

Lagomorpha and Rodentia

INTRODUCTION

Lagomorpha and Rodentia are sister groups, which together form the superorder Glires. Lagomorphs are a small order of herbivores, with 90 species in two families. In contrast, there are over 2000 species of rodents in 33 families, which account for 40% of all mammalian species. They have colonized every continent except for Antarctica and live in every climatic zone, from arid deserts to Arctic tundra, and they exploit a wider variety of plant foods, including nuts, seeds, and roots, and the group includes omnivores and even animalivores.

Dentition

The dentitions of lagomorphs and rodents share a common ground plan, which is a major factor in the success of these mammals. The most distinctive feature is the presence of curved, continuously growing incisors (Fig. 7.1A and B), which have extremely sharp edges and can be put to a multitude of uses, from cropping grass to gnawing some of the hardest substances in nature. There is one pair of upper incisors in rodents and two pairs in lagomorphs, while in all Glires there is one pair of lower incisors. These incisors owe their sharp edges to an asymmetrical distribution of enamel, which is confined to the anterior surfaces, with some extension onto the lateral surfaces (Fig. 7.1C). The remaining surfaces of the incisors are covered by a very thin layer of cementum that mediates attachment of the periodontal ligament fibers (Fig. 7.1A–C). Because enamel is much harder than dentine or cementum, the anterior surface wears more slowly than the oral surface, so that the functional surfaces acquire a sharp-edged gouge shape. The edge is maintained in good condition by deliberate sharpening movements of the jaws (Druzinsky, 1995).

As the incisors of rodents and lagomorphs erupt, the diameter gradually increases, so that the size of the tooth keeps pace with bodily growth. Each incisor has the shape of part of a spiral, which means that it is possible for the formative ends to be located within the jaws, while the incisors converge toward the front of the jaws, so that the functional tips lie alongside each other.

Canines are absent and the incisors are separated by a gap (**diastema**) from a battery of cheek teeth that are

adapted to efficient chewing of the food. The diastema allows manipulation of food, and also permits the anterior part of the oral cavity to be closed off from the posterior part by the intrusion of folds of the cheeks. This activity prevents debris of incisal gnawing from reaching the pharynx. As detailed later in this chapter, the number, morphology, and mode of use of the cheek teeth vary between taxa and between upper and lower jaws. In lagomorphs there are five or six cheek teeth per quadrant and zero to six in rodents.

The mandibular symphysis in lagomorphs and most rodents is not fused, which allows a degree of relative movement between the two halves of the jaws and permits twisting of each half around its long axis. These movements allow precise occlusion between the cheek teeth during mastication.

Wear and Eruption

The incisors of rabbits and rodents are subject to heavy wear from grazing and gnawing. Molars of lagomorphs and herbivorous rodents are also subject to wear from the diet and adventitious grit and soil (Chapter 3). Consequently, in many herbivorous rodents, the molars are hypsodont or hypselodont, and the cheek teeth are hypselodont in all lagomorphs (see Chapter 3).

The eruption rate of hypselodont teeth reflects the high rate of wear. For practical reasons, the continuously growing incisors of lagomorphs and rodents have been the experimental system of choice for studies investigating the eruptive mechanism. The “impeded” eruption rate—i.e., the rate measured for teeth in function—of the incisors of terrestrial rodents varies from 1.1 to 3.9 mm/week (e.g., Berkovitz, 1974) and from 1.6 to 7.0 mm/week in burrowing species (e.g., Manaro, 1959; Berkovitz and Faulkes, 2001; Müller et al., 2015; Wyss et al., 2016). In the rabbit this rate varies between 1.1 and 2.7 mm/week (Ness, 1956; Müller et al., 2014 [their Table 2: experimental studies only]). There are fewer data on hypselodont molars. In voles and lemmings, the impeded eruption rate of molars is 0.4–0.9 mm/week (von Koenigswald and Golenishev, 1979). In the rabbit, premolars grow at 0.9–2.1 mm/week (Wyss et al., 2016) and molars at

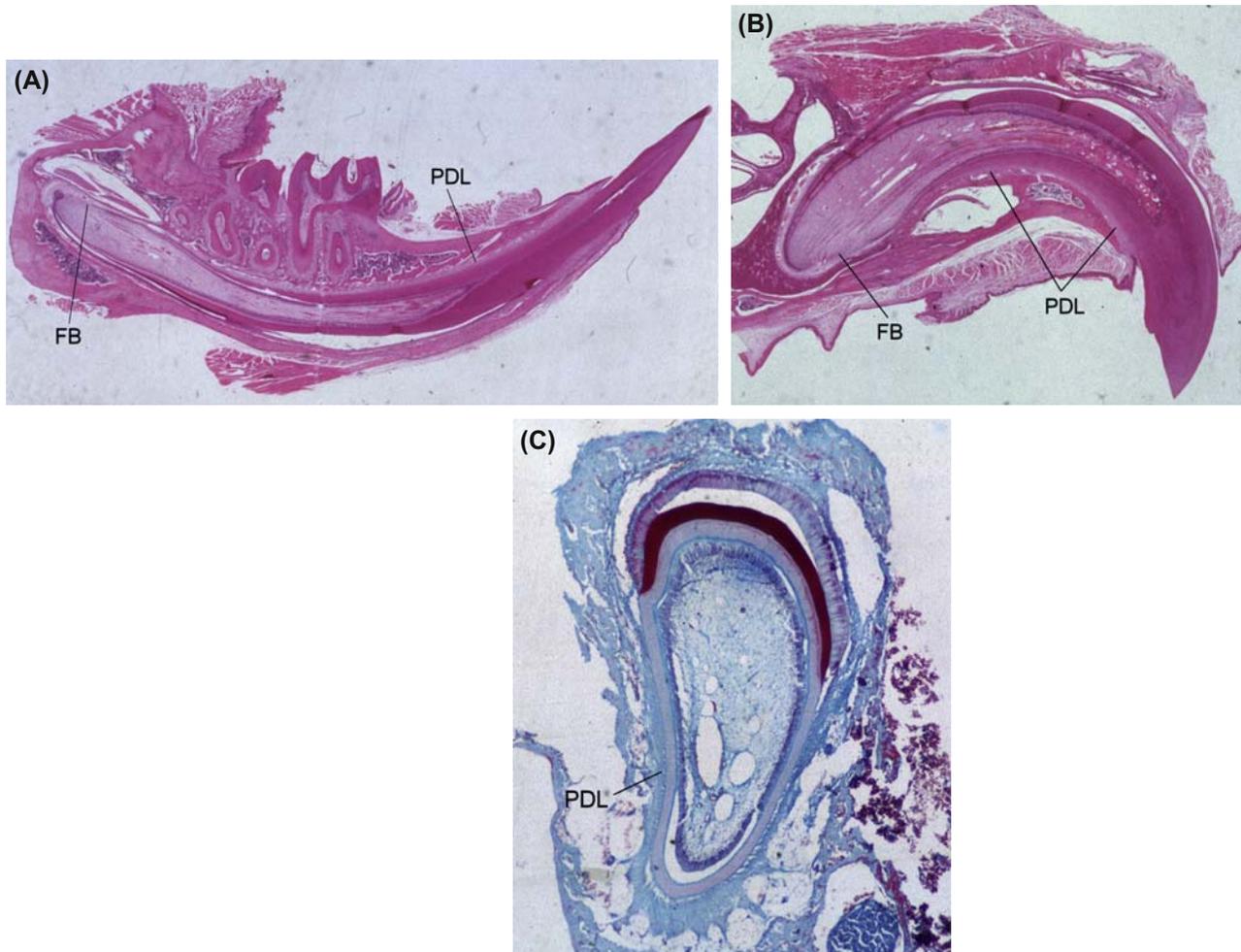


FIGURE 7.1 Histology of hypselodont incisors of the brown rat (*Rattus norvegicus*). (A) Longitudinal section of lower incisor. Original magnification $\times 11$. (B) Longitudinal section of upper incisor. Original magnification $\times 11$. (C) Transverse section of a lower incisor near the formative base, showing immature enamel matrix, stained dark red, on the anterior surface with some extension onto lateral surfaces but none on other surfaces. Original magnification $\times 55$. In all sections, periodontal ligament is present on surfaces not covered by enamel. *FB*, formative base; *PDL*, periodontal ligament. Hematoxylin and eosin. *Courtesy Dr. M. Robins.*

1.1–3.2 mm/week (Müller et al., 2014), depending on the abrasivity of the diet.

In experiments with diets of different abrasivities, the eruption rate of incisors was observed to be positively, but weakly, related to wear rate ($r^2 = 0.09\text{--}0.43$) (Müller et al., 2014, 2015). If the influence of interindividual variation is removed by using mean rates, eruption rate shows a much stronger relationship to wear rate and, moreover, the relationship seems to be the same for rabbits and guinea pigs (Fig. 7.2). As Müller et al. (2015) pointed out, their studies indicate that, even with soft foods that produce no wear, the incisors would still erupt at a certain rate, as indicated by the positive y-intercept in Fig. 7.2. The explanation for this is that lagomorphs and rodents employ deliberate movements to maintain the sharpness of the incisor edges and this activity maintains optimal tooth length when dietary abrasion is inadequate (Ness, 1956; Druzinsky, 1995).

The incisors of lagomorphs and rodents have considerable reserves of eruption potential that could, if needed, compensate for extremely high rates of wear or for tooth fracture. If the occlusal load on the incisors is removed by cutting the tooth out of occlusion, the resulting “unimpeded” eruption rate is much higher than the impeded rate: 2.9–7.0 mm/week in terrestrial rodents (Berkovitz and Thomas, 1969; Berkovitz, 1974; Berkovitz and Faulkes, 2001) and 5.0–7.0 mm/week in the rabbit (Ness, 1956; Moxham and Berkovitz, 1974). This ability can give rise to gross overgrowth of hypselodont teeth that lose contact with their opponents (Fig. 7.3), which can cause feeding problems, other pathologies, and eventual death. It has been suggested that these disturbances, which are major forms of dental pathology in pet rabbits and rodents (Crossley, 1995a,b; Meredith, 2007), could be due to feeding with insufficiently abrasive foods (Crossley, 1995a,b), but

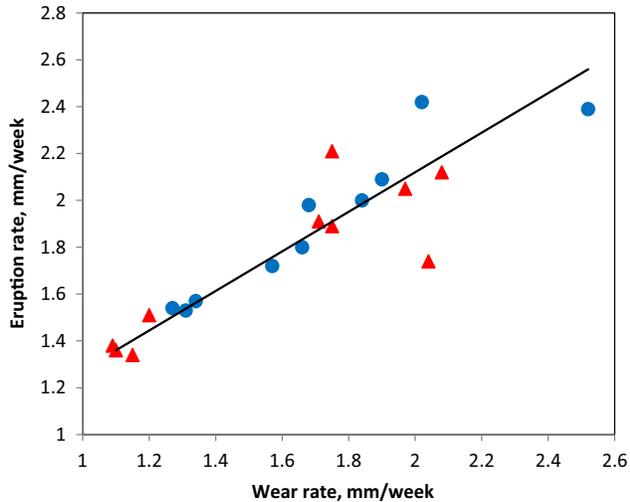


FIGURE 7.2 Plot of mean eruption rate against mean wear rate for rabbit and guinea pig incisors. *Triangles*, guinea pig; *circles*, rabbit. The line shows reduced major axis regression for the combined data set: eruption rate = $0.85(\text{wear rate}) + 0.42$. $r^2 = 0.81$. Data from Müller, J., Clauss, M., Codron, D., Schulz, E., Hummel, J., Fortelius, M., Kircher, P., Hatt, J.-M., 2014. Growth and wear of incisor and cheek teeth in domestic rabbits (*Oryctolagus cuniculus*) fed diets of different abrasiveness. *J. Exp. Zool.* 321A, 283–298; Müller, J., Clauss, M., Codron, D., Schulz, E., Hummel, J., Kircher, P., Hatt, J.-M., 2015. Tooth length and incisal wear and growth in guinea pigs (*Cavia porcellus*) fed diets of different abrasiveness. *J. Anim. Physiol. Anim. Nutr.* 99, 591–604.



FIGURE 7.3 North American beaver (*Castor canadensis*), showing an extreme example of overgrowth of a lower incisor that has become misaligned and lost contact with its opposing incisor. It has continued to grow in a circle and has penetrated the skin, and the tip has come to lie inside the back of the lower jaw. Such overgrowth is a physical obstacle to chewing and leads to death of the animal. The skull of a normal beaver is shown in Fig. 7.22. Original image width = 30 cm. Courtesy RCSHC/P 6

misalignments of the teeth, due to inherited defects or to acquired factors such as mineral deficiency, may also be responsible (Müller et al., 2014, 2015).

Digestion

The members of both groups are hindgut fermenters, in which cellulose fibers are broken down after the food has passed through the stomach and small intestine, within an enlarged cecum. In lagomorphs, and a large proportion of rodents (Hirakawa, 2001), the amount of nutrients extracted from food is maximized by **cecotrophy**. This process is essential for normal growth and maintenance. Two types of fecal pellets are produced (see Hirakawa, 2001, for details). Soft feces, containing the products of cellulose fermentation, are reingested immediately after voiding and the nutrients are assimilated during a further passage through the gut, which results in production of hard fecal pellets. These consist of residual food solids low in nutrients and are generally discarded, although it has been observed that some leporids acquire some nutrient by reingestion, mastication, and digestion of hard pellets when food is limited (Hirakawa, 2001).

LAGOMORPHA

This order comprises two families: the Leporidae (rabbits and hares) and the Ochotonidae (pikas). Lagomorphs originated in Asia and the two families diverged during the Eocene. The ochotonids were most abundant in terms of species, and were most widely distributed during the Miocene and Pliocene, but the number of species and their range were reduced sharply during the Pleistocene. In contrast, the leporids expanded later, during the late Miocene and Pliocene and today outnumber the ochotonids (62 species in 12 genera vs. 30 species in a single genus) (Ge et al., 2013). The more recent evolutionary fortunes of the two lagomorph families may be related to the climate becoming cooler and drier from the mid-Miocene onward, and to the emergence during the same period of C₄ plants, which tend to have a higher content of fiber and lignin than C₃ plants and so are less digestible (Ge et al., 2013). While both lagomorph families eat a wide range of plants, few ochotonids eat C₄ plant material, whereas C₄ plants compose up to 10% of the leporid diet.

Most of our knowledge of lagomorph dental biology has been obtained from studies of the domestic form of the **European rabbit** (*Oryctolagus cuniculus*). It is therefore appropriate to describe the dentition in Leporidae first.

Leporidae

The rabbits and hares are found in a variety of habitats, including forests and open scrub or savannah in Eurasia,

Africa, and North, Central, and northern South America. The European rabbit has also been introduced into Australia, New Zealand, and the rest of South America. Leporids eat a wide variety of herbaceous material. In the group as a whole, grasses account for about 30% of the plant food species (Ge et al., 2013). The dental formula of Leporidae is $I_1^2 C_0^0 P_2^3 M_3^3 = 28$.

All lagomorphs have one incisor in each lower quadrant and two incisors in each upper quadrant (Fig. 7.4). In the rabbit, the formative base of the anterior upper incisor lies between the tip of the premaxilla and the first cheek tooth, and that of the lower incisor lies immediately in front of the first cheek tooth (Fig. 7.5). Studies on the **domestic rabbit** (*O. cuniculus*) show that the six incisors differ in morphology, histology, and function (Hirschfeld et al., 1973). The lower incisors and the anterior upper incisors are wider anteriorly than posteriorly, so that the cross section is approximately D shaped. Enamel covers only the

labial and lateral surfaces, and these incisors develop sharp chisel edges used for biting. In the midline of the anterior surfaces of these teeth there is a longitudinal groove (see Fig. 7.4B). The lingual and lateral surfaces are covered with a thin layer of acellular cementum, which usually extends over the lateral enamel layer and sometimes also onto the labial enamel (Schmidt and Keil, 1971; Hirschfeld et al., 1973). The posterior upper incisors (often called “peg teeth”) lie directly behind the anterior incisors, are round in section, and have enamel on the labial and lingual surfaces but not on the lateral surfaces. A layer of acellular cementum covers all surfaces (Hirschfeld et al., 1973). The function of the posterior incisors is obscure. They may protect the palate from the cutting edges of the lower incisors, but some rabbits lack these teeth and do not show palatal damage (Dr. D.A. Crossley, personal communication). The first-formed tips of developing incisors have a thin layer of enamel on the surfaces that at later stages of growth are enamel free (Hirschfeld et al., 1973).

In the domestic rabbit, it is recognized that the posterior upper incisors are diphyodont (e.g., Hirschfeld et al., 1973; Ooë, 1980; Simoens et al., 1995). However, the homologies of the lower incisors and upper anterior incisors have been the subject of controversy. The most anterior tooth germ has already begun to secrete dentine at 17 days post-fertilization, while the second tooth germ, which lies posterior to the first, is only at the cap stage. The first tooth germ develops into a small tooth, which is shed at about 25 days, while the second develops into the functional lower incisor or upper anterior incisor. Some authors (e.g., Hirschfeld et al., 1973) have interpreted the first tooth germs as the deciduous precursors of the functional lower incisor and upper anterior incisor, which would then correspond to the primitive I_1 and I_1^1 , respectively, and the anterior rabbit dental formula would be $\frac{I_1^1 I_1^2}{I_1}$. Other authors (Moss-Salentijn, 1978; Ooë, 1980) have interpreted the first tooth germs as vestiges of the deciduous primitive I^1 and I_1 , which implies that the functional upper anterior incisors and lower incisor are retained deciduous forms of the primitive I^2 and I_2 or I_3 , which are not replaced. Moss-Salentijn (1978) considered that I_3 is retained, while Ooë (1980) believed the retained tooth is I_2 , so the anterior dental formula could be either $\frac{dI_2^2 I_3^3}{dI_2}$ or $\frac{dI_2^2 I_3^3}{dI_2}$, respectively. Simoens et al. (1995) observed in a wild rabbit a large supernumerary incisor medial to the usual anterior incisor and came to conclusions about the homology of the vestigial tooth germ that were similar to those of Ooë (1980), except that they described it and the anterior incisor as “monophyodont” rather than “deciduous.”

The incisor enamel of leporids is characterized by Hunter–Schreger bands (HSBs; see Chapter 2), which run from the inner to the outer surface (Martin, 2004).

The structure and relationships of the cheek teeth have been described by Michaeli et al. (1980), Crossley (1995b),

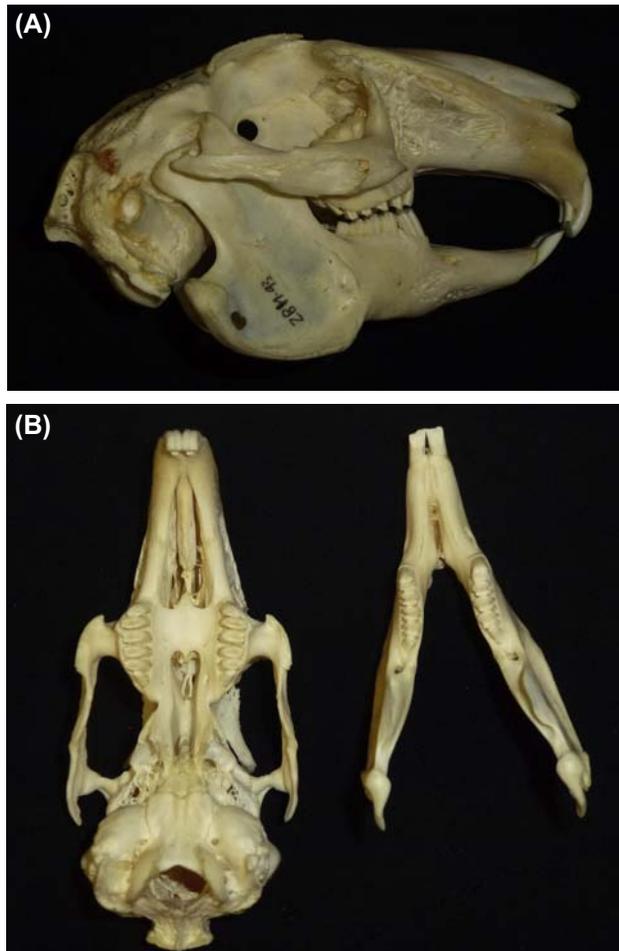


FIGURE 7.4 Domestic rabbit (*Oryctolagus cuniculus*). (A) Lateral view of skull, with mandible at maximum opening. Original image width = 10.4 cm. (B) Occlusal views of upper dentition (left) and lower dentition (right). Note the longitudinal groove on the front surface of the upper first incisors. Original image width = 9.3. Courtesy MoLSKCL. Cat. no. ZBM93.

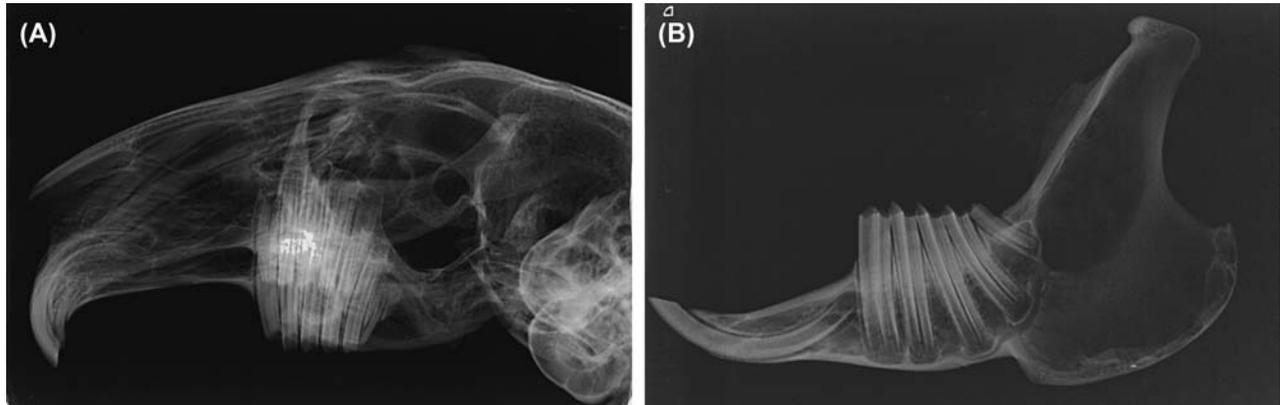


FIGURE 7.5 Domestic rabbit (*Oryctolagus cuniculus*). (A) Radiograph of upper jaw, showing the formative base of the incisor lying anterior to the first premolar. (B) Radiograph of lower jaw, showing location of the formative base of the incisor in front of the cheek teeth. Courtesy MoLSKCL. Cat. no. ZBM93.

and von Koenigswald et al. (2010). The premolars are diphyodont, but the deciduous teeth are short lived, erupting about a week after birth and being shed 2–3 weeks later. The permanent premolars are molarized and all the cheek teeth are hypselodont. The posterior dentition is strongly anisognathous: the lower cheek teeth form two straight rows, which lie well inside the rows of upper cheek teeth (Fig. 7.4B). When at rest, there is minimal contact between the upper and the lower molars.

Leporid cheek teeth possess transverse elevated ridges, which are generated by the action of wear on the underlying tooth structure (Fig. 7.4B). Each tooth is composed of two transverse lobes, the anteroloph(id) and the posteroloph(id), connected by a longitudinal bridge at their buccal aspect in upper molars and their lingual aspect in lower molars (Fig. 7.6A). The reentrant fold between the two lobes is filled with “bone-cementum”: a tissue that has the structure of osteonal bone (Fig. 7.6B) and begins to form while the

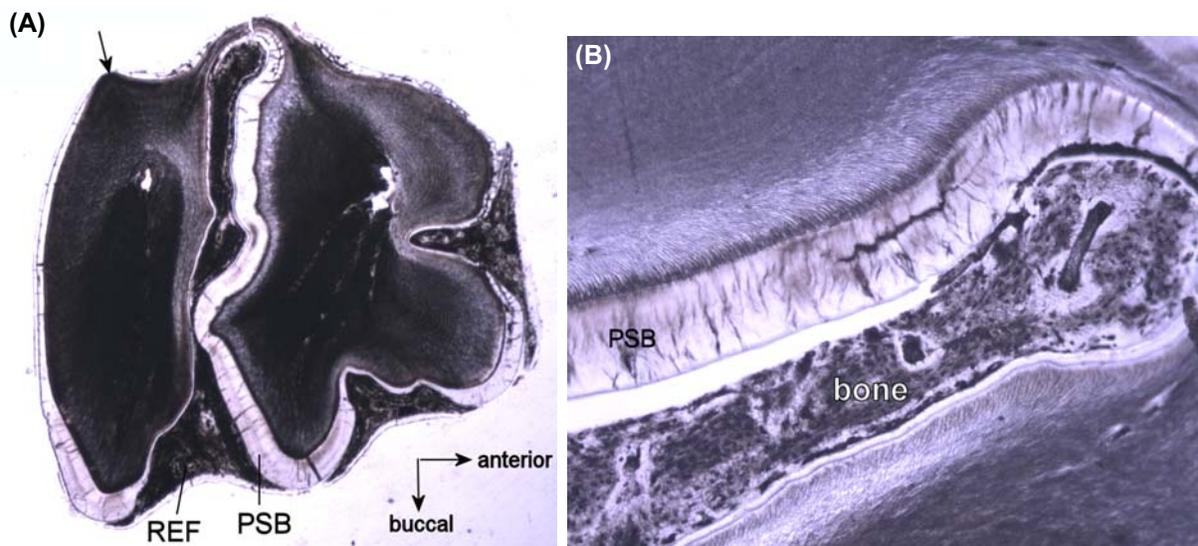


FIGURE 7.6 Structure of lagomorph molars. (A) *Oryctolagus cuniculus*. Transverse ground section of lower molar, showing bilobed structure and distribution of enamel. Arrow indicates enamel-free area on posterior–lingual corner. REF, reentrant fold; PSB, primary shearing blade. Original image width = 4.3 mm. (B) *Lepus europaeus*. Transverse ground section of molar, central section, near bridge connecting the two lobes (upper right), showing bone-cementum connecting the two lobes. On the upper margin of bone-cementum, the primary shearing blade (PSB) of thick enamel on the posterior margin of the anteroloph, with irregular Hunter–Schreger banding, is indicated. On the lower margin of bone, thin enamel on the anterior margin of the posteroloph is seen. Original image width = 1.05 mm. (A) Courtesy RCS Tomes Slide Collection. Cat. no. 1236. (B) Courtesy RCS Tomes Slide Collection. Cat. no. 1225.

anterolobe and posterolobe are still covered with ameloblasts (Michaeli et al., 1980). The teeth are covered with enamel, except at the angles of the “bridges,” and the outer layer of the tooth consists of a continuous layer of cementum (Michaeli et al., 1980). The thickness and structure of enamel are not uniform and it is the variation in these factors that determines the mechanical properties of the occlusal surfaces (von Koenigswald et al., 2010). Over most of the tooth surface, the enamel is thin (Fig. 7.6A) and has a uniformly radial structure. The enamel on the posterior surface of the anterolophid of the lower teeth is thickened and the Schmelzmuster consists of an inner layer of radial enamel and an outer layer of enamel with irregular prism decussation (Fig. 7.6B). These strips of thick enamel are termed “primary shearing blades” (PSBs). The corresponding structures in the upper teeth are located on the anterior surfaces of the anterolophids (Fig. 7.7B). The anteroloph of each upper tooth occludes with the posterolophid of the lower molar in the next most posterior tooth position (Fig. 7.7A and B). The PSBs form the main transverse

elevated ridges on the occlusal surfaces of functional teeth. In *Oryctolagus*, the enamel flanking the reentrant fold is thin and the anterior wall is crenulated. In *Romerolagus* and *Pronolagus*, a “composite secondary shearing blade” (composite SSB) is formed by a thickened strip of enamel on the posterior surface of the anterolobe and an adjacent, shorter strip on the anterolingual corner of the posterolobe: this blade forms an additional ridge on the occlusal surface of the tooth.

When the mandible is at rest, the mandibular condyle is positioned on the articular eminence of the temporomandibular joint and the tips of the lower incisors rest between the anterior and the posterior upper incisors (Crossley, 1995). Only a small amount of anterior movement is needed to engage the tips of the incisors, so that they can be used to cut plant material, which is executed by vertical movement of the mandible.

During chewing, the mandible is retracted slightly, so that the condyle rests within the glenoid fossa, which allows lateral movements of the mandible. Lateral

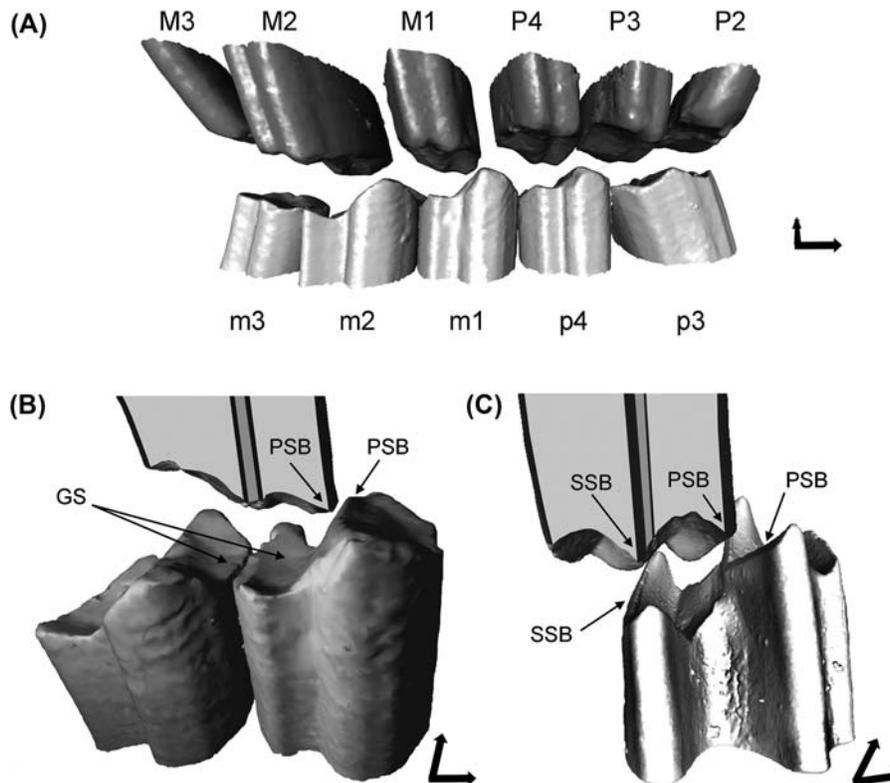


FIGURE 7.7 Virtual Occlusal Fingerprint Analyzer (OFA) models of lagomorph cheek teeth based on micro-computed tomography scans. (A) *Oryctolagus cuniculus* (KOE 4099): lingual view of upper and lower tooth rows. (B) Upper P⁴ (parasagittal section) and lower P₄ and M₁ of the same specimen during initial occlusion of the primary shearing blade in phase Ia. During phase Ib the upper tooth moves along the grinding surface. (C) *Ochotona alpina* (MB 100483): upper M¹ (parasagittal section) and lower M₁. During phase Ia the primary and the secondary shearing blades occlude simultaneously. In the schematic cross sections of the upper cheek teeth, the dental tissues are indicated: enamel (black), dentine (light gray), cementum (dark gray). GS, grinding surface of phase Ib; PSB, primary shearing blade; SSB, secondary shearing blade. Not to scale. From Von Koenigswald, W., Anders, U., Engels, S., Schultz, J.A., Ruf, L., 2010. Tooth morphology in fossil and extant Lagomorpha (Mammalia) reflects different mastication patterns. *J. Mammal. Evol.* 17: 275–299. By permission of Springer Verlag. Original artwork kindly provided by Professor W. Von Koenigswald.

movements are essential in chewing, as the lower cheek teeth have to be moved a considerable distance to occlude with the upper cheek teeth. From the point of maximum gape the mandible moves laterally and vertically during a fast closure phase and then, as the teeth contact the food, moves medially during a slow closure phase (power stroke): this takes the mandible to centric occlusion or beyond (Schwartz et al., 1989; Henderson et al., 2014). The power stroke has an anteroposterior as well as a lateral component. Food is broken down by a sequence of shearing and grinding during closure of the cheek teeth (von Koenigswald et al., 2010). In the initial phase (Ia), the PSBs shear vertically against their opposing counterparts (Fig. 7.7B) and cut fibrous foodstuffs, thanks to the opposing concave curvatures of the blades (see Fig. 1.4). At the end of this phase, the buccal tips of the lobes of the lower cheek teeth contact the bridge of the upper teeth. In the second phase (Ib), the PSBs are separated and lingual movement draws the enamel walls of the upper and lower reentrants across each other to produce a grinding action. This phase ends with the molars in centric occlusion.

The dentition of hares (*Lepus* spp.) is similar to that of rabbits (Fig. 7.8). The chewing action involves the same

vertical–lingual movement of the lower molars against the uppers but apparently continues into an additional phase. von Koenigswald et al. (2010) observed oblique wear marks that they considered to belong to a third phase of the power stroke (II'), corresponding to the phase II seen in some ungulates and primates (Chapter 1, Mastication). This phase presumably takes place during the movement of the mandible past the position of centric occlusion at the end of the power stroke (Schwartz et al., 1989; Henderson et al., 2014).

Ochotonidae

There is only one genus of pikas (*Ochotona*), which is distributed throughout Asia and North America. Pikas consume a wide variety of herbaceous plants, but grasses are a much smaller component of the diet than in that of rabbits and hares (Ge et al., 2013). The ochotonid dental formula is $I\frac{2}{1}C\frac{0}{0}P\frac{3}{2}M\frac{2}{3} = 26$.

The general structure of the dentition is very similar to that of leporids (Fig. 7.9). The principal difference is in the structure of the cheek teeth. As in leporids, the cheek teeth consist of an anterolobe and a posterolobe but, in the lower

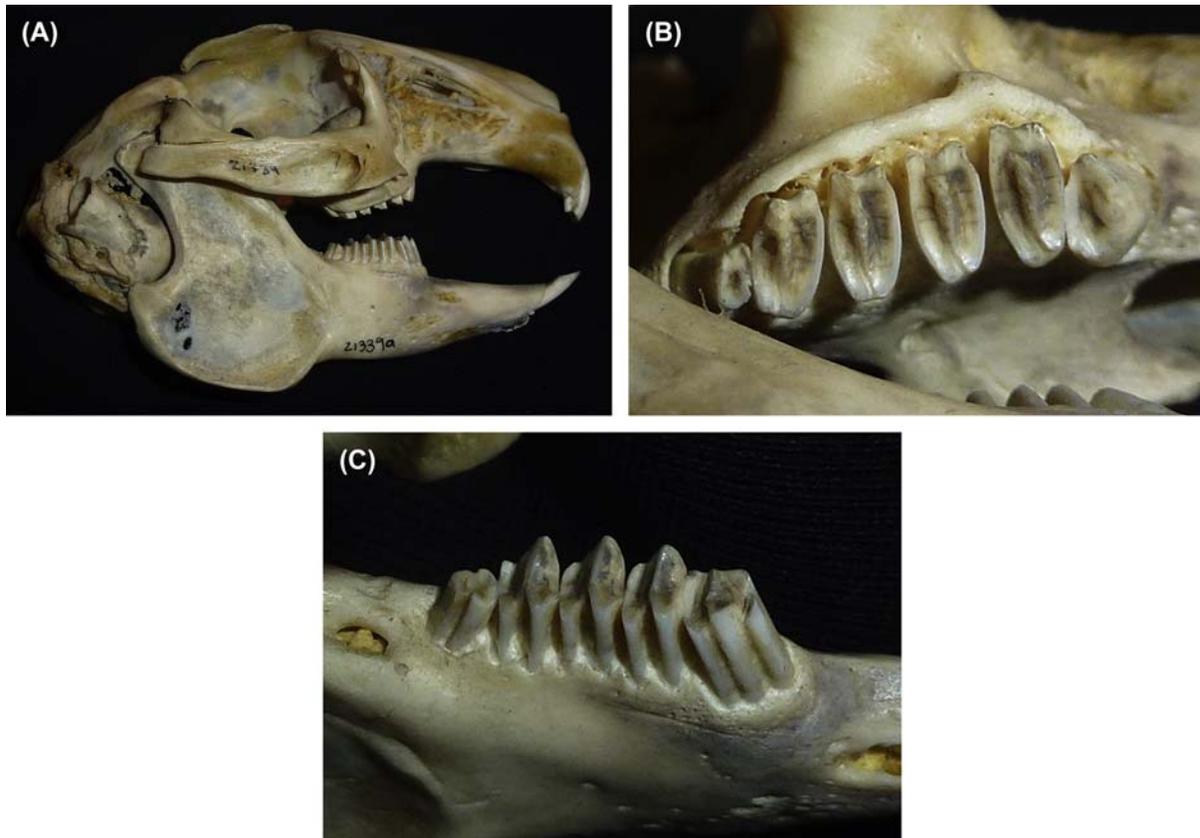


FIGURE 7.8 European hare (*Lepus timidus*). (A) Lateral view. Original image width = 99 mm. (B) Occlusal view of upper cheek teeth. Original image width = 26 mm. (C) Occlusal view of lower cheek teeth. Original image width = 31 mm. Courtesy UCL, Grant Museum of Zoology and Dr. P. Viscardi. Cat. no. LDUCZ-Z1339.

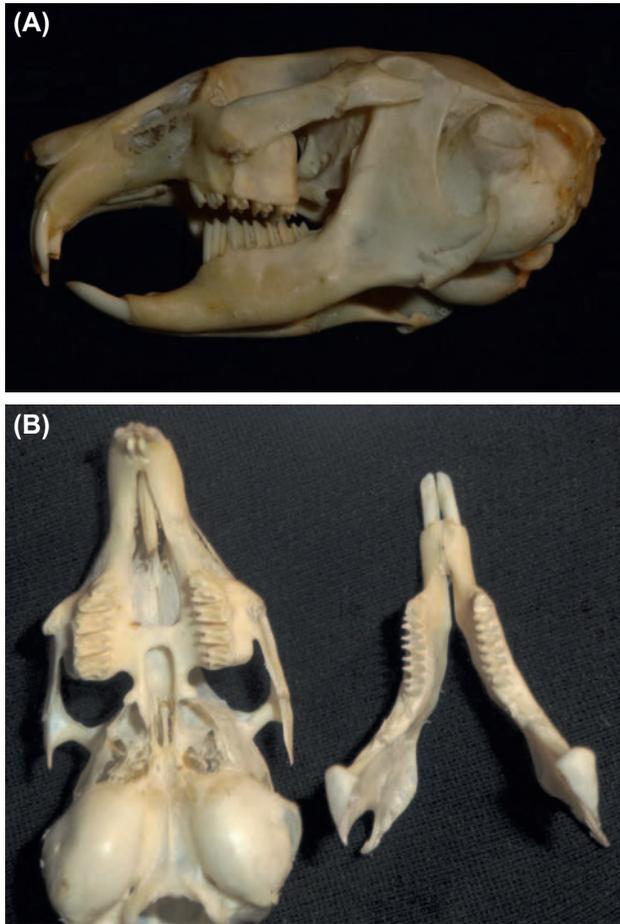


FIGURE 7.9 Pika (*Ochotona* sp.). (A) Lateral view of skull. Original image width = 4.6 cm. (B) Occlusal views of upper dentition (left) and lower dentition (right). Original image width = 5.0 cm. Courtesy of UCL, Grant Museum of Zoology, LDUCZ-Z416, and Dr. P. Viscardi.

teeth, the bridge connecting the two lobes is located at the midpoint instead of buccally or lingually (Fig. 7.9B) (von Koenigswald et al., 2010). Moreover, each tooth has, in addition to the PSB in the same place as in leporids, an SSB on the anterior surface of the posteroloph (uppers) or the posterior surface of the posterolophid (lowers). During the power stroke, the SSBs engage with each other simultaneously with the PSBs (Fig. 7.7C) and phase Ib does not involve grinding. The emphasis is thus on cutting fibrous materials.

The incisor enamel of ochotonids has two or three structurally distinct layers, of which only one contains HSBs (Martin, 2004).

RODENTIA

Rodents are mostly small mammals, with a few medium-sized and large species. They have adapted to a wide variety of ecological niches (MacDonald, 2006) and exploit all food sources (Landry, 1970; Samuels, 2009). Most

species are either herbivorous or omnivorous, but even herbivores will take some animal food, mainly insects and other arthropods. There are a few species of carnivorous murids, which feed on aquatic invertebrates, small vertebrates, birds and their eggs (*Hydromys*), or soft-bodied invertebrates such as worms (*Rhynchomys*). Landry (1970) suggested that the earliest rodents were omnivorous and that specialist herbivores, insectivores, and animalivores evolved during subsequent radiation of the group.

The classification of rodents has been controversial. Here we use an interpretation of the phylogeny and classification (Honeycutt, 2009) that recognizes five suborders: the squirrellike Sciuromorpha, three suborders of mouse-like rodents (Castorimorpha, Myomorpha, Anomaluromorpha), and the Hystricomorpha (Fig. 7.10).

In all rodents, the dentition consists of a single pair of sharp, continuously growing incisors in both upper and lower jaws, separated from a posterior battery of cheek teeth by a diastema (Fig. 7.11). Canines are absent. This type of dentition was present even in the earliest rodents and, together with the associated specializations of the skull and cranial musculature, has proved to be extremely versatile and is a major factor in the success of the rodents. As all rodents share the same basic masticatory system, there are numerous examples of convergence or parallelism among the adaptations to different diets (Wood, 1947).

Incisors

Rodent incisors are extremely versatile and are used to obtain food by cutting up grass and other plant material and to gain access to nutrients by gnawing through seed casings, shells, and bone. As they can break down most tough materials, the incisors are also frequently employed as tools, in excavating nest cavities, and in digging. Perhaps the most famous example of the use of the incisors as tools is provided by the beavers, who cut down trees by gnawing and use them to build dams and lodges.

The anterior surfaces of the incisors are smooth in most species, but in some species this surface has grooves running parallel with the tooth axis. Ohazama et al. (2010) found that, in 60/300 rodent species, there were between one and three grooves on the incisors of at least one jaw. Some grooves are due to localized thinning of enamel on the labial surface, while others are due to infolding of enamel of normal thickness. Molecular analysis of the development of grooves showed similarities to the development of cusps in cheek teeth (Ohazama et al., 2010).

The upper incisors have a smaller radius of curvature than the lower incisors, so their worn surfaces are more or less vertically oriented, while the lower incisors have a more gentle curvature and are more horizontally placed (Fig. 7.11). The position and orientation of the tips of the upper incisors vary according to the curvature of the teeth

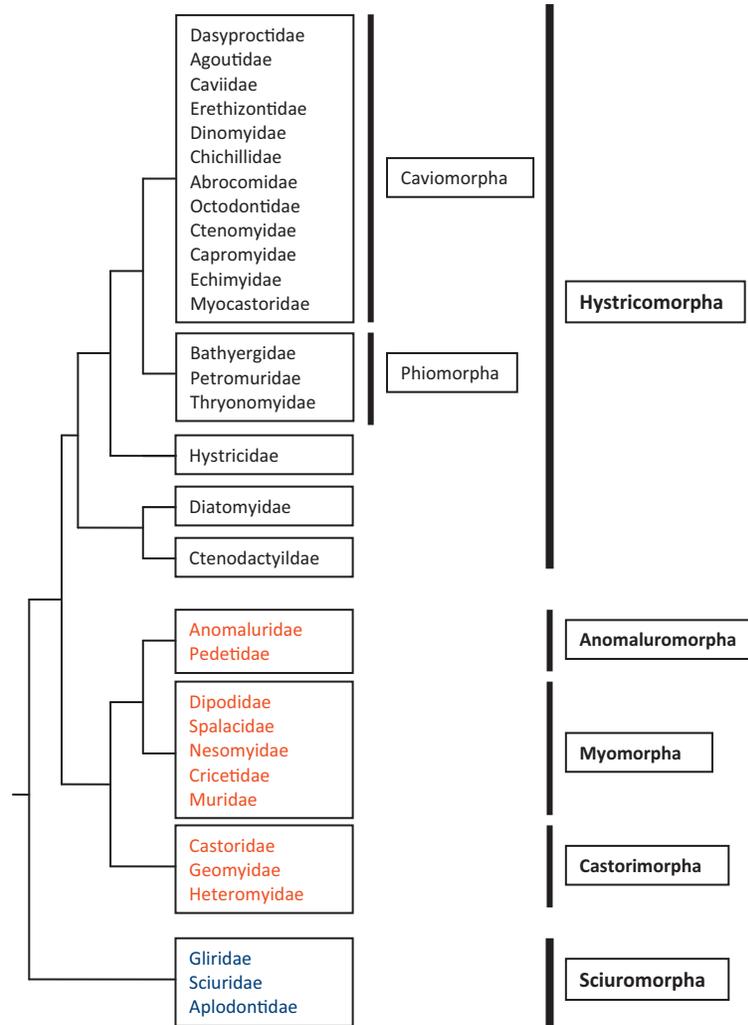


FIGURE 7.10 Phylogeny and classification of rodents. Simplified and modified from Honeycutt, R.O., 2009. *Rodents (Rodentia)*. In: Hedges, S.B., Kumar, S. (Eds.), *The timetree of life*. Oxford, Oxford University Press, pp. 490–494.



FIGURE 7.11 Lateral view of skull of North American porcupine (*Erethizon dorsatum*), to show the general organization of the rodent dentition. The upper and lower pairs of continuously growing incisors are large, chisel-edged, and covered with iron-pigmented enamel only on the labial aspect. Between the incisors and the molar rows is a wide diastema. The molars in this species are of limited growth. Original image width = 13.8 mm. Courtesy MoLSKCL. Cat. no. Z220.

(Hershkovitz, 1962). With moderate curvature, the wear facet at the incisal tip is positioned vertically (**orthodont**). The tips of more sharply curved incisors are directed posteriorly (**opisthodont**) and those of more gently curved incisors are directed anteriorly (**proodont** or **procumbent**). Because orthodont and opisthodont upper incisors have a relatively small radius of curvature, their formative bases are located in the region of the front cheek teeth, as in the cane rat (*Thryonomys*) (Fig. 7.12A) or porcupines (Fig. 7.12C). The formative bases of the more gently curved proodont incisors, in contrast, are located posterior to the last cheek tooth, as in the silvery mole rat (Fig. 7.12D). Lower incisors always have a greater radius of curvature than the uppers, so their formative bases lie posterior to the cheek teeth (Fig. 7.12C), in contrast to lagomorphs, in which they lie in front of the cheek teeth (Fig. 7.5B). In the case of procumbent lower incisors, the formative base can even be located within the ramus of the mandible, close to the articular condyle (Fig. 7.12B).

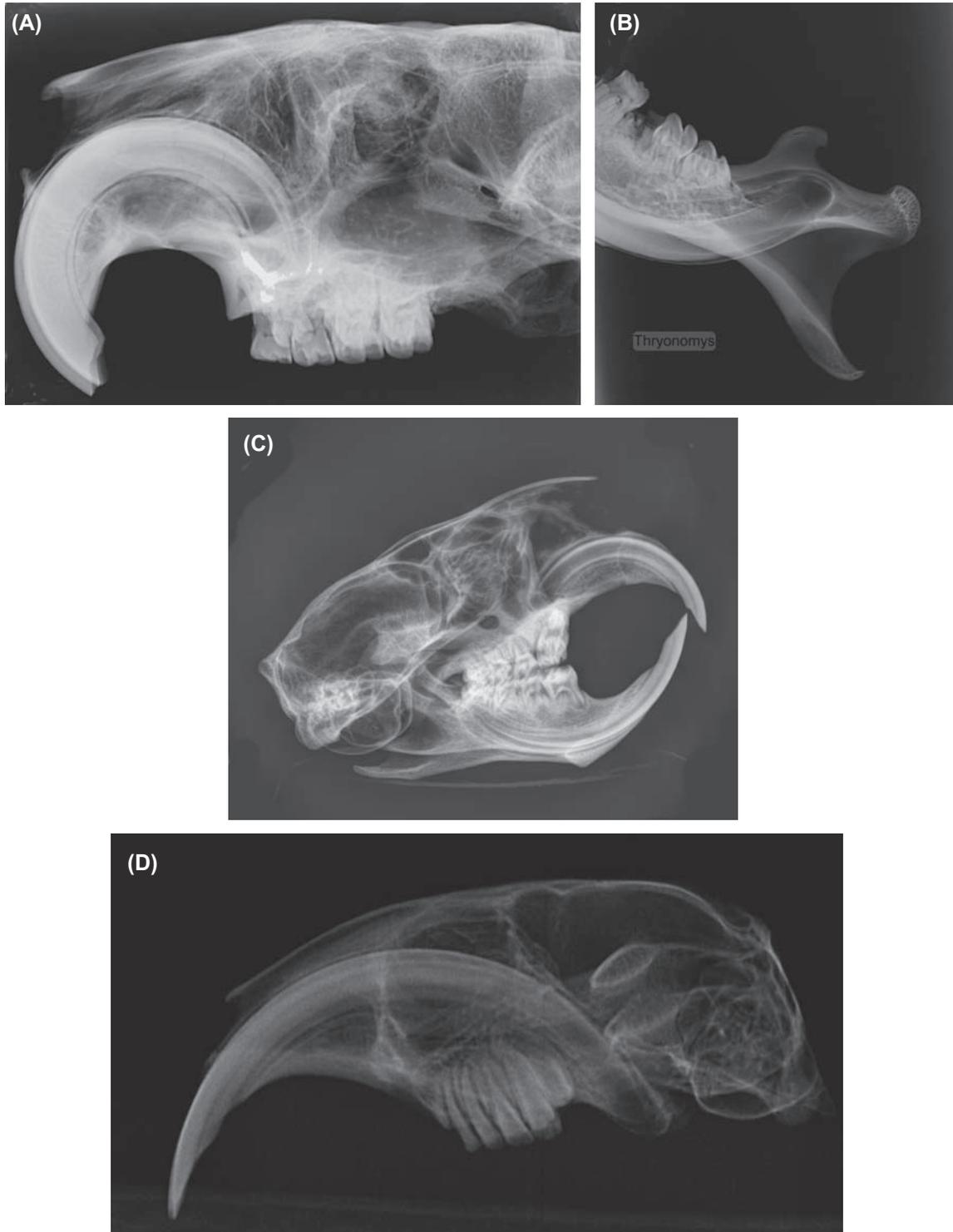


FIGURE 7.12 Radiographs of rodent skulls. (A) Cane rat (*Thryonomys*), upper incisor. (B) Cane rat (*Thryonomys*), posterior portion of lower molar, showing formative end in ascending ramus of the mandible. (C) North American porcupine (*Erethizon dorsatum*). (D) Silvery mole rat (*Heliophobius argenteocinereus*). This species has upper incisors with a greater radius of curvature than in most rodents and the formative base lies well posterior to the cheek teeth. Note also the developing molar at the back of the cheek tooth row, which will eventually move forward (horizontal succession). (A, B, D) Courtesy Dr. C.G. Faulkes. C Courtesy MoLSKCL. Cat. no. Z220.

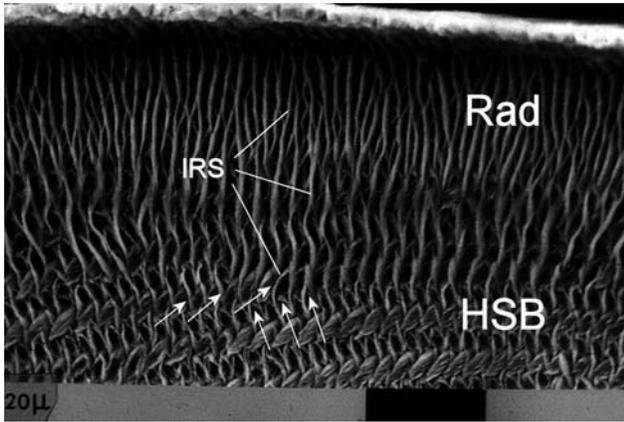


FIGURE 7.13 Transverse section through incisor of brown rat (*Rattus norvegicus*), etched with 1.0 mol/L HCl for 30 s and viewed by scanning electron microscopy. Inner layer consists of uniserial enamel with Hunter–Schreger bands (*HSB*) one prism thick. Arrows indicate direction of prisms in alternate bands. Outer layer consists of radial enamel (*Rad*) with parallel prisms. White layer at top is the iron-rich surface layer. *IRS*, intrarow sheets.

Incisor Structure

The structure of incisor enamel is a major factor in the creation and maintenance of the sharp incisal edge. In rodents, the basic Schmelzmuster is a two-layered structure, with an inner layer of decussating prisms and an outer layer of radial enamel (Fig. 7.13) (Boyde, 1978; Martin, 1997). In both layers, the prisms slope obliquely toward the functional tooth tip, and the prisms in the outer layer usually form a more acute angle with respect to the outer enamel surface than those in the inner layer (Fig. 7.14). The forward slope of the prisms increases the wear resistance, especially of the outer enamel, while the prism decussation in the inner

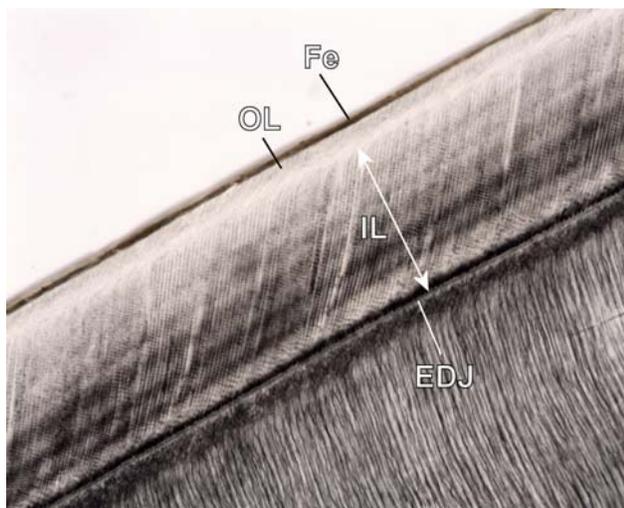


FIGURE 7.14 Longitudinal ground section of lower incisor of brown rat (*Rattus norvegicus*). *IL*, inner layer, comprising about 80% of the enamel thickness (double arrow), with prisms sloping toward the incisal tip at about 45 degrees to the enamel–dentine junction (*EDJ*). *OL*, outer layer with prisms at a more acute angle to the *EDJ*. *Fe*, brown, iron-pigmented surface layer. Original image width = 420 μm. Courtesy RCS Tomes Slide Collection. Cat. no. 1034.

enamel increases toughness. Primitively, the inner layer consisted of pauciserial enamel, with one to six layers of prisms per HSB (Martin, 1997), but among extant rodents, uniserial or multiserial enamel predominates. Uniserial enamel (one prism per HSB) is found in Sciuromorpha, Anomaluridae, and Myomorpha (Fig. 7.13). In sciuromorphs, the inner enamel occupies one-half of the thickness, the prisms are oriented approximately at right angles to the enamel–dentine junction, and interrow sheets are inconspicuous or absent. In myomorphs the inner enamel accounts for three-quarters of the thickness, the prisms in both inner and outer enamel, and interrow sheets are well developed (Boyde, 1978). Multiserial enamel (3–10 prisms per HSB), with prominent interrow sheets, is found in Hystricomorpha and Pedetidae (Boyde, 1978; Martin, 1997).

In most rodents, the enamel of the incisors (but not of the cheek teeth) appears brown because of the presence of ferric iron (Figs. 7.11 and 7.14). The nature of the pigmentation is described in Chapter 2. Its role has not been elucidated (Dumont et al., 2014). The iron enters the enamel at a late stage of development. When eruption is accelerated by trimming the tooth, there is no time for iron to enter the surface so that the labial enamel tooth surface loses its iron pigmentation and appears white as it enters the oral cavity (Risnes et al., 1996). White or pale yellow incisors are found in some species, e.g., animalivorous shrew rats.

Cheek Teeth

In basal rodents, the dental formula for the cheek teeth is $P\frac{2}{1}M\frac{3}{3}$. In many species, some or all of the premolars are lost, often as part of a process of reducing the length of the cheek tooth row. The reduction process involves alterations in the pattern of tooth replacement. Incisors do not have deciduous precursors in any rodent. The premolars of some species (American beaver [Castoridae], Arctic ground squirrel [Sciuridae], Chinchillidae, and the guinea pig [*Cavia porcellus*]) have deciduous precursors (Berkovitz, 1972; van Nievelt and Smith, 2005; Ungar, 2010). However, in some rodents the permanent premolars do not form and their place is taken by the deciduous generation (some caviomorphans and pliomorphans) (Wood, 1965; Ungar, 2010), whereas in others it is only the permanent generation that comes into function (some hystricomorphans) (Wood, 1965). Murids, cricetids, spalacids and nesomyids, and some glirids and dipodids have lost all premolars, so no teeth are replaced. In the guinea pig, the single deciduous cheek tooth is shed before birth, but shows evidence of attrition in utero (Fig. 7.15) (Berkovitz, 1972).

13–14 rodent families have hypselodont molars, 8–9 have hypselodont molars, and 7 have brachydont molars. Nesomyidae have brachydont and hypselodont members, Cricetidae have brachydont and hypselodont members, and Heteromyidae have members with all three molar types (Renvoisé and Michon, 2014).

In contrast to the restricted range of variation in the incisor teeth, there is a bewildering array of shapes and

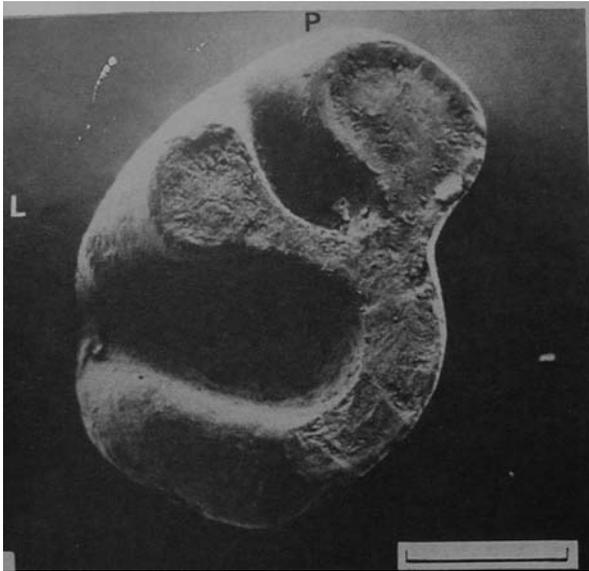


FIGURE 7.15 Deciduous premolar of guinea pig (*Cavia porcellus*), shed in utero and showing scratches due to wear. Scanning electron micrograph. Scale = 0.5 mm. From Berkovitz, B.K.B., 1972. *Ontogeny of tooth replacement in the guinea pig (Cavia cobaya)*. *Arch. Oral Biol.* 17, 711–718.

sizes of cheek teeth. Renvoisé and Montuire (2015) have provided a timely review of the recent major advances in the molecular biology of the mechanisms underlying the evolutionary diversification of rodent teeth.

Morphometric analysis suggests that variations in cranial morphology are related to diet (Samuels, 2009). Table 7.1 summarizes the data of Samuels (2009) on the principal cranial features of several groups defined, according to the predominant components of the diet, as omnivores, insectivores, carnivores, or herbivores. The last are subdivided into “specialist” herbivores, which subsist on tough, fibrous plant material, and “generalist” herbivores, which eat less-resistant items. Insectivores have the most lightly built skull and a reduced dentition. The robust skull of herbivores, with wide incisors and large molars, reflects the mechanical demands associated with processing large quantities of plant material. The narrow, elongated incisors of carnivores are adapted to penetrating flesh. The cranial morphology of omnivores is intermediate between those of herbivores and carnivores. The correlations between diet and cranial morphology are complicated by an additional factor: adaptations to digging. A third of the rodents in the specialist herbivore category of Samuels (2009) dig burrows using their lower incisors as picks, and four dig by lifting the head to move earth (Samuels and Van Valkenburgh, 2009). The craniodental features of digging rodents are strongly

TABLE 7.1 Morphological Features of Rodent Skulls in Relation to Diet

Feature	Generalist Herbivores	Specialist Herbivores	Insectivores	Carnivores	Omnivores
Skull shape	Wide, deep	Wide, deep	Elongated, not flattened	Dorsally flattened	Narrower and shallower than in herbivores
Rostrum	Wide, deep	Wide, deep	Elongated, narrow	Wide	Short
Zygomatic arches	Wide, thick	Wide, thick	Narrow, slender	Wide, robust	Moderately wide, robust
Temporal fossae	Large	Large	Small	Large	Moderately large
Upper incisors	Broad, transversely oriented Vertically elongated Tend to be opisthodont	Broad, transversely oriented Vertically elongated Tend to be proodont	Reduced: narrow and short anteroposteriorly Orthodont or moderately procumbent	Elongated Narrow but robust anteroposteriorly Orthodont	Narrow but robust anteroposteriorly Orthodont or moderately opisthodont or procumbent
Upper molar rows	Long rows Large molar area	Long rows Large molar area	Short rows Reduced molar area	Short rows Medium molar area	Medium–long rows Medium molar area
Upper molars	Predominantly hypsodont or hypselodont Folded	Predominantly hypsodont or hypselodont Folded	Brachydont Acrodont in species eating hard-cuticled insects	Brachydont Acrodont	Brachydont Cuspidate or folded

Data from Samuels, J.X., 2009. Cranial morphology and dietary habits of rodents. *Zool. J. Linn. Soc.* 156, 864–888.

influenced by these activities as well as by the nature of the diet (Topachevskii, 1976; Wilkins and Woods, 1983). For instance, rodents that use their teeth in digging have procumbent incisors, whereas head-lifting diggers have flattened skulls, and both groups have longer rostra and wide temporal fossae. The inclusion of rodents with features unrelated to feeding has a marked influence on the properties of the specialist herbivore group.

At an early stage of rodent evolution both upper and lower molars acquired a quadritubercular structure. In the upper molars transverse lophs are established between buccal and lingual pairs of cusps and are augmented by anterior and posterior cingula to form an occlusal surface with four transverse ridges. In some rodents a fifth middle loph has appeared to generate a five-crest pattern, and in others there is a bilophid pattern. The multicrest pattern has given rise to numerous complex molar patterns by infolding (plication) and other processes. The great variety of occlusal patterns on rodent molars has been thoroughly described and illustrated by Hershkovitz (1962) and Hillson (2005).

Rodents that consume a diet with relatively low proportions of plant material (omnivores, insectivores, animalivores) generally have elongated first molars and reduced third molars, and the molars tend to be brachydont, with up to four roots. Among herbivores, the molars tend to be equal in size, but in some, such as the capybara, the third molars are the largest. The greater wear attendant on processing plant material is compensated for by hypsodonty or hypselodonty of the molars (Gomes Rodrigues, 2015).

Molar Enamel Structure

von Koenigswald (2004) identified three types of Schmelzmuster in the enamel of rodent molars. P-type enamel consists largely of radial enamel, sometimes with weak, localized decussation. C-type enamel consists largely of radial enamel, with a ring of lamellar (uniserial) enamel at the base of the enamel cap. S-type enamel contains thick HSBs, 4–10 prisms wide, throughout the enamel cap, either in the inner enamel or in the outer enamel or through the whole enamel thickness. C- and S-type enamel are secondarily modified in hypsodont and hypselodont teeth, in response to changed mechanical demands. The distribution of Schmelzmuster of molar enamel among extant families is shown in Table 7.2 (note that data originate from both fossil and living species). There are correlations in structure between molars and incisors (von Koenigswald, 2004). Among extant families, P-type molar enamel in *Anomalurus* and *Myospalax*, and C-type molar enamel in most Myomorpha, are associated with uniserial incisor enamel. S-type molar enamel can be associated with uniserial incisor enamel (most Sciuromorpha and *Pedetes*) or multiserial incisor enamel (Hystricomorpha).

Molar enamel structure in rodents is highly adapted to function (von Koenigswald and Sander, 1997). The variations of enamel structure within molar crowns in many rodents are such that the side of an enamel ridge that first encounters the food during a power stroke (the “push” side) is usually composed of radial enamel, which is adapted to resisting wear. The remainder of the enamel layer is characterized by prism decussation, which resists crack propagation.

Temporomandibular Joint

Mastication in most rodents involves anteroposterior movement of the cheek tooth rows against each other. Furthermore, at rest, when the cheek teeth are in occlusion, the lower incisors lie well behind the upper incisors (Fig. 7.11). Thus, the lower jaw has to be protracted for the incisal edges to engage. This contrasts with the lagomorphs, in which the lower incisors lie just behind the upper incisors when the mandible is in the rest position (Fig. 7.4A). The jaw joint allows anteroposterior movement and also rotation of the articular condyle. The glenoid fossa lacks anterior and posterior processes and forms an anteroposteriorly oriented groove, while the mandibular condyle may have a rounded or longitudinally oriented fusiform shape (see Figs. 7.36B and 7.37).

Jaw-Closing Muscles

In rodents, the masseter muscle is usually the largest jaw-closing muscle (Turnbull, 1970; Cox and Jeffery, 2011), followed by the temporal and pterygoid muscles. It is widely accepted that in rodents the masseter has three divisions (Fig. 7.16). From the inside outward, these are, following the most widely used nomenclature: the **zygomatic–mandibular** (musculus zygomaticomandibularis), the **deep masseter** (musculus massetericus profundus), and the **superficial masseter** (musculus massetericus superficialis). It should be noted that the terminology of the muscles and the number of muscles recognized vary. It has long been recognized that there are four modes of organization of the **zygomatic–masseter system** (ZMS) in rodents: **protrogomorph**, **sciuromorph**, **myomorph**, and **hystricomorph**. At one time rodents were classified into three suborders named after the last three modes. The different ZMSs have evolved more than once during rodent evolution, so they do not map onto the phylogeny, but the older subordinal names persist (Fig. 7.10). To reduce possible confusion, we use the adjectival ending **-morph** to indicate the type of jaw musculature and **-morphan** to indicate membership of a taxonomic group.

The four ZMSs differ in the relative sizes of the muscles and in their attachments and directions of operation (Wood,

TABLE 7.2 Distribution of Molar Enamel Schmelzmuster Among Extant Families of Living Rodents

Suborder	Family	Schmelzmuster	
Sciuromorpha	Gliridae	(S) C-type	
	Sciuridae	S-type	
	Aplodontiidae	S-type	
Castorimorpha	Castoridae	S-type	
	Geomyidae	C-type and secondary modification	
	Heteromyidae	C-type and secondary modification	
Myomorpha	Dipodidae	C-type	
	Spalacidae Myospalacinae Spalacinae, Rhizomyinae:	? Secondary modification P-type → C-type	
	Nesomyidae	C-type	
	Cricetidae	C-type and secondary modification	
	Muridae	C-type and secondary modification	
	Anomaluromorpha	Anomaluridae	P-type
		Pedetidae	S-type
Hystricomorpha	Hystricidae	S-type	
	Ctenodactylidae	Secondary modification	
Hystricomorpha—Phiomorpha	Bathyergidae	S-type	
	Petromuridae	S-type	
	Thryonomyidae	S-type	
Hystricomorpha—Caviomorpha	Agoutidae	S-type and secondary modification	
	Caviidae	S-type and secondary modification	
	Erethizontidae	S-type	
	Dinomyidae	S-type and secondary modification	
	Chinchillidae	S-type and secondary modification	
	Abrocomidae	S-type and secondary modification	
	Octodontidae	S-type and secondary modification	
	Capromyidae	S-type and secondary modification	
Echimyidae	S-type		

Data from von Koenigswald, W., 2004. The three basic types of Schmelzmuster in fossil and living rodent molars and their distribution among rodent clades. *Paleontographica A* 270, 95–132. Data condensed and classification reorganized.

1965; Druzinsky, 2010a; Cox and Jeffery, 2011; Cox et al., 2012), as follows.

Protrogomorphy (Fig. 7.16A): this condition is found only in Aplodontiidae among living rodents. The zygomatic–mandibular muscle originates on the medial aspect of the zygomatic arch and inserts on the dorsolateral region of the mandible; it exerts a simple jaw-closing action. The deep masseter originates in a fossa on the ventral aspect of the zygomatic arch and inserts in the masseteric fossa of the mandible. It pulls the lower jaw upward,

slightly forward, and also laterally. The superficial masseter originates in a ventral fossa in the anterior (maxillary) region of the zygomatic arch, level with the premolars, and runs obliquely backward to insert on the ventral margin of the mandible, including the angular process. The temporal muscle originates over a wide region of the cranium and inserts on the coronoid process. As the mandible is protracted, the articular condyle is drawn forward down the glenoid fossa by the action of the superficial masseter, in conjunction with the anterior portion of the temporal and

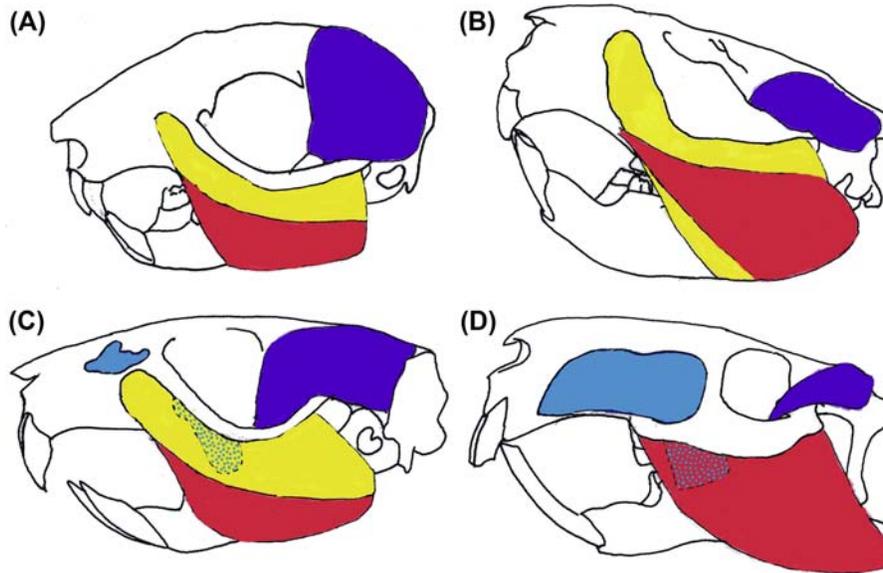


FIGURE 7.16 Diagrams indicating the relative size and arrangement of the jaw adductors in rodents. (A) Protrigomorphy (*Aplodontia*). (B) Sciuiromorphy (*Castor*). (C) Myomorphy (*Rattus*). (D) Hystricomorphy (*Lagidium*). Purple (dark), temporal; yellow, deep masseter; red, superficial masseter; blue (light), exposed portion of infraorbital zygomatic-mandibular. The portion of infraorbital zygomatic-mandibular underlying masseter muscles is indicated by a dotted area. Muscle outlines superimposed on drawings of skulls with reference to Wood, A.E., 1965. *Grades and clades among rodents*. *Evolution* 19, 115–130; Cox, P.G., Faulkes, C.G., 2014. *Digital dissection of the masticatory muscles of the naked mole-rat, *Heterocephalus glaber* (Mammalia, Rodentia)*. *PeerJ* 2:e448; <https://doi.org/10.7717/PEERJ.448>; Druzinsky, R.E., 2010a. *Functional anatomy of incisal biting in *Aplodontia rufa* and sciuiromorph rodents. Part 1: Masticatory muscles, skull shape and digging*. *Cells Tissue Org.* 191, 510–522.

the external pterygoid, while retraction is accomplished by the posterior fibers of the temporal and the digastric. Druzinsky (2010a) suggested that protrigomorphy as found in *Aplodontia* has features in common with the form of sciuiromorphy seen in sciurids, its sister group.

Sciuiromorphy (Fig. 7.16B): found in Sciuridae, Gliridae, and Castorimorpha. This differs from the protrigomorph ZMS in the expansion and reorientation of the deep masseter, which now originates from the snout anterior to the zygomatic arch and runs obliquely backward under the attachment of the superficial masseter. The reorientation of the deep masseter brings the fibers into closer alignment with those of the superficial masseter, and together the two muscles exert a stronger protractive action on the mandible.

Hystricomorphy (Fig. 7.16C): found in the Hystricomorpha, in the Anomaluroomorpha, and in the Dipodidae among the Myomorpha. The protractive action of the jaw muscles is enhanced by a different mechanism in this type of jaw musculature. The origin of the deep masseter is restricted to the zygomatic arch and does not extend onto the snout. Instead, the zygomatic-mandibular is prolonged forward through the infraorbital foramen and originates from the snout region. As with the reorientation of the deep masseter in sciuiromorphy, the fibers of the zygomatic-mandibular are realigned more closely with those of the superficial masseter.

Myomorphy (Fig. 7.16D): found among Myomorpha, except for the Dipodidae. This ZMS combines features of the sciuiromorph and hystricomorph modes, as both the deep masseter and the zygomatic-mandibular originate on the snout region.

In sciuiromorph, hystricomorph, and myomorph rodents, the anterior portion of the temporal muscle is lost and the origin of the posterior portion lies posterior to the coronoid process. The temporal muscle closes the jaws and, with the digastric and part of the zygomatic-mandibular, retracts the mandible. In some species the temporal muscle is much reduced.

Druzinsky (2010b) concluded that the protrigomorph ZMS of *Aplodontia* has a lower mechanical advantage and generates a lower bite force at the incisor tips compared with the sciuiromorph ZMS of the sciurid *Marmota*. However, the two systems did not differ in respect to the force transmitted down the incisor long axis.

From analyses of biting force and stress distribution during tooth use, Cox et al. (2012) concluded that the sciuiromorph squirrel (*Sciurus*) is morphologically better adapted for gnawing with its incisors than the hystricomorph guinea pig (*Cavia*), which, instead, has more efficient biting at the molars. These findings are in accord with the large proportion of nuts in the diet of squirrels and of softer vegetation in that of guinea pigs. The myomorph masticatory system of the rat (*Rattus*) is equally efficient for both incisal and molar biting.

Morphology of Molars

The structure of rodent molars was derived from the basic tritubercular pattern, and the molars of basal rodents had a number of features in common with those of other early placentals, including primates (Butler, 1980). They were cuspidate and the lower molars moved across the uppers in two phases: in an almost transverse direction in phase I, followed by a more anterior motion in phase II. Among many recent rodents the direction of movement of the lower molars is changed, so that they follow a single trajectory, which is oriented obliquely or anteroposteriorly rather than transversely. This involved changes in molar morphology. Butler (1985) defined four grades of molar form (Fig. 7.17).

- Grade A molars (Sciuromorpha) have a central basin surrounded by cusps. During phase I of chewing the lower molars move medially and also upward, so that the hypoconid occludes with the trigon basin and the protocone with the talonid basin. The movement in phase II is downward and obliquely forward.
- Grade B molars (cricketines and neotomines among Cricetidae, Dipodidae) have basins that are traversed by crests. Phase I movement is more oblique than in grade A and approximately in the same line as phase II of chewing, although there is the same rise and fall during the two phases as in grade A.

- Grade C molars (Castoridae, Hystricidae, Erethizontidae) have the cusps lower and flattened by planation. Chewing involves a single movement obliquely forward and wear facets formed on the occlusal surfaces of the cusps and crests form a single grinding surface.
- Grade D molars (Murinae, Anomaluridae, Pedetidae) are associated with chewing by a posterior–anterior movement of the lower molars: the occlusal surfaces are flattened by planation and the crests are aligned transversely, often in complex patterns, across the direction of motion.

To these grades, Lazzari et al. (2008) added grades O and M, found in Murinae. Grade M molars (as in *Cricetomys*: Fig. 7.35B) are cuspidate but the alignment of cusps forms gutters, which allow anteroposterior movement of opposing teeth. Grade O molars occur in only a few species. Like grade M molars, they are cuspidate, but anteroposterior movement is restricted by the absence of longitudinal gutters.

The molars of many rodents possess numerous cusps, e.g., eight or nine among murids, and the number of crests in grades C and D can be correspondingly high. In grades C and D, which are often hypselodont, the form of the crests is determined by longitudinal folding and the occlusal surfaces are flattened by wear (**planation**) (Hershkovitz,

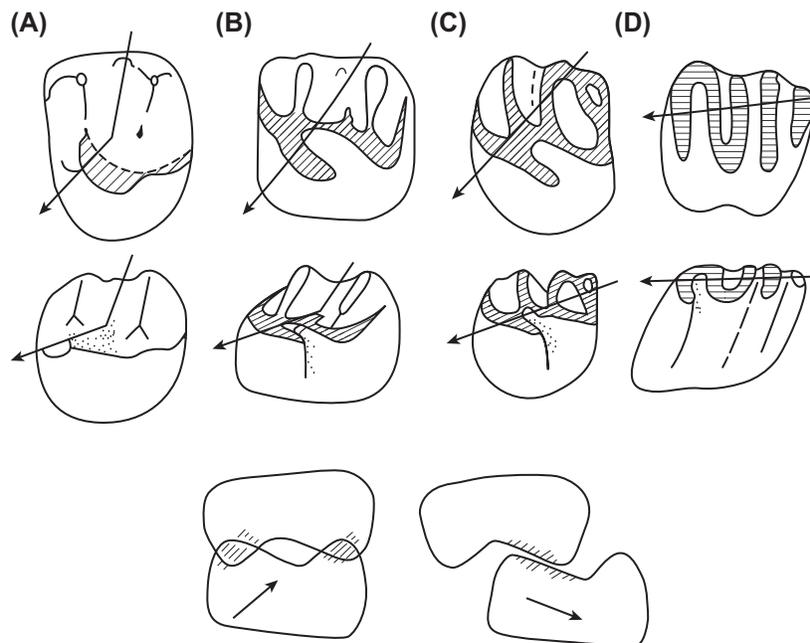


FIGURE 7.17 Four grades of molars in rodents. Top row: occlusal views of left upper molars in four species of rodents. Middle row: lingual–occlusal views of the same teeth. Grade A, sciurid; grade B, cricentodid; grade C, porcupine (*Erethizon*); grade D, pacarana (*Dinomys*). Arrows indicate path of the hypoconid during chewing. Bottom row: posterior view of teeth of grade B in phase I (left) and phase II (right) of mastication, to show the formation of wear facets. Shaded areas, wear facets. From: Butler, P.M., 1985. Homologies of molar cusps and crests, and their bearing on assessments of rodent phylogeny. In: Luckett, W.P., Hartenberger, J.L. (Eds.), *Evolutionary relationships among rodents*. NATO Advanced Science Institutes (ASI) Series (Series A: Life Sciences), vol. 92. Springer, Boston, pp. 381–401, Fig. 5. By permission of Springer Verlag.

1962). Rodent evolution is characterized by parallelism and convergence (Wood, 1947) and each of the different grades of molars has evolved more than once.

Rodent molar rows are tilted: the upper row buccally and the lower row lingually. Studies on a range of species suggest that there are three modes of chewing (Weijts, 1994). In the first group, e.g., mountain beaver (*Aplodontia*), golden hamster (*Mesocricetus*), and squirrel (*Eutamias*), chewing is **unilateral**: that is, only one side of the jaws is used at a time, and the two sides do not alternate regularly. Other rodents, e.g., guinea pig, capybara, and coypu (Hystricomorpha), and the mole rat *Tachyoryctes* (Myomorpha), employ **alternating** mastication: they chew first on one side of the jaw and then on the other in strict alternation, using an anteromedially directed power stroke. In other rodents (springhares, some murids and hystricomorphans), chewing is **bilateral**: the left and right molar rows are the same distance apart (isognathous), so both can occlude simultaneously and the power stroke is anteroposterior. Twice the grinding area of tooth surface is operative compared with unilateral chewing, resulting in more rapid breakdown of the food.

SCIUROMORPHA

Aplodontiidae

This family contains a single species, the **mountain beaver** (*Aplodontia rufa*), which is a burrowing rodent not related to the true beavers. It inhabits temperate forests in the mountain ranges of the western United States. The mountain beaver feeds on ferns and other soft vegetation, including shoots of trees and shrubs. It is coprophagous.

A. rufa (Fig. 7.18) retains more premolars than other rodents: the dental formula is $I \frac{1}{1} C \frac{0}{0} P \frac{2}{1} M \frac{3}{3} = 22$. They are the only extant protrogomorphous rodents. The mandible

needs to be protruded only a short distance for the upper and lower incisors to engage (Fig. 7.18A). All the cheek teeth are hypselodont. The first upper premolars are small and cylindrical, but the second upper premolars and the lower premolars are molarized and larger than the molars. In the upper jaw, the occlusal surfaces of P^2 and the molars are D shaped, with sharp corners, a slightly concave buccal surface, and a round palatal surface. The lower cheek teeth have a similar shape except that the rounded surface has a longitudinal groove and faces buccally, not lingually (Fig. 7.18B). Apart from the first upper premolars, each cheek tooth has a sharp longitudinal ridge: on the palatal surface of the uppers and the lingual surface of the lowers. The ridge appears on the occlusal surfaces as a pointed projection from the concave margin (Fig. 7.18B). During mastication, the articular condyle is located at the back of the glenoid fossa and the mandible is moved medially in the generalized mammalian chewing pattern by the temporals, the zygomatic–mandibulars, deep masseters, and internal pterygoids. There is little room for anteroposterior movement of the mandible because of the proximity of the lower and upper incisors. The rounded articular condyle (Fig. 7.18B) may be related to this restriction of movement. *Aplodontia* has a relatively large temporal muscle, which appears to be correlated with the wide, flat skull characteristic of burrowing rodents (Druzinsky, 2010a).

Sciuridae

The sciurids include the arboreal tree squirrels and ground-living forms (ground squirrels, marmots, chipmunks, and prairie dogs), which often live in burrows. There are over 270 species in 50 genera. Most species are omnivorous. The majority of the diet consists of a wide variety of plant materials, including flowers, nuts, fruits, and seeds plus, in ground-living forms, underground storage organs such as bulbs. Animal foods such as birds' eggs, insects, nestlings,

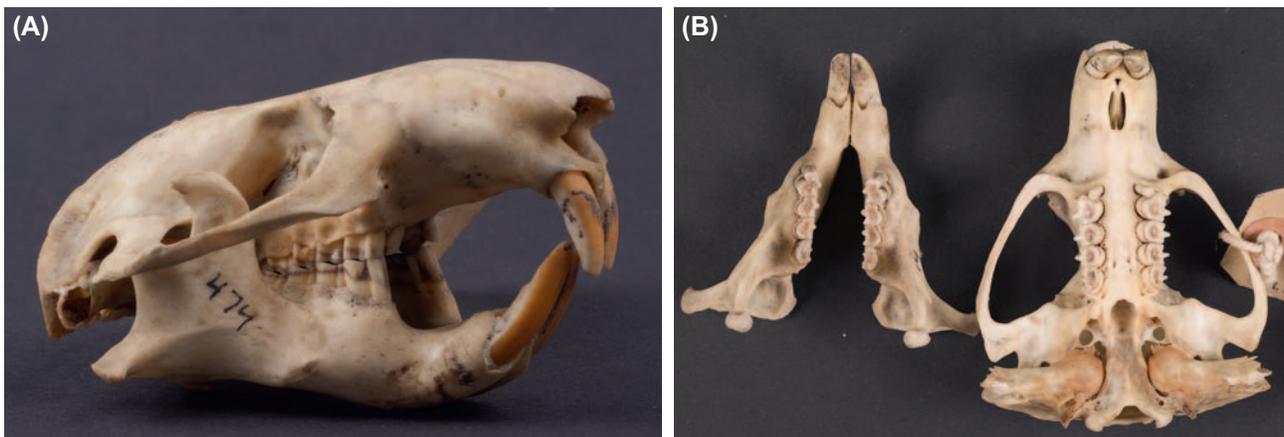


FIGURE 7.18 Mountain beaver (*Aplodontia rufa*). (A) Lateral view of skull. Original image width = 79 mm. (B) Occlusal views of upper dentition (right) and lower dentition (left). Note the rounded appearance of the condylar head. Original image width = 117 mm. Courtesy RCSOMA 262.1.

and small vertebrates are vital supplements, especially when plant foods are seasonally in short supply.

The dental formula is $I \frac{1}{1} C \frac{0}{0} P \frac{1-2}{1} M \frac{3}{3} = 20 - 22$. The molars are brachydont or hypsodont, but no sciurids have hypselodont teeth. The occlusal surfaces have complex ridge patterns in some species but, typically, the molars are bunodont, with relatively simple cusp patterns.

Giant squirrels (*Ratufa* sp.) (Fig. 7.19) spend most of their time in trees. They are omnivores, eating all kinds of plant food, together with birds' eggs and insects. The molars are quadritubercular and approximately square. The palatal margin of the uppers and the buccal margin of the lowers are bounded by continuous longitudinal crests. Transverse crests run lingually from the paracone and metacone in the upper molars. In the lower molars, the protoconid, metaconid, entoconid and hypoconid are connected by crests, which enclose a central pit. See Butler (1985) for details of molar structure.

The **red-legged sun squirrel** (*Heliosciurus rufobrachium*) (Fig. 7.20) is arboreal and has a diet like that of giant squirrels. The structure of the molars is similar to that in *Ratufa*. The upper molars have trapezoidal occlusal surfaces, the buccal margins being wider than the palatal. The occlusal surface of each molar is bounded anteriorly and posteriorly by prominent cingula.

The **Alpine marmot** (*Marmota marmota*) (Fig. 7.21) is a ground-living sciurid, which also has a varied diet, although one containing more grasses and herbaceous plants than those of arboreal sciurids. The dentition is similar to that of squirrels, except that the molar cusps are taller and more pointed (Fig. 7.21A). On the lower molars, the mesiobuccal cusps are particularly elongated and inclined anteriorly, giving the occlusal surfaces more rhomboid shape. The difference in width between the buccal and the lingual surfaces of the upper molars is greater than in



FIGURE 7.19 Giant squirrel (*Ratufa* sp.). Occlusal view of upper dentition and left lower dentition. Original image width = 8.2 cm. Courtesy QMBC.

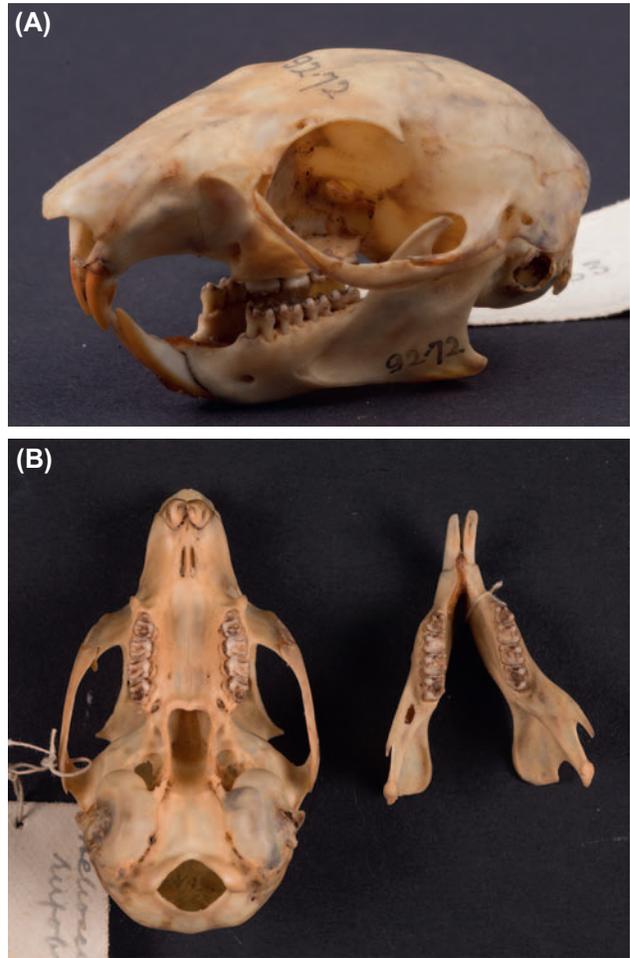


FIGURE 7.20 Sun squirrel (*Heliosciurus rufobrachium*). (A) Lateral view of skull. Original image width = 4 cm. (B) Occlusal views of upper dentition (left) and lower dentition (right). Original image width = 8.6 cm. Courtesy RCSOMA 258.63.

tree squirrels, so the occlusal surfaces are fan shaped (Fig. 7.21B).

CASTORIMORPHA

This suborder consists of three sciuriform families. The beavers (Castoridae) are large and semiaquatic, while the gophers (Geomyidae and Heteromyidae) are burrowing animals, often living in arid habitats and having a wide range of sizes. The dental formula is $I \frac{1}{1} C \frac{0}{0} P \frac{1}{1} M \frac{3}{3} = 20$.

Castoridae

This family contains two species of beaver: the **North American beaver** (*Castor canadensis*) and the **Eurasian beaver** (*Castor fiber*), which are the second largest rodents after capybaras (see “Caviidae”), weighing up to about 30 kg. They are well known for their ability to fell trees