The Aragonian type area revisited; comments on paleontology and stratigraphy

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In a recent study of van der Meulen and coauthors, the fossil rodents Fahlbuschia, Pseudofahlbuschia and Renzimys from the Aragonian type area (Calatayud Basin, Spain) were synonimized with Democricetodon. On the basis of the relative chronology provided by Daams and coauthors in an earlier study, these authors construed two evolutionary lineages, distinguished by size. One of these lineages contains Fahlbuschia koenigswaldi (Freudenthal, 1963) and the other one Democricetodon moralesi van der Meulen et al., 2004 but, in view of their great similarity, we consider D. moralesi to be a synonym of F. koenigswaldi.

The relative stratigraphic position of some fossil mammal localities is difficult to establish in the Aragonian type area because it is affected by folds and faults. Early studies of Daams and Freudenthal subdivided the local zone D into D1, D2, D3 and gave a scheme of the stratigraphy in which the fossiliferous locality Valdemoros 1A is considered to be older than Valdemoros 3B. But Daams and coauthors came to the opposite interpretation in a later study, and divided zone D in Da, Db, Dc, Dd. But, new field data presented here enforce the original interpretation in which Valdemoros 1A is older than Valdemoros 3B. This leads to the conclusion that the division of local zone D into Da to Dd has to be discarded, and substituted by the formerly proposed zonation D1–D3.

KEYWORDS

INTRODUCTION
Daams et al. (1977) created the Aragonian stage and Daams and Freudenthal (1981) presented a local zonation for the fossil mammal localities of the Aragonian type area. Their local zone D was subdivided into D1, D2 and D3 by Daams and Freudenthal (1988) and the two key localities, Valdemoros 1A (VA1A) and Valdemoros 3B (VA3B) were placed in zone D1 and D2, respectively, VA1A being older than VA3B. Daams et al. (1999a) proposed a new subdivision into Da, Db, Dc and Dd, and placed Valdemoros 3B in zone Dc and Valdemoros 1A in the higher zone Dd, supposing a fault separating them two.

On the basis of the Daams et al. (1999a) zonation, van der Meulen et al. (2004) presented a revision of the fossil rodents Democricetodon, Fahlbuschia, Pseudofahlbuschia and Renzimys from the Aragonian type area. They interpreted these populations to correspond to two evolutionary lineages: in many localities two species of different size are present, and in their interpretation the smaller ones form one lineage, and the larger ones a second lineage. We consider this
view an oversimplification, and propose that in many localities more than two species are present. Moreover, *Fahlbuschia koenigswaldi* and *Democricetodon moralesi*, placed in two different lineages by van der Meulen *et al.* (2004), are highly similar, and the latter one is, in our view, a synonym of *Fahlbuschia koenigswaldi*.

Van der Meulen *et al.* (2012), in an appendix entitled “Rebuttal of Freudenthal’s (2006) sequence of the Aragonian faunas”, rejected the interpretation of Freudenthal on the basis of a number of arguments. They hardly mentioned, however, Freudenthal’s most important argument: the fact that in the ravine W of VA3B one can see the horizontal beds that contain VA3B lying unconformably on the tilted beds that contain VA1A (Freudenthal, 2006, fig. 2). Apparently, VA3B is younger than VA1A.

**METHODS**

Fossil teeth Morphology Values (MV) are calculated as defined by Daams and Freudenthal (1988). Freudenthal (2004) changed that definition, but here we use the former one, since that was applied by van der Meulen *et al.* (2004).

$V'$ is the variability coefficient as defined by Freudenthal and Cuenca (1984). Tooth measurements are given in millimeters. Abbreviations used are explained in Table 1.

In this paper, we provide the geographic location of a number of localities in UTM coordinates, as taken in the field and checked on the topographic map 1:25,000, which uses the ED50 datum. We use data in this datum for the sake of coherency with the printed map. However, we also converted our data to the currently standard ETRS89 datum (see Table 2).

**TABLE 1. Abbreviations used**

<table>
<thead>
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<th>Localities</th>
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<tr>
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<tr>
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<td>Artesilla</td>
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<td>Buñol</td>
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<td>La Col</td>
</tr>
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<td>Moratilla</td>
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<td>Muela Alta</td>
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<tr>
<td>VL</td>
<td>Villafeliche</td>
</tr>
<tr>
<td>VR</td>
<td>Vargas</td>
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**TABLE 2. Conversion of UTM coordinates from ED50 to ETRS89 datum**

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<th>Localities</th>
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<td>VA3B</td>
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<td>626687 / 4560770</td>
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<td>Profile observation point</td>
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<td>626591 / 4560690</td>
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<td>Profile N end</td>
<td>626905 / 4561519</td>
<td>626796 / 4561309</td>
</tr>
<tr>
<td>Profile S end</td>
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<td>626452 / 4560566</td>
</tr>
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</table>

**PALEONTOLOGY**

Van der Meulen *et al.* (2004) synonymized *Fahlbuschia, Renzimys* and *Pseuodofahlbuschia* with *Democricetodon*; they placed the Spanish species in two evolutionary lineages. In many localities two species are present, a smaller and a larger one. It was assumed that the smaller ones formed one evolutionary lineage, and the larger species constitute another lineage. Their phrase “The faunal succession demonstrates that *D. moralesi* evolves to *D. jordensi*, which in its turn evolves to *D. lacombai*” implies a concept of evolution that we do not share. Faunal succession may demonstrate that one species is younger than another one, and the younger one cannot be the ancestor of the older one. It does not imply, however, that the older one is the ancestor of the younger one, not even that they are related. The concept of not more than two lineages is counter-argued by many localities where more than two species are present: Valdemoros 8A. According to van der Meulen *et al.* (2012, fig. 5), the locality of Valdemoros 8A contains *D. moralesi, D. franco nicus* and *Democricetodon* n. sp., which means that there are more than two lineages.

Vargas 4A. In several cases, e.g. the length of M1 of *D. moralesi* from Vargas 4A, the large variation ($V'$=29.5) indicates that the population is not homogeneous (see Fig. 1) and that, apart from *D. franco nicus*, two species are present.

Valdemoros 1A (VA1A). According to van der Meulen *et al.* (2004) there are no specimens with long mesolophid in VA1A, but, according to Freudenthal (1963), VA1A contains a badly preserved m1 (Coll. Utrecht, cat. nr. VA 257, measurements ±1.47x±1.02) of a *Democricetodon* (Fig. 2). It is much smaller than the minimum of *F. koenigswaldi* (1.64x1.15) and its mesolophid reaches the molar border. Freudenthal (1963) called it *Cricetodon cf. vindobonensis*. It may be *D. hispanicus* or *D. affinis* (Freudenthal and Daams, 1988). Van der Meulen *et al.* (2004) incorporated it in *F. koenigswaldi*. Apart from *F. koenigswaldi* and *Democricetodon* this locality contains several specimens of *Pseudofahlbuschia* (the two largest M1 in our Fig. 2); in other words VA1A contains three species of *Democricetodon/Fahlbuschia* and there must be at least three synchronous lineages.
Vargas 1A (VA1A). First mentioned by Freudenthal and Daams (1988), contains, according to these authors, *Democricetodon hispanicus*, *Fahlbuschia koenigswaldi*, and *Pseudofahlbuschia jordensi*. Van der Meulen et al. (2004) only mentioned *Democricetodon franconicus* and *Democricetodon moralesi*, the latter one corresponding to the material previously classified as *F. koenigswaldi*. However, the distribution of measurements (Fig. 3) makes it clear that at least three species are present. Furthermore, Freudenthal and Daams (1988, pg.: 167) remarked that the population of *F. koenigswaldi* from VR1A may contain some specimens of yet another species of *Democricetodon*, larger than *D. hispanicus* and of the same size as *F. koenigswaldi*; so, it is quite possible that four different lineages of *Democricetodon* and *Fahlbuschia* co-occur in this locality.

Casetón 1A and 2B. A similar situation is reported from Casetón 1A and Casetón 2B, where such a mixture of *F. koenigswaldi* with some species of *Democricetodon* is supported by the presence of maxillae with the short foramen incisivum considered to be characteristic of

![FIGURE 1.](image-url)

**FIGURE 1.** Length distribution of the molars m1 and M1 of *Democricetodon moralesi*, *Fahlbuschia decipiens* and *Fahlbuschia koenigswaldi*. Locality sequence and species attribution following van der Meulen et al. (2004). Number of specimens to the right of each bar. See Table 1 for abbreviations of molars and localities.
Democricetodon. These localities also contain some specimens of Pseuodofahlbuschia jordensi (Freudenthal and Daams, 1988).

Córcoles. Van der Meulen et al. (2004) synonymized F. sacedoniensis (at that time called F. corcolesi) with F. decipiens, in spite of the important morphological differences and lump the two species present at that locality (Fig. 4) into one. The presence of a second species is undeniable and Freudenthal (2006) called it F. cf. koenigswaldi. The size distribution is discontinuous and lumping the two species leads to very high-values for the variability coefficient V’ (e.g. 30.4 for the length of M3). Democricetodon is not recorded at Córcoles but exists in localities of similar age.

Buñol. Accompanying F. decipiens, several very small specimens in the collections of the University of Utrecht can be attributed to D. hispanicus (Fig. 5): m2 sin., BU 1600 (1.15x1.06); M2 sin., BU 1936 (1.18x1.11). M3 sin. BU 1983 (0.78x0.94) is doubtful. In addition to this, two specimens of m3 (BU 1638: 1.30x1.24; BU 2001: 1.32x1.21) are outside the normal distribution (leading to a variability coefficient V’ for the width of 31.8) and may represent yet another species. This could be F. koenigswaldi, and that would mean that F. decipiens cannot be the ancestor of F. koenigswaldi.

Moratilla 2. Apart from D. moralesi (=F. koenigswaldi) this locality is reported to contain D. franconicus. However, the size variation of m2 is so great that there must be a third species (see section on D. franconicus).

Democricetodon moralesi van der Meulen et al., 2004

In the differential diagnosis of this species van der Meulen et al. (2004) did not compare it with F. koenigswaldi. In their Remarks they stated: “The material from VA1A, Olmo Redondo 5, 8 and 9 was hitherto considered to belong to D. koenigswaldi by Freudenthal and Daams (1988) neglecting the different configurations of protolophule and metalophule of M2. These assemblages are here assigned to D. moralesi”.

In the following we will use MV to analyze the morphology of D. moralesi and compare it with F. koenigswaldi, following the locality sequence and specific assignment of van der Meulen et al. (2004), in order to keep the two species separated.

Protolophule of M2

In D. moralesi the MV of the protolophule of M2 ranges between 1.9 (COLA) and 4.38 (MOR2); in the type-locality, COLD, it is 3.16. In F. koenigswaldi MV ranges between 2.45 and 3.91 (Fig. 6). The range of MV of D. moralesi is almost twice that of F. koenigswaldi and covers the range of all koenigswaldi populations. So, we agree with van der Meulen et al. (2004) that the configuration is different, but we don’t agree with their conclusion. In our opinion, the extremely high variability of D. moralesi populations is due to the presence of two different species in varying numbers, and the MV obtained are questionable.
Eliminating from Figure 6 some extreme values (COLA, OR8 and MOR2), the remaining populations show a gradual increase of MV: all eight populations of *F. koenigswaldi* below the type-locality VA1A have a lower MV than in VA1A, and 13 of the 16 younger populations have a higher MV. Following this situation downwards we see that nearly all populations of *D. moralesi* are thought to be older than the type-locality COLD and their MV values are lower than in COLD.

**Metalophule of M2**

Seven of the eight populations of *F. koenigswaldi* below the type-locality VA1A have smaller MV than in VR1A; above VA1A half of them are smaller, the other half are larger (Fig. 7). In the *moralesi* populations the trend is very small, the *koenigswaldi* populations show a gradual increase of MV.

**Mesoloph of M1 and M2**

We did the same analysis for several other features, e.g. the length of the mesoloph of M1 and M2: no trend is observed; the two species are identical throughout their distribution.

**Synonymy of *D. moralesi* and *F. koenigswaldi***

From the above analysis we conclude that there is no difference in size between the two species (Fig. 1; Table 3); only the youngest populations of *F. koenigswaldi* are slightly larger, and the type-populations are identical. On the basis of morphology, our conclusion is that *D. moralesi* and *F. koenigswaldi* form an evolutionary unit. Since the type-population of *D. moralesi* (COLD) cannot be distinguished from the oldest populations of *F. koenigswaldi*, *D. moralesi* is a synonym of *F. koenigswaldi*. One might distinguish another species, based on one of the older populations of *D. moralesi*, e.g. VR1A, where MV are lower than in any *koenigswaldi* population; the problem is that in those populations a mixture may exist with an unnamed *Democricetodon* species.

The *koenigswaldi*-lineage continues upwards into *F. darocensis* (FREUDENTHAL AND DAAMS, 1988); its origin in *F. decipiens* is doubtful, because of the possible presence of *F. koenigswaldi* in Buñol (see above). The supposed ancestor -descendant relationship of *D. hispanicus*–*F. decipiens* must be rejected since in Buñol the two occur together.
Van der Meulen et al. (2004) stated: “The smaller sized material from VR1A, OR5, OR8 and OR9 was assigned (by Freudenthal and Daams, 1988) to D. hispanicus, despite the morphology of all these samples being similar to that of VA3B and significantly different from D. hispanicus”. However, no such material is present in OR8 and, in our opinion, the material from OR5, OR9 and VR1A is too poor to permit a reliable classification. In size, it is compatible with D. hispanicus. Morphologically, it may be assigned to any small Democricetodon. Morphologically, it may be assigned to any small Democricetodon.

Another problem is the role of VA3B. The collections of Museum Naturalis (Leiden, the Netherlands) contain a series of specimens from VA3B with catalogue numbers RGM147532–147549, which was collected shortly after the completion of Freudenthal’s Thesis, and donated by Utrecht University in 1969. During the 1976–1986 field campaigns Daams and Freudenthal tried to locate and sample VA3B as one of the original localities of Freudenthal (1963), and our recovery of Freudenthal’s original field notes has made it clear that the resulting new material, housed in Naturalis-Leiden under the numbers RGM268339–268371, is not from VA3B, but from a lower level, here called VA3AB (possibly equivalent to VA3A in Fig. 8). The composition of the two samples is completely different: the original VA3B collection of Freudenthal (1963) contains six specimens of Democricetodon and 59 of Pseuodofahlbuschia; in the VA3AB collection there are ten Democricetodon and five Pseuodofahlbuschia specimens. Among the Democricetodon there are three M2 and four M2, respectively; the other elements of the dentition are even less frequent and such numbers impede an evaluation of the morphology. On the other hand, Figure 8 suggests a correlation of VA3AB with VA11; in both localities Democricetodon dominates over Pseuodofahlbuschia.

**Democricetodon franconicus Fahlbusch, 1964**

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FIGURE 6. Morphology Values (MV) of the protolophule of M2. Locality sequence and taxonomic attribution following van der Meulen et al. (2004). Minimum population size n=5. See Table 1 for abbreviations of localities.

FIGURE 7. Morphology Values (MV) of the metalophule of M2. Locality sequence and taxonomic attribution following van der Meulen et al. (2004). Minimum population size n=5. See Table 1 for abbreviations of localities.
Among the about 20 localities with *D. franconicus*, recognized by van der Meulen et al. (2004), only five or six are sufficiently rich to permit a reliable analysis of the morphology, another five are marginal; measurements of several elements from MOR2 are so extremely variable that this population is certainly not homogeneous (V' for length and width of m2, 34.2 and 36.5). Moreover, the single M1 (1.94x1.32) and m2 (1.50x1.12) from VA3AB are larger than any *D. franconicus* specimen, including Erkertshofen, where n=200 (see Fig. 9).

The populations here under discussion are certainly not *D. franconicus*, as shown by Freudenthal (2006, pg.: 52), on the basis of morphology. Some of them may belong to *D. hispanicus*, others may not. The scarce material from VA3AB is neither *D. franconicus* nor *D. hispanicus*; for the moment we continue calling it *D. cf. affinis*.

### THE CORRELATION OF THE VALDEMOROS MAMMAL SITES

The species assignment by van der Meulen et al. (2004) strongly depends on their interpretation of the stratigraphy and tectonics of the area: all localities with *F. koenigswaldi* are younger than those with *D. moralesi*. A different interpretation of the locality sequence, as concluded by Freudenthal (2006), results in an alternating presence of the two species, but that is no problem since we consider them to be synonymous.

Additional field work has enabled us to enforce Freudenthal’s interpretation. Here, we focus on the relative position of the two key localities: Valdemoros 1A (VA1A) and Valdemoros 3B (VA3B), (Fig. 10). Both sites are located on the topographic map 1:25,000, 438-III, Villafeliche. Figures 11 and 12 (slightly modified after Freudenthal, 2006) represent the relative stratigraphic position of both localities, as observed from a point located at UTM 626700/4560900. According to van der Meulen et al. (2012), “this section gives an unrealistic blending of the different situations in the two separate valleys”. In our opinion, Figure 12 represents objective field observations and reproduces exactly the situation in the ravine West of VA3B. VA1A is projected into this section through a less than 300m lateral displacement following the strike direction of the strongly North-dipping strata. VA3B is located about 25m East of this ravine (see arrows in Fig. 10). The position of the beds is identical to the situation at VA1A: the steeply North-dipping silts and conglomerates that contain the fossil locality VA1A are unconformably overlain by subhorizontal marly beds and limestones. One may discuss the exact position of a specific fossil locality, but the tectonic structure of the two valleys is the same.

In both interpretations it is necessary to suppose a stratigraphic hiatus. Van der Meulen et al. (2012) assumed a hiatus in the VA3B section, between Valdemoros 3D and the overlying Valdemoros 3E. However, in that range the sediments are horizontal, concordant and apparently continuous; thus there is no field evidence of a hiatus at this position. On the contrary, there is strong evidence of a hiatus immediately above VA1A, where the beds change from dipping 60ºN to lying subhorizontal (Fig. 12), in only a few-meters distance.

The exact location of locality VA3B was slightly misplaced by Krijgsman et al. (1996). Here, we correlate the original log of Freudenthal (1963) with that of Krijgsman et al. (1996) and indicate the correct stratigraphic position.
of locality VA3B, just below the fourth limestone bank of the section (Fig. 8) -mb11 in Freudenthal (2006)- whereas Krijgsman et al. (1996) placed it on top of that limestone. That means that VA3B falls within a reversed polarity magnetozone.

The Aragón Section

Lithology and magnetic polarity of the Aragón Section were first published by Krijgsman et al. (1994); its location on the map was first given by Daams et al. (1999b). Magnetostratigraphic correlation is apparently based on the assumption of sedimentary continuity. However, the transition from steeply dipping to subhorizontal beds in a few meters distance immediately above VA1A proves the sequence to be discontinuous at this level. Therefore, in Figure 13 the magnetostratigraphic Aragón Section is split up, which allows to accommodate the hiatus that contains VA3B.

![Figure 8. Section of VA3B, modified from field notes of Freudenthal (1963), and correlated to the upper part of the Vargas section of Krijgsman et al. (1996). See Figure 10 for location and Table 1 for abbreviations of localities.](image)

![Figure 9. Length distribution of molars M1 and m2 of Democricetodon hispanicus and Democricetodon "franconicus". Number of specimens to the right of each bar. See Table 1 for abbreviations of localities.](image)
The Vargas Section

Lithology and magnetic polarity of the Vargas Section were first published by Krijgsman et al. (1996), but without an exact location. Daams et al. (1999) located it on the map and published a lithological log. According to their map, its top is in VR11 (=Umbrías Fm.). However, this is incompatible with the magnetostratigraphic log of Krijgsman et al. (1996, fig. 3): the upper part of that section contains localities like VA3B and VA3D and is the same as our Valdemoros 3B Section. We infer that Krijgsman et al. (1996) did not follow the trajectory drawn on the map of Daams et al. (1999a), but moved some 300 or 400m to the East, crossed the Rambla de Vargas, and added the Valdemoros 3B section on top of the lower part of the Vargas Section. Since the bed-to-bed correlation was uncertain, they added an unexposed stretch in the middle of their Vargas Section. Neither is the lower part compatible: a locality (FTE4) located at 40m in the

FIGURE 10. Map of the Aragonian type area, adapted from Daams et al. (1999b, fig. 2) with the location of Valdemoros 1A (VA1A) and Valdemoros 3B (VA3B) and the observation point in red (>) from which their relative position is reconstructed. Red arrows show the projection of localities VA1A and VA3B into section F-F’. A-A’: Aragón Section, V-V’: Vargas Section, F-F’: this study’s section of Figure 12. Numbers 4-11 are marker beds.
log of Krijgsman et al. (1996) appears at 90m-height in the log of Daams et al. (1999); in Krijgsman et al. (1996) the locality VR4A is situated 22m above the base of the section, whereas in Daams et al. (1999a) this is 60m.

Daams et al. (1999a) stated: “From our study of the geology of the area, it appears that the Valdemoros 3 area is separated from the type section by a N-S striking, approximately vertical normal fault, the Valdemoros 3 section belonging to the higher block”. Freudenthal (2006) showed that that fault does not affect the area of VA1A and VA3B and is therefore irrelevant for the correlation of the sections.

In view of these facts we think that only the VA3B Section is useful for determining the relative position of VA1A and VA3B; the Vargas Section should be discarded until information about its upper part is available. In our Figure 13, the magnetostratigraphic Vargas Section is split up at the level where Krijgsman et al. (1996) supposed an unexposed sequence.

**Proposed correlation**

Hiatuses, as well as unexposed sequences, imply that the magnetostratigraphic log may be incomplete: one or more chrons may be missing, and the correlation to the GPTS may allow various interpretations. In fact, VA3B was correlated to C5Cn.2n by Krijgsman et al. (1996), while Daams et al. (1999b) made a different interpretation and placed it in C5Bn.1n, and we propose here a correlation to C5ADr (Fig. 13).

On the other hand, VA1A was previously correlated to C5ADn (Krijgsman et al., 1996; Daams et al., 1999b), whereas we correlate it to C5Bn.2n or C5Cn.1n. In the Aragón Section, the interval below VA1A has no data, and on top of VA1A we place an important hiatus. Due to this incompleteness, VA1A is an isolated level in terms of magnetostratigraphy and it is impossible to decide a reliable paleomagnetic correlation for this locality. The reversed polarity interval C5Bn.2r may be either above or below VA1A.
According to van der Meulen et al. (2012), Freudenthal disregarded “the important role of the Armantes Section that was unambiguously correlated to the GPTS, as a result of which the type section could be calibrated with the aid of biostratigraphy”. As far as the biostratigraphy is concerned, Krijgsman et al. (1994) only mentioned the locality Armantes 1, the fauna of which has never been revised after the first publications (Freudenthal, 1963; de Bruijn, 1965, 1967), and said that no fossil record is available from 16.0 to 14.8 Ma, precisely the time that is crucial for the problem here under discussion. Therefore, the magnetostratigraphy of the Armantes Section does not contribute with relevant information to constrain the relative position of VA1A and VA3B. Daams et al. (1999b) changed the paleomagnetic calibration of the long reversal in the Vargas Section (containing localities FTE2 and FTE3) from C5Cr to C5Br, on the basis of the biostratigraphic correlation of fossil locality Armantes 1A. However, that locality has a peculiar faunal composition, unknown in the Villafeliche area, and the supposed correlation is not reliable.

Thanks to the data of van der Meulen et al. (2012; appendix, fig. II) it is now possible to refine the correlations across the Rambla de Vargas. In Figure 14, we identified the marker beds and some of the localities (VR8C and VR11) mentioned by van der Meulen et al. (2012) and came to the conclusion that the equivalent of VA3B may be found between mb10 and mb11.

**BIOSTRATIGRAPHY**

The Aragonian was divided into local zones A–G by Daams and Freudenthal (1981). In 1988, Daams and Freudenthal subdivided zone D into D1, D2 and D3. Daams et al. (1999a) changed the zonation into Da, Db and Dd, and placed Valdemoros 3B in zone Dc and Valdemoros 1A in the younger zone Dd. This zonation is considered incorrect because of the inverted sequence of VA3B and VA1A as discussed above. But that does not automatically restore the zonation D1–D3, because since its creation the number of fossiliferous localities has increased considerably.

In 1988 the biostratigraphy was quite simple: *Fahlbuschia koenigswaldi* is present in zone D1, and
replaced by *Pseuodofahlbuschia* in zone D2; zone D3 is characterized by *Fahlbuschia freudenthali* and *Renzimys lacombai*. *F. freudenthali* was considered to represent a lineage different from *F. koenigswaldi* and, in zone E, the *koenigswaldi*-lineage returned, represented by *F. darocensis*. Van der Meulen et al. (2004) did not recognize *F. freudenthali* and *F. darocensis*, a point of view that obscures the possibility that these species may be present in the new localities now available.

Therefore we refrain from proposing a new biostratigraphic scheme and provisionally accept the D1-D2-D3 division. However, as already hinted at by Daams and Freudenthal (1988), that zonation, apart from chronology, may include a climatic or biotopic component: the fossil sites are accumulations of transported material and the replacement of *F. koenigswaldi* by *Pseuodofahlbuschia* may be the result of different biotopes in the hinterland that acted as source areas of the fossiliferous sediments. If that assumption is correct, the zonation is still valid, but the zones may (partially) overlap in time.

**CONCLUSIONS**

The populations attributed to *D. moralesi* cannot be distinguished from *F. koenigswaldi*; *D. moralesi* is a junior synonym of *F. koenigswaldi*.

The Spanish populations attributed to *D. franconicus* represent several other species, and certainly not *D. franconicus*.

The biostratigraphy of the Aragonian by Daams et al. (1999a) fails, in our opinion, to conform to the stratigraphic superposition of localities in its type area. The zonation of Daams and Freudenthal (1988) remains thus as the best available scheme, though it may represent a combination of chronology and ecological factors.

**FIGURE 14.** Probable correlation of Valdemoros 3B North of the Rambla de Vargas. This correlation corresponds to the part of the Vargas Section of Daams et al. (1999a, fig. 4) between VR8C and VR9. Photography taken from UTM 626700/4561324, towards the West. Mb10 and mb11 are marker beds.
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