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GENERAL BIOLOGY

Patterns of Lateral Wear Facets on Molar Teeth of Voles (Arvicolinae)

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Among the modes of phytophagy described by Agadzhanyan, voles occupy a special place [1]. Large amounts of rough vegetables are masticated by either hypsodont or hypsodont molars. Their active flanks are enamel edges of the triangular prisms. The biomechanics of chewing movements is adjusted to predominantly anteroposterior mobility of the mandible relative to the maxilla [2, 3].

In some species, occlusal disturbances leave lateral wear facets on their upper and lower teeth. This phenomenon has been previously described in the root vole (*Microtus oeconomus*) [4]. This study considers the patterns of lateral wear facets in a number of species and genera out of the subfamily Arvicolinae. It is urgent to study this phenomenon because lateral wear facets may be indicators of mesowear on mammal teeth used for paleodietary reconstruction [5]. Mesowear has been already investigated in large-sized mammals [5, 6]. Voles are still little understood with regard to this aspect but deserve further consideration. In addition, the presence of facets should be taken into account when assessing the morphotypes of the masticatory surface pattern.

The patterns of lateral wear facets have been assessed in a sample of 15 species out of 10 genera of the vole subfamily Arvicolinae. A total of 1766 skulls from the following collections have been examined: Zoological Museum of the Moscow State University; Zoological Museum of the Institute of Biology and Soil Science, Far East Branch, Russian Academy of Sciences; Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences. Some of them were kindly provided by our colleagues. The patterns of facet development were analyzed in a laboratory colony of *M. oeconomus* ($n = 70$) by taking intravital imprints from the masticatory surface of molars [7].

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Lateral wear facets are pathological formations that occur as a result of functional changes. They are grooves in the lateral walls of the enamel prisms observed in the enamel and, as a rule, the dentine layers. They are the widest near the masticatory surface and vanish not reaching the gum (Fig. 1a). Facets are most often found on the lingual side of the lower molars and the buccal side of the upper molars. They run from the front to the back parts of the tooth and from the first to the third molars. At the initial stages, facets occur at the masticatory surface. When their development is maximal, they distribute along the most part of the outgoing angle. Wearing on the lateral sides of teeth changes the shape of the masticatory surface. In the laboratory colony of *M. oeconomus*, the interior outgoing angle of the first lower molar totally vanishes at the upper molar surface, which changes the morphotype of the masticatory surface (it becomes shorter).

The facets are distinguished from all other variants of changes in the shape of teeth with a smooth ground surface. In addition, they differ from the dentine tracts by their shape narrowing to the tooth root, as well as from the tooth chipping, in an ordered arrangement and even edges and from the sings of digestion by predators in the solid enamel outside the facets.

Analysis of intravital imprints collected from the molars of laboratory specimens of *M. oeconomus* revealed that facets may occur and vanish in the succeeding months. The results of our trial experiment suggest that wear facets occur on the lateral sides of teeth when an animal shifts to feeding on spongy food. Possibly, due to this spongy food, wearing of teeth does not compensate their growth. This causes an occlusal disturbance, when the lateral parts of upper teeth approach those of lower teeth. When abrasives are reintroduced into the diet, teeth wear out at a "normal" speed and facets do not occur. A tooth part with no facet grows, while the damaged part wears out, and the shape of the masticatory surface gradually recovers.

The surface of facets is distinguished from the masticatory one in that it has no signs of the abrasive effect

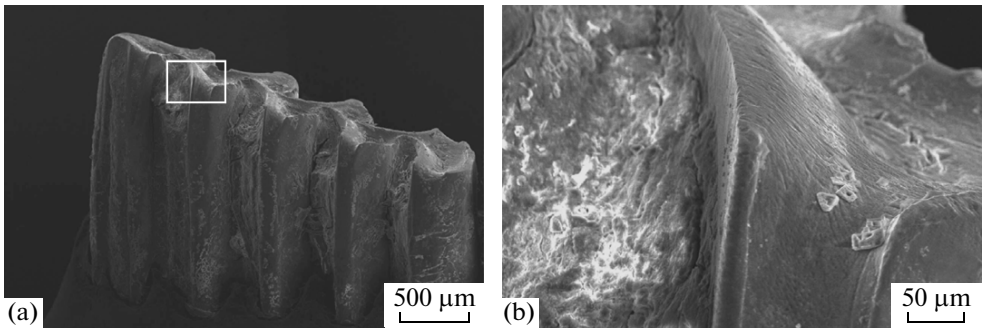

Fig. 1. The first lower molar of *M. oeconomus* with well-pronounced lateral wear facets: (a) magnification, 37×, (b) fragment of the photograph in Fig. 1a; magnification, 300×.

produced by food, which is possible during tooth-to-tooth friction. The microphotos show scratches on the molar tooth of *M. oeconomus* caused by chewing (Fig. 1b). They are parallel to each other and run along the tooth axis, indicating that there are no lateral movements of the jaws [8]. In meadow voles (*Microtus*), the forward movement of the jaws during chewing is considered a working one [9]. The mobile joint of mandibular branches in the symphysis enables the right and left jaw movements [2]. It may be suggested that the sides of the upper and lower teeth meet each other edge to edge during occlusion, when the lower jaw assumes a backward position.

The objects of study were selected according to Gromov's types of morphofunctional structures [2] responsible for "masticatory adaptations" in the subfamily. In order to find whether there are intraspecific differences in the frequency of lateral wear facets, we investigated the collections of one species from distant localities.

Lateral wear facets are pronounced in voles out of the genera *Microtus* and *Alticola*. These taxa have hypsodont molars with cement in the re-entrant angles without high dentine tracts. The highest proportion and expression of lateral wear facets was revealed in animals from the Polar Urals. The maximal proportion of animals with lateral wear facet on their molars (61 of 96 specimens) was found in the collection of Middendorff's voles (*M. middendorffii*) captured in the Polar Urals. *M. oeconomus* having lateral wear facets on their molars were detected in the samples from the Polar Urals (37 of 85 specimens), Chukchi Peninsula (11 of 58), and Yamal (12 of 122). No *M. oeconomus* specimens with lateral wear facets on the molars were found in two samples from the Middle Urals ($n = 111$, $n = 37$) and one sample from the Southern Urals ($n = 109$). The narrow-skulled vole (*M. gregalis*) with lateral wear facets were recorded in the collections from the Polar Urals (26 of 117 specimens), Middle Yamal (3 of 182), Southern Urals (3 of 26), and Southern Trans-Ural region (3 of 42). No animals of this species and having lateral wear facets on their molars were detected in the sample from the Middle Urals ($n = 31$). Among field voles ((*M. agrestis*), specimens with lateral wear facets were found in the samples from the Polar (24 of 116 specimens) and Middle (8 of 51) Urals. Lateral wear facets were found in 9 of 25 specimens of lemming voles (*Alticola* and *Aschizomis lemminus*) from the vicinities of the village of Egvekinot (Chukotka). All (13) specimens taken from the vicinities of the village of Pevek (Chukotka) developed highly pronounced facets after having been kept in the laboratory of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences. In large-eared voles (*Alticola macrotis*) captured near Tiksi ($n = 35$), no lateral wear facets of the molars were revealed.

In long-clawed mole voles (*Prometheomys shaposhnicovi*), lateral wear facets at the very initial stages were found in 11 of 137 specimens. Various mesowear traces were found in the genera *Ondatra*, *Clethrionomys*, *Dycrostonyx*, *Lemmus*, and *Myopus.* Nevertheless, they are not analogous to lateral wear facets on teeth of *Microtus.* In the studied sample of the muskrat (*Ondatra zibethicus*) from the Southern Yamal ($n = 98$), wearing of both enamel edges and dentine was observed in older specimens based on the enamel tissue disruption. The width of the wearing on the lateral edge of the prism decreases from the masticatory surface to the tooth root. They could be called facets along the dentine tracts. In the northern red-backed (*Cl. rutilus*) and grey red-backed (*Cl. rufocanus*) voles from the Polar Urals ($n = 33$ and 39, respectively), smoothed enamel edges and depleted dentine were most often observed on elements, where either a thinner enamel layer or dentine tracts are formed. In wood lemmings (*M. schisticolor*) from the Yenisei River ($n = 8$) and Siberian brown lemming (*L. sibiricus*) from Southern Yamal ($n = 30$), we did not find any lateral wear facets; only a slight smoothing along the dentine tracts were revealed.

In Arctic lemmings (*D. torquatus*) from Southern Yamal ($n = 43$) and yellow steppe lemmings (*E. luteus*) (Lake Zaysan, $n = 20$), no lateral wear facets were

found. Several specimens of steppe lemmings (*L. lagurus*) kept in the vivarium of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, ($n = 30$) had areas along the dentine tracts smoothed.

Consequently, lateral wear facets are commonly found in voles with rootless molars having a thick enamel covering and cement in the re-entrant angles, without high dentine tracts. Among the species studied, they have been found in representatives of the genera *Microtus* and *Alticola*. The density of facets may significantly vary in different parts of the range of the same species.

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