21

FOOD HABITS OF *"PRAEMEGACEROS" CAZIOTI* (DEPÉRET, 1897) FROM DRAGONARA CAVE (NW SARDINIA, ITALY)

INFERRED FROM CRANIAL MORPHOLOGY AND DENTAL WEAR

Maria Rita PALOMBO

PALOMBO, M.R. 2005. Food habits of *"Praemegaceros" cazioti* (Depéret, 1897) from Dragonara Cave (NW Sardinia, Italy) inferred from cranial morphology and dental wear. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 233-244.

Resum

S'ha estudiat l'adaptació alimentària de *"Praemegaceros" cazioti* (Depéret, 1897), en base a la rica mostra trobada als dipòsits del Pleistocè tardà de la cova de Dragonara (nord-oest de Sardenya, Itàlia). Amb aquest objecte, s'han pres en consideració els trets cranials, així com el gradient de desgast d'abrasió – atrició (mesodesgast), i els efectes produïts a l'esmalt dentari per les partícules contingudes als vegetals, per l'acidesa i/o duresa del menjar i per la força i direcció dels moviments mandibulars (microdesgast).

Els resultats de les anàlisis qualitatives i quantitatives són consistents amb una adaptació alimentària a una dieta mixta, tal com també ho són algunes característiques cranio-dentàries: en particular, el morro, més aviat quadrat, les grans àrees d'inserció del *musculus masseter*, el desenvolupament de la prominència massetèrica sobre el M^1, la profunditat i altura del *corpus* i *ramus* a l'*angulus mandibulae*, la superfície d'inserció reduïda del *musculus temporalis* a la mandíbula i les dents hipsodontes. Els resultats de la nostra anàlisi suggereixen que el cèrvid de la Cova Dragonara era un animal de dieta mixta, que va incrementar el consum d'herba en comparació amb el seu possible ancestre.

Paraules clau: *"Praemegaceros" cazioti*, Pleistocè tardà, Sardenya, morfologia cranio-dentària, microdesgast dentari, mesodesgast, adaptacions alimentàries.

Abstract

The dietary adaptation of *"Praemegaceros" cazioti* (Depéret, 1897) has been investigated on the basis of on the rich sample found in the Late Pleistocene deposits in Dragonara Cave (north-western Sardinia, Italy). To this end, we have taken into consideration cranial features as well as the abrasion-attrition wear gradient (mesowear) and the defects produced on tooth enamel by the particles contained in vegetables, by the acidity and/or hardness of food and by the strength and direction of jaw movements (microwears).

Results of qualitative and quantitative analyses of microwears are consistent with mixed-feeder dietary adaptation, as are some cranio-dental features: in particular the rather square muzzle, the large insertion areas of *musculus masseter*, the developed masseteric prominence above M^1; the depth and height of *corpus* and *ramus* at *angulus mandibulae*, the reduced insertion surface of *musculus temporalis* on the jaw and hypsodont teeth. Results of our analyses suggest that the cervid from Dragonara Cave was a mixed-feeder, increasing the consumption of grass as compared to its possible ancestor.

Keywords: *"Praemegaceros" cazioti*, Late Pleistocene, Sardinia, cranio-dental morphology, dental microwear, mesowear, dietary adaptation.

INTRODUCTION

Several morphological features of the herbivore skull, mandible and dentition can be correlated with dietary adaptations and used in estimating the feeding ecology of extinct taxa (e.g., Solounias & Dawson-Saunders, 1988; Janis, 1988; Solounias *et al.*, 1988; Solounias & Moelleken, 1993a,b; Janis, 1995; Caloi & Palombo, 1996; MacFadden & Shockey, 1997; Pérez-Barbería & Gordon, 1999; MacFadden, 2000; Pérez-Barbería & Gordon, 2001; Pérez-Barbería *et al.*, 2001; Williams & Kay, 2001; Mendoza *et al.*, 2002; Kaiser & Solounias, 2003; Mainland, 2003, and references therein).

As indicators of herbivore feeding behaviour, we can analyse cranio-dental morphology (see Mendoza *et al.*, 2002, and references therein), skull foramina (Solounias & Moelleken, 1999), the relative height of crown and the morphology of the occlusal surface of chewing teeth, which depend on combined attrition-abrasion actions (see Kaiser & Solounias, 2003, and references therein), the enamel scars produced during mastication by tooth-food and tooth-tooth contact (e.g., Resenberg, 1978; Solounias & Hayek, 1993; Solounias *et al.*, 2000; Solounias & Semprebon, 2002; Mainland, 1997; 2003; Teaford, 1988; 1991; 1994; Hayek *et al.*, 1991; Maas, 1991; Solounias & Moelleken, 1992; Palombo *et al.*, 2005).

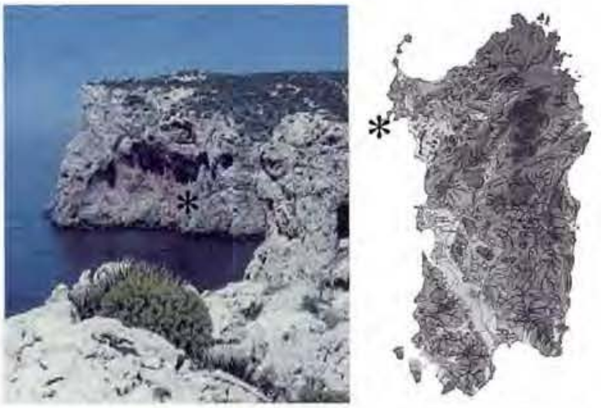

Fig. 1. Localisation of Dragonara Cave (Alghero, North-Western Sardinia).

Fig. 1. Localització de la cova Dragonara (L'Alguer, nord-oest de Sardenya).

Such features are obviously functionally constrained by the "baup-plane" inherited from the ancestor, as four main combined factors (phylogeny, morphogenetic structure, biological function, and environment), lead to the overall constructional morphology of each organism.

Moreover, it is worth noting that many ungulates are also opportunistic, and their diets can vary according to place or season or, sometimes, only occasionally. Though three main dietary classes (browser, grazer, mixed feeder) were generally considered, the type of food and lifestyle spectrum between typical grazer and browser is extremely varied, as highlighted by the heterogeneous feeding behaviour shown by so-called mixed feeders (see Kaiser & Solounias, 2003).

Deer, generally regarded as brachyodont herbivores inhabiting woodlands, are actually rather adaptable animals able to live in different environments (Geist, 1999). Among extant and Pleistocene cervids, many are mixed feeders, alternating seasonally, regionally or occasionally between browse and grass, though the feeding spectrum is extremely vast.

For instance, *Capreolus capreolus, Alces alces* and *Odocoileus virginianus,* are typical browsers*; Dama dama, Axis axis, Cervus canadensis, Rangifer tarandus* and species of the genus *Rusa* are feeders on fruit and foliage (trees and shrubs) as well as fresh-grasses, alternating their food according to the season, or even occasionally (meal-by-meal); *Elaphurus davidianus* and *Cervus albirostris* seems to be deer whose diet most resembles that of not strictly grazers (Hofmann, 1989; Cornelius *et al.*, 1999; Geist, 1999; Fortelius & Solounias, 2000; Cransac *et al.*, 2001; Stewart *et al.*, 2002), whereas the European *Cervus elaphus* feeds on the most available resources in its inhabited area (Groot Bruinderink & Hazebrock, 1995). Moreover, the feeding aptitude can change in particular environmental conditions, depending on the vegetation cover or the occurrence of unusual free ecological niches.

Accordingly, a multiple analytical approach (craniodental morphofunctional analysis, qualitative and quantitative studies of effects produced on tooth enamel during mastication) seems to be the most appropriate way to study the dietary preference of extinct mammals, especially in the case of the problematic group of deer. Research on the dietary adaptation of *"Praemegaceros" caziotí*[1] is of great interest, since this cervid is the only large herbivore existing in Sardinia during the Middle and Late Pleistocene. Consequently, *"P." caziotí* did not have any competitor for niche occupation and resource partitioning in Sardinia, whereas in Corsica, during the Middle Pleistocene, it had to compete with *C. elaphus rossii,* thus far not recorded in Sardinia (Pereira, 2001).

In the post-Tyrrhenian deposits of Dragonara Cave, more than 800 remains belonging to *"P." caziotí,* carefully described by Caloi & Malatesta (1974), were found. A preliminary analysis of the morpho-functional features of skull, mandible and *autopodium* (carpus, tarsus, metapodials and phalanges, Caloi & Palombo, 1991), as well as limb proportions, showed that the cervid from Dragonara Cave shared some cranial morphologies with grazers and was capable of agile, fast locomotion on prevalently hard and uneven ground (Caloi & Palombo, 1995; 1996).

In this paper, a multiple analytical approach is adopted in order to compare cranio-dental morphology with dental micro- and mesowear, using a large sample; this enables us to create support for further studies devoted to better defining the ecological niche of *"P." caziotí* from Sardinia and Corsica.

MATERIAL AND METHODS

We have examined the skulls, mandibles (Plate 1) and upper and lower teeth uncovered in the "post-Tyrrhenian" deposits filling the Dragonara Cave (Caloi & Malatesta, 1974) (Fig. 1). The specimens are currently kept at the "Museo di Paleontologia" at "La Sapienza" University in Rome (MPUR).

As far as craniodental morphology is concerned, we have analysed extant and fossil species as listed in the appendix.

Microwear analysis (see below) was done on casts of the enamel cusp of M^2 paracone. Analytical methods were adapted from those described by Solounias & Moelleken (1992) and Solounias & Semprebon (2002), for SEM and stereomicroscopic analysis respectively.

---

[1] It is worth noting that Joleaud (1914) proposed the name *Megaceroides,* as *Cervus* subgenus, with the type species *"Cervus" algericus,* for a fragmentary maxillary: subsequently, Arambourg (1932, 1938) ascribed a skull from the Late Pleistocene of Algeria and Morocco to this species. Mean similarities in skull characters between specimens from the Magreb and the megalocerine from Europe, first pointed out by Azzaroli (1952), have subsequently been widely debated (see e.g. Hadjoudis, 1990; Azzaroli & Mazza, 1992; Abbazzi, 2004; van der Made & Palombo, in press). All in all, it seems more correct to maintain the name *Megaceroides* only for the North African species. Nevertheless, the problem concerning the nomenclature of the genera referring to the tribu Megacerini is still unresolved. Assuming that the species ascribed to the so-called "*verticornis*" group and those to the "*giganteus*" group belong to two distinct lineages, what is the correct generic name to choose among those used thus far for the giant deer belonging to the "*verticornis*" group? The name "*Praemegaceros*", though not formally correct (see e.g. Azzaroli, 1979; Caloi & Palombo, 1996), was frequently employed, whereas other names, such as "*Ortogonoceros*" or "*Psekupsoceros*", have not been *de facto* widely utilised in more recent times. For this reason, to avoid additional confusion, we provisionally use the generic name "*Praemegaceros*" for European megalocerine as well as, of course, for the Sardinian and Corsican ones.

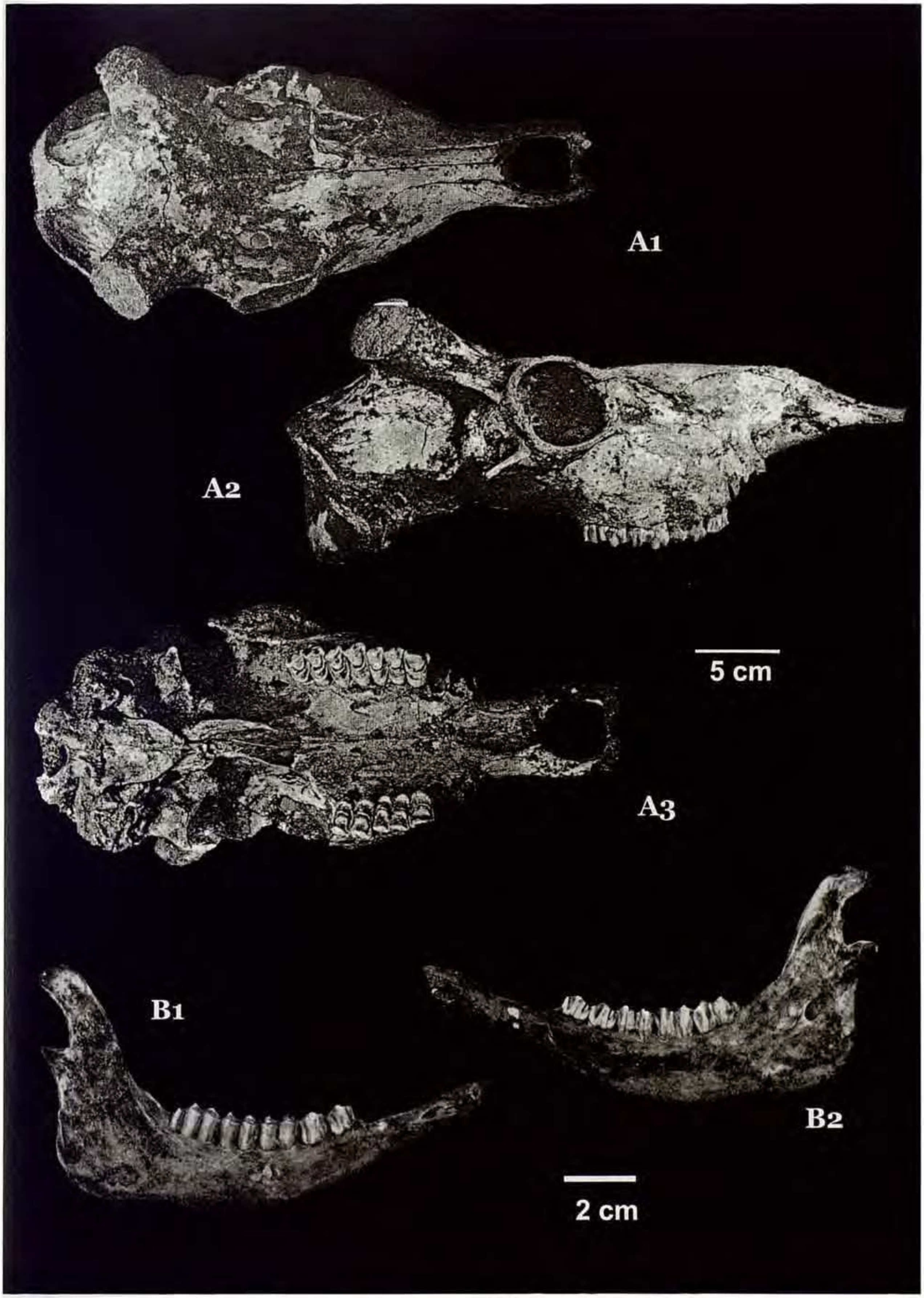

Plate 1. *"Praemegaceros" cazioti*, Dragonara Cave. Late Middle Pleistocene: A) skull (MPUR/V s.n.) in dorsal (1), lateral (2), ventral (2) view. B) mandible (MPUR/V 1/235) in lingual (1) and buccal (2) view.

Làmina 1. "Praemegaceros" cazioti, *cova Dragonara. Pleistocè Mitjà Tardà: A) crani (MPUR/V s.n.) en visió dorsal (1), lateral (2), i ventral (2). B) mandíbula (MPUR/V 1/235) en visió lingual (1) i bucal (2).*

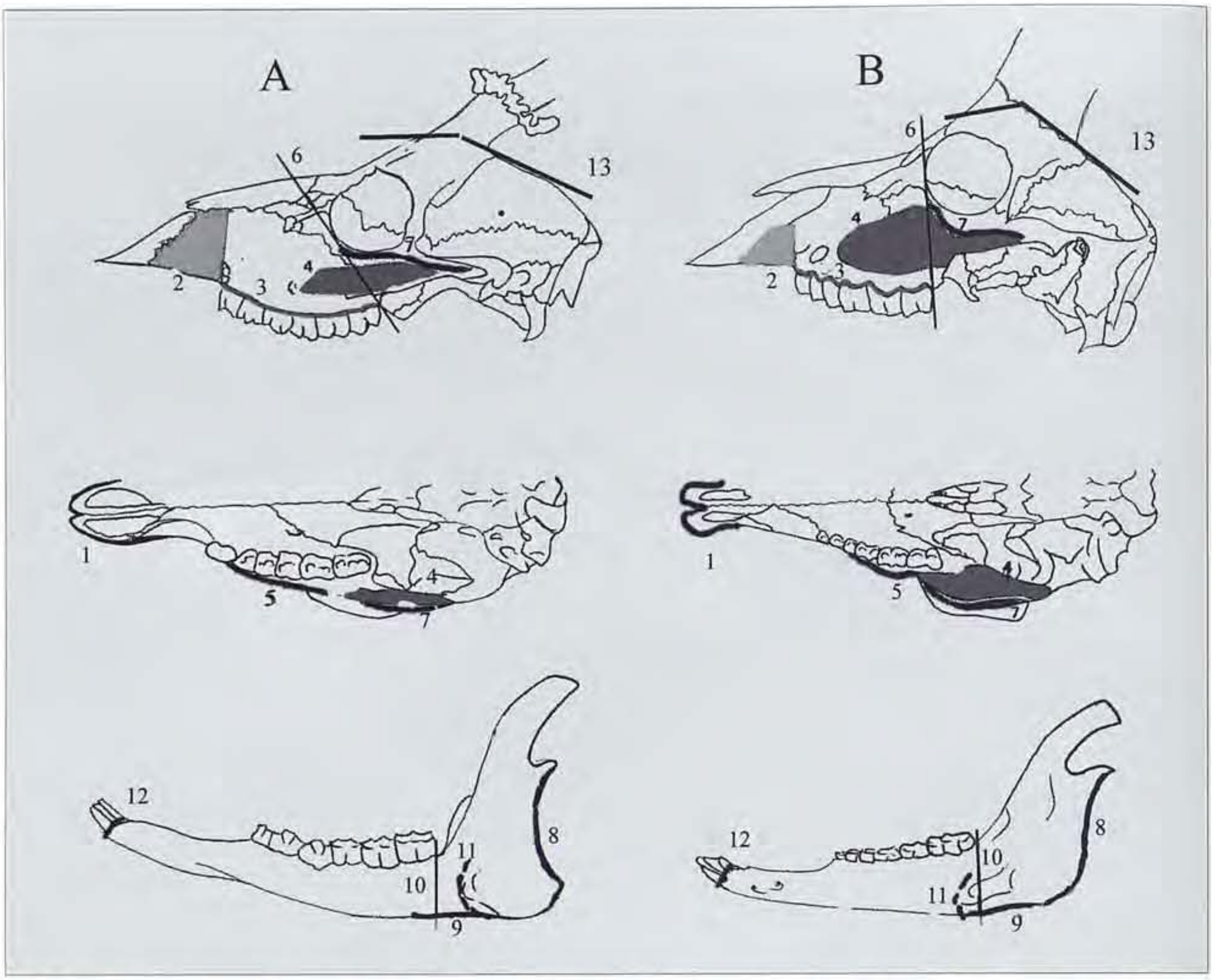

Fig. 2. Scheme of the main morphological features connected with masticatory modalities showed by a browser (A = *Capreolus capreolus*) and a mixed-feeder (B = *Capra hircus*) ruminants: 1 = shape and extent of the rostral premaxillary portion; 2 = development of the maxillary area anterior to P^2; 3 = shape of the alveolar margin; 4 = origin of the *m. masseter;* 5 = development of the *tuberculus faccialis;* 6 = position of the orbit; 7 = origin of the *m. zygomatico-mandibularis*; 8 = posterior part of *ramus mandibulae;* 9 = thickness of the *corpus mandibulae* between the *angulus mandibulae* and the *impressio vasculosa*; 10 = increase in height of the *corpus mandibulae* from P_2 to M_3; 11 = front extension of the *m. masseter* termination; 12 = alveolar line of incisive; 13 = Braincase angle; mt = moment arms of *temporalis* muscle; mm = moment arms of *masseter* muscle.

Fig. 2. *Esquema dels trets morfològics principals relacionats amb les modalitats masticatòries presentades per un remugant brostejador (A =* Capreolus capreolus*) i per un de dieta mixta (B =* Capra hircus*). 1, forma i extensió de la part premaxil·lar rostral; 2, desenvolupament de l'àrea maxil·lar anterior al* P^2*; 3, forma de la vorera alveolar; 4, origen del* musculus masseter*; 5, desenvolupament del* tuberculus faccialis*; 6, posició de l'òrbita; 7, origen del* m. zygomatico-mandibularis*; 8, part posterior del* ramus mandibulae*; 9, gruixa del* corpus mandibulae *entre l'*angulus mandibulae *i la* impressio vasculosa*; 10, increment en altura del* corpus mandibulae *des del* P_2 *al* M_3*; 11, extensió frontal de la terminació del* m. masseter*; 12, línia alveolar de la incisiva; 13, angle de la caixa craniana; mt, moment del m. temporalis; mm = moment del muscle masseter.*

The casts were first examined at 35x magnification using an Olympus stereomicroscope. Then, the casts, spatter-coated with 200 angstroms of gold, were analysed using a Cambridge Stereoscan 250. Photomicrographs were taken at 20 x, 35x, 200x and 500x magnification. The 20 x photomicrographs were taken in order to better check the region and orientation of the less magnified photomicrographs. The 35x photomicrographs were used for comparison with the images obtained with the light stereomicroscope. Both 200x and 500x photomicrographs were used for analysis in order to contrast results at different magnifications. Quantitative analysis was made using the Microwear 4.0 software programme, provided by Ungar (2001).

Mesowear analysis (see below) was performed according to the methodology proposed by Kaiser (2003). Analysis is focused on the buccal cutting edges of the enamel surfaces (paracone/ metacon), following methods proposed by Kaiser (2003) and Franz-Odendaal & Kaiser (2003). Moreover, according to our personal observation, as far as *"P." cazioti* is concerned, there are not significant differences between mesowear data resulting from the analysis of upper and lower last four (P^4-M^3) teeth. Consequently, also P_4-M_3 were considered, as well as upper ones, following the "four positions" method proposed by Kaiser (2003). We considered the following variables: occlusal relief, high or low (height of cusp divided by tooth length, respectively > or < 0,1) and cusp shape, defined as sharp, round and blunt, in decreasing order of facet development (Kaiser, 2003; Kaiser & Solounias, 2003).

CRANIO-DENTAL MORPHOLOGY

The characters tested are mainly those discussed by Solounias *et al.* (1988), Solounias & Dawson-Saunders (1988), Solounias & Moelleken (1993a,b), Solounias *et al.* (1995), MacFadden & Shockey (1997), Mendoza *et al.* (2002) for ruminants in general and adapted by Caloi & Palombo (1996), Croitor (1999; 2001) and Valli & Palombo (in press) specifically to cervids.

The most significant cranial features correlated with dietary preferences in ruminants, and valid for the fossil deer too, can be restricted to muzzle shape, the extension of the origin and insertion area of *masseter* muscle (on skull and mandible respectively), the shape and the depth of *angulus mandibulae*, the shape of the posterior outline of the vertical *ramus mandibulae* (Fig. 2).

Indeed, the outline of distal premaxillary bones and of the mandibular symphysial region are good indicators of the 'cropping mechanism', since the more selective feeding- browsing cervids (such as *C. capreolus*) have narrow muzzles and more pointed premaxillary outlines, whereas in mixed feeders (such as *D. dama*) the muzzle shows a squarer outline, like in grazers, allowing the most effective cutting of grasses growing in clusters on the ground.

Furthermore, the larger the origin and insertion areas of the *masseter* (*pars superficialis* and *profunda*) muscle, the more powerful chewing is. In addition, a long *masseter* muscle moment arm suggests powerful biting (see e.g. Vizcaíno & Bargo, 1998; Vizcaíno *et al.*, 1998). The shape of *angulus mandibulae* and the depth and height of the vertical *ramus* are also affected by the extension of insertion areas of the *masseter* (*pars superficialis* and *profunda*), *zygomaticomandibularis* and *pterigoideus* muscles. Cervids feeding on grasses, such as *E. davidianus*, have a deeper *angulus mandibulae* region; the condylus is in a higher position and articular surface is rather symmetrical and horizontal, as in grazers (Croitor, 1999; 2001). Conversely, the insertion of the *temporalis* muscle is wider in browser than in mixed- feeder cervids (Caloi & Palombo, 1995).

Some other cranial features may represent a useful tool in the attempt to detect deer feeding, but have to be employed more cautiously. For instance: 1) grazers have a more highly-developed masseteric prominence above the M^1, due to a stronger tendon of the *masseter superficialis* muscle than in browsers; nevertheless, *C. capreolus* shows relatively enlarged maxillary bones above M^1; 2) due to the larger origin of the *masseter* muscle on the maxillary bone of grazers, the orbit is usually positioned above M^2 in browsers, whereas it starts above M^3 or further back in grazers; nevertheless, in cervids, the orbit position is quite variable, also depending on structural characteristics; 3) Solounias *et al.* (1988) and Solounias & Dawson-Saunders (1988) consider a reduced area of maxillary bones in front of P^2 as a grazer feature; among cervids, the shape of this area appears quite uniform, and ecomorphological variations seem to be of little relevance; 4) the *corpus mandibulae* is usually larger and deeper in grazers due to the presence of hypsodont molars, though in cervids the increase in crow height seems does not significantly change the shape of the *corpus mandiblulae*; 4) it has been observed that grazers have equal or sub-equal size incisors, whereas in browsers the size differs, and the first incisor is more or less larger than the third (Gordon & Ilius, 1988; Janis & Ehrhardt, 1988); however, this feature is not evident in cervids and, moreover, the incisors of fossil taxa are rarely recorded; 5) sub-equal size incisors of grazers are usually combined with straight incisor arcades; cervids generally show a more or less rounded incisor arcade; moreover, this feature is also usually difficult to evaluate in fossils; 6) the high glenoid fossa (above the occlusal plane) and higher vertical *ramus mandibulae* of ruminant browsers have comparatively longer premolar tooth rows than grazers.

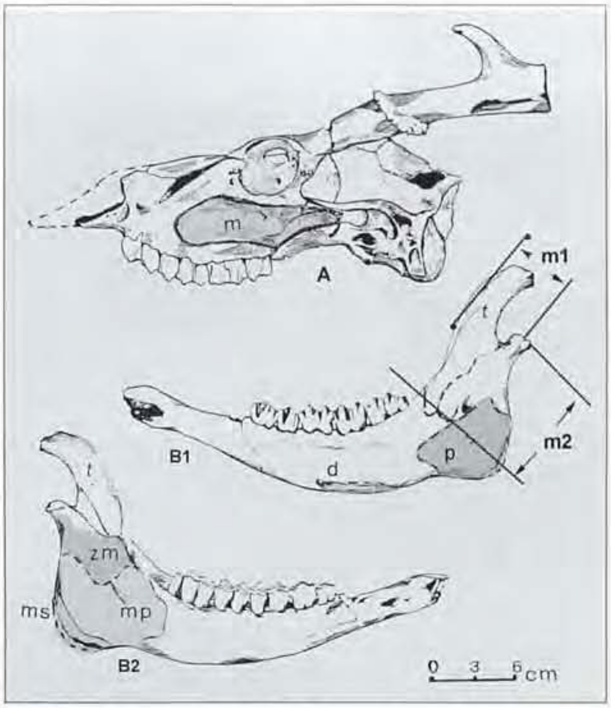

Fig. 3. *"Praemegaceros" cazioti*: skull (MPUR/V 1/1) and mandible (MPUR/V 1/235). Insertion areas of masticator muscles: d = *m. digastricus*; m = *pars profunda* and *pars superior* of *m. masseter*; mp = *pars profunda* of *m. masseter*; ms = *pars supeficialis* of *m. masseter*; p = *m. pterygoideus medialis*; t = *m. temporalis*; zm = *m. zygomatico-mandibularis.*

Fig. 3. "Praemegaceros" cazioti: *crani (MPUR/V 1/1) i mandibula (MPUR/V 1/235). Àrees d'inserció dels músculs mandibulars: d* = m. digastricus*; m* = pars profunda *i* pars superior *del* m. masseter*; mp* = pars profunda *del* m. masseter*; ms* = pars superficialis *del* m. masseter*; p* = m. pterygoideus medialis*; t* = m. temporalis*; zm* = m. zygomatico-mandibularis.

Other features, recognised as being distinctive from those of grazers, such as a narrow braincase angle and larger skull length in relation to body size (Mendoza *et al.*, 2002), cannot be taken into consideration when analysing insular specimens, because a larger skull, as well as the relative variation in skull/ brain case proportion, are features characterising most endemic insular mammals (Azzaroli, 1982; Palombo, 2001; Köhler & Moyà-Solà, 2003, 2004).

Furthermore, as is widely known, ungulates that feed on abrasive grasses with high silicophytolith contents have higher hypsodonty values than leaf-eating

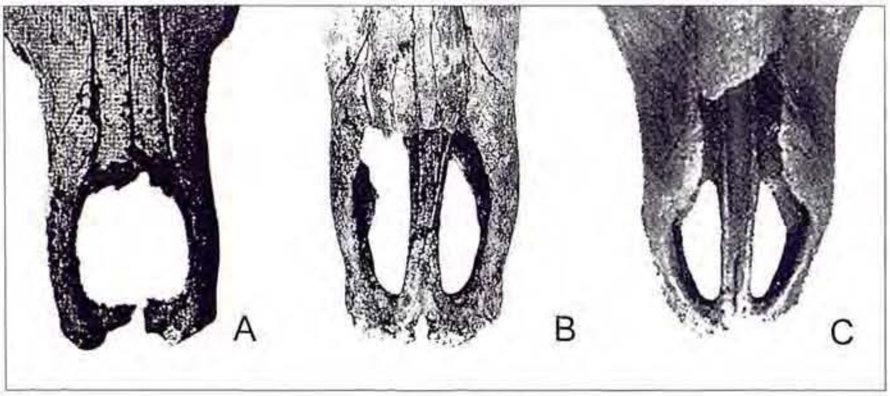

Fig. 4 . Premaxillary shape in A) *"Praemegaceros" cazioti* (MPUR/V1/1), B) *"Praemegaceros" obscurus* (late Villafranchian, Cava Liberatori-Tuscany, adapted from Abbazzi, 1995), C) *Megaloceros giganteus* (Holocene, Ireland, Museo Agenzia Nazionale per l'Ambiente, Roma).

Fig. 4. Forma del premaxil·lar a: A) "Praemegaceros" cazioti *(MPUR/V1/1), B)* "Praemegaceros" obscurus *(Villafranquià tardà, Cava Liberatori-Toscàna, adaptat de Abbazzi, 1995), C)* Megaloceros giganteus *(Holocè, Irlanda, Museo Agenzia Nazionale per l'Ambiente, Roma).*

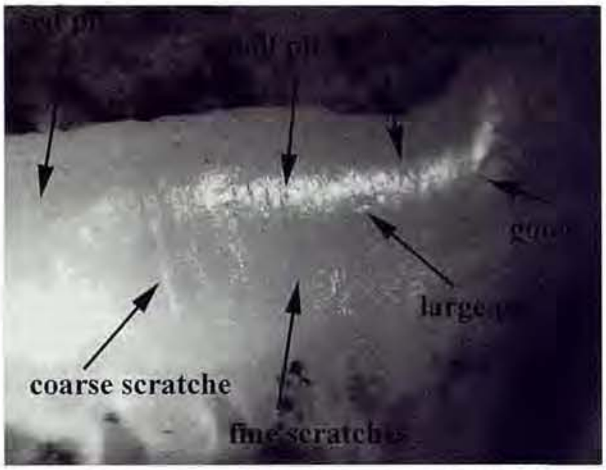

Fig. 5. *"Praemegaceros" cazioti*: second (lingual) enamel band of the paracone of a right M^2 (MPUR/V1/115). Microwear scars fotographed using stereomicroscope (magnification 40x).

Fig. 5. "Praemegaceros" cazioti*: segona (lingual) capa d'esmalt del paraconus d'un M^2 dret (MPUR/V1/115). Marques de microdesgast fotografiades amb un estereomicroscopi (40x).*

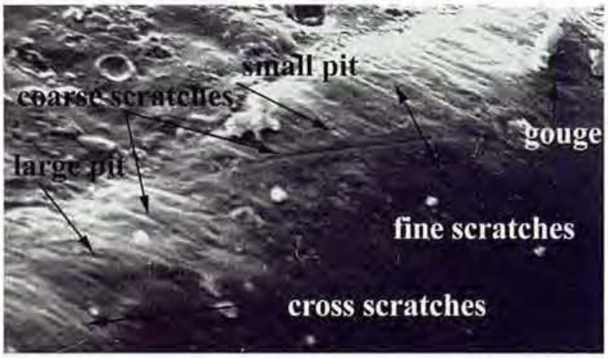

Fig. 6. *"Praemegaceros" cazioti*: M^2 (MPUR/V 1/116). SEM photomicrograph (magnification 60 x) of second enamel band of the paracone showing pits (large and small), scratches (coarse, crossed and fine), and gouges.

Fig. 6. "Praemegaceros" cazioti*: M^2 (MPUR/V 1/116). Microfotografia amb el SEM (60 x) de la segona capa d'esmalt del paraconus mostrant forats (grans i petits), ratllades (grolleres, creuades i fines), i clots.*

browsers (van Vale, 1960; Janis, 1988; Solounias & Dawson- Saunders, 1988; Jernvall & Fortelius, 2002). The criteria for assigning species to the three hypsodonty classes (brachydont, mesodont and hypsodonty) generally used for herbivores are based on the ratio of height to length of the second or third molar (upper or lower). The relative tooth crown height (hypsodonty index) is less than 0.8 for brachydont, 0.8–1.2 for mesodont and more than 1.2 for hypsodonty teeth. Although the hypsodonty index and diet are not strictly correlated (see e.g. Kaiser *et al.*, 2000; Fortelius *et al.*, 2002), an increase in dental crown height in populations belonging to the same species or genus might be regarded as an ecomorphological response to a change in diet.

As far as cervids are concerned, it is also more difficult to interpret the meaning of variations in the premolar/ molar length ratio (ruminant browsers have comparatively longer premolar tooth rows than grazers, Mendoza *et al.*, 2002) due to the evolutionary significance sometimes assumed by the increasing size of premolars in deer (Heintz, 1970).

In light of all this, the cranium of the Dragonara cervid (Fig. 3) shows some morphological features that, to a varying degree, are similar to those characterising mixed-feeder ruminants, whose feeding also includes some fresh-grasses, as well as drier herbs. Accordingly, the Dragonara cervid, like ruminant mixed-feeders, is similar to grazers in the following: having a square muzzle; a rough, large origin area of *musculus masseter;* a reduced insertion area of *musculus temporalis* on the jaw; a high, deep *corpus mandibulae* behind M3; a round outline of *angulus mandibulae* and little concave posterior outlines of *ramus verticalis;* moreover, the facial tubercle above M^1 is quite well developed, the orbit starting above M3; the glenoid fossa is high with respect to the occlusal plane; the teeth are hypsodont (Fig. 3; Plate 1). It is worth noting that among giant continental deer, *"P." obscurus* has quite an enlarged distal portion of premaxillary bones, even if less than in *"P." cazioti*, whereas the muzzle's shape of *Megaloceros giganteus*, as well as of *Eucladoceros*, is similar to that of browsers (Fig. 4).

MICROWEAR

Microwear analytical methods were developed at the end of the 1970s in an attempt to define dietary adaptation on the basis of scars produced during chewing on enamel occlusal surface by tooth /food (abrasion) and tooth/tooth (attrition) interaction. Differences in microwear patterning and formation processes depend on the physical properties of food (acidity, hardness, particles contained) and the strength and direction of jaw movements (magnitude and direction of chewing forces) affecting microwear patterns, notably their shape, size, distribution and density. Due to the very short time turnover (formation/obliteration) of wear patterns, microwear can provide information on the nature of the last few meals of the examined individual (Solounias *et al.*, 1994; Teaford & Oyen, 1989). Nevertheless, this rapid change can constitute a power point in research on extinct species: in this case, we can avoid the bias of short time occasional feeding and evaluate average dietary preferences over the course of time.

According to their microwear patterns and feeding preferences, artiodactyls were grouped in the following categories: 1) browsers, including: typical browsers (feeding mainly on foliage, ligneous plants) characterised by a high percentage of pits and few longitudinal, often crossed scratches; fruit/seed browsers, having a high number of coarse scratches and large pits; 2) grazers (eating more exclusively grasses), characterised by a high percentage of striation, especially fine parallel scratches; 3) mixed feeders (having a diet including a mixture of ligneous plants and grasses, with seasonal and/or spatial variation), with a more variable pattern; and, in addition, 4) fruit-seed browsers; 5) bark, coarse stem and leaf feeders, such as elephants, 6), rooters, such as some suids (Solounias & Semprebon, 2002).

Microscopic scars, analysed using light microscopy (35-40X) (Fig. 5) and at SEM (200X and 500X) on the second band of M^2 paracone (Fig. 6), can be arranged into three main categories: i) striations or scratches (linear depression whose length is always greater than its breadth; coarse scratches have a large bottom, fine scratches are thinner and straighter); ii) pits, large" or "small" (depressions whose length and breadth are approximately equal); iii) gouges (microwear scars larger and deeper than pits, with irregular edges) (Gordon, 1982, 1988; Solounias & Semprebon, 2002; Palombo, unpublished data) (Fig. 6).

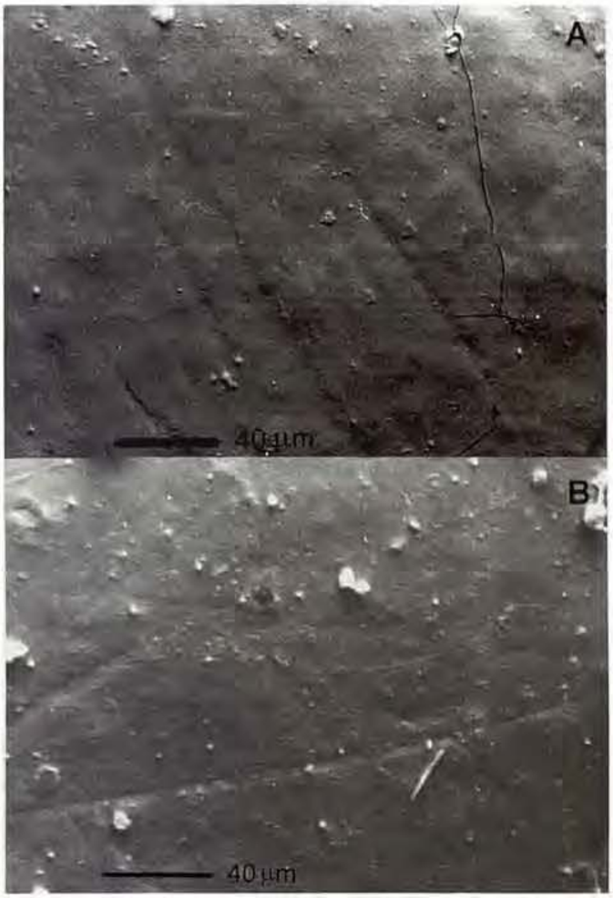

Fig. 7. *"Praemegaceros" cazioti*: SEM photomicrographs (magnification 500 x) of second enamel band of the paracone, 7a) M^2 (MPUR/V1/237) - the photomicrograph shows some parallel coarse stratches, several large pits quite abrasion that caused the polished feature of the enamel surface; 7b) M^2 (MPUR/V 1/123) - the photomicrograph shows both coarse scratches and fine crossed scratches, some times crossed, several pits and two gouges are also present.

Fig. 7. "Praemegaceros" cazioti*: microfotografies amb el SEM (500 x) de la segona capa d'esmalt del paraconus: 7a) M^2 (MPUR/V1/237) – la microfotografia mostra algunes ratllades grolleres paral·leles, alguns forats grans bastant desgastats degut al poliment de la superficie de l'esmalt; 7b) M^2 (MPUR/V 1/123) – la microfotografia mostra tant ratllades grolleres com fines, de vegades creuades, i també hi ha alguns forats i dos clots.*

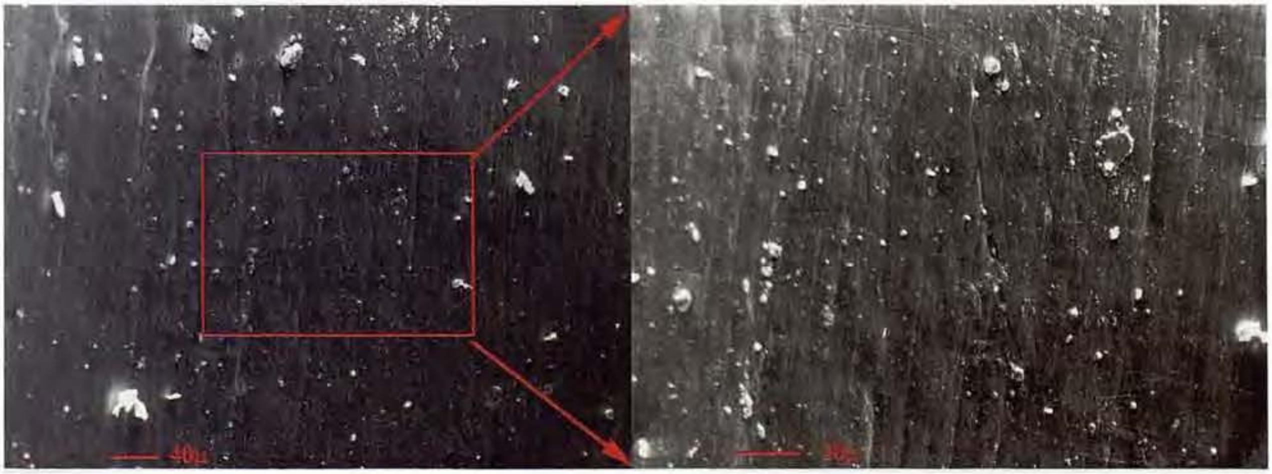

Fig. 8. *"Praemegaceros" cazioti*: very worn M^2 (MPUR/V1/122). SEM photomicrograph (magnification 500 x and 200 x) of an overscratched surface of second enamel band of the paracone, showing several parallel scratches (coarse and fine) and some large pits.

Fig. 8. "Praemegaceros" cazioti*: M^2 molt desgastat (MPUR/V1/122). Microfotografies amb el SEM (500 x i 200 x) d'una superficie extremadament ratllada de la segona capa d'esmalt del paraconus, mostrant algunes ratllades paral·leles (grolleres i primes) i alguns forats grans.*

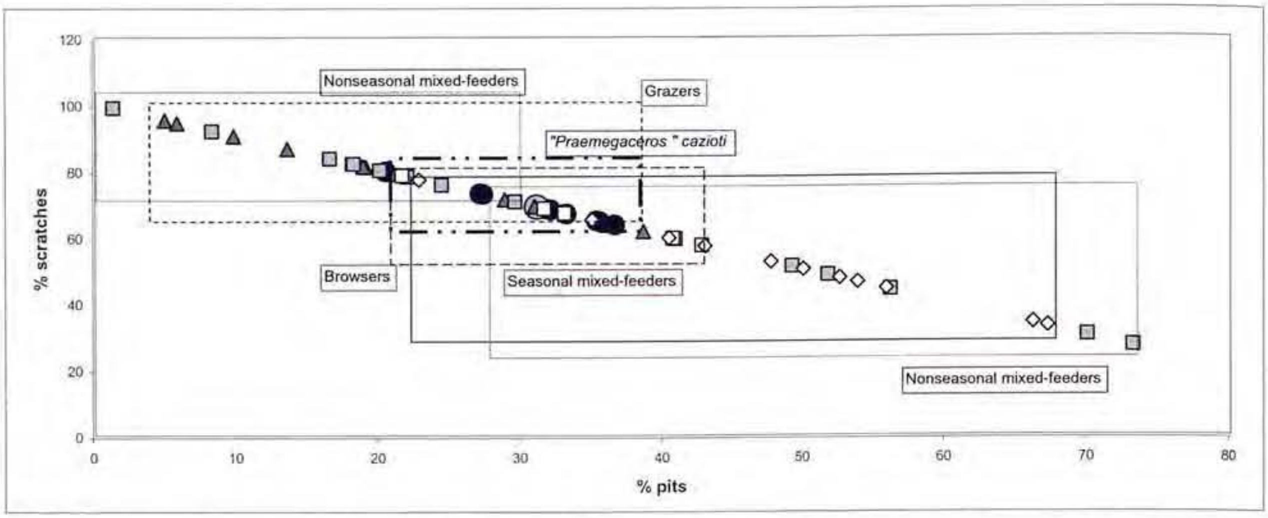

Fig. 9. Percentage of pits versus percentage of scratches for *"Praemegaceros" cazioti* and extant herbivores (average number of pits and scratches of extant species from Solounias & Semprebon, 2002).

Fig. 9. Percentatge de forats respecte el percentatge de ratllades per a "Praemegaceros" cazioti *i diversos herbivors vivents (nombre promig de forats i ratllades de les espècies vivents, a partir de Solounias & Semprebon, 2002).*

The microwear pattern shown by the cervid from Dragonara Cave (Fig. 7, 8) is characterised by a high percentage of scratches (Fig. 9) and, consequently, a low density of pits (Fig. 10), similar to those of extant "high scratch" mixed-feeder cervids such as *Axis axis* and *Cervus canadensis*, having average scratch numbers at the grazing end of the scratch range (Solounias & Semprebon, 2002). However, the average density of scratches is inferior to that of extant grazers. Accordingly, *"P." cazioti* from Dragonara is clearly distinct from browsers, and can be situated in the seasonal mixed-feeder group.

MESOWEAR

Dietary adaptation of fossil herbivores, or better certain kinds of wear, can also be inferred using the mesowear method (Fortelius & Solounias, 2000; Kaiser *et al.*, 2000; Kaiser & Solounias, 2003; Kaiser, 2003)

This method, already described in terms of facet development by Butler (1952) and Janis (1990), was considered by Fortelius & Solounias (2000) as a proxy to illustrate the average diet of a particular species living in a

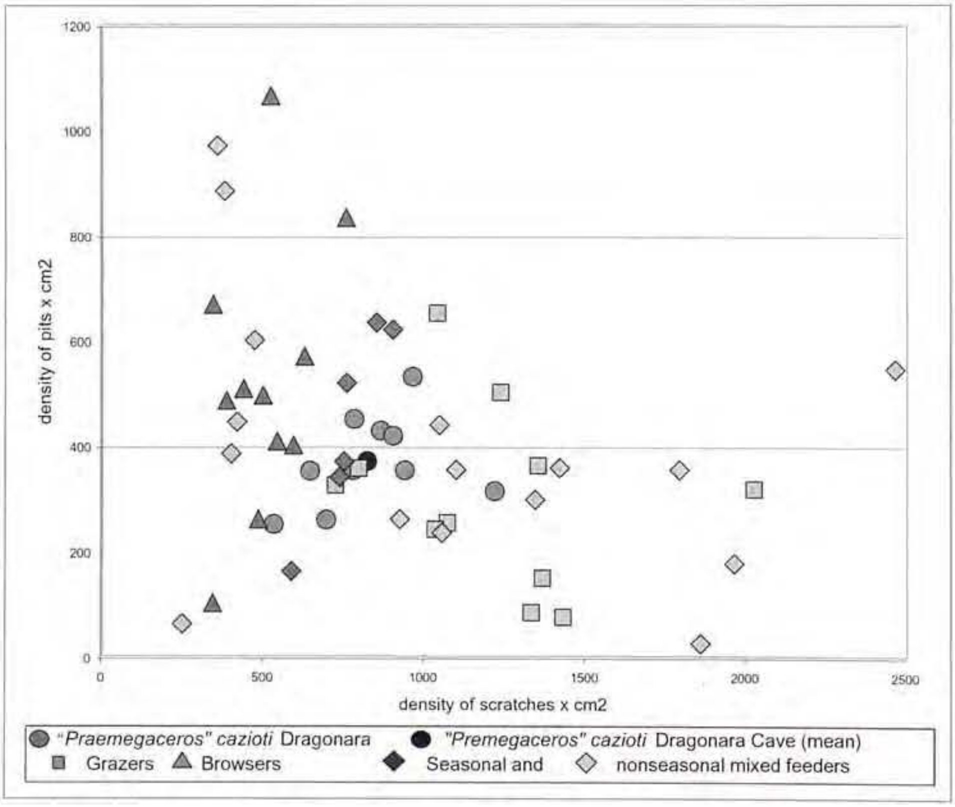

Fig. 10. Density of pits versus density of scratches for *"Praemegaceros" cazioti* and extant herbivores (average density of pits and scratches of extant species from Solounias & Semprebon, 2002).

Fig. 10. Densitat de forats respecte la densitat de ratllades per a "Praemegaceros" cazioti *i diversos herbivors vivents (nombre promig de forats i ratllades de les espècies vivents, a partir de Solounias & Semprebon, 2002).*

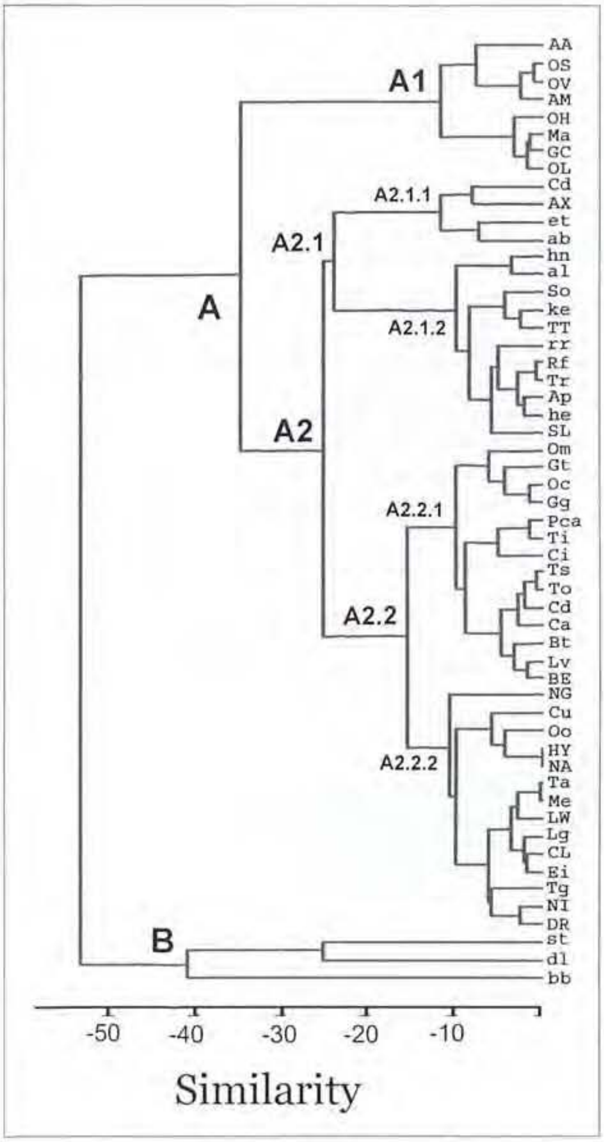

Fig. 11. Hierarchical cluster diagram based on recent cervid (data from Kaiser, 2003). The mesowear variables considered for cluster analysis (normalized Euclidean distance, NED) are: percent high occlusal relief, percent sharp cusps and percent blunt cusps.
Browser (upper case): AA *Alces alces*; BE *Boocercus euryceros*; EI *Ammodorcas clarkei*; GC *Giraffa camelopardalis*; LW *Litocranius talleri*; OH *Odocoileus hemionus* ; OJ *Okapia johnstoni*; OL *Capreolus capreolus* ; OV *Odocoileus virginianus*; TT *Tragelaphus strepsiceros*
Grazers (small case): ab *Alcelaphus buselaphus*; al *Alcelaphus lichtensteinii*; bb *Bison* bison; ct *Connochaetes*; dl *Damaliscus lunatus*; he *Hippotragus equines*; hn *Hippotragus niger*; ke *Kobus ellipsiprymnus*; rr *Redunca redunca*;
Mixed feeders (capital first): Ap *Axis porcinus*; Ax *Axis axis*; Bt *Budorcas taxicolor*; Ca *Capricornis sumatraensis*; Cc *Cervus canadensis*; Cd *Cervus duvauceli*; Ci *Capra ibex*; Cl *Camelus dromedarius*; Ru *Rusa unicolor*; Gg *Gazella granti*; Gt *Gazella thomsoni*; Lg *Lama lama*; Lv *Lama vicugna*; Ma *Antidorcas marsupialis*; Me *Aepyceros melampus*;
Oc *Ovis canadensis*; Om *Ovibos moschatus*; Oo *Ourebia ourebi*; Rf *Redunca fulvorufula*; Sc *Syncerus caffer*; St *Saiga tartarica*; Ta *Tragelaphus angas*; Ti *Tragelaphus imberbis*; To *Taurotragus oryx*; Tq *Tetracerus quadricornis*; Tr *Boselaphus tragocamelus*; Ts *Tragelaphus scriptus*; Pr.c *"Praemegaceros" cazioti*, Dragonara Cave

Fig. 11. *Diagrama d'agrupacions jeràrquiques basat en cèrvids recents (dades de Kaiser, 2003). Les variables de mesodesgast considerades per a l'anàlisi d'agrupaments (distància euclidea normalitzada, NED) són: percentatge de relleu oclussal alt, percentatge de cúspides agudes i percentatge de cúspides polides.*
Brostejadors (amb maiúscules): AA Alces alces; *BE* Boocercus euryceros; *EI* Ammodorcas clarkei; *GC* Giraffa camelopardalis; *LW* Litocranius talleri; *OH* Odocoileus hemionus ; *OJ* Okapia johnstoni; *OL* Capreolus capreolus ; *OV* Odocoileus virginianus; *TT* Tragelaphus strepsiceros
Pastadors (amb minúscules): ab Alcelaphus buselaphus; *al* Alcelaphus lichtensteinii; *bb* Bison bison; *ct* Connochaetes; *dl* Damaliscus lunatus; *he* Hippotragus equines; *hn* Hippotragus niger; *ke* Kobus ellipsiprymnus; *rr* Redunca redunca.
Dieta mixta (amb la primera lletra maiúscula): Ap Axis porcinus; *Ax* Axis axis; *Bt* Budorcas taxicolor; *Ca* Capricornis sumatraensis; *Cc* Cervus canadensis; *Cd* Cervus duvauceli; *Ci* Capra ibex; *Cl* Camelus dromedarius; *Ru* Rusa unicolor; *Gg* Gazella granti; *Gt* Gazella thomsoni; *Lg* Lama lama; *Lv* Lama vicugna; *Ma* Antidorcas marsupialis; *Me* Aepyceros melampus; *Oc* Ovis canadensis; *Om* Ovibos moschatus; *Oo* Ourebia ourebi; *Rf* Redunca fulvorufula; *Sc* Syncerus caffer; *St* Saiga tartarica; *Ta* Tragelaphus angas; *Ti* Tragelaphus imberbis; *To* Taurotragus oryx; *Tq* Tetracerus quadricornis; *Tr* Boselaphus tragocamelus; *Ts* Tragelaphus scriptus; *Pr.c* "Praemegaceros" cazioti, *cova Dragonara.*

particular time and environment, because this feature can provide an intermediate level of information, between hypsodont, reflecting long-term adaptation, and microwear, providing direct information regarding the nature of individual feeding.

Mesowear analysis is based on the degree of facet development on the occlusal surfaces of teeth. The development of tooth cusps depends on the relative amounts of attritive and abrasive wear of tooth-to-tooth contact (attrition) over food-to-tooth contact (abrasion). The more attrition prevails, the higher the tooth cusp relief (difference in height between cusp tips and inter cusp valleys), as lower occlusal stress permits higher occlusal relief.

According to Fortelius & Solounias (2000), apices were characterized as sharp, rounded, or blunt (in decreasing order of facet development), and the valleys between them either high or low. Four main groups have been recognised, ranging from abrasion-dominated to attrition-dominated and corresponding to the following trophic categories: grazers, graze-dominated mixed feeders, browse-dominated mixed feeders, and browsers.

The cusps of *"P." cazioti* from Dragonara Cave show a prevalently sharp shape, as seen in the buccal projection of the more or less worn teeth examined, confirming that attrition produced by tooth-on-tooth contact predominates, as usually observed in cervids, whereas the abrasion produced by food becomes more evident only on strongly worn molars. For example, the metacone of some M^2 belonging to senile individuals (MPUR/V 1/126) maintains a smooth cusp, confirming that a precise occlusion between the upper and lower teeth is maintained until the very latest wear stages. Moreover, this observation confirms what was already observed by Fortelius & Solounias (2000). "The ontogenetic changes that take place in the occlusal configuration are minor, or else restricted to very early and very late wear stages".

A cluster analysis in which mesowear features of *"P." cazioti* from Dragonara Cave have been compared with some extant ruminants (53 species among cervids, bovids, giraffids and camelids, data from Fortelius & Solounias, 2000) shows quite good resolution in dividing selected extant ruminants according to their dietary adaptation (Fig. 11). Indeed, we can recognize the major

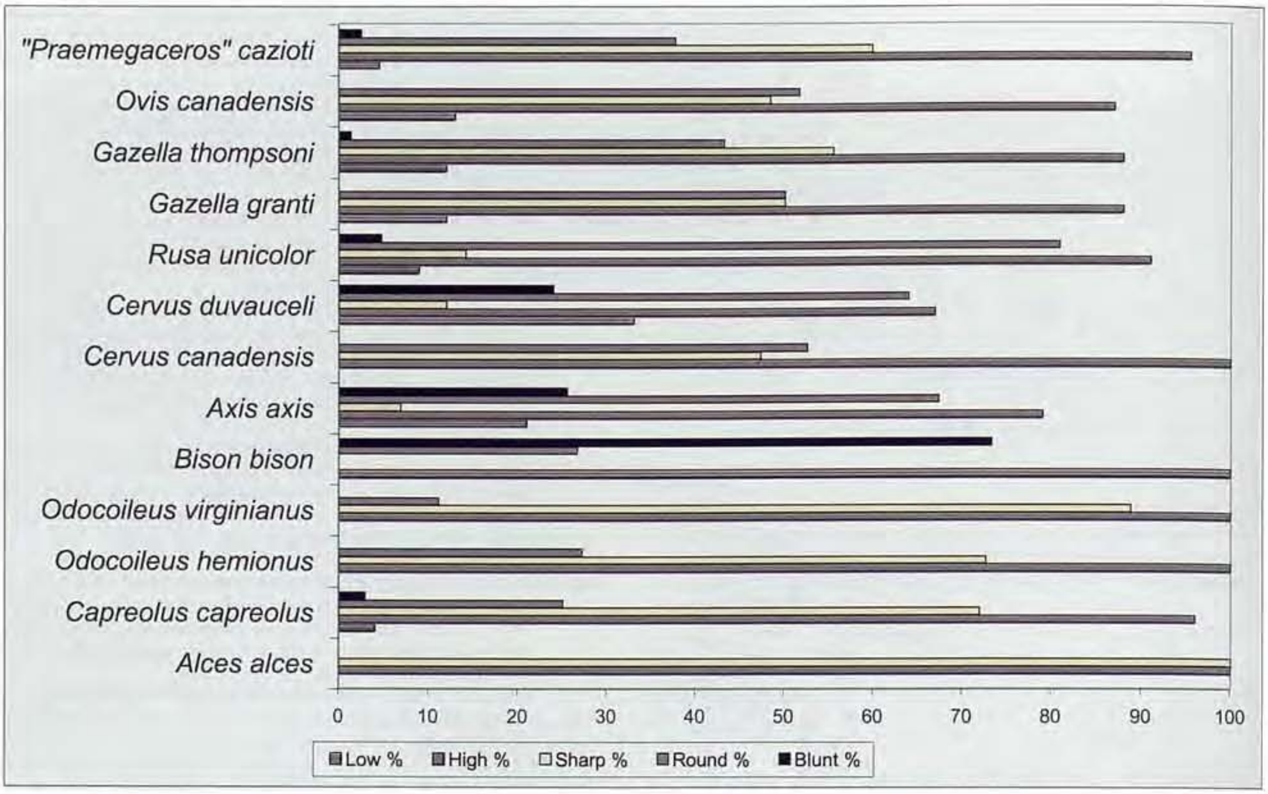

Fig. 12. Comparative histograms of mesowear variables based on "on tooth method". Data of extant species from Fortelius & Solounias (2000).

Fig. 12. Histogrames comparatius de variables de mesodesgast basades al "mètode sobre les dents". Dades de les espècies vivents, a partir de Fortelius & Solounias (2000).

clusters of typical grazers (A1) and of browsers and mixed-feeders (A2). Within the latter, we find the groups that include either mainly browsers (A2.1), or mixed-feeders (A2.2), the second divided into mixed versus grazer-feeders (A2.2.2) and more typical mixed-feeders (A2.2.1). *"P." cazioti* also falls among the latter, together with species such as *Gazella granti, G. thomsoni* and *Ovis canadensis* (see also Fig. 12), which are seasonal-regional mixed feeders, eating leaves but also grass and roughage, as often occurs among taxa regarded as representative of the "browsing-grazing transitional phase" (as far as microwear is concerned, see Solounias & Semprebon, 2000).

Taking all this into consideration, the mesowear method seems to be a less discriminatory tool in the attempt to detect minor differences in food exploitation, especially within a group where mixed-feeders are prevalent, as is the case with cervids.

REMARKS

Although in cervids, as well in each phylogenetic group, cranio-dental structure, morphology and proportions are constrained by their own evolutionary history, adaptation to a given trophic niche can involve some morphological skull and mandible features allowing optimal exploitation of feeding resources.

The skull and mandible of *"P." cazioti* from Dragonara show some features that, to a varying degree, are comparable to those of grazers: essentially, a square muzzle; rough, large origin area of *m. masseter*; non- hollow posterior border of vertical *ramus mandibulae*. Some other features are more frequent in mixed-feeders that eat large amounts of grasses. Cranium morphology suggests that the diet of the Dragonara cervid possibly included a larger amount of grasses than that of its hypothetical continental ancestor.

The microwear pattern agrees with cranium data. Dental microwear analysis of *"P." cazioti* from the Dragonara Cave enabled us to qualify it as a seasonal-mixed feeder, like some extant fallow deer characterised by similar pit density. However, its diet seems to have contained more gramineae, being presumably composed of harder vegetation than that of extant fallow deer species, even if sometimes it may have occasionally included ligneous plants and fruit, possibly during the milder months of the year. This could be connected with the contrasting seasonal conditions characterising Sardinia during the Late Pleistocene.

ACKNOWLEDGEMENTS

I am grateful to the Directors, Curators and Technicians of the Institutions listed in the Appendix who, at various times starting from 1980, offered me hospitality and assistance during my research. Special thanks to A.M.F. Valli for our interesting and useful discussions. I would also like to thank Sig. A. Mancini (CNR, Istituto di Geologia Ambientale e Geoingegneria) and G. D'Arpino (Dip. Scienze della Terra, "La Sapienza" University), who respectively assisted me with SEM and took the microphotographs. The English version has been revised by Prof. Mary Groeneweg, English Lecturer at the University of Cagliari.

REFERENCES

Abbazzi, L. 2004. An overview on *Praemegaceros* species from Pleistocene Italian localities, and remarks on the validity of the generic name *Praemegaceros* Portis 1920. *Rend. Fis. Acc. Lincei., s.9,* 15: 115-132.

Arambourg, C. 1932. Note preliminaire sur une nouvelle grotte à ossements des environs D'Alger. *Soc. Hist. Nat. Afrique du Nord,* 23: 154-162.

Arambourg, C. 1938. Mammifères fossiles du Maroc. *Soc. Sci. Nat. Maroc, Mem.,* 46: 1-74.

Azzaroli, A. 1952. La sistematica dei Cervi Giganti e i Cervi Nani delle isole. *Atti Soc. Tosc. Sci. Nat., Mem.(A),* 59: 119-127.

Azzaroli, A. 1979. Critical remarks on some Giant Deer (genus *Megaceros* Owen) from the Pleistocene of Europe. *Palaeont. It., n.s. 41,* 71: 5-16.

Azzaroli, A. 1982. Insularity and its effects on terrestrial vertebrates. *In* Montanaro Gallitelli, E. (ed.), *Proc. First Int. Meet. "Palaeontology, Essential of Historical Geology"* (Venice, 2-4 June 1981): 193-213.

Azzaroli, A. & Mazza, P. 1992. The cervid genus *Eucladoceros* in the Early Pleistocene of Tuscany. *Palaeont. Ital.,* 79: 43-100.

Butler, P.M. 1952. The milk-molars of Perissodactyla, with remarks on molar occlusion. *Proc. Zool. Soc. Lond,* 121: 777-817.

Caloi, L. & Malatesta, A. 1974. Il cervo pleistocenico di Sardegna. *Mem. Ist. It. Paleont. Umana, n.s.,* 2: 163-246.

Caloi, L. & Palombo, M.R. 1991. Morfologia e funzione della mano e del piede del megacerino del Pleistocene superiore di Dragonara (Sardegna, Italia). *Atti Acc._Peloritana Pericolanti,* 57 (1989), suppl. 1: 319-341.

Caloi, L. & Palombo, M.R. 1995. Functional aspects and ecological implications in Pleistocene endemic cervids of Sardinia, Sicily and Crete. *Geobios,* 28 (2): 247-258.

Caloi, L. & Palombo, M.R. 1996. Il megacerino di Dragonara, interpretazione funzionale di alcuni caratteri cranici. *Geologica Romana,* 31(1995): 29-40.

Cornelius, J., Casaer, J. & Herry, M. 1999. Impact of season, habitat and research techniques on diet composition of Roe Deer (*Capreolus capreolus*): a review. *J. Zool. London,* 248: 195-207.

Cransac, E., Cibien, C., Angibault, J.-M., Vincent, J.-M. & Hewison, A.J.M. 2001. Variation saisonnière du régime alimentaire du Chevreuil (*Capreolus capreolus*) selon le sexe en milieu forestier à forte densité (forêt demaniale de Dourdan). *Mammalia,* 65: 1-12.

Croitor, R. 1999. On systematic situation of "Moldavian Sambar deer" from the Pliocene of Moldova. *Boll.Soc. Paleont: It.,* 38 (1): 87-96.

Croitor, R. 2001. Functional morphology of fossil deer of Italy in condition of climate aridisation. *J. Morph.,* 248 (3): 554-565

Depéret, C. 1897. Etude de quelques gisement nouveaux de Vertébrés pléistocènes de l'ile de Corse. *Ann. Soc. Linnéenne Lyon,* 44: 111-128.

Fortelius, M., Eronen, J., Jernvall, J., Liping, L., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, A., Zhaoqun Zhang & Liping Zhou. 2002. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million year. *Evolutionary Ecology Research,* 4: 1005-1016.

Fortelius, M. & Solounias, N. 2000. Functional Characterization of Ungulate Molars Using the Abrasion-Attrition Wear Gradient: A New Method for Reconstructing Paleodiets. *American Museum Novitates,* 3301: 1-36.

Franz-Odendaal, T.A. & Kaiser, T.M. 2003. Differential mesowear in the maxillary and mandibular cheek dentition of some ruminants (Artiodactyla). *Ann. Zool. Fennici,* 40: 395-410.

Geist, V. 1999. *Deer of the world - Their evolution, behaviour and ecology.* Swan Hill Press. Shrewsbury (UK). 421 pp

Gordon, K.D. 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. *Am. J. Physi. Anthropol.,* 59: 195-215.

Gordon, K.D. 1988. A review of methodology and quantification in dental microwear analysis. *Scan. Misrosc,* 2: 1139-1147.

Gordon, I.J. & Illius, A.W. 1988. Incisor arcade structure and diet selection in ruminants. *Funct. Ecol.,* 2: 5-22.

Groot Bruinderink, G.W.T.A. & Hazebrock, E. 1995. Ingestion and diet of red deer (*Cervus elaphus* L.) in the Netherlands from 1954 till 1992. *Mammalia,* 59: 187-196.

Hadjoudis, H. 1990. *Megaceroides algericus* (Lydekker, 1890) du gisement des Phacoctères (Alger, Algérie). Etude critique de la position systématique de *Megaceroides. Quaternaire,* 1 (3-4): 247-258.

Hayek, L.-A.C., Bernor, R.L., Solounias, N. & Steigerwald, P. 1991. Preliminary studies of hipparionine horse diet as measured by tooth microwear. *Ann. Zool. Fenn.,* 3–4: 187–200.

Heintz, E. 1970. Les Cervidés villafranchiens de France et d'Espagne. *Bull. Mus. Nat. Hist. Nat.,* 22: 1-303.

Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia,* 78: 443-457.

Janis, C.M. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preferences. *Mémoirs de la Museum national d'Histoire naturelle, Paris,* 53: 367–387.

Janis, C.M. 1990. Correlation of cranial and dental variables with dietary preferences: a comparison of macropodoid and ungulate mammals. *Mem. Queensl. Mus.,* 28: 349-366.

Janis, C.M. 1995. Correlations between cranio-dental morphology and feeding behavior in ungulates: reciprocal illumination between living and fossil taxa. *In* Thomason, J.J. (ed.), *Functional Morphology in Vertebrate Paleontology*: 76-97. Cambridge University Press. Cambridge.

Janis, C.M. & Ehrhardt, D. 1988. Correlation of the relative muzzle width and relative incisor width with dietary preferences in ungulates. *Zool. J. Linn. Soc.,* 92: 267-284.

Jernvall, J. & Fortelius, M. 2002. Common mammals drive the evolutionary increase of hypsodonty in the Neogene. *Nature,* 417: 538–540.

Joleaud, L. 1914. Sur le *Cervus (Megaceroides) algericus* Leydekker (sic !) 1890. *Rec. Soc. Archéol . Costantine,* 49: 737-739.

Kaiser, T.M. 2003. The dietary regimes of two contemporaneous populations of *Hippotherium primigenium* (Perissodactyla, Equidae) from the Vallesian (Upper Miocene) of Southern Germany. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 198: 381-402.

Kaiser, T.M., Solounias, N., Fortelius, M., Bernor, R. & Schrenk, F. 2000. Tooth mesowear analysis on *Hippotherium primigenium* from the Vallesian Dinotheriensande (Germany) – a blind test study. *Carolinea,* 58: 103–114.

Kaiser, T.M. & Solounias, N. 2003. Extending the tooth mesowear method to extinct and extant equids. *Geodiversitas,* 25: 321-345.

Köhler, M. & Moyà-Solà, S. 2003. Parallel patterns in *Myotragus* and domesticated animals. *Abstracts Int. Symp: Insular Vertebrate Evolution, September 16-19 2003, Mallorca*: 31.

Köhler, M. & Moyà-Solà, S. 2004. Reduction of Brain and Sense Organs in the Fossil Insular Bovid *Myotragus. Brain Behav.,* 63: 125-140.

Maas, M.C. 1991. Enamel structure and microwear: an experimental study of the response of enamel to shearing forces. *Am. J. Physi. Anthropol.,* 85: 31-50.

MacFadden, B.J. 2000. Cenozoic mammalian herbivores from the Americas: reconstructing ancient diets and terrestrial communities. *Annu. Rev. Ecol. Syst.,* 31: 33-59.

MacFadden, B.J. & Shockey, B.J. 1997. Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: morphological and isotopic evidence. *Paleobiology,* 23: 77-100.

Mainland, I.L., 1997. A qualitative approach to dental microwear analysis. *In* Sinclair, A., Slater, E. & Gowlett, J. (eds.), *Archaeological Sciences 1995: Proceedings of a Conference on the Application of Scientific Methods to Archaeology* : 213-221. Oxford Books Monogr. Ser. 64. Oxford.

Mainland, I.L. 2003. Dental microwear in grazing and browsing Gotland sheep (*Ovis aries*) and its implication for dietary reconstruction. *Journ Archeol. Sc.*, 30: 1513-1527.

Mendoza, M., Janis, C.M. & Palmqvist, P. 2002. Characterizing complex craniodental patterns related to feeding behaviour in ungulates: a multivariate approach. *J. Zool., Lond.*, 258: 223-256.

Palombo, M.R. 2001. Paedomorphic features and allometric growth in *Elephas falconeri* skull from Spinagallo (Middle Pleistocene, Sicily). *In* Cavaretta, G., Gioia, P., Mussi, M. & Palombo, M.R. (eds.), *The World of Elephants*: 492-496. Pubbl. CNR. Roma.

Palombo, M.R, Filippi, M.L, Iacumin, P., Longinelli, A., Barbieri, M. & Maras, A. 2005. Coupling microwear and stable isotopes analyses for paleodiet reconstruction: The case study of Late Middle Pleistocene *Elephas (Palaeoloxodon antiquus* teeth from the Rome Area (Central Italy). *Quaternary International*, 126-128: 153-170.

Pereira, E., 2001. *Cervus elapus rossii* (Mammalia, Artiodactyla), an endemic new sub-species from the Middle Pleistocene in Corsica. *Paleovertebrata*, 30 (2-4): 189-213.

Pérez-Barberia, F.J. & Gordon,, I.J., 1999. The functional relationship between feeding type and jaw and cranial morphology in ungulates. *Oecologia*, 118: 118-157.

Pérez-Barbería, F.J. &, Gordon, I.J. 2001. Relationships between oral morphology and feeding style in the Ungulata: a phylogenetically controlled evaluation. *Proc. R. Soc. London*, B268: 1021-1030.

Pérez-Barbería, F.J., Gordon, I.J. & Nores, C. 2001. Evolutionary transitions among feeding styles and habitats in ungulates. *Evol. Ecol. Res.*, 3: 221-230.

Resenberg, J.M. 1978. Scanning electron microscopy of wear and occlusal events in some small herbivores. *In* Buttler, P.M. & Joysey, K.A. (eds.), *Development, Function and Evolution of Teeth*: 415-438. Academic Press.

Solounias, N. & Dawson-Saunders, B. 1988. Dietary adaptations and paleoecology of the late Miocene ruminants from Pikermi and Samos in Greece. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 65: 149-172.

Solounias, N., Fortelius, M. & Freeman, P. 1994. Molar wear rates in ruminants: a new approach. *Ann. Zool. Fenn.*, 31: 219–227.

Solounias, N. & Hayek, L.A. 1993. New methods of tooth microwear analysis and application to dietary determination of two extinct ruminants antelopes. *Journal of Zoology*, 229: 421-445.

Solounias, N., McGraw, W.S., Hayek, L.-A. & Werdelin, L. 2000. The paleodiet of the Giraffidae. *In* Vrba, E.S. & Schaller, G.B. (eds.), *Antelopes, Deer, and Relatives: Fossil Record, Behavioural Ecology, Systematics, and Conservation*: 84-95. Yale University Press. New Haven, CT.

Solounias, N. & Moelleken, S.M.C., 1992. Tooth microwear analysis of *Eotragus sansaniensis* (Mammalia: Ruminantia), one of the oldest known bovids. *J. Vertebr. Palaeontol.*, 12: 113-121.

Solounias, N. & Moelleken, S.M.C. 1993a. Tooth microwear and premaxillary shape of the archaic antelope. *Lethaia*, 26: 261-268.

Solounias, N. & Moelleken, S.M.C. 1993b. Dietary adaptation of some extinct ruminants determinated by premaxillary shape. *J. Mammal.*, 74: 1059-1071.

Solounias, N. & Moelleken, S.M.C. 1999. Dietary determination of extinct bovids through cranial foramina analysis, with radiographic application. *Ann. Mus. Goulandris*, 10: 267-290.

Solounias, N., Moelleken, S.M.C. & Plavcan, J.M. 1995. Predicting the diet of extinct bovids using masseteric morphology. *J. Vertebr. Paleontol.* 15: 795-805.

Solounias, N. & Semprebon, G. 2002. Advanced in the Reconstruction of Ungulate Ecomorphology with Application to Early Fossil Equids. *American Museum Novitates*, 3366: 1-49.

Solounias, N., Teaford, M.F. & Walker, A. 1988. Interpreting the diet of exinct ruminants: the case of a non-browsing giraffid. *Paleobiology*, 14: 287-300.

Stewart, K.M., Bowyer, R.T., Kie, J.G., Cimon, N.J. & Johnson, B.K. 2002. Termospatial disposition of elk, mule deer and cattle: resource partition and competitive displacement. *J. Mammal.*, 83: 229-244.

Teaford, M.F. 1988. A review of dental microwear and diet in modern mammals. *Scanning Microscopy*, 2 (2): 1149-1166.

Teaford, M.F. 1991. Dental microwear what can it tell us about diet and dental function? *In* Kelley, M.A. & Larsen, C.S. (eds.), *Advances in Dental Anthropology*: 341-356. Alan R. Liss. New York.

Teaford, M.F. 1994. Dental microwear and dental function. *Evol. Anthropol.* 3: 17-30.

Teaford, M.F. & Oyen, O.J. 1989. Differences in the rate of molar wear between monkeys raised on different diets. *J. Dental Researches*, 68: 1513-1518.

Ungar, P.S. 2001. *Microware software, Version 4.0. A semiautomated image analysis system for the quantification of dental microwear*. Fayetteville, AR.

Valli, A.M.F. & Palombo, M.R. In press. Le régime d'*Eucladoceros ctenoides* (Nesti 1841) reconstitué par la morphologie du crâne et par l'usure dentaire. *Eclogae Geol Helv.*

van Valen, L. 1960. A functional index of hypsodonty. *Evolution*, 14: 531–532.

Vizcaíno, S.F. & Bargo, M.S. 1998. The masticatory apparatus of the armadillo *Eutates* (Mammalia, Cingulata) and some allied genera: Paleobiology and evolution. *Paleobiology*, 24 (3): 371-383.

Vizcaíno, S.F., de Iuliis, G. & Bargo, M.S. 1998. Skull shape, masticatory apparatus, and diet of *Vassallia* and *Holmesina* (Mammalia: Xenarthra: Pampatheriidae). When anatomy con-strains destiny. *J. Mammal. Evol.*, 5: 293-321.

Williams, S.H. & Kay, R.F. 2001. A comparative test for adaptive explanations for hypsodonty in ungulates and rodents. *J. Mammal. Evol.*, 8: 207-229.

APPENDIX

Examined taxa: *Moschus moschiferus* Linnaeus 1758, *Muntiacus muntjak* (Zimmermann 1780) *Cervus elaphus* Linnaeus 1758; *Cervus albirostris* Pzevalski 1883; *Cervus canadensis* Exleben 1777; *Cervus duvaucelli* Cuvier 1823; *Capreolus capreolus* (Linnaeus 1758); *Dama dama* (Linnaeus 1758); *Dama clactoniana* (Falconer 1868) *Alces alces* (Linnaeus 1758); *Rusa unicolor* (Kerr 1792); *Rusa timorensis* (Blainville 1822); *Odocoileus virginianus* (Zimmermann 1780); *Odocoileus hemionus* (Rafinesque 1817, *Axis axis* (Exleben 1777); *Elaphurus davidianus* Milne Edwards 1899; *Rangifer tarandus* (Linnaeus 1758; *Megaloceros giganteus* Blumenbach 1803; *"Praemegaceros" obscurus* (Azzaroli, 1953*), Eucladoceros senesensis* Heintz 1970.

The specimens are kept at the following Institutions: Natural History Museum, London; Natuurmuseum, Rotterdam; Museum National d'Histoire Naturelle, Paris, Istitute de Paléontologie Humaine, Paris; Laboratoire départimental de Préhistoire du Lazaret, Nice; Naturhistorischen Museum, Basel; Museo di Scienze Naturali "La Specola", Firenze; Museo di geologia e Paleontologia, Firenze; Museo di Anatomia comparata, "La Sapienza" University of Rome; Museo di Paleontologia and Dipartimento di Scienze della Terra, "La Sapienza" University of Rome; Museo Civico di Zoologia, Rome; Istituto Italiano di Paleontologia Umana, Roma; Museo Preistorico Etnografico Pigorini, Roma.