Perissodactyla

INTRODUCTION

Ungulates

Perissodactyla is one of two groups of ungulates: mammals that walk on the tips of their toes (unguligrade locomotion). Most ungulates, including all perissodactyls, have hooves on their feet instead of claws. Perissodactyls are **odd-toed** ungulates, as the number of toes has been reduced: from the ancestral five to one in horses and three in rhinoceroses. Tapirs have three toes on the hind feet and four on the front feet. The Artiodactyla are **even-toed** ungulates, which have four toes (pigs, camels, hippopotamuses) or two (deer, sheep, cattle, and their allies). Ungulates are completely terrestrial and must gather food using the mouth, as the structure of their feet precludes grasping or climbing and has evolved primarily for locomotion. Most ungulates are proficient runners and many can reach high speeds. In the very large forms (rhinoceroses and hippopotamuses), however, the limbs are adapted to carrying large weights. The relationship between Artiodactyla and Perissodactyla is problematical (Tarver et al., 2016). In some phylogenies, they have been placed together in a clade of Euungulata (e.g., O'Leary et al., 2013), while in others, the two groups have a more distant relationship, the Perissodactyla being allied with Carnivora in a lineage that split from the Artiodactyla (e.g., Springer and Murphy, 2007; dos Reis et al., 2012).

Nearly all ungulates are herbivorous, although peccaries and pigs among the Artiodactyla are omnivorous. It is thought that the ancestral feeding style was browsing in "closed" habitats (forests and dense woodland). Grazing is likely to have evolved as forests became more open in response to climatic change. Mixed feeding would have evolved when grass became available in open spaces within woodland, and exclusive feeding on grass would have become possible as forests gave way, with continued drying of the climate, to open grassland (Pérez-Barbería et al., 2001).

Ungulates all possess a long row of five to seven large cheek teeth, separated by a diastema from the anterior teeth. Food is often gathered using the incisors, but the lips are either important ancillary organs in this process or, in rhinoceroses and hippopotamuses, the sole means of feeding. Canines are often absent and, when present, have a

role in aggression rather than in acquiring food. Because of the lengthening of the cheek tooth row and the presence of a long diastema, the facial region of the skull is also lengthened in ungulates (Fig. 12.1). The masseter complex is the largest component of the jaw-closing musculature (Turnbull, 1970). According to Greaves (2000, 2008), the large size of the masseter is responsible for a forward shift in the resultant vector of the jaw-closing musculature and this in turn maintains an optimum overall masticatory bite force when the facial portion of the skull is elongated.

As an adaptation to the increased wear due to grit and endogenous plant abrasives, molar teeth tend to be more hypsodont in grazing ungulates than among browsers (e.g., Janis, 1988; Archer and Sanson, 2002; Codron et al., 2007; Mendoza and Palmqvist, 2008; Damuth and Janis, 2011; Kubo and Yamada, 2014), as for herbivores in general (Chapter 3). Among ungulates, there are also morphological differences in addition to the degree of hypsodonty between browsers, grazers, and mixed feeders (Clauss et al., 2008). Browsers have narrow incisor arcades that are adapted to selective feeding, while grazers have wider arcades, which increase the mass of forage ingested per bite (Gordon et al., 1996) but reduce selectivity (Janis and Ehrhardt, 1988; Gordon and Illius, 1988; Spencer, 1995).

Pérez-Barbería and Gordon (2001) tested differences between browsers and grazers in several craniodental variables. When controlled for body mass, grazers had wider incisor arcades, more protruding incisors, taller M_3,

FIGURE 12.1 Skull of domesticated horse (*Equus ferus caballus*). *Copyright Kees Zwanenburg/Shutterstock.*

and total molar-row volume and occlusal surface area than browsers. However, when also controlled for phylogeny, the body mass, volume of the molar row, and height of M_3 were the only characters that differed significantly between feeding types. For grazers, large size enables them to consume large quantities of lower quality forage, while the greater hypsodonty and tooth volume reflect their more abrasive diet, as outlined earlier.

Mendoza and Palmqvist (2008) considered that phylogenetic correction removes valuable information about morphological adaptation and adopted a knowledge-discovery approach to analyzing the relationship of craniodental variables to feeding style. They identified two variables that, in combination with the hypsodonty index, discriminated between grazers, browsers, and mixed feeders inhabiting open grassland, closed habitats such as forest, or mixed habitats respectively. One variable was the muzzle width (measured on the maxilla) and the second was the size-adjusted anterior mandible length (measured between the alveolar margin of the first incisors and the boundary between P_4 and M_1) (Mendoza and Palmqvist, 2006). Each of these variables gave partial discrimination between diet/habitat combinations, but complete discrimination required the variable in combination with the hypsodonty index. For instance, muzzle width discriminated well between grazers and open-habitat browsers and mixed grazers, but in combination with the hypsodonty index, grazers could also be distinguished from members of other feeding categories that had wide muzzles. The mechanical significance of the anterior mandible length has not been elucidated. The relationship of anterior mandible length to diet and habitat offers unexpected insights. A group of specialized feeders, many of which live in open grasslands but have low values of the hypsodonty index, have mandibles with long anterior portions. Furthermore, as the anterior length of the mandible increases, the minimal hypsodonty index for open-habitat feeding increases.

Perissodactyla

The order Perissodactyla includes three families: the horses and their allies (Equidae, the only family in the suborder Hippomorpha), the rhinoceroses (Rhinocerotidae), and the tapirs (Tapiridae). The last two families are closely related and are grouped together as the Ceratomorpha. Perissodactyla is much smaller in terms of extant species than the even-toed ungulates (Artiodactyla; Chapter 14). The most successful are the horses, which exploit their ability to subsist on low-grade forage to compete successfully with artiodactyl ungulates. However, during the Eocene, perissodactyls were very diverse and contained a large number of species (Prothero, 2006).

All perissodactyls are hindgut-fermenting herbivores and include grazers, browsers, and mixed feeders. Whatever the feeding habits, the dentition of perissodactyls is dominated by a grinding battery of premolars and molars, which are often hypsodont. The degree of hypsodonty will be compared between different ungulates using the hypsodonty index for the third lower molar (M_3HI), as measured by Janis (1988), both in this chapter and in Chapter 13.

Data on the sequence and timing of tooth eruption and wear patterns in some perissodactyls are provided by Levine (1982), Ramzan et al. (2009), and Jones et al. (https://www.uaex.edu/publications/PDF/FSA-3123.pdf) (horse); Gibson (2011) (Baird's tapir); and Anderson (1966), Hitchins (1978), and Kitchener (1997) (rhinoceros).

HIPPOMORPHA

Equidae

This family contains the single genus *Equus*, which consists of three species of zebra, three of wild asses, and the wild horse (*Equus ferus*). The latter species includes Przewalski's wild horse and domesticated horses (Vilstrup et al., 2013).

The members of the horse family have the dental formula $I\frac{3}{3}C\frac{0-1}{0-1}P\frac{3-4}{3}M\frac{3}{3} = 36 - 42$. Canines usually appear only in males, and P^1, if it develops, is usually lost early. All of the other teeth are hypsodont. The deciduous dentition is $dI\frac{3}{3}dC\frac{0}{0}P\frac{3}{3}M\frac{3}{3} = 36$.

Dentition

The equid dentition is illustrated using the **domestic horse** (*Equus ferus caballus*). As shown in Fig. 12.1, the facial region of the skull is elongated and deep. The cheek teeth are separated from the anterior dentition by a wide diastema. The orbit is located posterior to the region occupied by the elongated roots of the cheek teeth. The body of the mandible is very deep, because of the very large area of attachment of the masseter muscles, which make up more than 50% of the total jaw adductor mass (Turnbull, 1970) and because the cheek tooth roots are tall.

The dentition of the horse is shown in Fig. 12.2. The incisors have a central invagination (**infundibulum**) filled with cementum. These teeth meet edge to edge and are used to grip and crop grass, in combination with movement of the head. The original surface wears away within a short time and the incisal surface acquires a characteristic morphology, shown in Fig. 12.2A. The wear surface has two concentric rings of enamel, which define an annulus of dentine. The center of the surface is filled with cementum. As a result of differential wear, the enamel rings are raised above the dentine annulus and the inner area of cementum, which both become concave. This structure facilitates gripping and cutting of grass between the incisors.

Most male horses develop upper and lower canines and these are stout, pointed teeth adapted for fighting. The
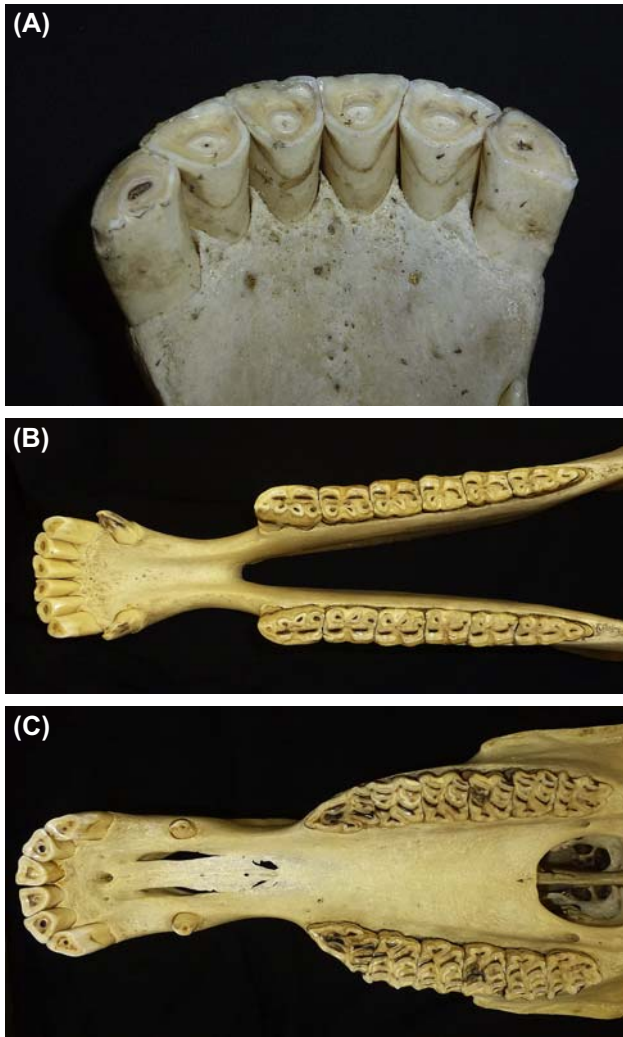
(A)

(B)

(C)

FIGURE 12.2 Dentition of domesticated horse (*Equus ferus caballus*). (A) Lower incisors and canines, occlusal view. Original image width = 9.8 cm. (B) Lower dentition, occlusal view. Original image width = 36.2 cm. (C) Upper dentition, occlusal view. Original image width = 26.9 cm. *Courtesy MoLSKCL.*

FIGURE 12.3 Domesticated horse (*Equus ferus caballus*). Wolf tooth in upper jaw. *Courtesy Wikipedia.*

lower canines lie anterior to the upper canines (Figs. 12.1 and 12.2), as in most mammals. They are less hypsodont than the incisors and cheek teeth, but the lower canines can have roots as long as 7 cm, which lie almost horizontally. The upper canines are curved and the crowns are more vertically oriented. Canines may erupt slowly up to about 10 years, when the root apices close. One or two canines develop in about 28% of mares, but they are smaller than in males and may be unerupted or aberrant. Deciduous canines may form but rarely erupt. The canines of domestic horses can cause injury, while malformed or impacted canines can be a source of infection. A detailed account of both the morphology and the eruption of canines, and the possible veterinary problems associated with these teeth, was given by Caldwell (2006).

The anterior premolars are vestigial teeth known as **wolf teeth** (Fig. 12.3). The prevalence of an upper anterior premolar is highly variable (13%−80%), and varies between breeds and between geographic areas (Hole, 2016). The prevalence may be higher in females than in males. An anterior premolar in the lower dentition is extremely rare. Morphologically, wolf teeth are variable in size, number of cusps, and length of roots. Misplaced or fractured wolf teeth can injure the oral mucosa and this is one reason for extraction by veterinary surgeons, although other reasons for extraction seem to be less well founded (Hole, 2016).

The cheek teeth are covered with a layer of cementum (Fig. 12.4). Instead of a thin layer of acellular cementum, as on the molars of lagomorphs and artiodactyls, the layer covering horse molars is very thick and is cellular (Sahara, 2014). It is deposited after the coronal enamel is completely formed. After the dental epithelium has been lost, osteoclasts resorb pits in the enamel surface and cementum is then laid down. Because of the pitting of the enamel, the cementum−enamel interface is much stronger than that in bovine teeth, in which cementum is deposited on intact enamel.

The enamel of horse cheek teeth has horizontal Hunter−Schreger bands (HSBs) (von Koenigswald et al., 2011). This increases toughness but, because the prisms are oriented at low angles with respect to the occlusal surface, the resistance to abrasion is relatively low.

All of the cheek teeth are highly hypsodont (Fig. 3.2). Janis (1988) found that the M_3HI is 5.70 for Przewalski's wild horse, the nearest extant relative to the domestic horse, and 5.79−8.73 among other Equidae. The premolars are all molarized, with a similar pattern of lophs compared to the molars. Of the six cheek teeth that are consistently present, P2 (most anterior) and M3 (most posterior) are roughly triangular, while the teeth between are rectangular. In the upper jaw, P^4 is the largest, and in the lower jaw, P_2 is the largest. In each upper cheek tooth there is a W-shaped ectoloph at the labial margin and lingual to this several
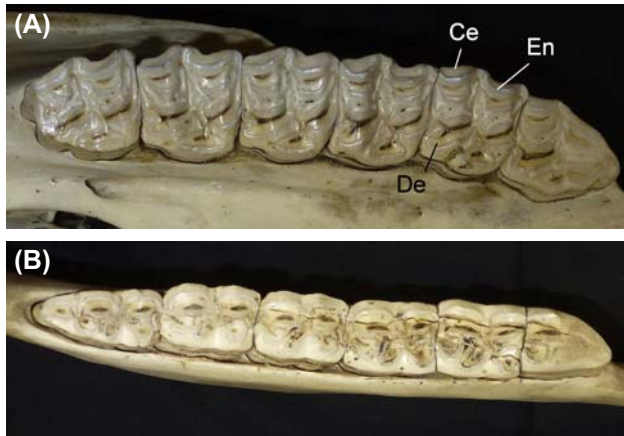
FIGURE 12.4   Domesticated horse (*Equus ferus caballus*). Loph pattern and thick outer layer of coronal cementum shown in occlusal views of (A) right upper molars and (B) left lower molars: anterior to right. Original image width = 27.9 cm (A) and 22.2 cm (B). *Ce*, coronal cementum; *De*, dentine; *En*, enamel. *Courtesy MoLSKCL.*

lophs, which run approximately parallel with the ectoloph. In the lower jaw, there is also an ectoloph, but with curvature opposite to that in the upper jaw, with loop-shaped lophs lingually. Both upper and lower occlusal surfaces are traversed by a labiolingual tract, which seems to have relatively low wear resistance because, at the point where lophs cross this tract, the enamel is relatively thin. With wear, these tracts lie below the adjacent regions, so the occlusal surfaces acquire gentle undulations (Fig. 12.4A and B). The occlusal surfaces of the cheek teeth lie on a transversely oriented, inverted U-shaped curve.

Feeding

Grass is brought into the mouth by the lips, gripped between the incisors, and cut between the sharp edges of the incisors as they are moved sideways. Although the lips can discriminate between grasses with different physical properties, such as between leaves and seed-bearing stalks, there is evidence that the lips are less efficient in this regard than the tongue used by cattle for grazing (Hongo and Akimoto, 2003). Horses gather enough food to fill the anterior part of the mouth before they begin to chew (Baker, 2002).

The articular condyles are cigar shaped and are oriented at a small angle (about 15 degrees) to the transverse axis in the horizontal plane (Fig. 12.5A). They also slope downward toward the midline at a similar angle (Baker, 2002). The glenoid fossa is bounded posteriorly by a prominent posterior process (Fig. 12.5B), but allows rotary and sliding movements. The masticatory cycle, starting with the mouth closed, follows the typical mammalian sequence of an opening stroke, in which the jaw moves laterally and downward, followed by a closing stroke, in which the mandible moves medially and upward, bringing the cheek teeth into contact, and finally by the power stroke, which

moves the occlusal surfaces of the opposing teeth against each other and thereby produces a grinding action (Baker, 2002; Bonin et al., 2006). A point midway between the temporomandibular joint condyles moves slightly caudally during jaw opening and anteriorly during jaw closing. The principal direction of the power stroke is transverse and upward. Baker (2002) suggested that continuing movement of the mandible brings the cheek teeth into occlusion on the balancing side. There is some evidence for a similar phenomenon in rabbits and pigs, but it seems likely that such contact does not produce significant attrition in horses (Weijs, 1994). Most horses chew consistently on one side of the mouth (Baker, 2002; Bonin et al., 2006), presumably changing sides at intervals, but some alternate between chewing sides (Baker, 2002).

The horse dentition, with the large size and relatively low relief of the tabular cheek teeth, operates as a mill, in which shear is applied to the food under compression. The efficiency of chewing is shown by the fact that, after correction for body size and phylogeny, equids reduce their food to a much smaller particle size than other perissodactyls and also than other herbivores that chew their food only once (nonruminants and other hindgut fermenters) (Fritz et al., 2009).

Wear of the Dentition

As is well known, features associated with the wear of horse incisors are consistent enough to provide a reliable method of aging (Cirelli, 2000). The principal index is the stage of wear of the infundibulum, which disappears at the age of 6 years from the lower central incisor and from the upper lateral by 12 years. Older horses can be aged using the shape of the worn incisors and the appearance of a groove on the labial surfaces of the lateral upper incisors (Galvayne's groove), which appears at 9−10 years and finally disappears at 30 years.

CERATOMORPHA

This suborder contains the tapirs and rhinoceroses, which each have three toes on their feet, although tapirs have a fourth toe, which is ordinarily not in contact with the ground but can be brought into use on soft ground.

Tapiridae

Tapirs are forest-dwelling, medium-large herbivores that feed on a wide variety of plant parts, principally leaves and fruit, but also herbaceous plants, moss, and succulents. All species have a large, muscular proboscis, which is very important in browsing. There are five species, of which four live in Central and South America and one in Asia. There are only small variations in the dentition, mainly in the relative sizes of the anterior teeth, as shown in the **Asian** or
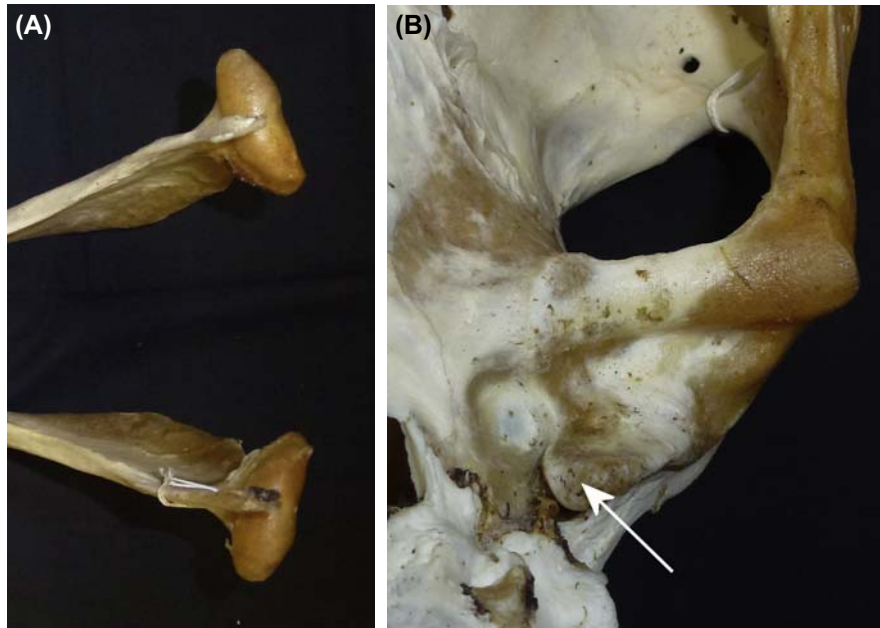
FIGURE 12.5 Domesticated horse (*Equus ferus caballus*). (A) Posterior end of mandible, showing form and angulation of articular condyles. Original image width = 21.4 cm. (B) Left glenoid fossa. *Arrow* indicates posterior process. Original image width = 11.7 cm. *Courtesy MoLSKCL.*

Malayan tapir (*Tapirus indicus*) (Fig. 12.6A) and **Baird's tapir** (*Tapirus bairdii*) (Fig. 12.6B). The dental formula is $I\frac{3}{3}C\frac{1}{1}P\frac{4}{3-4}M\frac{3}{3} = 42 - 44$. The cheek teeth are separated from the canines by a diastema (Fig. 12.6). The first and second incisors are chisel shaped but the upper third incisor is caniniform and is larger than the canine itself, which is reduced (Fig. 12.6 and 12.7A). The third upper incisor and the lower canine appear to sharpen against each other (Fig. 12.6A). The first upper premolars are T shaped, with a transverse loph connected to a labial loph. The remaining premolars are molarized. These teeth and also the molars are bilophodont (Fig. 12.7B). The transverse lophs are connected by a small ridge near the labial margin. In the lower jaw, all the incisors are chisel shaped and the canines are large and separated from the cheek teeth by a diastema, as in the upper jaw. The first premolars have three transverse lophs connected to a labial loph, while the second and third are molarized and, like the molars, are bilophodont (Fig. 12.7B).

The enamel structure in tapirs differs from that of equids in that HSBs follow a curved horizontal path and intersect the edges of shearing lophs at a large angle. This increases the resistance of the edge to wear (von Koenigswald et al., 2011).

Both the premolars and the molars increase in crown size from front to back (Fig. 12.7). A radiograph of the mandible of the specimen in Fig. 12.7A shows that this is reflected in the size of the roots of the molars and, possibly, also of the premolars (Fig. 12.7C).

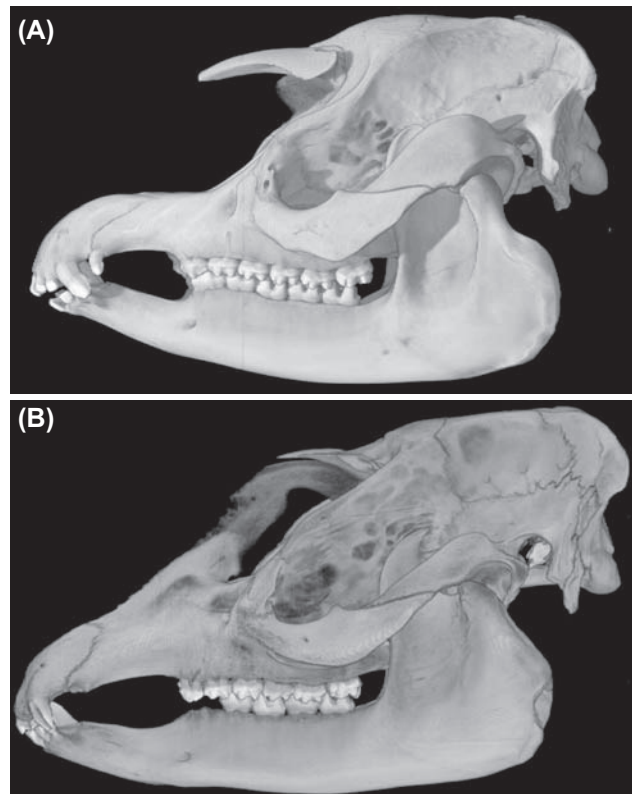The range of lateral motion of tapir jaws during mastication is reported to be less than in horses (Weijs, 1994).

FIGURE 12.6 Lateral views of skulls of tapirs (*Tapirus*). (A) Malayan tapir (*Tapirus indicus*). Original image width = 44.5 cm. *Courtesy Digimorph.com and Dr J.A. Maisano*. (B) Baird's tapir (*Tapirus bairdii*). Computed tomography image. Original image width = 37 cm. *(A) Courtesy MoLSKCL. Cat. no. Z302. (B) Courtesy Digimorph and Dr. J. A. Maisano.*
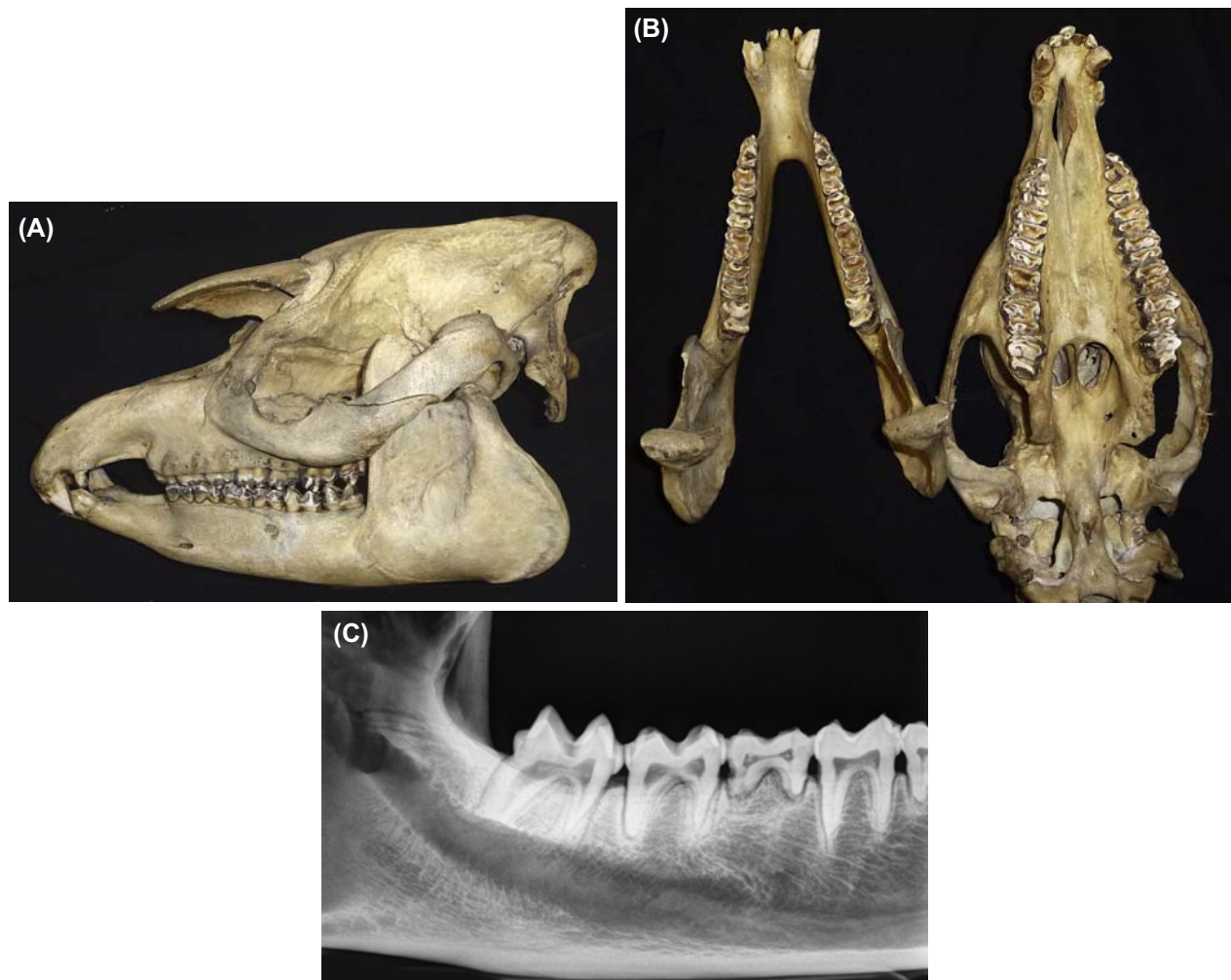
FIGURE 12.7 Tapir. Species unknown, but thought to be Malayan tapir from large lateral incisor. (A) Lateral view of skull. Original image width = 41.5 cm. (B) Occlusal view of upper dentition (right) and lower dentition (left). Original image width = 42.9 cm. (C) Radiograph of the mandible of the specimen seen in (A) and (B). *Courtesy MoLSKCL. Cat. no. Z302.*

The principal action of the cheek teeth on the food is probably shearing due to relative motion between the transverse lophs as they move vertically past one another (Janis and Fortelius, 1988).

In the specimen in Fig. 12.7A and B, the first molar is heavily worn down to the point at which an undivided occlusal surface remains, while the third molar has suffered very little wear. The eruption and wear chart provided by Gibson (2011) (for Baird's tapir) suggests that the animal was probably 8−9 years of age. The striking wear gradient in the molars is due to the time difference in eruption of about 5 years between M1 and M3.

Rhinocerotidae

There are five living species of rhinoceros: the white rhino and black rhino live in Africa, while the Indian, Javan, and Sumatran rhinos occur in southwest Asia. All are large herbivores. The white rhino is a grazer and the other species are browsers.

The dental formula is $I\frac{0-2}{0-1}C\frac{0}{1}P\frac{3-4}{3-4}M\frac{3}{3} = 26 - 36$. The upper molars are trilophodont (Fig. 12.8A). During mastication, the mandible rotates, sweeping the lophs of opposing molars across one another and cutting through the plant food (Fortelius, 1985). The lophs are maintained as efficient blades by a specialization of the enamel, in which the HSBs are vertical instead of horizontal as in equids or curved as in tapirs (von Koenigswald et al., 2011). Resistance to wear is increased because the constituent prisms are oriented parallel with the direction of abrasion at the functional surface of the loph (Rensberger and von Koenigswald, 1980), so sharp edges are maintained (Figs. 12.8 and 12.9). In addition, the vertical orientation of the HSBs may produce low ridges on the
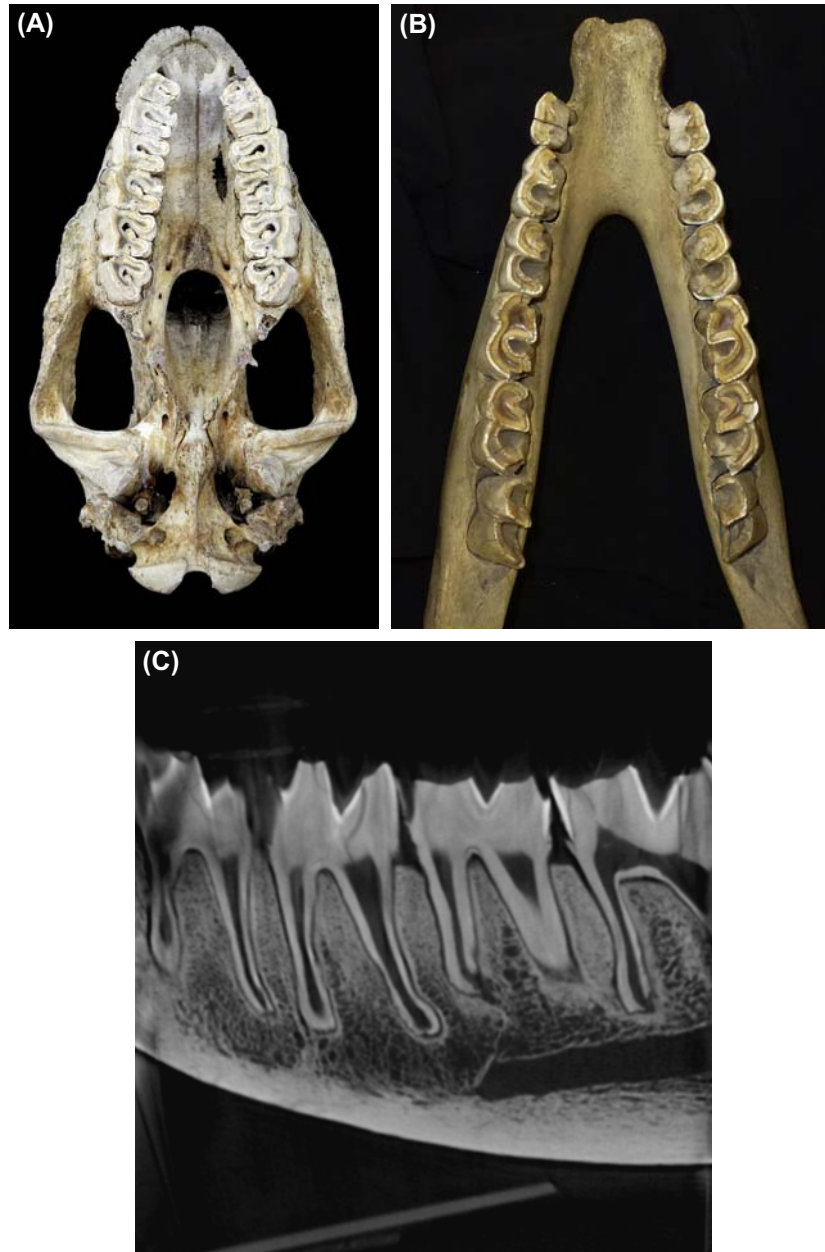
FIGURE 12.8 (A) Rhinoceros (species unknown), occlusal view of upper dentition. (B) Black rhinoceros (*Diceros bicornis*). Occlusal view of lower dentition. Original image width = 30.5 cm. (C) Computed tomography scan showing longitudinal slice through posterior cheek teeth of specimen seen in (B). *(A) ©Dreamtime.com, Dr. Ajay Kumar. (B and C) Courtesy MoLSKCL. Cat. no. Z804.*

worn edges of the lophs, which enhance abrasion (von Koenigswald et al., 2011). The teeth are supported by long, slender roots (Fig. 12.8C).

The **white rhinoceros** (*Ceratotherium simum*) is the largest rhinoceros (and the second largest land mammal, after elephants), males weighing up to 2300 kg. It inhabits savannah and grasslands of southern Africa. The white rhino has a square muzzle with a straight mouth adapted for grazing close to the ground. It lacks both incisors and canines, and has the dental formula $I\frac{0}{0}C\frac{0}{0}P\frac{3}{3}M\frac{3}{3} = 24$ (Fig. 12.9). The lips are used to gather vegetation, which

includes not only grass, but also herbaceous plants and fallen fruits. The white rhino is hypsodont ($M_3HI = 3.90$; Janis, 1988), in accordance with the increased wear associated with feeding close to the ground.

The **black rhinoceros** (*Diceros bicornis*) is a browser. It has a pointed upper lip, which is used to gather leaves. The dental formula is $I\frac{0}{0}C\frac{0}{0}P\frac{4}{4}M\frac{3}{3} = 28$, although the first premolar, especially the lower, is often missing (Anderson, 1966). The molars are mesodont ($M_3HI = 2.24$; Janis, 1988).

The **Indian rhinoceros** (*Rhinoceros unicornis*) is almost as large as the white rhinoceros. It is a mixed feeder:

FIGURE 12.9 White rhinoceros (*Ceratotherium simum*). (A) Lateral view of skull. Original image width = 49.4 cm. (B) Close-up of cheek teeth. Original image width = 31.8 cm. *Courtesy UCL Grant Museum of Zoology; Z767.*

FIGURE 12.10 Indian one-horned rhinoceros (*Rhinoceros unicornis*). Lateral view of skull. Note the procumbent lower incisors. Original image width = 54.7 cm. *Courtesy UCL Grant Museum of Zoology; Z232.*

that is, it feeds on grass but also browses leaves, shoots, and aquatic plants. The lower jaw bears a single pair of procumbent, tusklike incisors (Fig. 12.10). The molars are mesodont ($M_3HI = 1.59$; Janis, 1988).

The **Javan rhinoceros** (*Rhinoceros sondaicus*) and the **Sumatran rhinoceros** (*Dicerorhinus sumatrensis*) are much smaller than the Indian rhinoceros. They inhabit forests, where they browse on leaves, shoots, and fruits. The Sumatran rhinoceros, which is believed to be the most primitive member of the family, has a pair of upper incisors and a pair of lower canines. The dental formula is $I\frac{1}{0}C\frac{0}{1}P\frac{3}{3}M\frac{3}{3} = 28$.

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