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SHORT COMMUNICATION

Dental microwear in relation to changes in the direction of mastication during the evolution of Myodonta (Rodentia, Mammalia)

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Abstract Observations of dental microwear are used to analyse the correlation between changes in molar tooth crown morphology and the direction of masticatory movement during the evolution of Myodonta (Rodentia, Mammalia). The studied sample includes 36 specimens representing both superfamilies of Myodonta (Muroidea and Dipodoidea) spanning 16 dipodoid and 9 muroid species. Microscopic scratches on occlusal surfaces resulting from contact between opposite teeth during mastication are analysed. Using these features, we determine the direction of masticatory movements. Microwear patterns display diverse orientations among Dipodoidea: oblique in Sicistinae, Euchoreutinae and Zapodinae, propalinal in Dipodinae and intermediary in Allactaginae. Similarly, Muroidea exhibit the following orientations: oblique in Cricetinae and propalinal in Arvicolinae, Cricetomyinae, Gerbillinae and Murinae. These various chewing types illustrate different evolutionary grades within the superfamilies. Acquisition of the antero-posterior masticatory movement in Dipodoidea is related to flattening of the molar occlusal surface. However, in some muroid subfamilies, this direction of mastication is associated with low-crowned and cuspidate molars (Cricetomyinae, Murinae).

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Introduction

The infraorder Myodonta (Rodentia, Mammalia) is composed of two superfamilies, the Muroidea and the Dipodoidea, which include 1,336 and 51 living species, respectively (McKenna and Bell 1997; Nowak 1999). The oldest known Muroidea and Dipodoidea are from the Middle to Late Eocene of Asia (Dawson and Tong 1998; Emry et al. 1998; Wang and Dawson 1994). The common ancestor of these two superfamilies must have had bunodont molars, quadrangular lower molars and square upper molars (Marivaux et al. 2004). These characteristics are still present in extant Sicistinae, a subfamily of Dipodoidea. Ognev (1963) considered the dental morphology of Sicistinae as the most primitive among Dipodoidea, and Martin (1994) regarded them as a stem group for the extant Dipodoidea. As a result, and contrary to the situation in Muroidea, extant Dipodoidea display both primitive and derived dental morphologies. This study concentrates primarily on Dipodoidea because the patterns of mastication in those species with the relatively primitive dental morphologies likely approximate the condition in early myodont rodents.

We aimed to determine how morphological changes in the cheek teeth in myodont phylogeny correspond with modifications in the orientation of mastication. The orientation of mastication has been studied on the basis of dental microwear. Previously, this method was mainly used to infer diet in extinct and extant mammal species using images from a scanning electron microscope (SEM; Walker et al. 1978; Grine and Kay 1988; Lewis et al. 2000). Since the early 1990s, some authors have approached the same subject using optical microscopy, which can provide images of nearly similar quality (Solounias and Hayek 1993; Nelson et al. 2005; Merceron et al. 2005). More rarely, microwear has been used to study the mastication of large and small amniotes (Mills 1955; Butler 1980, 1985; Fiorillo 1998; Goswami et al. 2005) because the orientation of microwear striations reflects the dominant direction of jaw movements. Dental microwear directions were determined in this study using optical techniques to assess jaw movements in primitive and derived myodont rodents.

Materials and methods

Studied specimens were borrowed from the collections of the "Museum National d'Histoire Naturelle" (MNHN) of Paris, from the "Museum of Vertebrate Zoology" (MVZ) of Berkeley and from the "Centre de Biologie et de Gestion des Populations" of Montferrier-sur-Lez (CBGPM). A total of 36 specimens of Myodonta belonging to 16 dipodoid and 9 muroid species were examined. The taxonomy follows Nowak (1999). The Dipodoidea sample included seven Zapodinae (one *Eozapus setchuanus*, one *Zapus princeps*, one *Z. trinotatus*, two *Z. hudsonius* and two *Napaeozapus insignis*); six Allactaginae (one *Allactaga sibirica*, one *A. hotsoni*, one *A. major*, two *A. elater* and one *Alactagulus pumilio*); ten Dipodinae (two *Dipus sagitta*, one *Jaculus orientalis*, six *J. jaculus* and one *Stylodipus telum*); one Sicistinae (*Sicista betulina*); and one Euchoreutinae (*Euchoreutes naso*). The Muroidea sample included one Gerbillinae (*Meriones crassus*); two Myospalacinae (two *Myospalax fontanieri*); two Arvicolinae (two *Arvicola terrestris*); one Cricetomyinae (*Saccostomus campestris*); two Cricetinae (one *Cricetus cricetus* and one *Mesocricetus auratus*); and three Murinae (one *Apodemus sylvaticus*, one *Micromys minutus* and one *Arvicanthis ansorgei*).

Microwear features are generated on enamel dental facets during the course of mastication (Walker et al. 1978; Solounias and Hayek 1993). The number of pits (semi-circular scars) and scratches (elongated scars) vary with the properties of the last food items consumed (Merceron et al. 2004). Only scratches were considered during this study because their orientation identifies the direction of jaw movement during chewing. Angles were measured between scratch direction and the antero-posterior axis of the jugal tooth row. All measurements were made on the lingual facet of the entoconid of the second lower molar, which is the most widely used molar in microwear analysis (Solounias and Hayek 1993; Merceron et al. 2005). For two specimens (*E. setchuanus* and *S. betulina*), the preservation of this facet did not allow directionality of scratches to be measured correctly. In these cases, measurements were taken on a mesial facet of the first lower molar or on the vestibular facet of the third lower molar.

For this study, we used a LEICA® MZ 16 stereomicroscope. Compared to SEM, this method is cheaper, simpler and totally non-invasive (no need for coating). Dental elements were cleaned using alcohol and acetone to remove dirt or glue from the occlusal surface. Casts of the teeth were then made using polyvinylsiloxane and transparent epoxy resin, which was heated at 30°C during 8 h. Pictures of enamel facets were digitized in 256 grey levels using a LEICA® DFC 320 CCD-camera with either the ×80 or ×100 objective (depending on specimen size) and transmitted-light through the stereomicroscope (Fig. 1a–d). Statistics were calculated with the Statistica 7.1 program. An alpha level of 0.05 was assumed for all tests.

Results and discussion

Most of the casts (85%) allowed measurement of the angle defined by the orientation of the scratches and the antero-posterior axis of the tooth row (the other 15% are not included here). Scratch orientation varies slightly among the distinct facets of a molar, and measurements made on several facets in various molars of the same row showed negligible variation (less than 5°). This emphasizes that the buccal and lingual phases of mastication are about the same direction, or that the buccal phase is reduced, as observed in other rodents (Butler 1980). Intraspecific variation, measured mainly for *Jaculus jaculus*, is small when compared to interspecific variation (the standard deviation for this species is only 2.26°). Considering all specimens together, angle measurements between scratches and the tooth row axis vary from ca. 0° to 60°.

If significant differences between Dipodoidea subfamilies were observed, dispersion around a mean value was small for any subfamily (Fig. 2a–k). The ten Mann–Whitney U tests on the orientation of scratches in the different Dipodoidea subfamilies were all statistically significant except between Euchoreutinae and Zapodinae (U=87; p=0.607). The p value is less than 0.001 in all other cases except between Zapodinae and Sicistinae (U=98; p=0.011) and between Euchoreutinae and Sicistinae (U=8; p=0.037). Sicistinae display an oblique jaw movement during chewing (Fig. 2a). According to Butler (1985), an oblique pattern can be considered as primitive. Such a pattern is also observed within the Euchoreutinae and Zapodinae (Fig. 2b,c). It must be pointed out that similarities in scratch orientation among these latter three sub-families are associated with distinct occlusal morphologies. Molars are bunodont in Sicistinae, display high cusps in Euchoreutinae and transverse crests in Zapodinae, in which the molars are hypsolophodont. Molars of Dipodinae

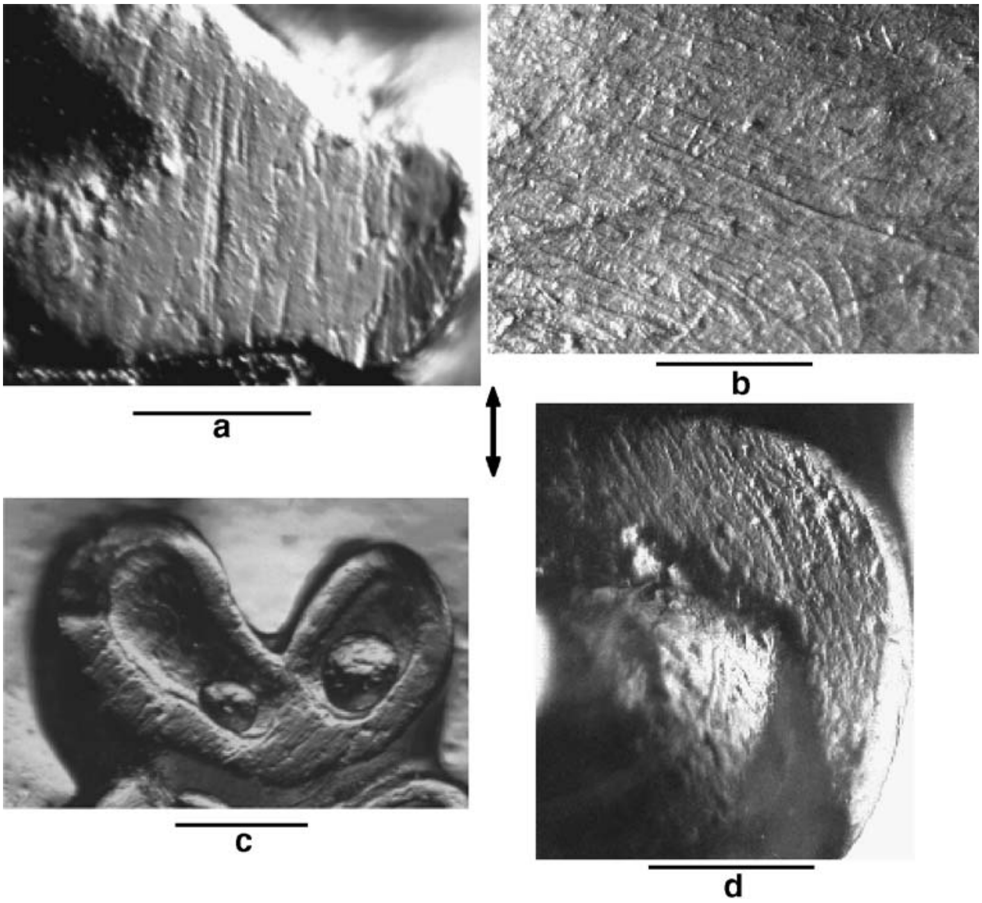

Fig. 1 Microwear pattern in Myodonta (Rodentia, Mammalia). **a** Occlusal view of the entoconid of the second lower molar (M_2) in the Dipodinae *Jaculus jaculus*, indicating a propalinal mastication, specimen MNHN CG 1989-16. **b** Occlusal view of the entoconid of M_2 in the Cricetinae *Cricetus cricetus*, indicating an oblique direction of mastication, specimen MNHN CG 1958-137. **c** Occlusal view of the mesial part of M_1 in the Zapodinae *Eozapus setchuanus*, indicating an oblique direction of mastication, specimen CBGPM HH9607-JY06. **d** Occlusal view of the entoconid of the M_2 in the Allactaginae *Allactaga sibirica*, indicating an oblique direction of mastication, specimen CBGPM NH9505-JB02. *Arrows* symbolize the axis of the jugal tooth row. Scale bar: 0.3 mm

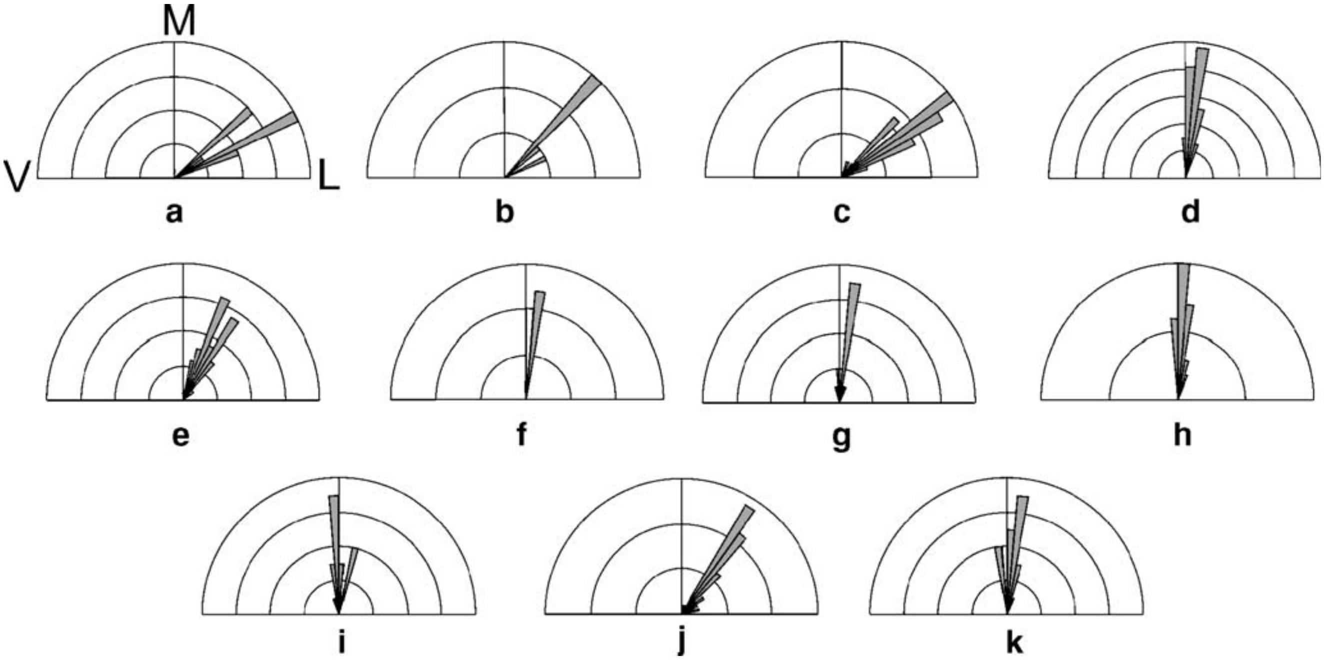

Fig. 2 Orientation of microwear scratches on lower molars in Myodonta. **a** Sicistinae, n=10 (m=57.9, sd=7.5); **b** Euchoreutinae, n=5 (m=46.8, sd=9.2); **c** Zapodinae, n=64 (m=51.15, sd=10.9); **d** Dipodinae, n=143 (m=7.1, sd=6.1); **e** Allactaginae, n=63 (m=26.1, sd=8.7); **f** *Myospalax*, n=24 (m=3.7, sd=3); **g** *Saccostomus*, n=14 (m=6.8, sd=6.2); **h** *Arvicola*, n=28 (m=0.6, sd=2.6); **i** *Meriones*, n=19 (m=0.8, sd=6.0); **j** Cricetinae, n=43 (m=40.2, sd=12.2); **k** Murinae, n=20 (m=3.5, sd=6.8). *M* Mesial, *V* vestibular, *L* lingual, *n* number of measured scratches, *m* mean angle, *sd* standard deviation

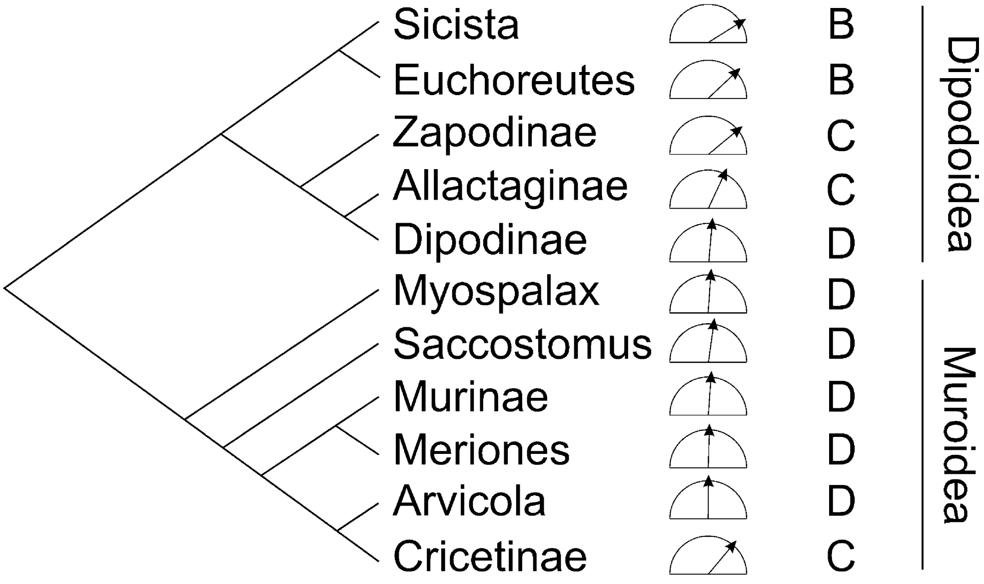

Fig. 3 Phylogeny and mastication orientation of some Myodont rodents. Molecular phylogeny adapted from Steppan et al. 2004. "Sicista + Euchoreutes" association according to Shenbrot 1992. *Arrows* represent the orientation of the masticatory jaw movement, same diagram orientation as Fig. 2. 'B', 'C' and 'D' correspond to Butler's grades of mastication. Although Cricetinae is the only Muroidea outside the D grade, it is considered to have the most primitive masticatory mechanism among Muroidea we sampled. We therefore conclude that propalinal mastication has been acquired many times during the course of myodont evolution

bear scratches having orientations that indicate propalinal (antero-posterior) mastication (Fig. 2d). Jaw movements are intermediate in Allactaginae (Fig. 2e).

Butler (1985) defined four major grades of rodent molar evolution as it relates to the orientation of mastication. None of the rodents studied here belongs to Butler's grade A, in which the masticatory movements display two distinct phases. Sicistinae and Euchoreutinae display grade B with an oblique chewing movement, despite differences in cusp morphologies. Zapodinae and Allactaginae illustrate grade C with a single oblique movement of chewing and a flattening of the occlusal surface. Nevertheless, having established significant differences of orientation and morphology between Zapodinae and Allactaginae, we propose here to split Butler's group C into C1 for species with an angle greater than 35° between scratches and the tooth row axis (as in Zapodinae, Fig. 2c) and C2 for those with an angle between 10° and 35° (as for Allactaginae, Fig. 2e). Dipodinae display a propalinal direction of mastication that characterizes D group.

Among the sampled Muroidea, only Cricetinae, which are ancestral to other Muroidea (Marivaux et al. 2004), have an oblique mastication. All others (*Meriones*, *Myospalax*, *Arvicola*, *Saccostomus*, *Murinae*) display a propalinal movement with statistically the same orientation confirmed by an analysis of variance ($F=2.21$; $df=4$; $p=0.08$). Contrary to Dipodoidea, in Muroidea, the propalinal chewing motion can be associated with two different crown morphologies: hypsodonty and flat-crowned molars in *Meriones*, *Myospalax* and *Arvicola*, and cuspidate teeth in *Saccostomus*, *Micromys*, *Apodemus* and *Arvicanthis*. Although species with similar masticatory direction can have different crown morphologies, the latter reflects a functional constraint relative to grinding efficiency. This is especially clear in lophodont Dipodoidea (Zapodinae and Allactaginae). Crests are roughly perpendicular to the direction of jaw movement, a fact already clearly recognized in rodents with hypsodont dentitions (Koenigswald et al. 1994). Similarly, cusps configuration in Murinae allow a propalinal masticatory direction with the lower cusps positioning in the grooves between the upper cusps (Butler 1985). Dipodinae, which are considered more derived than Sicistinae (Ognev 1963), display a propalinal direction of mastication associated with flat occlusal surfaces. Therefore, the acquisition of propalinal mastication in Dipodoidea seems to be associated with flattening of the molar occlusal surface (Fig. 3). However, this latter observation cannot be generalized to all rodents, as, for example, the Murinae with a propalinal chewing motion associated with cuspidate molars.

Conclusions

Dipodoidea display a wide spectrum of orientation of masticatory movements (Fig. 3). A highly oblique direction of mastication is present in Sicistinae, which display the most primitive dental morphology. In other subfamilies, the orientation tends to become more antero-posterior (Allactaginae) or even propalinal (Dipodinae). Dental morphologies among the Dipodoidea subfamilies reveal that the acquisition of propalinal mastication is associated with flattening of the molar occlusal surface. Among Muroidea, such an orientation can be associated either with flat-crowned molars (Gerbillinae, Myospalacinae, Arvicolinae) or cuspidate molars (Cricetomyinae, Murinae).

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