



Research

OPEN ACCESS

Morphological characteristics of the skull of Malayan tapir (*Tapirus indicus*)

Nur Asyiqin Firdaus Marzuki¹, Nurhidayat², Danang Dwi Cahyadi², Supratikno², Chairun Nisa², Srihadi Agungpriyono², Savitri Novelina^{2*}

¹Study Program of Veterinary Medicine, School of Veterinary Medicine and Biomedical Sciences, IPB University, Bogor, Indonesia

²Division of Anatomy Histology and Embryology, School of Veterinary Medicine and Biomedical Sciences, IPB University, Bogor, Indonesia

Abstract

Background The Malayan tapir (*Tapirus indicus*) is a notable herbivorous mammal found in Southeast Asia, recognized for its distinctive proboscis and coloration, along with its vital ecological role. According to the IUCN, this species is classified as a threatened species.

Objective: This study aimed to investigate the morphology of the skull of Malayan tapir, which is associated with feeding behavior.

Methods This study employed a descriptive method, comparing a skull specimen of a Malayan tapir to those of horses (*Equus* sp.). References regarding skull morphology and behavioral video of Brazilian tapirs (*T. terrestris*) were used for additional comparisons.

Results Tapir had a relatively rounder-shaped skull, shorter and thicker *os nasale*, deeper *fossa masseterica*, and wider *apertura cavum nasi* than the horse. The tapir skull specimen displayed an open eye socket, whereas the horse skull displayed a closed eye socket. Morphological observations of the tapir's behavioral videos showed that tapirs exhibited orthal masticatory movement, driven by brachydont teeth with bilophodont characteristics, which were very different from horses' hypsodont teeth, designed for lateral movement. The proboscis of the tapir is unique and has a more muscular structure than that of horses, including the nasal bones, which are shorter and thicker.

Conclusion These morphological differences influenced the feeding behavior and nocturnal activity of tapir species. This study contributes to broader conservation efforts aimed at conserving tapir populations and their habitats.

Keywords feeding behavior | morphology | proboscis | skull | tapir

Introduction

Tapir, also called Malayan tapir (*Tapirus indicus*), is a notable large herbivorous mammal that resides in densely forested areas and verdant jungles in Southeast Asia. The Malayan Tapir is a member of the Tapiridae family, which is classified within the order Perissodactyla, a taxonomic group consisting of ungulates with an odd number of toes. The taxonomic family Tapiridae consists of four currently existing species, including the Brazilian tapir, mountain tapir, and Baird's tapir, which can only be found in the South American region, with the Malayan tapir in the Southeast region. Tapirs have been positioned as an old lineage within the mammalian group through molecular phylogenetic investigations,

with their evolutionary origins dating back to the early Eocene period (Cozzuol *et al.*, 2013).

Malayan tapirs can be readily distinguished based on their distinctive coloration patterns. Pigmentation exhibits a distinct boundary, characterized by a white marking that originates posterior to the forelimbs and extends dorsally along the vertebral column to the caudal region. The distinctive black and white coloration of the tapir effectively blends the animal into its surrounding habitat (**Figure 1**). The measurements of head and body length spans range from 1.8 to 2.5 meters, while the height ranges from 0.9 to 1.1 meters. In addition, the weights can vary between 250 kg and 540 kg (Khan, 1997). They also have the longest proboscis among all tapir species (Witmer *et al.*, 1999).



Figure 1 External characteristic of tapir (*Tapirus indicus*) (Naturalistchu, 2024).

The current distribution of tapir species exhibits discontinuity due to historical environmental changes and the subsequent migration events of their predecessors. The dynamic nature of tapir distribution is a crucial aspect to consider when formulating management strategies and conservation plans (Garcia *et al.*, 2012). Tapirs encounter a range of challenges that pose danger to their cultural and ecological importance. These challenges encompass habitat degradation resulting from deforestation, illegal hunting activities, and the incidence of roadkill (Mahathir *et al.*, 2019). According to the International Union for Conservation of Nature (IUCN), the classification of these organisms is endangered, underscoring the pressing necessity for conservation endeavors aimed at protecting their continued existence (Traeholt *et al.*, 2016).

Tapir has garnered significant scholarly attention owing to its pivotal role in forest ecosystems and its designation as an endangered species. The aforementioned species is a crucial component of local biodiversity, as it plays a pivotal role in the dispersion of seeds and preservation of the overall well-being of its ecosystem. The morphological characteristics of Malayan tapir (*T. indicus*) have not been widely studied. However, understanding the skull morphology of this animal is crucial for supporting conservation efforts. In vertebrates, the skull is a bony structure that forms the upper part of the head. It is composed of several bones that fuse during development to form a single rigid structure. The skull protects the brain and sensory organs, and plays a crucial role in the development and function of these organs.

This study aimed to investigate the morphological characteristics of the skull of the Malayan tapir, which are associated with feeding behaviors, and their nocturnal activities, while comparing them with the skull of a horse (*Equus* sp.) and the Brazilian tapir (*T. terrestris*). This research provides additional information regarding the tapir skull as a reference for studying tapir physiology and behavior in ex situ and in situ conservation efforts for this animal.

Methods

Skull specimens

A specimen collection of a Malayan tapir's skull at the Laboratory of Anatomy, [delete temporary by editor for double anonymous review] was used in the present study. The materials used for this research were skulls of Malayan tapir. Horse

skull specimens from the laboratory collection were used for comparison, in addition to the literature, particularly for the Brazilian tapir. Horse specimens were used in this study because of their close phylogenetic relationship within the order Perissodactyla. This descriptive study examined the morphology of the skull of Malayan tapir, Brazilian tapir, and horse anatomy. This research was carried out from January to April 2024 at the Laboratory of Anatomy, [delete temporary by editor for double anonymous review]. In the present study, we did not seek ethical approval for the research since the cranial specimens were obtained from a scientific collection and no individuals were harmed.

Specimen observation

The Malayan tapir skull specimen was observed and photographed from lateral, dorsal, ventral, and caudal views, including the mandible. The pictures were then uploaded to Adobe Photoshop, and the processed images were labeled and named. The pictures were compared and discussed. In addition to the Malayan tapir and horse skull specimens, literature reviews for Brazilian tapirs and horses, as well as videos regarding Brazilian tapirs, Malayan tapirs, and horses, were used in this study.

Data analysis

Skull images were processed using Adobe Photoshop 2021 software. Parts of the skull were identified using an atlas (Nurhidayat *et al.*, 2016) and names based on the *Nomina Anatomica Veterinaria* (ICVGAN, 2017). These were then described and compared with those of horses and Brazilian tapirs based on anatomical characteristics and their feeding behavior.

Results

The facial bones (*ossa faciei*) observed in the present study were the *maxilla*, *os incisivum*, *os palatinum*, *os pterygoidus*, *os nasale*, *os lacrimale*, *os zygomaticum*, *os conchae nasalis ventralis*, *vomer*, *mandibula*, and *os hyoideum*. Among these, the last three bones were single, whereas the others were paired. In comparison, the skull of the Malayan tapir was barrel-shaped, whereas the skull of the horse was tapered. The *os nasale* in tapir was shorter than that in horses, making the *cavum nasi* wider. Tapir also tends to have a deeper *fossa masseterica* than horses. Tapir had an open orbit (eye socket) because of the lack of *arcus zygomaticus*. The dentition morphology of the tapir was different in that the upper incisor teeth were interlocked with the lower incisor, and their premolars had transverse ridges (**Figure 2**).

The dorsal part of the skull is formed by the squamous part of the *os occipitale*, *os interparietale*, *os parietale*, *os nasale*, *os frontale*, and *os incisivum*. It may be divided into *parietale*, *frontale*, *nasale*, and *incisivum* regions (**Figure 3**).

Os nasale of the tapir was thicker and shorter than that of the horses. The *arcus zygomaticus* was different, and the *orbita* did not have *processus zygomaticus* of *os frontale* like a horse, making it an open-eye socket. Tapir had four upper premolars, while the horse had three upper premolars. The lateral part of the skull may be divided into cranial, orbital,

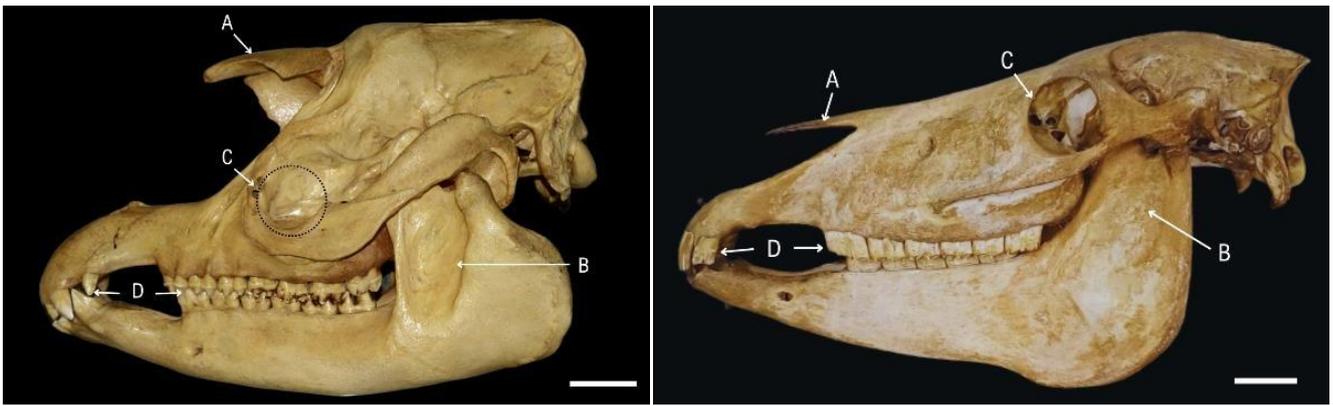


Figure 2 External appearance of the Malayan tapir (left) and horse (right) skulls. Scale bar: 5 cm. A. *Os nasale*; B. *Fossa masseterica*; C. *Orbita*; D. *Dentes*.

and maxillary regions (**Figure 3**).

The ventral view of the skull, exclusive of the *mandibula*, consists of *cranialis*, *choanae*, and *palatinum* regions. The occipital surface is formed by the occipital bone (**Figure 4**). The *mandibula* or lower jaw is the largest bone of the face. It carries the lower teeth and is articulated by the condyles of *os temporale* on both sides. *Mandibula* consisted of three *dentes incisivi*, two *dentes canini*, three *dentes premolares* and three *dentes molares* (**Figure 5**).

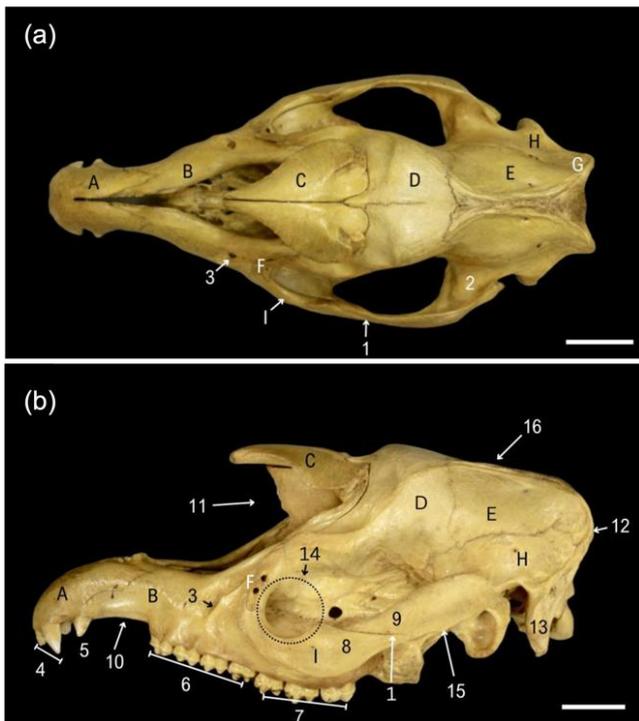


Figure 3 Malayan tapir skull in the (a) dorsal and (b) lateral view. A. *Os incisivum*; B. *Maxilla*; C. *Os nasale*; D. *Os frontale*; E. *Os parietale*; F. *Os lacrimale*; G. *Os occipitale*; H. *Os temporale*; I. *Os zygomaticum*. 1. *Arcus zygomaticus*; 2. *Fossa temporalis*; 3. *Foramen infraorbitale*; 4. *Dentes incisivi*; 5. *Dentes canini*; 6. *Dentes premolares*; 7. *Dentes molares*; 8. *Processus temporalis (os zygomaticum)*; 9. *Processus zygomaticum (os temporalis)*; 10. *Margo interalveolaris (diastema)*; 11. *Incisura nasoincisiva*; 12. *Crista nuchae*; 13. *Processus jugularis*; 14. *Orbita*; 15. *Crista facialis*; 16. *Crista sagittalis*; Scale bar: 5 cm.

Based on our observations of the behavioral videos on the chewing process between both Malayan and Brazilian tapirs

and horses, the tapirs' chewing motion is primarily orthal, with little to no lateral movement. As opposed to the horse chewing motion, the mastication movement of the horse is mostly lateral, which is characterized by a side-to-side or grinding motion. Obtaining a more comprehensive picture of tapirs from the frontal perspective is challenging because of the presence of their proboscis, which might hinder the accurate assessment of their chewing movement.

Discussion

Chewing, also known as the mastication process, is caused by different teeth morphology, and possibly due to the shape of the skull and jaw itself from their diet. The tooth morphology and wear patterns observed in these animals indicated a distinction in their chewing methods. Tapirs, known for their orthal chewing style, where the jaw primarily moves up and down, exhibit distinct dental characteristics that correspond to this chewing action, including a uniform wear pattern on their teeth resulting from limited sideways movements. Tapirs possess brachydont teeth with bilophodont characteristics featuring two transverse ridges or crests. This is in contrast to selenodont teeth found in most ungulates (Ryder, 1879). In addition, tapirs exhibit a restricted lateral chewing action. The mediolateral alignment of the lophs on the cheek teeth of tapirs suggests that they would likely exhibit chewing movements that are oriented towards the front and back (propalinal) rather than side-to-side (lateral) (Hohl *et al.*, 2020). Horses have hypsodont teeth, which means that they have high crowns, which erupt over the year due to their fibrous diet. They use their front incisors to grasp food and use their premolars and molars to grind food because of the rough occlusal surface of these teeth, which facilitates the grinding process (Dixon and Du Toit, 2010).

Obtaining a clear view of tapirs from the front perspective can be difficult because of their proboscis, which may obstruct accurate assessment of their chewing movement. When observed from the side, tapirs noticeably bulge their cheeks during chewing, which can create the impression that the process occurs laterally. However, when viewed from the front, cheek bulging appeared symmetrical on both sides, and there was no visible movement of the lower jaw. This ob-



Figure 4 Malayan tapir skull in the (a) ventral and (b) caudal view. A. *Os incisivum*; B. *Maxilla*; C. *Os palatinum*; D. *Os occipitale*; E. *Vomer*; F. *Os sphenoidale*; G. *Ostemporale*; 1. *Dentes incisivi*; 2. *Dentes canini*; 3. *Dentes molares*; 4. *Dentes molares*; 5. *Foramen palatinum minoris*; 6. *Foramen palatinum majus*; 7. *Processus zygomaticus*; 8. *Foramen magnum*; 9. *Condylus occipitalis*; 10. *Processus jugularis*; 11. *Crista nuchae*; 12. *Crista occipitalis externa*; 13. *Protuberantia occipitalis externa*; 14. *Processus retroarticularis*; 15. *Crista facialis*; Scale bar: 5cm.

servation aligns with that of Hohl *et al.* (2020). According to Holh *et al.* (2020), in species that exhibit a distinct sideways chewing action, such as horses, the lower jaw can be adjusted to move laterally, allowing the entire row of cheek teeth to come into contact while chewing. Another characteristic of tapir teeth is the noticeable interlocking of the third upper incisor with the third lower incisor and lower canine (**Figure 2**) when they come together, which indicates that there is not much sideways movement. Furthermore, the tapir has a chisel-shaped first and second incisors and a third upper incisor shaped like a canine tooth (caniniform). This sharp tooth helps the tapirs crush hard food and defend themselves.

The *crista sagittalis* of Malayan tapir and Brazilian tapir are visibly different in terms of height, although variations could occur. According to Van Valkenburgh (2007), a wide *crista sagittalis* makes it possible to increase the attachment area of the *m. temporalis*, which is one of the primary adductors of the jaw. Benefits from prominent *crista sagittalis*, such as those found in Brazilian tapir, may be associated with higher *m. temporalis* volume, which permits longer mastication ben-

efits, especially when eating tough food items with lower nutritional value (De Santis *et al.*, 2020). Nett *et al.* (2021) stated that tapirids such as llamas may have had their *crista sagittalis* height influenced by their diet. A tough, folivorous diet would have required tapirids to have large *crista sagittalis* and strong *m. temporalis* with long fibers for extended chewing (such as Brazilian tapir) rather than relying on high bite forces to crush hard-shelled seeds (such as Malayan tapir) (Dumbá *et al.*, 2018; Campos-Arceiz *et al.*, 2012). Horses possess *crista sagittalis* due to their diet of eating a tough diet, such as hays and grasses. The *m. temporalis* works in conjunction with the *m. masseter* for mastication.

Other differences between tapirs and horses are that the depression of *fossa masseterica* in tapirs is greater than that of horses and shorter *processus condylaris*. *Fossa masseterica* serves as an attachment to the *m. masseter*. However, *processus condylaris* enables the jaw to open and close like a hinge. Deep *fossa masseterica* has been suggested to be associated with a hard diet in animals. In general, animals with stronger jaws tend to have deeper *fossa masseterica*. It was

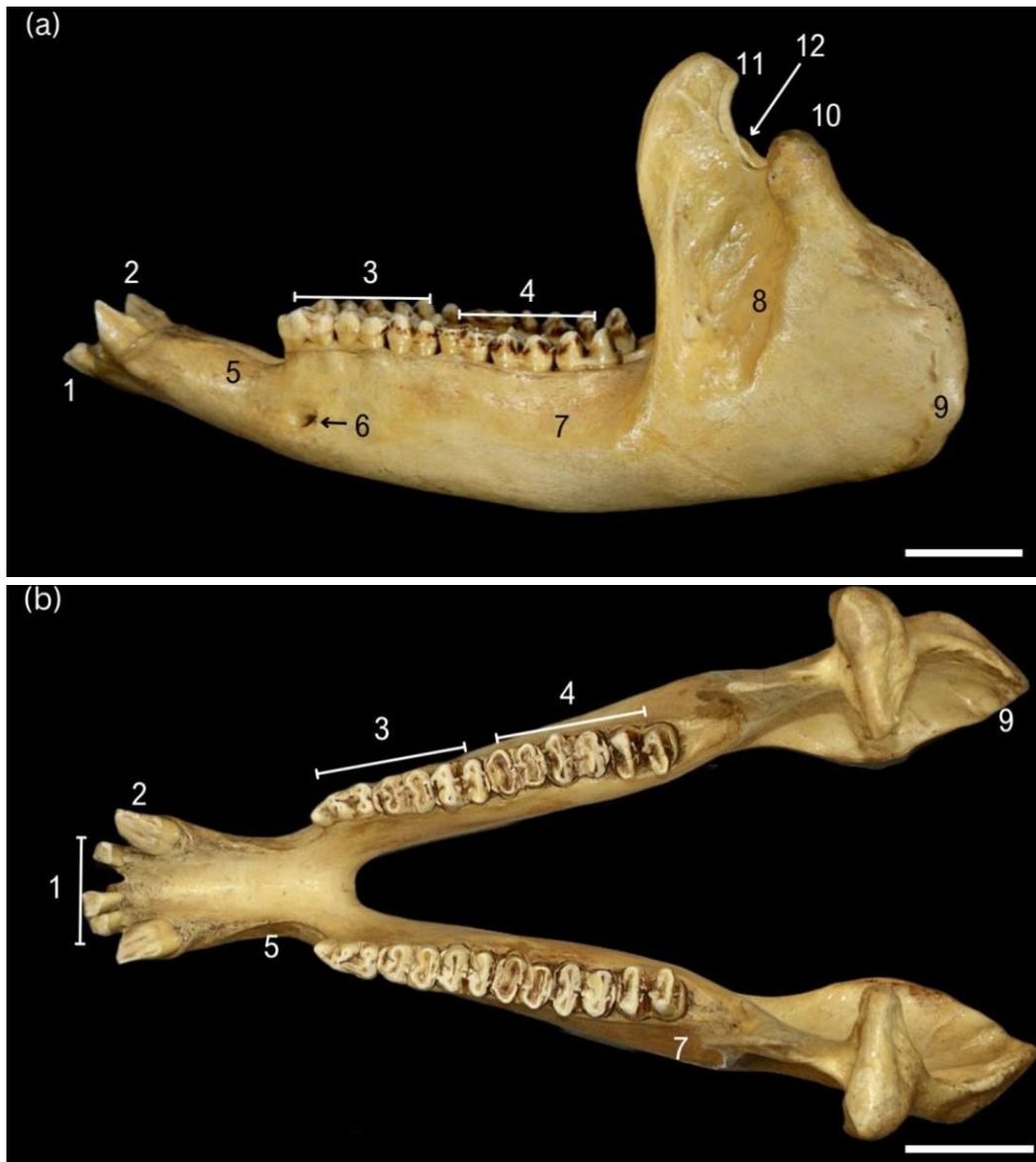


Figure 5 Mandibula of the Malayan tapir in (a) lateral and (b) dorsal view. 1. *Dentes incisivi*; 2. *Dentes canini*; 3. *Dentes premolares*; 4. *Dentes molares*; 5. *Margo interalveolaris (diastema)*; 6. *Foramen mentalis*; 7. *Corpus mandibulae*; 8. *Fossa masseterica*; 9. *Angulus mandibulae*; 10. *Caput mandibulae*; 11. *Processus coronoideus*; 12. *Incisura mandibulae*. Scale bar: 5cm.

observed that the *fossa masseterica* in the Malayan tapir is deeper and wider than that in the Brazilian tapir, as it is suggested that the Malayan tapir eats harder food than the Brazilian tapir.

Tapirs and horses have substantial variance in their *os nasale*. Tapirs possess an *os nasale* that is much more intricate than that of horses. *Os nasale* of the tapir is shorter than that of the horse because it is connected to the proboscis. Radinsky (1965) stated that in evolutionary terms, the presence of a proboscis has been associated with changes in three key skull characteristics: (1) enlargement of the nasal incision, resulting in the formation of the meatal diverticulum (Wall (1980) as a necessary condition for the development of a mobile proboscis); (2) disappearance of the nasal process of the *os incisivum* and its connection with the *os nasale* (i.e., the *sutura naso-incisiva* is absent); and (3) reduction in the length of the *os nasale*. These characteristics are found in tapirs, and

are part of what sets tapirs apart from other perissodactyls and most other living ungulates.

The proboscis of the tapirs is a flexible and fleshy appendage that originates from the tissues of the upper lip and nose. The structure has a tube-like shape that extends from a place behind and below the eye to a position in front of the upper jaw and hangs down below the lower lip. The paired nasal airways transverse the proboscis, starting at the nostrils located at the tip, and entering the nasal cavity at the level of the *os nasale*. The left and right sides of the airways remain distinct throughout their entire journey, separated by septal cartilage, which extends caudally and laterally (Witmer *et al.*, 1999). The length of the proboscis differed to some extent among the four existing species of *Tapirus*, with the Malayan tapir having the longest proboscis and the Brazilian tapir having the shortest. Witmer *et al.* (1999) reported that these differences could be observed in craniofacial osteology. For in-

stance, the *cavum nasi* of the Malayan tapir is significantly more arched than that of the Brazilian tapir, and the *os incisivum* is more rounded at the front of the former species. According to Clifford and Witmer (2004), the more arched *cavum nasi* in the Malayan tapir may be related to the need for a more extensive and flexible proboscis to reach and grasp foliage in its Southeast Asian habitat. This shape could also be an adaptation to navigate dense vegetation and access food sources that are not easily accessible to Brazilian tapirs.

The morphology of the snout region of horses is similar to that of other large ungulates but distinctively different from that of tapirs. Horses do not have a flexible proboscis similar to tapirs. The presence of a proboscis in tapirs necessitates significant restructuring of the entire head. A highly mobile proboscis may be linked to the reduction and retraction of bony and cartilaginous structures of the face to create space for movement. Furthermore, this reorganization would allow for the utilization of the current facial musculature for additional purposes and improved mechanical efficiency, which is in line with tapir morphology. Radinsky (1965) and Wall (1980) examined the skeletal signs of these changes. The *sutura naso-incisiva* moved downwards to a location situated behind the *orbita*. The *os incisivum* and *os nasale* no longer touch each other, causing the *maxilla* to form a portion of the narial border. The length of the skull anterior to the *orbita* is shorter, specifically the distance between the *orbita* and the hole below it, is shorter. In tapirs, the *septum nasi* is emarginate rostrally, meaning that it is not extended up to between the nostrils, as in horses. Consequently, the front part of a tapir's proboscis lacks any significant internal bone or cartilage structure and only the septal cartilage that functions to divide the right and left nostrils.

The proboscis of the tapir is upheld by several crucial facial muscles that have been adapted to facilitate mobility. The muscles encompassed in this category are *m. levator labii superioris*, *m. levator nasolabialis*, *m. caninus*, and *m. lateralis nasi*. *m. levator labii superioris* assists in raising the top lip and plays a role in the movement of the proboscis. The *m. levator nasolabialis* plays a role in the movement of the proboscis, aiding its flexibility and extension. *m. caninus* contributes to the movement of the proboscis by assisting in flexion and extension of the tubular structure. *Musculus lateralis nasi* is responsible for lateral movement of the proboscis (Witmer *et al.*, 1999). The tapir muscles, coupled with other soft and connective tissue components, create a muscular hydrostat. This structure enables the tapir to use its proboscis for tasks, such as gripping food and moving through thick vegetation.

Conclusion

In conclusion, the tapir skull exhibits several distinct features, including a barrel-shaped shape, a shorter and thicker nasal bone (*os nasale*), open eye sockets (orbits), and a wider cavity for the nose (*cavum nasi*) that allows for attachment of the proboscis muscle. Additionally, tapirs have a deeper masseteric fossa and low-crowned teeth, with transverse ridges on each set of teeth. These anatomical differences have influenced the feeding behavior of tapir species as well as their nocturnal activities.

Specimen collection This study used a collection of skull specimen from the Laboratory of Anatomy at the School of Veterinary Medicine and Biomedical Sciences, IPB University. Therefore, we did not seek ethical approval since the cranial specimens were sourced from a scientific collection and no individuals were harmed in the process.

Funding This research did not receive specific funding from any agencies.

Conflict of interest The authors declare that they have no conflicts of interest related to this research.

Author contribution NAF: Investigation, formal analysis, visualization, and writing – original draft; N, SN: Conceptualization, methodology, formal analysis, supervision, resources, and writing – review & editing; DDC, S: Data curation, and writing – review & editing; CN, SA: Validation and writing – review & editing.

Availability of data and materials The data underlying this article are available in the article.

Received 12 February 2025 | **Revised** 21 March 2025

Accepted 25 March 2025 | **Published online** 27 June 2025

References

- Campos-Arceiz A, Traeholt C, Jaffar R, Santamaria L, Corlett RT. 2012. Asian tapirs are no elephants when it comes to seed dispersal. *Biotropica*, 44(2): 220–227. DOI: [10.1111/j.1744-7429.2011.00784.x](https://doi.org/10.1111/j.1744-7429.2011.00784.x).
- Clifford AB, Witmer LM. 2004. Case studies in novel narial anatomy: 3. Structure and function of the nasal cavity of saiga (Artiodactyla: Bovidae: *Saiga tatarica*). *Journal of Zoology*, 264(3): 217–230. DOI: [10.1017/S0952836904005540](https://doi.org/10.1017/S0952836904005540).
- Cozzuol MA, Clozato CL, Holanda EC, Rodrigues FH, Nienow S, de Thoisy B, Fernandes Redondo RA, Santos F. 2013. A new species of tapir from the Amazon. *Journal of Mammalogy*, 94(6): 1331–1345. DOI: [10.1644/12-MAMM-A-169.1](https://doi.org/10.1644/12-MAMM-A-169.1).
- DeSantis LRG, Sharp AC, Schubert BW, Colbert MW, Wallace SC, Grine FE. 2020. Clarifying relationships between cranial form and function in tapirs, with implications for the dietary ecology of early hominins. *Scientific Reports*, 10(1): 8809. DOI: [10.1038/s41598-020-65586-w](https://doi.org/10.1038/s41598-020-65586-w).
- Dixon PM, Du Toit N. 2010. Dental anatomy. *In: Easley J, Dixon PM, Schumacher J* (eds). *Equine Dentistry*. 3rd ed. Pp 51–76. DOI: [10.1016/B978-0-7020-2980-6.00005-2](https://doi.org/10.1016/B978-0-7020-2980-6.00005-2).
- Dumbá LCCS, Parisi Dutra R, Cozzuol MA. 2018. Cranial geometric morphometric analysis of the genus *Tapirus* (Mammalia, Perissodactyla). *Journal of Mammalian Evolution*, 26(4): 545–555. DOI: [10.1007/s10914-018-9432-2](https://doi.org/10.1007/s10914-018-9432-2).
- Garcia MJ, Medici EP, Naranjo EJ, Novarino W, Leonardo RS. 2012. Distribution, habitat and adaptability of the genus *Tapirus*. *Integrative Zoology*, 7(4): 346–355. DOI: [10.1111/j.1749-4877.2012.00317.x](https://doi.org/10.1111/j.1749-4877.2012.00317.x).
- Hohl CJM, Codron D, Kaiser TM, Martin LF, Müller DWH, Hatt J, Clauss M. 2020. Chewing, dental morphology and wear in tapirs (*Tapirus* spp.) and a comparison of free-ranging and captive specimens. *PLoS ONE*, 15(6): e0234826. DOI: [10.1371/journal.pone.0234826](https://doi.org/10.1371/journal.pone.0234826).
- International Committee on Veterinary Gross Anatomical Nomenclature [ICVGAN]. 2017. *Nomina Anatomica Veterinaria*. 6th ed. Columbia (US): International Committee on Veterinary Gross Anatomical Nomenclature.
- Khan MKM. 1997. Status and action plan of the Malayan tapir (*Tapirus indicus*). *In: Brooks D, Bodmer R, Matola S* (eds). *Tapirs – Status Survey and Conservation Action Plan*. IUCN/SSC Tapir Specialist Group. Cambridge (UK): IUCN. Pp 24.
- Mahathir M, Donny Y, David M, Carl T, Noor JNJ. 2019. Habitat utilization of a translocated Malayan tapir in Senaling Inas Forest Reserve, Negeri Sembilan. *Journal of Sustainability Science and Management*, 14(4): 65–70.

- Naturalistchu. 2024. iNaturalist observation: <https://www.inaturalist.org/observations/246433250> (Accessed on 11 February 2025).
- Nett EM, Jaglowski B, Ravosa LJ, Ravosa DD, Ravosa MJ. 2021. Mechanical properties of food and masticatory behavior in llamas, *Llama glama*. *Journal of Mammalogy*, 102(5): 1375–1389. DOI: [10.1093/jmammal/gyab083](https://doi.org/10.1093/jmammal/gyab083).
- Nurhidayat, Nisa' C, Agungpriyono S, Setijanto H, Novelina S, Supratikno, Cahyadi DD. 2016. Osteologi dan Miologi Veteriner. Bogor (ID): IPB Press.
- Radinsky LB. 1965. Evolution of the tapiroid skeleton from *Heptodon* to *Tapirus*. *Bulletin of the Museum of Comparative Zoology*, 134: 69–106.
- Ryder JA. 1879. Further notes on the mechanical genesis of tooth forms. *Proceedings of the Academy of Natural Sciences of Philadelphia* 31(1): 47–51.
- Traeholt C, Novarino W, bin Saaban S, Shwe NM, Lynam A, Zainuddin Z, Simpson B, bin Mohd S. 2016. *Tapirus indicus*. The IUCN Red List of Threatened Species 2016: e.T21472A45173636. <https://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T21472A45173636.en>. (accessed 11 February 2025).
- Van Valkenburgh B. 2007. Déjà vu: The evolution of feeding morphologies in the Carnivora. *Integrative and Comparative Biology*, 47(1):147–163. DOI: [10.1093/icb/pcm016](https://doi.org/10.1093/icb/pcm016).
- Wall WP. 1980. Cranial evidence for a proboscis in Cadurcodon and a review of snout structure in the family Amarynodontidae (Perissodactyla, Rhinocerotidae). *Journal of Paleontology*, 54(5): 968–977.
- Witmer LM, Sampson SD, Salounias N. 1999. The proboscis of tapirs (Mammalia: Perissodactyla): a case study in novel nasal anatomy. *Journal of Zoology*, 249(3): 249–267. DOI: [10.1111/j.1469-7998.1999.tb00763.x](https://doi.org/10.1111/j.1469-7998.1999.tb00763.x).