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Trophic flexibility within the oldest Cervidae lineage to persist through the Miocene Climatic Optimum

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ABSTRACT

The oldest known Cervidae lineage, *Procervulus*, is a useful example for understanding the adaptations of mammalian clades to climatic and environmental changes. It appeared in the Lower Miocene (MN3), persisted through the Miocene Climatic Optimum, and became extinct at the onset of the Mid-Miocene general cooling. A combined approach of dental microwear and mesowear is undertaken to reconstruct its feeding behaviour to learn whether and how it responded to new environmental circumstances. None of the Early and Middle Miocene fossil taxa in the Calatayud–Daroca and Rubielos de Mora basins (NE Spain) had a wholly browser or grazer lifestyle, but rather dietary strategies equaling those of extant mixed feeders. However, members of *Procervulus* were sensitive to changes in the structure of ecosystems and vegetation that occurred during the Middle Miocene, and responded to these by substantially increasing the intake of grasses and abrasives. Despite this, it did not apparently display the sufficiently high trophic flexibility to bring about a change in its feeding style. Two possible, probably interrelated, causes can be pointed out; constraints imposed by both its small body size and its brachydont cheek teeth. If such a change in the feeding style was crucial for its survival, *Procervulus* disappeared as a consequence of an insufficient response to environmental changes because it may have been unable to compensate for the low nutritional content and abrasiveness of the new food items over a prolonged period. As the last *Procervulus* and the first bovids in the basin have similar dental wear signals, competition could be another possible explanation for its disappearance. Middle Miocene *Procervulus* could have been at a clear disadvantage after the advent of *Tethytragus*, whose teeth present morphologies that suggest better adaptation to grass-eating. Since diets tend to reflect habitats, the wear signals and assignments obtained from the Ramblian and earliest Aragonian cervids are indicative of humid climates and mixed environments, where closed areas were well developed and browse vegetation was abundant. In contrast, data from late Early and Middle Aragonian cervids and bovids reflect dry-seasonal and more open scenarios, with a higher diversity of grasses and abrasives.
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1. Introduction

An important interval in the global climatic and evolution of terrestrial mammalian faunas was the Early to Middle Miocene (Zachos et al., 2001). The cooling and rapid expansion of Antarctic continental ice-sheets that took place in the earliest Oligocene persisted until the latter part of the Oligocene, when a global and gradual warming trend reduced the extent of the ice (the warmest since the late Eocene; Flower and Kennett, 1994). From this point until the Middle Miocene the global ice volume remained low, and bottom water temperatures were slightly higher (Miller et al., 1991a; Wright et al., 1992). This warm and humid period, characterized by tropical and dry conditions in the basins of NE Spain (van der Meulen and Daams, 1992), peaked in the Middle Miocene Climatic Optimum, and was followed by a sudden decrease in temperature, the Mid-Miocene cooling, related to the reestablishment of the east Antarctic ice-sheet (Miller et al., 1991b; Zachos et al., 2001; Shevenell et al., 2004; Lewis et al., 2008).

This succession of events, associated with tectonic processes and sea-level oscillations, had enormous consequences on ecosystems, and therefore, on the further evolution of terrestrial mammalian faunas. Antarctica terrestrial organisms were obviously most affected (Lewis et al., 2008), but the European artiodactyls and perissodactyls also witnessed drastic changes in paleoenvironmental conditions (Zachos et al., 2001), and were some of the groups most significantly affected. Extinction, migration, or adaptation to the new conditions, for example, are some of the most important bioevents commonly attributed to major changes, and are well-known to have occurred during this epoch (Pickford and Morales, 1994).

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Therefore, the Early to Middle Miocene is one of the most remarkable and interesting intervals for investigating the influence of global climatic changes on local environments, and the adaptive response of mammals that were highly sensitive to the shifts occurred.

In order to obtain paleoclimatic and paleoenvironmental reconstructions as accurately as possible, we must look for the characterization of taxa that respond to changes in terms of adaptive strategies. Ruminants are particularly suitable for reconstruction, and consequently are among the most frequently utilized paleoecological indicators (Gordon and Illius, 1994). This is due to the fact that they are entirely dependent on different types of plants for nutrition and, therefore, adapted to a wide variety of habitats, and also because of their ubiquity at fossil sites.

Interestingly, we have a well-documented and continuous record (4 Ma) of a ruminant lineage (*Procervulus*, Cervidae) that persisted through the Miocene Climatic Optimum, but which became extinct at the onset of the Mid-Miocene cooling. We consider this lineage as a useful example for understanding the problems that certain mammalian clades encounter when trying to adapt to new local environmental conditions; perhaps by being unable to sufficiently exhibit the trophic flexibility to respond to a change in the structure of the vegetation. As *Procervulus* was also coincident with the first bovids in the basin (*Tethytragus*, Bovidae), both groups should have competed directly, and its disappearance could have also been a consequence of food competition with these new, though better morphologically adapted, taxa.

Since cervids and bovids from northeast Spain witnessed notable paleoenvironmental shifts that other authors have pointed out to have occurred during this temporal interval (van der Meulen and Daams, 1992), the main object of this study is to provide an accurate description of *Procervulus* feeding habits to learn whether and how this taxon responded to changes (dietary response). It could be expected that potential changes strong enough to promote certain important faunistic events would affect the abundance of vegetation and, consequently, would have an immediate and recordable effect on dietary signals. It is also our aim to better reconstruct the environmental context of northeast Spain during the Early and Middle Miocene by attempting to provide information on aridity and seasonality, how open the habitat was or how widespread grasses were.

2. Materials and methods

2.1. Geographical setting and data collection

We studied fossil material housed in the Museo Paleontológico de la Universidad de Zaragoza (Zaragoza, Spain), Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain) and Instituut voor Aardwetenschappen, Rijksuniv (Utrecht, Holland). The material belongs to the Neogene Calatayud–Daroca and Rubielos de Mora basins, which are located respectively in the north central and eastern Iberian Chain, NE Spain (Fig. 1). The basins of these areas display well exposed Early–Middle Miocene deposits containing a rich record of mammal remains. The presence of almost continuous sections with mammal localities make these basins ideal for defining mammalian continental stages, such as the Ramblian (Daams et al., 1987) and the Aragonian (Daams et al., 1977). Although the record is particularly rich in rodent communities, evidencing remarkable changes in climatic and environmental conditions, it is also characterized by an abundant presence of macromammals, among which ruminants are the dominant group.

As teeth are the basis of taxonomic research in the taxa investigated here, our study was applied to the dentition of cervids and bovids. We analyzed 72 dental specimens, after excluding unworn teeth and specimens in early and late wear (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002; Kaiser and Rössner, 2007), from the following 13 localities which span a temporal interval of approximately 4 Ma. The abbreviations used in text, tables and figures refer to large mammal locality names are as follows: *AGR* = Agreda, *MOR* = Moratilla and *AB1* = Alto de Ballester 1 in the Late Ramblian (Zone A, MN3); *SAM* = San Marco and *ART* = Artesilla in the Early Aragonian (Zone B and C, respectively, MN4); and *VALT* = Valtorres, *VDM1A* = Valdemoros 1A, *VDM3A* = Valdemoros 3A, *TOR1* = Torralba de Ribota 1, *MUN1* = Munébrega 1, *ARM3* = Armantes 3, *MUN3* = Munébrega 3 and *TOR5* = Torralba de Ribota 5 in the Middle Aragonian (Zone D, MN5). For an easier understanding of the text, the abbreviations of the localities after "*P*" or "*T*" are used to indicate a population of *Procervulus* or *Tethytragus*, respectively. The taxonomical study of most of the material belonging to *Procervulus* is included in Azanza (2000).

The fossil assemblage from these localities is varied and extensive, and is typically dominated by ruminants. *Procervulus* is one of the oldest Cervidae known and its dietary adaptations are thus of great interest. From the Upper Ramblian until the Middle Aragonian, *Procervulus* is the only member of Cervidae represented here and it coexisted with paleomerycids and occasionally with lagomerycids, other cervoid groups. There is a low diversity of bovids during this epoch and only *Tethytragus* has been distinguished.

Due to the shortage of material from *Procervulus* in the Middle Aragonian localities, it was decided to gather all the specimens to obtain more reliable dietary signals by assuming they belong to a single population which was extended through this interval (referred to here as "whole population"). In order to better understand the dietary assignments obtained because some samples are not statistically significant, we also realized variability studies by using as a reference the results obtained from the largest samples.

2.2. Dietary assessment methodologies

The type of vegetation available is one of the best indicators used to determine physical and ecological characteristics of the ecosystems in which herbivores lived. It is understandable, therefore, that paleodietary reconstructions have figured importantly in paleoecology and have been attempted extensively using a number of different approaches (Pérez-Barbería and Gordon, 1999; Fortelius and Solounias, 2000; Cerling et al., 2003). Among these, dental wear patterns are one of the most widely used by preserving signals directly related to the diet of an individual (Solounias and Semprebon, 2002; Merceron et al., 2005).

In this study, we undertook a combined analysis of microwear and mesowear procedures of dietary assessment on tooth material. The feeding of ungulates is traditionally explained along a browser/grazer continuum, with three broad categories typically recognized: browsers, mixed feeders and grazers (Hofmann and Stewart, 1972). Consequently, both methods discriminate between these categories in a wide variety of ungulate taxa.

Dental wear analysis deals mostly with the characterization of past environments (Merceron et al., 2004; Ungar et al., 2007) or dietary resource partitioning (Kaiser and Rössner, 2007) and competition studies (Valli and Palombo, 2008). However, only a few works have attempted to investigate how the diet within a genus or a species has historically varied through an important climatic event (Semprebon et al., 2004; Rivals and Solounias, 2007). Also, although micro- and mesowear have recently been used in tandem to shed light on the ancestral feeding state of Cervidae (DeMiguel et al., 2008) and on competition of early Spanish pecorans (DeMiguel et al., unpublished results), here we present the first attempt to use these methods to characterize the paleoenvironmental context of Spain. Information of such recent studies is also included here, to thus contribute to a better and a more complete paleoenvironmental reconstruction.

Dental microwear is the result of the abrasion of teeth by food items consumed during the last days prior to the death of an animal. The method applied for this study was performed following the procedure developed by Solounias and Moelleken (1992), which has

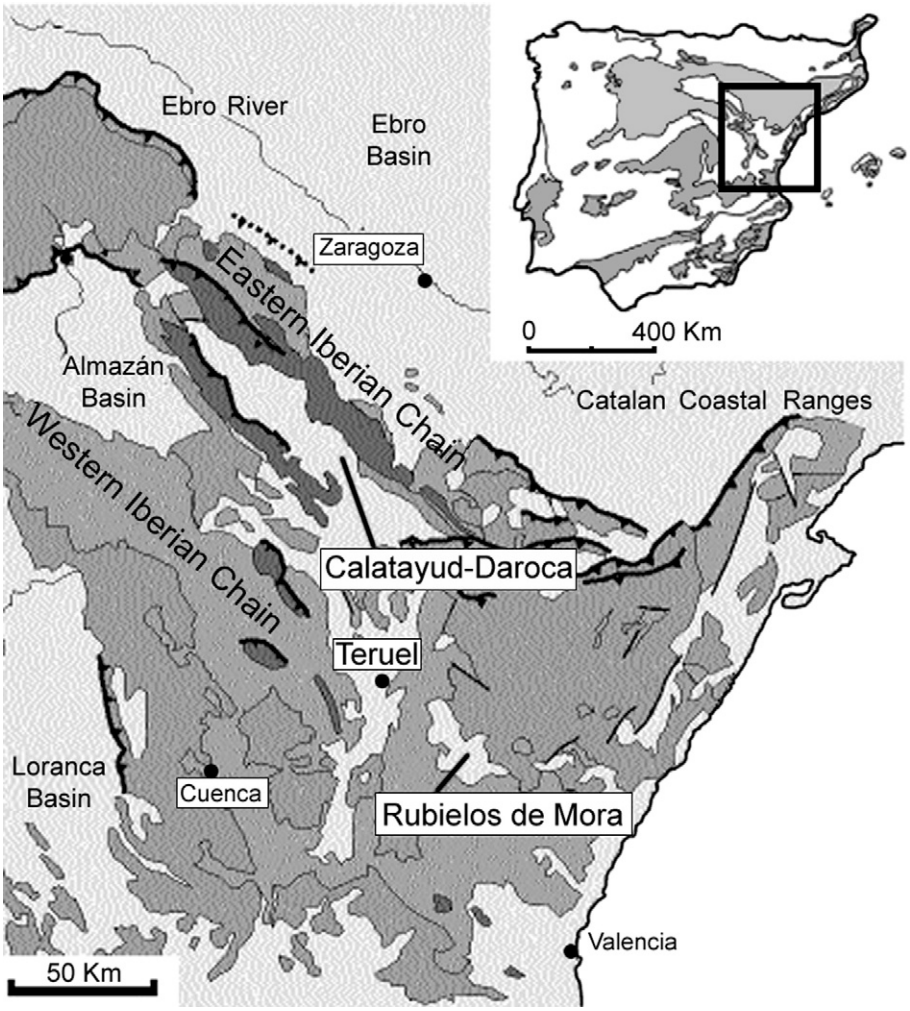

Fig. 1. Location map of the studied basins (Calatayud–Daroca and Rubielos de Mora) in the Iberian Chain (NE Spain).

been widely used by other authors. Microscopic marks were observed by means of an Environmental Scanning Electron Microscope (ESEM) FEI Quanta 200. Images were taken systematically in a surface of approximately 0.20 mm × 0.20 mm and were treated with specific microwear software. Scar dimensions were directly categorized on the basis of the ratio length/width (scratches: 4<ratio<100, pits: ratio = 4). The number of scratches and pits we obtained were then transformed into a density score in order to simplify the comparison of fossils with other extinct and extant ungulates (Rivals and Deniaux, 2003). In addition to scratch and pit densities, we also introduce large pits, cross scratches and scratch texture (Solounias and Semprebon, 2002) as qualitative variables to further analyze fossil cases where microwear was controversial or unclear. Analysis was performed using the dataset of 28 well-known extant ungulates compiled by Solounias and Moelleken (1994) and Solounias et al. (2000) and sharing the same protocol concerning high magnification (×500) and SEM. The study focused as far as possible on the anterior lingual blade of the paracone on the M^2 and the posterior buccal blade of the protoconid on the m_2 permanent because these facets are in occlusion together during the chewing–shearing phase and these teeth show an intermediate wear stage between the first and the third molar (Gordon, 1982). Dental microwear comparisons were made using a dataset (Solounias et al., 2000) composed of leaf ($N = 7$) and fruit ($N = 3$) browsers, seasonal ($N = 7$) and non-seasonal mixed feeder ($N = 4$), and grazers ($N = 7$).

Dental mesowear is based on the physical properties of food as reflected in the relative amounts of attritive and abrasive wear that they cause on the teeth (Fortelius and Solounias, 2000). Occlusal relief (characterised as either high or low) and the cusp shape (sharp, rounded, or blunt) of the apex of the paracone and metacone of M^1–M^3 and the metaconid and entoconid of m_1–m_3 were examined using a stereomicroscope Olympus SZ11 and qualitatively scored. Variables were also converted to a single score (mesowear score; unpublished method developed by M. Mihlbachler) as proposed in Semprebon and Rivals (2007). Thus, specimens with a combination of sharp cusps and high relief were assigned a value of 0; those with a combination of rounded cusps and high relief were assigned a value of 1; a combination of rounded cusps and low relief were assigned a value of 2; a combination of blunt cusps and low relief were assigned a value of 3. Mesowear values for each specimen within a sample were then averaged to obtain the global mesowear score for that sample. The comparative extant database of Fortelius and Solounias (2000) was followed as a reference from which samples represented by less than 10 individuals were removed in order to obtain a range in which distributions that look different become significantly different statistically. The mesowear patterns of fossils were therefore compared to those of a set of 54 extant ungulates partitioned into conservative fruit ($N = 5$) and leaf browsers ($N = 12$), conservative mixed feeders ($N = 26$) and conservative grazers ($N = 11$). The duikers, hyraxes, *Procavia capensis* and *Hyaemoschus aquaticus* ("MABRA", for "minute abraded brachydont") show quite unclear dental mesowear (Fortelius and Solounias, 2000).

Using the procedure described in DeMiguel et al. (2008), multivariate analyses were performed with SPSS 11.5 statistical

software to determine the most probable feeding categories of *Procervulus* and *Tethytragus* species. The microwear studies were developed using densities of scratches and pits as criterion variables, while the combination of rounded, blunt cusps and high relief were used for the mesowear analyses.

Hierarchical cluster analyses were first applied as an explorative technique for identifying herbivorous species groups and emphasizing any inherent structure, based on similarities in the dental wear pattern. The analyses were realized using the Euclidean distance and Ward's method. Discriminant analyses were then employed to evaluate the ability of the dental wear variables set with the purpose of distinguishing between the four conventional dietary classes of extant taxa and also to classify the fossil cases according to the model derived. For the discriminant mesowear analyses, two dietary classifications (conservative and radical), were used alternately as a grouping variable. A combined use of two parallel classifications will allow us to recognize those fossil taxa that, although being adapted to feed on mixed diet, are shifted toward the browse-dominated end or toward the grass-dominated end of the mixed feeder continuum. Also, comparison of results from both classifications will enable us to accommodate cases where dietary information is controversial or unclear (Fortelius and Solounias, 2000).

3. Results and description

Presented in Table 1 are micro- and mesowear summary results and also the number of specimens measured in the sample and the basin to which they belong.

3.1. Analysis of micro- and mesowear features

3.1.1. Procervulus (Ramblian and lower Aragonian localities)

In the previous studies carried out by DeMiguel et al. (2008, in prep.), diets of some *Procervulus* were investigated. Dental micro- and mesowear placed P_{AGR} and P_{MOR} within the class of browse-dominated mixed feeders, while suggested that P_{AB1} and P_{ART} most closely resemble to extant seasonal mixed feeders, and that the latter was a species more inclined to grazing.

3.1.2. P_{SAM}

It exhibits a microwear pattern (Fig. 2a) comprised of few scratches and an intermediate pit density (641 scratches/mm^2 and 446 pits/mm^2), similar to those of extant browsers. *Cephalophus dorsalis* is a typical extant frugivorous and displays similar microwear densities (626 scratches/mm^2 and 569 pits/mm^2) to this *Procervulus*. When its microwear is further studied, it has no large and deep puncturelike pits, or coarse scratches. This fact could suggest that it was not a fruit-browser, but may also be due to the scarce sample.

P_{SAM}, with an overall score of 0.5, is characterised by a combination of sharp (50%) and round cusps (50%) and by a predominance of high occlusal relief (100%). Thus, the mesowear signal (Fig. 2g) reveals a moderately abrasive diet, which is more similar to that of *Taurotragus oryx* and *Tragelaphus scriptus* extant mixed feeders.

Such a discrepancy in dental micro- and mesowear could indicate that it ingested a significant amount of ligneous items just before death, despite having an average signal characteristic of a relatively medium-abrasion diet. Since the mesowear is produced over a long feeding period in the animal's life (usually several weeks or months; Fortelius and Solounias, 2000) and the microwear is the direct result of the abrasive action during the last few meals (Solounias and Semprebon, 2002), the heterogeneity concerning P_{SAM} could indicate a difference between their average trophic practices and the last meals content. A possible interpretation for this would be a seasonal variability in the type of ingested food, with a prevailing mixed feeder strategy.

3.1.3. Procervulus (Middle Aragonian localities)

Most of the populations have similar microwear features (Table 1, Fig. 2b–f). Their teeth are mainly characterised by an intensive striated enamel surface and by intermediate pitting, similar to those of extant grazers. A clear difference is however evident in the amount of scratches of the following two populations. It was observed that P_{VDM3A} (Fig. 2c) displays the highest striation (1648 scratches/mm^2), suggesting more abrasives in its diet. It is apparent from examining the density of scratches that P_{VDM3A} shares strong affinities with extant non-seasonal mixed feeders. In contrast, P_{MUN1} (Fig. 2d) exhibits less striated enamel surfaces (981 scratches/mm^2), and this feature bears more resemblance to that of extant seasonal mixed feeders.

Middle Aragonian *Procervulus* display mesowear mostly comprised of high occlusal relief and sharp or rounded cusps, and have scores ranging between 0 and 1.5 (Table 1, Fig. 2h–n). When compared to extant ungulates, they fall into the ranges observed for browsers and mixed feeders (Semprebon and Rivals, 2007). A clear difference is however evident among the samples, and two trends are observed within the populations; those characterised mainly by a

Table 1
Summary of microwear and mesowear results. Number of individuals measured (*N*); standard deviation [SD]; scratches/mm^2 (*S*); pits/mm^2 (*P*); percentage of pits (%*p*); percentage of individuals with high (%*H*) and low (%*L*) mesowear relief; percentage of individuals with sharp (%*S*), rounded (%*R*) and blunt (%*B*) cusps; mesowear score (MS).

Locality	Basin	Microwear				Mesowear							Ref.
		N	*S*[SD]	*P*[SD]	%*p*[SD]	*N*	%*H*	%*L*	%*S*	%*R*	%*B*	MS	
Procervulus													
Ágreda	Calatayud–Daroca	2	675[174]	555[343]	43[9.8]	2	100	0	50	50	0	0.5	DeMiguel et al. (unpublished results)
Moratilla	Calatayud–Daroca	3	645[267.7]	642[26.3]	51[11]	2	100	0	50	50	0	0.5	DeMiguel et al. (unpublished results)
Alto Ballester 1	Rubielos de Mora	4	839[299.8]	534[183.9]	40[6.1]	13	92.3	7.7	14.3	85.7	0	0.8	DeMiguel et al. (unpublished results)
San Marco	Calatayud–Daroca	1	641[–]	446[–]	41[–]	1	100	0	50	50	0	0.5	This study
Artesilla	Calatayud–Daroca	13	1153[475.3]	864[406.5]	43[12.1]	40	92.5	7.5	13.75	75	11.25	1.012	DeMiguel et al. (2008)
Valtorres	Calatayud–Daroca	2	1291[199.4]	401[88.9]	24[1.2]	2	50	50	0	100	0	1.5	This study
Valdemoros 3A	Calatayud–Daroca	1	1684[–]	438[–]	21[–]	1	100	0	0	100	0	1	This study
Torralba Ribota 1	Calatayud–Daroca	–	–	–	–	2	100	0	25	75	0	0.75	This study
Munébrega 1	Calatayud–Daroca	1	981[–]	338[–]	26[–]	1	100	0	100	0	0	0	This study
Armantes 3	Calatayud–Daroca	–	–	–	–	2	100	0	0	100	0	1	This study
Munébrega 3	Calatayud–Daroca	2	1226[39.8]	364[220.9]	22[10]	2	100	0	50	50	0	0.5	This study
Torralba Ribota 5	Calatayud–Daroca	1	1237[–]	542[–]	30[–]	1	100	0	0	100	0	1	This study
Whole population		7	1276[207]	407[109]	24[4.9]	11	90.9	9.1	22.7	77.3	0	0.86	This study
Tethytragus													
Valdemoros 1A	Calatayud–Daroca	1	1432[–]	477[–]	26[–]	1	100	0	0	100	0	1	This study
Torralba Ribota 1	Calatayud–Daroca	–	–	–	–	1	100	0	0	100	0	1	This study

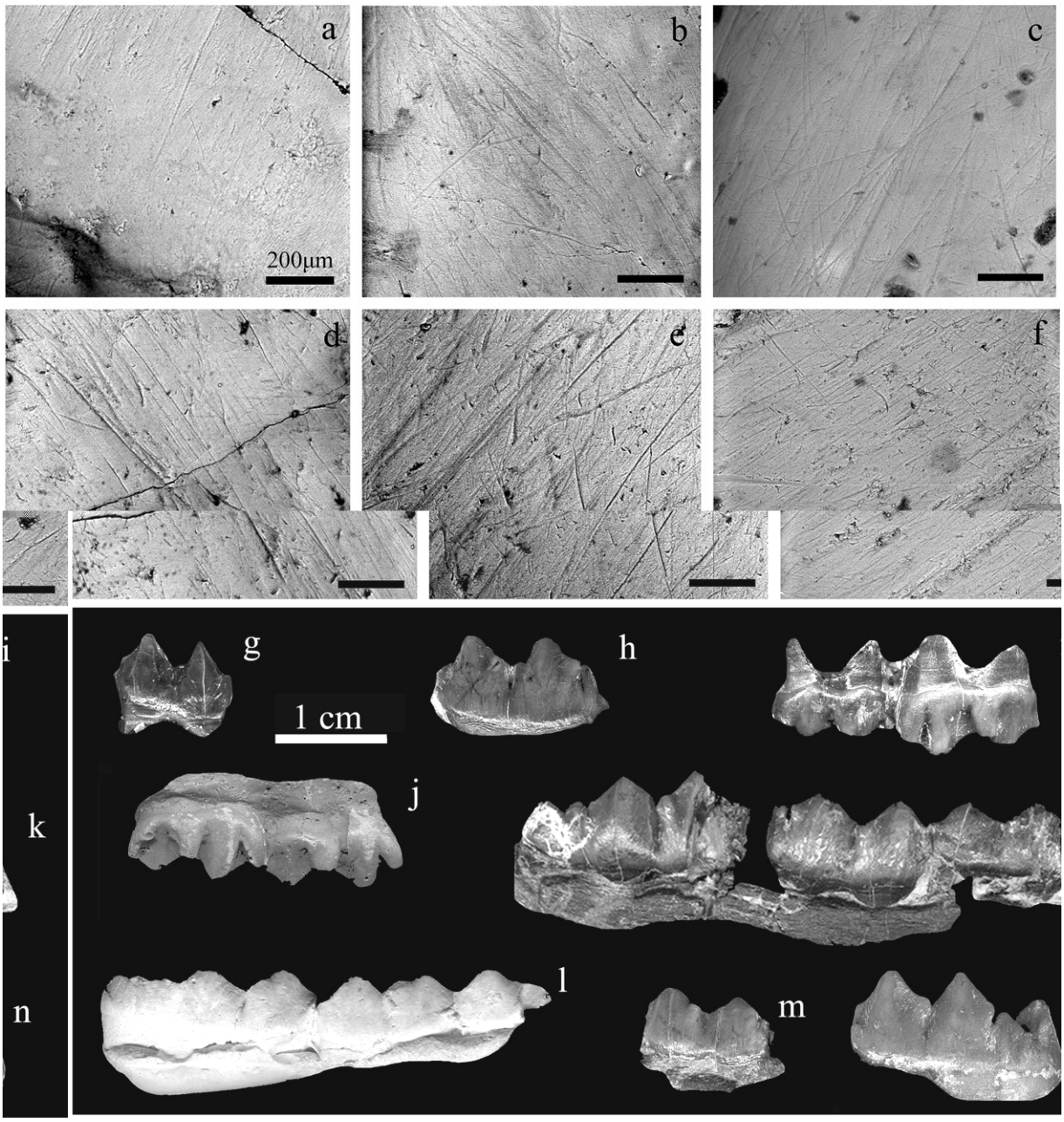

Fig. 2. ESEM photomicrographs at ×500 and mesowear features of selected *Procervulus* teeth. Microwear: specimens from San Marco (a; SAM/ss.: m_1), Valtorres (b; IVAU/VALT-56/501: m_2), Valdemoros 3A (c; IVAU/VA3A-501: M^2), Munébrega 1 (d; IVAU/MUN1-55/1119: m_2), Munébrega 3 (e; IVAU/MUN3-53/b0: m_2) and Torralba de Ribota 5 (f; IVAU/TOR5/ss.: m_3). Mesowear: specimens from San Marco (g; SAM/ss.: m_1), Valtorres (h; IVAU/VALT-56/501: m_2), Valdemoros 3A (i; IVAU/VA3A-501: M^1–M^2), Torralba de Ribota 1 (j; IVAU/ss.: M^2–M^3), Munébrega 1 (k; IVAU/MUN1-55/1119: m_1–m_3), Armantes 3 (l; IVAU/57-102 m_1–m_3), Munébrega 3 (m; IVAU/MUN3-53/b0: m_1) and Torralba de Ribota 5 (n; IVAU/TOR5/ss.: m_3).

high proportion of sharp cusps and scores between 0 and 0.75, indicating a significant attrition level (P_{TOR1}, P_{MUN1}, and P_{MUN3}; Fig 2j, k and m, respectively), and those showing strong rounding and scores ranging from 1 to 1.5, possibly because of fresh grass grazing (P_{VALT}, P_{VDM3A}, P_{ARM3}, and P_{TOR5}; Fig 2h, i, l and n). It must be noted that P_{VALT} has the highest score recorded in the sample (1.5).

When the "whole population" of *Procervulus* was analyzed (1276 scratches/mm^2 and 407 pits/mm^2), it was observed that its microwear pattern is almost exactly the same as that of P_{VALT} (1291 scratches/mm^2 and 401 pits/mm^2). The mesowear (90.9% High, 22.7%Sharp, 77.3%Rounded, 0.86MS) is however similar to that of P_{TOR1} (see Table 1), despite having a higher percentage of low occlusal relief (9.1%) that could be attributed to a higher degree of abrasion by the food consumed.

3.1.4. T_{VDM1A} and T_{TOR1}

The population from VDM1A is characterised by one of the highest scratch densities (1432 scratches/mm^2) on the shearing facets among the extinct fossils (Fig. 3a). This density is much higher than the average for the browsing ungulates (496 scratches/mm^2) and even higher to that of grazing ungulates (1231 scratches/mm^2). The pit density recorded for T_{VDM1A} (477 pits/mm^2) is higher than the value for the extant grazers (258.2 pits/mm^2) and is closer to that of some browsers (495.8 pits/mm^2). Such result could be indicator of dry, open environments (Solounias and Semprebon, 2002). Molar teeth of both T_{VDM1A} (Fig. 3b) and T_{TOR1} (Fig. 3c) displayed mesowear comprised of rounded cusps (100%) and high relief (100%), and a score of 1. This pattern is clearly different from the strict browser taxa, and reflects a moderately abrasive diet. Their percentages are close to