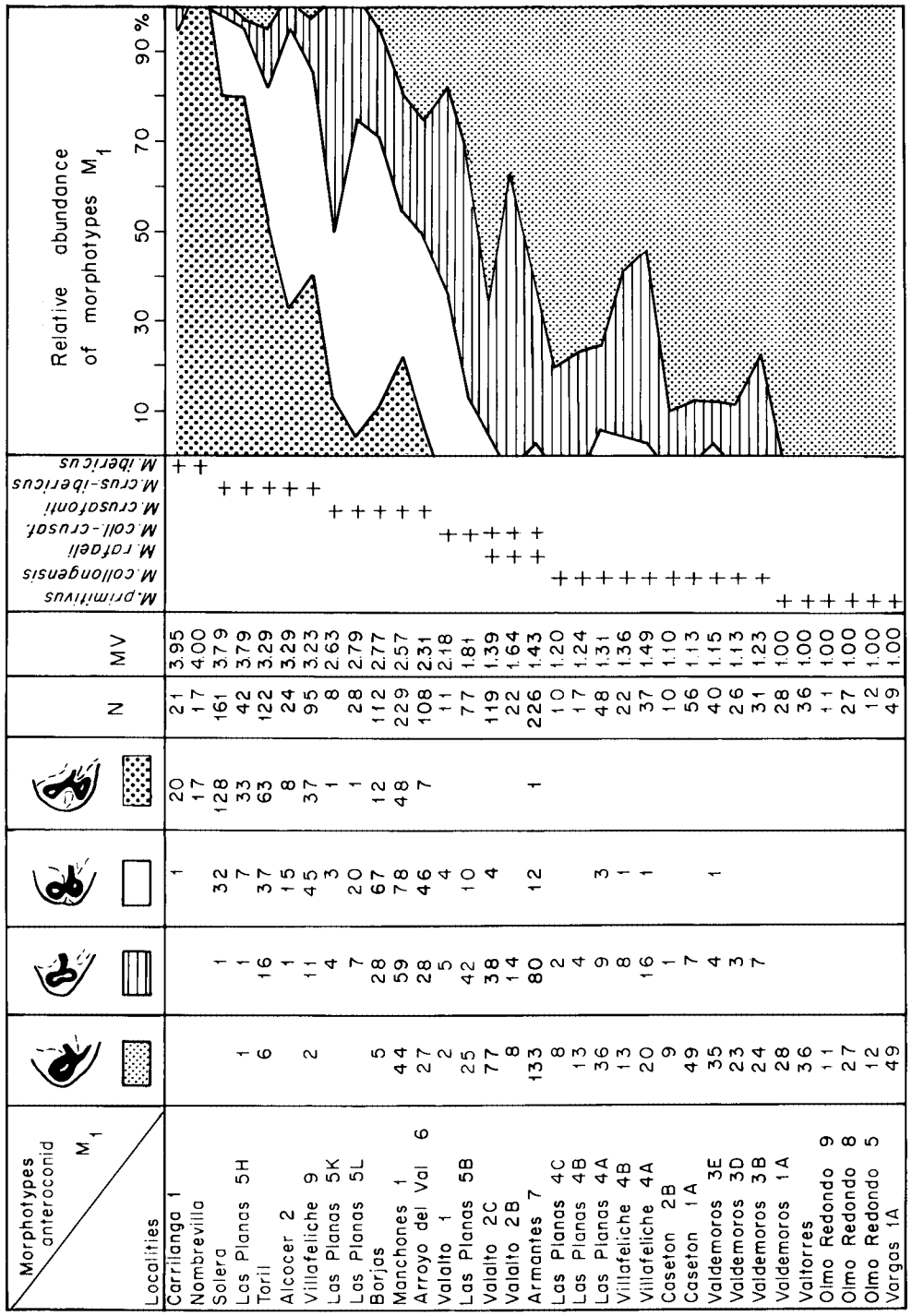


Fig. 3. Variation of the anteroconid in M_1 of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

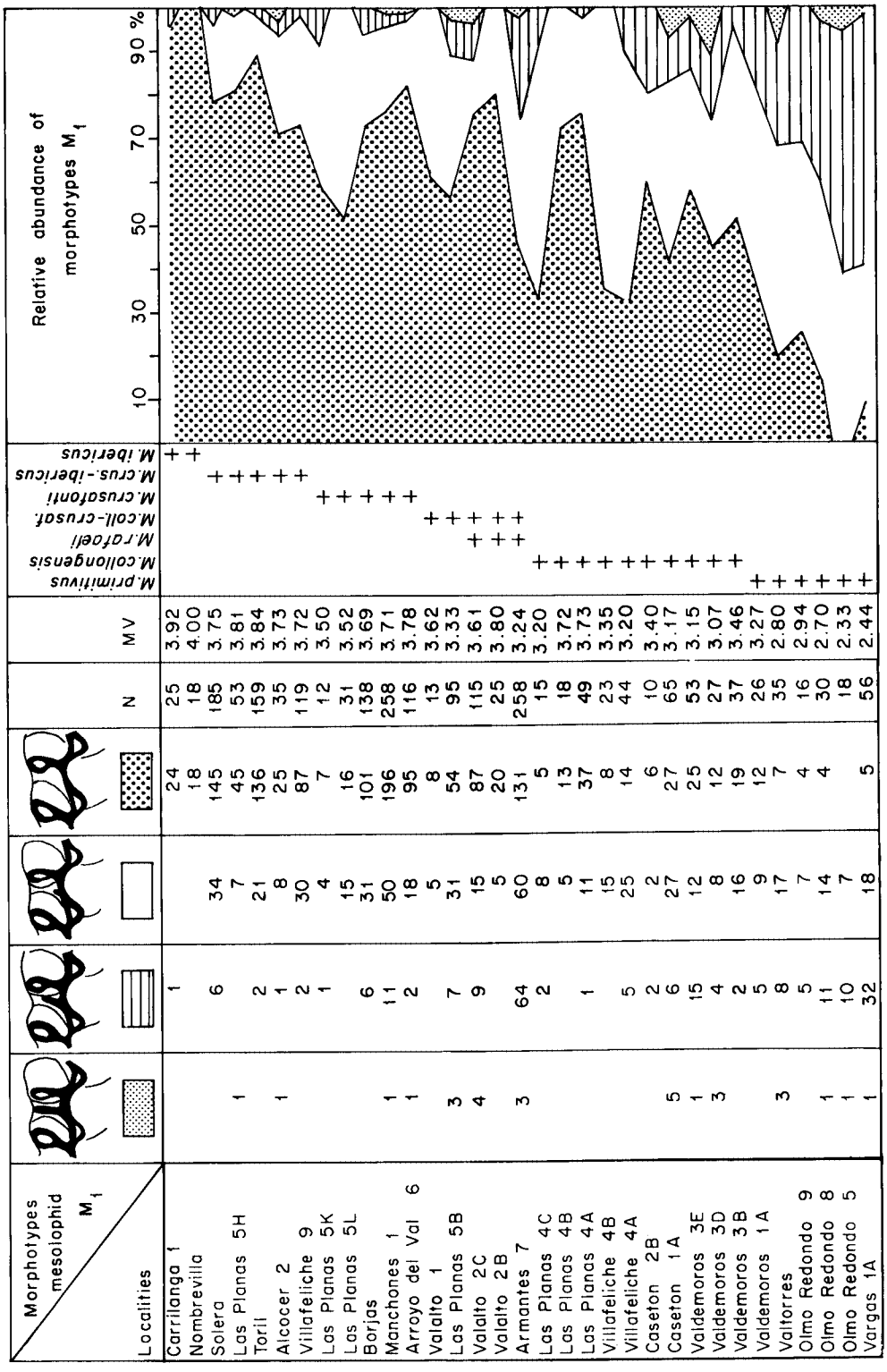


Fig. 4. Variation of the mesolophid in M_1 of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

specimens were not counted. The third type is an 8-shaped anteroconid. The furrow is deep and may reach the basis of the crown. This type is generally not confused with the preceding one, not even in worn specimens. The fourth type is the deeply split anteroconid which forms an X-pattern with the protoconid and metaconid. Attrition does not influence the appraisal of this feature, except for the extremely worn specimens where valleys and cusps are almost at the same level.

Fig. 3 shows a rather gradual change of morphotypes through the biostratigraphic sequence. *M. primitivus* has a simple anteroconid, in *M. eollongensis* the simple anteroconid is predominant, but the slightly subdivided one and even the 8-shaped type are present as well. The most common type in *M. crusafonti* is the 8-shaped anteroconid, whereas in *M. ibericus* the deeply split type is predominant.

Mesolophid of M_1 (Fig. 4)

Four stages have been distinguished: The mesolophid is considered to be long when it reaches the lingual border of the molar. The next stage is the medium-sized mesolophid, comprising the stages which are more or less half the length of the mesosinusid or longer, but without reaching the lingual border. The short mesolophid is a small protuberance of the ectolophid. The fourth type has no mesolophid. Freudenthal (1963, 1965, 1968) recognizes five stages of the mesolophid (absent, short, medium, long, and reaching the lingual border). Daams, who analyzed the material for the present study, could not distinguish satisfactorily between medium and long sensu Freudenthal, because of the subjectivity of stage assignment. By recognizing only four stages instead of five, this interpretation error is reduced.

Wear does not influence the appraisal of this character, but the observation is very subjective by the expectedly large amount of intermediate specimens. The main problem is the distinction between medium-sized and short. The error between short and absent is a lesser problem.

Fig. 4 shows that *M. primitivus* has on the average the longest mesolophids, and that in *M. ibericus* the mesolophid lacks almost completely. The mesolophids in *M. collongensis* and *M. crusafonti* are more or less of the same length. A trend towards reduction of the mesolophid is observed, but it is not a gradual one.

Lingual anterolophid of M_2 (Fig. 5)

Three stages are distinguished. This ridge is considered to be well-developed when it reaches the antero-lingual corner of the metaconid, thus closing a tiny anterosinusid. Specimens showing any trace of a lingual anterolophulid are assigned to the second morphotype and the third morphotype houses specimens with no trace of a lingual anterolophid at all. The appraisal of this character is hampered by two factors: not only wear is of influence, but also the longitudinal compression of the molar may cause the disappearance of this ridge.

Fig. 5 shows that long lingual anterolophids are most frequent in *M. primitivus* and some *M. collongensis* assemblages. The proportion of specimens without lingual anterolophid is highest in *M. ibericus* and in *M. collongensis* from Valdemoros 3B. A trend towards reduction of the lingual anterolophid is present, but it is not a gradual one.

Mesolophid of M_2 (Fig. 6)

The four morphotypes distinguished are the same as in M_1. Fig. 6 shows that the mesolophid is absent in *M. ibericus* and very variable in the other species.

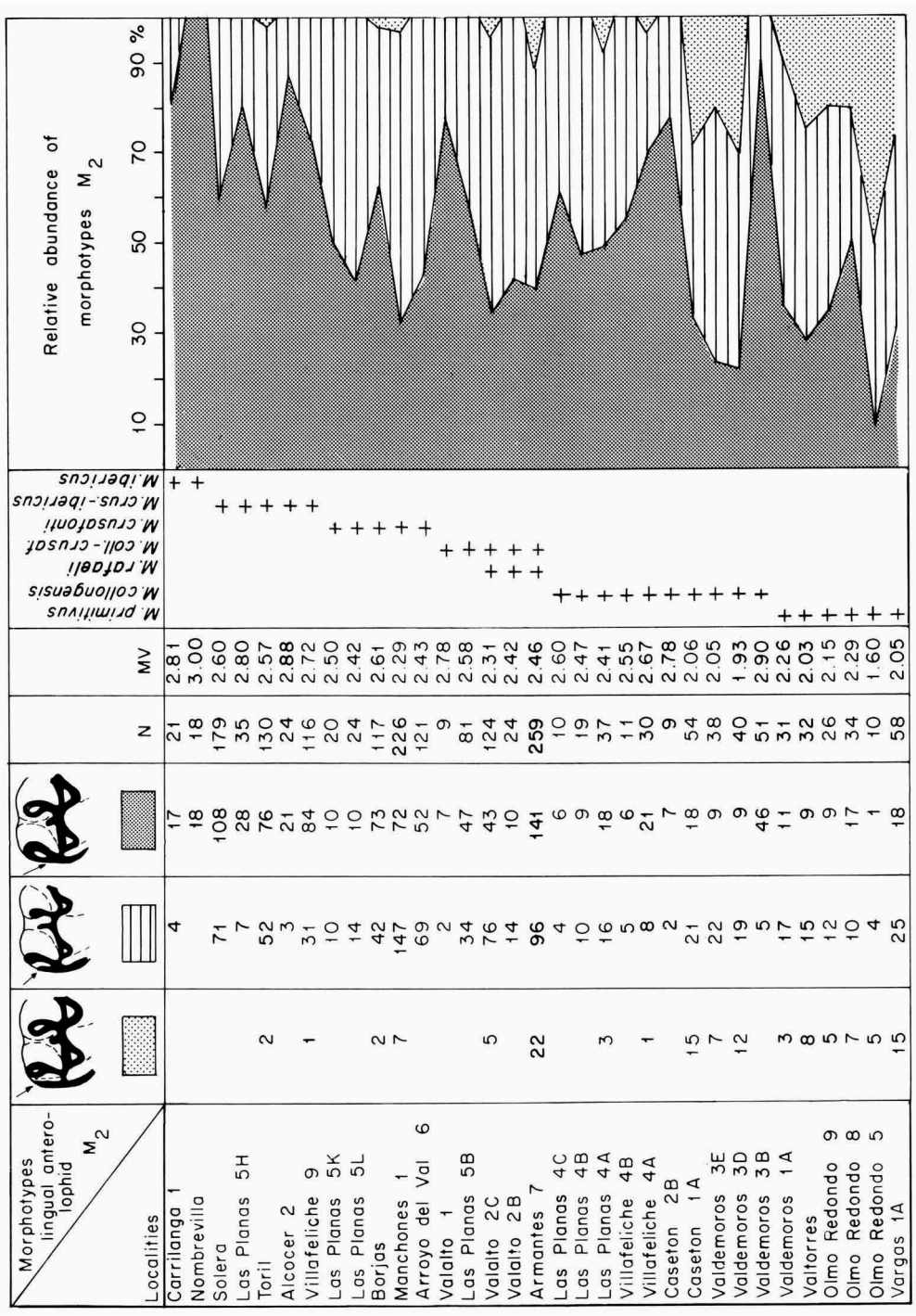


Fig. 5. Variation of the lingual anterolophid in M_2 of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

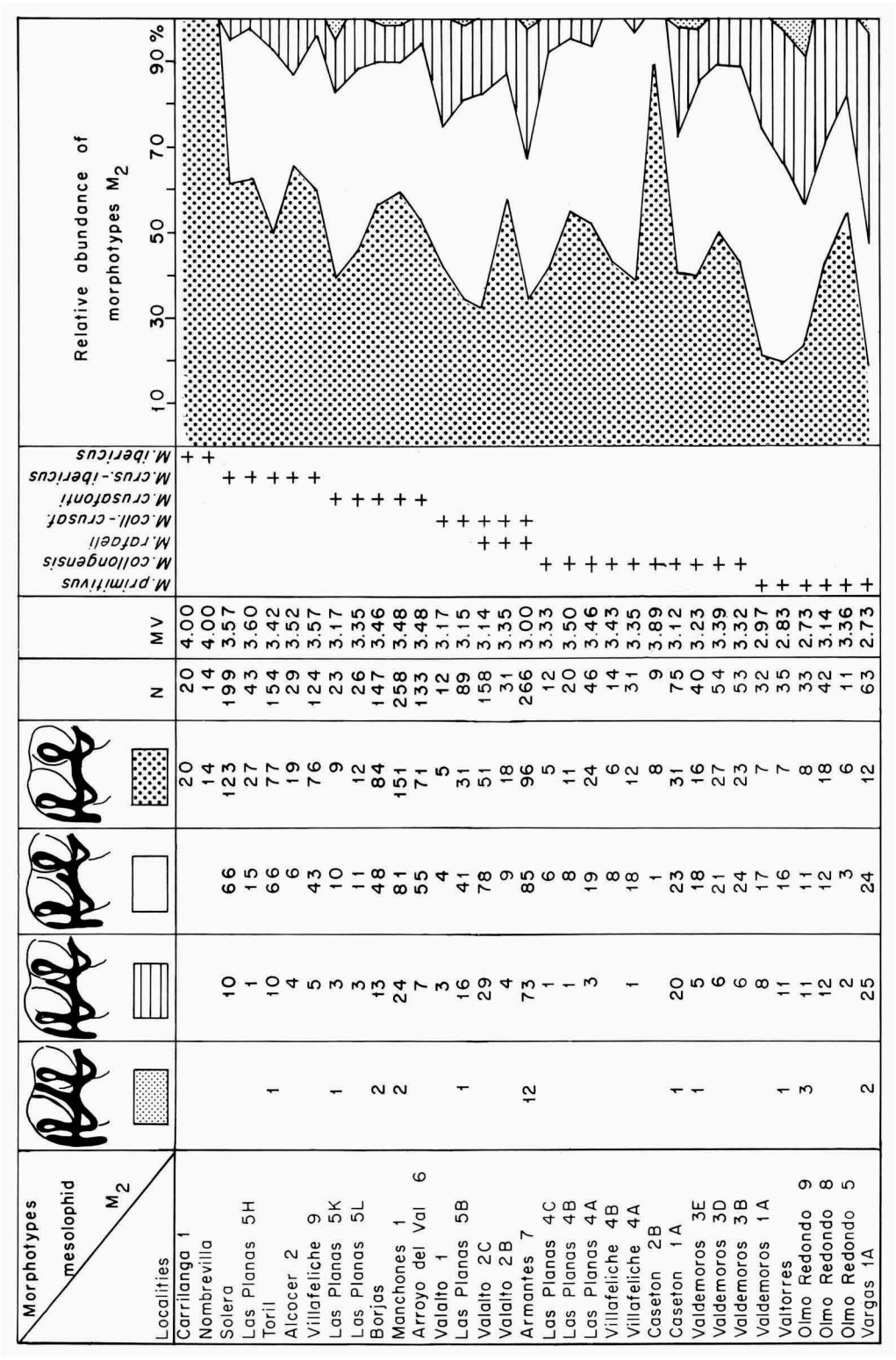


Fig. 6. Variation of the mesolophid in M_2 of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

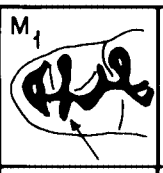
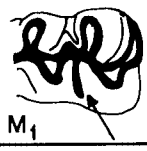
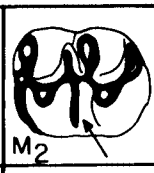
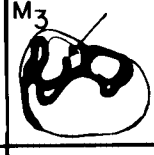
Morphotypes / Localities	M_1 	 M_1	 M_2	M_3 	*M. primitiv.*	*M. collong.*
Villafeliche 4B	2	-	-	-		+
Villafeliche 4A	2	-	-	-		+
Caseton 2B	-	-	-	-		+
Caseton 1A	2	1	-	3		+
Valdemoros 3E	-	-	-	-		+
Valdemoros 3D	-	-	-	1		+
Valdemoros 3B	3	-	-	-		+
Valdemoros 1A	-	-	-	-	+	
Valtorres	2	3	-	5	+	
Olmo Redondo 9	1	1	-	-	+	
Olmo Redondo 8	4	2	1	1	+	
Olmo Redondo 5	1	1	-	-	+	
Vargas 1A	7	-	-	1	+	

Fig. 7. Variation of some miscellaneous features in the lower molars of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

Miscellaneous features of the lower molars (Fig. 7)

In the lower assemblages of the composite section some rare features have been observed. In *M. primitivus* and *M. collongensis* some M_1 have a labial spur on the anterolophulid, which is generally short. Some M_1 and M_2 have an ectomesolophid. There are low numbers of M_3 with a short mesolophid in some assemblages of *M. primitivus* and *M. collongensis*. Wear does not influence the appraisal of these features.

Anterocone of M^1 (Fig. 8)

Four morphotypes are distinguished. The first one is figured as a simple one, but in reality the lingual part bears a very small extra cusp which can only be seen in unworn specimens. With the slightest degree of wear this little cusp disappears, and since it is so small that it consists of enamel only, it leaves no trace in the dentine wear pattern. The second morphotype is slightly subdivided and the furrow is not deep. With progressive wear this kind of anterocone turns into a simple bean-shaped cusp like in the first type. The anterolophule is generally connected to the lingual cusp of the anterocone. The third type is deeply split, and the wide or narrow furrow reaches the crown basis. There are intermediate specimens between the second and the third type, and wear influences the appraisal considerably. The fourth type is as deeply split as the third one, and is distinguished by the presence of a small cingulum ridge at the anterior border, in front of the anterocone; it may have a cusp shape, it may be a small isolated ridge, or it may be a continuation of the lingual anterocone cusp. Generally the anterolophule is connected to the middle part of the anterocone. This cusp is not always symmetrically split; either the lingual part or the labial one may be larger.

Fig. 8 shows that the simple and slightly subdivided anterocone is very rare in this lineage, and that the fourth type is predominant.

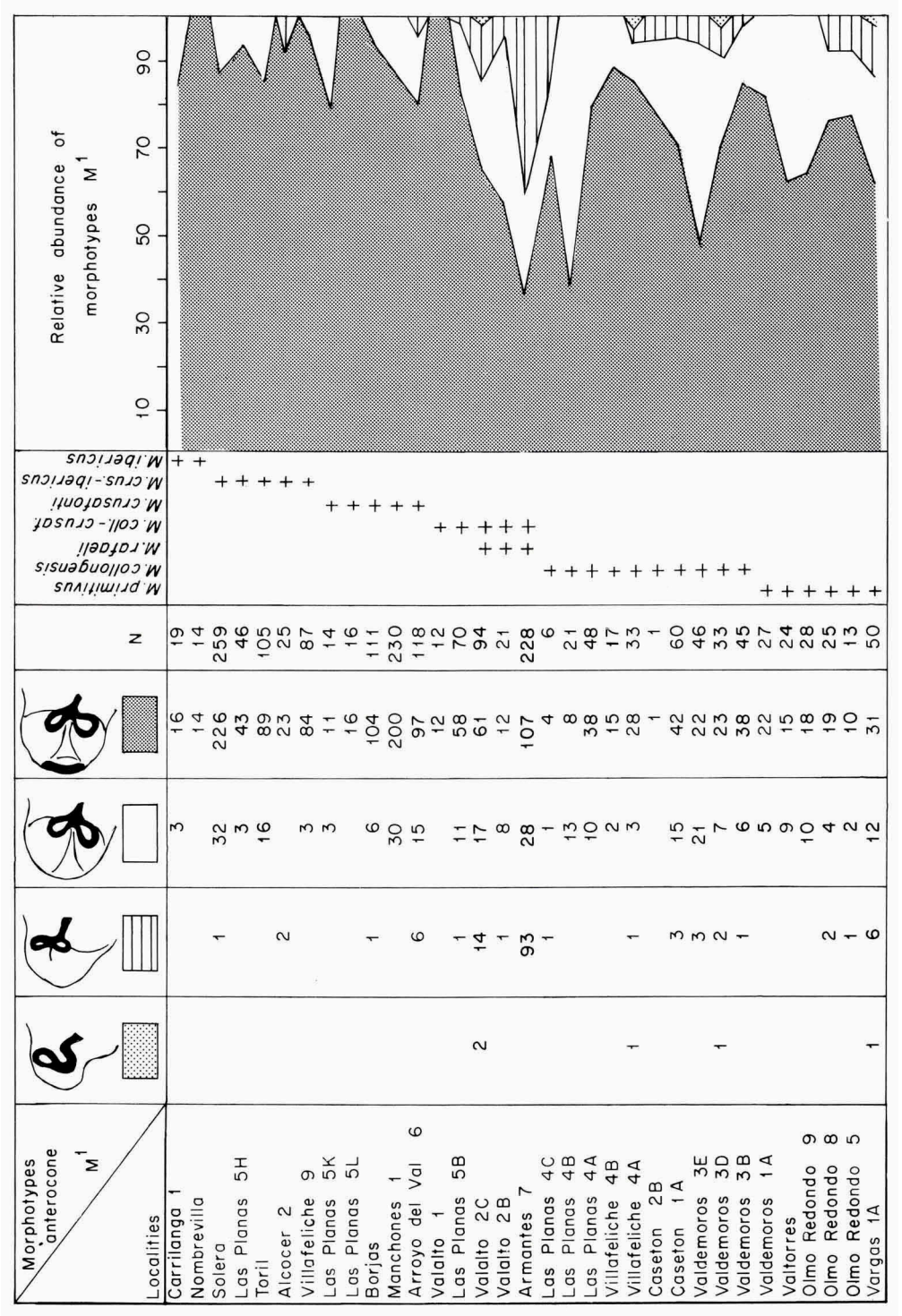


Fig. 8. Variation of the anterocone in M¹ of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

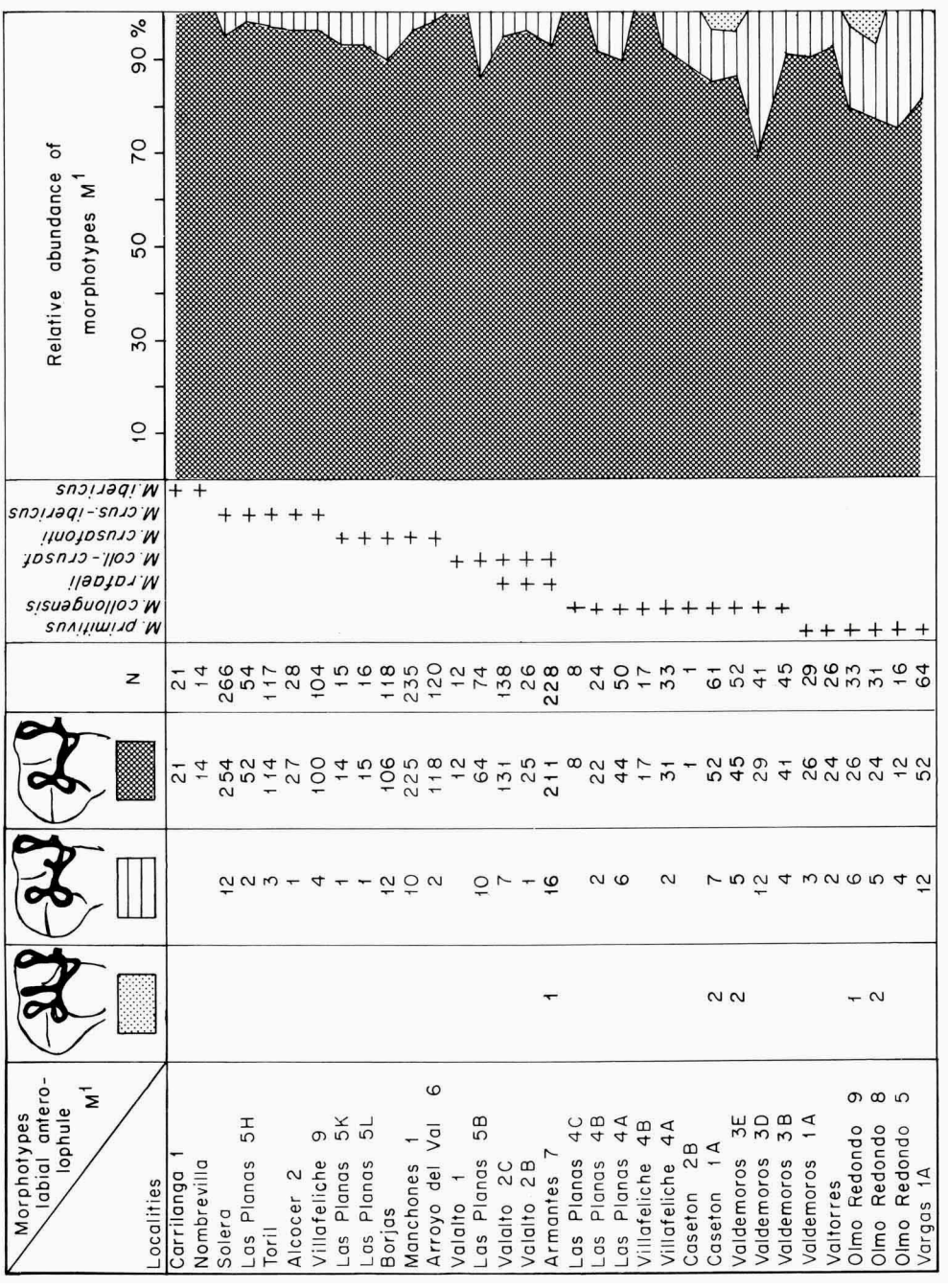


Fig. 9. Variation of the labial spur of the anterolophule in M¹ of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

Labial spur on the anterolophule of M^1 (Fig. 9)
Three morphotypes are distinguished. The first one has a long labial spur, reaching – or nearly reaching – the labial border of the molar. The second type has a short spur which may be transverse or may point obliquely backwards towards the anterior wall of the paracone. In fact the short spur may be a remnant of the anterior protolophule. The third type has no spur or anterior protolophule whatsoever. The appraisal of this feature is not subject to many errors, as the labial spur, if present, is either long or short, without any intermediate stages. Wear is not of influence either.

Fig. 9 shows that the long spur is only present in some assemblages of *M. primitivus* and *M. collongensis*, and a short one is present in almost all assemblages, with the exception of those of *M. ibericus*. Specimens without labial spur or anterior protolophule predominate in the entire lineage.

Ectoloph on the paracone of M^1 (Fig. 10)
Three stages are recognized. The first one lacks a posterior spur, the second one has a short protuberance, and the third type has a well-developed ectoloph, reaching the bottom of the mesosinus. The ectoloph may point obliquely backwards to the labial border of the molar; it may be more or less longitudinal, or it may have a postero-lingual direction. The appraisal of this character is hampered by wear and by the presence of intermediate specimens.

Fig. 10 demonstrates that *M. primitivus* and *M. collongensis* have poorly developed ectolophs on the paracone, and that the other assemblages have well-developed ectolophs, with the exception of *M. ibericus* from Carrilanga 1.

Mesoloph of M^1 (Fig. 11)
There are four morphotypes, defined in the same way as for the mesolophids of the lower molars. It appears from Fig. 11 that *M. primitivus* and *M. collongensis* have on the average medium-sized mesolophs, with the exception of *M. collongensis* from Caseton 1A. In the upper half of the composite section there is a gradual decrease of the mesoloph length, although *M. crusafonti* from Alcocer 2 has relatively long mesolophs. The major part of the M^1 of *M. ibericus* has no mesoloph.

Connection of the ectoloph with the mesoloph in M^1 (Fig. 12)
Two morphotypes have been distinguished. In the first one the posterior spur of the paracone is connected to the mesoloph. Generally in these specimens the mesoloph is long or medium-sized, but when the ectoloph points postero-linguad it may be connected to a short mesoloph. In the second type there is no connection. Specimens without mesoloph are represented separately in the third morphotype column of Fig. 12. Moderate wear is not of influence on the appraisal of this character, and intermediate specimens are hardly found.

It appears from Fig. 12 that in *M. primitivus* and *M. collongensis* few specimens have this connection, but it should be mentioned, that the paracone spur is not well-developed in these two species. In the assemblages from Armantes 7 to Solera the paracone spur is longer than in the previous assemblages and the connection is more frequent. In *M. ibericus* there are no specimens with the connection, but the majority of the *M. ibericus* material has no mesoloph.

Posterosinus of M^1 (Fig. 13)
Four morphotypes have been regognized. In the first type the metalophule is connected to the hypocone or to the entoloph just in front of this cusp, and the posteroloph is long

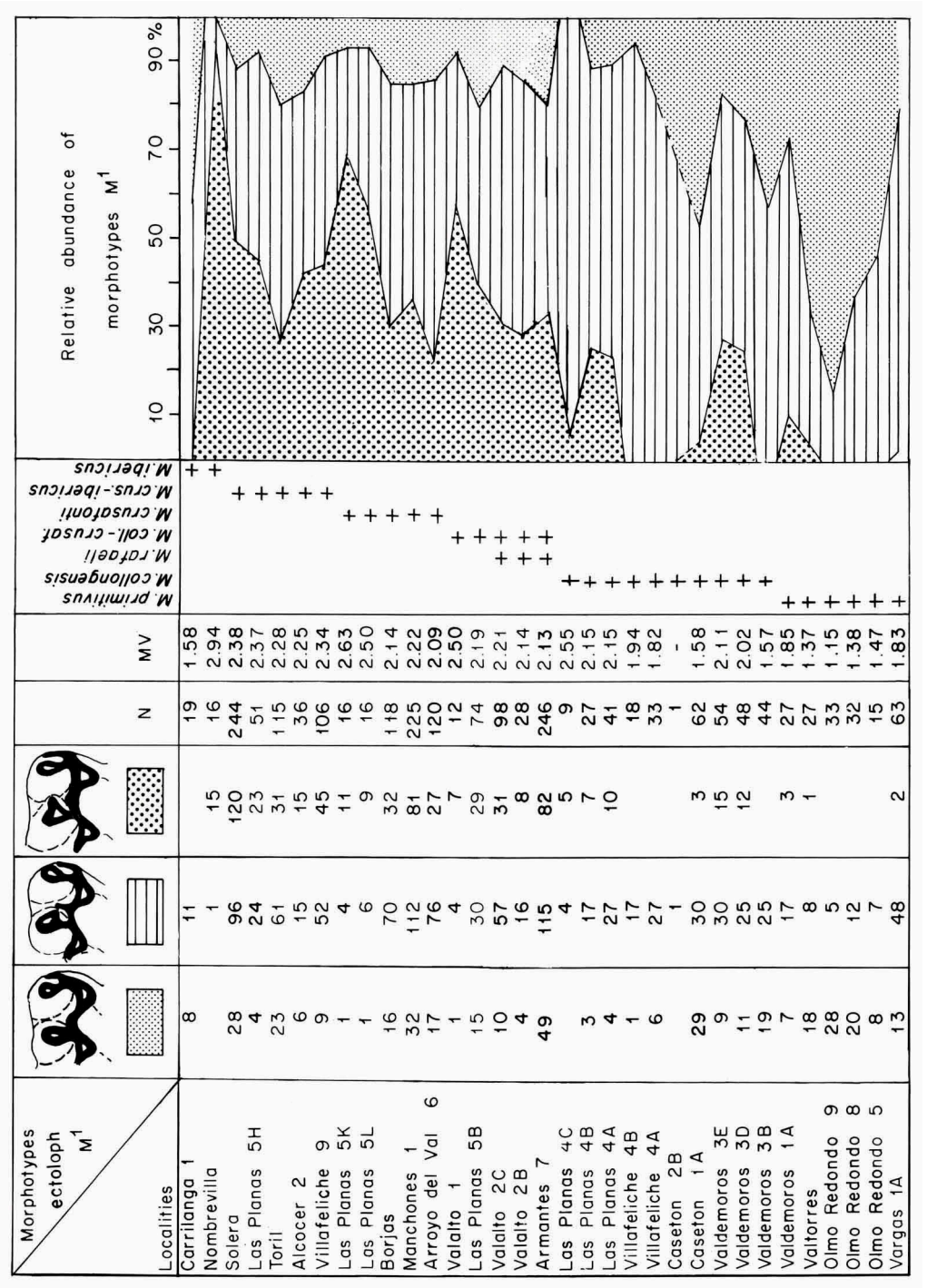


Fig. 10. Variation of the ectoloph in M¹ of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

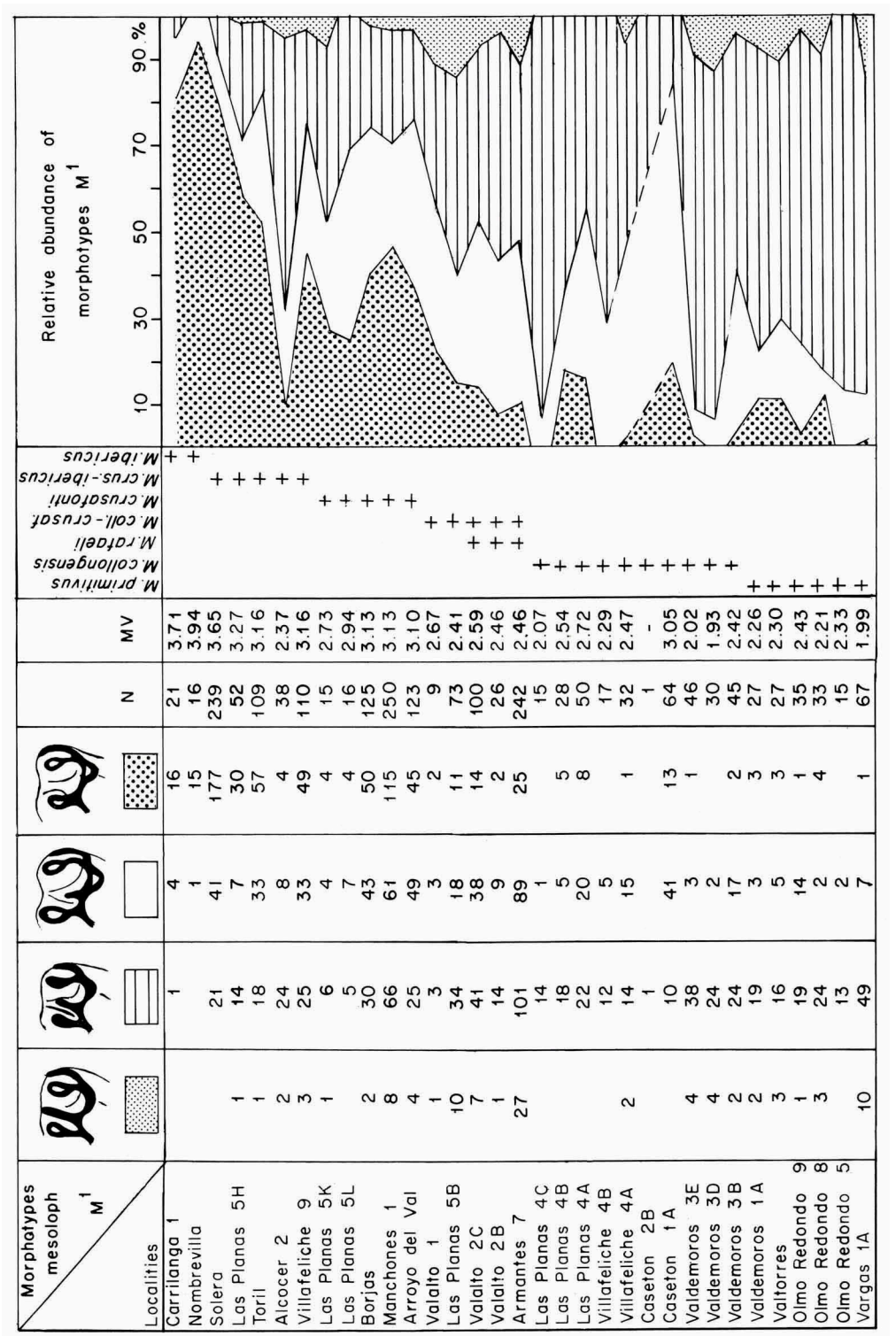


Fig. 11. Variation of the mesoloph in M¹ of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

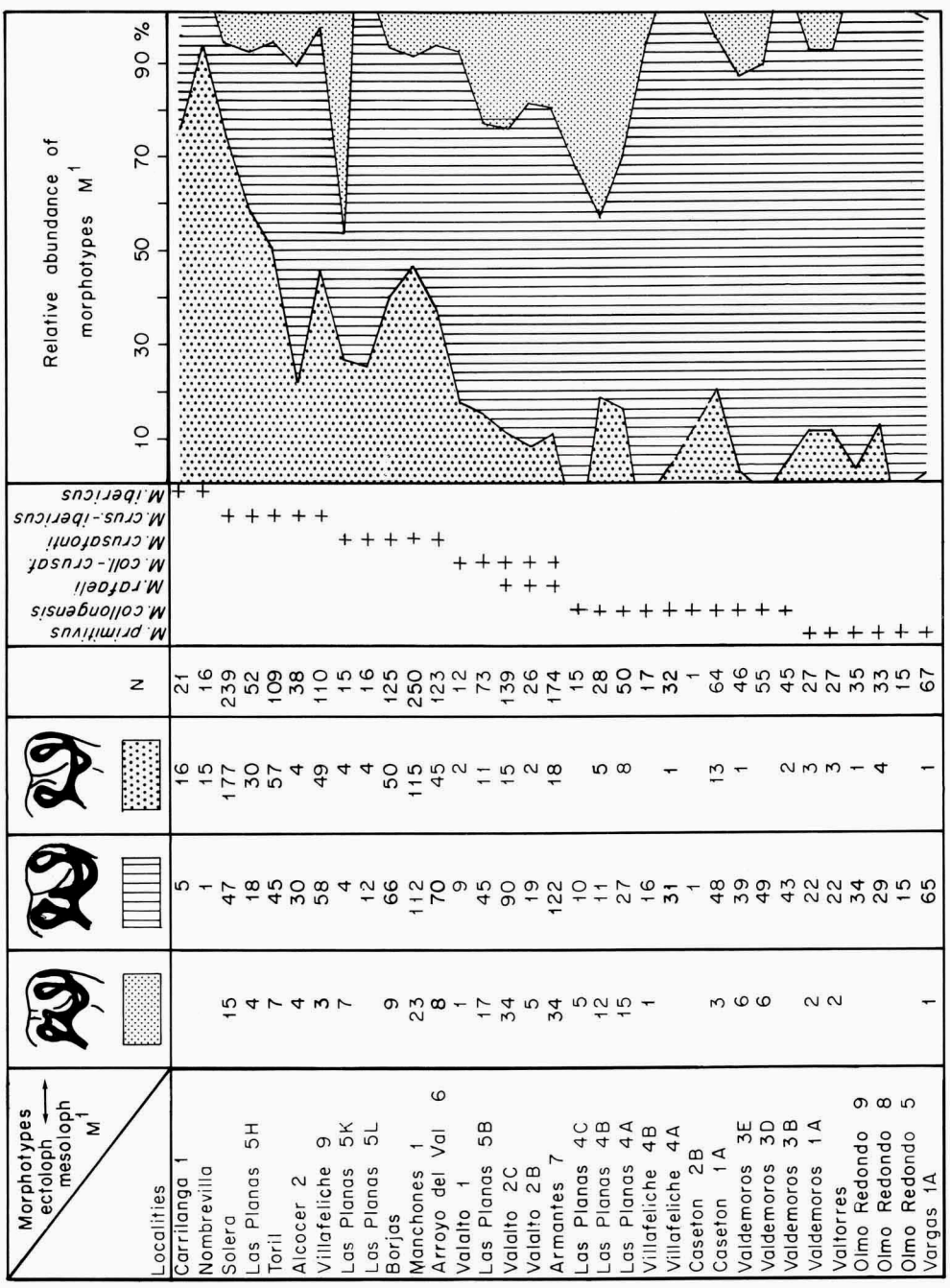


Fig. 12. Variation of the connection between ectoloph and mesoloph in M¹ of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

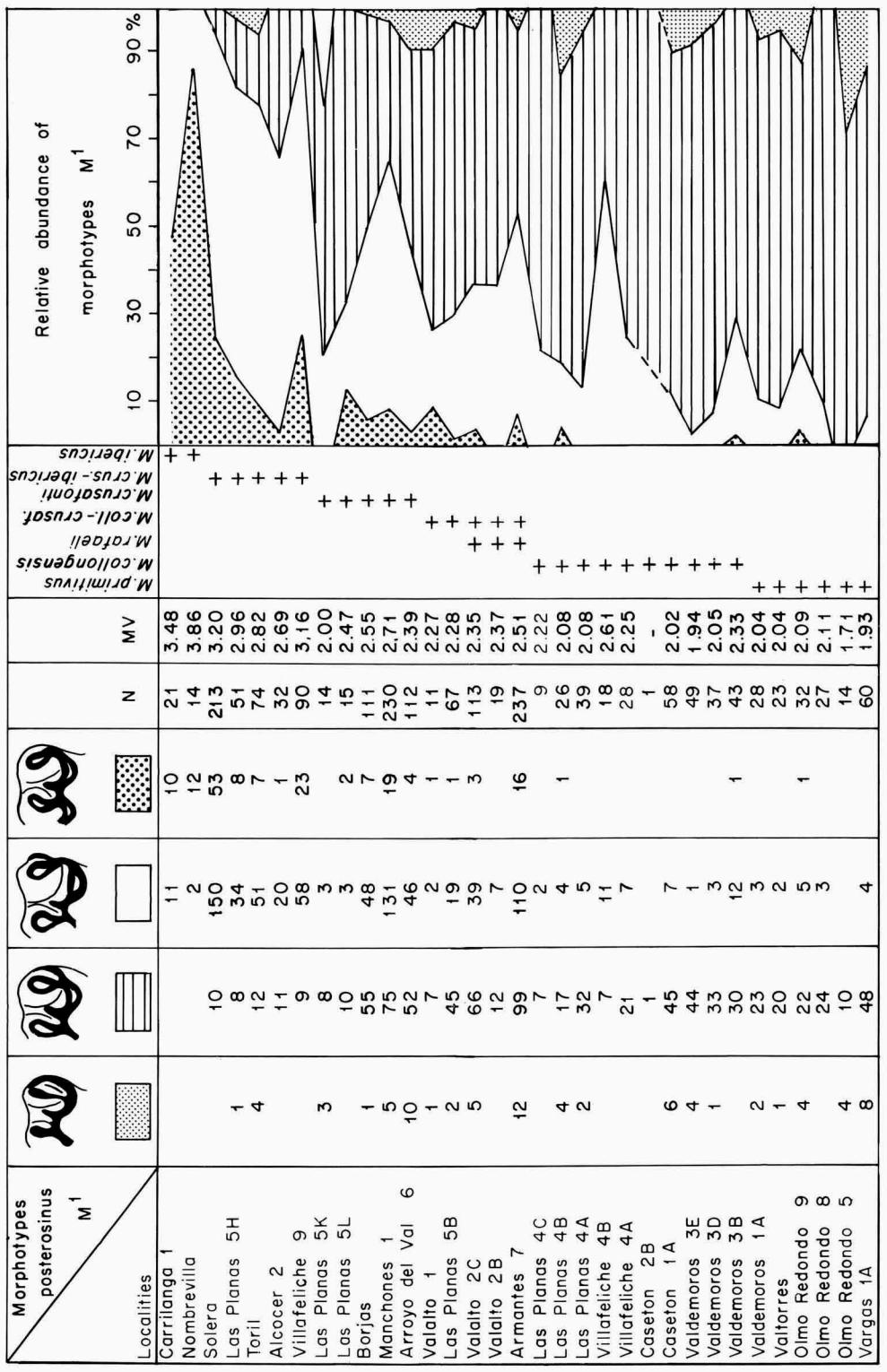


Fig. 13. Variation of the posterosinus in M¹ of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

and arched, enclosing a wide posterosinus. In the second type the metalophule is connected to the posteroloph just behind the hypocone. The posteroloph bends more inwards, enclosing a relatively small posterosinus. The third type presents a metalophule that points strongly backwards, and the posteroloph is a short labial ridge, enclosing a tiny posterosinus. The fourth type lacks posteroloph and posterosinus. The appraisal of this character is influenced by wear and by the presence of intermediate specimens. With moderate wear the error is largest in the distinction between the last three morphotypes.

Fig. 13 shows that there is a gradual trend towards reduction of the posterosinus. In nearly all assemblages from Vargas 1A to Las Planas 5K the second morphotype is predominant and from Villafeliche 9 to Carrilanga 1 the third type is the predominant one, with the exception of Nombrevilla.

Protolophule of M^2 (Fig. 14)

Five morphotypes have been distinguished. In the first type the protolophule points obliquely forward and it is connected to the anterolophule in front of the protocone. In the second morphotype the protolophule is transverse and connected to the protocone. The third morphotype also has a transverse protolophule, but it is connected to the entoloph behind the protocone. The paracone and protocone are not placed in opposition, but the paracone lies farther backwards. In the fourth type the entoloph is connected to the protocone indirectly through paracone and protolophule; for that reason the sinus is strongly curved forward. In the fifth type the protolophule is double. Moderate wear is hardly of influence on the appraisal of this feature, but intermediate specimens are present and do have influence.

Fig. 14 demonstrates that the first type is frequently present in most assemblages, and the third and fourth type gain importance in the higher levels of the composite section. The third type is the predominant one in *M. ibericus*. Specimens with double protolophule are more frequent in the lower levels.

Ectoloph on the paracone in M^2 (Fig. 15)

The same types are distinguished as in M^1. Fig. 15 shows that specimens with an ectoloph are more frequent in *M. primitivus* and *M. collongensis*. Specimens with a moderately developed ectoloph are present in all assemblages, and the type with a large ectoloph predominates in the upper part of the composite section.

Sinus of M^2 (Fig. 16)

Three morphotypes have been distinguished. The first type has a transverse sinus; in the second one the sinus is slightly curved forward, and in the third one it is strongly curved forward. The appraisal of this feature is not subject to wear. Intermediate specimens are present.

Fig. 16 shows that the predominant type in *M. primitivus* and *M. collongensis* is the transverse sinus. In all other assemblages the slightly or strongly curved sinus are more frequent.

Mesoloph of M^2 (Fig. 17)

The same four stages as in M^1 have been distinguished. Fig. 17 shows that there is a gradual trend towards the reduction of the mesoloph. In *M. ibericus* this ridge is almost absent.

Morphotypes protolophule M2
Localities
N
M.primitivus
M.collongensis
M.rafaeli
M.coll.-crusaf.
M.crusafonti
M.crus.-ibericus
M.ibericus
Relative abundance of morphotypes M2
10
30
50
70
90 %

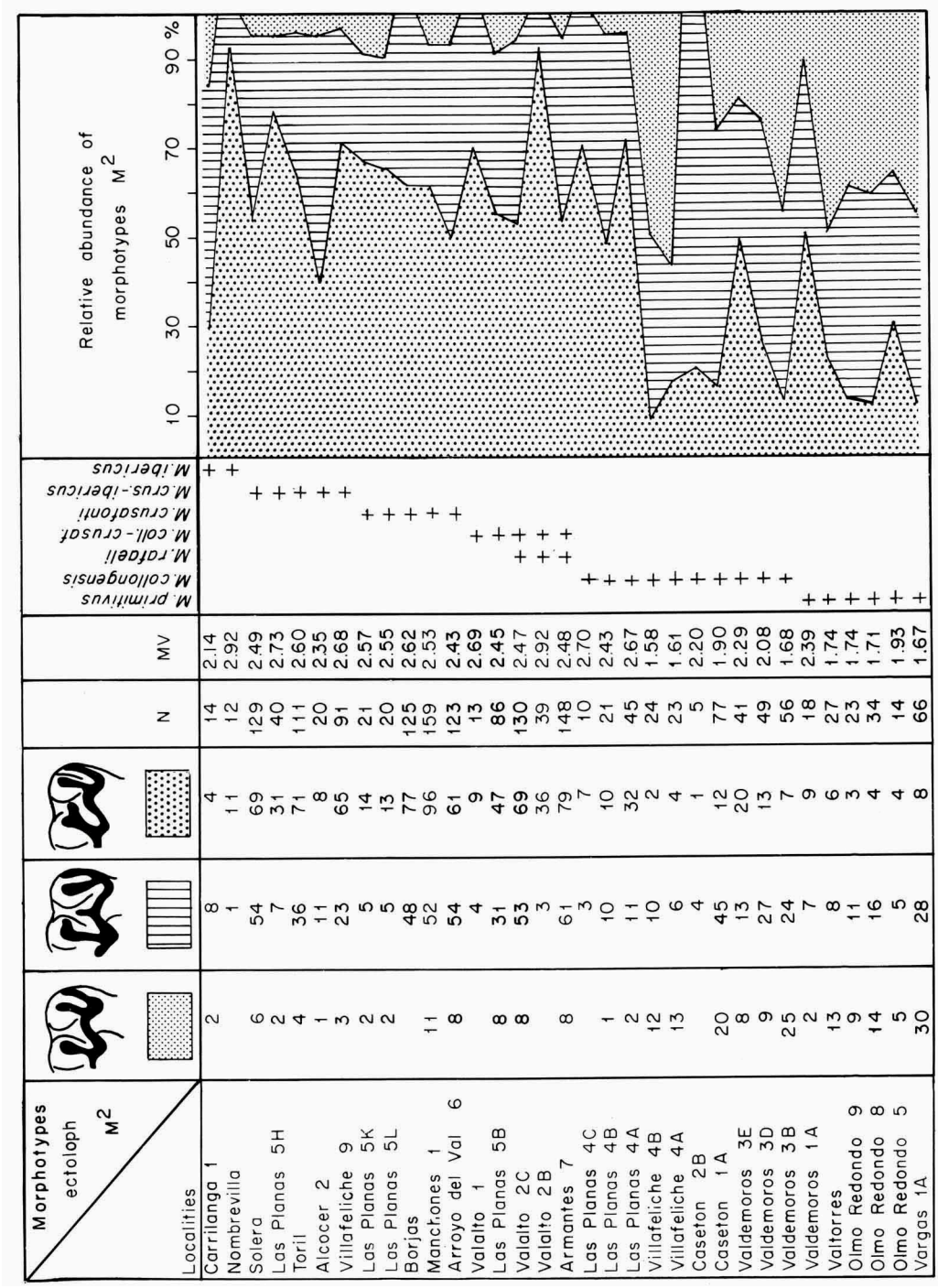


Fig. 15. Variation of the ectoloph in M² of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

← Fig. 14. Variation of the protolophule in M² of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

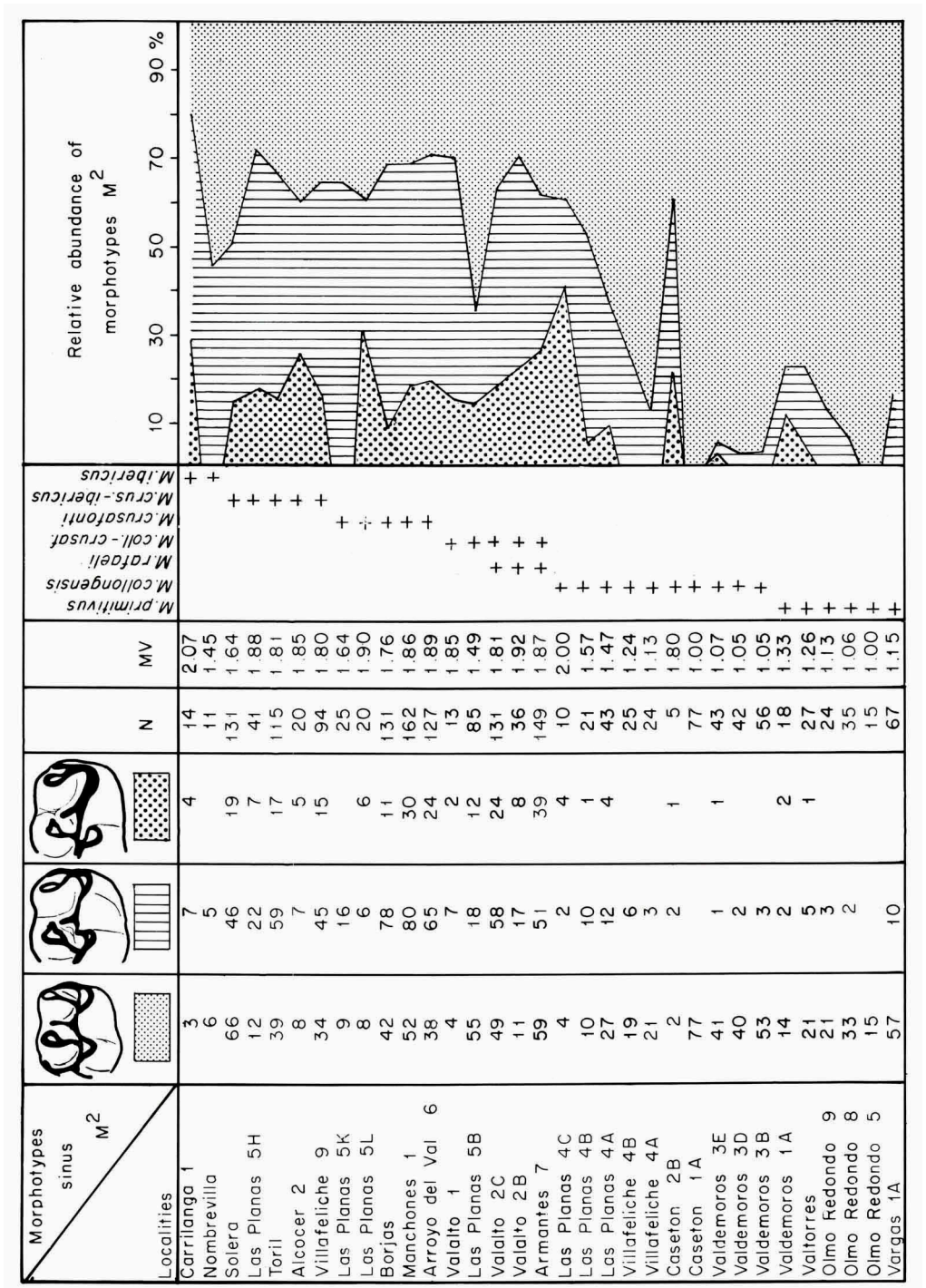


Fig. 16. Variation of the sinus in M² of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

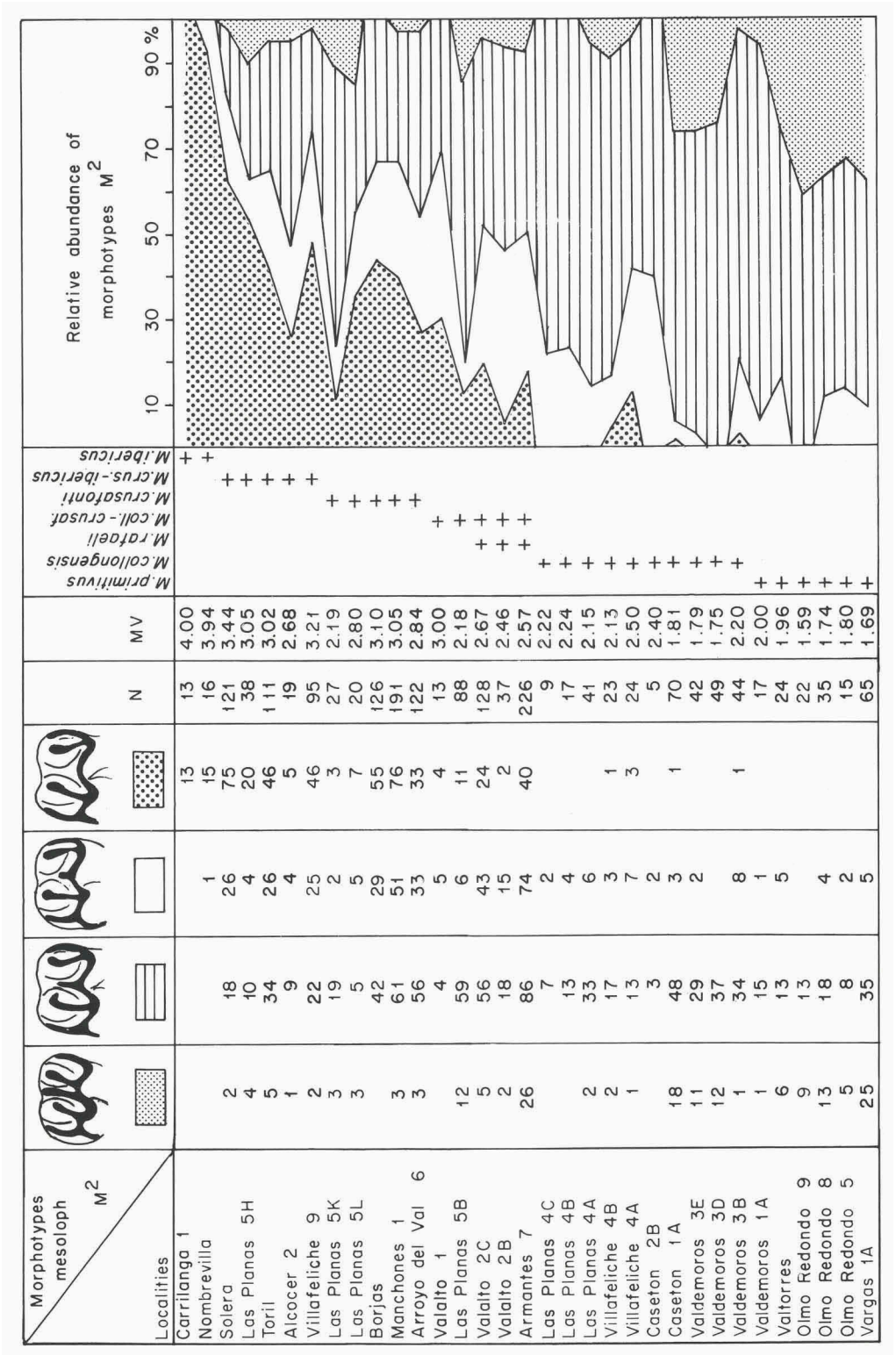


Fig. 17. Variation of the mesoloph in M^2 of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

Connection of the ectoloph with the mesoloph in M^2 (Fig. 18)
The same distinction has been made as in M^1. Fig. 18 shows that the connection is present in nearly all assemblages in more or less similar proportions, with the exception of *M. ibericus* in which mesolophs are practically absent.

Metalophule of M^2 (Fig. 19)
Five morphotypes have been recognized. In the first type the metalophule is transverse and connected to the hypocone. In the second type it is connected to the entoloph, in front of the hypocone. In the third morphotype the metalophule points obliquely backwards and it is connected to the posteroloph, just behind the hypocone. The fourth type has a more oblique metalophule, reducing the posterosinus to a small valley. The fifth type has a double metalophule. Moderate wear does not influence the appraisal of this character. Intermediate specimens are present but generally the error is not large. It is largest in choosing between the third and the fourth type.

Fig. 19 shows that the second type is predominant in *M. primitivus* and *M. collongensis*, and that the assemblages from Armantes 7 to Solera are characterized by a large variation of metalophule types, although the second type is the most frequent. In *M. ibericus* the fourth type predominates.

Morphology values of the mesoloph(id)s of M1 and M2 (Fig. 20)
In Fig. 20 the morphology values of the mesoloph(id)s of M1 and M2 have been plotted. First of all it is evident that the MV's are higher in the lower molars, implying that the mesolophids are shorter than the mesolophs. There may or may not be a positive correlation between the MV's of the four elements within each assemblage. E. g. *M. collongensis* from Valdemoros 3B and *M. crusafonti* from Las Planas 5K and 5L show positive correlations. On the other hand, in Olmo Redondo 5 the MV of the M_1 shows a negative correlation with the MV's of the other elements.

Furthermore it appears that in the lower part of the composite section the M^1 has more reduced mesolophs than the M^2, whereas in the upper part of the section this feature is more variable. The mesolophids present a reversed picture: in the uppper part the M_1 has more reduced mesolophids than the M_2, whereas in the lower part this feature is more variable.

Discussion
M. collongensis differs from *M. primitivus* by the following characters:
the presence of specimens of M_1 with slightly subdivided anteroconid;
the on the average shorter mesolophids in M_1 and M_2;
the shorter mesoloph in M^1;
the better developed ectoloph of the paracone in M^1;
the more frequent connection of the ectoloph with the mesoloph in M^1;
in the M_1 of *M. primitivus* the labial spur of the anterolophid and the ectomesolophid are more frequent.

Freudenthal (1963) mentions that 5 out of 15 M_3 of *M. primitivus* from its type locality Valtorres have a short mesolophid or a remnant of a posterior metalophulid, which would represent a less-reduced dental pattern than the one found in the M_3 of *M. collongensis*. However, this character is not or badly represented in other assemblages of *M. primitivus*, and it happens to be present in some assemblages of *M. collongensis* (Fig. 7). Therefore this character is not considered to be useful for specific separation.

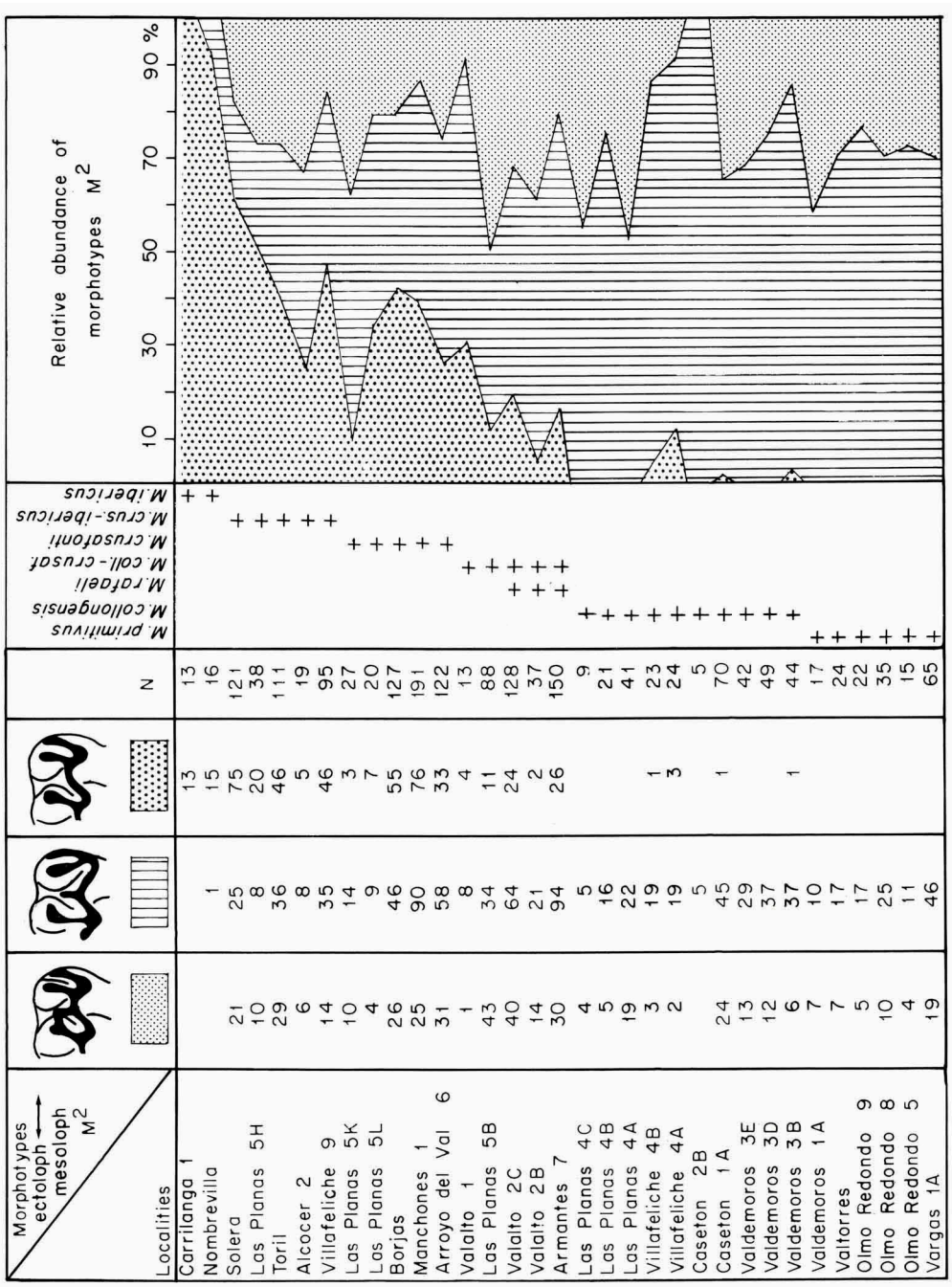


Fig. 18. Variation of the connection between ectoloph and mesoloph in M^2 of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

Localities	N	M.primitivus	M.collongensis	M.rafaeli	M.coll.-crusaf.	M.crusafonti	M.crus.-ibericus	M.ibericus
Carrilanga 1	10							+
Nombrevilla	16							+
Solera	98						+	
Las Planas 5H	33						+	
Toril	99						+	
Alcocer 2	18						+	
Villafeliche 9	89						+	
Las Planas 5K	22					+		
Las Planas 5L	19					+		
Borjas	122					+		
Manchones 1	181					+		
Arroyo del Val 6	104				+			
Valalto 1	12				+			
Las Planas 5B	84				+			
Valalto 2C	112				+			
Valalto 2B	31				+			
Armantes 7	216				+			
Las Planas 4C	9		+					
Las Planas 4B	16		+					
Las Planas 4A	36		+					
Villafeliche 4B	23		+					
Villafeliche 4A	23		+					
Caseton 2B	5		+					
Caseton 1A	78		+					
Valdemoros 3E	41		+					
Valdemoros 3D	47		+					
Valdemoros 3B	45		+					
Valdemoros 1A	17		+					
Valtorres	24		+					
Olmo Redondo 9	22		+					
Olmo Redondo 8	33		+					
Olmo Redondo 5	14		+					
Vargas 1A	59		+					

Localities	Morphotypes metalophule M2						
Carrilanga 1				10			
Nombrevilla				15	1		
Solera	7	14	4	34	39		
Las Planas 5H	2	9	3	13	6		
Toril	14	35	4	18	28		
Alcocer 2	4	5	1	5	3		
Villafeliche 9	20	32	6	11	20		
Las Planas 5K	3	12	3	1	3		
Las Planas 5L	3	9	2	2	3		
Borjas	18	44	9	25	26		
Manchones 1	18	93	10	39	21		
Arroyo del Val 6	2	66	7	17	12		
Valalto 1	3	3	1	1	4		
Las Planas 5B	21	39	11	5	8		
Valalto 2C	15	55	5	29	8		
Valalto 2B	6	6	4	12	3		
Armantes 7	17	131	16	28	24		
Las Planas 4C		7	2				
Las Planas 4B	2	11	3				
Las Planas 4A	16	16	2	1	1		
Villafeliche 4B	4	12	6		1		
Villafeliche 4A	4	13	6				
Caseton 2B	1	3		1			
Caseton 1A	17	51	6	3	1		
Valdemoros 3E	13	25	2		1		
Valdemoros 3D	11	33	2		1		
Valdemoros 3B	3	25	17				
Valdemoros 1A	7	7	3				
Valtorres	5	8	9		2		
Olmo Redondo 9	4	15		2	1		
Olmo Redondo 8	3	25	4	1			
Olmo Redondo 5	3	8	3				
Vargas 1A	7	33	11	5	3		

M. crusafonti differs from *M. collongensis* by the following features:
its larger size;
the much more complicated anteroconid of M_1;
the shorter mesolophids of M_1 and M_2;
the more reduced lingual anterolophid of M_2;
the better developed ectoloph of M^1;
the shorter mesolophs of M^1 and M^2;
the more reduced posterosinus of M^1 and M^2;
the large variation of the protolophule of M^2.

M. ibericus differs from *M. crusafonti* by the following characters:
its more complicated anteroconid;
its more reduced mesoloph(id)s in M1 and M2;
the absence of a labial spur on the anterolophule of M^1;
the more reduced posterosinus of M^1 and M^2;
the predominance of the posterior-transverse protolophule (morphotype 3) in M^2.

The evolutionary trends in the *M. primitivus – ibericus* lineage are towards:
larger size;
complexity of the anteroconid of M_1;
a strong reduction of the mesoloph(id)s of M1 and M2;
reduction of the lingual anterolophid in M_2;
loss of a labial spur on the anterolophule of M^1;
reduction of the posterosinus in M^1 and M^2;
forward curved sinus in M^2.

The trend towards size increase in this lineage is not a gradual one. In the Aragonian zones C and D this trend is not very conspicuous and subject to oscillations. But in zone E *M. collongensis* is definitely larger than the earlier associations. This may be interpreted in various ways.
1. Lack of documentation between zone D and E
2. Continuous documentation and a rapid size increase
3. Entry of an other *Megacricetodon* species, with similar dental pattern. The dental material from zone E may belong to this new species, or it may be a mixture of this species with *M. crusafonti* (Fig. 42). This hypothesis is supported by an abrupt change of various dental features. In comparison with the preceding associations from zone D *M. collongensis* from Las Planas 4A, 4B and 4C has much better developed ectolophs in M^1 and M^2, resulting in a connection with the medium-sized or long mesoloph. Moreover, the sinus of M^2 is more proverse in the Las Planas assemblages than in the preceding ones. All other dental characters do not differ significantly.

In this study the *Megacricetodon* assemblages from zone C and zone D appeared to be homogeneous. A study on recently collected samples in the Calamocha area of the Calatayud-Teruel Basin revealed however some faunas from zone D in which two *Megacricetodon* species are present: one of smaller size and the other one larger (Berends, pers. comm.). It is not impossible that the large-sized species be the ancestor

← Fig. 19. Variation of the position of the metalophule in M^2 of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

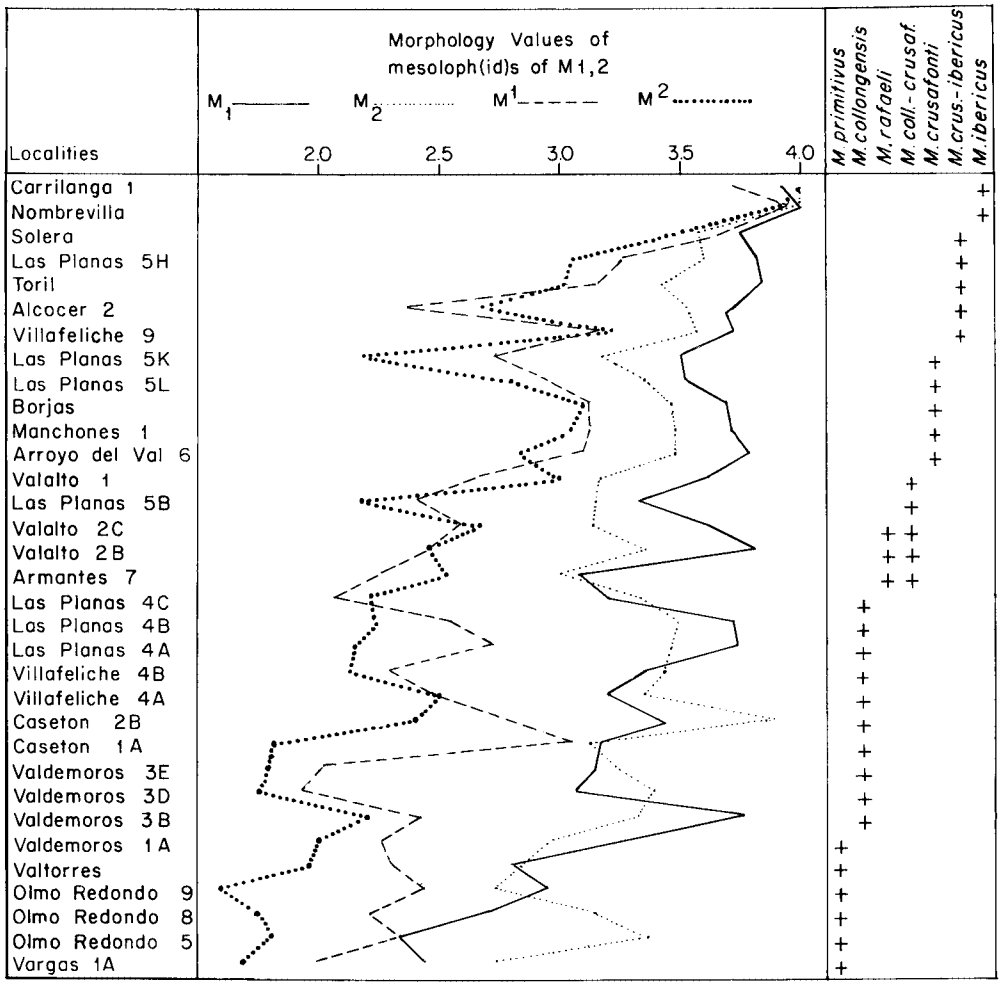


Fig. 20. Average length, expressed in morphology values (MV) of the mesoloph(id)s of M1,2 of the *M. primitivus – ibericus* lineage and of *M. rafaeli*.

of *M. crusafonti*, which is substituting *M. collongensis* during the time interval covered by zone E.

In this respect it is important to note, that our study of other cricetid genera (*Democricetodon, Fahlbuschia*, etc.) led us to subdivide zone D in D1, D2 and D3, and that zone D3 until now has not been recognized in our composite section of the Daroca-Villafeliche area. Zone D3 has been recognized in various localities in the Calamocha area, and is characterized – among other things – by the presence of a *Fahlbuschia* species, that is certainly not the ancestor of *F. darocensis* in zone E. So, the hypothesis of the immigration of a new *Megacricetodon* in zone E is supported by the more or less simultaneous immigration of *F. darocensis*, and on top of that the first appearance in our area of the genus *Cricetodon*.

Another discontinuity in the hypothetical *M. primitivus – ibericus* lineage concerns the lengths of the mesoloph(id)s in M1 and M2 (Fig. 20). In the lower part of the composite section (from Vargas 1A to Las Planas 4B) the M^2 has always longer

mesolophs than the M^1, whereas the relation between the mesolophids of M_1 and M_2 is more variable. In the upper part of the composite section (Armantes 7 to Carrilanga 1) it is just the other way around: M_1 has shorter mesolophids than M_2, and in the upper molars the situation is more variable.

In the Vallés-Penedés (Agustí, 1982) parts of the *M. primitivus – ibericus* lineage are present. In this area the lineage is not complete, due to a large marine interval. In Can Martí Vell 1 (zone C) two *Megacricetodon* species are present: the small-sized *M. primitivus* and a larger-sized *Megacricetodon* sp. This situation is comparable to that of the newly discovered localities in zone D of the Calamocha area. *M. ibericus* from both levels of Hostalets de Pierola have more or less the same dental pattern as the assemblage from Nombrevilla, but the size of teeth from Nombrevilla coincides more with the size of the specimens from the lower levels of Hostalets.

Sesé (1977) described *M. crusafonti* from the fissure filling of Escobosa de Calatañazor. Our own observations of this material revealed that the differences with *M. crusafonti* from Manchones 1 are such, that identification with that species must be excluded. In fact, the deeply split anteroconid in all M_1, the absence of mesoloph(id)s, the strongly reduced to absent posterosinus in M^1 and M^2 and the forward curved sinus of M^2 in the Escobosa assemblage agree well with the dental pattern of *M. ibericus* from Nombrevilla. Therefore the material from Escobosa is assigned to *M. ibericus*.

Comparison with Megacricetodon from France and Central Europe

In order to enable a good comparison with assemblages from other countries, we should have restudied them personally. But in the framework of this study it was not possible to visit foreign collections. Therefore we depend mainly on data from the literature. However, some material from French localities is present in the Leiden collections: *M. gersii* and *M. minor* from Sansan, *M. collongensis* from Vieux-Collonges, and *M. gregarius* from La Grive-St. Alban.

Aguilar (1980b) gave a new interpretation of the evolution of *Megacricetodon* during the Miocene, and created two new species: *M. gersii* from Sansan (*M. crusafonti* in Baudelot, 1972), and *M. germanicus* from Anwil (*M. gregarius* in Engesser, 1972). He recognized the *M. primitivus – gersii* lineage and supposed that *M. crusafonti* was an immigrant in Western Europe, replacing *M. gersii*.

M. gersii from Sansan agrees in size and dental pattern with the *M. collongensis – crusafonti* transitional assemblages from the Daroca-Villafeliche area, present in zones F and G1 (personal observations). *M. crusafonti* from Luc-sur-Orbieu (Aguilar, 1980) presents a remarkable resemblance in size and dental pattern with the *M. collongensis – crusafonti* transitional assemblages.

In this paper we did not want to describe the various intermediate evolutionary stages (*M. collongensis – crusafonti* and *M. crusafonti – M. ibericus*) as new species. The dental and metric features appear each to evolve independently, and therefore it is impossible to characterize adequately one of the transitional assemblages as a new species, without having to recognize transitional assemblages between this new species and its ancestor and/or its descendant. For that matter we do not recognize *M. gersii* in our succession, although it agrees well with our transitional assemblage *M. collongensis – crusafonti* from Las Planas 5B. We would be confronted with the same problem of having transitional assemblages between *M. collongensis and M. gersii*, and between *M. gersii* and *M. crusafonti*

The dental characters of *M. gregarius* from La Grive M (personal observations) agree with those of the *M. crusafonti – ibericus* transitional assemblages like those of

Toril, Las Planas 5H and Solera. Of the 76 M_1 studied, 5 specimens have a simple anteroconid, 2 have a slightly split one, in 13 the anteroconid is 8-shaped, and in 56 it is deeply split. This evolutionary stage would correspond to that of Toril and Las Planas 5H. The size of *M. gregarius* from La Grive M is, however, significantly larger, in spite of some overlap.

M. gregarius from La Grenatière (Aguilar, 1980a) appears to be a little more evolved than the same species from La Grive M, by the exclusive presence of M_1 with deeply split anteroconid. According to the descriptions of Aguilar (1980a), morphologically it should be situated between *M. crusafonti – ibericus* from Solera and *M. ibericus* from Nombrevilla. The size of *M. gregarius* from La Grenatière agrees more or less with that of the same species from La Grive M. In one feature *M. gregarius* is different from our *M. crusafonti – ibericus* transitional assemblages: its transverse sinus in M^2. In the Spanish material from zones F, G and H the sinus is frequently curved forward.

One may conclude that the few *Megacricetodon* assemblages from French localities have many features in common with representatives of the Spanish lineage. The trends in Spain and southern France towards size increase, more complex anteroconids, and loss of mesoloph(id)s and posterosinuses, go in tandem (Table 1). The few differences observed are attributed to geographical variation. If evolutionary rates are more or less the same in both areas, this implies that the faunas of Sansan and Luc-sur-Orbieu are older than the fauna of Manchones, and that their age is comparable to that of Las Planas 5B. The faunas of La Grive and La Grenatière would then be of an age comparable to that of Toril – Las Planas 5H – Solera.

Bulot (1980) described *M. bavaricus bezianensis* from the Lower Miocene locality of Bézian, which is supposed to be comparable in age to our zone D. The teeth are more or less of the same size as those of the *M. collongensis – crusafonti* transitional assemblage from Las Planas 5B, but the anteroconids of M_1 are less subdivided in Bézian. The general morphology of this species resembles surprisingly well that of the *M. collongensis – crusafonti* transitional assemblages from zones F and G1, and we think it is possible that *M. bezianensis* belongs to the same group as the *Megacricetodon* sp. from the three recently discovered localities from zone D in the Calamocha area (under study by Berends). It may also be the ancestor of *M. gersii* from Sansan.

Towards the east (Switzerland, Germany and Czechoslovakia) the data on large-sized *Megacricetodon* are even more scarce. In the Czech succession of Dolnice 3 to Strakonice, Fejfar (1974) describes *M.* cf. *collongensis* and *M.* aff. *collongensis*, in which a subdivision of anteroconids is not observed. The younger assemblage of *M. bavaricus* from Langenmoosen in the Bavarian 'Obere Süsswassermolasse' (Fahlbusch, 1964) has larger teeth than the above-mentioned Czech *Megacricetodon*, and shows split anteroconids in the M_1. The frequency of subdivided anteroconids and the size of the teeth in Langenmoosen agree more or less with those of the *M. collongensis – crusafonti* transitional assmblage from Las Planas 5B. The younger assemblages (Rosshaupten, Jettingen, Oggenhof) from the Bavarian Molasse, described by Fahlbusch (1964) as *M.* aff. *bavaricus* have larger teeth than *M. bavaricus* from Langenmoosen, but a progressive subdivision of the anteroconid of M_1 is not observed.

M. germanicus from Puttenhausen (Wu Wenyu, 1982) is of considerably larger size than the *M. collongensis – crusafonti* transitional assemblage from Las Planas 5B, but morphologically there are resemblances in M^1, M^2 and M_2. The subdivision of the anteroconid of M_1 is of the same degree as well, but in Puttenhausen the mesolophids are longer and labial and lingual spurs on the anterolophid are frequent. The small assemblages from Rosshaupten, Jettingen and Oggenhof, hitherto named *M.* aff. *bavaricus* fall

in the size and morphology range of *M. germanicus*, and should therefore be named as such.

M. germanicus Aguilar, 1980 from Anwil is more or less of the same size as *M. germanicus* from Southern Germany and *M. gregarius* from La Grive. An important difference among these assemblages is the shape of the anteroconid, mainly deeply split in La Grive, and round to slightly split in Anwil, and bean-shaped to bilobulated in Bavaria. As these localities are generally considered to be of similar age, we don't know the phylogenetic relationships of these species unless further documentation becomes available.

Resuming, it appears that in Central Europe there is an evident trend towards size increase, but trends towards reduction of mesoloph(id)s, reduction of posterosinus and progressive subdivision of the anteroconid are absent (Table 1). As a matter of fact the differences between the Central European *Megacricetodon* assemblages on the one hand and the Southwestern European ones on the other, are such that the Central European ones are better not considered as subspecies of *M. gregarius*. Therefore Aguilar (1980b) described the species from Anwil and Oggenhof as *M. germanicus*.

MEGACRICETODON SPP. FROM ARMANTES 7, VALALTO 2B AND 2C

Freudenthal (1963) described *Cricetodon* sp. from Armantes 7 and pointed at the possible presence of two species, due to the large size variation. However, he could not divide the assemblage into two groups. For the present study more material is available from Armantes 7, thanks to excavations carried out by de Bruijn in 1975.

Two localities near Daroca (Valalto 2B and 2C) revealed a similar inseparable mixture of two species. A detailed analysis was made of these three assemblages, focusing on Armantes 7, for being the richest one of the three.

Description

M_1 — Roughly two size groups can be distinguished (see Fig. 47): a small-sized group of which the length varies between 13.0 and 15.0, and the width varies between 7.5 and 9.2. And a large-sized group with the length varying between 15.0 and 17.5, and widths between 9.2 and 10.8.

Fig. 47 shows that the small-sized group has predominantly simple anteroconids and relatively long mesolophids. The large-sized group has more complicated anteroconids and shorter mesolophids (Fig. 48). The presence of two groups of different morphology and size is evident, although a complete separation is not possible, due to the presence of some intermediate specimens.

M_2 — The large size variation of this element also indicates the presence of two size groups (Fig. 49), of which the small-sized group appears to have relatively longer mesolophids than the other one.

The variation of the lingual anterolophid is more or less similar in both groups. In the small-sized group (length less than 12.0, width less than 10.0) 61 % have no lingual anterolophid, 27 % have a small one, and 12 % have a long one. In the large-sized group 62 % lack this ridge, 34 % have a small one, and 4 % have a long one. The presence of two groups of different size and slightly different dental pattern is obvious, but as in M_1, a complete separation into two groups is not possible.

M_3 — The size variation of this element is relatively large, but it is obvious that a separation into two groups is impossible (Fig. 55). Morphological features warranting a separation are not present either.

M^1 — The existence of two size groups is clear (Fig. 50). The dental pattern of the small-sized group (length less than 16.0, width less than 10.2) shows the following characteristics:
The anterocone is a slightly split cusp, of which the furrow does not reach the anterior border of the molar (Fig. 50). In worn specimens the anterocone takes a bean-shape. Only very few specimens have a deeply split anterocone.
The mesoloph varies between short and long, but the majority have a mesoloph of medium length (Fig. 51).
The posterosinus is well-developed (Fig. 52).
In 9 specimens (out of 106) the anterolophule has a labial spur.

The large-sized group shows the following characteristics:
The anterocone is deeply split with a small transverse cingulum ridge or cusp at the anterior border of the molar (Fig. 50).
The mesoloph is absent, short or of medium length; the short mesoloph predominates (Fig. 51).
The posterosinus is a reduced, tiny valley, or it is even absent (Fig. 52).
Only in 3 specimens out of 131 the anterolophule has a labial spur.

M^2 — The large size variation points at the presence of two groups, although the separation is not clear. The following characteristics are observed in the smaller specimens:
the mesoloph is of medium length or long (Fig. 53);
the sinus is predominantly transverse (Fig. 54);
the posterosinus is a well-developed wide valley.

The larger specimens display the following characteristics:
the mesoloph is on the average short (Fig. 53);
the sinus curves obliquely forward (Fig. 54);
the posterosinus is generally well-developed, but tends to be more reduced than in the smaller specimens.

M^3 — The size variation is quite large, but a separation into two groups is impossible (Fig. 56). Morphological features, warranting a separation, are not present.

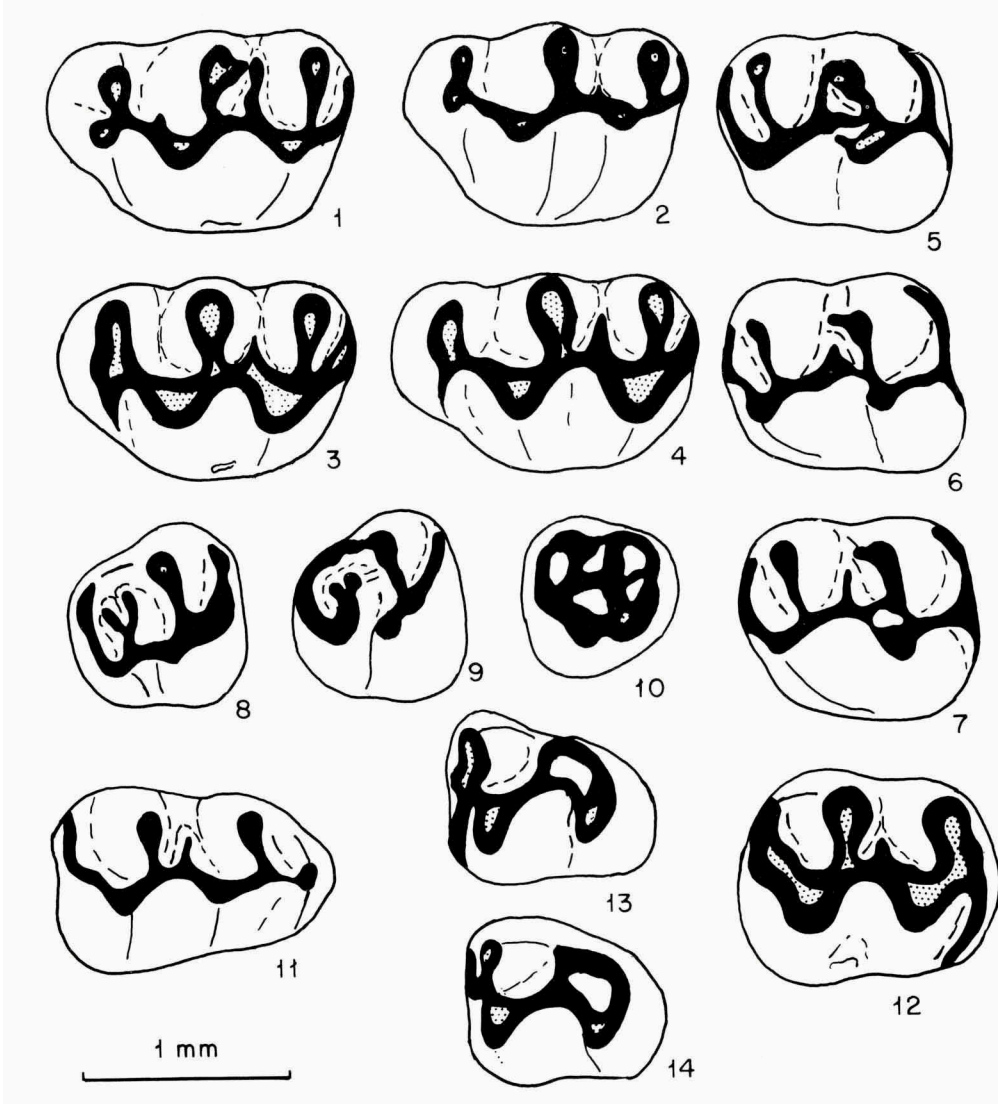
Discussion
It appears that the Armantes 7 material contains two *Megacricetodon* species, which differ in size and dental pattern. The first molars permit a separation of almost all specimens. Two species can be distinguished in the second molars as well, although the size and morphology overlap is larger than in the first molars. The distinction of the third molars is impossible. The size and dental pattern of the large-sized group agree well with those of *M. collongensis – crusafonti* from Las Planas 5B. But the small-sized group does not agree with any known *Megacricetodon* species. It is therefore described as a new species.

Megacricetodon rafaeli sp. nov.
Plate 1.

Holotype — M^1 sin., ARM7 1320, Plate 1, fig. 1.
Type locality — Armantes 7.
Derivatio nominis — *rafaeli* after Mr Rafael Estebán Lorente of Daroca, in recognition of his friendship and help.

Diagnosis — A *Megacricetodon* species of medium size with a slightly split anterocone, a simple anteroconid, relatively long mesoloph(id)s, and a wide posterosinus in M^1 and M^2.

Plate 1



Megacricetodon rafaeli sp. nov. from Armantes 7.

Fig. 1. M^1 sin., cat. no. 1320.
Fig. 2. M^1 sin., cat. no. 1314.
Fig. 3. M^1 sin., cat. no. 1336.
Fig. 4. M^1 sin., cat. no. 1337.
Fig. 5. M^2 dext., cat. no. 1602.
Fig. 6. M^2 dext., cat. no. 1609.
Fig. 7. M^2 dext., cat. no. 1591.
Fig. 11. M_1 dext., cat. no. 1267.
Fig. 12. M_2 dext., cat. no. 1740.

Megacricetodon rafaeli sp. nov. or *M. collongensis – crusafonti* from Armantes 7.

Fig. 8. M^3 dext., cat. no. 2010.
Fig. 9. M^3 dext., cat. no. 2007.
Fig. 10. M^3 sin., cat. no. 2025.
Fig. 13. M_3 dext., cat. no. 1851.
Fig. 14. M_3 sin., cat. no. 1858.

Differential diagnosis
M. rafaeli differs from *M. primitivus* by: its larger size; its slightly split anterocone; the slightly more reduced lingual anterolophid in M_2.

M. rafaeli differs from *M. collongensis* by: the slightly split anterocone of M^1; the longer mesolophids of M_1 and M_2; the somewhat more simple anteroconid of M_1.

Amongst other features *M. rafaeli* differs from *M. crusafonti* and *M. ibericus* by: its smaller size; the shape of the anterocone of M^1; the simple anteroconid of M_1; the longer mesoloph(id)s; the less reduced posterosinus of M^1 and M^2.

M. rafaeli differs from *M. minor* from Sansan by: its somewhat larger size; the shape of the anterocone; the scarcity of labial spurs on the anterolophule of M^1; the protolophule of M^2; in Armantes 7 it is double or simple, in Sansan it is predominantly double.

M. rafaeli differs from *M. debruijni* from Pedregueras 2C by: its somewhat larger size; its simple anteroconid; its longer mesolophids; the transverse sinus of M^2.

M. rafaeli differs from *M. similis* from Giggenhausen by: the longer mesolophids; the lower frequency of M_1 with a slightly split anteroconid; the simple protolophule of M^1; the badly developed labial spur on the anterolophule of M^1.

Discussion
In Valalto 2B and 2C *M. rafaeli* and *M. collongensis – crusafonti* are also present. In Valalto 2B *M. rafaeli* is represented by a few specimens only. *M. collongensis – crusafonti* from this locality agrees with the same transitional stage from Armantes 7. In the rather rich locality of Valalto 2C *M. rafaeli* is represented in the same relative proportions as in Armantes 7. The first molars from Valalto 2C can be separated into two size groups, except for only a few doubtful specimens. For the second molars the separation is more hazardous, and the third molars are inseparable (Fig. 56).

In Borjas a single M^1 with a slightly split anterocone might be attributed to the same group as *M. rafaeli*. Freudenthal (1966) mentions *M. similis* from Nombrevilla, represented by an M^1 and an M^3. We do not consider this poor material to be sufficient to warrant a specific determination.

As far as the anterocone and the size is concerned, *M. rafaeli* shows closest resemblances with *M. similis* from the Bavarian 'Obere Süsswassermolasse'. The former species is found at the base of the Upper Aragonian, and the localities containing *M. similis* are generally considered to belong to the uppermost Upper Aragonian. Anyway, these two species are probably closely related.

The M. rafaeli – similis group outside Spain
Hitherto no reference has been made of this group in French faunas. Bulot (1980) describes *M. primitivus* from Bézian, a fauna that may be correlated to our zone D. However, the species from Bézian does not agree with *M. primitivus* from the Calatayud-Teruel Basin. The teeth of the French form are larger, the mesoloph(id)s are longer and, most important of all, the anterocone is a slightly split cusp morphologically comparable to the anterocone of *M. rafaeli* and *M. similis*. Therefore, we consider the *M. primitivus* from Bézian to be a representative of the *M. rafaeli – similis* group.

The medium-sized *Megacricetodon* sp. from Puttenhausen (Wu Wenyu, 1982), represented by 6 teeth only, may be a representative of the *M. rafaeli – similis* group because of the not deeply split anterocone of M^1.

The medium-sized *M. rafaeli* and *M. similis* are thought to be related to each other because of the shape of the anterocone. The small-sized *M. debruijni* may have a slightly split anterocone as well, but on the other hand many specimens of this species have hardly split or simple anterocones. The *M. primitivus – ibericus* lineage has M^1's with deeply split anterocones, often with a small transverse enamel ridge along the anterior border.

THE *MEGACRICETODON* ASSEMBLAGE FROM SIMANCAS 2

The above-mentioned localities Armantes 7, Valalto 2B and Valalto 2C are not the only ones in which a large *Megacricetodon* is accompanied by one of medium size. García (in Alvarez & García, 1986) described a similar situation from the Upper Aragonian of Simancas 2 (Duero Basin): a larger one classified as a transitional stage between *M. crusafonti* and *M. ibericus*, and a smaller one described as a new species, *M. lopezae* García, 1986. The latter one differs from the first one by its smaller size and by the higher frequency of primitive morphotypes in both upper and lower molars.

In connection with the study of the assemblages from Armantes 7 and Valalto we restudied the material from Simancas 2, and came to results that deviate from the observations by García.Two well-separated size groups are observed in M^1, M_1 and M_2. There are some morphological differences between these two groups as well. In general the smaller species, *M. lopezae*, has relatively longer mesolophids. The smaller specimens of the – not differentiated – M^2 have relatively longer mesolophs than the larger specimens.

The anteroconid of M_1 in *M. lopezae* has the 8-shaped pattern; in the *M. crusafonti – ibericus* material it is X-shaped. García states that simple or slightly split anteroconids are present in *M. lopezae*, but according to our observations such morphotypes are absent. A few specimens in which the anteroconid is worn down to the crown basis do show a relatively simple pattern (slightly constricted), but in our view they are too much worn and they should not be counted in a morphology analysis. Simple anteroconids, as mentioned by García were not found, not even in very worn specimens.

The anterocone of M^1 has the same shape in both species. It is a deeply split cusp with a small transverse ridge at the anterior border of the molar in all specimens. This anterocone type is characteristic of the *M. primitivus – ibericus* lineage. The posterosinus of M^1 is more reduced in the smaller specimens than it is in the larger ones.

In M^2 a separation on the basis of size is not possible. In the smaller specimens the sinus is strongly curved forward, whereas in the larger specimens it is slightly curved forward or transverse.

In summary, *M. lopezae* is a medium-sized *Megacricetodon* species, characterized by a deeply split anterocone in M^1, an 8-shaped anteroconid in M_1, and a sharply curved sinus in M^2.

THE *M. MINOR – DEBRUIJNI* LINEAGE

In this group the same parameters as in the *M. primitivus – ibericus* lineage have been studied. In nearly all cases the same sets of morphotypes have been found, with the exception of the anteroconid of M_1. The reader is referred to the chapter on *M. primitivus – ibericus* for a description of these morphotypes.

Morphotypes anteroconid M_1 / Localities				N	*M.minor*	*M.debruijni*
Pedregueras 2C	23	17		40		+
Pedregueras 2A	6	6		12		+
Carrilanga 1	24	27	3	54		+
Nombrevilla	3	1		4	+	
Solera		1	1	2	+	
Las Planas 5H	2		1	3	+	
Toril	2			2	+	
Alcocer 2		1		1	+	
Villafeliche 9	1			1	+	
Las Planas 5K	1	1		2	+	
Borjas	3	1		4	+	
Manchones 1	10	2		12	+	
Arroyo del Val 6	2			2	+	
Las Planas 5B	5	1		6	+	

Fig. 21. Variation of the anteroconid in M_1 of *M. minor* and *M. debruijni*.

Anteroconid of M_1 (Fig. 21)
Only three morphotypes have been found. The first one is the round, simple anteroconid, the second one is slightly subdivided, and the third one is 8-shaped. Generally the anterolophulid is situated more labially than in the *M. primitivus – ibericus* lineage. Fig. 21 shows, that the simple anteroconid is predominant in *M. minor*, that the slightly subdivided type is common in *M. debruijni*, and that the 8-shaped type is scarcely represented in both species.

Mesolophid of M_1 (Fig. 22)
In *M. minor* long mesolophids are not very common, medium-sized mesolophids are the most frequent. Short mesolophids are common in both species, and specimens without mesolophid predominate in *M. debruijni*.

Miscellaneous features of M_1 (Fig. 23)
In several specimens of *M. debruijni* a short labial spur of the anterolophulid is present. An ectomesolophid is observed in some specimens of *M. minor* and *M. debruijni*.

Lingual anterolophid of M_2 (Fig. 24)
In both species the long lingual anterolophid is scarcely represented; short or absent lingual anterolophids are the common morphotypes.

Mesolophid of M_2 (Fig. 25)
Long mesolophids occur in both species, and medium-sized ones are common in *M. minor*, and in *M. debruijni* from Carrilanga 1. Short mesolophids and specimens without this ridge are common in the other assemblages of *M. debruijni*.

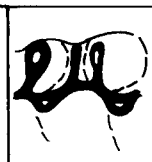
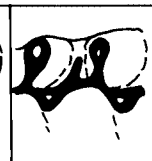
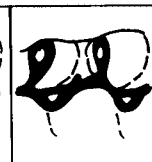
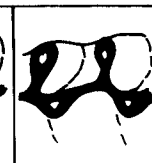
Morphotypes mesolophid M_1 / Localities					N	*M. minor*	*M. debruijni*
Pedregueras 2C			7	32	39		+
Pedregueras 2A		1	10	4	15		+
Carrilanga 1		12	24	28	64		+
Nombrevilla			5	1	6	+	
Solera				2	2	+	
Las Planas 5H		2		2	4	+	
Toril	1		1		2	+	
Alcocer 2				2	2	+	
Villafeliche 9			1		1	+	
Las Planas 5K	1	1			2	+	
Borjas	2	2			4	+	
Manchones 1	1	6	5		12	+	
Arroyo del Val 6		2			2	+	
Las Planas 5B		5		1	6	+	

Fig. 22. Variation of the mesolophid in M_1 of *M. minor* and *M. debruijni*.

Morphotypes M_1 / Localities			*M.minor*	*M.debruijni*
Pedregueras 2C	1	-		+
Pedregueras 2A	2	1		+
Carrilanga 1	-	1		+
Nombrevilla	-	-	+	
Solera	-	-	+	
Las Planas 5H	-	1	+	
Toril	-	-	+	
Alcocer 2	-	-	+	
Villafeliche 9	-	-	+	
Las Planas 5K	-	-	+	
Borjas	-	1	+	
Manchones 1	-	-	+	
Arroyo del Val 6	-	1	+	
Las Planas 5B	-	-	+	

Fig. 23. Variation of the labial spurs of the anterolophulid and ectolophid in M_1 of *M. minor* and *M. debruijni*.

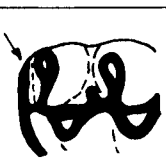
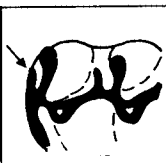
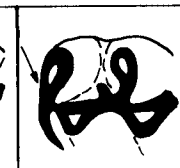
Morphotypes lingual antero-lophid M_2 / Localities				N	*M. minor*	*M. debruijni*
Pedregueras 2C	1	34	9	44		+
Pedregueras 2A		8	14	22		+
Carrilanga 1	2	14	35	51		+
Nombrevilla		2	7	9	+	
Las Planas 5H	1			1	+	
Toril		1	1	2	+	
Las Planas 5K		1	2	3	+	
Borjas	1	2	5	8	+	
Manchones 1	1	2	2	5	+	
Arroyo del Val 6		1	2	3	+	
Las Planas 5B		1	4	5	+	

Fig. 24. Variation of the lingual anterolophid in M_2 of *M. minor* and *M. debruijni*.

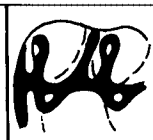
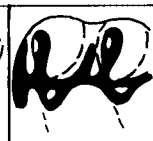
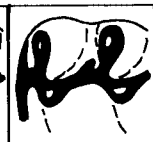
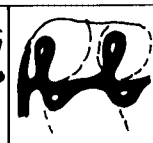
Morphotypes mesolophid M_2 / Localities					N	*M. minor*	*M. debruijni*
Pedregueras 2C		1	4	44	49		+
Pedregueras 2A	2	1	8	12	23		+
Carrilanga 1		18	22	19	59		+
Nombrevilla		2	5	2	9	+	
Las Planas 5H	1				1	+	
Toril			1	1	2	+	
Las Planas 5K		3			3	+	
Borjas	5	3	1	1	10	+	
Manchones 1		3		2	5	+	
Arroyo del Val 6	1	2			3	+	
Las Planas 5B		3	3		6	+	

Fig. 25. Variation of the mesolophid in M_2 of *M. minor* and *M. debruijni*.

Anterocone of M^1 (Fig. 26)

With the exception of 1 specimen from Manchones 1, the simple anterocone is restricted to the Vallesian assemblages. The slightly split anterocone is the most common type in Toril and younger assemblages. The deeply split anterocone is more common in the lower assemblages, and the fourth type (with anterior cingulum ridge) is frequent in Carrilanga 1 only.

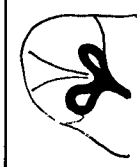
Localities \ Morphotypes anterocone M^1					N	*M. minor*	*M. debruijni*
Pedregueras 2C	5	28	1	1	35		+
Pedregueras 2A	6	7	1		14		+
Carrilanga 1	4	33	31	13	81		+
Nombrevilla	1	6		1	8	+	
Solera				1	1	+	
Las Planas 5H		4			4	+	
Toril		5	2		7	+	
Alcocer 2			2		2	+	
Villafeliche 9						+	
Las Planas 5K			3		3	+	
Borjas		1	2	1	4	+	
Manchones 1	1	6	2		9	+	
Arroyo del Val 6		1	1		2	+	
Las Planas 5B			5		5	+	

Fig. 26. Variation of the anterocone in M^1 of *M. minor* and *M. debruijni*.

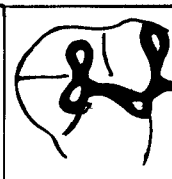
Localities \ Morphotypes labial antero-lophule M^1				N	*M. minor*	*M. debruijni*
Pedregueras 2C		1	39	40		+
Pedregueras 2A		1	15	16		+
Carrilanga 1		8	76	84		+
Nombrevilla			8	8	+	
Solera			1	1	+	
Las Planas 5H	4			4	+	
Toril	3	4	1	8	+	
Alcocer 2			3	3	+	
Las Planas 5K		1	3	4	+	
Borjas		3	1	4	+	
Manchones 1		7	4	11	+	
Arroyo del Val 6		2	1	3	+	
Las Planas 5B		5	1	6	+	

Fig. 27. Variation of the labial spur on the anterolophule in M^1 of *M. minor* and *M. debruijni*.

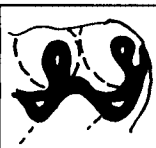
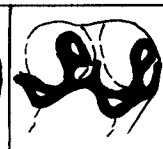
Morphotypes ectoloph M¹ / Localities				N	*M. minor*	*M. debruijni*
Pedregueras 2C	28	11		39		+
Pedregueras 2A	13	2		15		+
Carrilanga 1	42	33	8	83		+
Nombrevilla	4	2	3	9	+	
Solera		1		1	+	
Las Planas 5H	2	1		3	+	
Toril	1	3	4	8	+	
Alcocer 2	2	1	1	4	+	
Las Planas 5K		3	1	4	+	
Borjas	2	4		6	+	
Manchones 1	8	2		10	+	
Arroyo del Val 6	1	1		2	+	
Las Planas 5B		4	1	5	+	

Fig. 28. Variation of the ectoloph in M¹ of *M. minor* and *M. debruijni*.

Labial spur on the anterolophule of M¹ (Fig. 27)
Long labial spurs are only present in Toril and Las Planas 5H, whereas the short ones are more common in the lower assemblages and rare in the higher ones. Specimens without this ridge are more frequent in the Vallesian assemblages.

Ectoloph on the paracone of M¹ (Fig. 28)
This feature is quite variable. In *M. minor* from Manchones and in *M. debruijni* specimens without ectoloph predominate. Specimens with a small ectoloph are present in all assemblages in varying frequencies, and specimens with a large ectoloph are relatively well represented in *M. minor* from Toril.

Sinus of M¹ (Fig. 29)
Three morphotypes are distinguished: transverse, slightly curved forward and strongly curved forward. In both species the first and second type are predominant; the strongly curved sinus is more frequent in *M. debruijni* than it is in *M. minor*.

Mesoloph of M¹ (Fig. 30)
Long mesolophs are more frequent in *M. minor*, and medium-sized ones are common in both species. Specimens with short mesolophs and without mesolophs are more common in *M. debruijni*.

Connection between ectoloph and mesoloph in M¹ (Fig. 31)
In few specimens this connection is present. Generally the mesoloph is well developed (see Fig. 30), but the posterior spur of the paracone is absent or small in most specimens of both species (see Fig. 28).

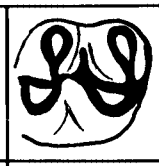
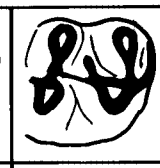
Morphotypes sinus M^1 / Localities				N	*M.minor*	*M.debruijni*
Pedregueras 2C	22	11	6	39		+
Pedregueras 2A	2	8	6	16		+
Carrilanga 1	18	55	12	85		+
Nombrevilla		6	2	8	+	
Solera		1		1	+	
Las Planas 5H	2	2		4	+	
Toril	7	1		8	+	
Alcocer 2		3	1	4	+	
Villafeliche 9					+	
Las Planas 5K	1	2	1	4	+	
Borjas		5		5	+	
Manchones 1	6	3		9	+	
Arroyo del Val 6		3		3	+	
Las Planas 5B	7			7	+	

Fig. 29. Variation of the sinus in M^1 of *M. minor* and *M. debruijni*.

Morphotypes mesoloph M^1 / Localities					N	*M. minor*	*M. debruijni*
Pedregueras 2C	1	17	20	2	40		+
Pedregueras 2A		11	3	2	16		+
Carrilanga 1	3	48	20	2	73		+
Nombrevilla		8	1		9	+	
Solera				1	1	+	
Las Planas 5H	1	2			3	+	
Toril	1	7			8	+	
Alcocer 2		3	1		4	+	
Las Planas 5K		4			4	+	
Borjas	1	4			5	+	
Manchones 1	1	7	1		9	+	
Arroyo del Val 6	1	1	1		3	+	
Las Planas 5B	3	2			5	+	

Fig. 30. Variation of the mesoloph in M^1 of *M. minor* and *M. debruijni*.

Posterosinus of M^1 (Fig. 32)

A wide posterosinus is most common in the Vallesian assemblages, a slightly reduced one, caused by the backward position of the metalophule is the most common morphotype in the Aragonian assemblages. The most reduced type is rare in this lineage.

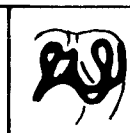
Morphotypes M¹ / Localities				N	*M.minor*	*M.debruijni*
Pedregueras 2C		38	2	40		+
Pedregueras 2A		14	2	16		+
Carrilanga 1	5	66	2	73		+
Nombrevilla	2	6		8	+	
Solera			1	1	+	
Las Planas 5H		4		4	+	
Toril	1	7		8	+	
Alcocer 2		4		4	+	
Las Planas 5K		4		4	+	
Borjas		5		5	+	
Manchones 1	1	8		9	+	
Arroyo del Val 6		3		3	+	
Las Planas 5B	1	6		7	+	

Fig. 31. Variation of the connection between ectoloph and mesoloph in M¹ of *M. minor* and *M. debruijni*.

Morphotypes posterosinus M¹ / Localities				N	*M. minor*	*M. debruijni*
Pedregueras 2C	34	5	1	40		+
Pedregueras 2A	10	4	2	16		+
Carrilanga 1	18	59		77		+
Nombrevilla	6	3		9	+	
Solera			1	1	+	
Las Planas 5H		3		3	+	
Toril	1	7		8	+	
Alcocer 2		3		3	+	
Las Planas 5K	1	3		4	+	
Borjas		5		5	+	
Manchones 1	2	6		8	+	
Arroyo del Val 6	1			1	+	
Las Planas 5B	2	3		5	+	

Fig. 32. Variation of the posterosinus in M¹ of *M. minor* and *M. debruijni*.

Protolophule of M² (Fig. 33)

The anterior protolophule is only present in *M. minor* and the second type (transverse) is relatively more common in *M. minor* than in *M. debruijni*. The third type (posterior transverse) is rare in *M. minor* and better represented in *M. debruijni*. The fourth type with the strongly curved sinus is the predominant type in *M. debruijni* and the fifth one with double protolophule is the most common one in *M. minor*.

Morphotypes protolophule M^2 / Localities						N	*M. minor*	*M. debruijni*
Pedregueras 2C			1	36	3	40		+
Pedregueras 2A			4	13	1	18		+
Carrilanga 1		2	9	59	3	73		+
Nombrevilla	2			1	4	7	+	
Las Planas 5H					1	1	+	
Toril				2	2	4	+	
Las Planas 5K	1	1			2	4	+	
Borjas	2	3		1	3	9	+	
Manchones 1		1			3	4	+	
Arroyo del Val 6			1			1	+	
Las Planas 5B		1			8	9	+	

Fig. 33. Variation of the position of the protolophule in M^2 of *M. minor* and *M. debruijni*.

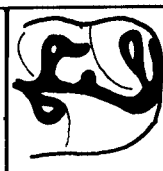
Morphotypes ectoloph M^2 / Localities				N	*M. minor*	*M. debruijni*
Pedregueras 2C	43	4	3	50		+
Pedregueras 2A	11	6	1	18		+
Carrilanga 1	31	36	8	75		+
Nombrevilla	4	1	2	7	+	
Las Planas 5H	1			1	+	
Toril	2	1		3	+	
Las Planas 5K		4		4	+	
Borjas	4	4	2	10	+	
Manchones 1	2	2	1	5	+	
Las Planas 5B	1	4	4	9	+	

Fig. 34. Variation of the ectoloph in M^2 of *M. minor* and *M. debruijni*.

Ectoloph on the paracone of M^2 (Fig. 34)
A well-developed ectoloph is relatively better represented in *M. minor* than in *M. debruijni*, and the small ectoloph is well-represented in both species. Paracones without an ectoloph are relatively more frequent in *M. debruijni*.

Sinus of M^2 (Fig. 35)
The transverse sinus is frequent in *M. minor*, the slightly curved type is rare in both species, and the strongly curved sinus is frequent in *M. debruijni*.

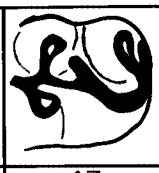
Morphotypes sinus M^2 / Localities				N	*M.minor*	*M.debruijni*
Pedregueras 2C	3		47	50		+
Pedregueras 2A			18	18		+
Carrilanga 1	5	6	64	75		+
Nombrevilla	4		3	7	+	
Las Planas 5H	1			1	+	
Toril		1	2	3	+	
Las Planas 5K	4			4	+	
Borjas	8	1	1	10	+	
Manchones 1	5			5	+	
Arroyo del Val 6	1			1	+	
Las Planas 5B	9			9	+	

Fig. 35. Variation of the sinus in M^2 of *M. minor* and *M. debruijni*.

Morphotypes mesoloph M^2 / Localities					N	*M. minor*	*M. debruijni*
Pedregueras 2C	3	35	1		39		+
Pedregueras 2A	5	11	2		18		+
Carrilanga 1	10	54	6	3	73		+
Nombrevilla	3	4			7	+	
Las Planas 5H	1				1	+	
Toril	1	3			4	+	
Las Planas 5K		4			4	+	
Borjas	4	3		2	9	+	
Manchones 1	1	3			4	+	
Arroyo del Val 6		1			1	+	
Las Planas 5B	2	8			10	+	

Fig. 36. Variation of the mesoloph in M^2 of *M. minor* and *M. debruijni*.

Mesoloph of M^2 (Fig. 36)
Long and medium-sized mesolophs are present in both species, whereas specimens with short mesoloph or without mesoloph are mainly present in *M. debruijni*.

Connection between ectoloph and mesoloph in M^2 (Fig. 37)
In general the ectoloph is not large, and the mesoloph is well developed in both species. As a result the ectoloph and the mesoloph are connected in a small part of the specimens only. This feature presents no differences between *M. minor* and *M. debruijni*.

Localities \ Morphotypes ectoloph ←→ mesoloph M2				N	*M.minor*	*M.debruijni*
Pedregueras 2C	4	46		50		+
Pedregueras 2A		18		18		+
Carrilanga 1	14	56	3	73		+
Nombrevilla	2	5		7	+	
Las Planas 5H		1		1	+	
Toril	1	2		3	+	
Las Planas 5K	2	2		4	+	
Borjas	1	6	2	9	+	
Manchones 1		5		5	+	
Las Planas 5B	2	7		9	+	

Fig. 37. Variation of the connection between ectoloph and mesoloph in M^2 of *M. minor* and *M. debruijni*.

Localities \ Morphotypes metalophule M2						N	*M.minor*	*M.debruijni*
Pedregueras 2C	12	23		1	4	40		+
Pedregueras 2A	2	14		1	1	18		+
Carrilanga 1	27	25	8	3	3	66		+
Nombrevilla	1	4			2	7	+	
Las Planas 5H		1				1	+	
Toril		3			1	4	+	
Las Planas 5K		4				4	+	
Borjas	4	1	1		3	9	+	
Manchones 1	1				3	4	+	
Arroyo del Val 6			1			1	+	
Las Planas 5B	2	8				10	+	

Fig. 38. Variation of the position of the metalophule in M^2 of *M. minor* and *M. debruijni*.

Metalophule of M^2 (Fig. 38)

The transverse and anterior metalophules are well represented in both species. The third type (slightly posterior) is scarce in both species, the fourth type (strongly posterior) occurs only in *M. debruijni* (though in small numbers), and the fifth type (double metalophule) occurs in both species.

Discussion

M. debruijni differs from *M. minor* by the following features:
the slightly subdivided anteroconid of many M_1;
the on the average shorter mesoloph(id)s of M_1, M_2 and M^1;

the less deeply split anterocone of M^1;
the absence of a labial spur on the anterolophule of M^1;
the wider posterosinus of M^1;
the single protolophule of M^2;
the strongly curved sinus of M^1 and M^2.

M. minor differs from *M. primitivus* by:
the presence of M_1's with slightly split anteroconid;
the more reduced lingual anterolophid of M_2;
the better developed labial spur on the anterolophule of M^1;
the more frequent double protolophule of M^2.

M. minor differs from *M. collongensis* by:
its smalller size;
the longer mesolophids of M_1 and M_2;
the better developed labial spur on the anterolophule of M^1;
the more frequent double protolophule of M^2.

The trends of the *M. minor – debruijni* lineage are towards:
slight subdivision of the anteroconid;
reduction of the mesolophids of M_1 and M_2;
simplification of the anterocone of M^1;
reduction of the labial spur on the anterolophule of M^1;
reduction of the mesolophs of M^1 and to a lesser extent of M^2;
widening of the posterosinus of M^1;
strong forward curvature of the sinus of M^2, with the related change of the shape of the protolophule.

The general trend of this lineage is towards a simplification of the dental pattern, which is most apparent in the mesoloph(id)s of M1 and M2. There is no trend in the sizes.

García in Alvarez & García (1986) described *M. freudenthali* from the Lower Vallesian of Ampudia 9 in the Duero Basin. This small-sized *Megacricetodon* species is supposed to differ from *M. debruijni* by the absence of M_1 with divided anteroconid, by the higher frequency of M^1 with simple anterocone and by the higher frequency of long mesoloph(id)s and posteroloph(id)s.

However, our own observations on the type material from Ampudia 9 revealed some contradictions between the description of García and our appreciation of the diagnostic features. In the 5 specimens of M_1 3 have a subdivided anteroconid and 2 have a simple one. Out of 7 M^1, 5 specimens have a slightly subdivided anterocone and 2 represent the simple type. The variation of these two features coincides with that of *M. debruijni*.

As for the length of the mesoloph(id)s it is a fact that in the assemblage from Ampudia 9 these ridges are on the average longer than they are in *M. debruijni* from its type locality Pedregueras 2C. We consider this feature, however, to fall within the range of variation of *M. debruijni*.

The fourth distinctive feature of *M. freudenthali* would be the longer posteroloph(id)s, but it appears that the variation of these ridges is more or less similar to that of *M. debruijni*.

Other characteristic features of *M. debruijni*, such as the length of the lingual anterolophid of M_2, the badly developed ectoloph on the paracone of M^1 and M^2, the

well-developed posterosinus of M^1, the backward pointing metalophule and the strongly proverse sinus of M^2 are also present in *M. freudenthali* in comparable proportions, there are no reasons to consider *M. freudenthali* and *M. debruijni* as two different species. *M. freudenthali* is a junior synonym of *M. debruijni*.

The M. minor – debruijni lineage outside of Spain

Data on this lineage are very scarce outside Spain. Of course it is present in Sansan, the type locality of *M. minor*. The assemblage from Las Planas 5B agrees in all its features with the one from Sansan. Other localities with related forms (*M.* aff. *minor*) are the 'Obere Süsswassermolasse' (Fahlbusch, 1964) and Anwil (Engesser, 1972), but, with the exception of Anwil, *M.* aff. *minor* is too poorly represented to allow a good comparison. The size of the teeth of *M.* aff. *minor* is on the average smaller than that of *M. minor*, but that seems to be the only difference observed hitherto. Faunas with *M. debruijni* are not (yet) known outside Spain.

Daxner (1967) describes *Megacricetodon (Mesocricetodon) minutus* from the Pannonian of Inzersdorf and Brunn-Vösendorf (Austria), characterized by its small size, a slightly split anterocone in M^1, and by a strongly curved sinus in M^1 and M^2. Unfortunately only 2 M^1 and 1 M^2 from these two localities are known, and a good comparison with our Spanish material is impossible. Nevertheless, the features of the three available teeth agree well with those of *M. debruijni* from Pedregueras 2A and 2C. If more material would become available from the Austrian localities and if the size and morphology ranges would coincide with the Spanish species, this might imply that *M. debruijni* and*M. minutus* are synonyms. The publication date of *M. debruijni* is 24-2-1968, that of *M. minutus* May 1968, so *M. minutus* might be a junior synonym of *M. debruijni*.

MEASUREMENTS

Size (Figs. 39, 40, 44-65, Tables 2-9)

Roughly we can make a subdivision into three size groups:

1) Small-sized: *M. primitivus*, *M. collongensis* from zone D, *M. minor*, and *M. debruijni*.
2) Medium-sized: *M. collongensis* from zone E and *M. rafaeli*.
3) Large-sized: *M. collongensis – crusafonti* transitional form, *M. crusafonti*, *M. crusafonti – ibericus* transitional form, *M. ibericus*.

Length/width ratios (Tables 10-12)

For each specimen the ratio length/width was taken, and the average of these ratios per assemblage is given in Tables 10-12. The M_1 of *M. primitivus* and *M. collongensis* appear to be relatively blunt, whereas the M_1 of *M. minor* is on the average more slender. The M_2 of *M. minor* and *M. debruijni* appear to be more slender than the same element in the other species (Table 11). The M_3 of *M. primitivus* and *M. collongensis* is relatively short in comparison with the other species (Table 12). The length/width ratios of the upper molars give less results, and therefore the distribution tables for these parameters are omitted. It may be mentioned that the M^3 of *M. primitivus* is relatively short.

Length/width ratios may be obtained in one of two different ways. The first one is the one mentioned above. The second one is simply dividing the average length of each element by the average width. In some cases the results of these two methods coincide more or less, but in several assemblages the results are strongly different. Deviations of up to 20 % may occur. Therefore we consider the second method insufficiently reliable.

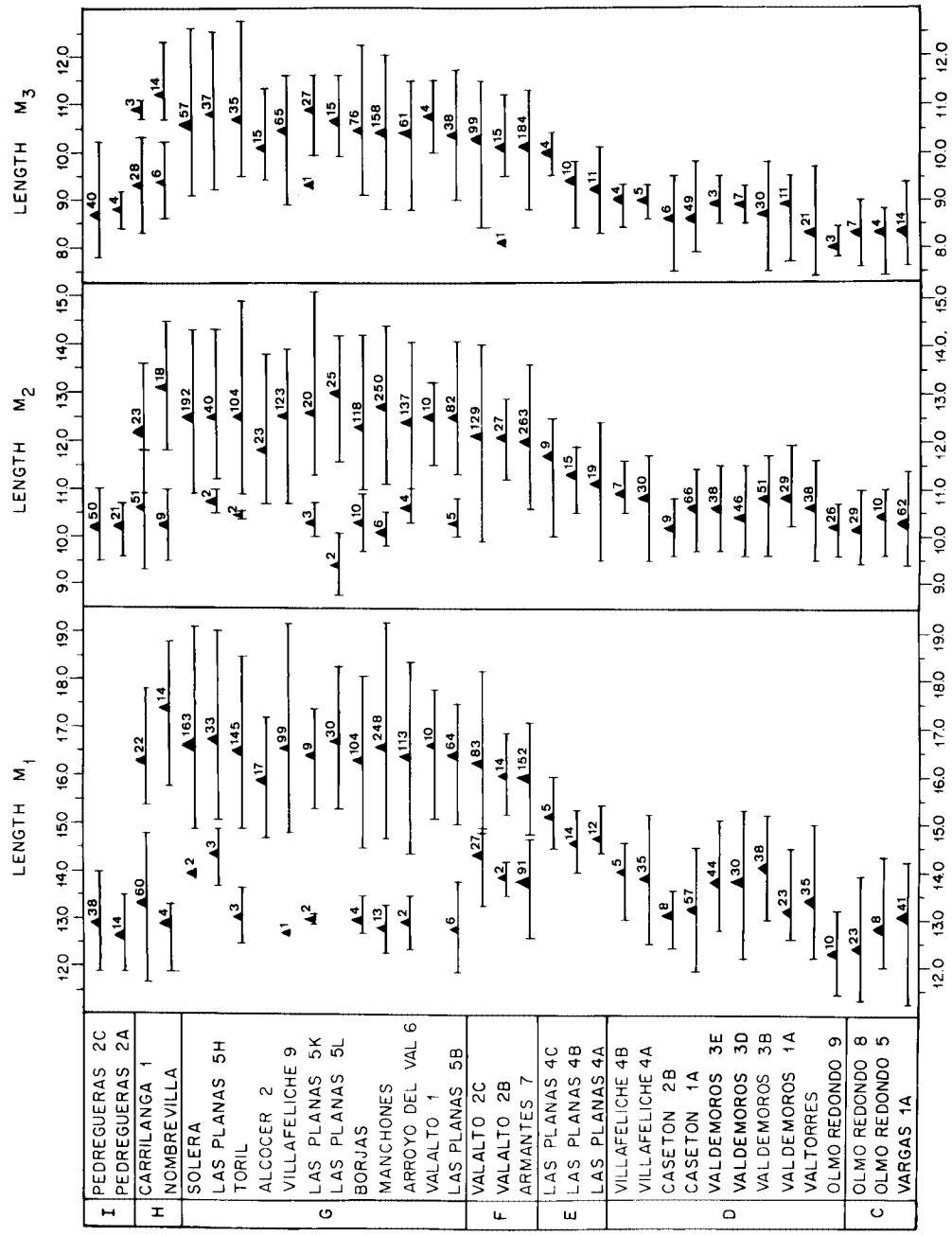


Fig. 39. Distribution of the length ranges of the lower molars of the *M. primitivus – M. ibericus* lineage, of *M. rafaeli* and of the *M. minor – M. debruijni* lineage.

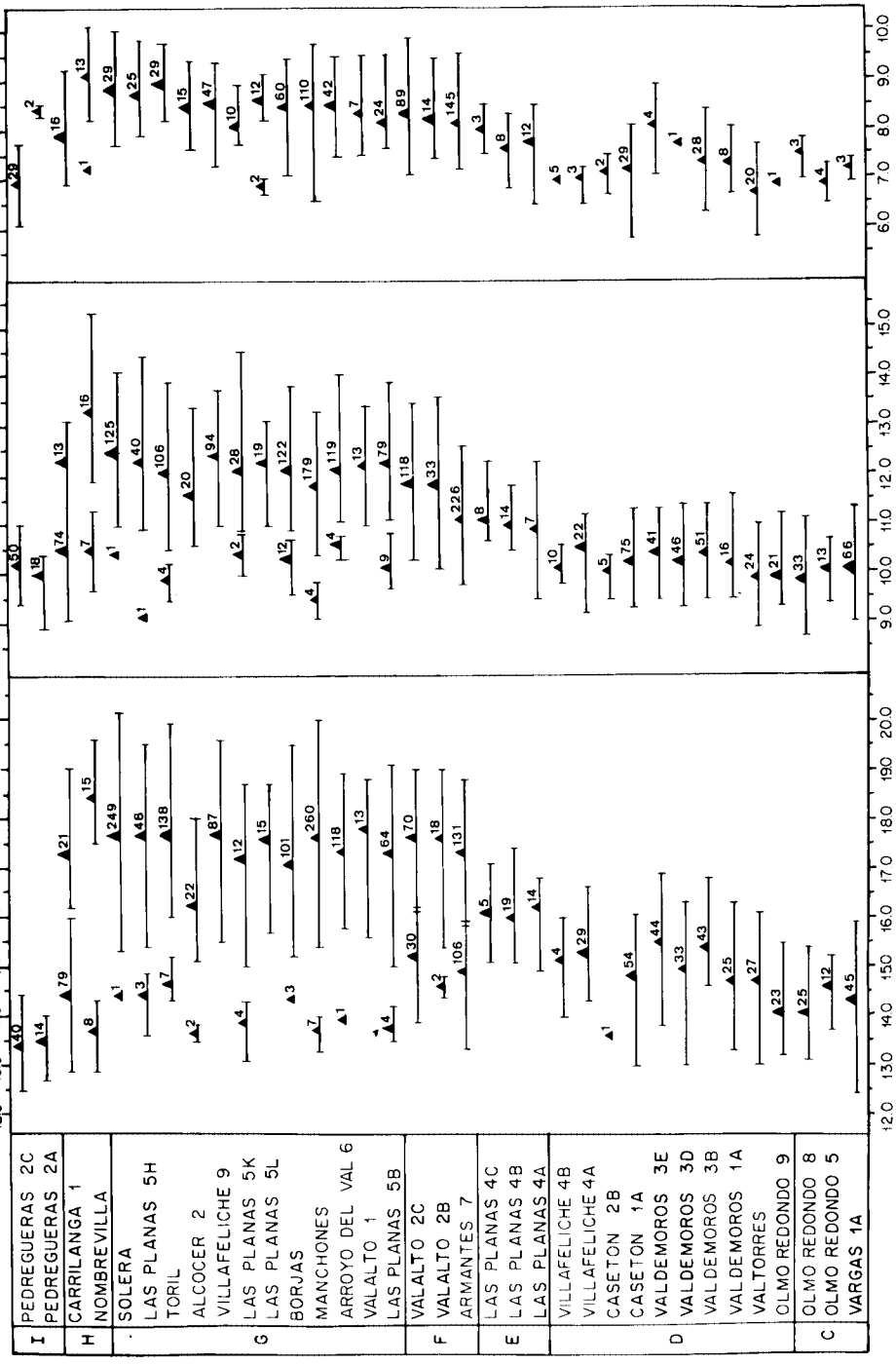


Fig. 40. Distribution of the length ranges of the upper molars of the *M. primitivus* – *M. ibericus* lineage, of *M. rafaeli* and of the *M. minor* – *M. debruijni* lineage.

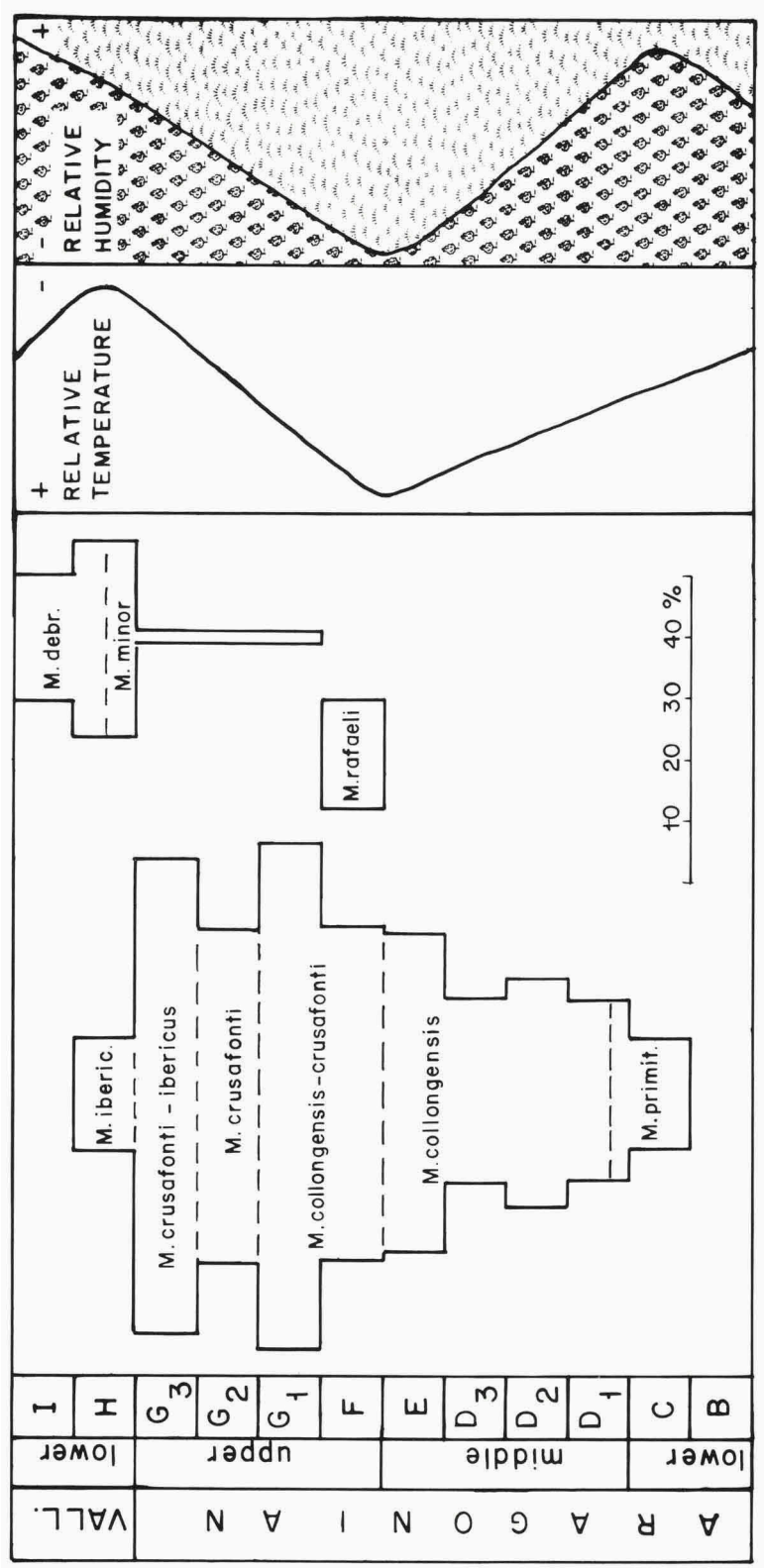


Fig. 41. Relative abundance – in percentages of the total rodent fauna – of the *Megacricetodon* species in the Aragonian-Lower Vallesian of the Daroca-Calamocha-Bañón area in the Calatayud-Teruel Basin.

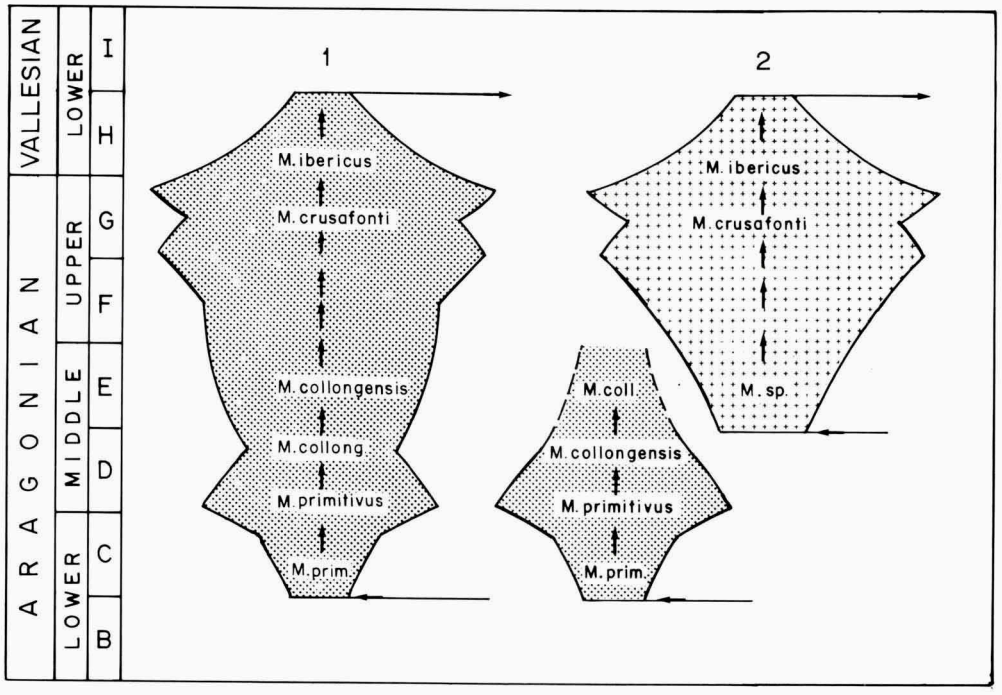


Fig. 42. The two hypotheses of the evolution of the *M. primitivus – M. ibericus* lineage; 1: the continuous line; 2: the line interrupted by a hypothetical immigrant.

Biogeography

Freudenthal (1965) compared extensively the Spanish, French and Bavarian *Megacricetodon* species, and mentioned the differences in size and morphological trends between the assemblages of the various geographic areas. The much more abundant material available now permits us to shed some more light on the evolution of this group.

In the lower levels of the Aragonian *M. collongensis* is present in all three areas and does not present significant differences between one area and another. In the following level (zone E) *M. bavaricus* is significantly different from *M. collongensis* from Spain. *M. gersii* from the South of France (zone G) is similar to the *M. collongensis – crusafonti* transitional assemblages from zone F and the lower part of zone G, but it differs considerably from *M. germanicus* in Central Europe.

M. gersii and *M. collongensis – crusafonti* are also very different from *M. collongensis* from zone D. For Spain we suggested the possibility of the entry, during the time interval covered by zone E (and perhaps zone F), of an immigrant that would gradually substitute *M. collongensis*. It is not impossible that this process took place in Central Europe and the South of France as well. During the above-mentioned time interval more migrations took place in Spain, such as the entry of *Cricetodon* (zone E), *Paraglirulus werenfelsi* (zone E), *M. rafaeli* (zone F),and *M. minor* (zone G).

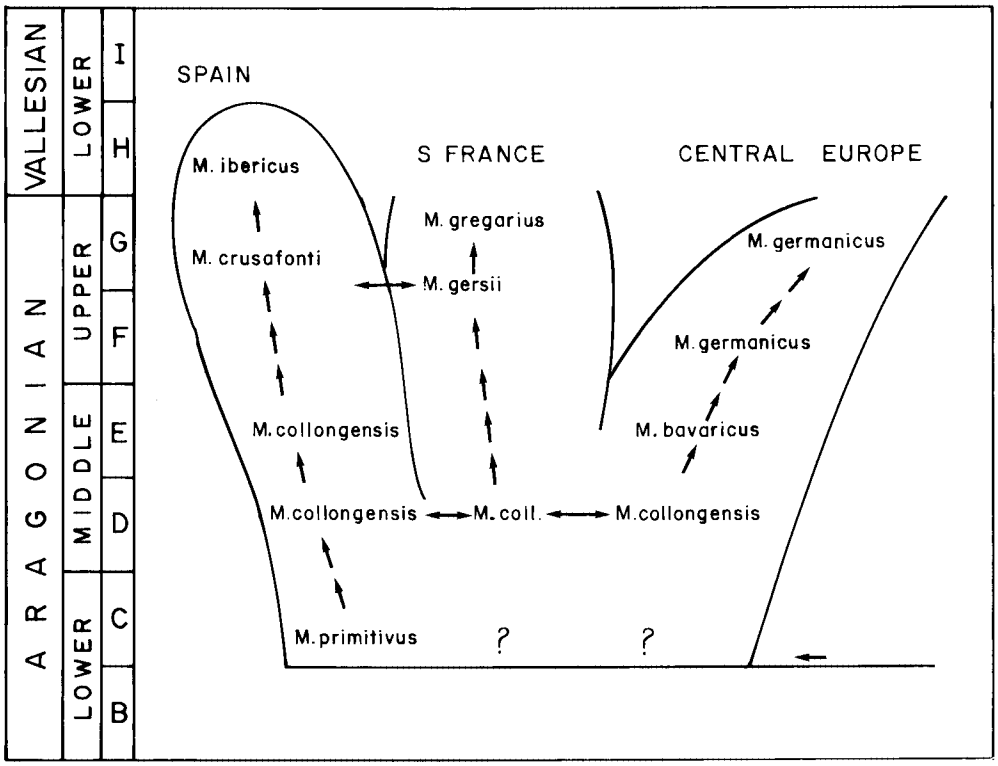


Fig. 43. Supposed phylogenetical relationships among various *Megacricetodon* species in the Miocene of Europe.

During the Late Aragonian the differences between the various areas became more pronounced. The Central European *Megacricetodon* associations differ considerably from the Spanish-French ones. This is not only true for the large-sized lineage, but also for *M. minor* from Spain and Southern France on the one hand, and *M.* aff. *minor* from Central Europe on the other. During the same time interval the differences between Spanish *Megacricetodon* associations on the one hand and Southern French ones on the other, is of minor importance (Fig. 43).

Paleoecological interpretation

M. primitivus is an immigrant into Spain in the Early Aragonian (zone C). Its immigration coincides with those of *Fahlbuschia* and *Eumyarion* and with a considerable increase of the Eomyidae. *M. primitivus* is not present in large numbers (14-29 %, Table 13). This period has been interpreted (Daams & van der Meulen, 1984) as being more humid than the preceding interval (zone B) and the next one (zone D). According to the same authors the temperature increased from zone B, through C and D to E.

In zone D *Megacricetodon* is more abundant and it is associated with large amounts of *Fahlbuschia*. *Heteroxerus* is common and *Pseudodryomys simplicidens*, *Microdyromys*

and *Armantomys* are commonly present as well. This period is supposed to be a dry and relatively warm interval (Daams & van der Meulen, 1984).

A major turn-over of the accompanying fauna seems to take place in the Las Planas 4 localities (zone E). Immigrants at this level are *Cricetodon* and *Paraglirulus*, though in low numbers. *Heteroxerus* is represented by three species, *Microdyromys koenigswaldi* is replaced by *M. monspeliensis* (Daams, 1981) and *Pseudodryomys simplicidens* is absent in the faunas beyond zone D. The size of the teeth of *M. collongensis* from Las Planas 4A, 4B and 4C is larger than that of the same species from zone D. Moreover some elements (M_2, M^1, M^2) show a relatively large size variation, suggesting a possible heterogeneity, although the low number of observations does not permit a decision on this point. Daams & van der Meulen (1984) considered this interval the warmest and driest period in the Aragonian/Vallesian succession of micromammals, in which *Megacricetodon* is by far the most abundant rodent.

The following group of faunas (Valalto 2B, 2C and Armantes 7) consists mainly of *Megacricetodon* as well. In these assemblages a heterogeneity of the material is conspicuous in M^1 and M_1 on the basis of size and morphology. The heterogeneity of this *Megacricetodon* material has been the only reason to distinguish between zone E and zone F. There is a great resemblance in the composition of the faunas from these two zones. In zone F *Heteroxerus* is also represented by three species and *Paraglirulus* and *Cricetodon* are also present in low numbers. Zone E has been correlated with the Langhian (Steininger & Rögl, 1983), which has been interpreted by other authors as having been a tropical period.

The basis of zone G has been defined by Daams & Freudenthal (1981) by the entry of *M. minor*, though this species is scarcely represented. The faunas are dominated by the larger *Megacricetodon* lineage. Differences with the preceding zone are the presence of Gliridae species such as *Myomimus dehmi*, *Muscardinus thaleri*, *Myoglis meini*, *Eliomys truci* and in some faunas Eomyidae are present (*Eomyops catalaunicus*). *Cricetodon* is more abundant than before. This period has been interpreted as being slightly more humid and during this time a decrease of the temperature is supposed to have taken place (Daams & van der Meulen, 1984). These trends would have persisted until the close of the Vallesian.

The Lower Vallesian faunas contain less *Megacricetodon* than the Upper Aragonian ones. *Myomimus dehmi* is a common rodent and other differences are the result of evolutionary trends in the *Cricetodon – Hispanomys* lineage and in the *Muscardinus thaleri – hispanicus* lineage (Daams, 1985). In Carrilanga 1 the representative of the *Megacricetodon* lineage of small size (*M. debruijni*) is more abundant than the large *Megacricetodon* (*M. ibericus*). This phenomenon has not been observed in the preceding zone. The two Pedregueras localities only contain *M. debruijni*, and *M. ibericus* is absent. The climatic trends continue being towards lower temperatures and increased humidity.

It appears that the evolutionary trends of both lineages of *Megacricetodon* are independent of ecological and climatic fluctuations. As for the habitat preference of our numerous *Megacricetodon* assemblages conclusions are hazardous. *Megacricetodon* enters into Spain in a relatively wet period, but it is most abundant in the relatively dry and warm periods. Perhaps the large *Megacricetodon* has preferred higher temperatures and had no special preference for humid or dry habitat.

The small *Megacricetodon* may have been different in this aspect. *M. minor* is the most common cricetid in the fauna of Sansan, while *M. gersii* is rather scarce. Sansan contains a fauna from a humid and tropical climate (Daams & van der Meulen, 1984).In Spain the small *Megacricetodon* (*M. debruijni*) dominates in the localities of Carrilanga 1 and Pedregueras 2A and 2C. These are supposed to represent a wet climate because of

the presence of Castoridae and of *Muscardinus hispanicus*. Perhaps the representatives of the *Megacricetodon* lineage of small size have favoured relatively moist biotopes. This interpretation would coincide with the climatic trends in the Late Vallesian and Turolian. The Upper Vallesian is void of *Megacricetodon*, and from the Late Vallesian onwards there is a trend again towards a drier climate (López et al., 1987).

The habitat preference of *M. rafaeli* is more questionable. Its acme is in zone F, one possible specimen is present in Borjas and one in Nombrevilla. This species is an immigrant into Spain during or just after the greatest warmth in a dry climate, and it disappears nearly completely when the trends towards lower temperature and wetter climate begin.

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Table 1. Comparison of evolutionary trends and significant dental features of the *M. primitivus* – *M. ibericus* lineage and related species from Spain, France and Central Europe.

Evolutionary trends and dental features	Spain	France	Centr. Europe
size increase	present in zones C to F afterwards absent	present	present
subdivision of anteroconid in M_1	very prominent	prominent	weak
reduction mesoloph(id)s	very prominent	prominent	weak
reduction lingual anterolophid in M_2	generally weak, but prominent in upper levels	?	?
loss of labial spur on anterolophule M^1	present	?	?
reduction posterosinus in $M^{1,2}$	prominent	prominent	weak
trend towards proverse sinus in $M^{1,2}$	prominent	prominent	weak
double metalophule M^2	frequent in zones F and G	?	absent
ectoloph on paracone in $M^{1,2}$	well-represented	well-represented	weak

Local biozonation																			N	*M. primitivus*	*M. collongensis*	*M. rafaeli*	*M. collongensis-crusafonti*	*M. crusafonti*	*M. crusafonti-ibericus*	*M. ibericus*	*M. minor*	*M. debruijni*
I	Pedregueras 2C		1	10	18	4	3	2											38									+
I	Pedregueras 2A		1	5	5	2	1												14									+
H	Carrilanga 1		4	2	10	21	12	8	3	2	3	10	4	2	1				84							+		+
H	Nombrevilla		1	1	1	1					1	1	2	4	3	2	1		18							+	+	
G	Solera						1	1	3	12	19	38	35	25	17	10	3	1	165					+		+		
G	Las Planas 5H						1	1	2	2	3	12	1	8	1	2	2	1	36						+		+	
G	Toril				1	1	1		1	7	13	28	35	16	4	2	2		111					+		+		
G	Alcocer 2								2	4	4	2	1	4					17						+			
G	Villafeliche 9				1				2	4	10	28	28	21	3	2		1	100						+		+	
G	Las Planas 5K				1	1				1	1	3	2	2					11					+			+	
G	Las Planas 5L									3	1	11	3	5	5	2			30					+			+	
G	Borjas				2	1	1		4	7	20	30	24	12	5	2			108				+			+		
G	Manchones 1			1	9	2	1		5	17	38	65	45	41	26	6	4	1	261					+			+	
G	Arroyo del Val 6			1			1	2	2	9	19	37	22	16	4	1			114					+			+	
G	Valalto 1									1		4	2	1	2				10				+					
G	Las Planas 5B		1	1	2	1	1			6	9	14	20	14	1				70				+				+	
F	Valalto 2C					1	3	13	13	10	25	19	19	13		2	1		119		+	+						
F	Valalto 2B						2			5	3	5	1						16		+	+						
F	Armantes 7				5	20	27	36	13	26	41	49	27	7					251		+	+						
E	Las Planas 4C							1	1	1	1	1							5		+							
E	Las Planas 4B							6	6	2									14		+							
E	Las Planas 4A							3	2	5	2								12		+							
D	Villafeliche 4B				1			3	1										5		+							
D	Villafeliche 4A				4	9	8	8	4	2									35		+							
D	Casetón 2B			1	2	4	1												8		+							
D	Casetón 1A		1	5	12	23	11	4	1										57		+							
D	Valdemoros 3E				2	12	13	13	3	1									44		+							
D	Valdemoros 3D			1		8	11	7	2	1									30		+							
D	Valdemoros 3B				2	3	12	12	7	2									38		+							
D	Valdemoros 1A				11	8	3	1											23	+								
D	Valtorres			3	9	8	5	5	4	1									35	+								
D	Olmo Redondo 9	1	3	1	3	2													10	+								
C	Olmo Redondo 8	1	5	7	6	2	2												23	+								
C	Olmo Redondo 5			1	5	1		1											8	+								
C	Vargas 1A	1	1	6	9	7	15	2											41	+								
			12.0		13.0		14.0		15.0		16.0		17.0		18.0		19.0											

Table 2. Numerical histogram of the length of M_1 of *Megacricetodon* from the Aragonian and Lower Vallesian of the Calatayud-Daroca area.

Local biozonation	Locality															N	*M. primitivus*	*M. collongensis*	*M. rafaeli*	*M. collongensis-crusafonti*	*M. crusafonti*	*M. crusafonti-ibericus*	*M. ibericus*	*M. minor*	*M. debruijni*
I	Pedregueras 2C		1	9	18	12										40									+
	Pedregueras 2A			4	12	5										21									+
H	Carrilanga 1		1	2	13	22	14	10	5	2	4	1				74							+		+
	Nombrevilla		1		1	6	1	2	2	3	4	4	2	1		27							+	+	
G	Solera					1	12	28	46	49	41	13	2			192					+				
	Las Planas 5H					3	5	6	8	6	6	7	1			42						+		+	
	Toril				1	2	2	14	41	44	19		2	1		106					+		+		
	Alcocer 2					4	6	4	4	2	1	2				23						+			
	Villafeliche 9					2	1	12	35	45	21	7				123						+			
	Las Planas 5K				1	3	2	2	2	7	3	2			1	23					+			+	
	Las Planas 5L	1			1			2	2	9	9		3			27					+			+	
	Borjas			2	4	5	8	28	38	27	12	3	1			128				+			+		
	Manchones 1			3	2	1	8	20	71	94	39	16	3			257					+			+	
	Arroyo del Val 6				1	3	7	19	56	34	16	6	1			144					+			+	
	Valalto 1							1	3	5	1					10				+					
	Las Planas 5B				4	1	3	7	28	26	11	2	1			87				+				+	
F	Valalto 2C			1	1	2	21	26	25	29	20	3	1			129			+	+					
	Valalto 2B						3	8	11	5						27			+	+					
	Armantes 7				4	23	50	34	45	55	28	4				243			+	+					
E	Las Planas 4C				1		1	3	2	2						9		+							
	Las Planas 4B					4	6	5								15		+							
	Las Planas 4A		1		2	1	6	6	3							19		+							
D	Villafeliche 4B					5	1	1								7		+							
	Villafeliche 4A			3	2	12	11	2								30		+							
	Casetón 2B			3	3	3										9		+							
	Casetón 1A			5	13	35	13									66		+							
	Valdemoros 3E			2	13	16	6	1								38		+							
	Valdemoros 3D			4	21	17	3	1								46		+							
	Valdemoros 3B			3	5	24	18	1								51		+							
	Valdemoros 1A				7	17	4	1								29	+								
	Valtorres		1	6	5	15	5	6								38	+								
	Olmo Redondo 9			8	8	10										26	+								
C	Olmo Redondo 8		2	8	11	7	1									29	+								
	Olmo Redondo 5			1	4	3	2									10	+								
	Vargas 1A		1	17	21	18	5									62	+								

Scale: 9.0 10.0 11.0 12.0 13.0 14.0 15.0

Table 3. Numerical histogram of the length of M_2 of *Megacricetodon* from the Aragonian and Lower Vallesian of the Calatayud-Daroca area.

Local biozonation														N	*M. primitivus*	*M. collongensis*	*M. rafaeli*	*M. collongensis-crusafonti*	*M. crusafonti*	*M. crusafonti-ibericus*	*M. ibericus*	*M. minor*	*M. debruijni*
I	Pedregueras 2C		1	7	8	2	1	1						20									+
	Pedregueras 2A			1	1	2								4									+
H	Carrilanga 1			3	5	8	8	4	1	2				31							+		+
	Nombrevilla				1	2	2	1	6	4	1	3		20							+	+	
G	Solera					2	6	14	20	11	3		1	57				+		+			
	Las Planas 5H					1	3	10	10	5	6		2	37					+		+		
	Toril						3	13	14	9	4		2	35				+		+			
	Alcocer 2					2	7		3	3				15					+		+		
	Villafeliche 9				1	2	8	16	27	9	2			65					+		+		
	Las Planas 5K					5	4	5	6	3	2		2	27				+			+		
	Las Planas 5L						1	4	7	2	1			15				+			+		
	Borjas					4	7	26	23	11	2	3		76				+		+			
	Manchones 1				3	9	24	36	63	20	2	1		158				+			+		
	Arroyo del Val 6				1	2	11	17	21	8	1			61				+			+		
	Valalto 1							1	2		1			4				+			+		
	Las Planas 5B					4	6	13	8	5	2			38				+			+		
F	Valalto 2C			1	1	2	15	40	24	16	1			100			+	+					
	Valalto 2B			1			6	5	2	2				16			+	+					
	Armantes 7				3	9	48	75	42	9	1			187			+	+					
E	Las Planas 4C						1	3						4		+							
	Las Planas 4B			1		5	6							12		+							
	Las Planas 4A			1	2	2	2	1						8		+							
D	Villafeliche 4B			1		3								4		+							
	Villafeliche 4A				2	3								5		+							
	Casetón 2B		1		3		1							5		+							
	Casetón 1A		1	11	22	9	6							49		+							
	Valdemoros 3E				2		1							3		+							
	Valdemoros 3D				3	4								7		+							
	Valdemoros 3B	1		7	12	9	1							30		+							
	Valdemoros 1A		1	2	2	6								11	+								
	Valtorres	2	5	5	7	1	1							21	+								
	Olmo Redondo 9		2	1										3	+								
C	Olmo Redondo 8		2	3	1	1								7	+								
	Olmo Redondo 5	1		1	2									4	+								
	Vargas 1A		5	3	5	1								14	+								
			8.0		9.0		10.0		11.0		12.0												

Table 4. Numerical histogram of the length of M_3 of *Megacricetodon* from the Aragonian and Lower Vallesian of the Calatayud-Daroca area.

Local biozonation																			N	*M. primitivus*	*M. collongensis*	*M. rafaeli*	*M. collongensis-crusafonti*	*M. crusafonti*	*M. crusafonti-ibericus*	*M. ibericus*	*M. minor*	*M. debruijni*
I	Pedregueras 2C	3	7	10	14	5													39									+
I	Pedregueras 2A		1	3	8	2													14									+
H	Carrilanga 1		1	5	15	21	19	13	4	3	6	5	5	2		1			100							+		+
H	Nombrevilla				3	1	1		1				4	6	1	2	2		21							+	+	
G	Solera					1		2	10	13	34	41	43	70	21	11	2		250					+		+		
G	Las Planas 5H				1		2	1	1	5	7	6	8	6	8	4	2		51						+		+	
G	Toril					4	1	2		7	28	21	34	24	17	1	6		145					+		+		
G	Alcocer 2			1	1		1	4	3	8	1	3	2						23						+		+	
G	Villafeliche 9								1	4	15	15	14	20	14	2	2		87						+		+	
G	Las Planas 5K					3		2			2	3	3	2	1				16					+			+	
G	Las Planas 5L								1	1	3	1	2	5	2				15					+			+	
G	Borjas					3		2	8	16	13	29	23	5	2	2	1		104				+			+		
G	Manchones 1			1	5	1		2	7	29	29	39	66	44	32	10	1	1	267					+			+	
G	Arroyo del Val 6				1					12	15	17	41	16	11	6			119					+			+	
G	Valalto 1								1			2	4	3	3				13				+				+	
G	Las Planas 5B				3	1		4		5	10	15	9	13	6	2			68				+				+	
F	Valalto 2C				1	4	6	7	9	6	7	19	18	12	4	1			94			+	+					
F	Valalto 2B						1		2	1	4	4	4	1	3				20			+	+					
F	Armantes 7			1	1	18	31	40	18	7	28	36	39	10	7				244			+	+					
E	Las Planas 4C							2		1		2							5		+							
E	Las Planas 4B					1		8	3	4	1	3							20		+							
E	Las Planas 4A						1	2	1	6	7	2		1	1				21		+							
D	Villafeliche 4B					1		3	2	5	2								13		+							
D	Villafeliche 4A					1	7	8	10	2	1								29		+							
D	Casetón 2B				1														1		+							
D	Casetón 1A			3	2	9	18	16	3	3									54		+							
D	Valdemoros 3E				1	3	10	10	7	7	6								44		+							
D	Valdemoros 3D			2	1	3	9	9	7	2									33		+							
D	Valdemoros 3B						8	17	15	3	1								44		+							
D	Valdemoros 1A			2	3	6	7	8		1									27	+								
D	Valtorres		1		1	6	8	7	1	1									25	+								
D	Olmo Redondo 9			4	8	7	3	1											23	+								
C	Olmo Redondo 8		1	5	5	7	5	2											25	+								
C	Olmo Redondo 5				1	3	5	3											12	+								
C	Vargas 1A	1		1	12	13	14	3	1										45	+								
		12.0		13.0		14.0		15.0		16.0		17.0		18.0		19.0		20.0										

Table 5. Numerical histogram of the length of M[1] of *Megacricetodon* from the Aragonian and Lower Vallesian of the Calatayud-Daroca area.

Local biozonation	Locality															N	*M. primitivus*	*M. collongensis*	*M. rafaeli*	*M. collongensis-crusafonti*	*M. crusafonti*	*M. crusafonti-ibericus*	*M. ibericus*	*M. minor*	*M. debruijni*
I	Pedregueras 2C	1	11	24	11	1										48									+
	Pedregueras 2A	1		3	14											18									+
H	Carrilanga 1		4	7	33	17	10	5	5	5	1					87							+		+
	Nombrevilla				2	3	1	1	2	2	4	3	3		1	22							+	+	
G	Solera				1		8	22	27	33	28	6	1			126					+		+		
	Las Planas 5H		1			4	4	5	7	11	6	1	1	1		41						+		+	
	Toril			2	2	7	11	28	30	19	9	2				110					+		+		
	Alcocer 2					4	6	2	6	1	1					20						+			
	Villafeliche 9						3	21	25	27	16	2				94						+			
	Las Planas 5K				2	4	2	10	2	5	1	2	1	1		30					+			+	
	Las Planas 5L						2	3	5	7	2					19					+				
	Borjas			2	4	7	13	35	41	20	11	1				134				+			+		
	Manchones 1		1	3	3	9	40	67	41	18	1					183					+			+	
	Arroyo del Val 6				2	3	14	37	34	28	6	1	1			128					+			+	
	Valalto 1						1	2	7	2	1					13				+					
	Las Planas 5B			1	6	2	9	12	25	25	7	1				88				+				+	
F	Valalto 2C				1	12	20	28	28	22	6	1				118			+	+					
	Valalto 2B				1	3	1	11	13	2	1	1				33			+	+					
	Armantes 7			5	15	47	39	47	42	23	5					223			+	+					
E	Las Planas 4C					5	2		1							8		+							
	Las Planas 4B					8	5	1								14		+							
	Las Planas 4A		1	1		7	4		2							15		+							
D	Villafeliche 4B			7	3	3										13		+							
	Villafeliche 4A		1		8	8	5									22		+							
	Casetón 2B			2	3											5		+							
	Casetón 1A		1	16	33	20	5									75		+							
	Valdemoros 3E			6	19	13	3									41		+							
	Valdemoros 3D		4	9	20	9	4									46		+							
	Valdemoros 3B		1	9	14	21	6									51		+							
	Valdemoros 1A		1	4	7	2	1	1								16	+								
	Valtorres	2	4	8	6	1	1									22	+								
	Olmo Redondo 9		5	8	4	3	1									21	+								
C	Olmo Redondo 8	5	3	12	8	3	2									33	+								
	Olmo Redondo 5		1	4	5	3										13	+								
	Vargas 1A		9	16	26	13	2									66	+								
		9.0		10.0		11.0		12.0		13.0		14.0		15.0											

Table 6. Numerical histogram of the length of M2 of *Megacricetodon* from the Aragonian and Lower Vallesian of the Calatayud-Daroca area.

Local biozonation												N	*M. primitivus*	*M. collongensis*	*M. rafaeli*	*M. collongensis-crusafonti*	*M. crusafonti*	*M. crusafonti-ibericus*	*M. ibericus*	*M. minor*	*M. debruijni*
I	Pedregueras 2C			3	10	10	2	3	1			29									+
	Pedregueras 2A							1	1			2									+
H	Carrilanga 1				1	2	6	3	2	2		16							+		+
	Nombrevilla					2	1	2	3	4	3	16							+	+	
G	Solera						2	5	10	9	2	29					+		+		
	Las Planas 5H						1	7	10	5	2	25						+		+	
	Toril							5	10	9	5	29					+		+		
	Alcocer 2						4	4	2	5		15						+		+	
	Villafeliche 9					1	2	17	17	10		47						+		+	
	Las Planas 5K						5	2	3			10					+			+	
	Las Planas 5L				1	1		4	7	1		14					+			+	
	Borjas					3	5	17	20	13		58				+			+		
	Manchones 1				2	2	14	30	41	21	1	111					+			+	
	Arroyo del Val 6					7	16	11	5	3		42					+			+	
	Valalto 1						2	2	2		1	7				+				+	
	Las Planas 5B						7	7	9	7	1	24				+				+	
F	Valalto 2C					1	16	29	28	13	2	89			+	+					
	Valalto 2B					1	5	1	5	2		14			+	+					
	Armantes 7			1		6	40	50	37	7	2	143			+	+					
E	Las Planas 4C						1	1	1			3		+							
	Las Planas 4B				1	3	1	3				8		+							
	Las Planas 4A			1	1	1	3	5	1			12		+							
D	Villafeliche 4B				1	4						5		+							
	Villafeliche 4A				1	2						3		+							
	Casetón 2B				1		1					2		+							
	Casetón 1A	1			7	14	6	1				29		+							
	Valdemoros 3E					1	1		2	1		5		+							
	Valdemoros 3D						1					1		+							
	Valdemoros 3B			2	6	8	4					20		+							
	Valdemoros 1A				2	2	3	1				8	+								
	Valtorres	1		4	10	4	1					20	+								
	Olmo Redondo 9				1							1	+								
C	Olmo Redondo 8					1	2					3	+								
	Olmo Redondo 5				2	2						4	+								
	Vargas 1A				1	2						3	+								
		6.0			7.0			8.0			9.0			10.0								

Table 7. Numerical histogram of the length of M^3 of *Megacricetodon* from the Aragonian and Lower Vallesian of the Calatayud-Daroca area.

Table 8. Measurements of the *Megacricetodon primitivus – ibericus* lineage and *M. rafaeli* in the Aragonian and Lower Vallesian of the Daroca-Calatayud area.

M_1	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Carrilanga 1	22	15.4	16.3	17.8	24	8.7	10.0	11.1	*iber.*
Nombrevilla	19	15.8	17.3	18.6	20	9.8	10.7	11.8	*iber.*
Solera	163	14.8	16.6	19.1	175	8.4	10.4	11.6	*crus.–iber.*
Las Planas 5H	33	14.9	16.7	19.0	41	8.9	10.1	11.8	*crus.–iber.*
Toril	108	14.9	16.5	18.5	145	9.0	10.2	11.8	*crus.–iber.*
Alcocer 2	17	14.7	15.9	17.2	28	7.8	9.7	10.9	*crus.–iber.*
Villafeliche 9	99	14.8	16.5	19.2	107	8.8	10.1	11.5	*crus.–iber.*
Las Planas 5K	9	15.3	16.4	17.4	10	8.8	9.5	10.1	*crus.*
Las Planas 5L	30	15.3	16.7	18.3	31	9.1	10.1	11.7	*crus.*
Borjas	104	14.5	16.3	18.1	118	8.3	9.8	11.4	*crus.*
Manchones 1	238	14.7	16.6	19.2	238	8.7	10.0	11.8	*crus.*
Arroyo del Val 6	113	14.4	16.4	18.4	113	8.6	9.9	11.6	*crus.*
Valalto 1	10	15.1	16.6	17.8	11	9.5	10.4	10.8	*coll.–crus.*
Las Planas 5B	64	15.0	16.4	17.5	79	8.7	9.8	10.8	*coll.–crus.*
Valalto 2C	27	13.3	14.3	14.9	30	8.0	8.9	9.4	*raf.*
Valalto 2C	83	14.8	16.2	18.2	99	8.9	10.1	11.1	*coll.–crus.*
Valalto 2B	2	13.8	13.9	13.9	2	8.5	8.6	8.6	*raf.*
Valalto 2B	14	15.0	15.7	16.5	20	9.1	9.4	11.2	*coll.–crus.*
Armantes 7	57	12.9	13.8	14.7	62	7.7	8.7	9.7	*raf.*
Armantes 7	119	14.8	16.0	17.4	118	9.0	9.8	10.8	*coll.–crus.*
Las Planas 4C	5	14.4	15.5	16.0	9	8.0	9.2	10.4	*coll.*
Las Planas 4B	14	14.0	14.6	15.3	15	8.4	9.2	9.8	*coll.*
Las Planas 4A	11	14.1	14.9	15.8	11	8.4	9.4	10.2	*coll.*
Villafeliche 4B	5	13.0	14.0	14.6	5	8.4	8.7	9.1	*coll.*
Villafeliche 4A	35	12.5	13.8	15.2	43	7.8	8.7	9.7	*coll.*
Casetón 2B	8	12.4	13.0	13.6	10	7.7	8.1	8.9	*coll.*
Casetón 1A	57	11.9	13.2	14.5	63	7.6	8.4	9.1	*coll.*
Valdemoros 3E	44	12.8	13.8	15.1	48	7.9	8.8	9.8	*coll.*
Valdemoros 3D	30	12.2	13.7	15.3	35	7.0	8.6	9.9	*coll.*
Valdemoros 3B	38	13.0	14.1	15.2	36	8.1	8.9	9.6	*coll.*
Valdemoros 1A	22	12.6	13.2	14.5	22	7.9	8.6	9.1	*prim.*
Valtorres	36	12.2	13.4	15.0	36	7.4	8.6	9.8	*prim.*
Olmo Redondo 9	10	11.4	12.3	13.2	16	7.4	8.1	8.8	*prim.*
Olmo Redondo 8	23	11.3	12.4	13.9	30	6.9	8.0	9.0	*prim.*
Olmo Redondo 5	8	12.0	12.9	14.3	13	7.5	8.3	9.2	*prim.*
Vargas 1A	41	11.2	13.1	14.2	51	6.9	8.2	9.2	*prim.*

M_2	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Carrilanga 1	23	10.9	12.2	13.6	23	9.6	10.3	11.3	*iber.*
Nombrevilla	18	11.8	13.1	14.5	18	9.9	11.0	12.5	*iber.*
Solera	192	10.9	12.5	14.3	192	8.9	10.6	11.8	*crus.–iber.*
Las Planas 5H	41	10.6	12.5	14.3	51	8.7	10.3	11.9	*crus.–iber.*
Toril	124	10.9	12.5	14.9	134	9.1	10.4	11.9	*crus.–iber.*
Alcocer 2	23	10.7	11.8	13.8	29	8.6	10.0	11.7	*crus.–iber.*
Villafeliche 9	123	10.7	12.6	13.9	121	9.1	10.4	11.7	*crus.–iber.*
Las Planas 5K	20	10.6	12.6	15.1	23	8.9	10.3	11.6	*crus.*
Las Planas 5L	25	11.7	12.9	14.2	26	9.8	10.5	11.3	*crus.*
Borjas	118	10.7	12.3	14.2	124	8.9	10.1	11.9	*crus.*
Manchones 1	250	11.1	12.7	14.4	250	9.0	10.5	11.9	*crus.*
Arroyo del Val 6	137	11.0	12.4	14.1	137	9.2	10.3	11.6	*crus.*
Valalto 1	10	11.5	12.5	13.2	11	9.7	10.3	10.9	*coll.–crus.*
Las Planas 5B	82	11.3	12.5	14.1	87	9.0	10.1	11.2	*coll.–crus.*

M_2 continued	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Valalto 2C	129	9.9	12.2	14.0	141	8.1	9.9	11.3	*coll.–crus.* + *raf.*
Valalto 2B	27	11.2	12.1	12.9	33	8.8	10.0	11.0	*coll.–crus.* + *raf.*
Armantes 7	263	10.6	12.0	13.6	263	7.8	9.9	11.3	*coll.–crus.* + *raf.*
Las Planas 4C	9	10.0	11.7	12.5	11	8.4	9.3	10.2	*coll.*
Las Planas 4B	15	10.5	11.3	11.9	15	8.8	9.4	9.8	*coll.*
Las Planas 4A	19	9.5	11.3	12.4	20	8.8	9.5	10.4	*coll.*
Villafeliche 4B	7	10.5	10.9	11.6	7	9.0	9.4	9.8	*coll.*
Villafeliche 4A	30	9.5	10.8	11.7	31	7.9	9.0	9.8	*coll.*
Casetón 2B	9	9.6	10.2	10.8	9	7.8	8.6	9.2	*coll.*
Casetón 1A	66	9.7	10.6	11.4	67	7.9	8.8	9.5	*coll.*
Valdemoros 3E	38	9.7	10.6	11.5	39	7.8	8.7	9.3	*coll.*
Valdemoros 3D	46	9.6	10.4	11.5	44	7.9	8.6	9.5	*coll.*
Valdemoros 3B	51	9.6	10.8	11.7	50	8.4	9.2	10.0	*coll.*
Valdemoros 1A	29	10.2	10.8	11.9	29	8.1	9.0	9.8	*prim.*
Valtorres	38	9.5	10.6	11.6	39	8.1	9.5	10.1	*prim.*
Olmo Redondo 9	26	9.6	10.2	10.7	29	7.7	8.4	8.9	*prim.*
Olmo Redondo 8	29	9.4	10.2	11.0	38	7.4	8.3	9.0	*prim.*
Olmo Redondo 5	10	9.6	10.5	11.0	10	8.1	8.6	9.2	*prim.*
Vargas 1A	62	9.4	10.3	11.4	62	7.6	8.6	9.6	*prim.*

M_3	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Carrilanga 1	3	10.7	10.9	11.1	3	8.9	9.3	9.8	*iber.*
Nombrevilla	14	10.7	11.2	12.3	14	8.4	9.3	9.8	*iber.*
Solera	57	9.1	10.6	12.6	57	7.5	8.9	10.3	*crus.–iber.*
Las Planas 5H	35	9.7	10.9	12.5	43	7.5	8.7	10.2	*crus.–iber.*
Toril	45	9.5	10.8	12.7	47	7.7	8.7	10.2	*crus.–iber.*
Alcocer 2	15	9.4	10.2	11.3	17	7.6	8.5	9.4	*crus.–iber.*
Villafeliche 9	65	8.9	10.5	11.6	68	7.6	8.6	9.6	*crus.–iber.*
Las Planas 5K	18	10.0	10.9	12.8	18	7.5	8.9	10.8	*crus.*
Las Planas 5L	15	9.9	10.7	11.6	14	7.9	8.7	9.2	*crus.*
Borjas	71	9.1	10.5	12.2	82	7.2	8.6	9.9	*crus.*
Manchones 1	158	8.8	10.4	12.0	158	7.0	8.6	10.1	*crus.*
Arroyo del Val 6	61	8.8	10.4	11.5	58	7.4	8.6	9.8	*crus.*
Valalto 1	4	10.0	10.8	11.5	5	8.9	9.2	9.7	*coll.–crus.*
Las Planas 5B	35	9.2	10.4	11.7	36	7.8	8.7	9.9	*coll.–crus.*
Valalto 2C	99	8.4	10.4	11.5	111	7.3	8.4	10.2	*coll.–crus.* + *raf.*
Valalto 2B	15	9.5	10.2	11.2	16	7.4	8.3	8.9	*coll.–crus.* + *raf.*
Armantes 7	184	8.8	10.1	11.3	184	7.2	8.1	9.7	*coll.–crus.* + *raf.*
Las Planas 4C	4	9.5	10.0	10.4	5	7.1	7.9	8.4	*coll.*
Las Planas 4B	10	8.4	9.4	9.8	10	7.3	7.9	8.3	*coll.*
Las Planas 4A	11	8.3	9.2	10.1	12	7.4	7.9	8.4	*coll.*
Villafeliche 4B	4	8.4	9.0	9.3	4	7.4	7.5	7.6	*coll.*
Villafeliche 4A	5	8.6	9.0	9.3	5	7.3	7.7	8.0	*coll.*
Casetón 2B	5	7.5	8.7	9.5	5	6.7	7.3	8.3	*coll.*
Casetón 1A	49	7.9	8.8	9.8	49	6.4	7.4	8.8	*coll.*
Valdemoros 3E	3	8.5	8.9	9.5	5	7.0	7.7	8.0	*coll.*
Valdemoros 3D	7	8.5	8.9	9.3	6	7.1	7.4	7.7	*coll.*
Valdemoros 3B	30	7.5	8.7	9.8	31	6.3	7.4	7.9	*coll.*
Valdemoros 1A	11	7.7	8.9	9.5	11	6.8	7.7	8.3	*prim.*
Valtorres	21	7.4	8.3	9.7	21	6.3	7.4	8.6	*prim.*
Olmo Redondo 9	3	7.8	8.0	8.4	3	6.6	6.8	7.1	*prim.*
Olmo Redondo 8	7	7.6	8.3	9.0	7	6.7	7.1	7.4	*prim.*
Olmo Redondo 5	4	7.4	8.3	8.8	5	6.6	7.1	7.5	*prim.*
Vargas 1A	14	7.6	8.4	9.4	15	6.5	7.1	8.0	*prim.*

M^1	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Carrilanga 1	21	16.2	17.3	19.0	21	9.6	11.0	12.3	*iber.*
Nombrevilla	15	17.5	18.4	19.6	16	9.9	11.3	13.1	*iber.*
Nombrevilla	1	—	15.0	—	0	—	—	—	*sim.*
Solera	249	15.3	17.7	20.2	249	9.1	11.2	13.1	*crus.–iber.*
Las Planas 5H	48	15.4	17.7	19.6	60	9.3	11.0	12.5	*crus.–iber.*
Toril	138	16.0	17.7	19.9	158	9.5	11.2	12.8	*crus.–iber.*
Alcocer 2	23	14.9	16.3	18.0	35	8.8	10.1	12.0	*crus.–iber.*
Villafeliche 9	87	15.5	17.7	19.6	102	10.0	11.2	12.5	*crus.–iber.*
Las Planas 5K	13	15.0	17.2	18.7	17	9.6	10.9	12.0	*crus.*
Las Planas 5L	15	15.7	17.6	18.7	16	9.6	11.1	12.3	*crus.*
Borjas	1	—	15.2	—	1	—	9.2	—	*sim.*
Borjas	101	15.2	17.1	19.5	115	9.2	10.8	12.8	*crus.*
Manchones 1	260	15.4	17.6	20.0	260	9.4	11.0	12.6	*crus.*
Arroyo del Val 6	118	15.7	17.4	19.0	118	9.3	10.9	12.7	*crus.*
Valalto 1	13	15.6	17.8	18.8	13	10.7	11.4	12.2	*coll.–crus.*
Las Planas 5B	64	15.0	17.4	19.3	77	8.9	10.9	12.1	*coll.–crus.*
Valalto 2C	30	13.9	15.2	16.2	43	8.9	9.7	10.6	*raf.*
Valalto 2C	70	16.1	17.6	19.0	96	9.8	11.2	12.1	*coll.–crus.*
Valalto 2B	2	14.8	15.2	15.6	4	9.2	9.8	10.3	*raf.*
Valalto 2B	18	15.5	17.4	18.9	27	9.6	10.9	12.1	*coll.–crus.*
Armantes 7	105	13.4	15.2	15.9	105	8.9	9.5	10.2	*raf.*
Armantes 7	137	15.8	17.3	18.9	137	9.9	11.0	12.5	*coll.–crus.*
Las Planas 4C	5	15.1	16.1	17.2	8	8.9	10.2	11.2	*coll.*
Las Planas 4B	19	15.1	16.0	17.4	20	9.1	10.2	11.2	*coll.*
Las Planas 4A	24	14.9	16.7	18.7	23	9.5	10.3	11.5	*coll.*
Villafeliche 4B	4	14.1	15.0	16.0	4	9.4	9.7	10.2	*coll.*
Villafeliche 4A	29	14.3	15.4	16.6	34	8.5	9.5	10.3	*coll.*
Casetón 2B	1	—	13.6	—	1	—	8.6	—	*coll.*
Casetón 1A	54	13.0	14.8	16.4	61	8.2	9.2	10.4	*coll.*
Valdemoros 3E	44	13.8	15.4	16.9	54	8.6	9.7	10.7	*coll.*
Valdemoros 3D	33	13.0	15.0	16.3	46	8.2	9.3	10.6	*coll.*
Valdemoros 3B	43	14.6	15.4	16.8	43	8.5	9.6	10.5	*coll.*
Valdemoros 1A	25	13.3	14.7	16.3	27	8.0	9.0	9.7	*prim.*
Valtorres	27	13.0	14.7	16.1	27	8.1	9.2	10.0	*prim.*
Olmo Redondo 9	24	13.2	14.0	15.5	29	8.1	8.8	9.6	*prim.*
Olmo Redondo 8	25	12.9	14.0	15.4	31	8.1	8.9	10.0	*prim.*
Olmo Redondo 5	12	13.7	14.6	15.2	14	8.3	9.1	10.0	*prim.*
Vargas 1A	45	12.4	14.3	15.9	66	7.9	9.0	10.2	*prim.*

M^2	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Carrilanga 1	13	11.4	12.3	13.1	14	9.7	10.9	11.5	*iber.*
Nombrevilla	16	11.9	13.3	15.3	15	9.8	11.1	12.3	*iber.*
Solera	125	10.6	12.4	14.1	125	9.8	10.9	11.9	*crus.–iber.*
Las Planas 5H	40	10.5	12.3	14.5	40	9.0	10.4	11.6	*crus.–iber.*
Toril	106	10.5	12.1	13.9	108	9.1	10.6	12.3	*crus.–iber.*
Alcocer 2	20	10.6	11.7	13.4	19	8.9	10.0	10.9	*crus.–iber.*
Villafeliche 9	94	11.0	12.4	13.7	92	9.4	10.7	11.8	*crus.–iber.*
Las Planas 5K	27	10.2	12.1	14.5	26	8.0	10.6	12.4	*crus.*
Las Planas 5L	19	11.0	12.3	13.1	20	9.7	10.6	11.5	*crus.*
Borjas	122	10.9	12.1	13.8	123	9.4	10.6	12.0	*crus.*
Manchones 1	179	10.4	11.8	13.3	179	9.2	10.7	12.3	*crus.*
Arroyo del Val 6	119	11.1	12.1	14.0	118	9.2	10.6	12.0	*crus.*
Valalto 1	13	11.0	12.2	13.4	12	10.0	10.9	12.4	*coll.–crus.*
Las Planas 5B	79	11.1	12.3	13.9	74	8.9	10.6	11.8	*coll.–crus.*
Valalto 2C	118	10.3	11.9	13.5	121	9.0	10.5	11.6	*coll.–crus.* + *raf.*

M^2 continued	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Valalto 2B	33	10.1	11.9	13.6	32	9.3	10.4	11.3	*coll.–crus.* + *raf.*
Armantes 7	226	9.8	11.1	12.6	226	8.8	10.3	11.5	*coll.–crus.* + *raf.*
Las Planas 4C	8	10.7	11.1	12.3	6	9.0	9.6	10.3	*coll.*
Las Planas 4B	14	10.5	11.0	11.8	13	9.1	9.8	10.2	*coll.*
Las Planas 4A	14	9.5	11.0	12.3	13	8.1	9.8	10.6	*coll.*
Villafeliche 4B	10	9.8	10.1	10.6	10	8.9	9.2	9.6	*coll.*
Villafeliche 4A	22	9.2	10.5	11.2	22	8.7	9.3	10.4	*coll.*
Casetón 2B	5	9.5	10.0	10.4	5	8.7	9.1	9.5	*coll.*
Casetón 1A	75	9.3	10.3	11.3	74	7.9	9.1	10.3	*coll.*
Valdemoros 3E	41	9.5	10.4	11.3	38	8.2	8.9	9.7	*coll.*
Valdemoros 3D	46	9.3	10.2	11.4	47	8.0	9.0	10.7	*coll.*
Valdemoros 3B	52	9.5	10.4	11.4	55	8.4	9.4	10.2	*coll.*
Valdemoros 1A	16	9.5	10.2	11.6	17	8.4	9.4	10.2	*prim.*
Valtorres	24	8.9	9.9	11.0	22	8.0	9.0	9.8	*prim.*
Olmo Redondo 9	21	9.3	9.9	11.2	22	7.7	8.6	9.5	*prim.*
Olmo Redondo 8	33	8.7	9.8	11.1	34	8.0	8.7	9.5	*prim.*
Olmo Redondo 5	13	9.4	10.1	10.7	15	7.7	8.8	9.8	*prim.*
Vargas 1A	66	9.0	10.1	11.3	64	8.1	8.9	9.6	*prim.*

M^3	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Carrilanga 1	1	—	9.2	—	1	—	9.0	—	*iber.*
Nombrevilla	13	8.2	9.1	10.1	13	8.2	9.2	10.2	*iber.*
Solera	29	7.7	8.9	10.0	29	7.8	8.8	9.7	*crus.–iber.*
Las Planas 5H	25	7.9	8.7	9.8	26	7.6	8.6	9.4	*crus.–iber.*
Toril	29	8.2	9.0	9.7	30	8.0	8.8	9.9	*crus.–iber.*
Alcocer 2	15	7.6	8.5	9.4	15	7.2	8.5	9.6	*crus.–iber.*
Villafeliche 9	47	7.3	8.6	9.4	47	7.7	8.7	9.7	*crus.–iber.*
Las Planas 5K	10	7.7	8.1	8.9	8	7.8	8.2	8.5	*crus.*
Las Planas 5L	12	8.2	8.6	9.1	11	7.8	8.5	9.7	*crus.*
Borjas	60	7.1	8.5	9.4	60	7.5	8.5	9.9	*crus.*
Manchones 1	110	6.8	8.5	9.7	110	7.4	8.5	10.2	*crus.*
Arroyo del Val 6	42	7.5	8.5	9.5	40	7.5	8.6	9.7	*crus.*
Valalto 1	7	7.5	8.3	9.5	7	8.0	8.6	9.2	*coll.–crus.*
Las Planas 5B	6	7.6	8.3	9.5	6	8.0	8.8	9.6	*coll.–crus.*
Valalto 2C	89	7.1	8.4	9.8	87	7.3	8.4	9.3	*coll.–crus.* + *raf.*
Valalto 2B	14	7.4	8.3	9.4	14	7.9	8.5	9.2	*coll.–crus.* + *raf.*
Armantes 7	145	7.2	8.2	9.5	145	7.1	8.4	9.5	*coll.–crus.* + *raf.*
Las Planas 4C	3	7.5	8.0	8.5	3	7.9	8.0	8.1	*coll.*
Las Planas 4B	8	6.8	7.6	8.3	7	7.2	7.7	8.4	*coll.*
Las Planas 4A	12	6.5	7.7	8.5	11	7.1	7.8	8.3	*coll.*
Villafeliche 4B	5	6.9	7.0	7.0	5	7.2	7.6	8.0	*coll.*
Villafeliche 4A	3	6.5	7.0	7.2	3	6.6	6.9	7.1	*coll.*
Casetón 2B	2	6.7	7.1	7.5	2	—	7.5	—	*coll.*
Casetón 1A	29	5.8	7.1	8.1	28	6.9	7.5	8.1	*coll.*
Valdemoros 3E	5	7.1	8.3	9.4	5	7.6	8.4	9.3	*coll.*
Valdemoros 3D	1	—	7.7	—	1	—	7.4	—	*coll.*
Valdemoros 3B	28	6.3	7.3	8.4	28	6.8	7.7	8.6	*coll.*
Valdemoros 1A	8	6.7	7.3	8.1	8	7.4	7.8	8.3	*prim.*
Valtorres	20	5.8	6.7	7.7	20	6.8	7.5	8.0	*prim.*
Olmo Redondo 9	1	—	6.9	—	1	—	7.5	—	*prim.*
Olmo Redondo 8	3	7.0	7.5	7.8	3	7.5	7.8	8.1	*prim.*
Olmo Redondo 5	4	6.5	6.9	7.3	4	7.0	7.5	8.0	*prim.*
Vargas 1A	5	6.9	7.2	7.4	5	7.1	7.5	7.9	*prim.*

Table 9. Measurements of *Megacricetodon minor* and *M. debruijni* from the Upper Aragonian and Lower Vallesian of the Daroca-Calatayud area.

M_1	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Pedregueras 2C	40	11.9	12.8	14.0	40	7.1	7.8	8.9	*debruijni*
Pedregueras 2A	14	11.9	12.6	13.5	16	7.3	7.7	8.0	*debruijni*
Carrilanga 1	60	11.7	13.3	14.8	64	7.4	8.3	9.2	*debruijni*
Nombrevilla	5	11.9	12.8	13.3	6	7.7	8.2	8.5	*minor*
Solera	2	13.9	14.0	14.0	2	8.5	8.8	9.1	*minor*
Las Planas 5H	3	13.7	14.2	14.7	3	7.8	8.6	9.2	*minor*
Toril	3	12.5	13.2	13.6	3	7.7	7.9	8.2	*minor*
Villafeliche 9	1	—	12.7	—	1	—	7.8	—	*minor*
Las Planas 5K	2	12.9	13.0	13.1	2	7.6	7.7	7.8	*minor*
Borjas	4	12.7	13.0	13.5	4	7.3	7.6	7.9	*minor*
Manchones 1	10	12.3	12.8	13.3	10	7.8	8.0	8.5	*minor*
Arroyo del Val 6	3	12.4	13.1	13.7	4	7.4	7.8	8.2	*minor*
Las Planas 5B	6	11.9	12.8	13.8	6	7.3	7.7	8.1	*minor*

M_2	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Pedregueras 2C	50	9.5	10.2	11.0	50	7.4	8.2	9.0	*debruijni*
Pedregueras 2A	21	9.6	10.2	10.7	22	7.6	8.2	8.6	*debruijni*
Carrilanga 1	51	9.3	10.7	11.8	53	7.7	8.6	9.3	*debruijni*
Nombrevilla	9	9.5	10.5	11.0	9	7.9	8.3	8.8	*minor*
Las Planas 5H	1	—	10.5	—	1	—	7.7	—	*minor*
Toril	2	10.4	10.5	10.5	2	—	8.4	—	*minor*
Las Planas 5K	3	10.0	10.4	10.7	3	7.9	8.4	9.7	*minor*
Las Planas 5L	2	8.8	9.5	10.1	2	—	7.9	—	*minor*
Borjas	10	9.7	10.3	10.9	9	7.7	8.0	8.3	*minor*
Manchones 1	6	9.8	10.1	10.5	6	8.3	8.7	9.1	*minor*
Arroyo del Val 6	4	10.3	10.6	11.0	4	8.5	8.8	9.3	*minor*
Las Planas 5B	5	10.0	10.3	10.8	6	7.7	7.9	8.1	*minor*

M_3	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Pedregueras 2C	40	7.8	8.7	10.2	40	6.1	6.9	7.4	*debruijni*
Pedregueras 2A	4	8.4	8.8	9.2	3	6.8	7.0	7.1.	*debruijni*
Carrilanga 1	28	8.3	9.3	10.3	27	6.8	7.7	9.0	*debruijni*
Nombrevilla	6	8.6	9.4	10.2	6	6.9	7.5	8.3	*minor*
Las Planas 5H	2	9.2	9.5	9.7	2	7.2	7.4	7.6	*minor*
Las Planas 5K	2	—	9.3	—	2	7.3	7.6	7.8	*minor*
Las Planas 5B	3	9.0	9.1	9.3	3	6.9	7.2	7.5	*minor*

M^1	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Pedregueras 2C	40	12.5	13.4	14.4	40	7.9	8.5	9.0	*debruijni*
Pedregueras 2A	14	12.7	13.5	14.0	15	8.0	8.6	9.0	*debruijni*
Carrilanga 1	79	12.9	14.4	16.0	84	8.2	9.3	10.2	*debruijni*
Nombrevilla	8	12.9	13.7	14.3	9	8.5	8.7	9.2	*minor*
Solera	1	—	14.3	—	1	—	9.3	—	*minor*
Las Planas 5H	4	13.6	14.4	15.4	4	8.3	8.8	9.4	*minor*
Toril	7	14.2	14.6	15.2	8	8.1	9.2	9.8	*minor*
Alcocer 2	2	13.2	13.5	13.8	2	8.4	8.7	9.0	*minor*
Las Planas 5K	3	14.0	14.1	14.3	4	8.1	8.4	8.8	*minor*
Borjas	3	14.3	14.4	14.4	5	8.1	8.8	9.2	*minor*
Manchones 1	7	13.3	13.7	14.0	7	8.1	8.6	9.0	*minor*
Arroyo del Val 6	1	—	13.9	—	3	7.8	8.6	9.0	*minor*
Las Planas 5B	4	13.5	13.7	14.2	4	8.1	8.5	8.8	*minor*

M^2	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Pedregueras 2C	50	9.4	10.2	11.0	50	8.0	8.7	9.5	*debruijni*
Pedregueras 2A	18	8.9	10.0	10.4	18	8.0	8.8	9.6	*debruijni*
Carrilanga 1	74	9.0	10.5	11.3	73	7.7	9.2	10.2	*debruijni*
Nombrevilla	7	9.7	10.5	11.3	6	8.5	9.1	9.8	*minor*
Las Planas 5H	1	—	9.1	—	1	—	9.0	—	*minor*
Toril	4	9.5	9.9	10.2	4	8.7	8.8	9.1	*minor*
Las Planas 5K	2	10.0	10.4	10.8	2	8.8	8.9	8.9	*minor*
Borjas	12	9.6	10.4	11.0	12	8.6	9.3	10.0	*minor*
Manchones 1	4	9.1	9.5	9.8	4	8.5	8.8	9.1	*minor*
Arroyo del Val 6	4	10.3	10.6	10.8	4	9.2	9.8	10.1	*minor*
Las Planas 5B	9	9.7	10.3	10.8	9	8.2	8.8	9.6	*minor*

M^3	Length				Width				
	n	min.	mean	max.	n	min.	mean	max.	species
Pedregueras 2C	29	6.1	6.9	7.7	29	6.0	7.0	7.9	*debruijni*
Pedregueras 2A	2	8.3	8.4	8.5	2	8.5	8.8	9.0	*debruijni*
Carrilanga 1	15	6.9	7.9	9.0	15	7.1	8.0	9.0	*debruijni*
Nombrevilla	1	—	7.2	—	1	—	7.2	—	*minor*
Las Planas 5L	2	6.7	6.9	7.0	2	7.1	7.4	7.7	*minor*

Table 10. Sorted length/width ratios of the M_1 of *Megacricetodon* species from the Aragonian and Lower Vallesian of the Calatayud-Daroca area.

L/W	N	Localities	Species							
1.717	8	Las Planas 5K			*cru.*					
1.705	4	Borjas						*min.*		
1.689	2	Las Planas 5K						*min.*		
1.679	3	Arroyo del Val 6						*min.*		
1.678	64	Las Planas 5B		*col.-cru.*						
1.670	14	Valalto 2B		*col.-cru.*						
1.664	6	Las Planas 5B						*min.*		
1.663	100	Borjas			*cru.*					
1.660	238	Manchones 1			*cru.*					
1.659	3	Toril						*min.*		
1.657	113	Arroyo del Val 6			*cru.*					
1.656	3	Las Planas 5H						*min.*		
1.656	30	Las Planas 5H				*cru.-ib.*				
1.656	157	Solera				*cru.-ib.*				
1.651	29	Las Planas 5L			*cru.*					
1.647	95	Villafeliche 9				*cru.-ib.*				
1.641	17	Alcocer 2				*cru.-ib.*				
1.641	5	Las Planas 4C	*col.*							
1.641	40	Pedregueras 2C							*deb.*	
1.640	14	Pedregueras 2A							*deb.*	
1.637	22	Carrilanga 1					*ib.*			
1.633	119	Armantes 7		*col.-cru.*						
1.628	1	Villafeliche 9						*min.*		
1.623	108	Toril				*cru.-ib.*				
1.617	19	Nombrevilla					*ib.*			
1.616	2	Valalto 2B								*raf.*
1.609	5	Villafeliche 4B	*col.*							
1.607	10	Valalto 1		*col.-cru.*						
1.607	27	Valalto 2C								*raf.*
1.607	8	Casetón 2B	*col.*							
1.604	83	Valalto 2C		*col.-cru.*						
1.600	10	Manchones 1						*min.*		
1.596	35	Villafeliche 4A	*col.*							
1.592	60	Carrilanga 1							*deb.*	
1.592	41	Vargas 1A	*pri.*							
1.591	2	Solera						*min.*		
1.587	14	Las Planas 4B	*col.*							
1.586	57	Armantes 7								*raf.*
1.585	11	Las Planas 4A	*col.*							
1.584	38	Valdemoros 3B	*col.*							
1.575	57	Casetón 1A	*col.*							
1.575	30	Valdemoros 3D	*col.*							
1.571	44	Valdemoros 3E	*col.*							
1.563	23	Olmo Redondo 8	*pri.*							
1.561	5	Nombrevilla						*min.*		
1.558	36	Valtorres	*pri.*							
1.552	8	Olmo Redondo 5	*pri.*							
1.535	22	Valdemoros 1A	*pri.*							
1.522	10	Olmo Redondo 9	*pri.*							

Table 11. Sorted length/width ratios of the M_2 of *Megacricetodon* species from the Aragonian and Lower Vallesian of the Calatayud-Daroca area.

L/W	N	Localities	Species							
1.364	1	Las Planas 5H						*min.*		
1.308	5	Las Planas 5B						*min.*		
1.285	10	Borjas						*min.*		
1.265	9	Nombrevilla						*min.*		
1.258	9	Las Planas 4C		*col.*						
1.244	50	Pedregueras 2C							*deb.*	
1.244	2	Toril						*min.*		
1.244	3	Las Planas 5K						*min.*		
1.239	21	Pedregueras 2A							*deb.*	
1.238	82	Las Planas 5B			*col.-cru.*					
1.237	51	Carrilanga 1							*deb.*	
1.232	129	Valalto 2C			*col.-cru.*					*raf.*
1.231	10	Valalto 1			*col.-cru.*					
1.229	25	Las Planas 5L				*cru.*				
1.229	38	Valdemoros 3E		*col.*						
1.226	29	Olmo Redondo 8	*pri.*							
1.221	27	Valalto 2B			*col.-cru.*					*raf.*
1.220	20	Las Planas 5K				*cru.*				
1.220	26	Olmo Redondo 9	*pri.*							
1.219	118	Borjas				*cru.*				
1.212	41	Las Planas 5H					*cru.-ib.*			
1.212	263	Armantes 7			*col.-cru.*					*raf.*
1.211	123	Villafeliche 9					*cru.-ib.*			
1.210	250	Manchones 1				*cru.*				
1.208	46	Valdemoros 3D		*col.*						
1.207	124	Toril					*cru.-ib.*			
1.206	23	Alcocer 2					*cru.-ib.*			
1.206	66	Casetón 1A		*col.*						
1.205	62	Vargas 1A	*pri.*							
1.205	4	Arroyo del Val 6						*min.*		
1.204	137	Arroyo del Val 6				*cru.*				
1.203	5	Las Planas 5L						*min.*		
1.202	15	Las Planas 4B		*col.*						
1.202	30	Villafeliche 4A		*col.*						
1.200	29	Valdemoros 1A	*pri.*							
1.200	10	Olmo Redondo 5	*pri.*							
1.194	192	Solera					*cru.-ib.*			
1.191	18	Nombrevilla						*ib.*		
1.190	9	Casetón 2B		*col.*						
1.189	19	Las Planas 4A		*col.*						
1.186	23	Carrilanga 1						*ib.*		
1.174	51	Valdemoros 3B		*col.*						
1.165	38	Valtorres	*pri.*							
1.160	7	Villafeliche 4B		*col.*						

Table 12. Sorted length/width ratios of the M_3 of *Megacricetodon* species from the Aragonian and Lower Vallesian of the Calatayud-Daroca area.

L/W	N	Localities	Species							
1.279	2	Las Planas 5H						*min.*		
1.275	3	Las Planas 5B						*min.*		
1.272	4	Pedregueras 2A							*deb.*	
1.266	4	Las Planas 4C	*col.*							
1.263	35	Las Planas 5H				*cru.-ib.*				
1.261	40	Pedregueras 2C							*deb.*	
1.253	6	Nombrevilla						*min.*		
1.247	184	Armantes 7		*col.-cru.*						*raf.*
1.238	99	Valalto 2C		*col.-cru.*						*raf.*
1.236	45	Toril				*cru.-ib.*				
1.233	2	Las Planas 5K						*min.*		
1.231	18	Las Planas 5K			*cru.*					
1.230	71	Borjas			*cru.*					
1.229	15	Las Planas 5L			*cru.*					
1.229	57	Solera				*cru.-ib.*				
1.226	65	Villafeliche 9				*cru.-ib.*				
1.225	15	Valalto 2B		*col.-cru.*						*raf.*
1.210	15	Alcocer 2				*cru.-ib.*				
1.209	158	Manchones 1			*cru.*					
1.209	61	Arroyo del Val 6			*cru.*					
1.209	28	Carrilanga 1							*deb.*	
1.207	35	Las Planas 5B		*col.-cru.*						
1.204	14	Nombrevilla					*ib.*			
1.200	4	Villafeliche 4B	*col.*							
1.199	7	Valdemoros 3D	*col.*							
1.190	10	Las Planas 4B	*col.*							
1.190	49	Casetón 1A	*col.*							
1.189	3	Valdemoros 3E	*col.*							
1.186	5	Casetón 2B	*col.*							
1.179	4	Olmo Redondo 5	*pri.*							
1.178	14	Vargas 1A	*pri.*							
1.177	3	Carrilanga 1					*ib.*			
1.176	30	Valdemoros 3B	*col.*							
1.176	5	Villafeliche 4A	*col.*							
1.174	7	Olmo Redondo 8	*pri.*							
1.171	3	Olmo Redondo 9	*pri.*							
1.165	11	Las Planas 4A	*col.*							
1.162	4	Valalto 1		*col.-cru.*						
1.156	11	Valdemoros 1A	*pri.*							
1.122	21	Valtorres	*pri.*							

Table 13. Relative abundance, in percentages of the total rodent fauna, of the *Megacricetodon* species in the Aragonian/Lower Vallesian of the Daroca-Calamocha area in the Calatayud-Teruel Basin. Percentages under 1 % are indicated by an *; an x indicates, that the percentage can not be calculated because the composition of the fauna is unknown.

Localities	*M. primitivus*	*M. collongensis*	*M. rafaeli*	*M. collongensis-crusafonti*	*M. crusafonti*	*M. crusafonti-ibericus*	*M. ibericus*	*M. minor*	*M. debruijni*	Local biozonation
Pedregueras 2C									24	I
Pedregueras 2A									13	
Carrilanga 1							15		46	H
Nombrevilla			*				29	15		
Solera						80		*		G
Las Planas 5H						77		3		
Toril						77		2		
Alcocer 2						76		1		
Villafeliche 9						95		*		
Las Planas 5K					56			7		
Las Planas 5L					89			1		
Borjas			*		68			3		
Manchones 1					46			1		
Arroyo del Val 6					x			x		
Valalto 1				71						
Las Planas 5B				84						
Valalto 2C			19	53						F
Valalto 2B			8	69						
Armantes 7			22	46						
Las Planas 4C		70								E
Las Planas 4B		50								
Las Planas 4A		47								
Villafeliche 4B		31								D
Villafeliche 4A		25								
Casetón 2B		8								
Casetón 1A		32								
Valdemoros 3E		46								
Valdemoros 3D		64								
Valdemoros 3B		39								
Valdemoros 1A	50									
Valtorres	87									
Olmo Redondo 9	34									
Olmo Redondo 8	29									C
Olmo Redondo 5	14									
Vargas 1A	16									

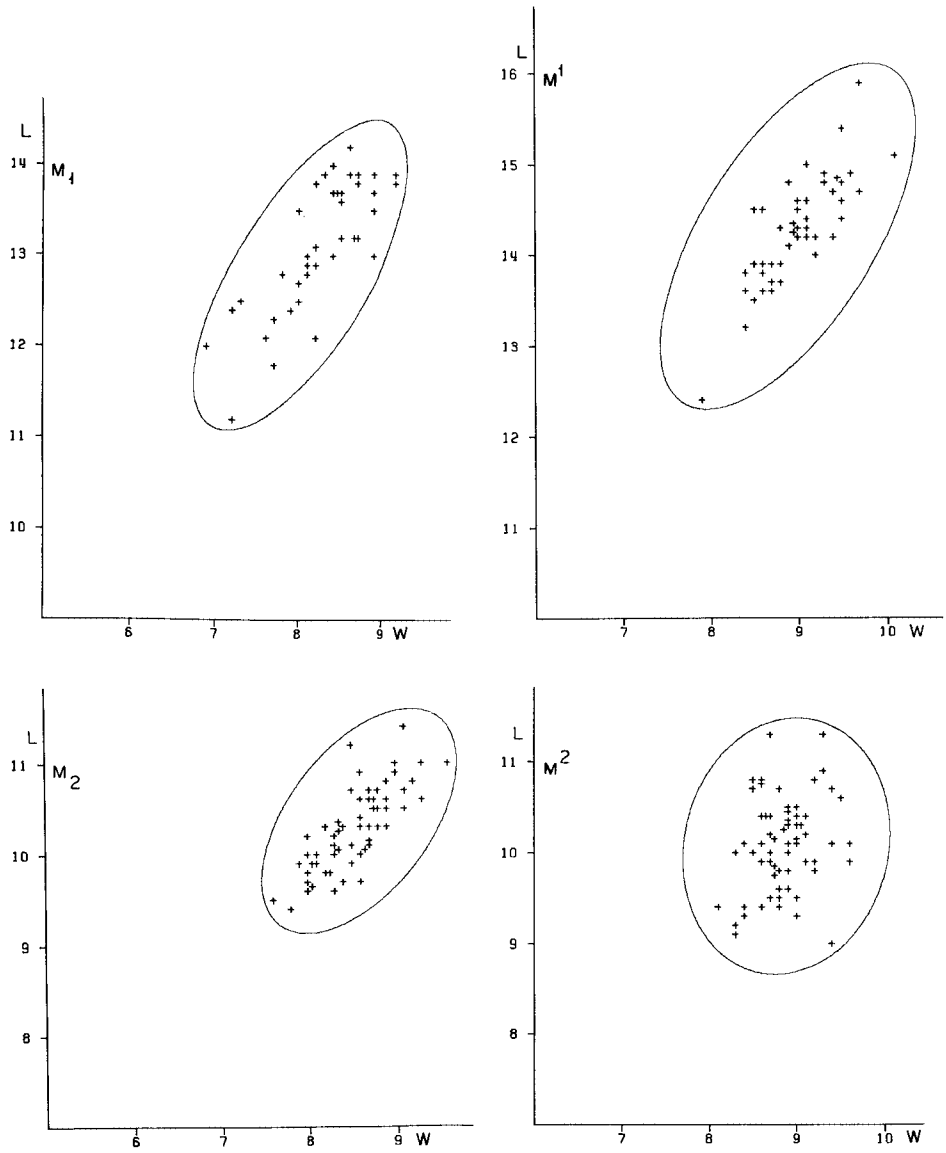

Fig. 44. Length/Width scatter diagrams of M1,2 of *M. primitivus* from Vargas 1A.

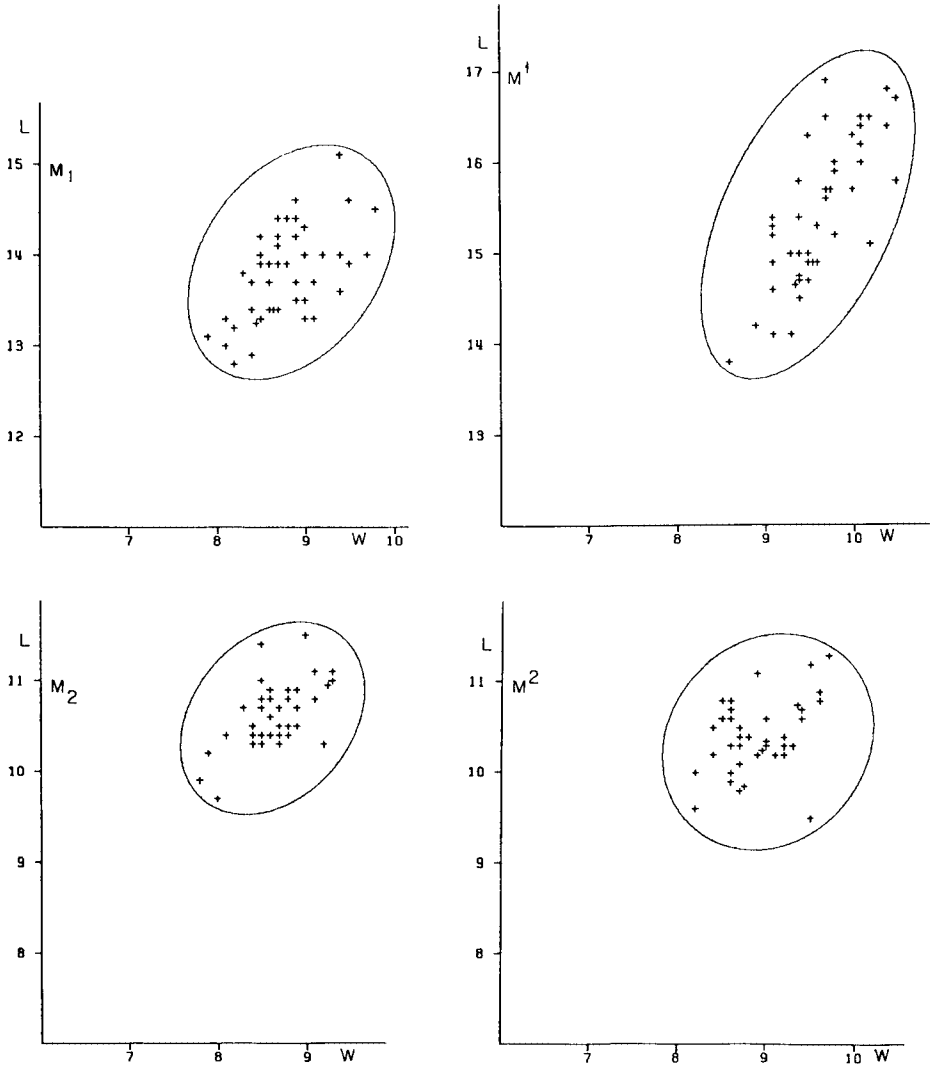

Fig. 45. Length/Width scatter diagrams of M1,2 of *M. collongensis* from Valdemoros 3E.

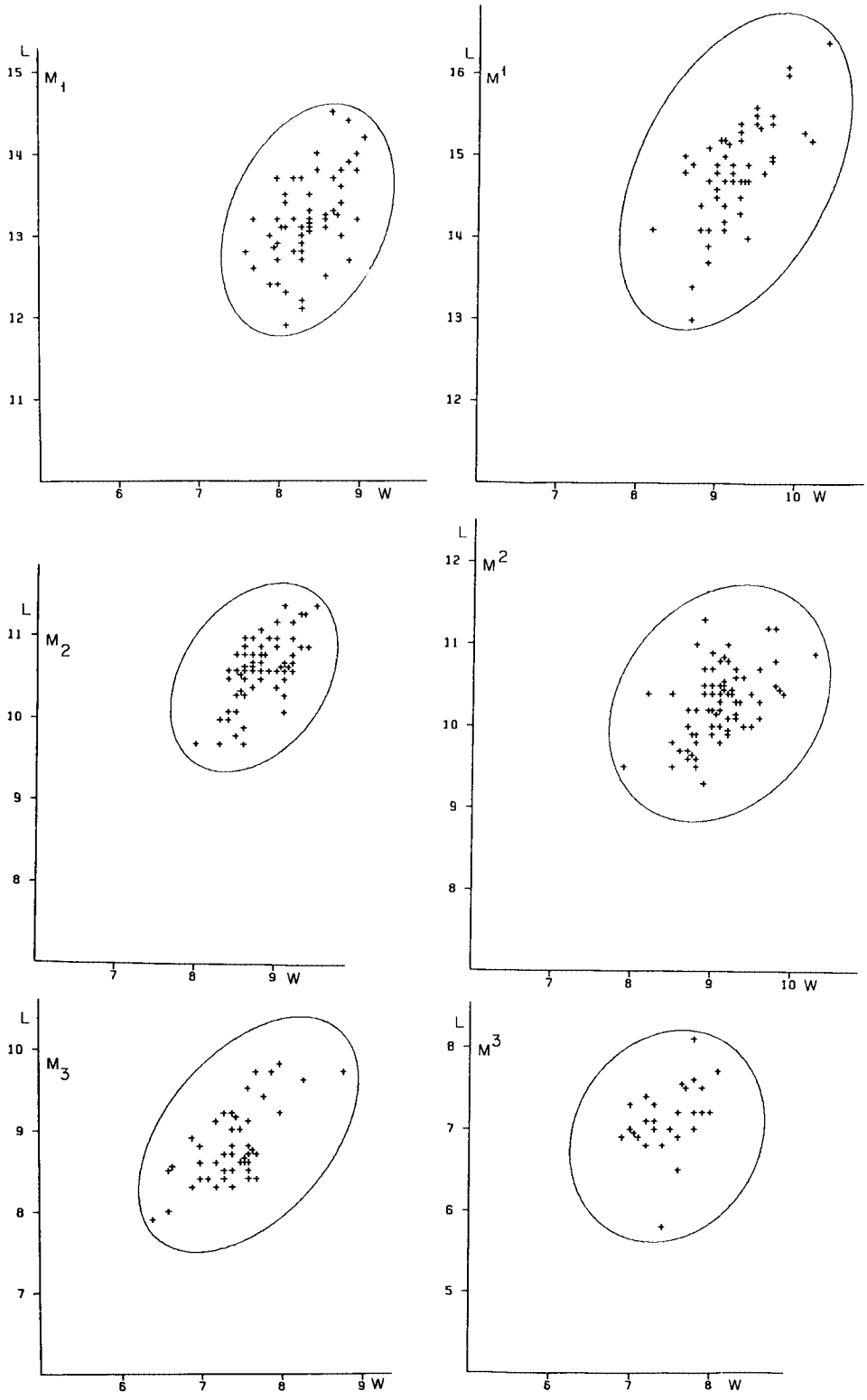

Fig. 46. Length/Width scatter diagrams of the molars of *M. collongensis* from Caseton 1A.

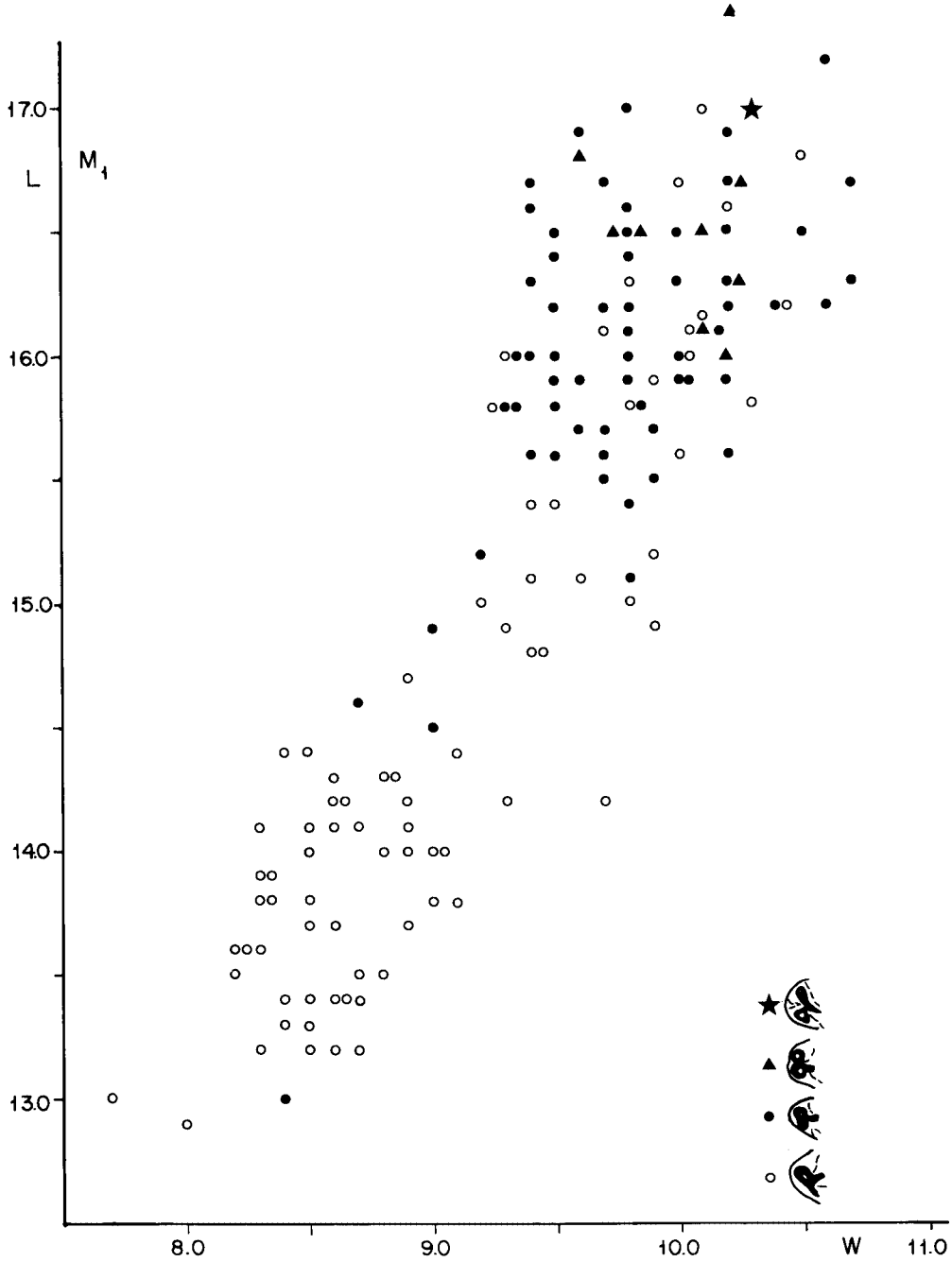

Fig. 47. Length/Width scatter diagrams of M_1 of *M. rafaeli* and *M. collongensis – crusafonti* from Armantes 7. Symbols indicate morphotypes of the anteroconid.

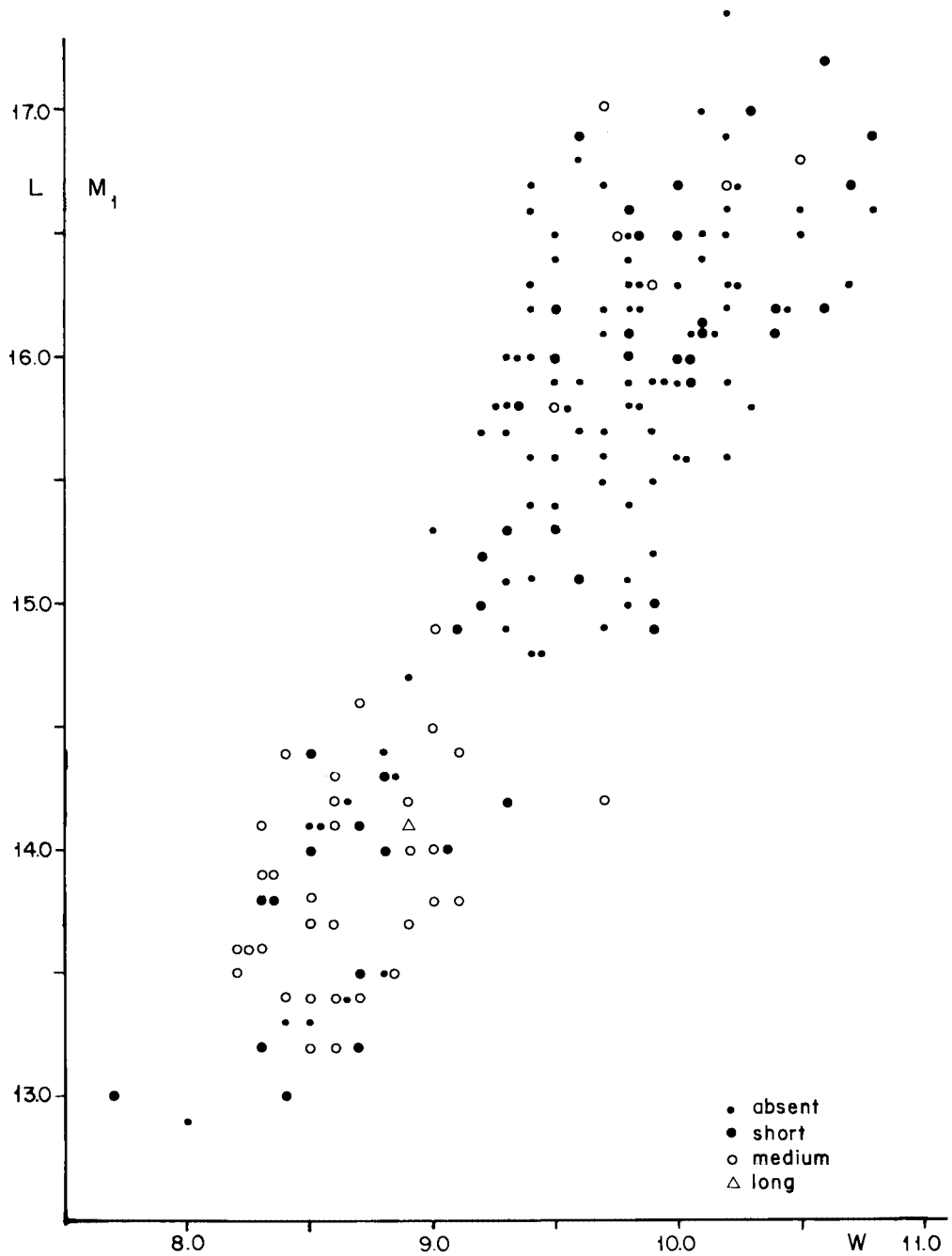

Fig. 48. Length/Width scatter diagrams of M_1 of *M. rafaeli* and *M. collongensis – crusafonti* from Armantes 7. Symbols indicate morphotypes of the mesolophid.

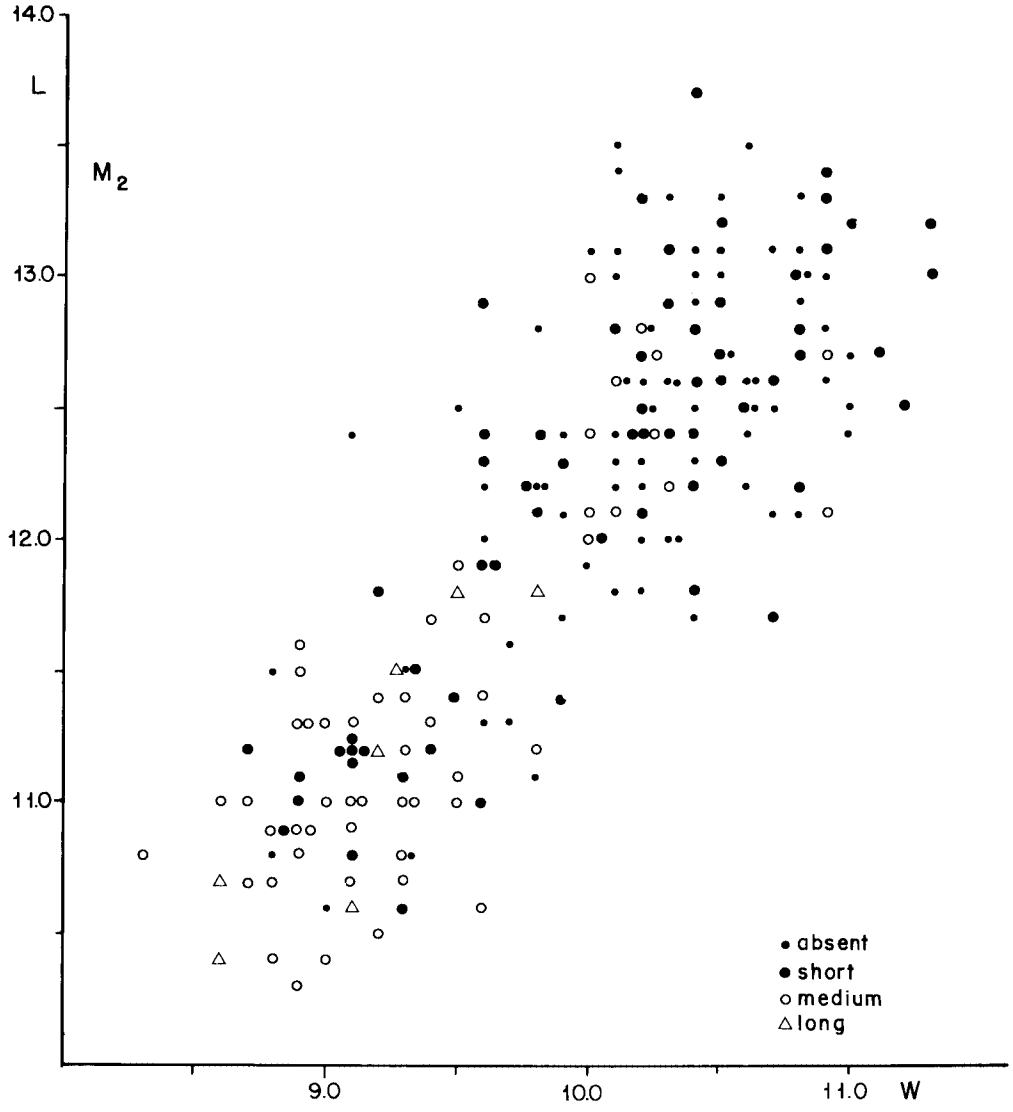

Fig. 49. Length/Width scatter diagrams of M_2 of *M. rafaeli* and *M. collongensis – crusafonti* from Armantes 7. Symbols indicate morphotypes of the mesolophid.

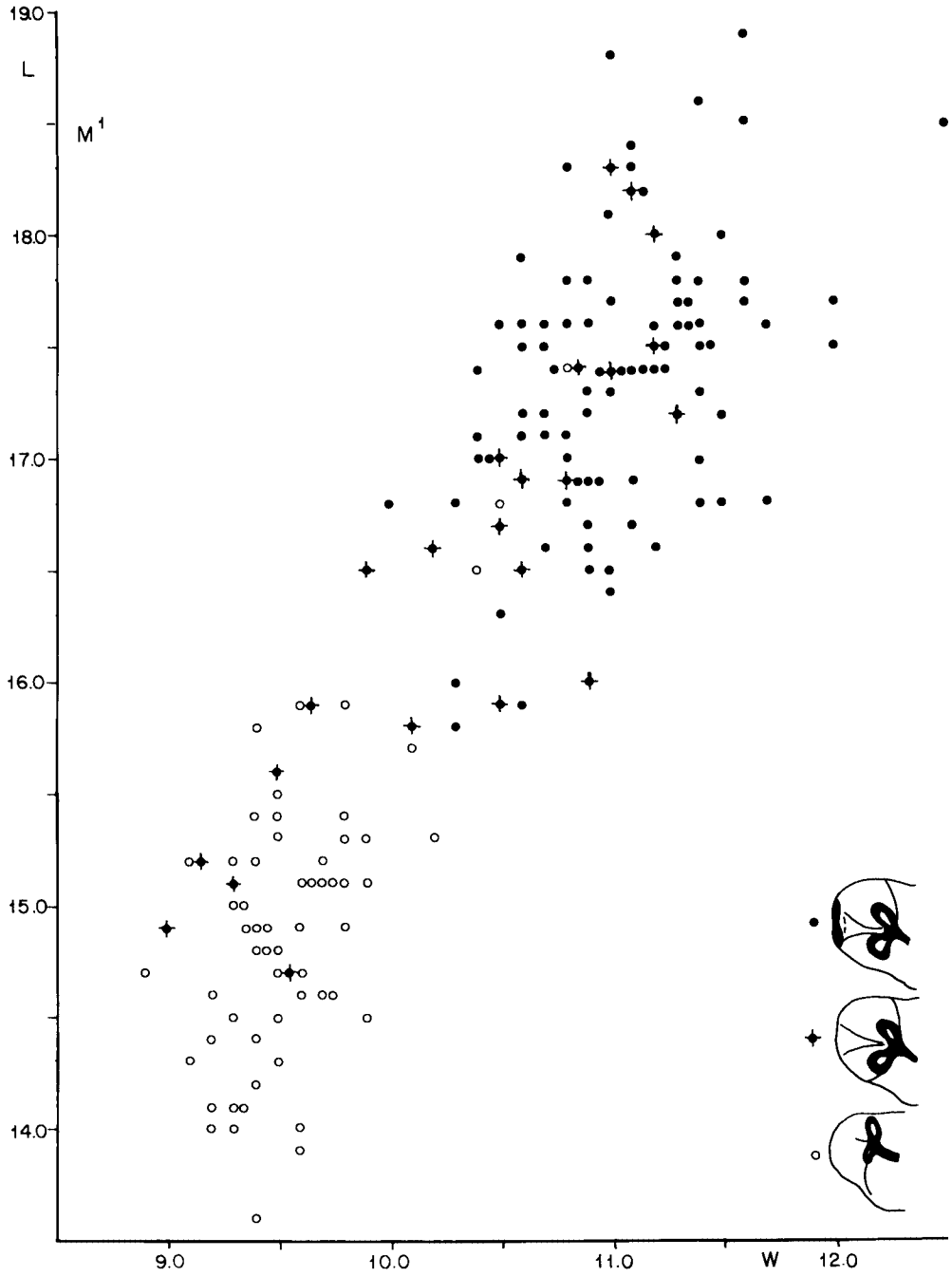

Fig. 50. Length/Width scatter diagrams of M^1 of *M. rafaeli* and *M. collongensis – crusafonti* from Armantes 7. Symbols indicate morphotypes of the anterocone.

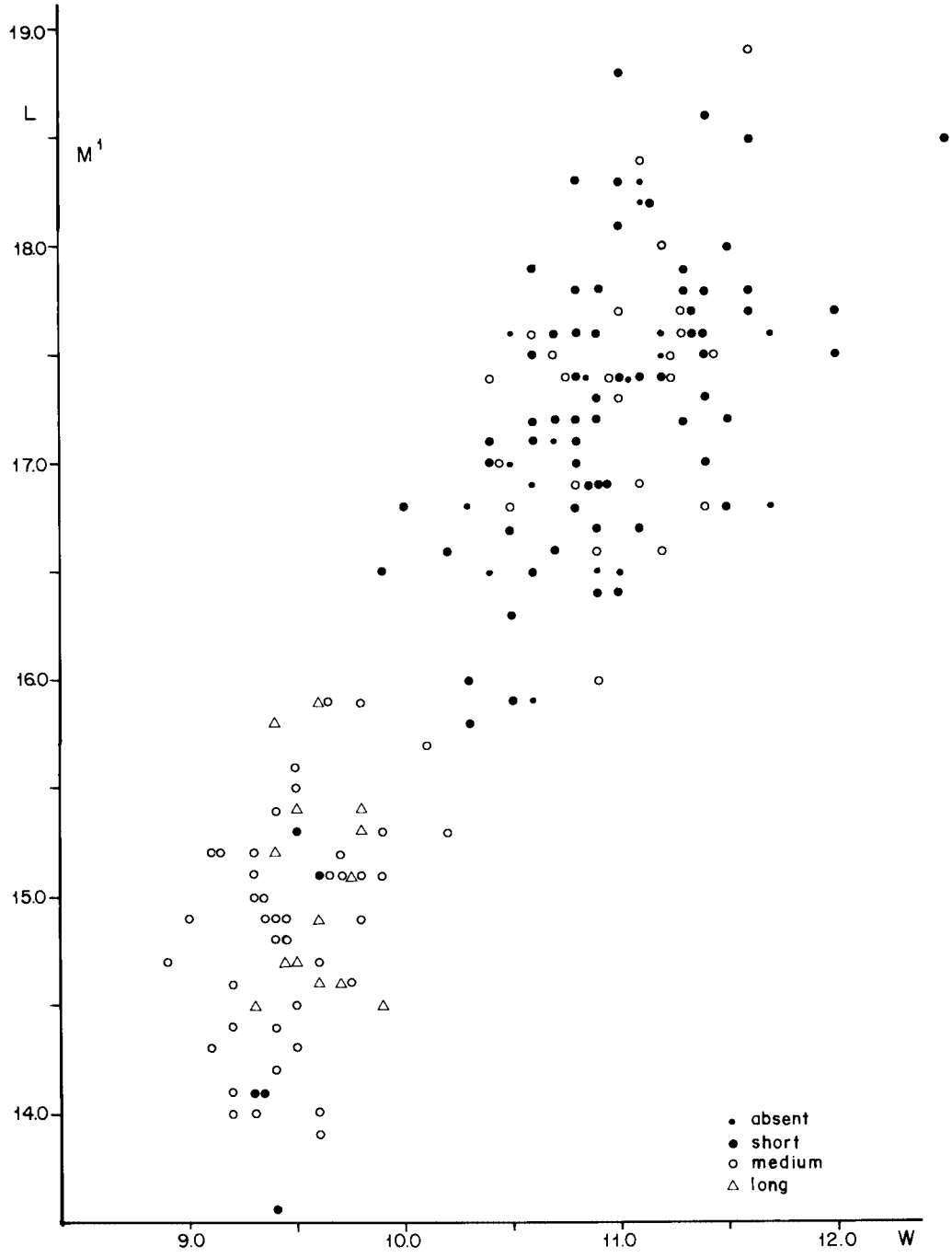

Fig. 51. Length/Width scatter diagrams of M^1 of *M. rafaeli* and *M. collongensis – crusafonti* from Armantes 7. Symbols indicate morphotypes of the mesoloph.

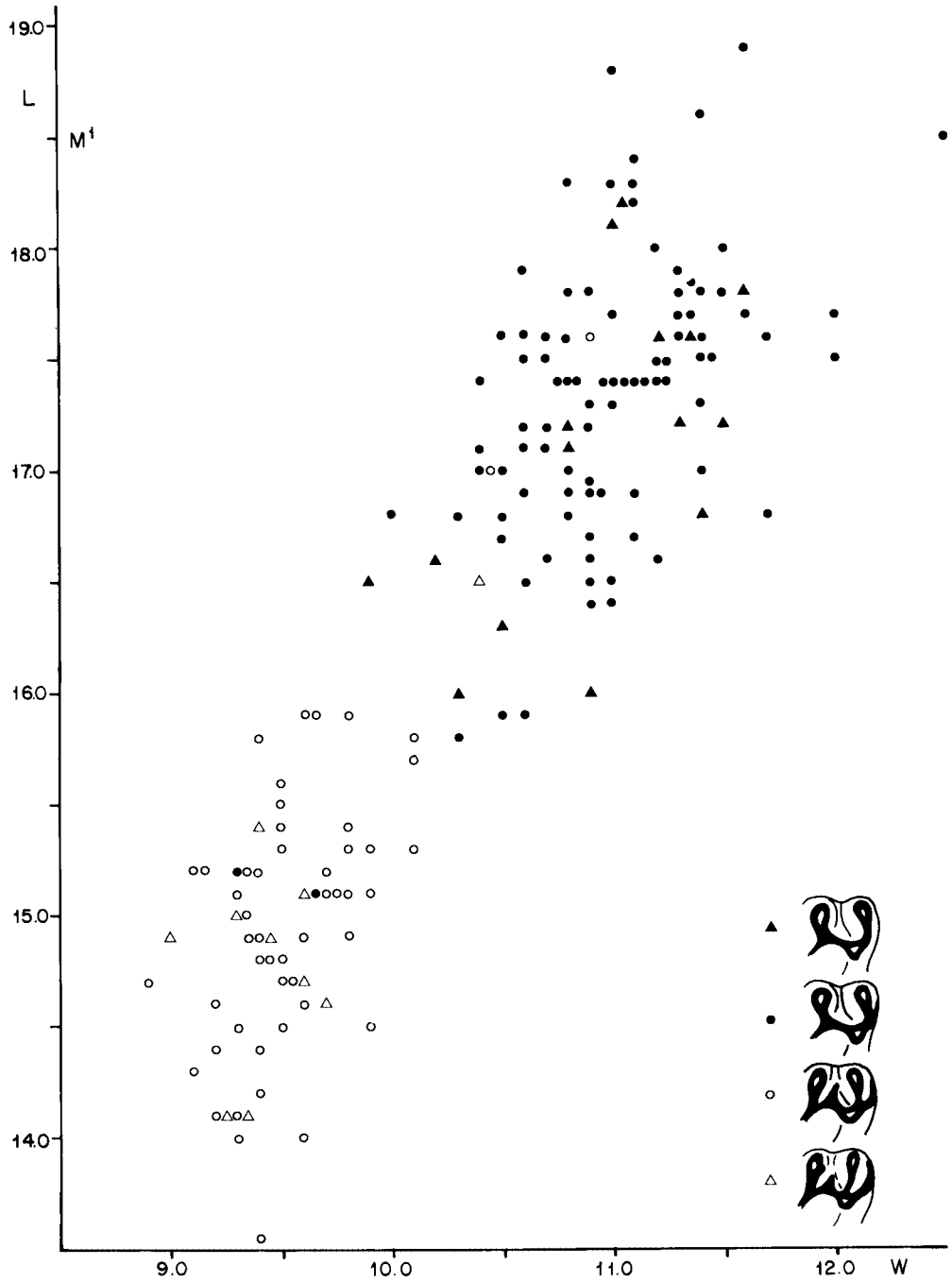

Fig. 52. Length/Width scatter diagrams of M^1 of *M. rafaeli* and *M. collongensis – crusafonti* from Armantes 7. Symbols indicate morphotypes of the posterosinus.

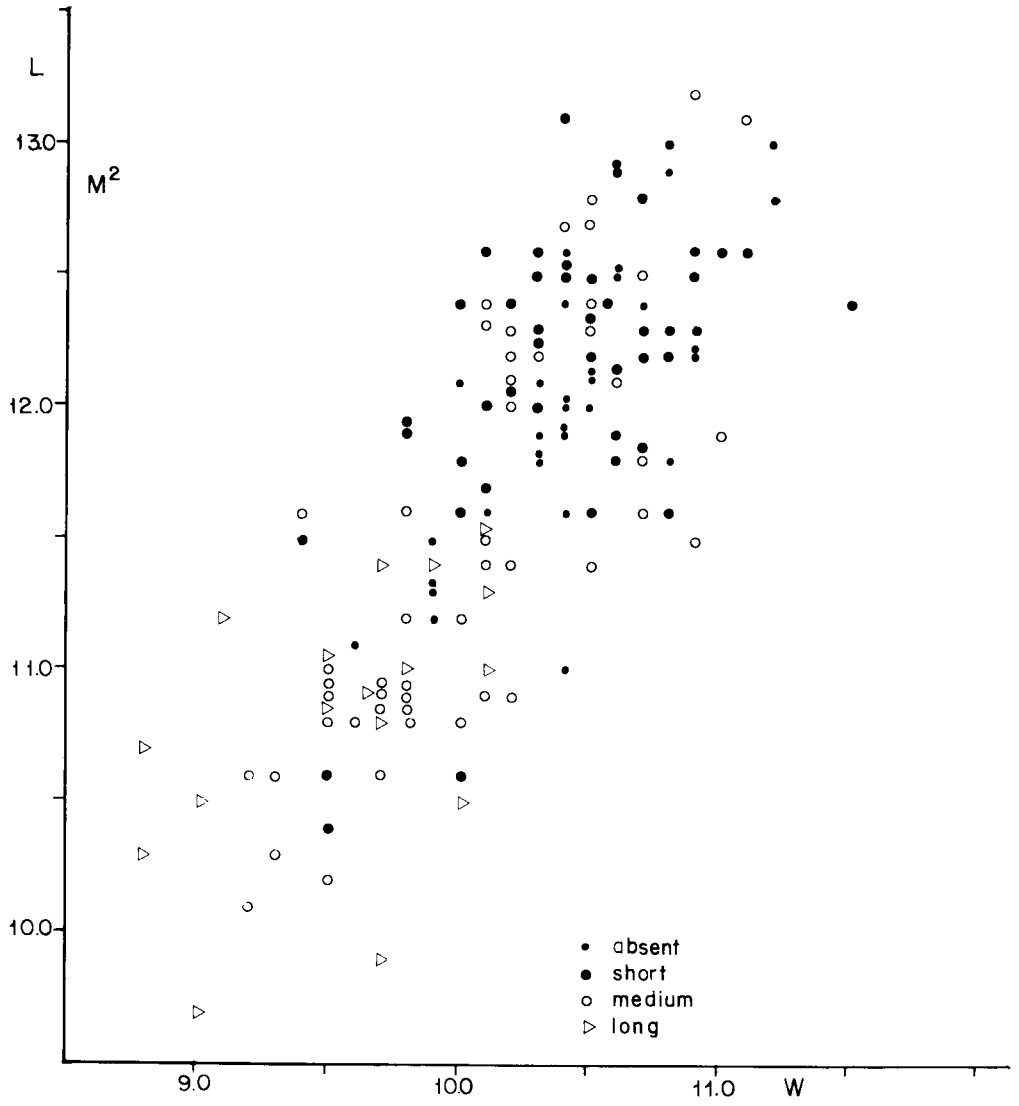

Fig. 53. Length/Width scatter diagrams of M^2 of *M. rafaeli* and *M. collongensis – crusafonti* from Armantes 7. Symbols indicate morphotypes of the mesoloph.

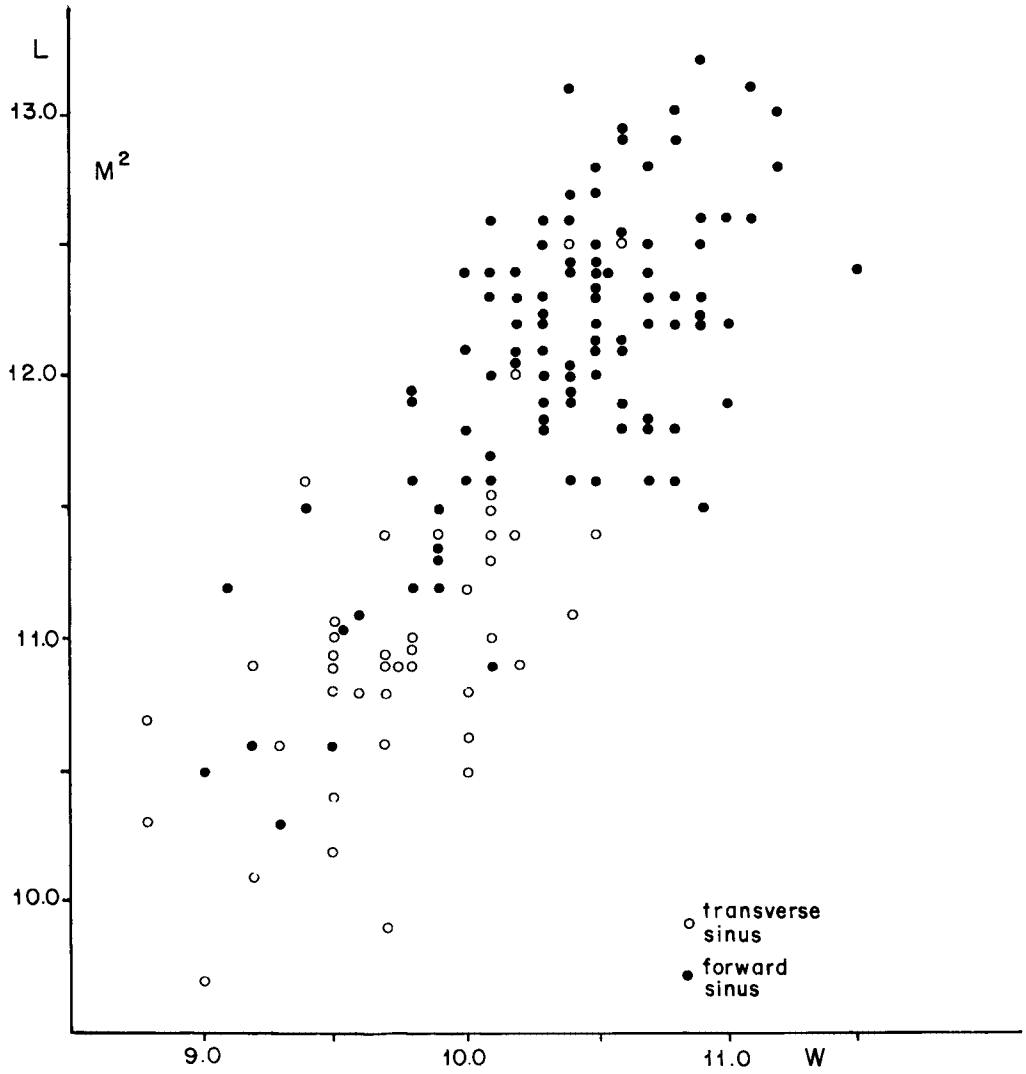

Fig. 54. Length/Width scatter diagrams of M^2 of *M. rafaeli* and *M. collongensis – crusafonti* from Armantes 7. Symbols indicate morphotypes of the sinus.

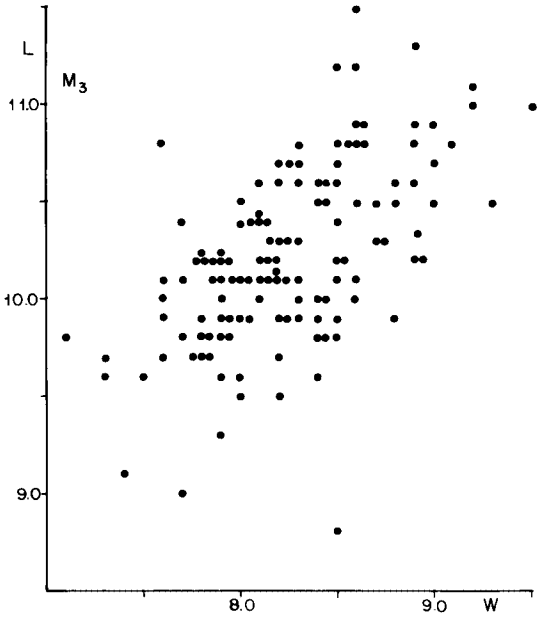

Fig. 55. Length/Width scatter diagrams of M_3 of *M. rafaeli* and *M. collongensis – crusafonti* from Armantes 7.

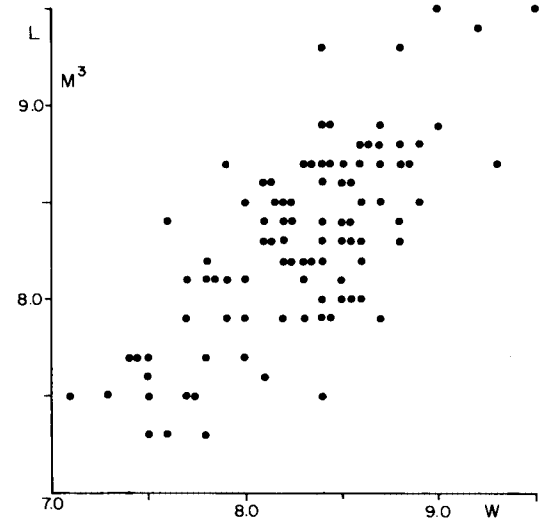

Fig. 56. Length/Width scatter diagrams of M^3 of *M. rafaeli* and *M. collongensis – crusafonti* from Armantes 7.

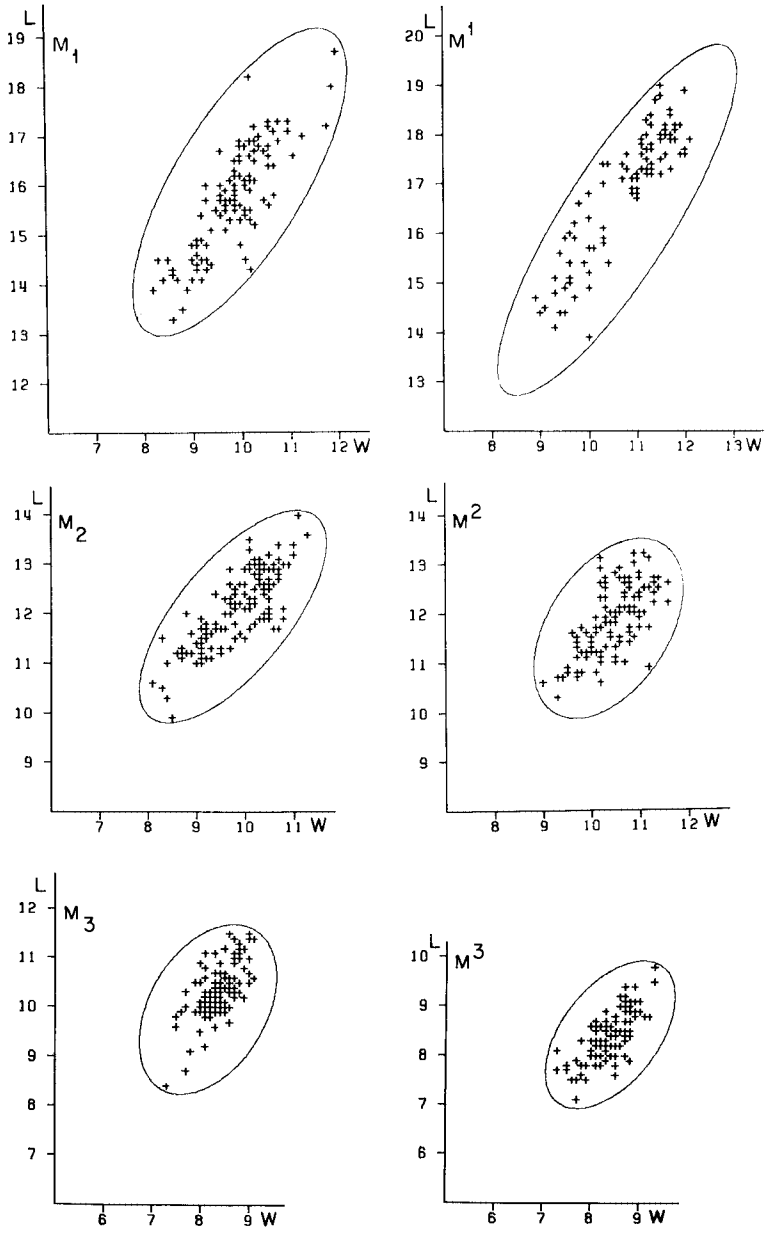

Fig. 57. Length/Width scatter diagrams of the molars of *M. rafaeli* and *M. collongensis – crusafonti* from Valalto 2C.

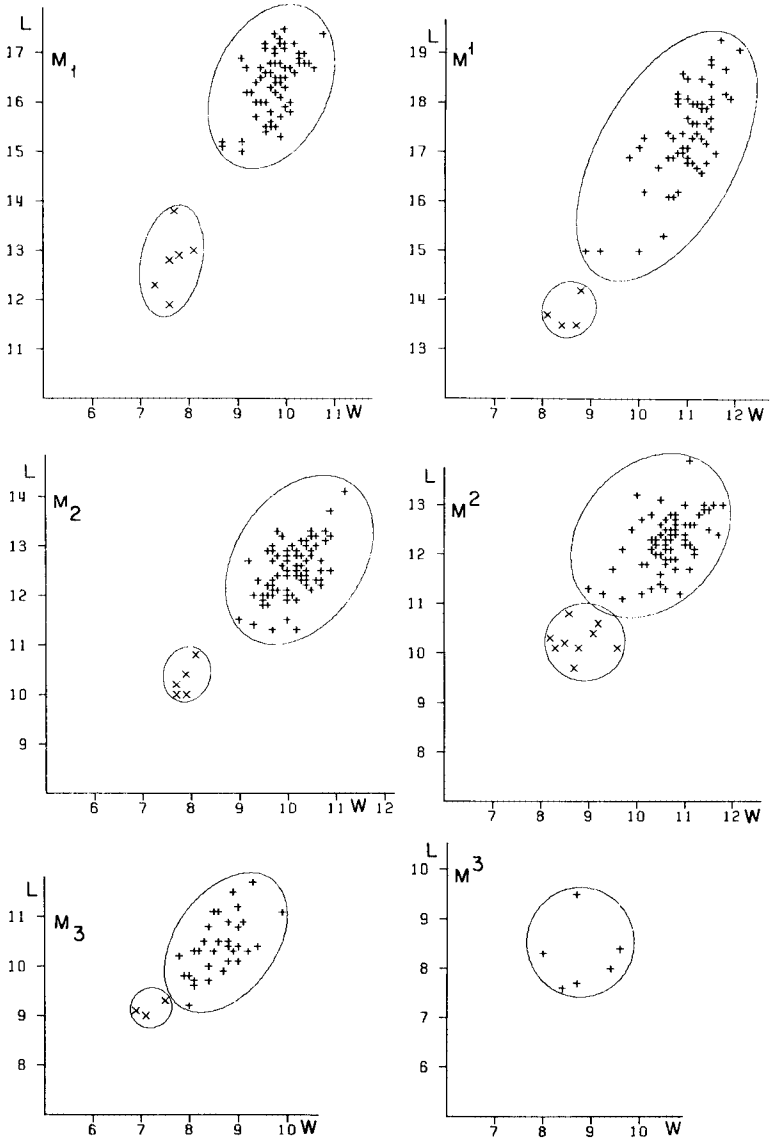

Fig. 58. Length/Width scatter diagrams of the molars of *M. minor* (×) and *M. collongensis – crusafonti* (+) from Las Planas 5B.

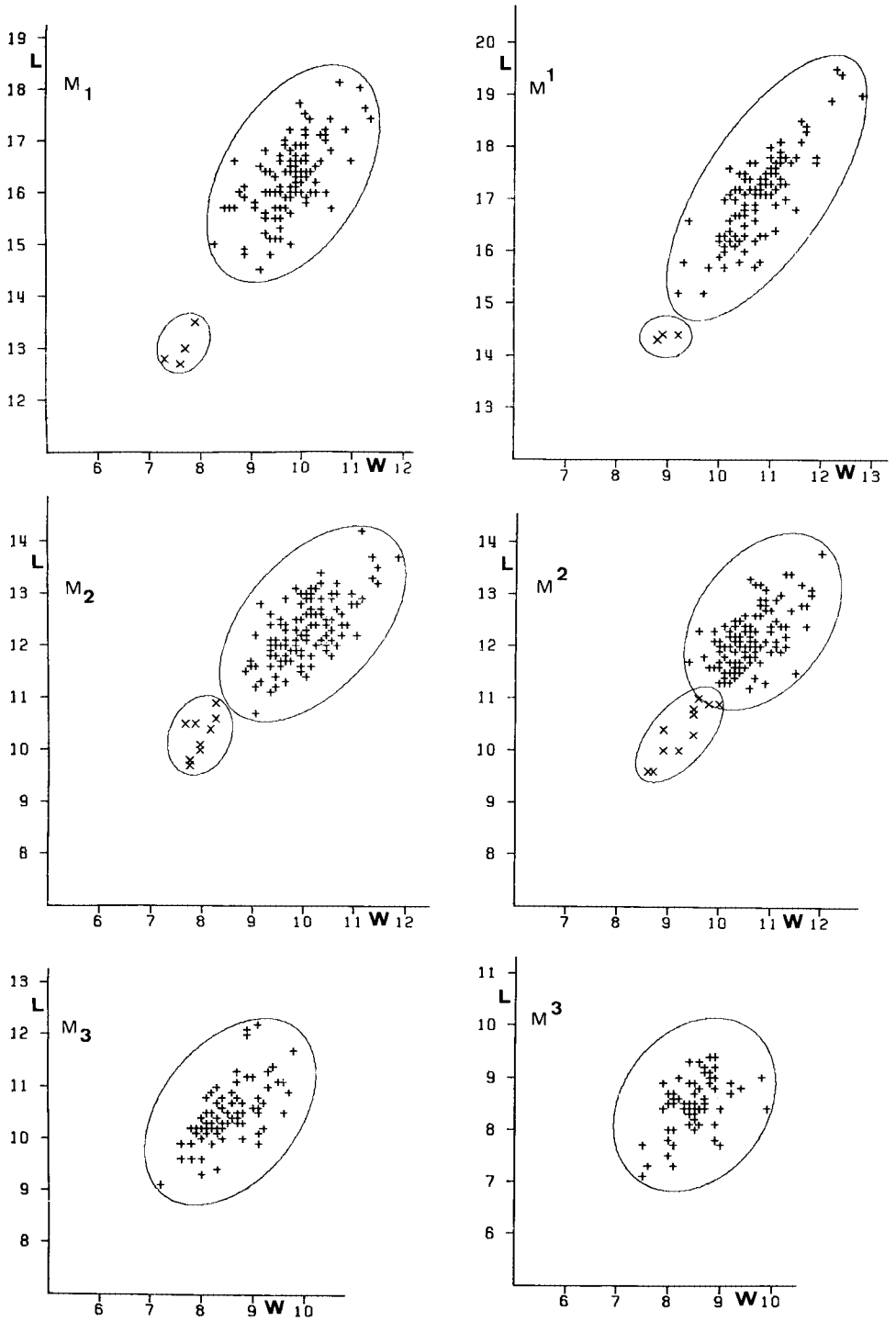

Fig. 59. Length/Width scatter diagrams of the molars of *M. minor* (×) and *M. crusafonti* (+) from Borjas.

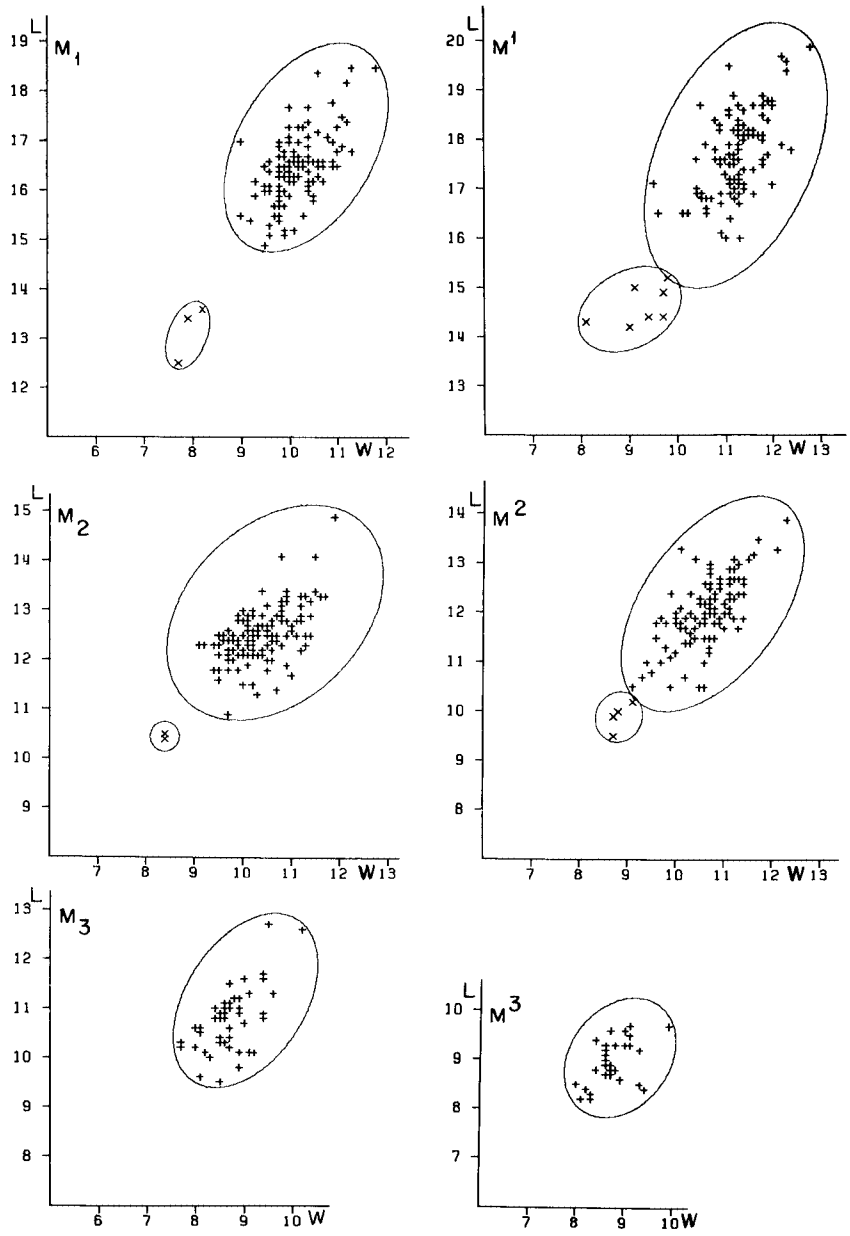

Fig. 60. Length/Width scatter diagrams of the molars of *M. minor* (×) and *M. crusafonti – ibericus* (+) from Toril.

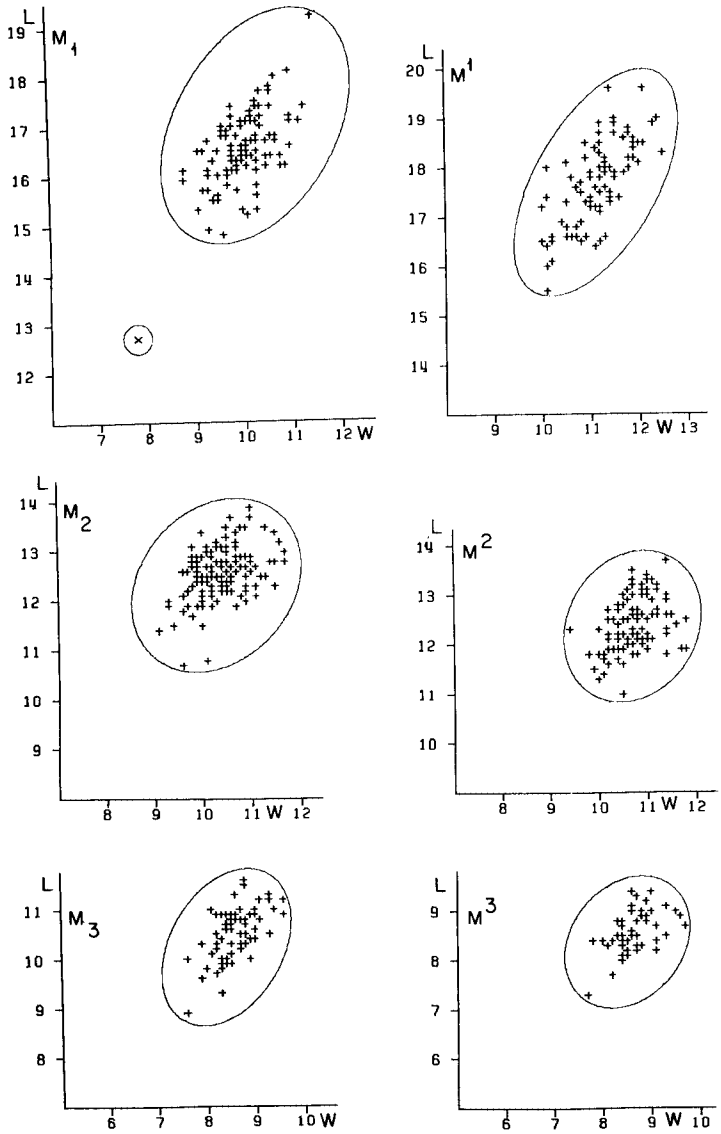

Fig. 61. Length/Width scatter diagrams of the molars of *M. minor* (×) and *M. crusafonti – ibericus* (+) from Villafeliche 9.

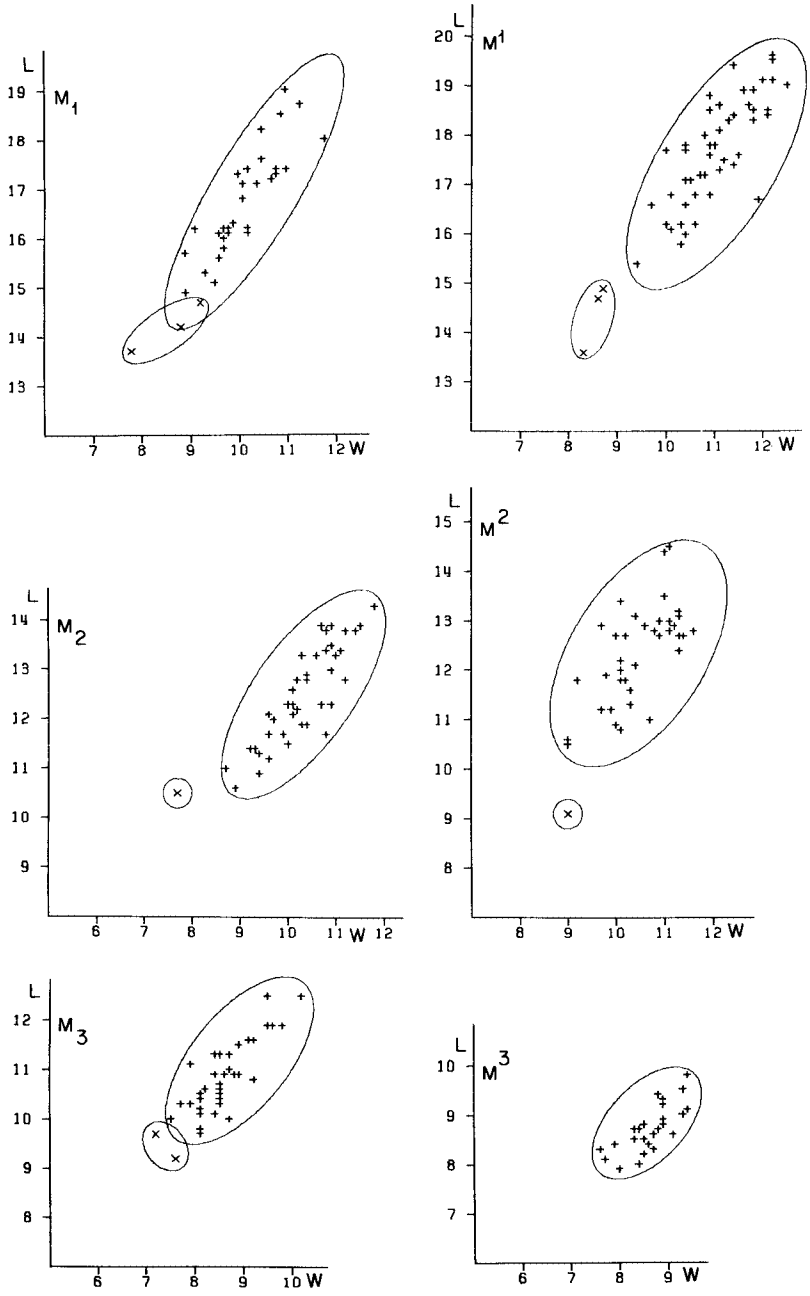

Fig. 62. Length/Width scatter diagrams of the molars of *M. minor* (×) and *M. crusafonti – ibericus* (+) from Las Planas 5H.

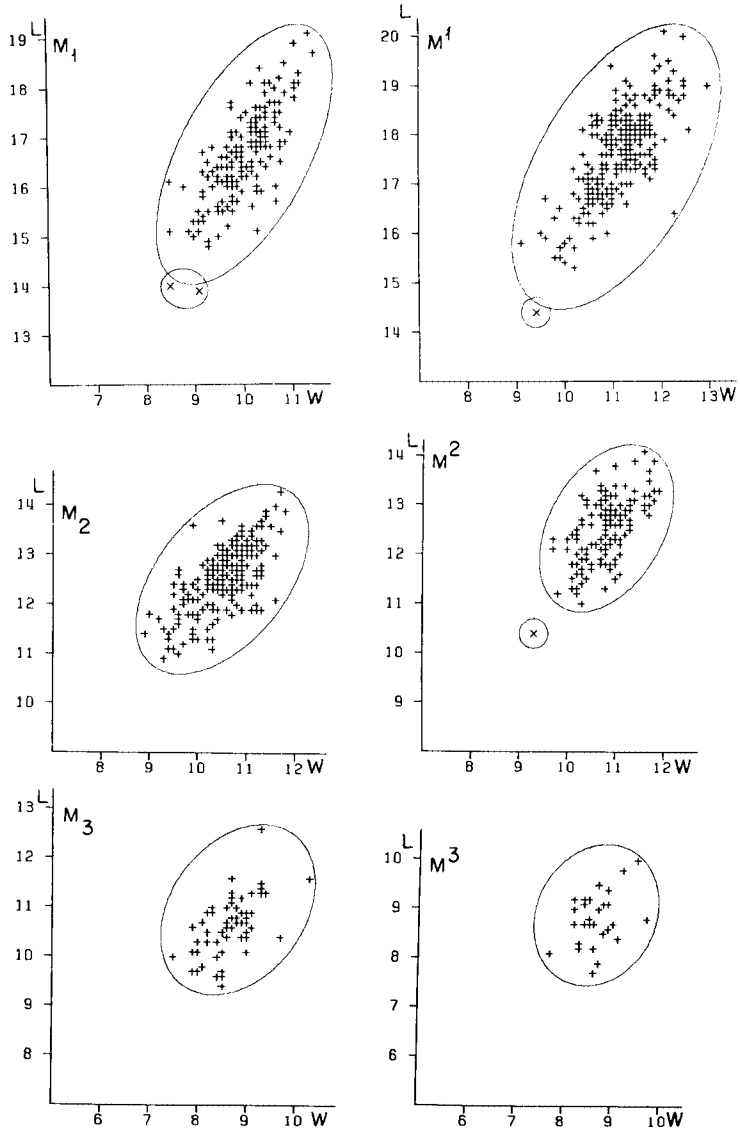

Fig. 63. Length/Width scatter diagrams of the molars of *M. minor* (×) and *M. crusafonti – ibericus* (+) from Solera.

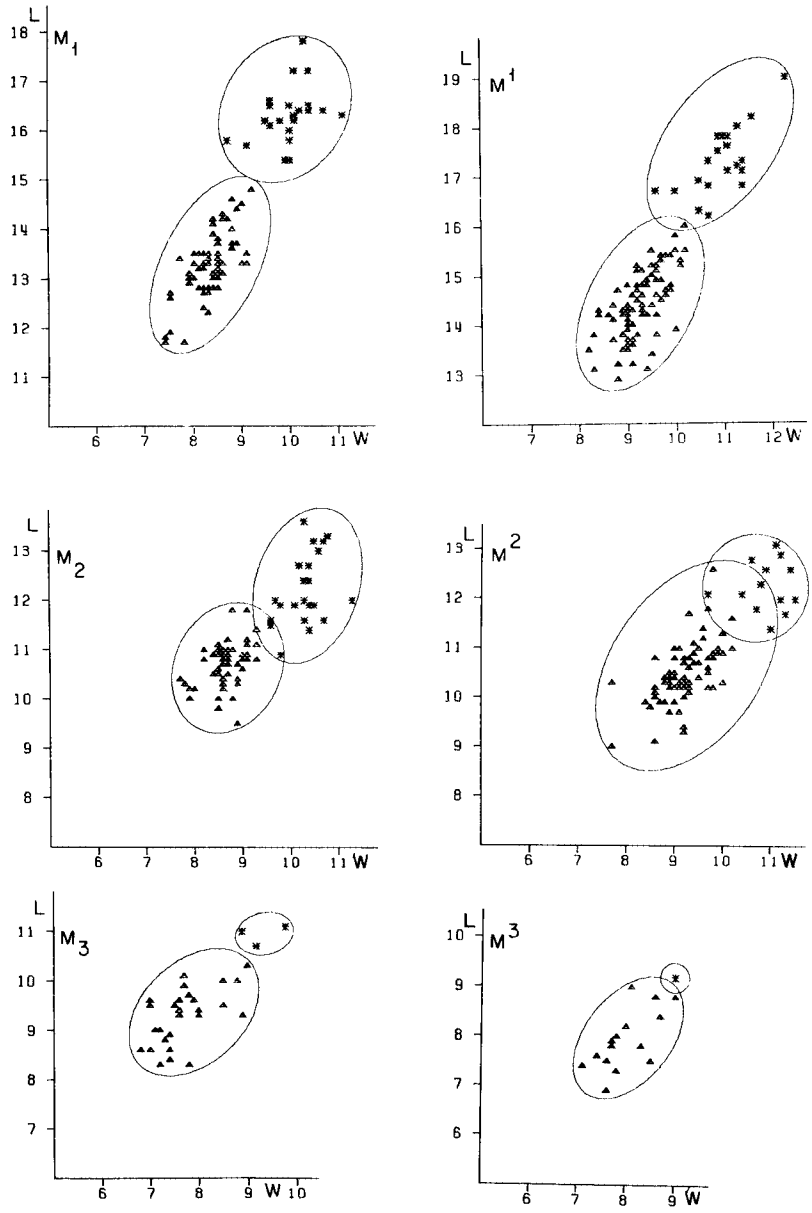

Fig. 64. Length/Width scatter diagrams of the molars of *M. debruijni* (▲) and *M. ibericus* (*) from Carrilanga 1.

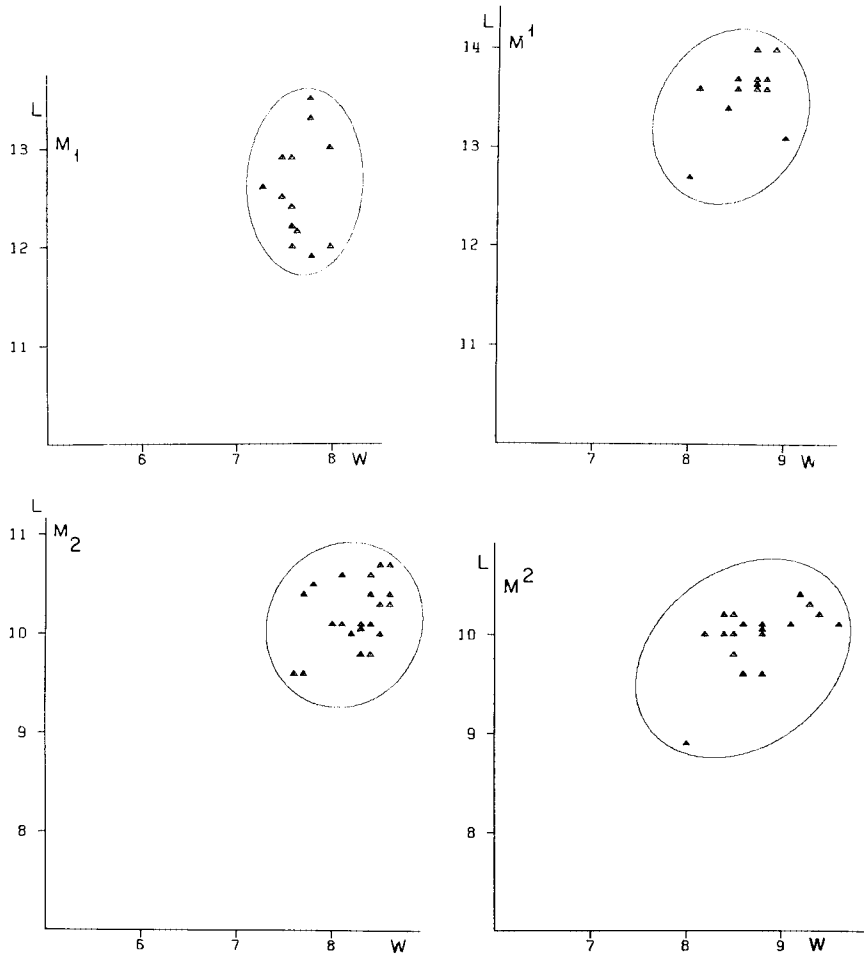

Fig. 65. Length/Width scatter diagrams of M1,2 of *M. debruijni* from Pedregueras 2A.