Comparative Anatomy of the Gastrointestinal Tract in Eutheria

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mucus protection, might play a role in the development of ulcers. On the other hand, Aranzales and Alves (2013) compile different defence mechanisms – physiological, histological, cytological and neurohumoral – that protect the mucosal lining of the equine stomach.

27.4.4.2 Gastric digestion in the horse

This short section will report information that was obtained by studies on domestic horses, *Equus caballus*. Bacteria in the caecum of fossil equids from the middle Miocene indicate that these animals were already large-intestine fermenters (Schmitz-Münker and Franzen, 1988). The digestive process in the stomach depends on activities of enzymes from the food, as well as from microorganisms and from gastric juice (Meyer, 1986). In the fornix gastricus, which is lined with non-glandular squamous epithelium, the number of microbes amounts to 10^9/g gastric contents and microbial activity degrades the easily digestible carbohydrates (sugars and starch), as well as some proteins, which are mainly degraded by proteinases of plant origin. In the pars proventricularis or oesophagea, there is, as Geyer and Drepper (1973) write, an active lactic acid producing microflora (especially *Lactobacillus bifidus*), which degrades a large part of the soluble carbohydrates into lactic acid. In those parts of the stomach with secreting mucosa, the gastric contents becomes more acid and protein degradation increases. According to Geyer and Drepper (1973), amylolytic and proteolytic digestion takes place close to each other. The acidity of the stomach lies between pH 1.6 in the pars glandularis of the stomach and 6.0 in the pars proventricularis. Proteolytic activity is minimal in the pars proventricularis, amounting to only 0.6% of the value reached in the small intestine, but in the pars glandularis as much as 10% of the small intestinal value is reached (Hintz, 1975). Most equine individuals compensate, as Edouard et al. (2008) described, for a decline in forage digestibility when eating grass forages; they increase in their voluntary intake. This response is different from that of cattle, in which intake declines on decrease in forage quality.

The horse habitually relies more on cellulose as an energy source than ruminants (Gwynne and Bell, 1968). Hindgut fermenters are less efficient in assimilating protein than ruminants, as Pastor et al. (2006) write. Even though the hindgut fermenter is only two-thirds as efficient as a ruminant in assimilating protein, it can process twice as much food per unit time because it does not have to wait for a rumen to be emptied (Bell, 1971). In a wonderful investigation on feral horses in the Camargue, southern France, Duncan (1991) compares these (E) with cattle (R) of similar size and found the following relationships:

(a) Intake of organic matter: E > R;
(b) Passage rate: E > R;
(c) Intake rate: E > R;
(d) Nutrient extraction: E > R;
(e) Rate of digestion: E < R.

Using microbial fermentation for alloenzymatic digestion, as the host's own digestive enzymes are not sufficient to make sufficient amounts of nutrients available, incubation of the digestive tract with microbes has to be accomplished. This also holds true in perissodactyla, which are large-intestine fermenters. Crowell-Davis and Caudel (1989) studied this process in equine foals: When given choice between maternal faeces and material from another mare, equine foals sniff on both materials equally, but practice coprophagy only of maternal faeces.

27.5 Rhinocerotidae

The rhinocerotoids, sister taxon to the tapiroids within the infraorder Ceratomorpha, developed higher crowned teeth and adopted various strategies for dealing with more fibrous vegetation, including increased body size (Colbert and Schoch, 1998). In terms of diversity and longevity, the Rhinocerotidae represent a really successful group during the Oligocene radiation (Radinsky, 1966). The late Oligocene was the time when *Rhinoceros unicornis*, the Indian rhinoceros, separated from the two-horned Asian and African rhinos (Steiner and Ryder, 2011). Tougard et al. (2001) estimated that the paleontological emergence of the genus *Dicerorhinus* has to be dated in the Lower Miocene (between 23 and 16 Myr, Carroll, 1988). Today, there exist four rhinocerotid genera and five species (Grubb, 2005); they are treated in monographic style by Meister and Owen-Smith (1997): *Ceratotherium simum*; Van Strien (1997): *Dicerorhinus sumatrensis*; Adcock and Emslie (1997): *Diceros bicornis*; Schenkel (1997): *Rhinoceros sondaicus*; Laurie (1997): *Rhinoceros unicornis*. The monophyly of the five recent rhinoceros species (Tougard et al., 2001) is well established from morphological and paleontological data. Strong support is provided for the split between *Diceros* and *Ceratothorium* 17.1 ± 2.5 year before present; the divergence of *Rhinoceros* is dated about 11.7 ± 1.9 million years ago (Tougard et al., 2001).

Although not a single rhinocerotid species can presently be found in North America, Rhinocerotidae from that continent represented one of the largest, longest, and most complete records of a mammalian family (Prothero, 2005) as well as one of the most successful groups of mammals in North America (Prothero, 1998). According to this author, the most striking thing about the pattern of rhinocerotid evolution is that of stasis: Most species appear suddenly and then are unchanged through most of

their history. During the Miocene Rhinocerotidae occurred in enormous herds, especially in the High Plains of North America. Ecologically they were very diverse. "There were large hippolike grazers (*Teleoceras*, *Brachypotherium*, and *Peraceras superciliosum*); prehensile-lipped browsers; four independent examples of dwarfing (*Peraceras hessei*, *Teleoceras meridianum*, and still undescribed species of *Teleoceras* and *Diceratherium*); pig-sized herding rhinos (*Menoceras arikarense*); and many other less specialized kinds. Rhinocerotids occupied the large-bodied herbivorous niches in North America from the early Oligocene to the end of the Miocene" (page 595, Prothero, 1998). In their Old World evolution, rhinoceroses changed, as Kahlke and Lacombat (2008) describe it, from cursorily mixed feeders of central Asian origin to heavy, highly specialised grazers in the Plio-Pleistocene tundra of Central Europe.

27.5.1 Food of the Rhinocerotidae

The reader should refer to Tab. 5.4. Ecologically, most Miocene (26 to 7 MYBP) rhinoceroses were brush or leaf eaters; later they adapted to hard and dry brush vegetation (Heissig, 1999b). Much later, between 44,000 and 24,000, rhinos eat considerable amounts of forbs, and Willerslev et al. (2014) show for some rhino species that they eat considerably more graminoids than horses.

In the following, a short account of the food of rhinoceroses will be given in the systematic differentiation supplied by Groves (1983, 1997): There are five recent species of four genera in two tribes in the family Rhinocerotidae. In tribe Dicerotini, two species are grouped, namely, *Diceros bicornis* (black rhinoceros) and *Ceratotherium simum* (white rhino); in tribe Rhinocerotini, the genus *Rhinoceros* consists of two species (*sondaicus*, Javan rhino, and *unicornis*, Indian rhino), as well as of *Dicerorhinus sumatrensis*, the Sumatran rhino.

The black rhino, *Diceros bicornis*, is predominantly a browser with woody dwarf shrubs, small trees and forbs providing the bulk of the diet (Hillman-Smith and Groves, 1994; Kaiser and Kahlke, 2005). According to Hall-Martin et al. (1982), this species selects against herbs, as well as against grass and sedges. Adcock and Emslie (1997) write that this species eats from small bushes, including *Acacia* species, but rarely eats plant parts that grow higher than 2 m. In a study comparing digestion of the black rhinoceros with the horse, Clauss et al. (2006) observed that these rhinos achieved only relatively low digestion coefficients when compared with the horse, a species of similar gastrointestinal morphology. The warning statement of Foose (1982) is corroborated that extrapolation from morphology to physiological details between species of different families should be avoided.

In contrast to the black rhino, a strict browser, the white rhino, *Ceratotherium simum*, is entirely graminivorous (Groves, 1972; Kaiser and Kahlke, 2005) or a "pure grazer" (Meister and Owen-Smith, 1997). The two handbooks of Mills and Hes (1997) and of Skinner and Chimimba (2005) on South African mammals make more detailed comparisons of both species possible. However, the stenophagous dependence of *Ceratotherium simum* on grass does not exclude seasonal variability of grassland usage, as has been described by Shrader and Perrin (2006).

Schenkel (1997) characterises the food of the Javan rhinoceros, *Rhinoceros sondaicus*, as that of a true browser; young trees, bushes, shrubs and lianas represent the items that are eaten by that South East Asian species. *R. sondaicus*, is classified by Kaiser and Kahlke (2005) as browser. Schenkel (1997) mentions that the food of this species is composed of more than 100 plant species.

Rhinoceros unicornis, Indian rhino, as described by Laurie (1997) is very diverse, but long grasses of the genus *Saccharum* represent the main food item. Additionally, the author observed 180 plant species as food items in Nepal. Food of *R. unicornis*, characterised by Laurie et al. (1983), consists of 70 to 89% of grass, but food composition shows seasonal changes. Sarma et al. (2012) indicates that Indian rhinos prefer wet grassland in all seasons of the year. *R. unicornis* was also studied by Steinheim et al. (2005) in Nepal. These authors found an effective fermentation of cellulose in this species, it feeds on grass, which represents 63%, while browse contributes 28% to the food, this species has to be called a grazer; according to Laurie et al. (1983) grasses even make up between 70 and 89% of the diet in Nepal. It also eats fruits, leaves, branches sedges and ferns, aquatic plants and agricultural crops as additional material. Laurie et al. (1983) observed high seasonal variability.

The Sumatran rhinoceros, *Dicerorhinus sumatrensis*, eats, as Hubback (1939) and van Strien (1997) remark, a diversity of plants, leaves and twigs, but also herbs and succulent leaves, but grass and sedges growing along streams are never eaten. According to Groves and Kurt (1972), the food of this species consists of fruit, leaves, twigs, bark and saplings (Kaiser, 2003); *Dicerorhinus sumatrensis* is a true browser (Kaiser and Kahlke, 2005).

From the data presented by the literature and cited above, one can classify Rhinocerotidae into two feeding groups, two species that can be called grazers, namely *Ceratotherium simum* (white rhino, totally graminivorous), and *Rhinoceros unicornis* (Indian rhinoceros) with a high percentage of grass in its food. On the other hand, *Diceros bicornis* (Black rhino), *Rhinoceros sondaicus* (Javan rhinoceros) and *Dicerorhinus sumatrensis* (Sumatran rhinoceros) are browsers.

27.5.2 Anatomy of the stomach of Rhinocerotidae

Thomas (1801) describes the stomach of *Rhinoceros unicornis*, Indian rhino. In external appearance, it is very similar to the equine stomach, as is shown in illustrations that were originally published by Owen (1862) (Fig. 5.82). It is unilocular and composite, i.e. it is partly covered with squamous epithelium on a non-glandular tunica mucosa (Burne, 1905; Bhattacharya and Chakraborty, 1993). The mucosa in the fornix and proximal corpus is covered by a white, thick and non-glandular tunica mucosa, which is covered with a squamous epithelium with fine rugae (Fig. 5.82 B). A well-defined border separates this mucosal section from a much thicker pars glandularis. On the cardiac side of the pars pylorica the stomach has its smallest circumference. The total straight length of the stomach is 122 cm in a male and 81 cm in a female, but the length of the lesser curvature is only 53 cm (Owen, 1862).

The stomach of the Sumatran rhinoceros, *Dicerorhinus sumatrensis*, is different from that of the Indian rhino, as Garrod (1873) writes. There is no constriction between cardiac and pyloric portion of the organ, but there is a peculiar diverticulum in the region of the fornix gastricus (Fig. 5.83), which is lined by non-glandular mucosa and covered by a squamous epithelium. Near the lesser
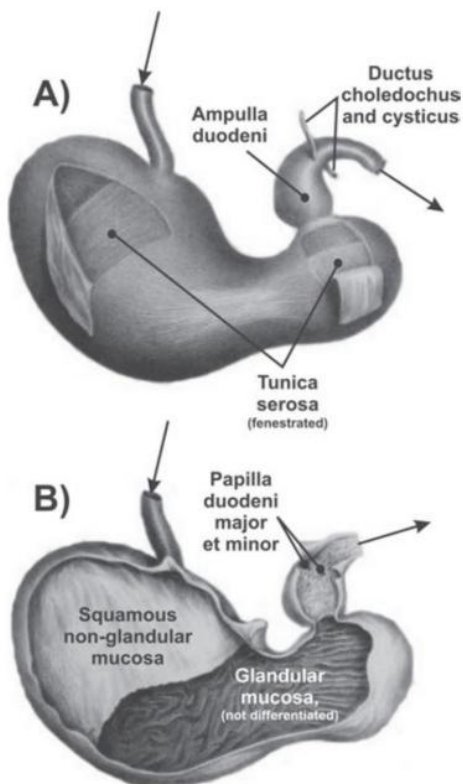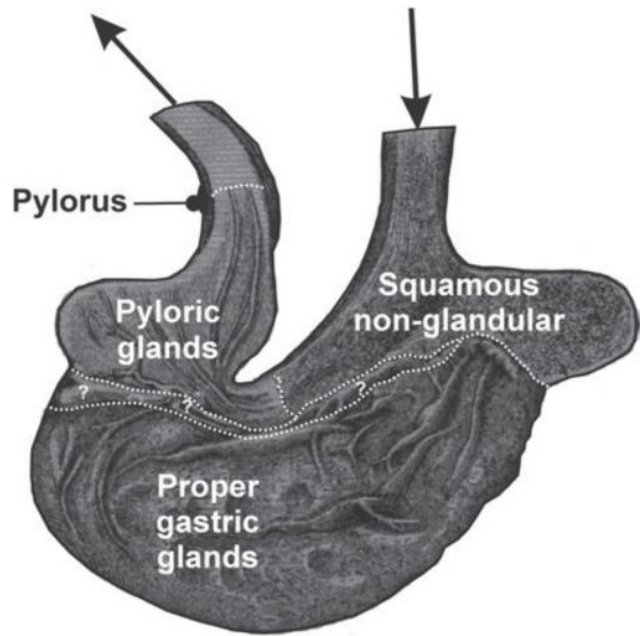

Fig. 5.83: Opened stomach of the Sumatran rhinoceros, *Dicerorhinus sumatrensis*. In the area with question mark, cardiac glands are not clearly delimited. Adapted from Garrod (1873).

curvature Cave and Aumonier (1963) mention a "cobblestone" surface, which is cornified and papillated (Fig. 5.84). "The "cobblestone" area of the *Dicerorhinus* (the author writes "*Didermocerus*") *sumatrensis* stomach must

Fig. 5.82: External (A) and internal (B) aspects of the stomach of *Rhinoceros unicornis*. Adapted from Owen (1862).
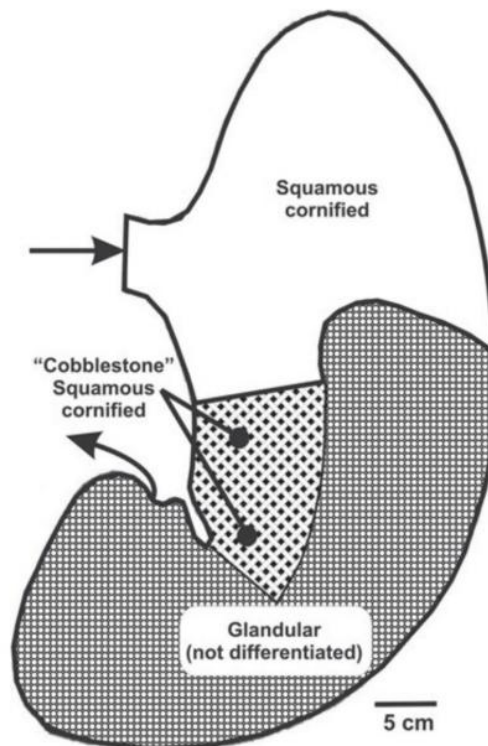

Fig. 5.84: Mucosal lining of the stomach of *Dicerorhinus sumatrensis*. Adapted from Cave and Aumonier (1963).

be regarded as a specialised prolongation of the cardiac mucosal field" (page 35). The authors speculate that "milling" of gastric contents occurs in this mucosal zone. The length of the above-mentioned diverticulum is 28 cm and its diameter is 13 cm. The mucosa in the fundus and parts of the corpus, as well as of the fornical diverticulum, is much plicated and looks white and opaque. The pars pylorica and the corpus gastricum are covered with a thick glandular mucosa. Between both types of mucosa – glandular and non-glandular – the bordering line is abrupt and of a type of the margo plicatus of the equine stomach. For two other rhinocerotid species a composite stomach is described. Clemens and Maloiy (1982) mention for the black rhino of Africa, *Diceros bicornis*, that the cranial one-half to two-thirds of the stomach are lined with stratified squamous tissue. On the other hand, a smooth white squamous epithelium occupies about one-third of the total gastric area of *Rhinoceros sondaicus*, the Javan rhinoceros (Garrod, 1877). In the gastric zone lined with a non-glandular mucosa, Clemens and Maloiy (1983) found for the browsing black rhinoceros, *Diceros bicornis*, that the apparent digestibility of cell wall material, cellulose and hemicellulose is higher than in the glandular part of the organ ("caudal stomach"). On the other hand, energy uptake from the pars proventricularis ("cranial stomach") is considerably lower than in the pars glandularis ("caudal stomach").

27.6 Tapiridae

The tapiroid and the rhinocerotid lineage, together forming the suborder Ceratomorpha (McKenna and Bell, 1997), diverged, as Colbert and Schoch (1998) write, from a common ancestor in the early Eocene (~50 Mya.). The two superfamilies Tapiroidea and Rhinocertoidea are considered as sister-groups by Janis (1984). The recent family Tapiridae has only four established (Grubb, 2005a), as well as a recently described fifth species (Cozzuol et al., 2011, 2013), *Tapirus kabomani*, the little brown tapir or "tapir negrito" (Antelo Aguilar, 2014) from western Amazonia. Cerqueira (1982) presents information about the three, already well-established species from Ibero-America, represented by *Tapirus pinchaque*, the Andean form, which occupied the rising Andes during the Pliocene/Pleistocene; *T. terrestris* lives in the lowlands east of the Andes; and *T. bairdi* might have differentiated from the latter. *T. terrestris* and *T. bairdi* seem to occupy similar habitats. *Tapirus indicus*, from Sumatra, Malaysia, Thailand and Myanmar (IUCN, 2011) prefers secondary lowland forest in flat and damp areas, as Novarino et al. (2005) describe.

All species of the family belong to the genus *Tapirus*. Ancestors of tapirs "were common in all northern continents in the early Eocene. Subsequently, separate families differentiated in North America, Europe, and Asia" (Carroll, 1988, page 530). The earliest species of the family Tapiridae, *Prototapir*, "appeared in the early Oligocene in Europe and the Middle Oligocene in North America" (page 531). Holanda and Ferrero (2013) stated that the genus *Tapirus* immigrated to South America and represents a lineage that has diversified in South America. Fluctuations in tapir distribution were observed by Holanda et al. (2012): In the Pleistocene *Tapirus terrestris* could be found in southern Brazil. The South American tapir species *T. terrestris* and *T. pinchaque* are closely related, but the tapir of Central America, *T. bairdii*, and the Asian species, *T. indicus*, diverged from them earlier (Ashley et al., 1996). According to Holanda et al. (2011), the distribution of fossil tapirs was similar to the actual distribution.

27.6.1 Food of the Tapiridae

In relation to tapir food, reference should be made to Tab. 5.4. The four well-established species of tapirs, *Tapirus bairdii* (Baird's tapir), *T. pinchaque* (Mountain tapir), *T. terrestris* (South American or Brazilian or lowland tapir), *T. indicus* (Malaysian tapir), eat similar types of food: twigs, fruits and leaves (IUCN, 2011). They disperse seeds of the fruits they have eaten (Olmos, 1997). Tapirs and their kin might specialise in consuming a high amount of foliage with a moderate amount of fibre content (Schoch, 1989).

27.6.1.1 Food of *Tapirus bairdii*
The Central American or Baird's tapir, *Tapirus bairdii*, is a completely herbivorous species, eating a wide variety of leaves, twigs, flowers and bark (Naranjo, 2001), as well as "fleshy fruits" (Eisenberg and Redford, 1999; García et al., 2006, Fig. 5.85). In the state of Quintana Roo, Mexico, the majority of plants eaten are herbs and bushes (Pérez Cortez and Matus Pérez, 2010). According to García et al. (2006), this species is able to eat approximately 15 kg of vegetation per day, consisting of leaves, stems and a small amount of fruits (Naranjo Piñera, 1995). Depending on the availability of food items, tapirs can shift their foraging strategy among habitat types and seasons (Naranjo, 2009), but also habitat differences between geographical regions can be responsible for variable food composition (Henry et al., 2000). The most noticeable changes in proportions of food items ingested by Baird's tapir throughout the year are those related to fruit consumption. This type of food is related with seed dispersal, described by O'Farrill et al. (2006). However, according to Naranjo Piñera and Cruz Aldán (1998), the contribution of fruits