Palaeobiology of tragulids (Mammalia: Artiodactyla: Ruminantia)

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I hereby confirm that my thesis entitled “**Palaeobiology of tragulids (Mammalia: Artiodactyla: Ruminantia)”** is the result of my own original work. Furthermore, I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the approval of the Ludwig-Maximilians-Universität München.

Contents

Abstract of the thesis

Tragulidae is a family of the order Artiodactyla and suborder Ruminantia. Its representatives are closely related to deer, antelopes and their relatives. Fossil evidence from Asia suggests an origin of the Tragulidae in the Eocene at least 34 million years ago, with a climax during the Miocene and subsequent decline until present. They were well represented with over 30 species grouped in the genera *Archaeotragulus*, *Afrotragulus*, *Iberomeryx*, *Dorcabune*, *Dorcatherium*, *Siamotragulus*, and *Yunnanotherium*, which were completely replaced by the infraorder Pecora. Fossil tragulids had a broad geographical distribution in Asia, Africa, and Europe, including different morphotypes (small to large species) and diverse diet preferences (e.g. intermediate feeders, browsers and grazers). Nowadays tragulids are represented by only ten species classified in the genera *Tragulus, Moschiola* and *Hyemoschus.* They are exclusively distributed in the Indo-Malayan and Afro-tropical regions and feeding predominantly on fruits. Compared with their fossil relatives, their restricted recent distribution, low species richness and similar phenotype have stimulated the idea that recent tragulids represent “living fossils”. However, comparative studies between fossil and living relatives are very rare, and even the idea that living tragulids have become “frozen” in their evolution has been recently questioned. In this context, the aim of this work is an analysis of the body mass and the morphological diversity of the dentition and skulls of tragulids through time including fossil and living species. Among the studied taxa, the detailed description of a so far unstudied tragulid material from the Miocene of Pakistan has completed previous knowledge on ancient diversity. The methodology used here comprised comparative morphometrics of teeth and skulls as well as digital 3D reconstruction of a fossil skull. The results evidence a broad range of body sizes (from 1.0 kg to more than 100.0 kg) amongst fossil species, contrasting with the limited size range (1.0 kg to 15.0 kg) of the living species. From the late Eocene to present, the analysis of median body mass per 2.0 mya showed a peak between 16.0 mya to 4.0 mya,

including species with less than 17.9 kg (that includes the range of living species) and between 18.0 kg to 34.9 kg (only fossil species) as the most diverse class. If we consider the food preferences of fossil tragulids (≤ 17.9 kg and medium-sized species: 18.0 kg-34.9 kg), all categories from grazers, browsers and intermediate feeders have been reported, but not frugivores as in the living species. The study of the skulls of extant tragulids helped to understand their character disparity. With this, a hitherto undocumented difference in the neurocranium geometry among Asian tragulids was quantified: *Tragulus javanicus* and *T. kanchil* are relatively tall and their neurocrania are globose, while the heigth of the skull is less pronounced in *T. napu* and *Moschiola* spp and somewhat flattened, more comparable to *Hyemoschus aquaticus* of Africa. Here, it is hypothesized that a flatter skull might be related to dietary habits and mastication movements and/or to diving and under-water locomotion to escape from predator as previously reported. In addition, I have assembled a chart providing revised taxonomic assessments of the specimens of *Moschiola* and *Tragulus* included in my analysis. The descriptions of the fossil skull of *Dorcatherium crassum* improve the understanding on its external morphology as well as its affinities with living species. This fossil has a strong neurocranium with some hyper-developed elements, such as the sagittal and nuchal crests as well as highlight the canine tooth and its alveola. The general morphology is similar to living species, but its hyper-developed morphology is not comparable to living ones, and was probably adapted morpho-functionally to the acquisition and processing of hard food items. Compared with *Tragulus, Moschiola* and *Hyemoschus,* the skull of *Dt. crassum* is bigger, but it is similar in some bone proportions calculated here. In general *Dt. crassum* is more similar to *H. aquaticus* than to other living species, supporting their close affinity as reported in previous studies based on other characters (limbs, teeth, partial skulls). The flattened skull of both species support this close affinity. A formerly unreported great morphological diversity in the dentition of fossil tragulids was documented by an analysis of material from the Miocene

of Pakistan. Thus, of seven species previously known from the Siwaliks, based on the height of the tooth crown and related morphological features, only four are here recognized: *Dorcatherium nagrii*, *Dt. minus*, *Dt. majus* and *Dorcabune anthracotheroides*. In addition, we extend the diversity with the new species *Dorcatherium dehmi* and unexpectedly we extend the distribution into the Siwaliks for *Dt. naui* and *Dt. guntianum* previously recorded exclusively from Europe. Thus, the detailed analysis of morphology and the morphometric variables enabled distinguishing tragulid species that were previously masked by overlapping size. Accordingly, the variation described above coincides with data from the limited literature and it is in line with other groups previously misinterpreted as ‘living ancestors’ or ‘living fossils’, which were shown to be part of a greater morphological diversity than previously thought. However, considering that ancient diversity of tragulids was greater than the one of current representatives, and the living species belong to a group that is mostly extinct and such, by definition, provide deficient samples, it is difficult to assess with these data, which are plesiomorphic or derived characters. However, my results suggest a similar palaeobiology in fossil and living tragulids. Finally, the outcomes presented in this Ph.D. thesis clearly enhance the understanding of morphological diversity and palaeobiology of these mammals, but at the same time, reinforce the importance of studies on tragulids in order to improve the understanding on their origin and evolution.

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CHAPTER 1

Introduction

1.1 Family Tragulidae

Phylogentic studies based on molecular and morphological data support the monophyly of Ruminantia as well as their families (Hernández Fernández and Vrba 2005; Hassanin et al. 2012). Among these families, Tragulidae Milne Edward, 1864 (chrevrotains or mouse deer) are traditionally considered the sister group to all other extant ruminant families (a clade named Pecora), namely Giraffidae (giraffes and okapis), Antilocapridae (pronghorns), Moschidae (musk deer), Cervidae (deer) and Bovidae (cattle, sheep, goats and antelopes) (Janis and Scott 1987; Hernández Fernández and Vrba 2005: Figure 1.1). The basal position of tragulids within Ruminantia is unambiguously supported by molecular data that make them the first branching-clade of the extant ruminant radiation (Métais and Vislobokova 2007; Hernández Fernández and Vrba 2005; Figure 1.1).

The modern representatives of Tragulidae are allocated to three genera (*Hyemoschus*, *Tragulus* and *Moschiola*) with ten species formally accepted occurring in tropical Asia and Africa. The fossil species are grouped in seven genera (*Archaeotragulus*, *Afrotragulus*, *Iberomeryx*, *Dorcabune*, *Dorcatherium*, *Siamotragulus*, and *Yunnanotherium*) with at least 33 species described so far (Rössner 2007; Mennecart 2011; Sánchez et al. 2010: Table I). The family originated in Asia at least 34 mya (Métais et al. 2001; Benammi et al. 2001). During the Miocene, it reached its maximum diversity as reflected by the high number of species, wide geographical distribution (Asia, Africa and Europe), high variety of morphotypes (with tiny to large-bodied species), as well as in its diverse food habit strategies that range from browsing to grazing (Kaiser and Rössner 2007; Ungar et al. 2012; Clauss and Rössner 2014).

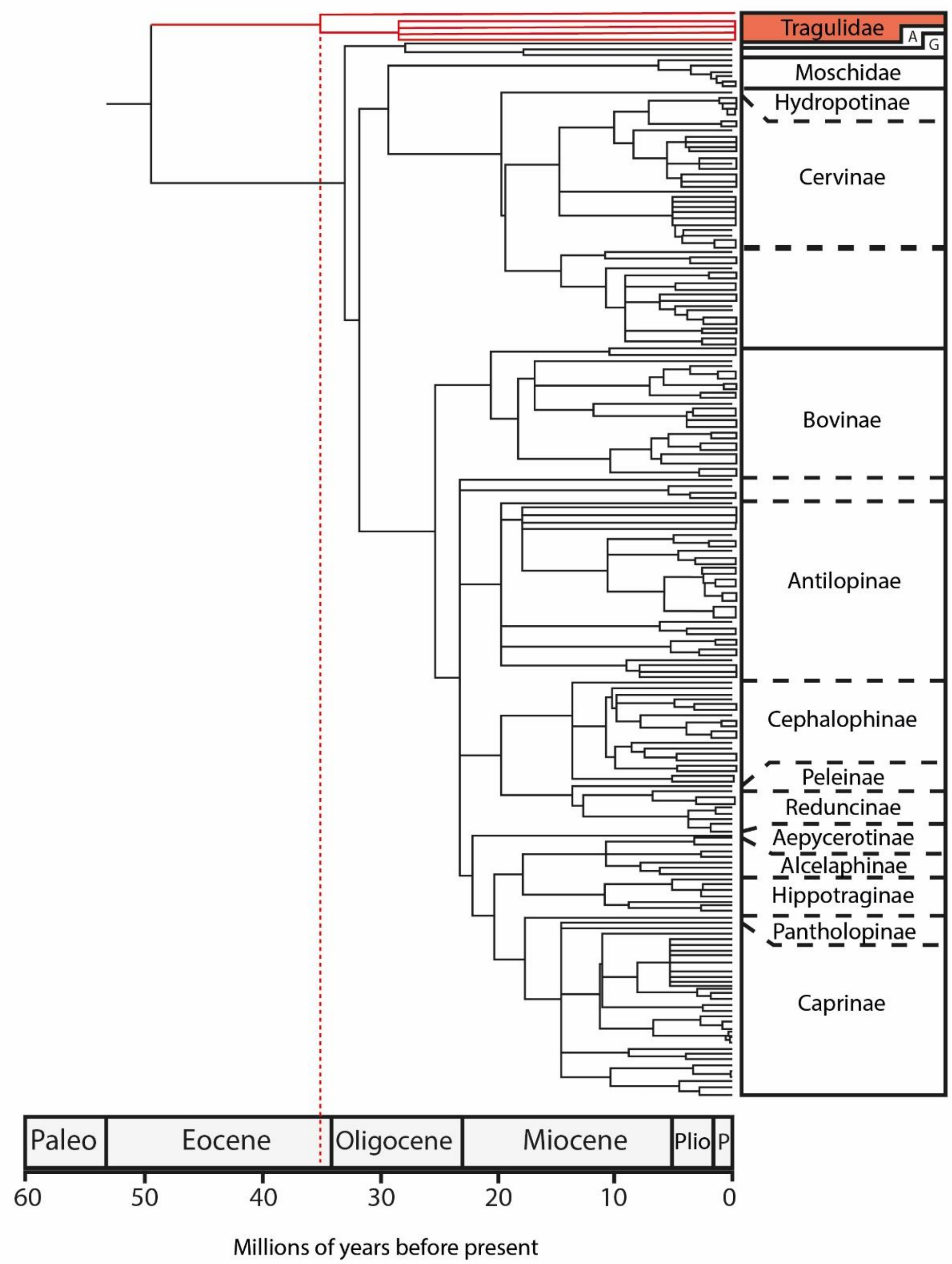

Figure 1.1. Phylogenetic tree of ruminant species including estimated times of divergence. The family Tragulidae (in red) is sister to all other clades. A: Antilocapridae; G: Giraffidae. (Modified from Hernández Fernández and Vrba 2005). The use of this figure has permission from John Wiley and Sons, License number: 4424150661908.

Tragulids share with other members of the Ruminantia the fusion of the cuboid and navicular bones in the tarsus, which is a unique specialization of the suborder (Janis 1984). On the other hand, the autapomorphic features that separate the tragulids from all other ruminants are (1) the malleolar bone, which is fused to the distal end of the tibia (except in *Dorcatherium naui* and *Hyemoschus aquaticus*: Aiglstorfer et al. 2014); (2) an ectocuneiform fused with the cubonavicular in the tarsus; (3) a temporal bone without postglenoid process; (4) a very small external exposure of the mastoid in the temporal bone; (5) and a closed postorbital bar (for details see: Gentry 1978; Janis 1984; Milne-Edward 1864; Rössner 2007). In addition, tragulids have bunoselenodont and selenodont dentition (Rössner 2007). Bunoselenodont tragulids have rounded cusps with less developed crests, whereas selenodont forms have, in addition to elongated crests, non-rounded cusps with flat internal walls. Thus, selenodonty in tragulids (as in all ruminants) is determined by the longitudinal extension and vertical development of the crests, and also by the flattening of the main cusps (Sánchez et al. 2010). According the Sánchez et al. (2010) the crests of the bunoselenodont taxa (e.g. some *Dorcatherium* sp. and *Dorcabune*) are variable in their vertical and longitudinal extension within certain limits. As a result, the lower molars of these forms have very pointed main cusps. On the other hand, the lower molars of selenodont tragulids (e.g. *Afrotragulus*, *Siamotragulus*, *Yunnanotherium*, *Moschiola* and *Tragulus*) are characterized by the presence of flat main cusps with crests that are not only elongated, but also very vertically developed (Sánchez et al. 2010). Thus, the existence of large to tiny-sized selenodont tragulids that overlap with most of the size range of *Dorcatherium* suggests that the enhanced selenodonty in tragulids evolved independently of body size and is not an allometric by-product (Sánchez et al. 2010).

1.2 Fossil representatives

Seven genera with at least 33 species have been described so far from the fossil record (Table I). The remains of *Archaeotragulus krabiensis* of the late Eocene from Krabi Basin, South Thailand, represent the oldest occurrence of a tragulid (Métais et al. 2001; Benammi et al. 2001), whereas Oligocene records are dubious or unclear. In fact, Mennecart et al. (2011, 2018b) considered *Iberomeryx* from the Oligocene (27.0 Ma to 32.0 Ma) of western Europe to represent another tragulid genus, a proposal that was followed scarcely so far, but not criticized either (e.g. Barry 2014; Sánchez et al. 2014; Kostopoulos and Sen 2016).

Table I. Tragulid species (fossil and living) and their spatiotemporal distribution so far described (modified from Pickford 2001 and Rössner 2007 and complemented with data from Mennecart et al. 2011; Sánchez et al. 2010; 2014; Kostopoulos and Sen 2016).

Genus	**Species**	**Spatiotemporal distribution**
Archaeotragulus Metais et al., 2001	*A. krabiensis* Metais et al., 2001	37.0-34.0 Ma (Eocene), Asia
Iberomeryx Gabunia, 1964	*I. minor* (Filhol, 1882)	33.9-28.4 Ma (Oligocene), Europe
	I. parvus Gabunia, 1964	28.4-23.0 Ma (Oligocene), Georgia and Turkey
Dorcatherium Kaup, 1833	*Dt. pigotti* Whitworth, 1958	23.0-11.6 Ma (Miocene), East Africa
	Dt. chappuisi Arambourg, 1933	18.5-12.0 Ma (Miocene), Africa
	Dt. minus Lydekker, 1876	18.3-5.1 Ma (Miocene), Asia
	Dt. crassum (Lartet, 1851)	17.8-13.0 Ma (Miocene), Europe
	Dt. iririensis Pickford, 2002	17.8 Ma (Miocene), East Africa
	Dt. vindebonense von Meyer, 1846	17.2-7.2 Ma (Miocene), Europe
	Dt. guntianum von Meyer, 1846	16.5-13.3 Ma (Miocene), Europe
	Dt. peneckei (Hoffmann, 1893)	15.1-14.8 Ma (Miocene), Europe
	Dt. orientale Qui Zhanxiang and Gu Yumin, 1991	15.9-11.6 (Miocene), China
	Dt. minimus West, 1980	14.2-11.2 Ma (Miocene), South Asia
	Dt. majus Lydekker, 1876	14.0-5.1 Ma (Miocene), South Asia
	Dt. nagrii Prasad, 1970	14.2-3.5 Ma (Miocene), South Asia
	Dt. naui Kaup and Scholl, 1834	12.3-7.6 Ma (Miocene), Europe
	Dt. jourdani (Déperet, 1887)	11.2-7.6 Ma (Miocene), Europe
	Dt. puyhauberti Arambourg and Piveteau, 1929	11.2-5.3 Ma (Miocene), Europe
	Dt. maliki Kostopoulos and Sen, 2016	9.6-9.4 Ma (Miocene), Eastern Europe
	Dt. bulgaricum Bakalov and Nikolov, 1962	5.3-2.5 Ma (?Pliocene), Bulgaria
Siamotragulus Thomas et al., 1990	*S. songhorensis* (Whitworth, 1958)	22.0-17.0 Ma (Miocene), Africa
	S. bugtiensis Ginsburg et al., 2001	19.5-18.0 Ma (Miocene), South Asia
	S. sanyathanai Thomas et al., 1990	14.8-11.2 Ma (Miocene), Southeast Asia
	S. indicus (Forster Cooper, 1915)	(Miocene), Pakistan
Dorcabune Pilgrim, 1910	*Db. welcommi* Ginsburg et al., 2001	19.5-18.0 Ma (Miocene), South Asia

	Db. nagrii Pilgrim, 1915	15.1-14.8 Ma (Miocene), South Asia
	Db. anthracotheroides Pilgrim, 1910	14.1-10.1 Ma (Miocene), South Asia
	Db. sindiense Pilgrim, 1915	11.6-5.3 Ma (Miocene), Pakistan
	Db. progressus (Yan, 1978)	(Miocene), China
	Db. liuchengense Han, 1974	(Pleistocene), China
Afrotragulus Sánchez et al., 2010	*A. moruorotensis* (Pickford, 2001)	19.0-16.8 Ma (Miocene), East Africa
	A. parvus (Whitworth, 1958)	18.5-17.0 Ma (Miocene), East Africa
Yunannotherium Han, 1986	*Y. simplex* Han, 1986	8.0-7.4 Ma (Miocene), China
Tragulus Brisson, 1762	*T. javanicus* (Osbeck, 1765)	Extant, Southeast Asia
	T. kanchil (Raffles, 1821)	Extant, Southeast Asia
	T. napu (Cuvier, 1822)	Extant, Southeast Asia
	T. nigricans Thomas, 1892	Extant, Southeast Asia
	T. versicolor Thomas, 1910	Extant, Southeast Asia
	T. williamsoni Kloss, 1916	Extant, Southeast Asia
Moschiola Gray, 1853	*M. meminna* (Erxleben, 1777)	Extant, Sri Lanka, Dry Zone
	M. kathygre Groves and Meijaard, 2005	Extant, Sri Lanka, Wet Zone
	M. indica (Gray, 1852)	Extant, India
Hyemoschus Gray, 1845	*H. aquaticus* (Ogilby, 1841)	Extant, West Africa

Likewise, according to Barry et al. (2013), *Dorcatherium* ([sic] or perhaps *Siamotragulus*) was present in the latest Oligocene (at least 28.1 Ma - 23.0 Ma) and earliest Miocene of the Chitarwata (at least 22.0 Ma and perhaps as old as 26.0 Ma) and Vihowa Formations (at least 19.1 Ma - 11.2 Ma). However, the age of the lower Chitarwata Formation is controversial (Lindsay et al. 2005; Antoine et al. 2013; Métais et al. 2017).

Tragulids became quite abundant during the Miocene, represented by the genera *Afrotragulus*, *Dorcatherium*, *Dorcabune*, *Siamotragulus* and *Yunannotherium* (Rössner 2007; Sánchez et al. 2010, 2014). Species richness peaked during the Early/Middle Miocene of Africa as well as Eurasia (Eronen and Rössner 2007; Clauss and Rössner 2014), with more than 30 species (Whitworth 1958; Pickford 2001; Rössner 2007; Geraads 2010) and up to four or more sympatric species (Rössner and Heissig 2013; Barry 2014). *Dorcatherium* is the most diverse fossil genus of Tragulidae with material recorded from Europe, Asia and Africa (Pickford 2001; Table I). However, species delimitation within the genus has been based primarily on morphometric variables being an approximation criticized for its ambiguity (e.g. Sánchez et al. 2010, 2014). Several authors indicated that a new revision of *Dorcatherium*, considering not only metric variables, is necessary and urgent (e.g. Rössner 2007; Alba et al 2014; Barry 2014). In this context, Sánchez et al. (2010) erected the genus *Afrotragulus*, in which they included the tiny *A. parvus* originally described as member of the genus *Dorcatherium*. Later, Sánchez et al. (2014) evaluated material (teeth and post-cranial bones) of tragulids from Africa (Uganda) and transferred *Dorcatherium songhorensis* Whitworth, 1958 to the genus *Siamotragulus* Thomas et al., 1990. Thus, the study of the morphological variation along with metric variables has demonstrated its importance to understand the evolution of the Tragulidae, since for example, this taxonomic modification reordered the species diversity in Africa, while *Siamotragulus* is no longer a genus endemic to Asia (Rössner 2007; Sánchez et al. 2010).

The species of the genus *Dorcabune* are the largest tragulids with bunodont molars, being only present in Asia. They did not receive much attention since their first description (Pilgrim 1910, 1915; Colbert 1935). The genus is morphologically close to or even more primitive than the genus *Anthracotherium* (Anthracotheriidae, Artiodactyla) and clearly more primitive than *Dorcatherium* (Pilgrim 1915; Gentry 1978). The genera *Archaeotragulus* and *Yunannotherium* are monotypic, and so far have been found only on the Asian continent (Pickford 2001; Rössner 2007; Sánchez et al. 2010, 2014).

The simultaneous existence of tragulids in Africa (ca. 22.5 mya, Whitworth 1958; Pickford 2001) and Asia (Chitarwata Formation, Pakistan, at least 22.0 mya, Antoine et al. 2013) represents an enigma, because the land corridor between Asia and Africa was estimated to be younger (19.0 Ma to 16.0 Ma, Made 1999). In this context, Rössner (2017) suggested complex Miocene tragulid migrations, from Asia to Africa, and from Asia and Africa to Europe. However, it is still unclear how *Dorcatherium* reached Africa from Asia or vice versa before the existence of the "*Gomphotherium*-land bridge".

In Europe, *Dorcatherium* is recorded from the Early Miocene (minimum appearance datum ca. 17.8 mya), probably through successive heterochronous dispersal events from the East/Southeast to the West/Southwest of Europe, rather than a synchronous appearance (Rössner 2017). Mennecart et al. (2018b) proposed that Bachitheriidae migration linked western to southeastern Europe in the "*Bachitherium* dispersal event", in which *Iberomeryx* from the Earliest Oligocene of Georgia would have participated because it appears simultaneously in Europe. The recently described *Dorcatherium maliki* from Küçükçekmece West (Late Miocene) in the European Turkey (Kostopoulos and Sen 2016), and the discovery of the previously exclusively European species *Dt. naui* (Middle Miocene to Late Miocene) and *Dt. guntianum* (Early to Middle Miocene) in the Siwaliks of Pakistan (chapter 5 in this thesis) support the migration event proposed by Mennecart (2018). Accordingly, Miocene *Dorcatherium* is recorded from Europe, Asia and Africa, whereas *Siamotragulus* is known from Asia and Africa and *Dorcabune* currently only from Asia. Thus, according to Sánchez et al. (2010), in strict biogeographic terms, *Afrotragulus* and *Dorcatherium* could be considered the "African" branch of the Tragulidae, since both are recorded first in the African Early Miocene, whereas *Dorcabune* and *Siamotragulus* could be considered the "Asian" branch, recorded first in Asia almost synchronously. In addition, the presence of *Afrotragulus* in the Early Miocene of Africa and the increasingly high species diversity of the Tragulidae during the course of the early Miocene, strongly suggests that these ruminants underwent a strong radiation event or events prior to the early Miocene (Sánchez et al. 2010).

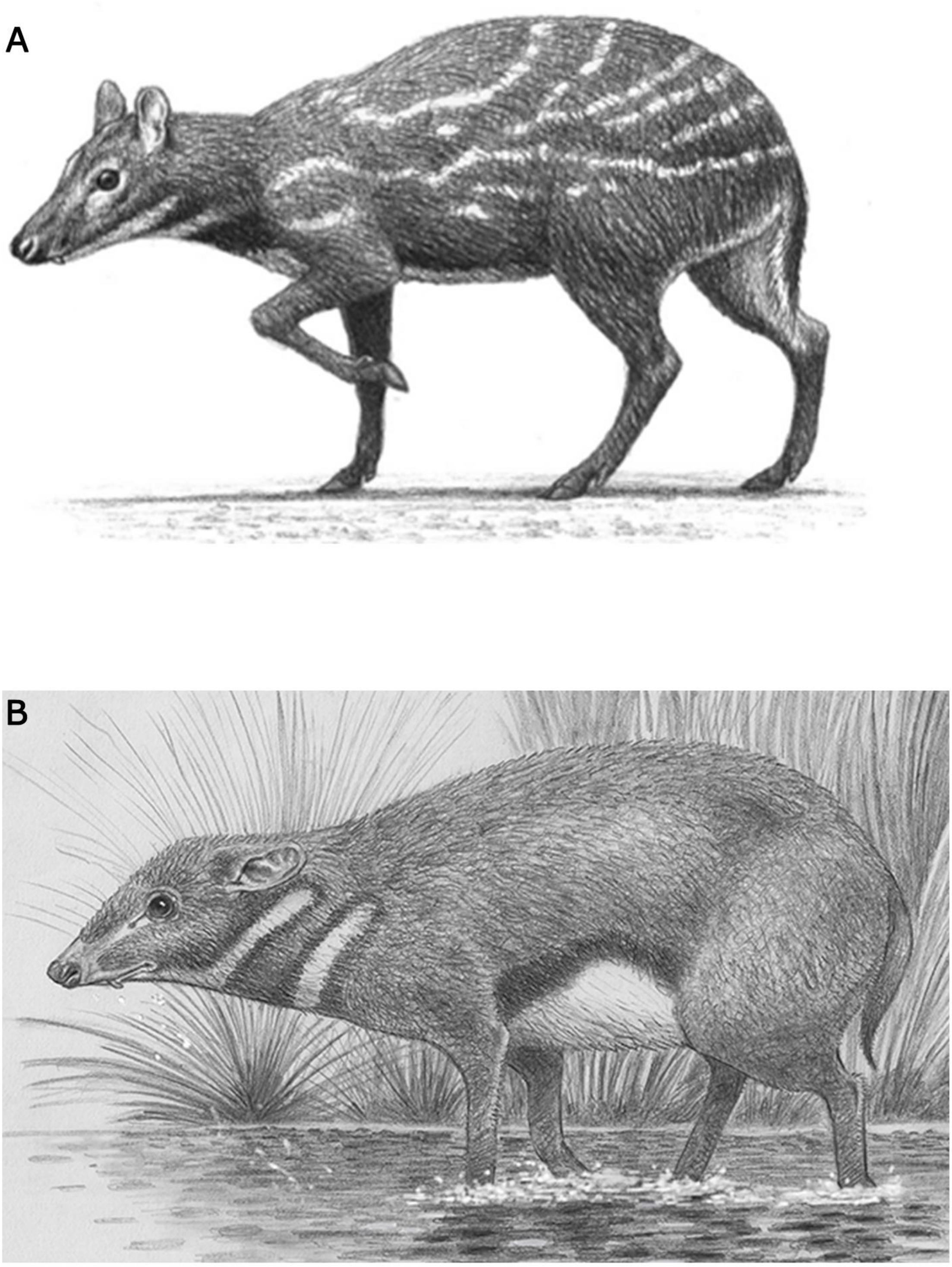

Figure 1.2. *Dorcatherium* from the Miocene. **A**) life reconstruction of an adult male from Europe; **B**) life reconstruction for *Dorcatherium* sp. from Africa. Both images have permission from the illustrators: **A)** Maurio Antón; **B**) Israel M. Sánchez.

1.3 Living species

Ten living species of tragulids, distributed in tropical Africa and Asia, are currently recognized (Groves and Grubb 2011; Meijaard 2011; Table I). According to Meijaard and Groves (2004a), the genus *Tragulus* is distributed widely across the mainland and many islands of Southeast Asia with the following six species: *Tragulus javanicus* (only on Java), *T. williamsoni* (northern Thailand, but also southern China; see Meijaard et al. 2017), *T. kanchil* and *T. napu* (both in Southeast Asia, but not on Java), *T. nigricans* (Philippines) and *T. versicolor* (southern Vietnam). The genus *Moschiola* with three species is present in India with *M. indica* (southern India), while in Sri Lanka, and probably Nepal and China are present *M. meminna* (dry zone of Sri Lanka), *M. kathygre* (wet zone of Sri Lanka), as well as a fourth species that has not yet been formally described (Chasen 1940; Geist 1998; Groves and Meijaard 2005; Baral et al. 2009, Meijaard et al. 2017, Guzmán and Rössner 2018). A third genus is the monotypic *Hyemoschus*, with *H. aquaticus* only found in Africa, from Sierra Leone to Uganda (Groves and Meijaard 2005; Dubost 1964, 2017: Figure 1.3).

The monophyly of these living tragulids is strongly supported in a phylogenetic analysis combining morphological, ethological and molecular information (Hernández Fernández and Vrba 2005: Figure 1.1). The five living pecoran families (Antilocapridae, Bovidae, Cervidae, Giraffidae and Moschidae) are classically grouped as higher ruminants and are distinguished from tragulids by numerous morphological characters (Janis and Scott 1987), leaving Tragulidae the sister group to all other ruminants (Figure 1.1).

The living Tragulidae are known to be reclusive, shy animals hiding in dense understorey in the tropics (http://www.iucnredlist.org) of Asia and Africa, where fruits are available at least nine months of the year (Heydon and Bolloh 1997). They are selective feeders, with a frugivorous diet (Dubost 1984; Meijaard 2011).

Figure 1.3. Living species: **A**) *Tragulus* sp. of individual in Hellabrunn Zoo, Munich, Germany (source: cover of Mammalian Biology, 90, 2018); **B**) *Moschiola* sp. swimming to escape a brown mongoose; **C**) *Tragulus napu* caught in a river after having spent 60 min hiding underwater (b and c: Meijaard et al. 2010); **D**) *Hyemoschus aquaticus* (Source: Dubost 2017). **E**) stuffed tragulids in the Natural History Museum of Stuttgart, Germany: left *Hyemoschus aquaticus*, middle: *Moschiola meminna*, right: *Tragulus* sp. Images: a, authorized by Frank E. Zachos (Managing Editor Mammalian Biology); b and c, permission from Elsevier, License number: 4422460743785. d, authorized by Gérard Dubost (picture owner), e) taken by Jonathan Guzmán Sandoval

Tragulids flee into water when encountered by predators (Figure 1.3B) and their species are among the smallest living ruminants (from 1.7 to 16 kg) with *T. javanicus* (1.7 to 2.1 kg, 50 to 53 cm head-body-length) counting as the smallest living hoofed mammal (Meijaard 2011). The small body size, anatomy and physiology of the digestive tract, frugivorous diet, males with sabre-like upper canines, lack of bony horns, short legs and neck, etc. were interpreted previously as conserved ancestral ruminant traits. Consequently, the extant Tragulidae were considered "living fossils" (e.g. Janis 1984; Thenius 2000).

The above contrasts the suggestion, that the extant tragulids represent a novel intra-tragulid evolutionary response to the high level of competition among modern ruminants (Clauss and Rössner 2014). The previous assumption of "little change through time" is now challenged by new lines of evidence.

1.4 Objectives of the dissertation

Due to possession of many unique features opposed to other living ruminants (e.g. small body size, frugivory, habitat in rain forest undergrowth), tragulids were claimed to be "living fossils" (Janis 1984, Thenius 2000). However, comparisons between their fossil and extant diversity are rather limited (Milne Edwards 1864; Sánchez et al. 2014) and new lines of evidence, lead to the question on a potential diversity disparity of their phenotypes over time. Accordingly, the main objectives of this thesis are:

To analyze the morphology and diversity of dentition and skull features of extinct tragulids through space and time to identify and quantify the degree of similarity with extant tragulids. The more specific goals of this thesis include the following:

1. Documentation of body mass diversity in the family Tragulidae through time,
2. Comparative analysis of skull morphometry and morphology of living species,
3. First description of the best preserved skull of *Dorcatherium crassum* and first digital segmentation of a fossil tragulid skull including comparison with living species,
4. Description of the so far largest sample of tragulid fossils from the Siwalik Group in Pakistan.

The study of these topics compose the following chapters of this thesis. Each of these chapters was written to stand on its own as an independent manuscript. However, as all the individual chapters converge to same main objective, some overlap in their content is unavoidable.

CHAPTER 2

Dentition-based assessment of disparity in past and present phenotype variability in Tragulidae

2.1 Introduction

Contemporary survivors of ancient evolutionary lineages with limited diversity and, hence, restricted geographical distribution, are often considered to be relict species with conserved ancestral phenotypes providing important information on the past of clades and biota. However, the proven misconception of evolutionary stasis excludes that extant impoverished clades have conserved ancient phenotypes (e.g. see Grandcolas et al. 2014). There are numerous examples of previously misinterpreted 'living ancestors' or 'living fossils', which were shown to be part of a greater morphological diversity than previously thought, as for example the Chinese gymnosperm *Ginkgo* spp. (e.g. Royer et al. 2003), the coelacant fish *Latimeria* from the Indian Ocean (e.g. Casane and Laurenti 2013; Friedman and Coates 2006), the archosaurian Crocodilia (e.g. Buckley et al. 2000), the bony fish Teleostei (e.g. Clarke and Friedman 2018), other groups with more genetic diversity than previously thought as the horseshoe crabs Limulidae (e.g. Obst et al. 2012), the New Zealand reptile *Sphenodon* spp., (e.g. Jones et al. 2009; Subramanian et al. 2009; Hay et al. 2008) or even extinct species with a social behaviour unknown in extant relatives as the fossil opossum *Pucadelphys andinus* from Bolivia (e.g. Ladeveze et al. 2014). In this paper, we take up the 'living fossil' case of tragulids (Janis 1980; Thenius 2000), which has recently been questioned (Clauss and Rössner 2014). Tragulidae are a clade of artiodactyl mammals with a long, well-recorded, but severly understudied evolutionary history (Rössner 2007). Living members of the group, African chevrotains and Asian mouse-deer were described as 'living fossils' by Janis (1984) and Thenius (2000). Their restricted geographical distribution, low species richness and phenotypic similarity within the family members, despite disjunct distribution ranges, spurred the idea of a conserved ancestral phenotype, i.e. a mosaic character suite of pig-like plesiomorphic and ruminant-like apomorphic artiodactyl features (Gentry and Hooker 1988; Janis and Scott 1987).

According to Groves and Grubb (2011), present-day tragulids comprise three genera and ten species: *Tragulus* with six species (Meijaard and Groves 2004a), widely distributed across the mainland and many islands of Southeast Asia; *Moschiola* with three species in India, Sri Lanka, and probably Nepal and China (Chasen 1940; Geist 1998; Groves and Meijaard 2005; Baral et al. 2009; Meijaard et al. 2017; Guzmán and Rössner 2018), and the monotypic *Hyemoschus* with *H. aquaticus* in Africa, from Sierra Leone to Uganda (Groves and Meijaard 2005; Dubost 1964). All these species are among the smallest living ruminants (from 1.7 to 16.0 kg) with *T. javanicus* (1.7 to 2.1 kg, 50.0 to 53.0 cm head-body-length) even considered the smallest living hoofed mammal (Meijaard 2011). All are known to be reclusive, shy animals hiding in dense understorey and fleeing into water when encountered by predators. They are selective feeders with a major component of fruit and additional browsing (Dubost 1984; Meijaard 2011). They are restricted to the tropical climate zone (http://www.iucnredlist.org) with availability of fruit for at least nine months of the year (Heydon and Bolloh 1997).

The small body size and related morpho-physiological variables in living tragulids (e.g. anatomy and physiology of digestive tract, frugivorous diet) were interpreted previously to represent conserved ancestral ruminant traits (e.g. Janis 1984; Thenius 2000), but were suggested recently to be a novel intra-tragulid evolutionary response to the highly competitive ecology among modern ruminants (Clauss and Rössner 2014). This leads to the question on potential diversity disparity in fossil and extant tragulid phenotypes, and triggered the present study.

In this context, generally, tooth size is correlated with body size and, hence, serves as body size indicator (e.g. Damuth and Mc Fadden 1990). On the other hand, body size is highly correlated with morpho-physiological traits/constraits in herbivorous mammals (Clauss et al. 2003), as well as related to dietary specifics (Tejcada-Lara et al. 2018). Thus, estimates of body size for fossil species allow for the assessment of fossil phenotype diversity. In this respect, the fact that the fossil record of mammals has a generally high portion of teeth is advantageous. Moreover, fossil tragulid species were basically established on comparative tooth metrics. Thus, the species described so far (see for reviews Pickford 2001; Rössner 2007; Sánchez et al. 2010, 2014; Kostopoulos and Sen 2016) provide a reasonable framework for the quantification of past tragulid phenotype diversity.

They document that the clade diverged in the Eocene from the ruminant stem lineage, prior to the diversification of Pecora, one of the largest large mammal group of the modern world (Groves and Grubb 2011), which encompasses antelopes, buffaloes, deer and kin, giraffes, pronghorns and several extinct clades (Janis and Scott 1987; Gentry and Hooker 1988; Métais et al. 2001; Hernández-Fernández and Vrba 2005; Mennecart et al. 2010).

The hypothesis we tested here is that extinct and extant tragulids do not differ in phenotype ranges, according to the traditional assumption of conserved ancestral adaptation. Thus, based on neontological/palaeontological comparisons (e.g. Sánchez et al. 2010, 2014) and considering that relict species belong to groups or biotas that are mostly extinct (Grandcolas et al. 2014), we predict that the phenotype diversity of extant tragulids species represents only a moderate subset of the extinct phenotypic variation.

2.2 Material and Methods

Geochronological Framework

In order to provide a geochronological framework for our analysis through time, we compiled a data set from documented occurrences for all tragulid species studied here (Table II). The temporal occurrences of species were obtained from "The Paleobiology Database" (www.paleobiodb.org), and the "NOW" database (www.http://www.helsinki.fi) and were adjusted according to the literature (Pickford 2001; Geraads 2010; Ungar et al. 2012; Rössner and Heissig 2013; Clauss and Rössner 2014; Aiglstorfer et al. 2014; Kostopoulos and Sen 2016; Rössner 2017). Listings of *Dorcatherium naui* older than European Land Mammal Unit MN9, were considered here as *Dt. crassum*, with the exception of Przeworno 1 and 2 in Poland (Czyzewska and Stefaniak 1994; see Alba et al. 2011) due to a previous mistaken junior synonymy of *Dt. crassum* with *Dt. naui* (Sánchez et al. 2011; Rössner and Heissig 2013).

Late Middle Miocene *Dt. naui* records from Abocador de Can Mata in Spain (Alba et al. 2011) and Gratkorn in Austria (Gross et al. 2011) are neither entered in the NOW or the Paleobiology Database, but were taken into account in the present paper. *Dorcatherium rogeri* was considered a junior synonym of *Dt. vindebonense* (Thenius 1952), *Dt. libiensis* a junior synonym of *Dt. pigotti* (Geraads 2010) and *Dt. songhorensis* is considered a junior synonym of *Siamotragulus songhorensis* (Sánchez et al. 2014). For correlation of different and regional age concepts we used van der Made (1999), Qiu et al. (1999), Hilgen et al. (2012), Reichenbacher et al. (2013), and Sant et al. (2017).

For each species, we considered minimum first and maximum last occurrence data, resulting from the different sources, unless literature offers more accurate information (Table II).

Table II. Studied species with their spatiotemporal distribution and estimation of body mass. Body mass for *Hyemoschus*, *Moschiola* and *Tragulus* species (except *Tragulus nigricans* and *Moschiola meminna*) were extracted from Meijaard (2011). Table modified from Pickford 2001 and Rössner 2007 and complemented with data from Mennecart et al. 2011; Sánchez et al. 2010; 2014; Kostopoulos and Sen 2016; Meijaard and Groves 2004; Groves and Meijaard 2005; Groves and Grubb 2011.

Genus	Species	Spatiotemporal distribution	**Bodymass (kg)** Mean (min-max)
Archaeotragulus Metais et al., 2001	*A. krabiensis* Metais et al., 2001	37.0-34.0 Ma (Eocene), Asia	4.7 kg (4.5-4.9)
Iberomeryx Gabunia, 1964	*I. minor* (Filhol, 1882)	33.9-28.4 Ma (Oligocene), Europe	1.6 kg (1.2-2.5)
	I. parvus Gabunia, 1964	28.4-23.0 Ma (Oligocene), Georgia and Turkey	3.3 kg (2.4-4.4)
Dorcatherium Kaup, 1833	*Dt. pigotti* Whitworth, 1958	23.0-11.6 Ma (Miocene), East Africa	11.6 kg (6.8-18.0)
	Dt. chappuisi Arambourg, 1933	18.5-12.0 Ma (Miocene), Africa	29.9 kg (27.6-31.5)
	Dt. minus Lydekker, 1876	18.3-5.1 Ma (Miocene), Asia	22.8 kg (14.0-29.9)
	Dt. crassum (Lartet, 1851)	17.8-13.0 Ma (Miocene), Europe	24.9 kg (18.6-34.0)
	Dt. iririensis Pickford, 2002	17.8 Ma (Miocene), East Africa	22.3 kg (19.2-25.5)
	Dt. vindebonense von Meyer, 1846	17.2-7.2 Ma (Miocene), Europe	49.0 kg (45.3-51.9)
	Dt. guntianum von Meyer, 1846	16.5-13.3 Ma (Miocene), Europe	12.4 kg (9.6-14.5)
	Dt. peneckei (Hoffmann, 1893)	15.1-14.8 Ma (Miocene), Europe	71.2 kg [n=1]
	Dt. minimus West, 1980	14.2-11.2 Ma (Miocene), South Asia	1.0 kg [n=1]
	Dt. majus Lydekker, 1876	14.0-5.1 Ma (Miocene), South Asia	77.0 kg (59.1-99.6)
	Dt. nagrii Prasad, 1970	14.2-3.5 Ma (Miocene), South Asia	4.5 kg (3.3-7.0)
	Dt. naui Kaup and Scholl, 1834	12.3-7.6 Ma (Miocene), Europe	30.4 kg (19.7-47.5)
	Dt. jourdani (Déperet, 1887)	11.2-7.6 Ma (Miocene), Europe	20.9 kg (20.3-21.5)
	Dt. puyhauberti Arambourg and Piveteau, 1929	11.2-5.3 Ma (Miocene), Europe	19.3 kg [n=1]
	Dt. maliki Kostopoulos and Sen, 2016	9.6-9.4 Ma (Miocene), Eastern Europe	33.8 kg (29.1-38.4)
Siamotragulus Thomas et al., 1990	*S. songhorensis* (Whitworth, 1958)	22.0-17.0 Ma (Miocene), Africa	5.6 kg (3.6-7.0)
	S. bugtiensis Ginsburg et al., 2001	19.5-18.0 Ma (Miocene), South Asia	6.9 kg (6.8-7.0)
	S. sanyathanai Thomas et al., 1990	14.8-11.2 Ma (Miocene), Southeast Asia	6.2 kg [n=1]
Dorcabune Pilgrim, 1910	*Db. welcommi* Ginsburg et al., 2001	19.5-18.0 Ma (Miocene), South Asia	20.3 kg [n=1]
	Db. nagrii Pilgrim, 1915	15.1-14.8 Ma (Miocene), South Asia	52.5 kg (51.9-53.1)
	Db. anthracotheroides Pilgrim, 1910	14.1-10.1 Ma (Miocene), South Asia	111.5 kg (72.6-139.4)
Afrotragulus Sánchez et al., 2010	*A. moruorotensis* (Pickford, 2001)	19.0-16.8 Ma (Miocene), East Africa	1.0 kg [n=1]
	A. parvus (Whitworth, 1958)	18.5-17.0 Ma (Miocene), East Africa	2.7 kg (2.0-4.2)
Yunannotherium Han, 1986	*Y. simplex* Han, 1986	8.0-7.4 Ma (Miocene), China	5.1 kg (4.4-5.7)
Tragulus Brisson, 1762	*T. javanicus* (Osbeck, 1765)	Extant, Southeast Asia	1.9 kg (1.7-2.1)
	T. kanchil (Raffles, 1821)	Extant, Southeast Asia	2.0 kg (1.5-2.5)
	T. napu (Cuvier, 1822)	Extant, Southeast Asia	4.0 kg (3.5-4.5)
	T. nigricans Thomas, 1892	Extant, Southeast Asia	2.9 kg
Moschiola Gray, 1853	*M. meminna* (Erxleben, 1777)	Extant, Sri Lanka, Dry Zone	2.5 kg
	M. indica (Gray, 1852)	Extant, India	3.0 kg
Hyemoschus Gray, 1845	*H. aquaticus* (Ogilby, 1841)	Extant, West Africa	12.0 kg (7.0-16.0)

Data Set and Measurements

We compiled measurements of 1572 permanent postcanine teeth of 27 extinct species of the genera *Archaeotragulus*, *Afrotragulus*, *Dorcabune*, *Dorcatherium*, *Iberomeryx*, *Siamotragulus* and *Yunannotheium*, and seven extant species belonging to the genera *Hyemoschus*, *Moschiola* and *Tragulus*. The data set mainly encompasses measurements performed by the authors and completed with measurements from the literature (Appendix 2, Table 2.1). For each tooth position (premolars [2, 3, 4] and molars [1, 2, 3], we measured length (l) and width (w) with an analogue caliper, and we considered the "anterior width" as width according to Rössner (1995) (Figure 2.1, Tables III and IV).

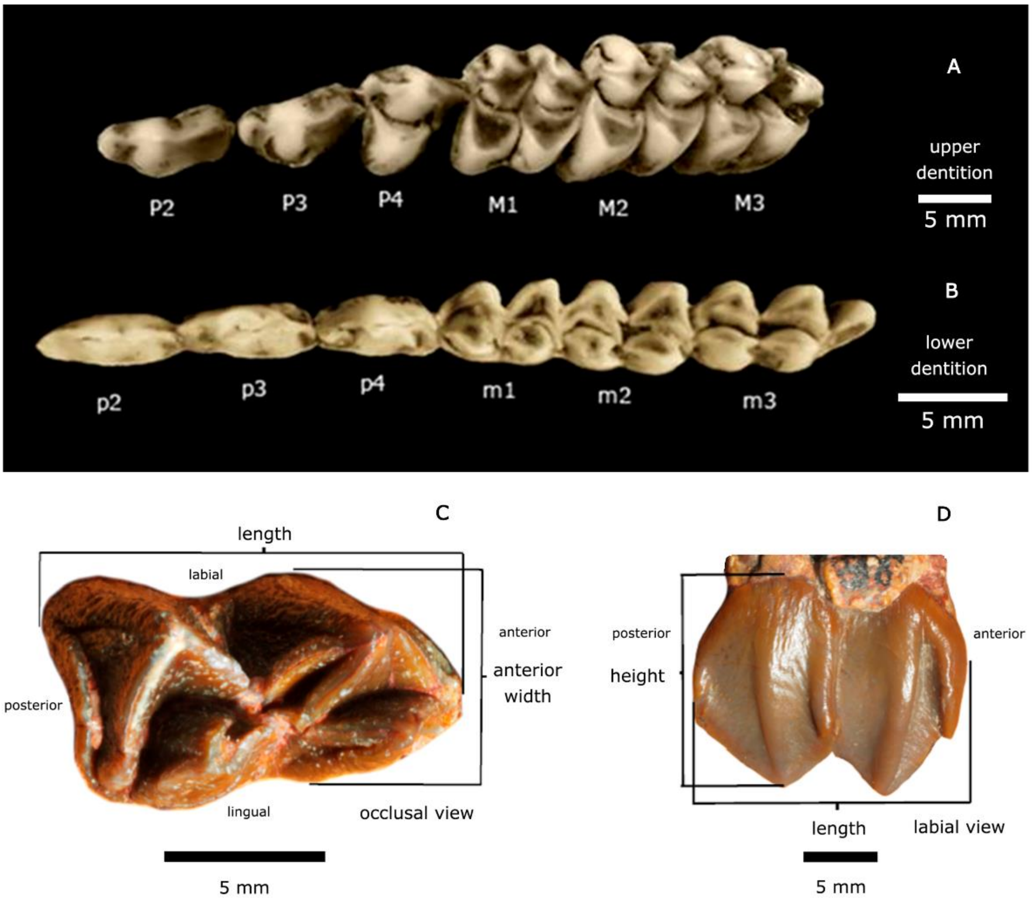

Figure 2.1. A: exemplified left upper and **B:** right lower tragulid dentition of *Hyemoschus aquaticus.* Specimen H-30 15.03.63 property of Gérard Dubost (Paris, France) currently stored at Bayerische Staassammlung für Paläontologie und Geologie, München, Germany. **C**: occlusal view of lower left molar where length and anterior width measurements are indicated, **D**: labial view of upper right molar where length and height measurements are indicated.

Body Mass

Estimation.-

Based on the relationship between tooth size, body size, and body mass in mammals (often demonstrated in previous studies, e.g. Damuth and Mc Fadden 1990), we estimated body mass of extinct and some extant tragulids, via allometric equation (log body mass = $a + b$ log x; where a is the intercept, b is the slope, and x is the tooth length: either second lower molar length (SLML) or second upper molar length (SUML) or third upper molar length (TUML). In general, Janis (1990) demonstrated that molar length shows significant correlation with body mass for all ungulates ($r^2 = .93 - .94$). Hence, we selected the equation derived from SLML for "ruminants only" ($r^2 = .93$; intercept = 1.118 and slope = 3.337) provided by Janis (1990, in Damuth and Mc Fadden 1990: Table 16.8) and used in previous work on fossil tragulids (Rössner 2010; Alba et al. 2011; Aiglstorfer et al. 2014). For *Dorcatherium puyhauberti* and *Dt. minimus* the m2 length was not available. Hence, for *Dt. puyhauberti* SUML for "ruminants only" ($r^2 = .93$; intercept = 1.068 and slope = 3.360) was used, while for *Dt. minimus* TUML for "all selenodonts" ($r^2 = .90$; intercept = 0.94 and slope = 3.12) was used (Janis 1990). Body mass for extant species was taken from Meijaard (2011), except for *Tragulus nigricans* and *Moschiola indica* of which we calculated it. The median for body mass was plotted for each species within a geochronological framework, to obtain a first understanding about the phenotype diversity of fossil and living tragulids (Figure 2.2).

Description through time.

The fossil species studied here, cover a mean time span of 4.6 Ma (SD = 3.6 Ma; minimum time span of 0.2 Ma for *Dorcatherium maliki* and maximum time span of 13.2 Ma for *Dt. minus*: see Table I). Therefore, to describe the body mass from the present to the oldest tragulid record (38.0 Ma), we calculated the median body mass for all species each 2.0 Ma, being a resolution high enough to register changes in the phenotype through time (Table IV). The median was used instead the mean, because at values above 34.0 kg, body mass shows an irregular distribution (only five species between 49.0 kg [*Dt. vindebonense*] to 111.5 kg [*Dorcabune anthracotheroides*]; Table I), being the mean very sensitive to extreme values.

Similarities/differences in tragulids with same body mass

In order to compare directly and unambiguously the differences/similarities in tragulids, we established six body mass classes, using the body mass of the largest living species, *Hyemoschus aquaticus*, as unit (7.0 – 15.0 kg; e.g. Dubost 1978; Kingdon 1979; Dubost 1984; Meijaard 2011); plus 2.9 kg of range of uncertainty = 17.9 kg). Thus the following classes were established: 0.1 - 17.9 kg, 18.0 – 34.9 kg, 35.0 – 51.9 kg, 52.0 – 68.9 kg, 69.0 – 85.9 kg and ≥ 86.0 kg (Tables III and IV). In this context, for each these body mass classes we calculate the dental Occlusal Surface Area (OSA), the Occlusal Tooth Area (OTA) and length and width patterns along tooth rows (these analyses are described below) (Figure 2.3). Descriptive statistics of length and width per tooth position are reported for each body mass class (Tables III and IV), and are plotted for each specimen studied here (Figures 2.4A and 2.4B).

Estimation of the Occlusal Surface Area (OSA and OTA)

The occlusal surface area of the postcanine tooth row is related to the quantity, abrasiveness and mechanical resistance to comminution of the ingested food, with grazers having a larger occlusal surface area to grind coarse foods, while browsers have a smaller and narrower post-canine tooth row, with more-prominent dental crests adapted to puncturing the cell walls of browsed material (Pérez-Barbería and Gordon 2001 and references therein). In this context, for each tooth position per species (e.g. p2 of *Dt. minus*), we obtained its area (length and width were multiplied), also called Occlusal Tooth Area: OTA (Famoso et al. 2013). Then, mean OTA for each premolar and molar position (upper and lower) per species were totalled and we obtained the mean Occlusal Surface Area: OSA (Vizcaino et al. 2006). In order to compare OSA between body mass diversity, the correlation between log OSA taken as dependent variable and log body mass as independent variable were calculated with non-parametric "*rs*" Spearman or "*r*" Pearson parametric Correlation Coefficients (Table VI), after assessment of normality/homoscedasticity (Shapiro-Wilk and Levene's test) (Hawkins 2005; Dytham 2011). Eventually, OSA values were plotted against body mass class (Figure 2.3). Occlusal Surface Area and body mass variables were log-transformed to reduce the heteroscedasticity of the data as for example the dispersion associated with high values (Vizcaino et al. 2006) (Appendix 2, Table 2.2 and 2.3).

Dentition Proportions

In order to compare inter-specific patterns in length and width along tooth rows, we provide univariate plots for upper and lower dentition of each species (Figures 2.5 and 2.6). Through this way of presenting the measurement data, proportional differences that exist between the different tooth positions are visually and metrically accessible (Pickford and Laurent 2014). In the present case, we are searching differences/similarities between tragulid species from the Eocene to the present.

Abbreviations

Institutions.- SNSB — BSPG = Staatliche Naturwissenschaftliche Sammlungen Bayerns — Bayerische Staatssammlung für Paläontologie und Geologie München, Germany; NMW = Naturhistorisches Museum Wien, Austria; UMZC = University Museum of Zoology Cambridge, England; ZMH = Biozentrum Grindel Zoologisches Museum Universität Hamburg, Germany; MCNM = Museo de Ciencias Naturales Madrid, Spain; NMA = Naturmuseum Augsburg, Augsburg, Germany.

Genera and Teeth.- for premolar teeth, P = upper premolars (e.g. P2); p = lower premolar (e.g. p3); for molar teeth, M = upper molar (e.g. M1), m = lower molar (e.g. m2); for genera, *Dt*. = *Dorcatherium*, *Db*. = *Dorcabune*.

Table III. Descriptive statistics for lower teeth per body mass class of the studied tragulid species. N = number specimens studied. Min = minimun value. Max=maximun value. SD = Standard deviation.

Lower teeth			m1	m2	m3	p2	p3	p4
Living spp. 0.1-17.9 kg	length (mm)	N (Min-Max)	62 (4.1-10.3)	57 (5.1-10.2)	46 (7.8-14.3)	39 (4.1-8.5)	45 (5.2-9.5)	43 (4.6-9.3)
		Mean±SD	6.4±1.4	7.0±1.1	9.6±1.4	5.8±1.2	6.6±1.0	6.3±1.2
	width (mm)	N (Min-Max)	62 (2.7-6.5)	57 (3.4-7.4)	46 (3.5-7.1)	39 (1.7-3.0)	45 (1.9 - 3.4)	43 (2.4-4.1)
		Mean±SD	4.0±0.9	4.7±0.9	4.7±0.8	2.1±0.3	2.5±0.4	2.9±0.5
Fossil spp. 0.1-17.9 kg	length (mm)	N (Min-Max)	57 (4.4-9.6)	81 (4.6-11.0)	101 (6.7-16.7)	12 (3.8-8.6)	20 (3.0-10.0)	39 (3.9-9.6)
		Mean±SD	6.7±1.5	7.3±1.4	11.8±2.9	6.8 ±1.3	7.8±2.0	6.9 ±1.8
	width (mm)	N (Min-Max)	56 (2.2-6.6)	81 (2.6-7.1)	100 (2.7-8.3)	12 (2.3-3.0)	20 (1.2-3.6)	38 (1.8-4.3)
		Mean±SD	4.0±1.3	4.4±1.0	5.4±1.4	2.6 ±0.2	2.9±0.7	3.2±0.8
Fossil spp. 18.0-34.9 kg	length (mm)	N (Min-Max)	55 (9.8-12.7)	66 (10.2-14.7)	48 (15.4-20.1)	19 (9.9-13.5)	28 (10.5-14.6)	35 (10.0-13.8)
		Mean±SD	11.2±0.6	12.3±0.9	18.0±1.3	11.5±1.2	12.7±0.9	11.9±0.9
	width (mm)	N (Min-Max)	55 (5.0-8.3)	66 (6.4-9.5)	48 (6.8-9.7)	18 (3.1-5.0)	27 (3.5-5.5)	36 (4.4-6.0)
		Mean±SD	6.7±0.7	7.8±0.8	8.3±0.8	4.1±0.6	4.7±0.4	5.3±0.5
Fossil spp. 35.0-51.9 kg	length (mm)	N (Min-Max)	-	3 (14.5-15.1)	2 (21.1-22.9)	-	2 (14.7-14.9)	-
		Mean±SD	-	14.8±0.3	22.0±1.3	-	14.8±0.1	-
	width (mm)	N (Min-Max)	-	3 (9.7-10.2)	2 (10.4-10.7)	-	2 (5.6-6.0)	-
		Mean±SD	-	9.9±0.3	10.6±0.2	-	5.8±0.3	-
Fossil spp. 52.0-68.9 kg	length (mm)	N (Min-Max)	1	2 (15.1-15.2)	4 (21.7-23.1)	-	-	-
		Mean±SD	13.8	15.2±0.1	22.5±0.6	-	-	-
	width (mm)	N (Min-Max)	1	2 (11.0-12.0)	4 (10.4-12.8)	-	-	-
		Mean±SD	10.0	11.5±0.7	11.3±1.1	-	-	-
Fossil spp. 69.0-85.9 kg	length (mm)	N (Min-Max)	16 (13.0-16.0)	19 (15.7-18.3)	19 (20.0-28.4)	1	4 (15.5-17.7)	13 (13.1-17.3)
		Mean±SD	14.7±0.9	16.9±0.7	24.0±2.1	14.3	16.5±1.0	14.9±1.4
	width (mm)	N (Min-Max)	16 (7.7-10.2)	19 (9.3-12.3)	19 (10.5-13.3)	1	3 (5.2-5.9)	13 (5.4-9.3)
		Mean±SD	9.0±0.7	10.6±0.9	11.7±0.9	4.3	5.6±0.4	6.7±1.0
Fossil spp. > 86 kg	length (mm)	N (Min-Max)	5 (15.4-19.3)	7 (16.7-20.3)	6 (26.0-30.9)	-	1	1
		Mean±SD	17.3±1.6	18.9±1.3	28.8±1.6	-	17.8	16.6
	width (mm)	N (Min-Max)	5 (9.0-14.0)	7 (11.5-14.7)	6 (13.0-16.0)	-	1 (6.9-6.9)	1 (8.4-8.4)
		Mean±SD	11.5±1.9	13.0±1.1	14.3±1.0	-	-	-

Table IV. Descriptive statistics for upper teeth per body mass class of the studied tragulid species. N = number specimens studied. Min = minimun value. Max=maximun value. SD = Standard deviation.

Upper teeth			**M1**	**M2**	**M3**	**P2**	**P3**	**P4**
Living spp. 0.1-17.9 kg	length (mm)	N (Min-Max)	55 (3.9-8.8)	56 (5.2-10.0)	49 (5.6-10.2	35 (5.6-9.9)	44 (4.6-10.0)	47 (3.7-8.8)
		Mean±SD	6.1±1.3	7.0±1.2	7.1±1.2	6.9±1.2	6.6±1.2	5.2±1.1
	width (mm)	N (Min-Max)	55.0 (4.5-9.9)	56.0 (5.2-11.2)	49.0 (5.0-12.0)	35.0 (2.2-4.4)	44.0 (2.8-7.6)	47.0 (4.0-8.5)
		Mean ± SD	6.3±1.4	7.3±1.4	7.5±1.6	2.9±0.6	4.0±1.0	5.4±1.0
Fossil spp. 0.1-17.9 kg	length (mm)	N (Min-Max)	38 (4.5-8.7)	56 (4.0-9.9)	41 (4.6-10.6)	7 (4.3-10.5)	9 (4.2-10.8)	10 (3.8-8.3)
		Mean±SD	6.5±1.3	7.6±1.4	8.0±1.5	8.0±2.5	7.8±2.1	6.4±1.5
	width (mm)	N (Min-Max)	38 (4.5-9.7)	55 (4.3-11.4)	41 (4.0-12.3)	6 (2.0-4.9)	9 (3.0-6.5)	12 (4.4-9.7)
		Mean±SD	6.9±1.6	8.0±1.8	8.8±2.0	3.6±1.1	4.8±1.1	7.1±1.6
Fossil spp. 18.0-34.9 kg	length (mm)	N (Min-Max)	27 (9.3-13.1)	33 (10.5-13.7)	26 (10.7-15.5)	6 (11.5-13.0)	5 (9.9-12.0)	11 (8.1-12.5)
		Mean±SD	10.6±0.8	11.9±0.9	12.5±1.1	12.1±0.7	11.1±0.8	9.4±1.2
	width (mm)	N (Min-Max)	26 (10.0-13.8)	33 (11.1-15.1)	26 (11.3-15.8)	6 (5.0-7.2)	5 (5.7-8.5)	11.0 (8.0-12.8)
		Mean±SD	11.4±1.0	13.1±1.1	13.5±1.2	5.7±0.8	6.9±1.1	9.5±1.2
Fossil spp. 35.0-51.9 kg	length (mm)	N (Min-Max)	3 (13.3-14.0)	4 (14.6-16.9)	1	2 (14.9-17.3)	1	1
		Mean±SD	13.6±0.4	15.8±1.0	16.8	16.1±1.7	15.5	12.7
	width (mm)	N (Min-Max)	3 (13.7-15.5)	4 (16.1-17.0)	1	2 (7.2-7.4)	1	1
		Mean±SD	14.7±0.9	16.7±0.4	17.7	7.3±0.1	9.7	12.1
Fossil spp. 52.0-68.9 kg	length (mm)	N (Min-Max)	2 (14.0-15.2)	1	2 (14.6-14.8)			
		Mean±SD	14.6±0.8	13.4	14.7±0.1			
	width (mm)	N (Min-Max)	2 (16.0-17.6)	1	2 (16.7-16.8)			
		Mean±SD	16.8±1.1	14.4	16.8±0.1			
Fossil spp. 69-85 kg	length (mm)	N (Min–Max)	3 (14.8-15.3)	12 (16.5-19.6)	8 (17.3-20.5)			1
		Mean±SD	15.0±0.3	18.4±0.9	19.3±1.1			14.0
	width (mm)	N (Min-Max)	2 (14.7-14.8)	12 (16.8-22.8)	8 (17.1-22.0)			1
		Mean±SD	14.8±0.0	19.5±1.8	19.5±1.7			15.0
Fossil spp. > 86 kg	length (mm)	N (Min-Max)	1	3 (19.4-21.7)	4 (18.8-21.4)			
		Mean±SD	18.0	20.7±1.2	19.7±1.2			
	width (mm)	N (Min-Max)	1	3 (21.0-25.7)	4 (21.3-25.8)			
		Mean ± SD	23.1	22.9 ± 2.5	22.9 ± 2.0			

2.3 Results

Body mass estimations (kg) and deep time distribution

Our body mass estimations of fossil tragulids encompass a range of species from 1.0 kg (e.g. *Dorcatherium minimus* and *Afrotragulus moruorotensis*) to more than 100.0 kg (*Dorcabune anthracotheroides*) (Table I). The greatest diversity and the widest range of body masses (from 1.0 kg to 111.5 kg) occurred during the Miocene, whereas the Pliocene and the Quarternary almost lack tragulid records. Thus, there is a sharp cut between phenotype diversity in the Miocene and the present (Figure 2.2). When the median body mass is analyzed each 2.0 mya from 36.0 mya to the present, a distribution to right side of the time scale can be observed, with a peak of body mass and species richness between 16.0 mya to 4.0 mya (Figure 2.2 and Table V). In more detail, from 36.0 mya to 24.0 mya the body mass fluctuated between 1.6 kg and 4.7 kg and grouped species as *Archaeotragulus krabiensis*, *Iberomeryx minor* and *I. parvus*. At 22.0 mya, there was increase in median body mass of 11.6 kg to decrease to median body mass 6.3 kg at 18.0 mya, with a concomintant increase of species number from one to six respectively (Figure 2.2 and Table V). Here the following species are present: *Afrotragulus moruorotensis*, *Siamotragulus songhorensis*, *Dorcatherium pigotti* and *Dorcabune welcommi*. From 16.0 mya to 4.0 mya, median body mass fluctuated between 17.4 kg and 21.1 kg, being also the time with the greatest number of species (between 4 to 12 species; Figure 2.2 and Table V). At that time, the following species were present, for example, *Dorcatherium minus*, *Dt. maliki*, *Dorcabune anthracotheroides*, *Siamotragulus sanyathanai* and *Yunannotherium simplex*, among others. From 2.0 mya to the present, the median body mass ranges between 2.9 kg and 4.5 kg, with *Dorcatherium nagrii* being the youngest fossil species considered here (Figure 2.2 and Table V).

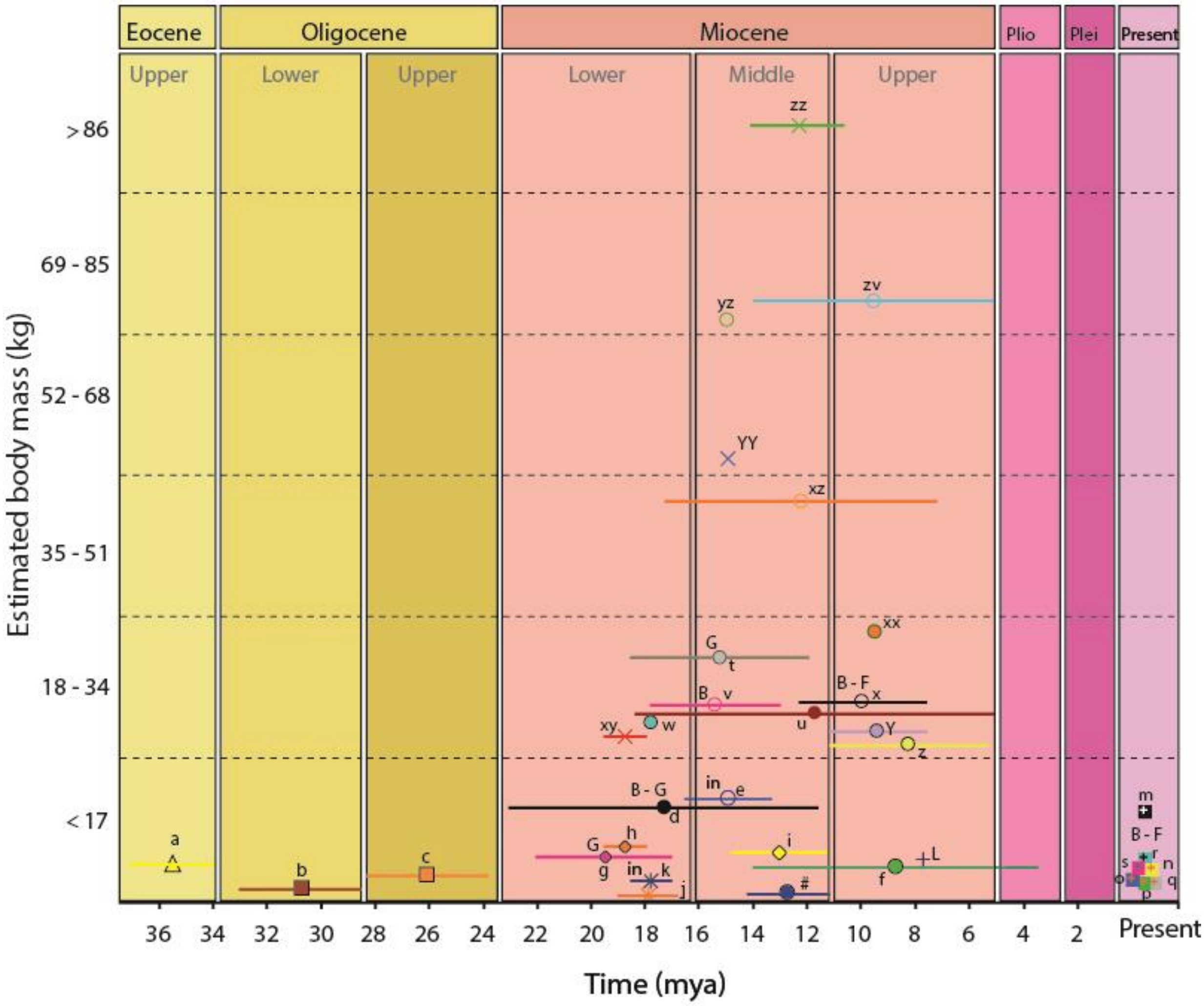

Figure 2.2. Body mass class (kg) v/s time (mya), for 34 fossil and living tragulid species (27 fossil species and 7 living species). Each symbol represents a species and lines temporal occurrence. The body mass for *Hyemoschus*, *Moschiola* and *Tragulus* species (except *T. nigricans* and *Moschiola indica*) were extracted from Meijaard (2011). ***a***: *Archaeotragulus krabiensis*, **b**: *Iberomeryx parvus*, **c**: *I. minor*, ***d***: *Dorcatherium pigotti*, ***e***: *Dt. guntianum*, ***f***: *Dt. nagrii*, ***g***: *Siamotragulus songhorensis*, ***h***: *S. bugtiensis*, ***i***: *S. sanyathanai*, ***j***: *Afrotragulus moruorotensis*, ***k***: *A. parvus*, ***l***: *Yunannotherium simplex*, ***m***: *Hyemoschus aquaticus*, ***n***: *Moschiola indica*, ***o***: *M. meminna*, ***p***: *Tragulus javanicus*, ***q***: *T. kanchil*, ***r***: *T. napu*, **s:** *T. nigricans*, ***t***: *Dt. chappuissi*, ***u***: *Dt. minus*, ***v***: *Dt. crassum*, ***w***: *Dt. iririensis*, ***x***: *Dt. naui*, ***y***: *Dt. jourdani*, ***z***: *Dt. puyhauberti*, ***xx***: *Dt. maliki*, ***xy***: *Db. welcomi*, ***xz***: *Dt. vindebonense*, ***yy***: *Db. nagrii*, ***yz***: *Dt. peneckei*, **zv:** *Dt. majus*, **zz**: *Db. anthracotheroides*, #: *Dt. minimus*. **G**: Grazer, **in**: Intermediate feeder, **B**: Browser, **F**: Frugivore. **Plio**: Pliocene, **Plei**: Pleistocene.

Table V. Median body mass (kg), plotted at 2.0 Ma intervals, for 34 fossil and living tragulid species (27 fossil species and 7 living species). The number of species, median, minimum and maximum body mass values are presented.

Time (mya)	Number of species	Body Mass (kg)	
		Median	Min - Max
Present	7	2.9	1.9 - 12.0
2.0 – 3.9	1	4.5	4.5
4.0 – 5.9	4	21.1	4.5 – 77.0
6.0 – 7.9	7	21.9	4.5 – 77.0
8.0 – 9.9	8	26.6	4.5 – 77.0
10.0 – 11.9	11	20.9	1.0 – 111.5
12.0 – 13.9	12	23.9	1.0 – 111.5
14.0 – 15.9	10	23.9	1.0 – 71.2
16.0 – 17.9	10	17.4	1.0 – 49.0
18.0 – 19.9	6	6.3	1.0 – 20.3
20.0 – 21.9	2	8.6	5.6 – 11.6
22.0 – 23.9	1	-	11.6
24.0 – 25.9	1	-	3.3
26.0 – 27.9	1	-	3.3
28.0 – 29.9	1	-	1.6
30.0 – 31.9	1	-	1.6
32.0 – 33.9	1	-	1.6
34.0 – 35.9	1	-	4.7
36.0 – 37.9	1	-	4.7

Body mass class

The extant tragulids' (genera *Hyemoschus*, *Moschiola* and *Tragulus*) body mass values define the limit of the lowest class (≤ 17.9 kg). Except for *Hyemoschus aquaticus*, which averages 12.0 kg, the others clearly are even smaller species, whose body mass varies from 1.0 kg to 5.0 kg (Figure 2.2). The few known Palaeogene tragulids *Archaeotragulus krabiensis*, *Iberomeryx minor*, and *I. parvus* fall within that lower body mass range of the class of living tragulids with no more than 5.0 kg. The greatest diversity of tragulid body mass in general occurred during the Miocene, from which all six body mass classes are recorded. Among these, class ≤ 17.9 kg was the most diverse with 10 species closely followed by class 18.0 kg to 34.9 kg with 9 species (Figure 2.2). Within the Miocene, the greatest diversity and the widest range of body masses (from 1.0 kg to 111.5 kg) occurred during the Middle Miocene (15.9 mya to 11.6 mya). In contrast to the Early Miocene, for the Late Miocene a wider range of body mass classes are recorded in general, but there are more species in class 18.0 kg to 34.9 kg than during the Early Miocene. Since there are only few tragulid records from most of the Pliocene and the Quarternary mostly not considered in this study a sharp cut between phenotype diversity in the Miocene and the present can be observed (Figure 2.2).

Occlusal Surface Area (OSA)

For all fossil and living species here studied, the molars are generally square (upper), rectangular (lower), and/or trapezoidal shape in occlusal view, while the premolars vary from triangular in the maxilla (especially P4) to rectangular, elongated and slender in the mandible (Figure 2.1 A, B). For these teeth, there is a positive correlation between tooth width and tooth length, no matter which tooth position (Figure 2.4a, B). Regarding the lower dentition we found a positive relationship between the OSA and body mass (Table VI). For the species less than 18.0 kg (fossil and living) the length and width of lower molars has more or less similar proportions , while the premolars are more slender (Figure 2.3 and Figure 2.4 A). There was only a single fossil species in the 18.0 kg to 34.9 kg body mass class, but the total OSA of premolars was greater in species of a body mass of ≤ 17.9 kg (Figure 2.4). There were not enough data to analyze all other body mass classes (Figure 2.3).

The upper dentition shows positive allometry of total OSA (Table VI). Here, the premolars and molars were longer and wider in fossil than in living species (Figure 2.4 B). For premolars, the width is 76.4% and 68.9% respectively of the length in fossil and living species, while the molars were wider than long; 6.8% wider in fossil and 4.5% in living species. The fossil species have a slightly greater total OSA, being the molar OSA higher than premolar OSA (Figure 2.3).

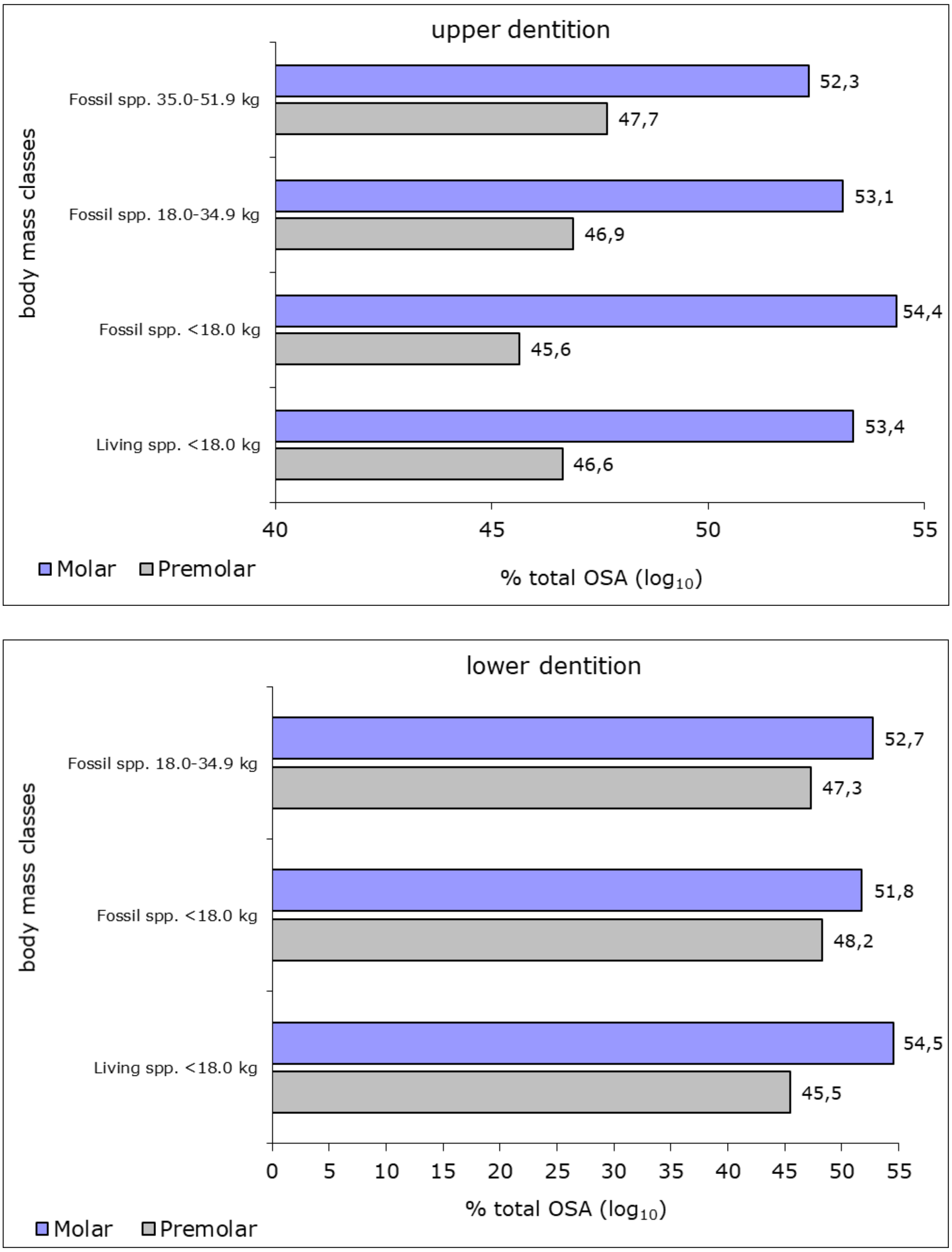

Figure 2.3. Upper and lower Occlusal Surface Area (OSA) of the permanent dentition (premolar and molar) for the different body masses studied (Raw data in Appendix 2, Tables 2.2 and 2.3).

Table VI. Ordinary Least Squares Regression between the Total Occlusal Surface Area (Total OSA) and body mass for upper and lower teeth, of fossil and living tragulid species.

Body Mass	**Species considered in the analysis with data for the Total OSA (= premolar OSA + molar OSA)**	**Ordinary Least Squares Regression**				
		r^2	**Slope**	**Std error estimate**	**Intercept**	***p*-value**
Lower dentition All species > 0.0 kg (n = 16 spp.)	Fossil spp.: *Archaeotragulus krabiensis, Dorcatherium pigotti, Dt. guntianum, Dt. nagrii, Dt. chappuisi, Dt. crassum, Dt. naui, Dt. maliki, Dt. majus, Yunannotherium simplex.* Living spp.: *Hyemoschus aquaticus, Moschiola indica, M. meminna, Tragulus javanicus, T. kanchil, Tragulus napu.*	0.97	1.10	0.04	3.13	< *0.0001*
Species ≤ 17.9 kg (n = 11 spp.)	Fossil spp.: *Archaeotragulus krabiensis, Dorcatherium pigotti, Dt. guntianum, Dt. nagrii, Yunannotherium simplex.* Living spp.: *Hyemoschus aquaticus, Moschiola indica, M. meminna, Tragulus javanicus, T. kanchil, Tragulus napu.*	0.94	0.92	0.07	3.23	< *0.0001*
Upper dentition All species > 0.0 kg (n = 14 spp.)	Fossil spp.: *Iberomeryx minor, Afrotragulus parvus, Dorcatherium guntianum, Dt. chappuisi, Dt. minus, Dt. naui, Dt. vindebonense.* Living spp.: *Hyemoschus aquaticus, Moschiola indica, M. meminna, Tragulus javanicus, T. kanchil, T. napu.*	0.97	1.28	0,06	0,05	< 0.0001
Species ≤ 17.9 kg (n = 9 spp.)	Fossil spp.: *Iberomeryx minor, Afrotragulus parvus, Dorcatherium guntianum.* Living spp.: *Hyemoschus aquaticus, Moschiola indica, M. meminna, Tragulus javanicus, T. kanchil, T. napu.*	0.91	1.10	0.12	3.48	<0.0002

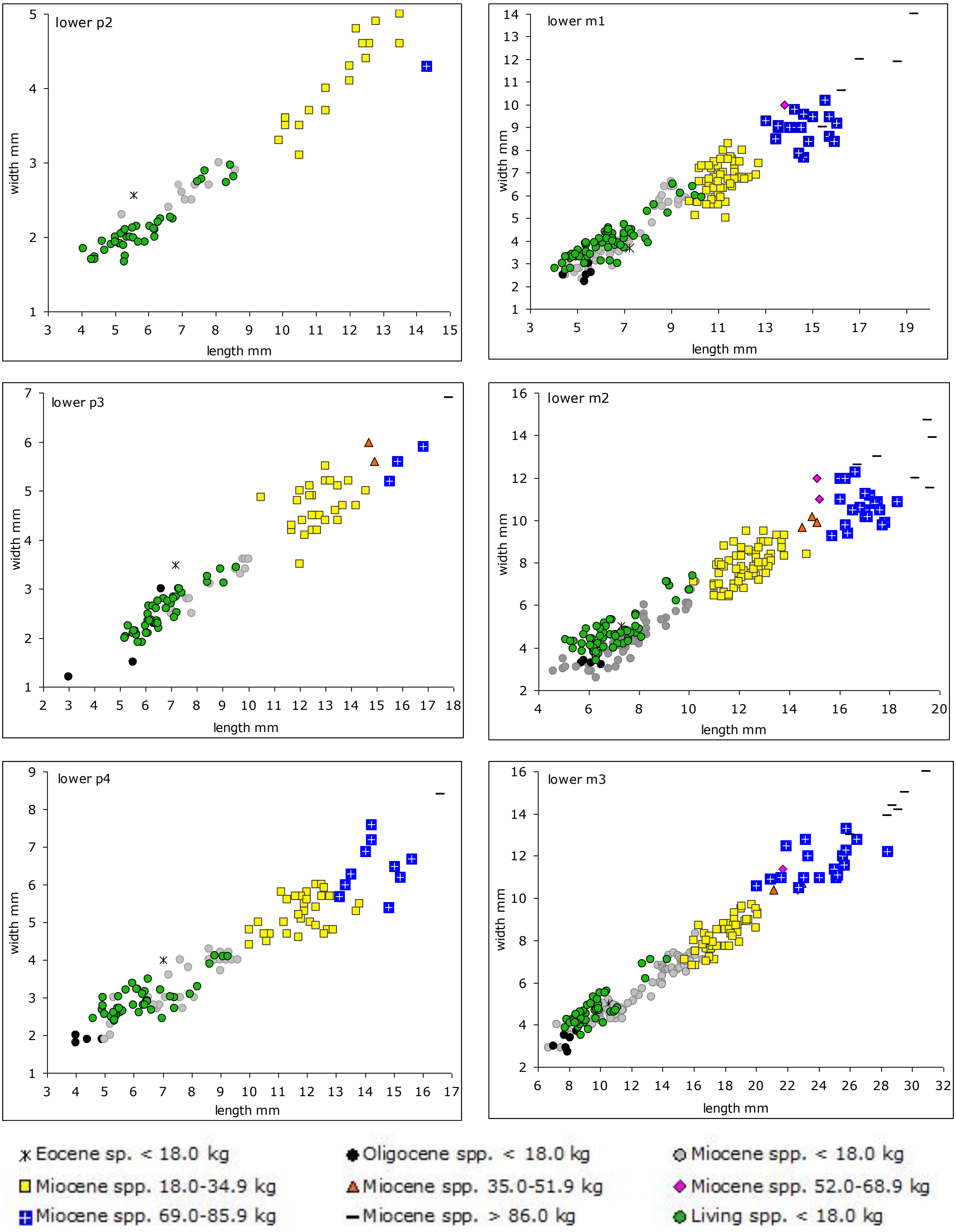

Figure 2.4A. Width vs. length (mm) for the lower teeth of tragulid species categorized in body mass classes established here.

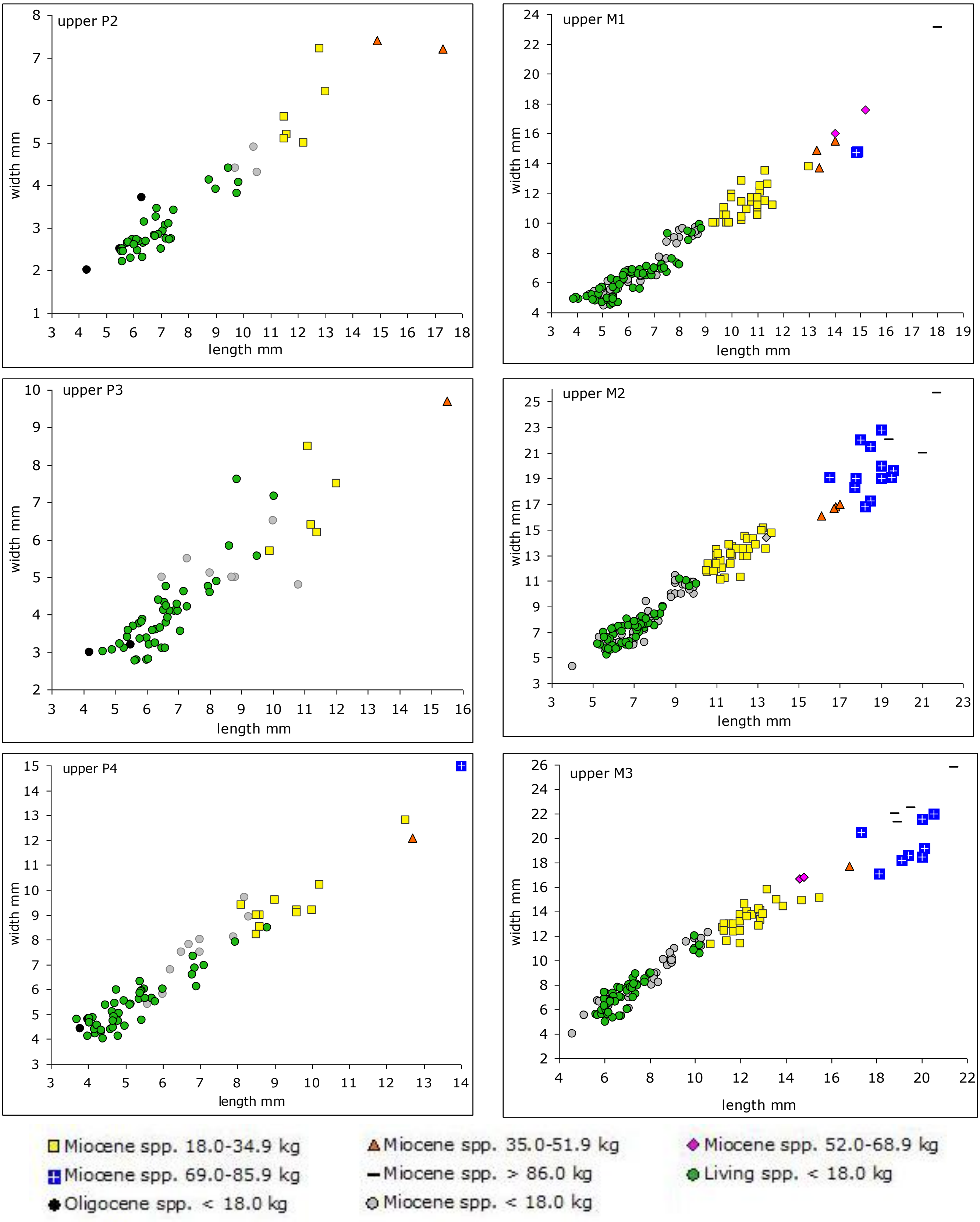

Figure 2.4B. Width vs. length (mm) for the upper teeth of tragulid species categorized in body mass classes established here.

Dentition proportions in Tragulidae

With slight differences, the length and width pattern of the full postcanine dentition (lower and upper) is similar between fossil and living species (Figures 2.5 and 2.6). The lower molar row has similar proportions in length in fossil and living tragulids, showing a clear increase from m1 to m3, but being more pronounced in the heavier species of a body mass range from 18.0 kg to < 86.0 kg (Figure 2.5 A). The width increases from m1 to m2, but decreases slightly towards m3 in fossil tragulids and coincides with m2 in living tragulids. However, for heavier species (18.0 kg to < 86.0 kg), this increase in width was constant from m1 to m3 (Figure 2.5 B). In general, the lower premolar row increases in length fom p2 to p3, being the only exception *Dorcatherium chappuisi*, whose p3 is smaller than p2. From p3 to m1, in the majority of the species, the length decreases, except in living species *Hyemoschus aquaticus* and *Tragulus javanicus*, where they do not vary, and the fossil *Dt. nagrii* where there is a notable increase of the length from p3 to m1 (Figure 2.5 A). The width of the lower premolar row shows a general pattern with only a slight increase from p2 to p4, (the increase is even less in the living species). However, in the heavy species, e.g. *Dorcabune anthracotheroides*, the p2-p4 increase is more pronounced. The width usually increases from p2 and m3, being more pronounced in the larger species (Figure 2.5 B).

Regarding the upper molar row, the majority of the tragulids (fossil and living species) show a length increase from M1 to M2, with M3 having the same size as M2 (Figure 2.6 A). Exceptions from that, with M3 smaller than M2, are the fossil species *Siamotragulus bugtiensis*, *Dorcatherium chappuisi* and *Dorcabune anthracotheroides* and the living species *Moschiola indica*, *M. meminna* and *Tragulus napu* (Figure 2.6 A). The upper premolar row shows in the majority of species a decrease from P2 to P4. However, the fossil species *Afrotragulus parvus* shows the same length from P2 to M1, and *Siamotragulus sanyathanai* shows an increase of the length from P2 to P3, but a decrease to P4. In almost all species, between P4 and M1, there is an increase in length, except for *Dorcatherium maliki*, where M1 is smaller than P4 (Figure 2.6 A). With few exceptions, there is an increase in width from P2 to M3, which is very clear in heavyweight species. Exceptions, where M3 is less wide than M2, are the fossil species *Siamotragulus bugtiensis*, *Afrotragulus moruorotensis*, *Dorcatherium puyhauberti* and *Dt. majus* and the living species *Moschiola meminna*. M2 and M3 have the same width in living *Hyemoschus aquaticus* and *Tragulus kanchil* (Figure 2.6 B).

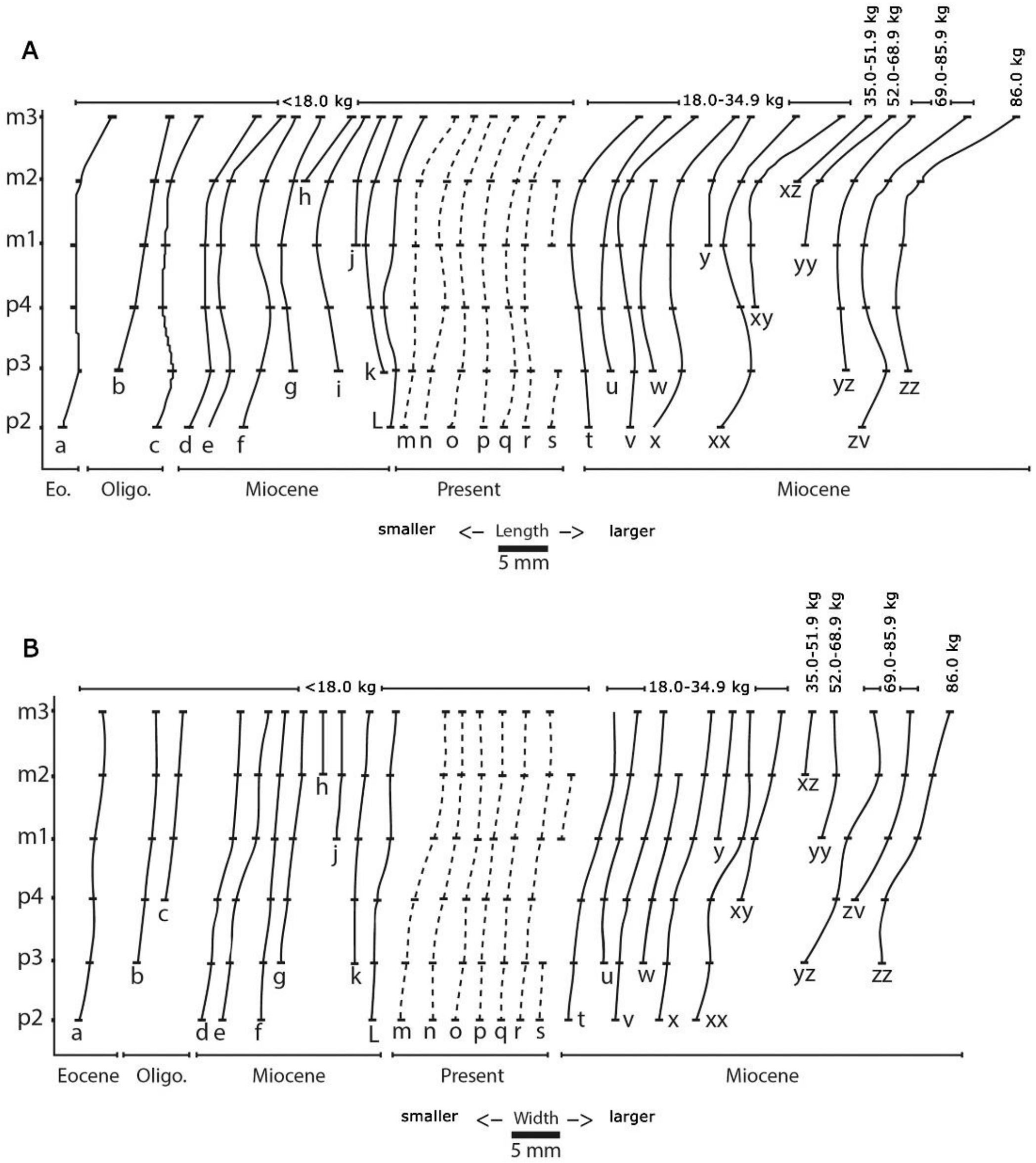

Figure 2.5. A: length and **B**: width pattern of lower dentition in fossil and living species of Tragulidae. ***a***: *Archaeotragulus krabiensis*, ***b***: *Iberomeryx parvus*, ***c***: *I. minor*, ***d***: *Dorcatherium pigotti*, ***e***: *Dt. guntianum*, ***f***: *Dt. nagrii*, ***g***: *Siamotragulus songhorensis*, ***h***: *S. bugtiensis*, ***i***: *S. sanyathanai*, ***j***: *Afrotragulus moruorotensis*, ***k***: *A. parvus*, ***l***: *Yunannotherium simplex*, ***m***: *Hyemoschus aquaticus*, ***n***: *Moschiola indica*, ***o***: *M. meminna*, ***p***: *Tragulus javanicus*, ***q***: *T. kanchil*, ***r***: *T. napu*, ***s***: *T. nigricans*, ***t***: *Dt. chappuisi*, ***u***: *Dt. minus*, ***v***: *Dt. crassum*, ***w***: *Dt. iririensis*.

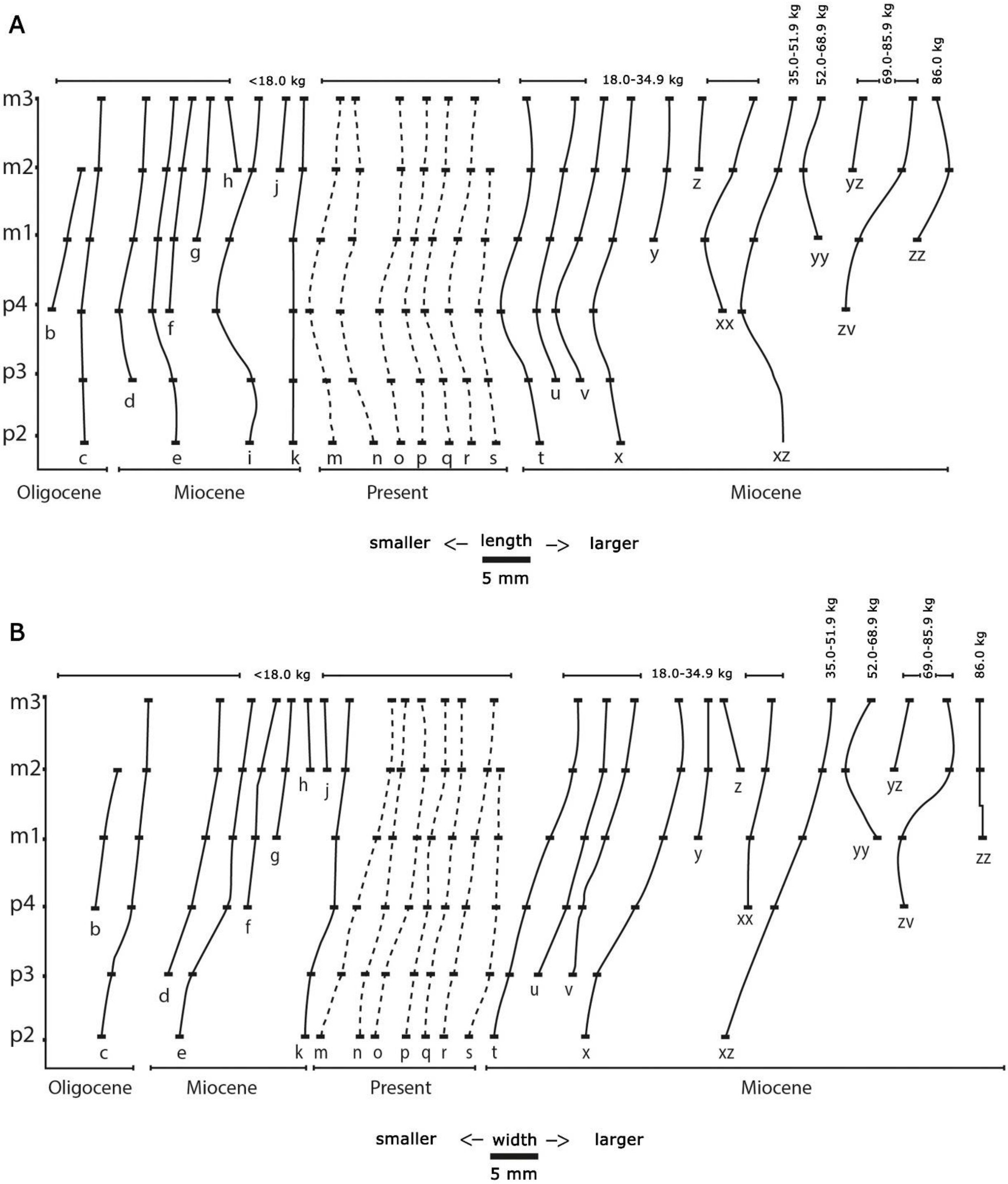

Figure 2.6. A: length and **B**: width pattern of upper dentition in fossil and living species of Tragulidae. ***b***: *Iberomeryx parvus*, ***c***: *I. minor*, ***d***: *Dorcatherium pigotti*, ***e***: *Dt. guntianum*, ***f***: *Dt. nagrii*, ***g***: *Siamotragulus songhorensis*, ***h***: *S. bugtiensis*, ***i***: *S. sanyathanai*, ***j***: *Afrotragulus moruorotensis*, ***k***: *A. parvus*, ***l***: *Yunannotherium simplex*, ***m***: *Hyemoschus aquaticus*, ***n***: *Moschiola indica*, ***o***: *M. meminna*, ***p***: *Tragulus javanicus*, ***q***: *T. kanchil*, ***r***: *T. napu*, **s:** *T. nigricans*, ***t***: *Dt. chappuissi*, ***u***: *Dt. minus*, ***v***: *Dt. crassum*, ***w***: *Dt. iririensis*, ***x***: *Dt. naui*, ***y***: *Dt. jourdani*, ***z***: *Dt. puyhauberti*, ***xx***: *Dt. maliki*, ***xy***: *Db. welcommi*, ***xz***: *Dt. vindebonense*, ***yy***: *Db. nagrii*, ***yz***: *Dt. peneckei*, **zv:** *Dt. majus*, ***zz***: *Db. anthracotheroides.*

2.4 Discussion

The postcanine tooth areas of Tragulidae (OSA) show positive allometry. Therefore, they match with data from the literature on herbivore mammals (Gould 1975). The length increases from M1 to M3 in fossil tragulids was reported to be diagnostic by Rössner (2007). This is confirmed here for the majority of fossil and living tragulids (Figure 2.4). However, the increase in width is differently correlated with the increase of length in fossil and living tragulids and between the tooth positions. While molars and P4s are less affected, all other premolars are more slender in living than in fossil tragulids (Figure 2.4). This is in accordance with the lack of lingual tooth crown elements in the living species.

External appearance, behavior, and ecology of living African and Asian tragulids is documented to be quite similar among them and, hence, easily lead to the assumption that living species represent a phenotype that persisted possibly over more than 40 mya since divergence from the stem lineage (Janis 1984, Thenius 2000, Hernández-Fernández and Vrba 2005). Thus, the aquatic escape behaviour shared among *Hyemoschus aquaticus*, *Tragulus napu* and *Moschiola* spp. is interpreted as a symplesiomorphic trait, suggesting that it could be probably ancestral to all members of Tragulidae (Meijaard et al. 2010). Moreover, it has been hypothesized that the presence of a substantial arteria carotis interna instead of a rete mirabile epidurale in *H. aquaticus* and two species of *Tragulus* either represents a plesiomorphy for ruminants, or an apomorphic feature of extant tragulids (O'Brien 2015). Guzmán and Rössner (2018) found that crania of *Tragulus javanicus* and *T. kanchil* are relatively tall, with globose neurocrania, while cranial height is less pronounced and somewhat flattened in specimens of *T. napu* and *Moschiola* spp., and thus resembling more that of *H. aquaticus*. Given the similarity of *H. aquaticus,* which is closer related to fossil *Dorcatherium* than to extant *Tragulus* and *Moschiola* (e.g. Mennecart and Costeur 2016), to *T. napu* and *Moschiola* spp. the authors argue in favour of a flat skull constituting a plesiomorphic character state, whereas a globose neurocranium would probably represent an apomorphic character state. In tragulids, fundamental differences exist in skull and limb anatomy (Milne Edwards 1864; Carlsson 1926; Sánchez et al. 2014), as well as in life history traits (Dubost et al. 2011 and references therein). Based on extinct and extant tragulids' morphological characters, a recent phylogenetic analysis inferred a split of the lineages leading to *Hyemoschus* and *Tragulus* + *Moschiola*, respectively, being no younger than 20.0 mya (Sánchez et al. 2014). In any case, the living tragulids comprise a mixture of ancestral as well as derived characters and are most likely more misleading than enlightening for inferring the evolutionary history of the family (see Grandcolas et al. 2014).

Our analysis provides evidence for a substantial range of body sizes among tragulids from the past, not comparable to what we observe today. In that context, a closer look at body size biology is of interest. Body size is the result of mutual interactions between intrinsic and extrinsic factors (Peter 1985; Damuth and McFadden 1990). Among these, tooth morphology, food composition, and digestion features are key factors. Ruminantia, including tragulids, are equipped with the most complex stomach structure known from mammals (Langer 1988). A subdivison in several chambers facilitate a time-consuming, but effective retention and rumination strategy (Illius and Gordon 1992). Whereas most ruminants (bovids, cervids, giraffes, antilocaprids) have four chambers, tragulids have only three, lacking the omasum (Clauss and Rössner 2014 and references therein). This deviation from the common pattern is accompanied by the frugivorous diet, being a rather rare adaptation among living ruminants (Dubost 1978). The observation that browsing ruminants are predominantly smaller-sized species compared to grazing ruminants (e.g. Owen-Smith 1988; Gagnon and Chew 2000) is transferable to fruit-eating ruminants, even without exceptions (Dubost 1978; Heydon and Bulloh 1997). The fact that browsing as well as fruit-eating ruminants are selective feeders, living on high-quality food with a lower fiber/protein ratio than large ruminants, makes small and large ruminants highly comparable but not necessarily what concerns the digestive strategy.

High-quality food does not need specific morpho-physiological adaptations beyond what general herbivores show. Indeed, relative metabolic requirements increase with decreasing body weight. Not only do smaller herbivores have greater metabolic requirements than do larger ones, but also their gut capacity relative to these requirements is less. Thus, larger herbivores have a relative larger digestive storage capacity than do smaller ones, and can afford a longer passage time (Janis 1976).

Our data allows for the comparison of fossil and living species on the basis of their body mass. This information provides indirect evidence correlated with dentition morphometrics. In this context, smaller species (< 18.0 kg) have a relatively smaller postcanine surface area (total OSA: Figure 2.3) and non-molariform premolars. These features are correlated with the processing of items of herbage that are high in protein content and that require minimal fermentation such as fruits, young leaves, buds, berries, etc. Indeed, these dentition characteristics are highly correlated with the frugivorous diet of the extant tragulid *Hyemoschus aquaticus* and *Tragulus* species (Dubost 1978; Heydon and Bulloh 1997). Secondarily, these dentition characteristics can be associated to the fossil species *Dorcatherium pigotti* (11.6 kg; Table II), which has been classified a likely browser generalist rather than a frugivorous species, based on paleodiet reconstructions (Ungar et al. 2012). Other smaller fossil species like *Afrotragulus parvus* (2.7 kg) have been reconstructed as intermediate feeders, while *Siamotragulus songhorensis* (5.6 kg) was a variable grazer and *Dorcatherium guntianum* (12.4 kg) a grass-dominated mixed feeder (Ungar et al. 2012; Kaiser and Rössner 2007) despite their lower body mass and slender dentition (Pickford 2002; Sánchez et al. 2012). On the other hand, the medium-sized *Dt. crassum* (24.9 kg) is considered a browser, but *Dt. naui* (30.4 kg) a frugivorous browser just as the extant species (Kaiser and Rössner 2007; Merceron 2009; Aiglstorfer et al. 2014), and *D. chappuisi* (29.9 kg; Ungar et al. 2012) a grazer. Also, our data show a greater length of lower m3 in these medium-sized tragulids. The issue is, whether this m3 length represents a specialization related to food habits. But clearly, when compared with living tragulids, body mass and diet for fossil species cannot be correlated. In other words, smaller fossil species are not necessarily frugivorous like similar-sized extant tragulids. Moreover, the geographic, ecological, and temporal segregation between living tragulids should result in different suites of selective pressures. Accordingly, it is unlikely that a broad diversity associated with diet in the small and medium-sized fossil tragulids is represented today by only frugivorous species. Indeed, Yapa and Ratnavira (2013) reported that grasses, bark, herbs, seedlings, fruits, berries and the accidentally ingested insect constitute the diet of *Moschiola kathygre*. Therefore, an extensive comparative study on African and Asian living species dealing with these aspects of their biology is necessary.

Herbivorous mammals of larger body size are able to use forage of lower quality (Bell 1969, 1971; Jarmann 1968, 1974; Demment and Van Soest 1985; Clauss et al. 2003), due to morphophysiological features of the gastrointestinal tract. This opens up a higher flexibility in foraging, especially advantageous at difficult temporary environmental/climatic conditions and highly competitive guild structures. On the other hand, larger mammals tend to mature sexually at a later age, have longer gestation times, and fewer offspring (Peters 1985), all of which results in a significantly lower reproductive rate. Accordingly, there may be an associated higher risk of evolutionary failure. According to Owen-Smith (1988) and Van Soest (1996), larger herbivorous mammals show more flexibility regarding their diet, due to their lower specific metabolic requirements, by thriving on lower quality forage and/or by ingesting lesser amounts of regular quality forage per day. All living tragulids are small, and there are no significant differences in gestation length (ranging from five to six months), litter size (1 or 2 fawns) and longevity (ca. 13 or 15 years) (Meijaard 2011).

Our body mass estimations show (Figure 2.2, Table V), from small to larger extinct tragulids, that these species did not prosper in open, grassland-dominated ecosystems during the Miocene (Janis 1993; Janis 2008; Zachos 2001). The diversification of pecoran species with their high competitivity and much more efficient fiber consumption, probably displaced the rather unsuccessful grazing tragulids (Ungar et al. 2012). On the other hand, browsing tragulids were affected by the reduction and/or dissappearance of their habitats at the expense of the grassland. This, in association with the arrival of pecoran competitors, must have detonated their extinction. In this context, the actual frugivorous diet could be considered an adaptation as answer to selection pressures encountered during the Miocene. It is probable that the actual frugivorous diet of the Asian and African mouse-deers is a recently acquired condition and, in a certain sense, more "sophisticated" than the feeding habit of the tragulid ancestor. Accordingly, based on the data here analyzed and the available paleodiet reconstructions (Ungar et al. 2012; Kaiser and Rössner 2007), it is highly probable that the frugivorous adaptation of tragulids does not necessarily represent an ancestral state for this family (e.g. Janis 1984; Thenius 2000), but rather a novel intra-tragulid evolutionary response as has been hypothesized before (Clauss and Rössner 2014). Obviously, this scenario can change if there would exist a still not recorded frugivorous tragulid fossil. That today there are only small-sized species is probably due to the higher diversity of these phenotypes during the Miocene. The high variation that existed in the past was the basis on which natural selection (directional natural selection in this case) acted upon and of which small phenotypes were favoured that led to the development of the extant tragulids. Notwithstanding, whether the small body size of living tragulids represents an ancient or derived trait remains unclear (e.g. Grandcolas et al. 2014). In this context, the small size and short straight horns of antilopine artiodactyls was commonly thought to represent an ancient type of bovid body plan. However, Bärmann (2014) concluded that small body size and short horns are likely derived instead of primitive traits, and that the ancestor of Antilopine was probably very similar to modern gazelles. In the case of tragulids, more samples and new approaches should be considered to advance our knowledge on that topic.

2.5 Conclusions

Our body mass estimations give evidence for the existence of a wide body size range of tragulid species from the past, which is not comparable to what we have today (Figure 2.2). The peak occurred during the Miocene between 16.0 mya to 4.0 mya with a median body mass that fluctuated between 17.4 kg and 21.1 kg. Among the body mass classes, the class ≤ 17.9 kg with 10 species and the class 18.0 kg to 34.9 kg with 9 species, were the most diverse ones during the Miocene (Table V). The disparity in body size of fossil and extant tragulids hints at a much wider spectrum of phenotypes in the past. Although our empiric analyses are restricted to tooth measurements, the directly related body mass is known to be tightly linked with ecological and physiological parameters. Here, we hypothesized that directional natural selection would have favoured the small phenotype of tragulids in compensation for the increasing interspecific competition among crown ruminants and Miocene climate change. Finally, we found that the phenotype diversity of extant tragulids species represents only a moderate subset of the extinct phenotypic variation, and consequently we validated our hypothesis.

CHAPTER 3

Skull morphometrics of *Tragulus* and *Moschiola* for an improved classification of tragulid collections

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3.1 Introduction

Mouse deer are neither deer nor mice, but rather belong to the Tragulidae, a family of ruminants closely related to deer, antelopes and their kin (see Hernández Fernández and Vrba, 2005; Hassanin et al. 2012) that includes the smallest living artiodactyls (shoulder height 20 cm). Fossil evidence from Asia suggests that the Tragulidae evolved in the Eocene, at least 34 mya (Métais et al. 2001; Benammi et al. 2001). Present-day Tragulidae are subdivided into three genera, i.e. *Tragulus*, *Moschiola*, and *Hyemoschus*. While *Hyemoschus* is a monospecific genus that exclusively occurs in central Africa, *Tragulus* and *Moschiola* each include several species. *Moschiola* comes from India and Sri Lanka, and *Tragulus* is distributed widely across the mainland and many islands of South-East Asia (Meijaard 2011; Groves and Grubb 2011).

The taxonomic history of *Tragulus* and *Moschiola* is complicated (for details see Meijaard and Groves 2004; and Groves and Meijaard 2005). Previous phenomic analyses have produced a plethora of conflicting results that triggered dispute over the number of species and validity of some of the historic species delimitations (e.g. see Raffles 1822; Gray 1836; Milne-Edwards 1864; Gray 1873; Miller 1911). The first major taxonomic revision of *Tragulus* Brisson, 1762 was provided by Chasen (1940), who lumped all the *Tragulus* species of the time (i.e. between two and five, depending on the author) to two species and numerous subspecies, i.e. *T. javanicus* (greater mouse-deer) with 27 subspecies, and *T. kanchil* (lesser mouse-deer), with 26 subspecies. This classification had to be corrected in terms of nomenclatural issues into *T. napu* (greater mouse-deer) and *T. javanicus* (lesser mouse-deer) (van Bemmel 1949). *Moschiola* specimens were first described as *Moschus* (Erxleben 1777). Subsequently, Indian and Sri Lankan tragulids were assigned to yet another genus, *Memina* (Gray 1821), a preoccupied and hence invalid name. In 1843, Gray referred the Southeast Asian mouse deer to *Tragulus*. Finally, Thomas (1916), Flerov (1931), Groves and Grubb (1982), Groves and Meijaard (2005), and Groves and Grubb (2011) recommended that the Indian and Sri Lankan tragulids be accommodated in *Moschiola* Gray 1952. In addition to being distinctly different with regard to overall skull morphology, *Tragulus* and *Moschiola* differ from one another in the morphology of the median metacarpals and metatarsals.

Taxonomic assignments and labelling of tragulid specimens in zoological collections reflects the complex history of classification of these animals. Species splitting and lumping during the 19th century, along with the concurrent use of the revisions by Chasen (1940) and van Bemmel (1949), have led to confusion in collections and publications. For example, Carlsson (1926) described *Tragulus* embryos that he assigned to *T. napu* and *T. kanchil*; however, these two species names are mutually exclusive according to Chasen (1940) and van Bemmel (1949). Smit-van Dort (1988, 1989) mentioned the sympatric occurrence of *T. javanicus* and *T. napu*. While this coincides with Chasen (1940), it is impossible according to van Bemmel (1949). Nevertheless, most subsequent authors followed a three-species concept for the Asian tragulids (i.e. two Indo-Malayan and one Indian-Sri Lankan species) (e.g. Smit-van Dort 1988, 1989; Corbet and Hill 1992; Endo et al. 2004a). The most recent taxonomic revisions of *Tragulus* and *Moschiola* were provided by Meijaard and Groves (2004) and Groves and Meijaard (2005), who proposed substantial changes. These authors used extensive data sets of skull and coat variables to reassess the alpha taxonomy. As a result, sseveral of the subspecies established by Chasen (1940) were elevated to species rank. Seven spieces in *Tragulus* and three (or four, see below) in *Moschiola* species, all with relatively restricted geographical distributions, are currently recognized, including *T. javanicus* (only in Java), *T. williamsoni* (Northern Thailand, but also southern China; see Meijaard et al. 2017), *T. kanchil* and *T. napu* (both in Southeast Asia but not in Java), *T. nigricans* (Philippines), *T. versicolor* (southern Vietnam). *M. indica* (southern India), *M. meminna* (dry zone of Sri Lanka), *M. kathygre* (wet zone of Sri Lanka), as well as a fourth species that has not been formally described to date. Although, there seems to be general agreement in recent systematic studies (Kuznetsov et al. 2004; Hérnandez-Fernández and Vrba 2005; Sánchez et al. 2014; Mennecart and Costeur 2016b; Jun-Jie Hu et al. 2016 [with consistently incorrect spelling of "*Tuagulus williamsoni*"]) and reviews (e.g. Grubb 2005; Rössner 2007; Meijaard 2011; Yapa and Ratnavira 2013) regarding the two-Asian-genera concept of the living Tragulidae and the number of species per genus, the classification by Chasen (1940) and keys in Smit-van Dort (1989) continue to be used (e.g. Wooding et al. 2007; O'Brien 2015), due probably to the fact that specimens kept in collections are often still labelled based on these old works, rather than the newer and more accurate studies. The use of an out-dated taxonomy in papers focusing on the phenotype is not only the cause for time consuming and arduous disentanglement, but also rather the source of fundamental misinterpretations of molecular studies with deposition of DNA sequences in public databases. It is noteworthy in this context that the phylogeography of *Tragulus* provided in the only molecular phylogenetic analysis on tragulids available to date (Endo et al. 2004b citing Meijaard and Groves 2004) includes regions where, according to Meijaard and Groves (2004), only *T. napu* and *T. kanchil* occur. However, Endo et al. (2004b) recovered three main clades (bootstrap support from 52 to 100%) in these areas, the first containing specimens assigned to two sub-clades of *T. javanicus*, one from the Malayan Peninsula (Pahang) and the other from Laos (Vientiane). The second clade includes specimens assigned to *T. javanicus* from Borneo Island (Sabah), while the third comprises two specimens of *T. napu* from Borneo Island (Sabah) and Pulau Tioman. Although the data clustering in itself is (more or less) congruent with the distribution of *Tragulus* species depicted in Meijaard and Groves, (2004, page 98) (see above), the taxonomy used by Endo et al. (2004b) does not correspond to the revision, and the reference DNA sequences deposited in Genbank (see https://www.ncbi.nlm.nih.gov/genbank/) under *T. javanicus* do in fact not belong to this species, but rather to *T. kanchil* based on the body size.

In preparation for a larger research project on tragulid morphology we measured morphometric variables of 43 skulls of *Tragulus* and *Moschiola* reposited in several European collections that still use the conventional three-species concept for Asian tragulids. To be able to apply the latest taxonomic revisions to these specimens, we performed a morphometric characterization based on the same basic methodologies used by Meijaard and Groves (2004) and Groves and Meijaard (2005). The morphometric variables included in our analysis include many variables also used in Meijaard and Groves (2004) and Groves and Meijaard (2005), but also some not considered previously. By using a different sample set of specimens than in the aforementioned studies, albeit much smaller, we are able to provide an independent scrutiny of the newest *Tragulus* and *Moschiola* taxonomy.

3.2 Material and methods

Thirty-four skulls of *Tragulus* from Java, Borneo, Sumatra, Sunda Islands and Thailand, and nine skulls of *Moschiola* from Sri Lanka and India (according to specimen labels and collection catalogues) were analyzed; only adult individuals showing the erupted upper third molar were used. Specimen and repository information is provided in Appendix 3, Table 3.1. For each skull, 25 craniodental morphometric variables were measured with a digital caliper (accuracy 0.01 mm), partially following Meijaard and Groves (2004) (Figure 3.1). Moreover, the product of the zygomatic width (ZW) and condylobasal length (CBL) was calculated and the result then multiplied by 100 to quantifying overall skull geometry per genus/provenance group (Figure 3.5 and Table VII). To perform taxonomically independent analyses, we removed all species-specific names from our data matrix, but retained the genus names and geographical provenances, because the differences between *Tragulus* and *Moschiola* are well established (e.g. Hérnandez Fernández and Vrba 2005; Sánchez et al. 2014; Mennecart and Costeur 2016a,b) and are not an objective of this study. Principal Component Analysis (PCA) with the morphometric variables transformed to $\log_{10}$ was used to delimit discrete groups. Incomplete measurements of individual variables (e.g. because of distortion or incomplete preservation of the skull) were completed mathematically by calculating the mean of that variable from all other specimens with the same sex and geographic provenance. The genus-provenance groups were characterized by descriptive statistics: mean ± standard deviation, minimum and maximum values. All statistical analyses were performed using the free software PAST 3.14 (Hammer et al. 2001).

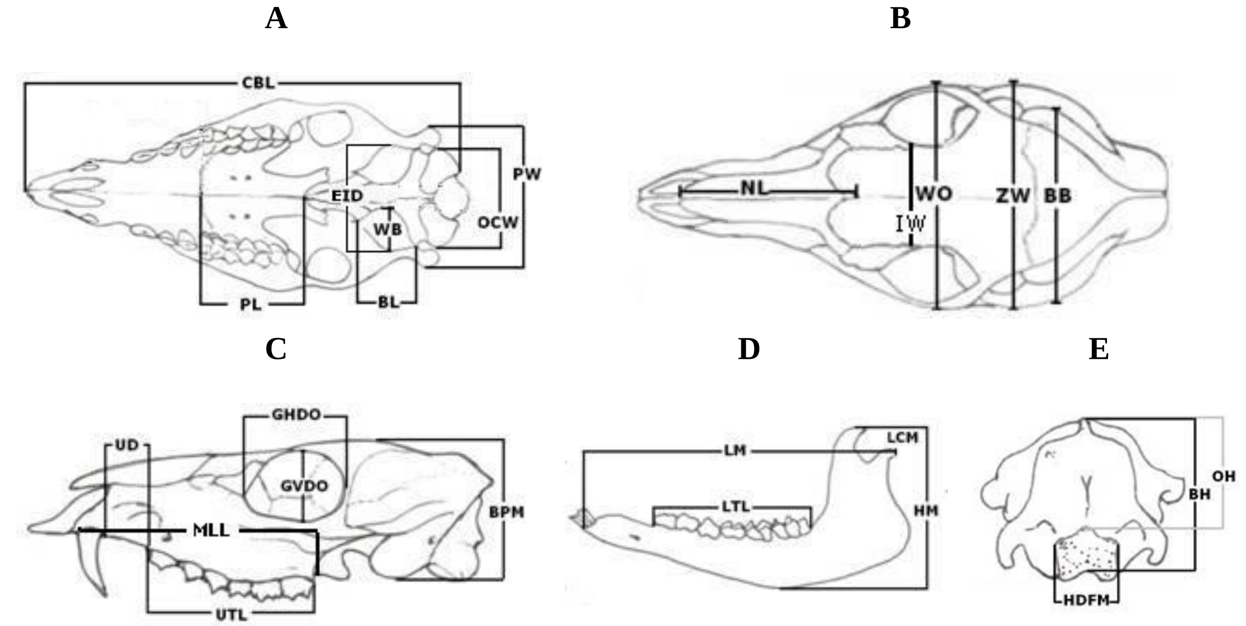


Figure 3.1. Standard measurements used in the analysis. **A**) ventral view of cranium, **B**) dorsal view of cranium, **C**) lateral view of cranium, **D**) external lateral view of mandible, **E**) caudal view of cranium. Variables indicated with an asterisk (*) taken from Meijaard and Groves (2004). Abbreviations: condylobasal length (CBL*); palatine length (PL); nasal length (median) (NL*); zygomatic width (ZW*); width across orbits (WO*); largest dorsoventral diameter of orbits (GVDO); largest anteroposterior diameter of orbits (GHDO); length of tympanic bulla (BL); width of tympanic bulla (WB*); external bullar distance (EID); occipital condylar width (OCW*); paraoccipital width (PW*); laterolateral diameter of foramen magnum (HDFM); width of braincase (BB*); interorbital width (IW); maxillar lateral length (MLL) measured to anterior side of canine tooth; occipital height dorsal of ophistion (OH*); occipital height dorsal of basion (BH*); length of mandibular condyle (LCM); height between tympanic bulla and parietal bone (BPM); length of upper tooth row (UTL); length of lower tooth row (LTL); length of upper diastema (UD); height of mandible (HM); length of mandible (LM*).

3.3 Results

The PCA reveals that the first two components account for more than 67.8 % of total variance (PC 1: 54.5 % and PC 2: 13.3 %) (Figure 3.2) overlap of the geographic groups is moderate (Figure 3.3).

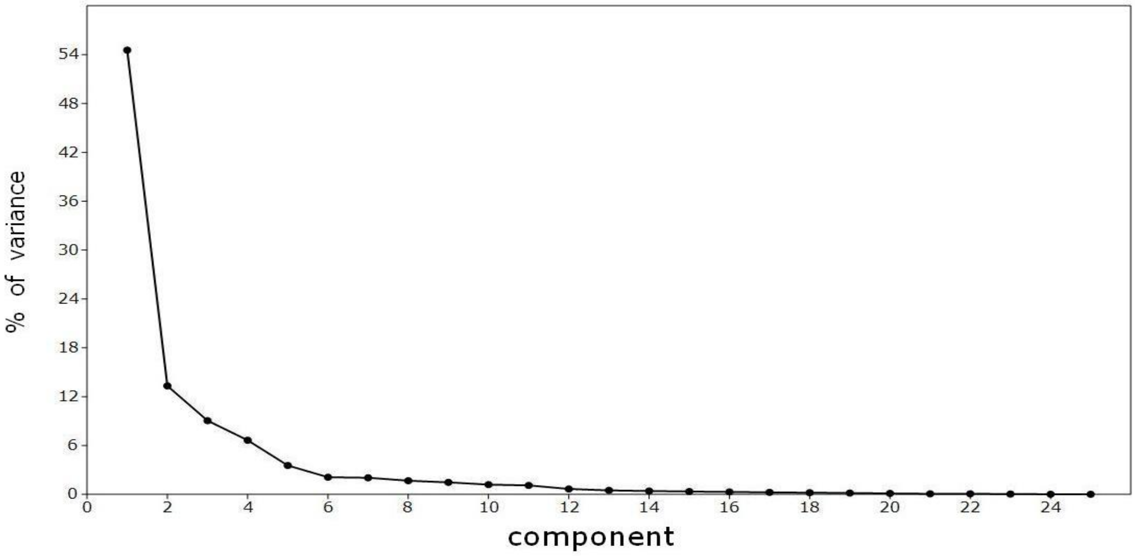


Figure 3.2. Distribution of total of variance expressed by components of the Principal Component Analysis.

All morphological variables have positive factor loadings for PC1, with moderate to high correlations, and hence permit definition of this component as a size vector (Figure 3.4A). Factor loadings are positive and negative for PC2; this component is associated with form. The specimens from Sumatra are the only ones to form two groups within PC1, the larger-sized specimens on the left and the smaller-sized to the right of the axis (Figure 3.3). The lengths of the palatine (PL) and nasal (NL) exhibit the highest factor loadings (0.34 and 0.30, respectively) for this component, and hence clearly contribute to separating three groups of *Tragulus* skulls, i.e the first comprising specimens from Sumatra & Thailand, the second those from Java, and the third comprised of specimens from Borneo, Sumatra and Sunda Islands.

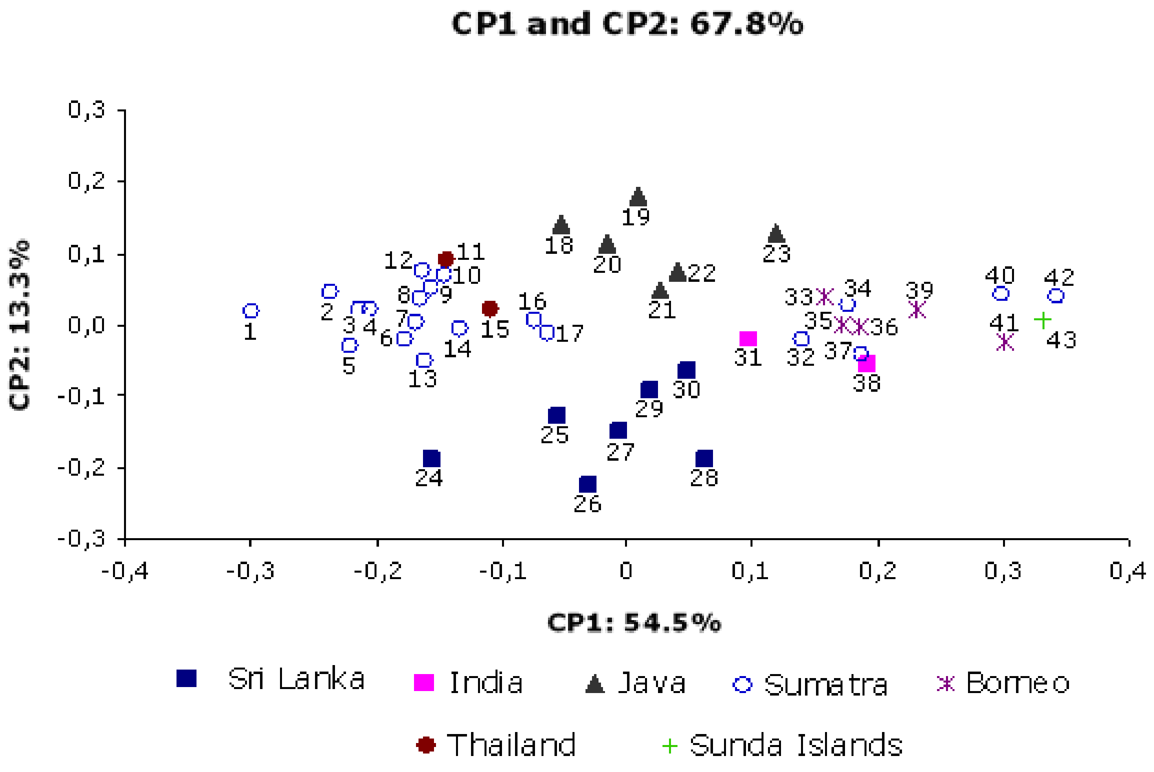
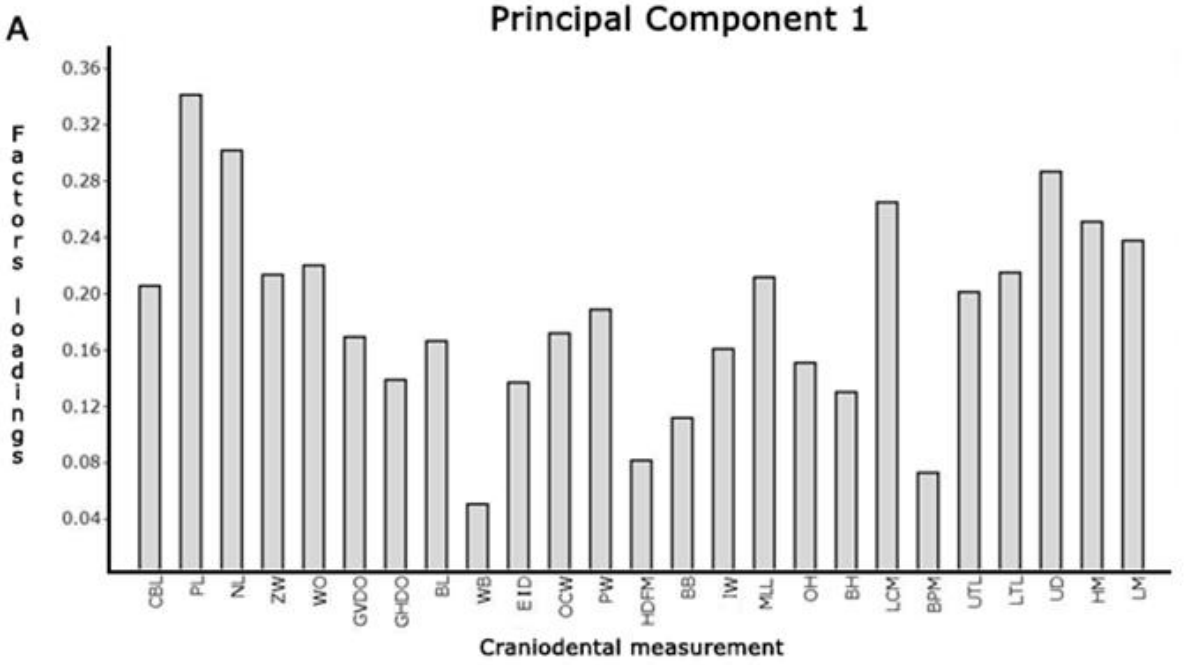


Figure 3.3. Components 1 and 2 of Principal Component Analysis generated with morphometric skull variables of tragulids from six geographical areas. Square symbols (blue and pink) are individuals of *Moschiola*, other symbols are *Tragulus*. Individual numbers are affiliated to specimen in Appendix 1.

a moderate to high separation of the two genera; *Tragulus* shows more positive values, while *Moschiola* has more negative values, suggesting that the shape of the cranium differs between the two genera. The variables with the highest factor loadings that support this segregation are the occipital height above ophistion (OH) and the length of the upper diastema (UD) (0.63 and 0.37, respectively) (Figure 3.3 and Figure 3.4B). The specimens of *Moschiola* fall into two groups according to their provenance, i.e. either from India and or Sri Lanka (Figure 3.3 and Figure 3.4A).



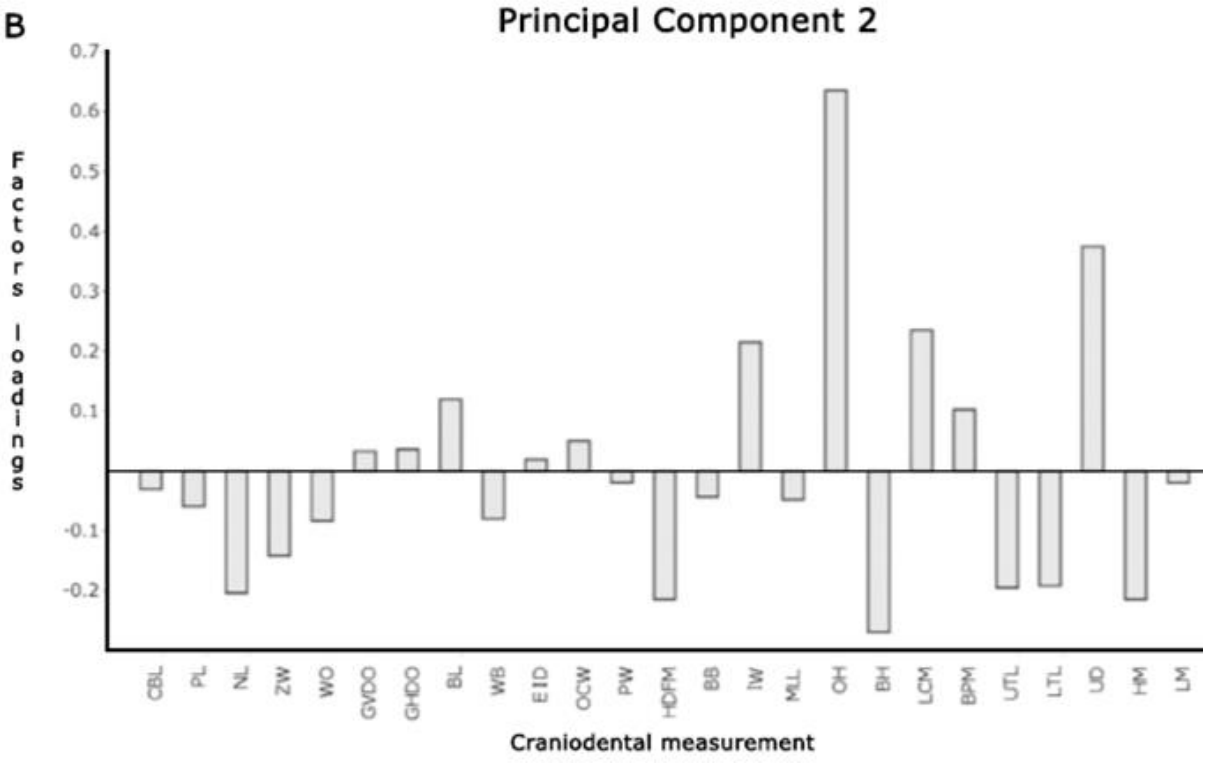


Figure 3.4. Factor loadings from Principal Component Analysis: **A**) Principal Component 1; **B**) Principal Component 2.

Table VII. Summary statistics (mean ± standard deviation; minimum and maximum) of specimen measurements according to variables explained in Figure 3.1 and as recovered from PCA analysis (Figure 3.3). Specimens were classified in genus-provenance groups. n = number of specimens studied; nd = no data. Further abbreviations see legend Figure 3.1. Measurements are in mm.

	Moschiola		*Tragulus*		
Character	*Sri Lanka* n = 7	*India* n = 2	*Java* n = 6	*Sumatra+Borneo* +Sunda Islands n = 11	*Sumatra+Thailand* n = 17
CBL	91.4±3.0 86.6-96.2	103.4±3.3 101.1-105.7	92.1±2.4 89.7-96.5	102.8±5.2 97.3-112.1	85.2±2.4 81.3-89.9
PL	19.6±1.8 17.3-22.5	22.0±3.9 19.2-24.8	20.5±1.1 19.2-22.4	22.1±1.6 19.5-24.5	16.4±1.6 12.9-20.0
NL	30.7±2.0 27.8-33.7	29.0±1.6 27.9-30.1	27.5±1.8 25.8-29.6	31.3±3.3 25.3-36.3	23.8±2.4 20.1-28.8
ZW	47.2±3.0 42.1-51.8	52.8±0.8 52.2-53.3	43.8±2.6 41.8-48.6	48.5±1.7 46.5-51.6	40.3±1.3 38.8-43.1
WO	46.4±2.6 41.4-49.1	49.6±2.4 47.9-51.3	44.7±2.6 42.0-49.1	49.7±2.0 46.2-51.8	40.5±1.2 38.8-43.8
GVDO	20.1±0.8 18.9-21.5	21.8 ±0.0 21.7-21.8	20.4±0.9 19.1-21.5	23.5±1.1 21.7-25.1	19.7±0.8 18.0-20.9
GHDO	22.9±0.5 22.3-23.7	24.7±1.9 23.4-26.1	23.6±0.5 22.7-24.2	25.9±0.8 24.8-26.9	22.6±0.7 21.6-23.8
BL	17.4±1.1 16.0-18.8	nd	18.6±0.7 17.9-19.8	21.1 ± 1.1 19.4-22.8	17.9±1.2 16.2-19.8
WB	9.2±0.5 8.7-9.9	9.6±0.0 nd	8.9±0.6 8.4-10.0	9.3±0.9 7.9-11.0	8.9±0.6 7.9-10.0
EID	26.8±0.7 25.5-27.8	nd	26.9±0.6 26.1-27.8	30.0±0.9 28.3-31.3	26.2±0.9 24.9-28.2
OCW	19.8±0.7 18.9-20.7	23.5±0.0 nd	20.6±0.5 19.9-21.5	25.2±0.9 22.1-24.8	19.6±0.7 18.4-20.7
PW	27.8±0.9 26.4-29.3	31.7±0.0 nd	28.1±0.4 27.5-28.8	30.6±1.6 27.9-32.9	25.6±0.9 24.4-27.4
HDFM	12.2±1.4 10.4-13.8	11.8±0.0 nd	11.0±0.7 10.1-12.3	12.6±0.9 10.9-13.8	11.5±1.1 9.4-13.5
BB	32.3±1.1 30.9-33.7	34.0±4.0 31.1-36.9	31.9±1.3 30.9-34.5	34.3±1.2 32.8-36.1	31.1±1.1 29.9-33.4
IW	23.1±1.0 21.6-24.2	26.0±1.7 24.8-27.2	26.6±1.5 24.5-28.5	29.5±1.6 27.1-32.0	25.2±1.0 23.8-27.8
MLL	49.0±1.6 47.0-51.1	53.6±2.3 52.0-55.3	49.3±3.0 46.1-54.4	53.9±5.9 38.0-59.4	44.9±2.3 40.6-48.6
OH	16.8±2.3 13.9-20.7	21.5±0.0 nd	25.6±3.0 20.5-29.1	21.8±1.6 19.7-24.0	19.2±1.9 14.3-21.6
BH	26.9±0.8 25.5-28.8	29.5±1.7 28.3-30.7	21.3±4.6 16.5-28.3	30.5±0.9 29.0-31.5	26.5±1.1 24.9-28.1
LCM	6.6±0.6 6.2-7.9	6.9±0.2 6.8-7.0	7.7±0.4 7.4-8.5	9.0±0.5 8.1-9.8	6.9±0.6 5.8-8.2
BPM	34.6±1.4 32.5-36.1	nd	36.2±2.1 32.6-38.9	40.0±1.1 37.6-41.5	37.3±1.3 35.7-39.4
UTL	37.3±1.1 35.5-38.7	37.6±1.0 36.9-38.3	34.1±3.0 31.4-38.9	38.7±1.5 36.9-41.2	32.1±1.6 29.6-34.6
LTL	41.7±1.6 39.4-44.1	41.7±0.9 40.7-42.0	38.4±2.5 36.4-42.1	43.5±1.4 41.8-46.4	35.5±2.0 32.1-38.8
UD	9.8±1.1 8.5-11.4	12.9±0.8 12.4-13.5	12.3±1.7 10.1-14.3	13.0±1.7 10.8-16.3	10.4±1.8 8.0-14.7
HM	39.6±2.7 36.4-43.1	40.8±2.3 39.1-42.4	36.8±4.0 34.1-44.6	39.1±1.8 35.8-41.4	31.3±1.6 28.7-33.9
LM	77.4±4.6 68.9-82.0	84.3±5.3 80.6-88.1	78.4±3.4 73.5-83.1	87.2±4.1 81.8-94.1	70.5±2.9 66.7-76.0

The factor scores for PC2 produced *Tragulus* skulls from Borneo, Sumatra & Sunda Islands have the longest condylobasal length (CBL) (mean and standard deviation = 102.8 ± 4.5 mm), followed by skulls from Java (92.1 ± 2.4 mm) and Sumatra & Thailand (85.2 ± 2.4 mm). For *Moschiola*, the specimens from India (103.4 ± 3.3 mm) are longer than those from Sri Lanka (91.4 ± 3.0 mm) specimens (Table VII). The same tendency is apparent in both genera with regard to the variables palatine length (PL) and nasal length (NL) (Table VII). *Tragulus* specimens from Borneo, Sumatra & Sunda Islands possess the greatest zygomatic width (ZW) (48.5 ± 1.7 mm), followed by the specimens from Java (43.8 ± 2.6 mm) and Sumatra & Thailand (40.3 ± 1.3 mm). The *Moschiola* skulls from India are wider (52.8 ± 0.8 mm) than those from Sri Lanka (47.2 ± 3.0 mm) (Table VII). All skulls show a CBL more or less twice as long as the ZW. However, ZW may reach >50 % of the CBL in the *Moschiola* specimens from India and Sri Lanka, whereas it remains <50 % in *Tragulus* (Figure 3.5). This latter difference explains the stocky overall appearance of the *Moschiola* skull (Figure 3.6).

There are still other differences with regard to the form of the cranium between *Tragulus* and *Moschiola*. For example, specimens of *Tragulus javanicus* and *T. kanchil* show an inflated (globose) neurocranium and the sagittal crest is weak or absent, while *Moschiola* and *T. napu* skulls have non-globose neurocrania and the sagittal crest is more pronounced (Figure 3.6). These differences are further pronounced by the height of the opisthion (OH) in PC2 (Figure 3.3 and, Figure 3.4B), which yields the largest values in *T. javanicus*, followed by *M. indica* + *T. napu* with medium, and *T. kanchil* with the smallest values (Table VII).

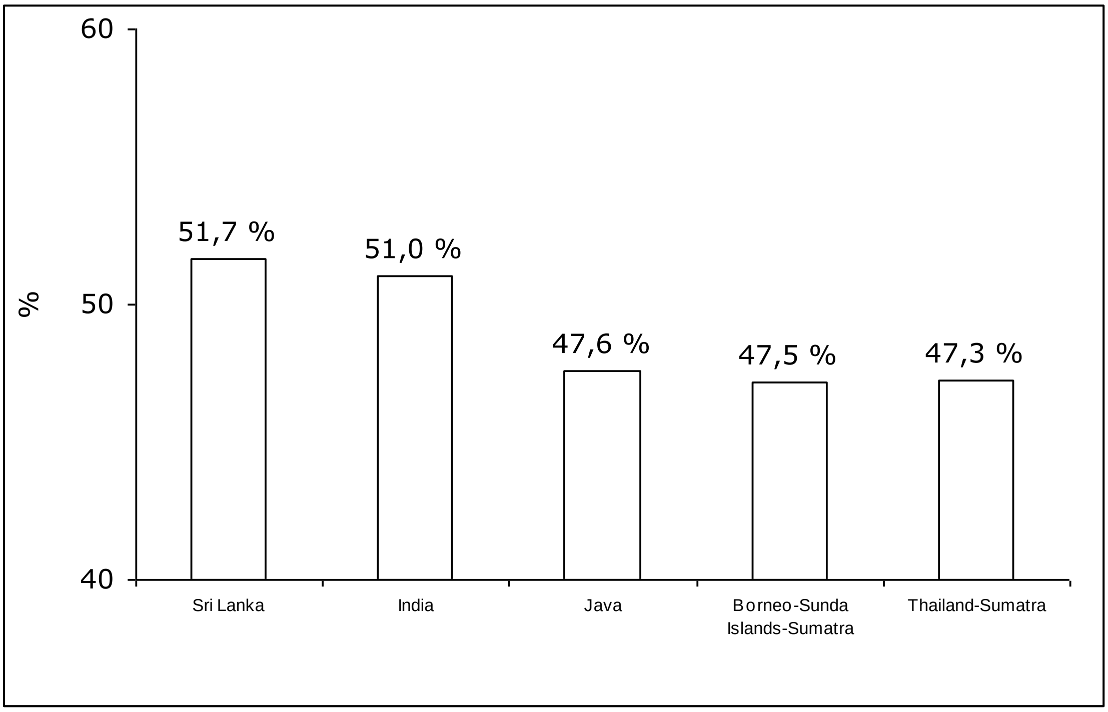


Figure 3.5. Percentage proportion of zygomatic width (ZW) to condylobasal length (CBL) (ZW/CBL*100) for tragulid skulls from Sri Lanka, India, Java, Borneo Sumatra, Sunda Islands, and Thailand.

3.4 Discussion

Since the recognition of *Tragulus* and *Moschiola* as different genera (i.e. Groves and Grubb 1982), several methodological approximations have corroborated this distinction (Meijaard and Groves 2004; Groves and Meijaard 2005; Hernández Fernández and Vrba 2005; Sánchez et al. 2014; Mennecart and Costeur 2016a,b). Our multivariate data provide support for the morphological distinction between the crania of these genera, with predominantly positive values for PC2 for specimens of *Tragulus* and negative values for *Moschiola* (Figure 3.3).

On the other hand, the number of species in each of the two genera is still debated, and estimates in literature appear to be biased by constraints in taxon sampling (e.g. Chasen 1940; van Bemmel 1949; Smit-van Dort 1989; Meijaard and Groves 2004; Groves and Meijaard 2005). Our PCA provides evidence in support of the existence of three morphometric clusters of *Tragulus* skulls and two clusters of *Moschiola* skulls (see Figure 3.3 and explanations above), and thus concur the recent taxonomic review by Meijaard and Groves (2004) for *Tragulus* and Groves and Meijaard (2005) for *Moschiola*.

The data gathered by Meijaard and Groves (2004) served as the basis for the formal description of *T. napu* (corresponds to our Borneo, Sumatra and Sunda Islands specimens), *Tragulus kanchil* (corresponds to our Sumatra plus Thailand specimens) and *T. javanicus* (corresponds to our Java specimens). The delimitation of these species in our analysis, as well as in Meijaard and Groves (2004), is based on the size and overall positive correlation of the factor loadings on PC1. The absolute size of the *Tragulus napu* specimens from Borneo, Sumatra, and the Sunda Islands also corresponds to that given in Meijaard and Groves (2004) (e.g. LCB from 97.3 mm to 112.1 mm; Table VII and Table VIII). The larger size and relatively small auditory bullae clearly distinguish *T. napu* from the other species of the genus. This is especially relevant since *T. kanchil* also lives in Sumatra, but is notably smaller (Figures 3.3 and 3.6).

Tragulus kanchil is morphologically distinct from, and allopatric to, *T. javanicus*. The taxon is widely distributed in SE Asia (e.g. Sumatra, Thailand, Borneo, Malayan and mainland Asia) with several subspecies. Specimens from Java stand out in our analysis because of their long and high mandibles (HM), narrow tympanic bullae (WB) and narrow braincase (BB) (Table VII). This result is congruent with Meijaard and Groves (2004), who proposed based on their analyses that only a single taxon, *T. javanicus*, occurs in Java. Moreover, our results add support to and reinforce the separation of *T. javanicus* from *T. kanchil* (Figure 3.3, specimens from Java versus specimens from Sumatra and Thailand). Based on these results, we infer that the DNA sequences of tragulid individuals from the Malayan Peninsula, Laos, and Borneo in Endo et al. (2004b citing Meijaard and Groves 2004) cannot stem from *T. javanicus*. The geographical distribution of *T. kanchil* partly overlaps with that of *T. napu*, but not with that of *T. javanicus*. The individuals identified as *T. javanicus* by Endo et al. (2004a), most likely belong to *T. kanchil* based on body size that is similar to that in *T. javanicus*.

The ranges of morphological variation recovered through PCA for *Moschiola* clearly segregates the individuals from India from those from Sri Lanka (Figure 3.3). Here, the revision by Groves and Meijaard (2005) served as a basis for the formal diagnosis of *M. indica* (corresponds to our India specimens) and for the separation of the *Moschiola* from Sri Lanka (corresponds to our Sri Lanka specimens). *Moschiola indica* is the largest (and monotypic) species in India, where it occurs from the southern tip of the subcontinent to approximately 24°N in both the east (Mandla, Hoshangabad, Palamu) and west (Rajasthan). The measurements obtained by Groves and Meijaard (2005) for condyle basal length (CBL) have a mean of 101.1 mm ± 4.9 mm (range 95.0 - 108.1 mm) and a zygomatic width (ZW) of 52.2 mm ± 1.6 mm (range 50.0 - 54.5 mm). This is entirely consistent with our results (CBL 103.4 mm ± 3.3 mm, ZW 52.8± 0.8 mm, Tables VII and VIII). The following species occur in Sri Lanka according to Groves and Meijaard (2005): *Moschiola kathygre* in the humid region with CBL ranging from 90.6 mm to 99.9 mm (mean = 96.4 mm ± 5.08 mm); *M. meminna* in the dry area (CBL ranging from 88.2 mm to 95.7 mm; mean 91.9 mm ± 3.2 mm), and a third, yet-undescribed species (CBL = 97.3 mm [n=1]). Although the mean values are suggestive of the existence of different species in Sri Lanka (Groves and Meijaard 2005), the wide overlap of the CBL ranges does not permit the safe discrimination of these species.

The diagnostic variables for *M. meminna* overlap with those of the other two species described for Sri Lanka (*M. kathygre* and the undescribed species) (Groves and Meijaard 2005:

Table VIII), and thus render the identification of our crania based only on morphometry impossible; qualitative characters that can be used to distinguish the species are not yet available. In addition to cranium morphometry, Groves and Meijaard (2005) included coat coloration, external body dimensions (e.g. body-head size, tail, ear) and habitat distribution (wet or dry zone) into their analyses and established well-defined traits for the species of *Moschiola* in India and Sri Lanka. Unfortunately, precise information on the provenance of our specimens from Sri Lanka is not available, neither from the labels nor the collection catalogue, and we did not analyze fur coloration or external morphology. We therefore refer to these specimens as *Moschiola* sp. to avoid errors in assignment (Table VIII).

Table VIII. Comparison of value ranges of variables mandibular length (LM), condylobasal length (CBL/LCB) (or length of mandible, LM), and zygomatic width (ZW) of *Tragulus* and *Moschiola* species from this study, as well as Meijaard and Groves (2004) and Groves and Meijaard (2005). LM values considered instead of CBL values* for *T. javanicus*, because CBL for *T. javanicus* is not included in Meijaard and Groves (2004). Measurements are in mm.

	This study		**Meijaard and Groves (2004)**	
Species	**CBL/LM(*)**	**ZW**	**CBL/LM(*)**	**ZW**
Tragulus javanicus (Java)	73.5-83.1*	41.8-48.6	72.8-78.8*	40.4-44.2
Tragulus napu (Borneo, Sumatra, and Sunda Islands)	97.3-110.6	46.5-51.6	96.8-116.3	45.0-52.7
Tragulus kanchil (Sumatra and Thailand)	81.3-89.9	38.8-43.1	81.4-101.8	38.5-48.1

Species	**This study**		**Groves and Meijaard (2005)**	
	CBL	**ZW**	**LCB**	**ZW**
Moschiola indica (India)	101.1-105.7	52.2-53.3	95.0-108.1	50.0-54.5
Moschiola spp. (Sri Lanka)	86.6-96.2	42.1-51.8	91.1-97.3	46.0-49.3
Moschiola meminna (Sri Lanka)	-	-	88.2-95.7	43.8-49.4
Moschiola kathygre (Sri Lanka)	-	-	90.6-99. 9	44.9-50.9
Moschiola sp. undescribed (Sri Lanka)	-	-	97.3	49.3

Nevertheless, our data support the separation of the individuals from India from those from Sri Lanka. In other words, our data concur with Groves and Meijaard (2005) in that *M. indica* is distinctly different (larger) from *Moschiola* from Sri Lanka. We cannot confirm that *Moschiola* is monotypic as proposed by Mennecart and Costeur (2016a). Since this latter study only considered specimens from Sri Lanka, *M. indica* was *per se* excluded. The taxonomic assignments of most of the skulls as stated in the different collection catalogues (Appendix 3, Table 3.1) are confirmed by our analyses. However, the identification of some of the specimens was refuted and evidence provided for reassignment. Since most labels attached to the skulls show outdated and/or invalid taxonomic assignments, they may cause continued confusion. Based on the results obtained from our analysis (PCA: factor loadings), we recommend to the keepers of zoological collections holding older tragulid material to measure nasal length, palatine length, condylobasal length, zygomatic width, and occipital height dorsal of ophistion (NL, PL, CBL, ZW, and OH in Figure 3.1) to obtain a reliable data set for taxonomic assignment. Moreover, we were able to confidently assign an enigmatic specimen labelled "Sunda Islands" (NMB C2950) to *Tragulus napu*.

The crania of *Tragulus javanicus* and *T. kanchil* are relatively tall and the neurocrania are globose, while cranial heigth is less pronounced in specimens of *T. napu* and *Moschiola* spp. and somewhat flattened, more comparable to *Hyemoschus aquaticus* of Africa (Figure 3.6). These differences in cranial shape might be related to differences in dietary habits and mastication movements, as the neurocranium is largely shaped by the attachment areas of the chewing muscles. However, no comparative studies on the dietary habits of tragulids are available, and functional morphology of the tragulid mastication has not been assessed to substantiate or refute this speculation. Another possible explanation for the differences in cranial morphology might be related to the fact that *Moschiola* and *T. napu* commonly escape from predators through diving and under-water locomotion (Meijaard et al. 2010). Under-water locomotion is perhaps facilitated by a flatter, more hydrodynamic skull shape. Escape from predators through diving and movement under water has not been reported to date in *T. kanchil* and *T. javanicus*. Finally, the larger degree of correspondence in skull geometry between *T. javanicus* and *T. kanchil* might indicate a closer phylogenetic relationship of these species.

Figure 3.6. Skull morphology in three different species of Tragulidae. Top image = *Moschiola indica* (ZSM 1906/6); middle image = *Tragulus napu* (NMB C2950), and bottom image = *T. kanchil* (NMB 3735). Scale bar represents 10 mm

Several studies have demonstrated that *Hyemoschus aquaticus* from Africa, which is also characterized by a flattened skull, is closer related to the fossil *Dorcatherium* than to the extant *Tragulus* and *Moschiola* (Rössner 2010; Sánchez et al. 2014; Mennecart and Costeur 2016b). Thus, if the shape of the *Hyemoschus* skull is also present in *Dorcatherium,* this would then argue in favor of a plesiomorphic character state, whereas a globose neurocranium would probably represent a derived character in *Tragulus kanchil* and *T. javanicus*.

3.5 Conclusions

One result of the increased use of the phylogenetic species concept in zoology is the splitting of long-standing and widely accepted species that were established before on the basis of other species concepts (e.g. biological species concept). The raising number of new species of mammals, generated primarily through the promotion of sub-species to the rank of species, has been criticized as producing taxonomic inflation or, in other words, artificial increase of the number of species. On the other hand, Zachos et al. (2013) states that species splitting must not be deemed bad *per se*, and taxonomic inflation is not necessarily the consequence of splitting, but rather of inappropriate application of the phylogenetic species concept or the naive interpretation of inconclusive data. The data/strong evidence available today on tragulids provides a strong argument in favor of splitting the historical species (Meijaard and Groves 2004; Groves and Meijaard 2005; Meijaard et al. 2017). We agree with Groves (2013) in that classifications must always be open to be tested on the basis of additional data and new analytical approaches complementing the information available to avoid or reduce the problem of species inertia (Gippoliti et al. 2017) and species inflation (Zachos et al. 2013).

Our study provides independent evidence corroborating the recently suggested species splitting into/delimitation of *Tragulus kanchil*, *T. napu*, *T. javanicus, M. indica,* and Sri Lankan tragulids (Meijaard and Groves 2004; Groves and Meijaard 2005). *Tragulus napu* stands out among the *Tragulus* species because of the larger cranium with a flatter and more robust overall appearance, while the crania of *T. javanicus* and *T. kanchil* are smaller and more delicate. *Moschiola indica* from India is larger than *M. meminna* and *M. kathygre* from Sri Lanka (Groves and Meijaard 2005). *Moschiola* can be separated from *Tragulus* by a more robust skull and clear sagittal crest; instead, *Tragulus* (with the exception of *T. napu*) possesses a more delicate skull and weak or absent sagittal crest. There are general differences in the overall skull geometry of *Moschiola* + *T. napu* and *T. kanchil* + *T. javanicus* that we have quantified for the first time in the present study. A more flattened versus a globose neurocranium is a morphological skull difference that is support for a closer phylogenetic relationship between *T. kanchil* and *T. javanicus*, but the adaptational significance of this difference, if any, remains elusive. Sri Lankan *Moschiola meminna* and *M. kathygre* cannot presently be safely discriminated based on morphology, but we anticipate that future studies on osteology of *Moschiola* can provide new morphological information for the discrimination of these species (see Meijaard et al. 2017).

Although this study is based on a statistically not significant sample size, comparison of the results to recently conducted extensive investigations ensures that it makes a contribution. Our results add to the clarification and update of taxonomical assignments of tragulid material in public collections and helps to lessen the bias for future of taxonomical studies of living Asian tragulids. It is a pilot study with regard to the quantification of skull geometry in tragulids. We recommend that museums update their records for Asian tragulids based on the most recent taxonomy using nasal length, palatine length, zygomatic width, condylobasal length, and occipital height dorsal of ophistion. Moreover, we strongly recommend that geneticists working on Asian tragulids ensure that they identify the species correctly before filing molecular data in GenBank or elsewhere. Greater efforts in better understanding Indo-Malayan tragulid diversity and distribution patterns is of cardinal importance when considering the current loss and fragmentation of tragulid habitats (e.g. Adila et al. 2017). Conservational measures are urgently needed.

CHAPTER 4

New skull record of Miocene *Dorcatherium crassum* (Lartet, 1851) from Walda 2 (Germany)

4.1 Introduction

The fossil chevrotains (Artiodactyla, Tragulidae) were diverse small to medium-sized ruminants that originated in the Eocene at least 34.0 mya, where they diverged from the ruminant stem lineage prior to the diversification of Pecora (for both opinions see Janis and Scott 1987; Gentry and Hooker 1988; Métais et al. 2001; Hernández Fernández and Vrba 2005; Hassanin et al. 2012). Tragulids are characterized by the presence of a single elongated lacrimal orifice situated just inside the rim of the orbit, and lack bony horns which are prominent features of pecoran ruminant artiodactyls (Gentry 1978; Groves and Grubb 2011). The male possesses large sabre-like upper canines, while these are much smaller in the female (Janis 1984; Rössner 2007). They were common in Eurasia and Africa; their species number peaked during the Middle Miocene, when several of the species lived sympatrically before decline until present (Unger et al. 2012; Barry 2014). The extant tragulids differ from the extinct ones by their lower phenotypic diversity comprising only small body sizes, and a relict distribution in the Southeast-Asian and Afrotropical regions (Meijaard 2011; Groves and Grubb 2011).

Dorcatherium crassum is a common terrestrial faunal element in the Miocene of Europe, as the widespread fossil remains reflect (Aiglstorfer et al. 2014). The species appeared in

Central Europe earlier than in Western / Southwestern Europe. The first appearance of *Dt. crassum* equals to the minimum appearance datum of the genus *Dorcatherium* in this continent (Rössner 2017). *Dorcatherium crassum* was first described by Lartet (1851) on the basis of postcranial material from Sansan, France, but without the designation of a holotype; Morales et al. (2012) recently established a neotype based on a left mandible from Sansan.

Dorcatherium crassum forms with the contemporaneous *Dt. vindebonense* and the younger *Dt. naui*, the group of medium-sized Central European *Dorcatherium* with bunoselenodont teeth (Rössner 2010). Because of the similar morphology and size the validity of *Dt. crassum* has been repeatedly questioned by several authors (see Rössner and Heissig 2013; Alba et al. 2014), who considered it a junior synonym of the type species *Dt. naui* from Germany. However, a thorough re-examination of the considerable variability of teeth and post-cranial morphology from different places in Europe showed that both species are well supported, for example, by their differences in tooth crown height and proximal inter-metacarpal region (e.g. Rössner 2010; Alba et al. 2011, 2014; Sánchez et al. 2011; Morales et al. 2012). *Dt. crassum* is also considered to be very similar in skeleton and body mass to the living aquaphilic tragulid *Hyemoschus aquaticus* from Africa (Milne-Edwards 1864; Carlsoon 1926; Dubost 1978; Gentry 1978; Barrette 1982). Milne-Edwards (1864) noticed the strong osteological and odontological similarity between the fossil “deer” *Dicrocerus* ? *crassus* Lartet, 1839 from Sansan (France) and the living *Hyemoschus aquaticus*. Thus he included the fossil species in his newly erected family Tragulidae and *Hyemoschus*. However, Schlosser (1916) finally affiliated it to the genus *Dorcatherium.*

Recently, Mennecart and Cousteur (2016) studied the petrosal bone and bony labyrinth morphology among living *Tragulus*, *Moschiola* and *Hyemoschus* and *Dt. crassum*. They found most morphological accordance in *Dt. crassum* and *Hyemoschus aquaticus*, but a comparison of skull anatomy among these species was not possible. Data on cranial anatomy for *Dt. crassum* are scarce as well as fossil tragulids. In this context, based on the morphology and metric variables of attached teeth, Seehuber (2015) attributed a female skull from Thierhaupten 2 (Germany, Middle Miocene) to *Dt. crassum,* but despite the relatively good state of preservation, he did not provide details about its morphology. The description of another relatively well-preserved partial skull from France (Mennecart et al. 2018a) has added more anatomical information (external morphology, dentition, petrosal bone and bony labyrinth) to the knowledge of *Dt. crassum*. However, the latter study compared merely superficially with living species. Another skull from Germany (Steinheim am Albuch, Middle Miocene) was figured but not described by Gentry et al. (1999); its taxonomic affiliation is still unclear (Mennecart et al. 2018). In addition, de Bonis et al. (1998) described superficially a skull fragment of a small *Dorcatherium* sp. from Thymiana B of the middle Miocene in the island of Chios in Greece.

It is evident from the preceding paragraph that skull material of fossil tragulids is not abundant, not very well preserved and poorly known, as well as comparison with the living relatives is missing. Here we describe the external morphology of another, so far undescribed skull of *Dorcatherium crassum* from the lower Middle Miocene of Germany. We compare it to the external morphology of the living species and discuss some morpho-functional and palaeoecological aspects.

4.2 Material and Methods

This study is based on a single well-preserved skull of *Dorcatherium crassum* from Walda 2 (Landkreis Augsburg, Bayern) in southern Germany. This locality (Figure 4.1) is located in Miocene deposits of the Northern Alpine Foreland Basin and correlated with unit MN5 (De Bruijn et al. 1992) of the European Land Mammal Chronology. Its fluvial sediments are characterized by ochres and reddish brown sands. The studied specimen is currently stored at the Naturmuseum Augsburg in Germany, however the inventory number is in process. Thus, here we refer to the specimen as NMA-Walda 2. Cranial and dental measurements of bones and attached teeth were made in millimeters with a digital caliper.

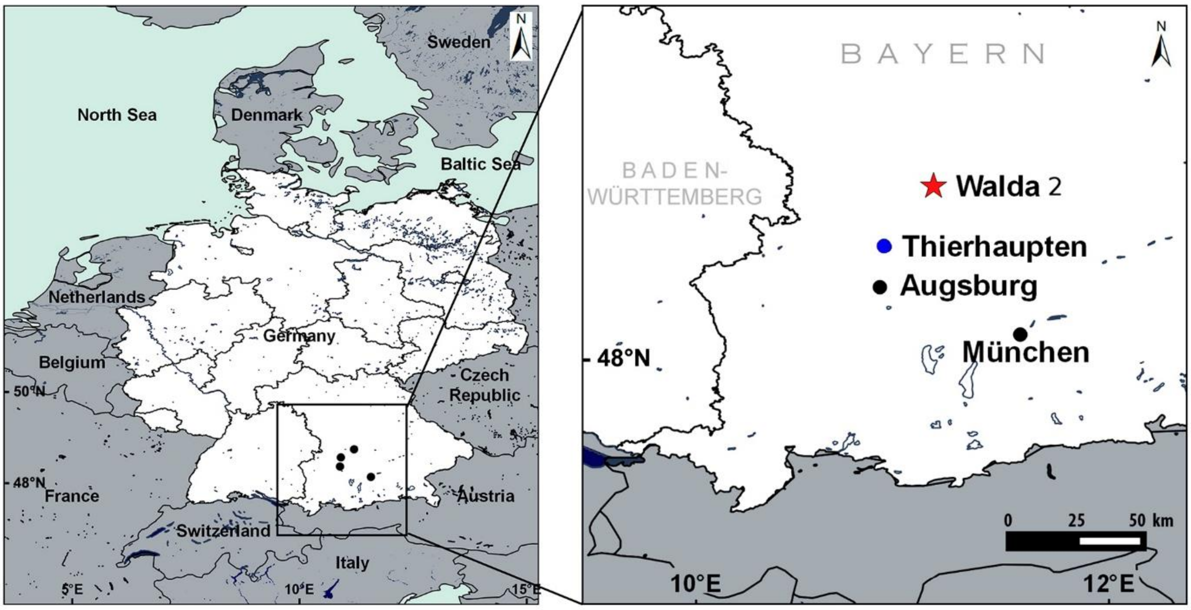


Figure 4.1. Map indicating the geographic position of the locality Walda 2 (red star) from where the described *Dorcatherium crassum* skull was collected. Also the locality Thierphaupten from the *Dt. crassum* described by Seehuber (2015) is indicated.

Because the skull is partially reconstructed (Figure 4.2), a high resolution computer tomography was performed in order to separate between original and artifical anatomy. The specimen was scanned at the Bavarian Natural History Collections facility with a phoenix x-ray nanotom m (GE Sensing & Inspection Technologies GmbH, Wunstorf / Hannover, Germany) at 120 kV voltage and 40 µA current with a 0.2 mm copper filter. 1,330 x-ray slices were generated, which yielded a volume data set with the following dimensions: 1592 x 2909 x 1498 mm with 6.6 µm voxel size. The slices obtained in the scanning procedure were segmented one by one by hand using the software Amira (version 6.1.4; Visage Imaging, Berlin, Germany). The 3D model is available at: https://data.ub.uni-muenchen.de/ and was performed using the free software: MorphoDig version 1.5.3 64-bit, available at: https://www.morphomuseum.com/.

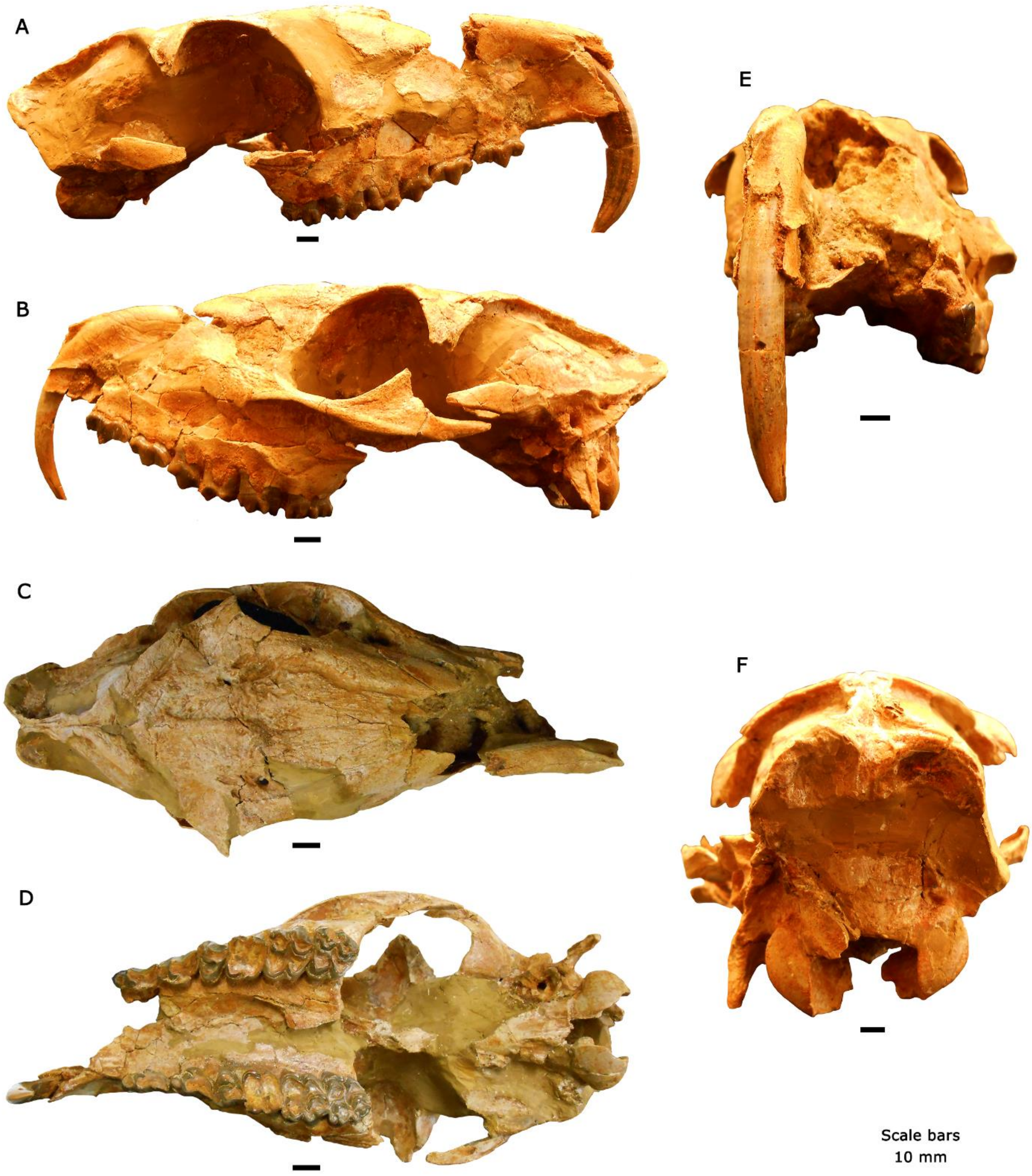


Figure 4.2. Original skull of *Dorcatherium crassum* NMA-Walda 2 studied here. **A**) rigth lateral view of cranium, **B**) left lateral view of cranium, **C**) dorsal view of cranium, **D**) ventral view of cranium, **E**) rostral view of cranium, **F**) caudal view of cranium.

The skull nomenclature employed in this study follows Moore (1981) and Carlsson (1926), the dental nomenclature is according to Bärmann and Rössner (2011). The measurements taken on teeth (length and width) are defined in Rössner (1995). We follow in part the taxonomic classification proposed by Sánchez et al. (2014). This is not based on a complete reconstruction of phylogeny of Tragulidae, but it is the only by now. The *Dorcatherium crassum* skull described here was identified according to characters of attached dentition with the help of Rössner (2010), Morales et al. (2012) and Aiglstorfer et al. (2014).

Metric variables of NMA-Walda 2 were compared to living tragulids. Thus, twenty skulls from *Hyemoschus aquaticus* (n = 3), *Moschiola meminna* (n = 3), *Tragulus javanicus* (n = 2), *T. napu* (n = 7), and *T. kanchil* (n = 4) were analyzed. Because the skull of *Dt. crassum* is a male adult (enlarged canine and third upper molar erupted), it was exclusively compared with adult males of the living species. To enrich the sample we considered the morphometric variables of *Dt. crassum* from Thierhaupten (Seehuber 2015) and partially studied here. Specimen and repository information is provided in the Table IX and Table XII and Appendix 4, Table 4.1. For each skull, 14 cranio-dental morphometric variables were measured with a digital caliper (accuracy 0.01 mm) following Guzmán and Rössner (2018) (Figure 4.3).

The product of the maxillar length and condylobasal length was calculated and the result multiplied by 100 to quantify overall skull geometry per species. The same procedure was followed with the length of upper tooth row and the length of upper diastema (Table I, variables **o**, **p** and **q**). Principal Component Analysis (PCA) of the morphometric variables transformed to $\log_{10}$ was used to delimit the species in the morpho-space. With this analysis, we do not intend to evaluate the complete relations between the morphometric skull variables of the living tragulids and *Dt. crassum* species. We only want to describe the affinities in the morphometric space of *Dt. crassum* among some living species. The statistical analyses were performed using free software PAST 3.14 (Hammer et al. 2001).

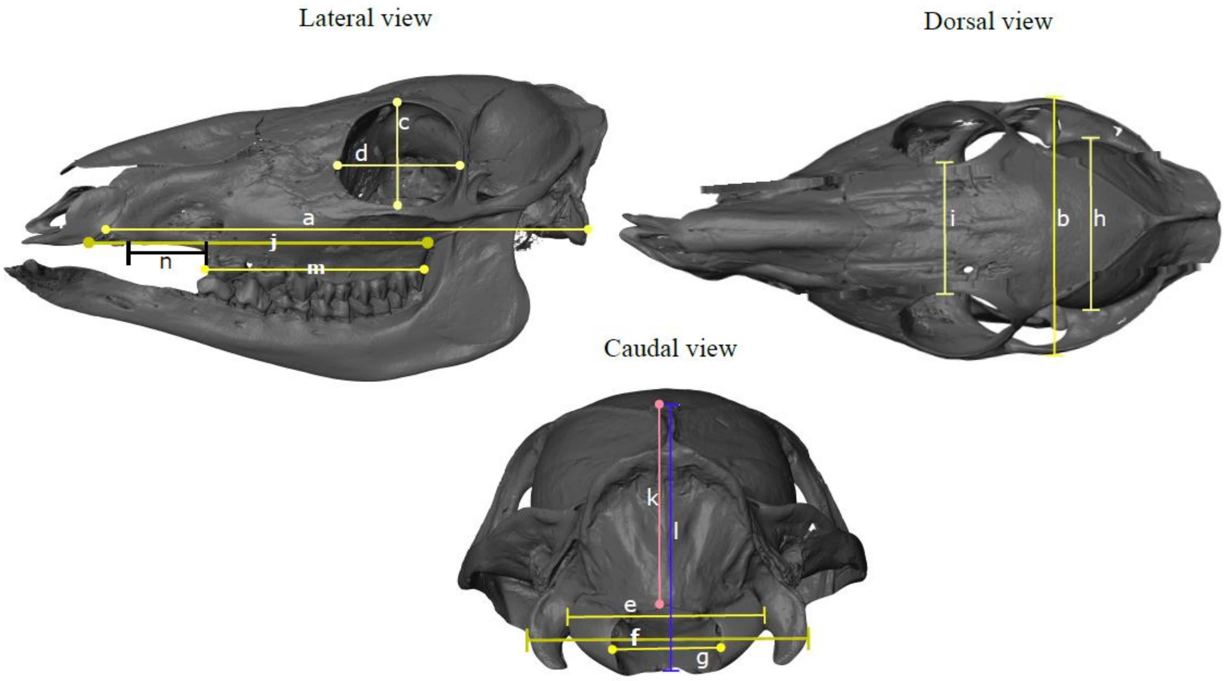


Figure 4.3. Standard measurements used in the analysis depicted on a skull of *Hyemoschus aquaticus* (H – 30). **a**: condylobasal length (measured from the occipital condyle to anterior side of the canine); **b**: zygomatic width; **c**: largest dorsoventral diameter of orbits; **d**: largest anteroposterior diameter of orbits; **e**: occipital condylar width; **f**: paraoccipital width; **g**: latero-lateral diameter of foramen magnum; **h**: width of braincase; **i**: interorbital width; **j**: maxillar lateral length; **k**: height dorsal ophistion; **l**: height dorsal basion; **m**: length of upper tooth row; **n**: length of upper diastema. Proportions not depicted in this figure. **o**: proportion of the maxillar length (**o** = [j/a]*100); **p** = proportion of the length of upper tooth row (**p** = [m/a]*100); **q** = proportion of the length of upper diastema (**q** = [n/a]*100).

Institutional abbreviations:

NMA, Naturmuseum Augsburg, Germany; SNSB – BSPG, The Bavarian Natural History Collections - Bavarian State Collection of Paleontology and Geology, Munich, Germany; NMB, Natural History Museum Basel, Switzerland; SMNS, State Museum of Natural History Stuttgart, Germany; NHMW, Natural History Museum Vienna, Austria.

Systematic Paleontology

Class **Mammalia** Linnaeus, 1758

Order **Artiodactyla** Owen, 1848

Suborder **Ruminantia** Scopoli, 1777

Family **Tragulidae** Milne-Edwards, 1864

Genus ***Dorcatherium*** Kaup, 1833

Type Species ***Dorcatherium naui*** Kaup and Scholl, 1834

Dorcatherium crassum (Lartet, 1851)

Figures 4.2, 4.4

Neotype: Recently established by Morales et al. (2012) based on a left mandible of type locality of Sansan, France.

Type locality: Sansan, Molasse marine de Salles, Gers, France, Middle Miocene, MN6 (Rössner 2010).

Stratigraphic range: Early Miocene (MN4a) – to Middle Miocene (MN6) (Morales et al. 2012, Aiglstorfer et al. 2014; Rössner 2017) potentially (MN7) (Mennecart et al. 2018).

Geographical distribution. Germany, Austria, Switzerland, France, Spain.

Material studied: NMA-Walda 2, a well-preserved skull of *Dorcatherium crassum* from Germany with dentition containing the skull roof represented by both frontal and parietal bones, a, right and left maxilla with right canine in alveola and left and right complete postcanine tooth rows (P2 to M3), fragmented basicranium represented by basioccipital, paroccipital process. Also left squamosal and jugal bones are present (Figure 4.2).

4.3 Results

Skull: NMA – Walda 2 is partially fragmented and deformed, but a number of structures are preserved as well as its general morphology (Figures 4.2 and 4.4). The 3D model of NMA-Walda 2 is available at: https://data.ub.uni-muenchen.de/.

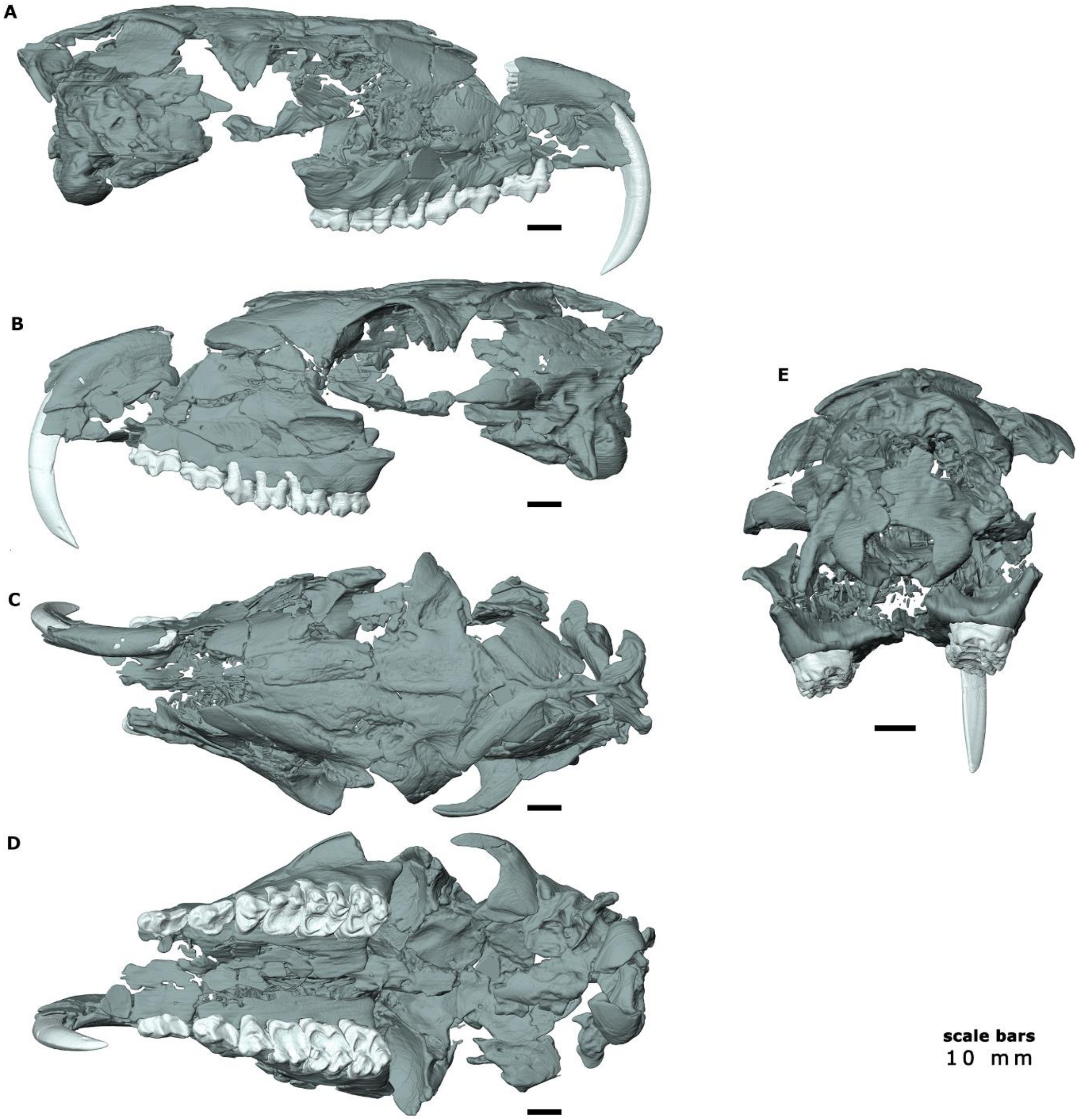
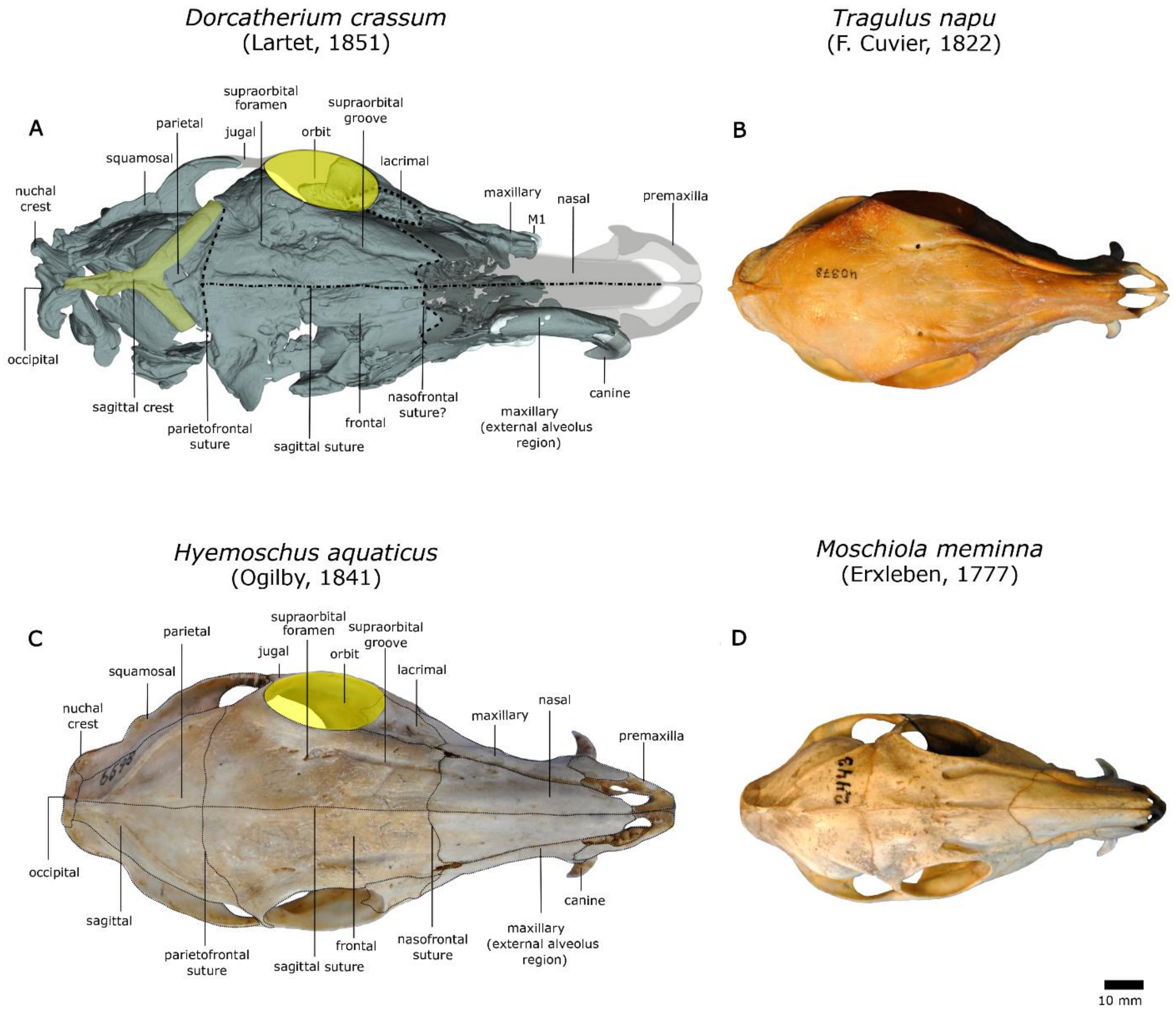


Figure 4.4. 3D reconstruction of the external skull morphology of *Dorcatherium crassum* NMA-Walda 2 here studied. **A**) right lateral view of cranium, **B**) left lateral view of cranium, **C**) dorsal view of cranium, **D**) ventral view of cranium, **E**) caudal view of cranium.

Sutures are strongly fused; therefore the identification of the limits between bones was not possible, but it have been inferred by comparision with living tragulids species (Figures 4.5 to 4.7). The skull roof is fully preserved and represented by left and right occipitals, parietals and frontals, while both nasal bones are destroyed. The dorsal surface of the skull roof is almost parallel to the occlusal surface of the cheek teeth. The nasal bones are completely broken and it is not possible to see, if the nasals and maxillary bones were in contact or not (Figure 4.5). Because the preserved anterior part of the frontal is anterior to the orbit, it is highly probable that nasal bones reached this area of the skull. In the living *Hyemoschus aquaticus* the nasal and frontal are in contact at level of P3, and extended anteriorly to anterior part of canine alveola (Figure 4.5, Figure 4.6).

Apparently (and by inference) the naso-frontal suture of NMA - Walda 2 has a W-shape (Figure 4.5) as in *H. aquaticus* and in *Dt. crassum* from Contres. Despite the sagittal crest is damaged, it is strongly developed and slightly convex, separating into left and right temporal lines in the middle of the braincase (Figure 4.5 A) alike in *Dt. crassum* from Contres and Thierhaupten (Mennecart et al. 2018a) and *H. aquaticus*. In NMA-Walda 2 (and the others) it is a wide ridge and passes at the dorso-caudal skull edge to the well-developed and strong nuchal crest, forming the framing external crest of the occipital. The sagittal crest has a height of 4.17 mm in the more posterior part, almost in the confluence with the nuchal crest. In *H. aquaticus* the same pattern is evident, but weakly developed (Figure 4.5).


Dorcatherium crassum (Lartet, 1851)

Tragulus napu (F. Cuvier, 1822)

Hyemoschus aquaticus (Ogilby, 1841)

Moschiola meminna (Erxleben, 1777)

Figure 4.5. Dorsal view of tragulid crania. **A**) 3D reconstruction of the external skull-morphology of NMA-Walda 2; yellow colour indicates orbit and sagittal crest, grey colour indicates the hypothetical nasal bone and premaxilla. **B**, **C**, and **D** living species, yellow colour indicates the orbit.

The frontal bones and the anterior part of the parietal bones form an almost flat surface, between orbits the supraorbital groove is well developed. In dorsal view these grooves run from more or less the level of the middle of the orbits to the naso-frontal suture at the level of P3-P4. In *Tragulus*, *Hyemoschus* and *Moschiola* these grooves present the same morphology and variation, as well as the skull from France (Mennecart et al. 2018a). Part of the sagittal suture is located over a protuberance that extends from the middle of the frontal bones to parietofrontal suture (Figure 4.5 A).

The premaxillae are not recorded. Right maxilla and the canine are partially preserved (Figure 4.6). On the left side the maxilla is damaged and the zygomatic arch is partially preserved (Figure 4.5 A). The right and left tooth row is preserved from P2 to M3, however, the dentition is in a very advanced state of wear. In lateral view the neurocranium is flat more similar to living *Hyemoschus aquaticus* than the "globose" shape reported for *Tragulus javanicus* (Guzmán and Rössner 2018) (Figure 4.4 A, D, Figure 4.6). The right maxilla is highly damaged and the infraorbital foramen is destroyed. The dorsalpart of the right maxilla is convex and contains a long alveola for the upper canine. The diastema is short relative to the long tooth row. It is similar to the length of P2+P3 and comparable in relative length to *H. aquaticus* (Figure 4.6). In NMA-Walda 2 the maxillary ramus of the zygomatic arch is horizontally arranged and almost parallel to the roof of the skull (Figure 4.6). The anterior border of the zygomatic arch is above M2 and M3, coinciding with the position in *Hyemoschus aquaticus*. The postorbital bar is destroyed, but a fragment associated with the frontal bone is conserved (Figure 4.2). As in the living species it is primarily composed of the jugal and oriented more or less horizontally.

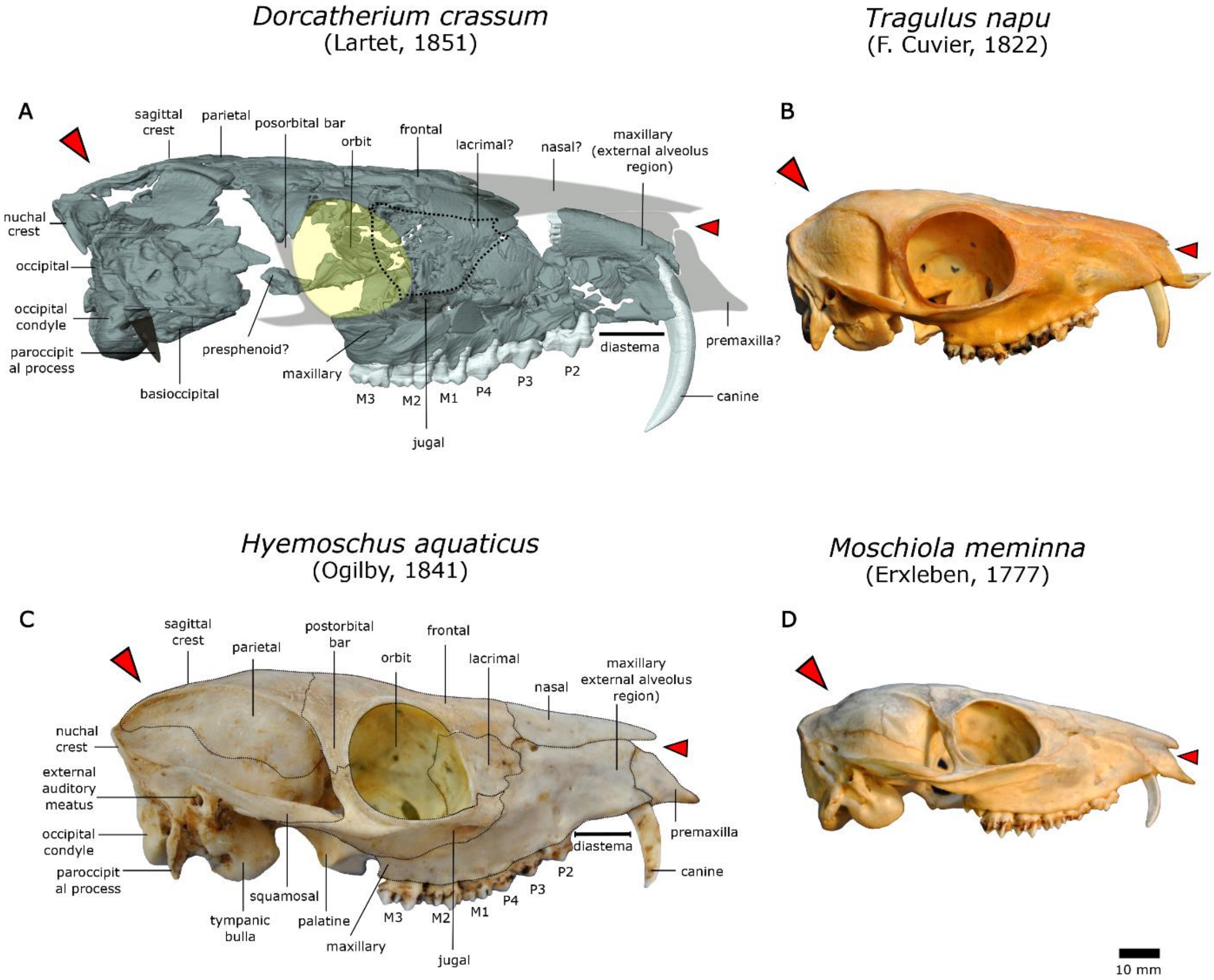


Figure 4.6. Lateral view of tragulid crania. **A**) 3D reconstruction of the external skull-morphology of NMA-Walda 2; yellow colour indicates the orbit; grey colour indicates the hypothetical postorbital bar, nasal and premaxilla. **B**, **C**, and **D** living species, yellow colour indicates the orbit. Big red arrows point to the differences for the saggital crest. The small red arrows point to (assumed) contact between the maxillary and the premaxilla.

The squamosal bone forms a flat portion of the lateral wall of the braincase. This projects horizontally from the neurocranium, then bends 90º anteriorly and joins with the jugal bone at level of the postorbital bar forming the zygomatic process (Figure 4.5 A). The orbit apparently is trapezoid-like with very rounded corners; the ventral part extends more to anterior than the dorsal part. The orbit is highly variable in living tragulids, being rounded, rectangular or even more triangular (Figure 4.6). The ventral elements of the rostrum are highly damaged (maxilla, palatine) or destroyed (premaxilla) (Figure 4.7), while the basicranium is partially preserved (occipital bone, paroccipital process, basioccipital). The occipital condyle is longer than high. The paroccipital process is long and wide, with the base broader than the tip it projects lateral of occipital condyle. The foramen magnum is deformed, but more or less circular (Figure 4.7 and Figure 4.8).

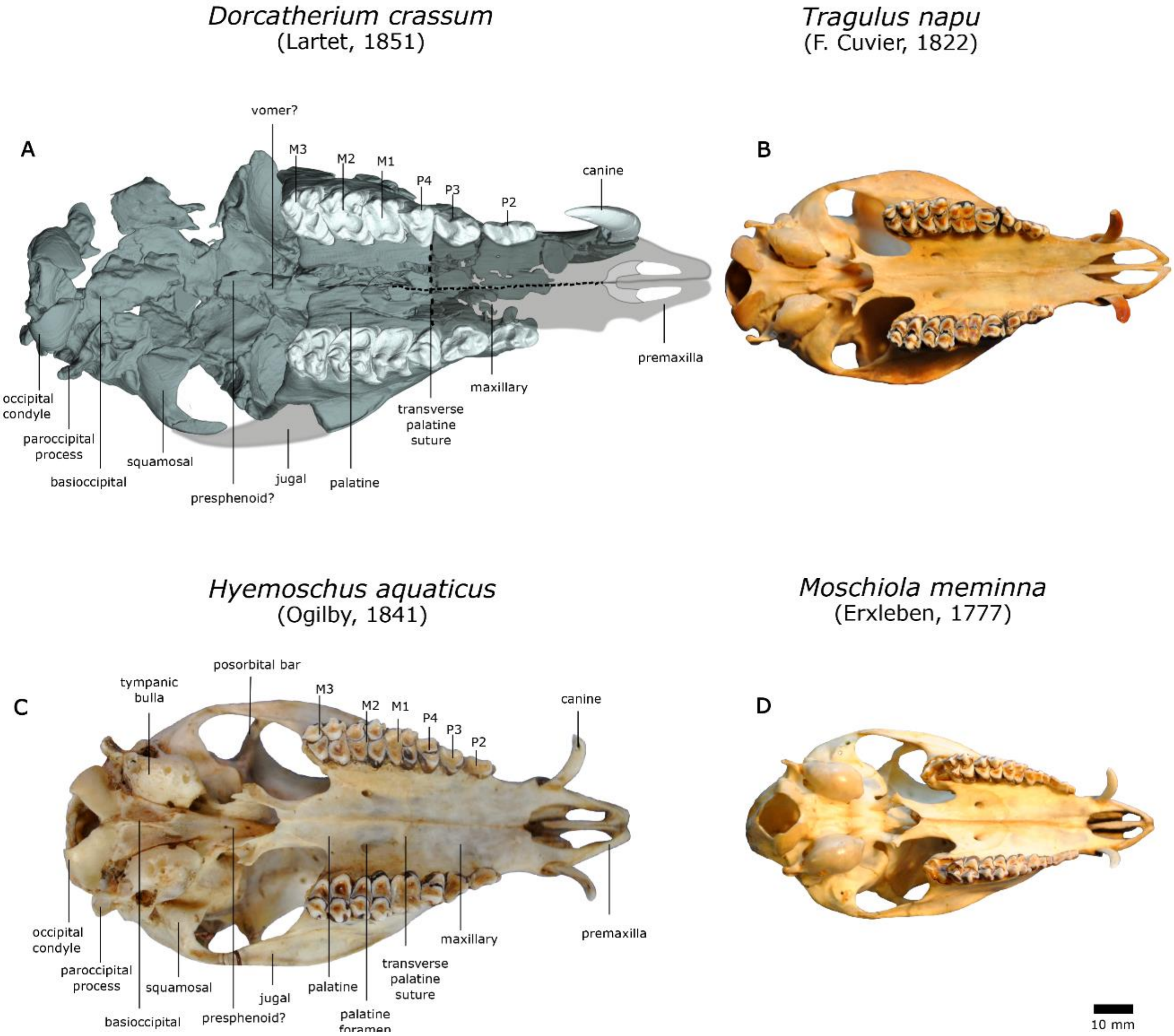


Figure 4.7. Ventral view of tragulid crania. **A**) 3D reconstruction of the external skull-morphology of NMA-Walda 2, grey colour indicates hypothetical jugal and premaxilla. **B**, **C**, and **D** living species.

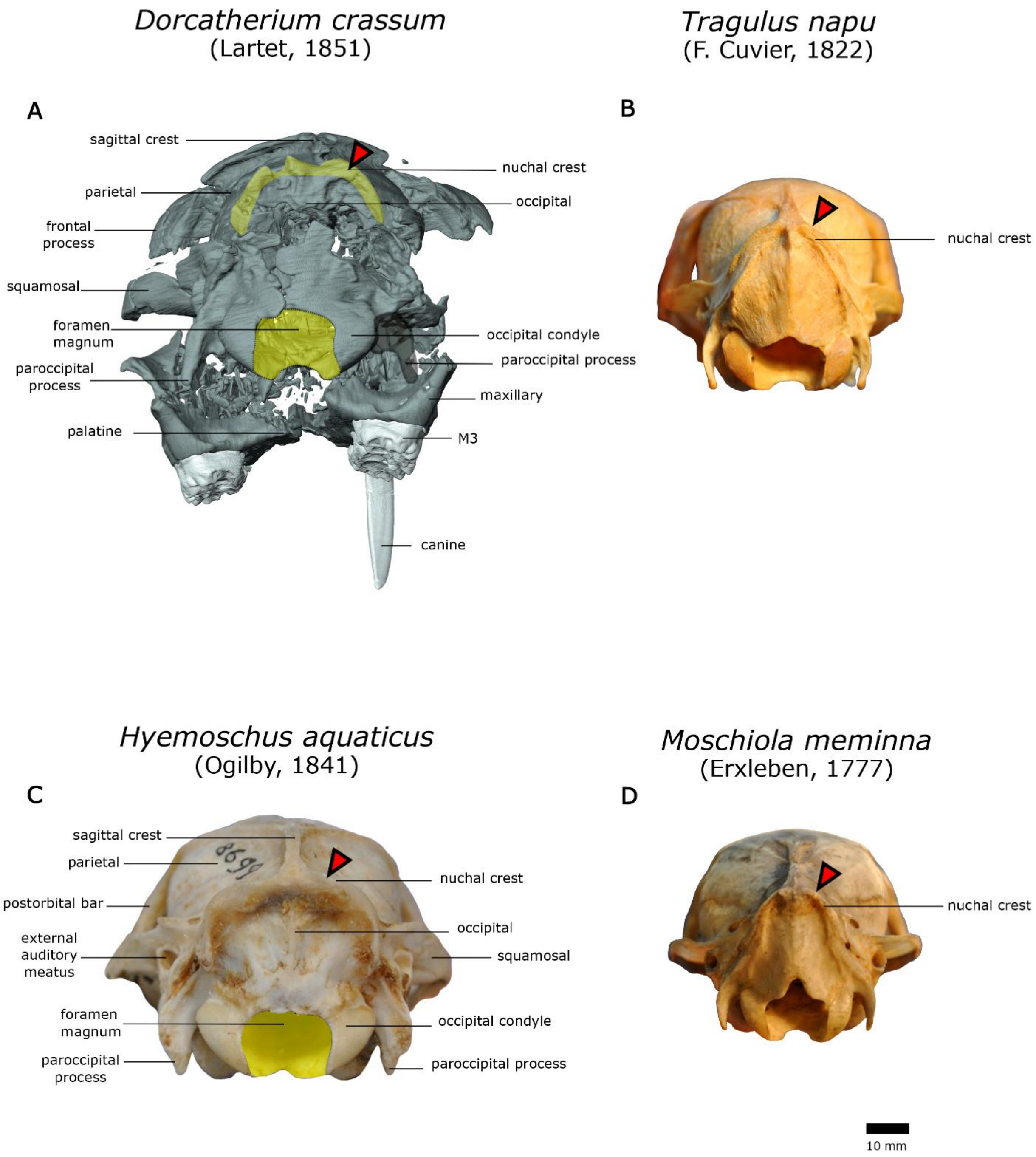


Figure 4.8. Caudal view of tragulid crania. **A**) 3D reconstruction of the external skull-morphology of NMA-Walda 2, yellow colour indicates the nuchal crest and foramen magnum. **B**, **C**, and **D** living species, yellow colour indicates the foramen magnum. Red arrows point to the saggital crest.

Table IX. Cranio-dental variables of fossil specimens of *Dorcatherium crassum* and for extant tragulid species of the genera *Hyemoschus*, *Moschiola* and *Tragulus* here studied. Measurements from a to n are in mm. From o to q the values are proportions in %. Variables o: proportion of the maxillar length (o = [j/a]*100); **p**: proportion of the length of upper tooth row (p = [m/a]*100); **q**: proportion of the length of upper diastema (q =[n/a]*100). (Details of measurements variables are given in Figure 4.3). n.d. = no data

Species	Collection museum and inventory number	Cranio-dental variables measured in mm														Cranio-dental proportions (%)		
		a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q
Dorcatherium crassum (NMA-Walda 2)	NMA-Walda 2	173.0	80.0	38.3	36.4	35.0	44.6	17.9	46.6	52.0	102.4	37.9	51.9	72.5	21.2	59.2	12.3	41.9
Dorcatherium crassum (Thierhaupten)	NMA-2012-1/2131	153.0	84.3	27.5	34.1	29.9	38.4	15.2	50.0	46.9	nd	34.0	45.0	66.3	nd	nd	nd	nd
Hyemoschus aquaticus	NHMW-5407	139.3	62.9	24.2	27.1	31.6	43.5	16.3	42.7	33.8	73.4	26.9	41.4	50.4	13.7	52.7	9.8	36.2
Hyemoschus aquaticus	SNSB-BSPG H-30	139.9	63.7	25.9	28.4	30.8	44.2	16.9	42.0	32.0	73.5	27.3	40.9	50.0	15.4	52.5	11.0	35.7
Hyemoschus aquaticus	NHMW 40827	142.9	64.0	25.7	29.3	31.9	44.9	15.6	44.2	33.1	73.7	26.8	41.0	52.3	12.0	51.6	8.4	36.6
Moschiola meminna	SNSB-ZSM 1911-2163	91.0	46.6	20.1	22.3	18.9	27.3	13.2	32.4	22.3	47.6	13.9	26.2	37.1	9.1	52.3	10.0	40.7
Moschiola meminna	NHMB C-1366	87.6	45.3	18.9	22.8	19.6	28.1	11.9	31.8	24.2	49.7	17.9	27.2	38.5	9.4	56.7	10.7	43.9
Moschiola meminna	NHMB 1429	89.6	47.5	19.9	23.0	20.2	27.1	11.3	32.9	23.4	51.1	18.0	27.2	36.6	11.4	57.1	12.7	40.9
Moschiola meminna	NHMB 2328	84.6	42.1	19.4	23.3	19.7	26.4	13.7	30.9	21.6	47.6	14.7	25.5	35.5	8.5	56.3	10.1	42.0
Tragulus javanicus	SMNS 16874	88.9	41.8	21.1	23.5	20.2	28.8	10.8	31.0	26.6	46.6	27.1	19.9	31.4	10.6	52.4	11.9	35.3
Tragulus javanicus	SMNS 16876	94.5	45.3	21.5	24.2	21.5	27.8	12.3	34.5	28.5	54.4	29.1	19.9	36.9	12.2	57.5	12.9	39.0
Tragulus napu	SNSB-ZSM 09-411	97.7	47.1	24.5	25.4	22.2	28.9	11.9	32.8	28.6	38.0	24.0	29.1	38.2	11.6	38.9	11.9	39.0
Tragulus napu	SNSB-ZSM 1909/233	106.7	49.9	25.1	26.9	23.3	30.2	13.6	35.7	30.2	57.9	21.3	31.3	41.2	13.4	54.2	12.6	38.6
Tragulus napu	NHMW 1923	96.7	49.3	22.7	25.4	22.8	30.7	12.6	35.4	29.8	53.2	22.7	31.5	38.0	12.4	55.1	12.8	39.3
Tragulus napu	NHMW 40826	99.0	46.5	23.3	25.0	22.1	27.9	13.0	33.8	27.4	53.2	22.4	30.5	36.9	11.4	53.7	11.5	37.2
Tragulus napu	NHMW 40378	100.0	47.3	21.7	25.9	22.8	29.8	11.6	33.1	30.0	54.2	19.7	29.0	38.5	12.7	54.2	12.7	38.5
Tragulus napu	SNSB-ZSM 1903-9443	99.0	50.4	25.0	26.9	23.4	32.8	12.3	36.0	30.8	59.4	23.2	30.9	40.2	14.5	59.9	14.7	40.6
Tragulus napu	NHMW B6014	95.3	46.8	22.3	24.8	22.3	30.4	13.4	33.9	27.3	53.1	22.0	31.1	37.9	11.3	55.7	11.8	39.8
Tragulus kanchil	NHMB C3808	83.8	39.1	20.1	22.7	19.4	24.8	13.5	31.5	24.9	41.4	18.8	27.9	29.9	14.7	49.4	17.5	35.7
Tragulus kanchil	NHMB C3798	83.8	39.3	19.6	22.4	19.3	25.8	11.2	30.5	25.1	40.6	20.9	26.2	29.6	8.0	48.4	9.5	35.3
Tragulus kanchil	NHMW 1473	83.8	43.1	20.1	23.6	20.5	26.6	10.9	33.4	26.3	47.2	20.9	27.9	34.1	9.6	56.3	11.4	40.7
Tragulus kanchil	SNSB-ZSM 1964-233	87.9	40.4	20.7	23.8	18.9	26.1	10.5	29.9	25.4	48.6	20.9	26.8	33.9	10.5	55.2	11.9	38.5

Dentition: The teeth are in a very advanced state of wear but in sufficient condition to be described. They are preserved *in situ* on the maxillary bone (Figure 4.4 and Figure 4.9). Their general morphology is bunoselenodont with wrinkled enamel. In occlusal view the molars are square shaped with increase in overall size from M1 to M3. There is a strong cingulum running around the lingual base of the molars, being best developed in the protocone. The parastyle, paracone column, and mesostyle are labially prominent in contrast to the weak metacone column. The metaconule complex has a v-shape. The postprotocrista is shorter than the preprotocrista.

The P2 is slightly longer than P3, and P4 is the shortest premolar tooth. P2 has two roots and three cusps; the anterior cingulum is weak. The P3 has three cusps and triangular shape in occlusal view. The labial cones are higher than the lingual cone and the posterior part is wider than the anterior. Its cingulum is well developed, but more in the middle and anterior part. The P4 is wider than long and surrounded (except on the labial side) by a strong cingulum. The lingual cone is smaller than labial cone. The canine is very long and curved, with at least 50 % housed in a long maxillary alveola. The alveola runs along the maxillonasal suture and extends back to the level of P2 - P3, similar to living tragulids.

The apical region of the canine ends with a posteriorwards orientation, but does not extend to the level of the anterior border of P2 (Figure 4.3).

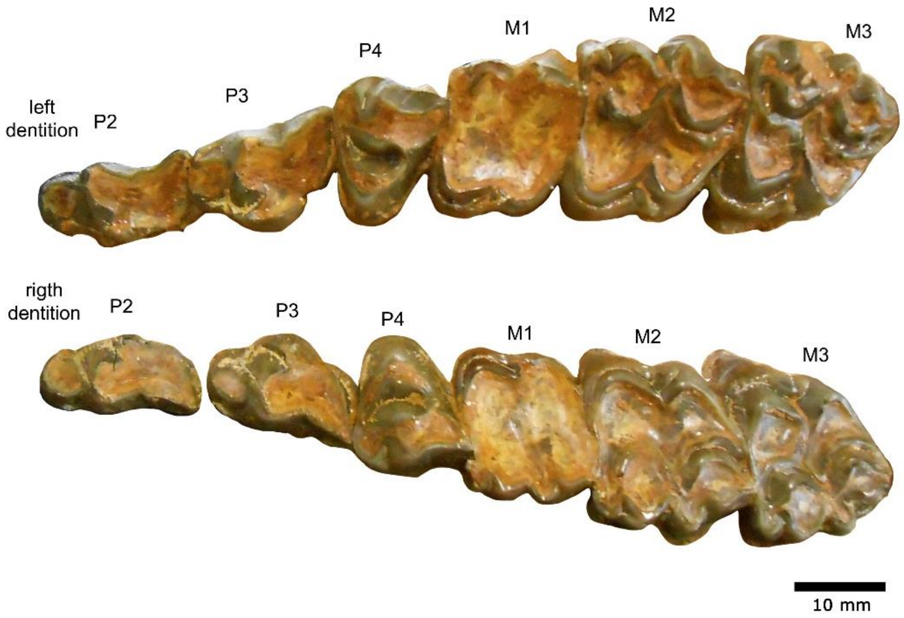


Figure 4.9. Occlusal view of upper dentition of NMA-Walda 2 here studied. Top figure: left tooth row; bottom figure: right tooth row. The metric data for these teeth are given in the figure 4.10 and Table XII. Provenance, collection museum and inventory number in Appendix Chapter 4, Table 4.1. Premolars: P2, P3, P4. Molars: M1, M2, M3.

Comparative morphometric analysis: the first two components of the Principal Component Analysis (PCA) accounted for more than 91.0 % of the total variance with the PC 1: 84.6 % and PC 2: 6.4 % (Table X). All morphometric variables had positive factor loadings for PC 1 and hence permit definition of this component as a size vector (Table III), while PC 2 had positive and negative factor loadings; it is associated with the form. PC 1 clearly separated *Dt. crassum* of Walda 2 and Thierhaupten from all living species; *H. aquaticus* was closer to *Dt. crassum* than the *Tragulus* and *Moschiola* species studied.

Table X. Distribution of the % variance expressed by components of the Principal Component Analysis.

PC Component	% of variance	PC Component	% of variance
1	84.57	8	0.49
2	6.42	9	0.20
3	3.11	10	0.13
4	1.76	11	0.11
5	1.63	12	0.08
6	0.77	13	0.05
7	0.68	14	0.02

The larger-sized species (*Dt. crassum* and *H. aquaticus*) are on the right and the medium and smaller-sized species (*Tragulus javanicus*, *T. kanchil*, *T. napu* and *Moschiola meminna*) on the left of the x-axis (Figure 4.10). The length of the maxillary and the upper tooth row had the highest factor loadings (0.32 and 0.31 respectively: Table XI) for this component, and hence clearly contribute to the separation of *Dt. crassum* from the other living species. The factor scores for PC 2 overlap between the living and fossil species, but there is moderate separation of *M. meminna* and *H. aquaticus* from *Dt. crassum* (Figure 4.10). The height of dorsal ophistion (HDO) had the highest factor loading (0.69) and supports this segregation (Table XI).

Table XI. Factors loadings for Principal Component 1 (PC1) and Principal Component 2 (PC2), from the Principal Component Analysis.

Figure 4.3	**Cranio-dental variables here studied**	**Principal Component**	
		PC1	**PC2**
a	Condylobasal length	0.3091	-0.0959
b	Zygomatic width	0.2949	-0.1334
c	Largest dorsoventral diameter of orbits	0.2086	0.1400
d	Largest anteroposterior diameter of orbits	0.1787	0.0577
e	Occipital condylar width	0.2670	-0.0716
f	Paraoccipital width	0.2591	-0.1587
g	Laterolateral diameter of foramen magnum	0.1785	-0.2603
h	Width of braicase	0.2024	-0.0650
i	Interorbital width	0.2861	0.2739
j	Maxillar lateral length	0.3260	-0.1289
k	Height dorsal ophistion	0.2746	0.6909
l	Height dorsal basion	0.3068	-0.3681
m	Length of upper tooth row	0.3176	-0.1717
n	Length of upper diastema	0.2690	0.3372

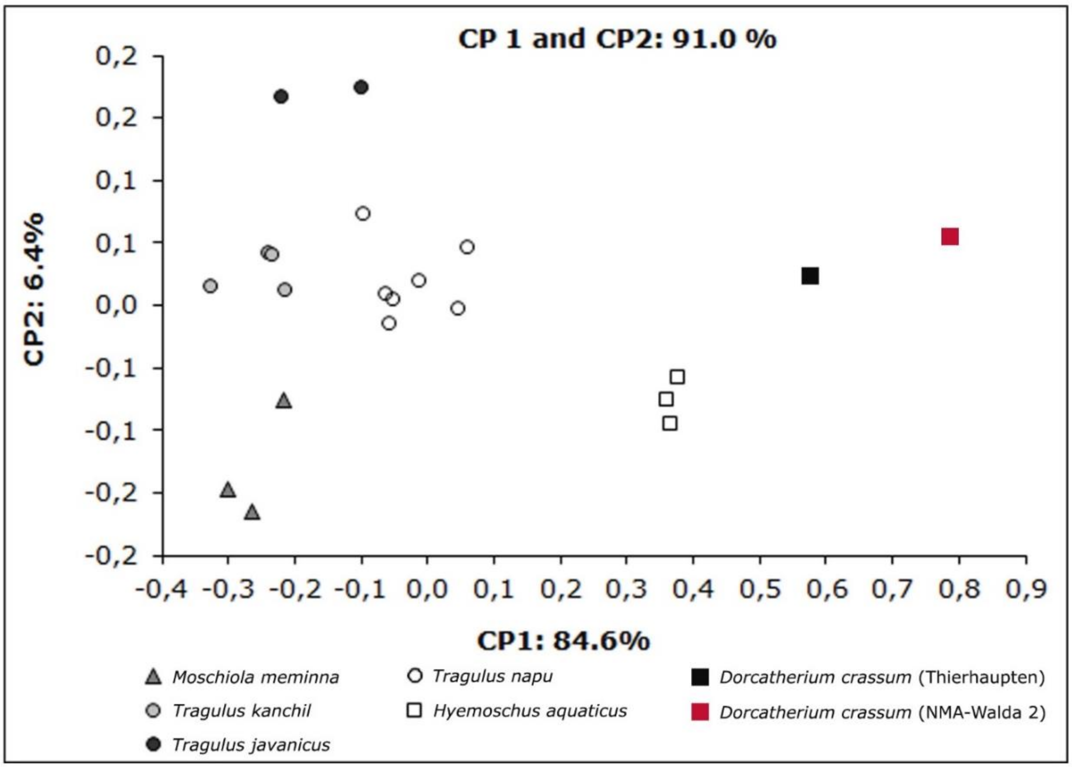


Figure 4.10. Components 1 and 2 of Principal Analysis generated with morphometric variables (Raw data, Table XII) from 22 individuals of 5 living tragulids species and one of the fossil species *Dorcatherium crassum*.

Compared to the living species studied here, *Dorcatherium crassum* had the longest skull length (condylobasal length), followed by the skulls of *Hyemoschus aquaticus* and *Tragulus napu* (Table IX). The larger skull, the proportions of the maxillary bone, diastema and the tooth row (with respect to the condylobasal length) for *Dt. crassum* are in the same range as the living species studied (Table IX), but closest to *M. meminna*. For dentition, *Dt. crassum* is clearly greater than living species (Figure 4.11).

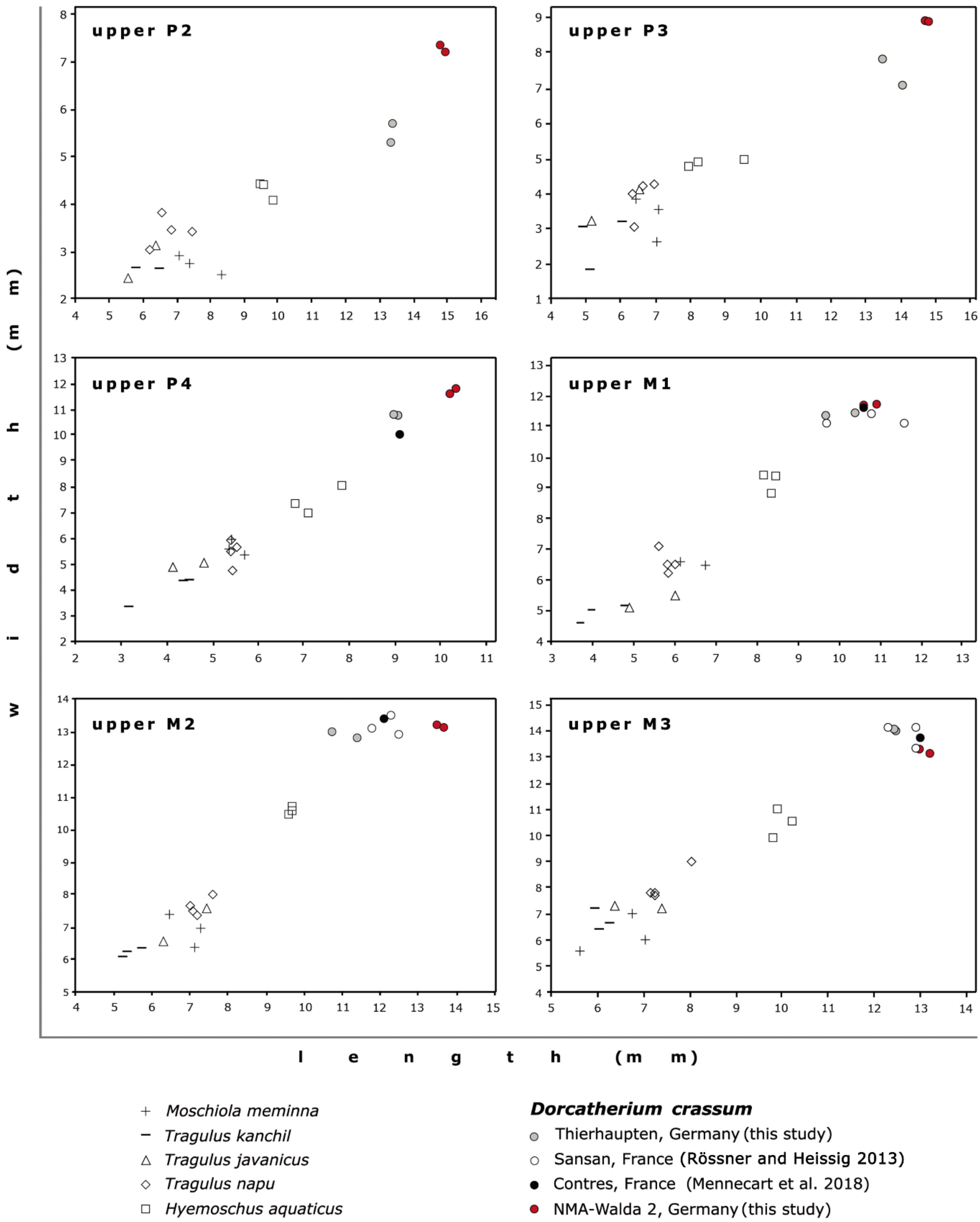


Figure 4.11. Biplot of the width vs. length (mm) for the upper teeth of tragulid species here studied. Data from *Dorcatherium crassum* from Sansan based on Rössner and Heissig (2013) and for *Dt. crassum* from Contres based on Mennecart et al., (2018). (Raw data, Table XII)

Table XII. Dental variables of fossil specimens of *Dorcatherium crassum* and for extant tragulids species of the genera *Hyemoschus*, *Moschiola* and *Tragulus* here studied. Measurements are mm. Data for *Dt. crassum* from Sansan based on Rössner and Heissig (2013) and for *Dt. crassum* from Contres: Mennecart et al. (2018). F = female; M = male; U = undetermined. sin.: sinistral side, dex.: dextral side.

Species	**Collection museum and inventory number**	**Geographical provenance**	**Sex**	**P2**		**P3**		**P4**		**M1**		**M2**		**M3**	
				l	**w**	**l**	**w**	**l**	**w**	**l**	**w**	**l**	**w**	**l**	**w**
Dorcatherium crassum	NMA-Walda 2 (sin.)	Walda 2	M	14.8	7.4	14.7	8.9	10.3	11.8	10.9	11.7	13.5	13.2	13.2	13.1
Dorcatherium crassum	NMA-Walda 2 (dex.)	Walda 2	M	14.9	7.2	14.8	8.9	10.2	11.6	10.6	11.7	13.7	13.1	13.0	13.3
Dorcatherium crassum	NMA-2012-1/2131 (sin.)	Tierhaupthen	F	13.3	5.3	13.5	7.8	9.1	10.7	10.4	11.4	10.8	13.0	12.5	14.0
Dorcatherium crassum	NMA-2012-1/2131 (dex.)	Tierhaupthen	F	13,4	5.7	14.1	7.1	9.0	10.8	9.7	11.3	11.4	12.8	12.4	14.0
Dorcatherium crassum	MNHN-SS-2300	Sansan	U	nd	nd	nd	nd	nd	sd	9.7	11.1	11.8	13.1	12.3	14.1
Dorcatherium crassum	MNHN-SS10857	Sansan	U	nd	nd	nd	nd	nd	sd	11.6	11.1	12.5	12.9	12.9	13.3
Dorcatherium crassum	MNHN-SS 1015	Sansan	U	nd	nd	nd	nd	nd	sd	10.8	11.4	12.3	13.5	12.9	14.1
Dorcatherium crassum	NMB-Fa.213	Contres	U	nd	nd	nd	nd	9.1	10	10.6	11.6	12.1	13.4	13.0	13.7
Hyemoschus aquaticus	NMB-5407	Cameroon	M	9.5	4.4	8.3	4.9	6.8	7.3	8.5	9.4	9.7	10.7	9.9	11.0
Hyemoschus aquaticus	SNSB-BSPG H-30	Gabon	M	9.6	4.4	9.6	5.0	7.9	8.0	8.2	9.4	9.6	10.5	9.8	9.9
Hyemoschus aquaticus	NHMW-40827	Congo	M	9.9	4.1	7.9	4.8	7.1	7.0	8.4	8.8	9.7	10.6	10.2	10.5
Moschiola meminna	NMB-1366	Sri Lanka	M	7.4	2.7	7.1	3.6	5.4	6.0	6.2	6.6	7.3	7.0	7.0	6.0
Moschiola meminna	NMB-1429	Sri Lanka	M	7.1	2.9	6.4	3.9	5.4	5.6	6.1	6.6	6.5	7.4	6.8	7.0
Moschiola meminna	NMB-2328	Sri Lanka	M	8.3	2.5	7.0	2.6	5.7	5.4	6.7	6.5	7.1	6.4	5.6	5.6
Tragulus javanicus	SMNS-16874	Java	M	5.6	2.4	5.2	3.2	4.1	4.9	4.9	5.1	6.4	6.6	6.4	7.4
Tragulus javanicus	SMNS-16876	Java	M	6.4	3.1	6.5	4.1	4.8	5.0	6.0	5.5	7.4	7.6	7.4	7.2
Tragulus napu	NHMW-1923	Borneo	M	7.5	3.4	7.0	4.3	5.5	5.6	5.8	6.5	7.1	7.5	7.2	7.7
Tragulus napu	NHMW-40826	Borneo	M	6.2	3.0	6.3	4.0	5.4	5.5	6.0	6.5	7.0	7.7	7.3	7.8
Tragulus napu	NHMW-40378	Sumatra	M	6.6	3.8	6.4	3.1	5.4	6.0	5.6	7.1	7.6	8.0	8.0	9.0
Tragulus napu	NHMW-B6014	Sumatra	M	6.8	3.5	6.6	4.2	5.5	4.8	5.8	6.2	7.2	7.4	7.2	7.8
Tragulus kanchil	NMB-3808	Sumatra	M	nd	nd	5.1	1.8	3.2	3.3	3.7	4.6	5.3	6.3	5.9	7.2
Tragulus kanchil	NMB-3798	Sumatra	M	5.8	2.6	4.9	3.1	4.4	4.4	4.0	5.1	5.2	6.1	6.3	6.6
Tragulus kanchil	NHMW-1473	Sumatra	M	6.5	2.6	6.0	3.2	4.5	4.4	4.8	5.2	5.7	6.4	6.0	6.4

4.4 Discussion

Dorcatherium crassum forms with the contemporary *Dt. vindebonense* the group of medium-sized Central European *Dorcatherium* representatives with bunoselenodont teeth (Rössner 2010) and here, our described specimen matches in teeth (e.g. see Rössner 2010; Sánchez et al. 2011; Morales et al. 2012), skull size and morphology (Seehuber 2015; Mennecart et al. 2018a) with *Dt. crassum* and therefore, unambiguously associate our specimen with this species (Figure 4.9.2). Comparison of teeth measurements are showing that NMA-Walda 2 is larger than *Dt. guntianum* (Rössner and Heissig 2013) and smaller than *Dt. vindebonense* (Rössner 2010; Alba et al. 2011) and *Dt. peneckei* (Rössner and Heissig 2013).

Dt. crassum is considered to be very similar in its skeleton and body mass to *Hyemoschus aquaticus* from Africa (Milne-Edwards 1864; Carlsson 1926; Dubost 1978; Gentry 1978; Barrette 1982). Recently Mennecart et al. (2018a) described the remains of a partial and very fragmented skull from France and reported that it is much closer to *H. aquaticus* than to other living tragulids. Other evidence associated with the skulls comes from the morphology of the petrosal bone and bony labyrinth, which present greater morphological accordance for *Dt. crassum* and *H. aquaticus* than for *Moschiola* and *Tragulus* species (Mennecart and Cousteur 2016). The strong similarity of *Dorcatherium* and *Hyemoschus* has often been mentioned (e.g. Gentry 1978b) and the two genera have sometimes been synonymised (Milne-Edwards 1864). However, according to Rössner (2007) in its more selenodont cheek teeth, lacking p1 and no cingulum, less robust jaws and lack of contact between premaxilla and nasals (missing in NMA-Walda 2), *Hyemoschus* contrasts with *Dorcatherium*, distinction supported by phylogenetic analysis (Sánchez et al. 2014). In this context, our data for NMA-Walda 2 skull, along with the morphometric variables shows that *Dt. crassum* is the largest species when comparing with the living species, which morphology is more consistent with *Tragulus napu* and *T. kanchil* than *H. aquaticus* (Figure 4.10). The above described, reinforce even more the need to evaluate the distinction of the two genera.

NMA-Walda 2 here referred to *Dorcatherium crassum* has a robust and strong morphological appearance, accented by some remarkable morphological characters (Figure 4.4; 3D model available at: https://data.ub.uni-muenchen.de/). This robustness was previously reported by Mennecart et al. (2018a) for a partial skull of *Dt. crassum* of France. These authors called it hyper-developed compared to its recent relatives that are either rather delicate (*Tragulus* and *Moschiola*) or *Hyemoschus aquaticus* which is intermediate. We found that *Tragulus javanicus* and *T. kanchil* stand out by having little developed and delicate crania; the crania of *T. napu*, *Moschiola meminna* and *M. indica* are larger, and the cranium of *H. aquaticus* is the most robust with strongest developed neurocranium crests and therefore we agree with Mennecart et al. (2018a). Compared with the species in *Tragulus* and *Moschiola*, *Dorcatherium crassum* and *Hyemoschus aquaticus* have a orbit poorly developed (dorsoventral and anteroposterior diameter), being the later species more similar than other two living tragulids. Considering that a nocturnal or crepuscular way of life has been documented for *Hyemoschus* (Dubost 1975) a nocturnal behaviour of this extinct species is also possible. Recently Guzmán and Rössner (2018) reported that the crania of *T. javanicus* and *T. kanchil* are relatively tall and the neurocrania are globose, while cranial height is less pronounced in specimens of *T. napu* and *Moschiola* and somewhat flattened, more comparable to *H. aquaticus* of Africa. Here NMA - Walda 2 looks more like *H. aquaticus*, but, with a hyper-developed morphology (Figures 4.4) where the neurocranium with sagittal and nuchal crests as well as the canine tooth and its alveola are important. According to Mennecart et al. (2018a) the position of the naso-frontal suture of *Dorcatherium crassum* (Contres, France) is located at the level of the center of the orbits in dorsal view (Figure 4.5A). But for NMA-Walda 2 the preserved anterior part of the frontal is anterior to the orbit and, it is highly probable that nasal bones reached this area of the skull. In this context, for the living *Hyemoschus aquaticus* the nasal and frontal are in contact to at level of P3, and extended anteriorly to anterior part of canine alveola (Figure 4.5, Figure 4.6) and consequently we do not agree with Mennecart et al. (2018a). About lacrimal bones are almost completely destroyed and are not informative. However for a skull fragment Bonis et al. (1998; figure 11, 416e) described in the front of the orbit a large lacrymal bone of triangular shape and flat without a lacrymal fissure, while in living tragulids, they are apparently larger (Figure 4.6 A).

Dt. crassum is considered a medium-sized tragulid (Rössner 2010) and the reconstruction of its paleodiet classifies it as a browser (Kaiser and Rössner 2007). Considering that browsers come in many shapes and sizes (e.g. from giraffes and elephants to koalas and primates) and consume a broader variety of food items that includes storage structures (seeds, fruits, and roots), metabolically active tissues (leaves, stems, and flowers) and other products such as nectar or tree exudates (Ungar 2010), the general morphology of this species indicates that its skull may have played a role more for consuming harder food (e.g. roots, seeds, leaves) than softer ones (e.g. fruit flesh, flowers, nectar). Its neurocranium is largely shaped by enlarged attachment areas of the chewing muscles, likewise adapted for this type of hard food acquisition and processing. If hard items formed part of the diet of *Dt. crassum*, it is also probable that the enlargement of canines fulfilled the function of removing /excavating tools for sediment and/or forest vegetation in the active search for foods such as roots and/or seeds. In some fossorial rodents, the incisors are the main tool for breaking up the soil and building tunnels. This adaptation is characterized by conspicuous procumbent incisors with long roots and extreme adpatation of the skull (Hildebrand 1985). Up to now the great development of the canines has only been associated with intraspecific combats (Rössner

2007) as in living tragulids (Dubost 1965, Ralls et al. 1975) and the Chinese water deer, which uses it for stabbing and tearing when fighting (Cooke and Farell 1998). Apparently, the adaptation to a frugivorous diet (e.g. fruit flesh, flowers, nectar) and to a smaller degree to small invertebrates, fish and small mammals (Dubost 1964, 1978) would be associated with the less well-developed cranium and canines in *H. aquaticus* as well as in the genera *Tragulus* (Heydon and Bulloh 1997) and *Moschiola* (Yapa and Ratnavira 2013).

4.5 Conclusion

Despite the commonness of *Dorcatherium crassum* in the European Miocene, descriptions of skulls were hitherto only based on fragmentary material. Thus the skull described herein is the most complete published to date, which allowed us to more completely describe its morphology, make measurements, calculate some proportions, analyze morphometric data and compare it to living species, respectively. This morphometrics information of the skull compared in the morpho-space with living relatives, had never been described before in any fossil tragulid, and increases our knowledge of the morphometric characters of this species. As in other studies, our analyses reinforce the morphological similarity of this fossil species to the living *Hyemoschus aquaticus* from Africa. However, it was not possible to analyze the nasal bones or the premaxillae, whose characters are considered key to discriminate among the genera of this family. The cranium of *Dorcatherium crassum* exhibits pronounced crests and zygomatic arches, considered by some authors as hyper-developed. It is important to note that the sagittal and nucal crests permitted the insertion of a strong musculature, associated with acquisition and processing of food, among other things.

We also hypothesize that the enlargement of the canine teeth would be associated with the search for seeds, roots, fruits, etc. among the vegetation and/or in the ground, having a function in excavating as well as in combat and defense. The relatively flat configuration of the cranium of *Dt. crassum* is similar to that reported for its living relatives *Hyemoschus aquaticus* and *Tragulus napu*, which on escaping leap into water and submerge, while walking on the substrate. As a consequence, a flatter skull would make this structure more hydrodynamic and thus more useful for escaping.

CHAPTER 5

Miocene tragulids from Pakistan

5.1 Introduction

The lithostratigraphic Siwalik Group on the Indian Subcontinent consists of deposits of ancient rivers that accumulated from the beginning of the Miocene through the late Pliocene (Barry et al. 2002). The preserved sediments are highly fossiliferous and ruminant artiodactyls are the predominant element of the macromammal assemblages. Among those, the family Tragulidae makes up an important portion (Barry et al. 1995; Flynn 1995; Barry et al. 2002; Barry 2014; Flynn et al. 2016) which fossil remains (teeth and postcrania) are abundant and stored in various public collections around the world (Geraads 2010; Barry 2014), including the SNSB – BSPG in Munich, Germany (Gentry et al. 1999; Rössner 2017).

The oldest tragulid record reported from the Pakistani Siwalik sediments stems from the Vihowa Formation (18.7 mya to 22.0 mya) and from the Chitarwata Formation (22.0 mya to possibly 26.0 mya) (Barry 2014). Lydekker (1876) was the first to report on fossil tragulids from Asia based on specimens from the Siwalik Hills, describing specimens of *Dorcatherium*. Kaup had established the genus in 1833 based on *Dt. naui* specimens from Eppelsheim in Germany. Thirty years later, Pilgrim (1910) widened the knowledge on Asian tragulid diversity by establishing *Dorcabune anthracotheroides*. Fossil tragulids from the Siwalik Hills comprise *Dorcatherium majus* Lydekker, 1876, *Dt. minus* Lydekker, 1876, *Dt. nagrii* Prasad, 1970, and *Dt. minimus* West, 1980, as well as the large *Dorcabune anthracotheroides*, the medium-sized *Db. nagrii* Pilgrim, 1915, and *Db. sindiense* Pilgrim, 1915. Also *Db. liuchengense* Han, 1974. *Db. progressus* (Yan, 1978) and *Db. welcommi* Ginsburg, Morales and Soria 2001 were recorded from Asia, but not from the Siwaliks (Pickford 2001; Rössner 2007). A large portion of the specimens from Siwalik was assigned to *Dorcatherium* sp., without further determination to the species level (e.g. Lydekker 1876; Colbert 1935; Antoine et al. 2013; Barry 2014; Flynn et al. 2014; Khan et al. 2017) and the validity of some species can be questioned. In fact, when Lydekker (1876) erected *Dorcatherium majus*, he also described "*Dt*. *majus* var b" and *Dorcatherium* sp. Later, Colbert (1935) studied and revised both *Dorcatherium* and *Dorcabune* and pointed out that "hypsodont" molars characterize Asian *Dorcatherium* whereas *Dorcabune* has "bunodont" molars. Also, Colbert (1935) found some *Dorcatherium* specimens to be sufficiently distinct from all known species (smaller than *Dt*. *minus*), but did not describe them as new species. Subsequently, those specimens were classified as *Dt*. *nagrii* by Prasad (1970). Gaur (1992) revised the genus *Dorcatherium* and assigned other specimens from Colbert (1935) to *Dt*. *majus* and *Dt*. *nagrii* to *Dt*. *minus*. Moreover, Colbert (1935) revised *Dorcabune*, accepting only the following entities: *Dorcabune sindiense*, *Db*. *anthracotheroides* (synonym of *Db*. *hyaemoschoides*), and *Db*. *nagrii* (synonymous with *Db*. *latidens*).

More recently, Flynn et al. (1995) studied new fossil mammal findings from the Siwalik Hills and proposed eight tragulid species of the genera *Dorcabune* and *Dorcatherium*. Three were preliminarily named *Dt*. A, *Dt*. B, and *Dt*. C, while another specimen was assigned to cf. *Dt*. *nagrii*. Khan and Akthar (2011) described a tooth found in the Chinji Formation (northern Pakistan), suggesting that it also belongs to that latter species. Most recently, Barry (2014) proposed the existence of at least 18 Siwalik tragulid species based exclusively on astragalus size and shape. He assigned all but one *Dorcabune* astragalus morphotype to the previously described species. Thus, since their establishment as genera, the four *Dorcatherium* and three *Dorcabune* species are recognized and the differentiation within the genera is based on tooth size only. Additionally, Barry (2014) described partial metapodials, indicating that they may stem from two different species because of size differences. The metapodials match those of *Siamotragulus,* a genus previously described from the Lower Miocene Bugti Beds in Central Pakistan (Ginsburg et al. 2001), but not found in the Siwalik Hills. Thus the systematics above described is being used in a number of further papers, listing supplementary tragulid material from the Pakistani Siwaliks (e.g. Sankhyan 1981; Vasishat et al. 1985; Gaur 1992; Farooq et al. 2007a, b, c, 2008; Khan et al. 2005, 2010, 2012; Iqbal et al. 2011; Khan and Akhtar 2005, 2011, 2013, 2017, Batool et al. 2014; Samiullah et al. 2015; Sehgal 2015).

In this study, we describe and interprete new dental material of Tragulidae from the Siwalik Hills in Pakistan to enhance the knowledge on Miocene tragulid diversity and its spatio-temporal distribution. The specimens where collected in 1955/1956 during a joint expedition of the Institute of Palaeontology and Historical Geology, Ludwig-Maximilians-Universität München, and the Bayerische Staatssammlung für Paläontologie und Geologie (both Munich, Germany) (Dehm et al. 1958) from places near Chinji, Nagri and Dhok Pathan (Figure 5.1). The specimens identified here are characterized by features that are indicative of Miocene tragulid representatives (e.g. Lydekker 1876; Pilgrim 1915; Colbert 1935; Mottl 1961; Fahlbusch 1985; Rössner 2007). These features comprise a strong cingulum on upper molars, brachyodonty with different degrees of tooth crown height the absence of a mesostylid and the presence of an “M-structure” in lower molars and fourth lower deciduous premolar, length and width increase from M1 to M3, as well as the slender morphology of lower and upper premolars (except in P4) due to hardly or no lingual crown elements. Moreover, the presence of a “*Dorcatherium* platform” (Sánchez et al. 2010, 2014) indicates that the studied teeth belong to *Dorcatherium* Kaup, 1833 or *Dorcabune* Pilgrim, 1910. Size and morphology of some of the specimens studied here match with the European species *Dorcatherium naui* and *Dt. guntianum*, until now reported only from Europe, while other specimens belong to a new species that is described here.

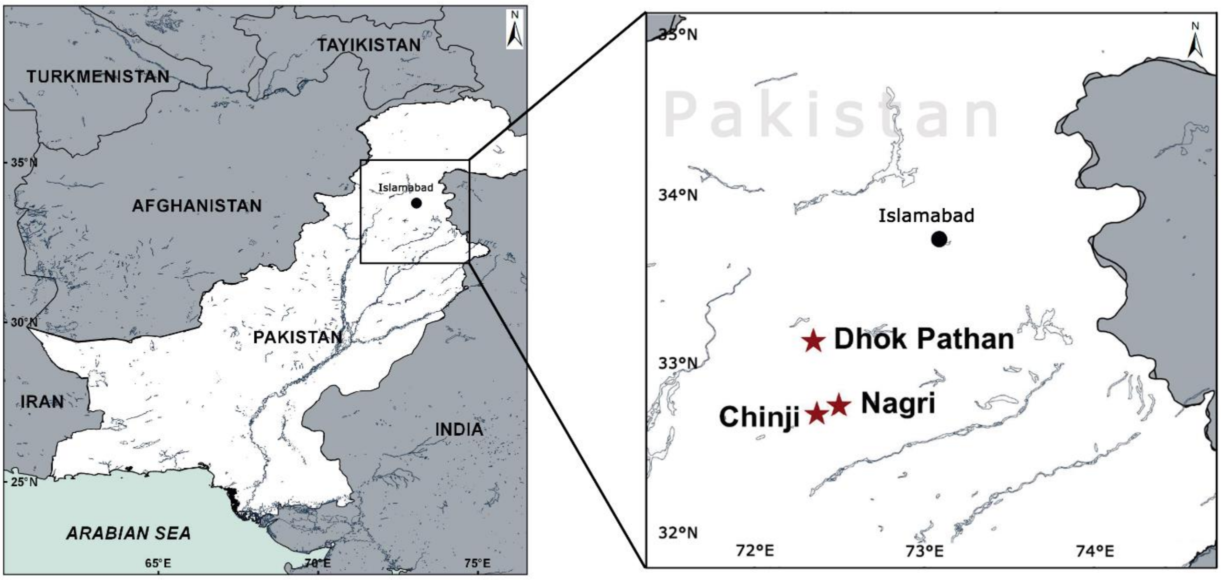


Figure 5.1. Location of the study area in the North of Pakistan. Collecting areas of tragulid remains from the Siwalik Group investigated here are indicated with asterisks (modified from Dehm et al. 1958; Barry et al. 2013; Khan et al. 2017).

5.2 Material and methods

Institutional abbreviations: AMNH: American Museum of Natural History, New York, USA; BM: British Museum, London, United Kingdom; GSI: Geological Survey of India, Calcutta, India; LMU: Ludwig-Maximilians-Universität München, Munich, Germany; SNSB-BSPG: Staatliche Naturwissenschaftliche Sammlungen Bayerns - Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.

Genus, tooth and measurement abbreviations: aw: anterior width, d: lower deciduous tooth, D: upper deciduous tooth, dex.: dextral side, *Db.*: *Dorcabune*, *Dt.*: *Dorcatherium*, h: height, hi: hypsodonty index, l: length, lab.: labial view, lin.: lingual view, m: lower molar, M: upper molar, occ: occlusal view, P: upper premolar, p: lower premolar, sin.: sinistral side, w: width.

Material: the fossil remains described in this paper comprise 213 teeth, mostly *in situ* in mandible or maxillary fragments. They are housed at the Staatliche Naturwissenschaftliche Sammlungen Bayerns – Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany (SNSB – BSPG) under the inventory numbers SNSB – BSPG 1956 II ... (omitted in the text), 1961 XIX ..., 1966 II ..., 1968 XVIII. For comparison, we studied casts of teeth of *Dorcatherium majus*, *Dt. minus* and *Dt. nagrii* obtained from originals stored at the AMNH, BM, and GSI that were described in part by Colbert (1935). Additionally, we compared the samples with type material of *Dorcatherium guntianum* and casts of type material of *Dt. naui* and *Dt. crassum* stored at the SNSB – BSPG.

Anatomical definitions and taxonomic affiliation: Terminology for tooth crown elements follows Bärmann and Rössner (2011). In addition, we use the term "M-structure" (according to Mottl 1961), which is synonymous with the crest-complex comprising the "internal postmetacristid", "external postmetacristid", "internal postprotocristid", and "external postprotocristid". Further, we use the term "*Dorcatherium* platform" (Sánchez et al. 2010 fig. 4; Sánchez et al. 2014, Figure 5.2) for the hyper-developed and widely curved preprotocristid that contacts with a very short premetacristid, a structure only present in *Dorcatherium* and *Dorcabune* species (Figure 5.2A, C). The holotypes of Siwalik tragulid species are exclusively based on upper teeth or maxilla fragments with upper teeth. However, crania with articulated mandibles or lower teeth that can be associated with the same individual are not available. When Prasad (1970) established *Dt. nagrii*, he proposed upper (M1, M2, M3, P4) and lower (m1, m2, m3) teeth as type material, however, both upper and lower dentition are not from the same individual. The same is true for all the *Dorcabune* species established by Pilgrim (1915).

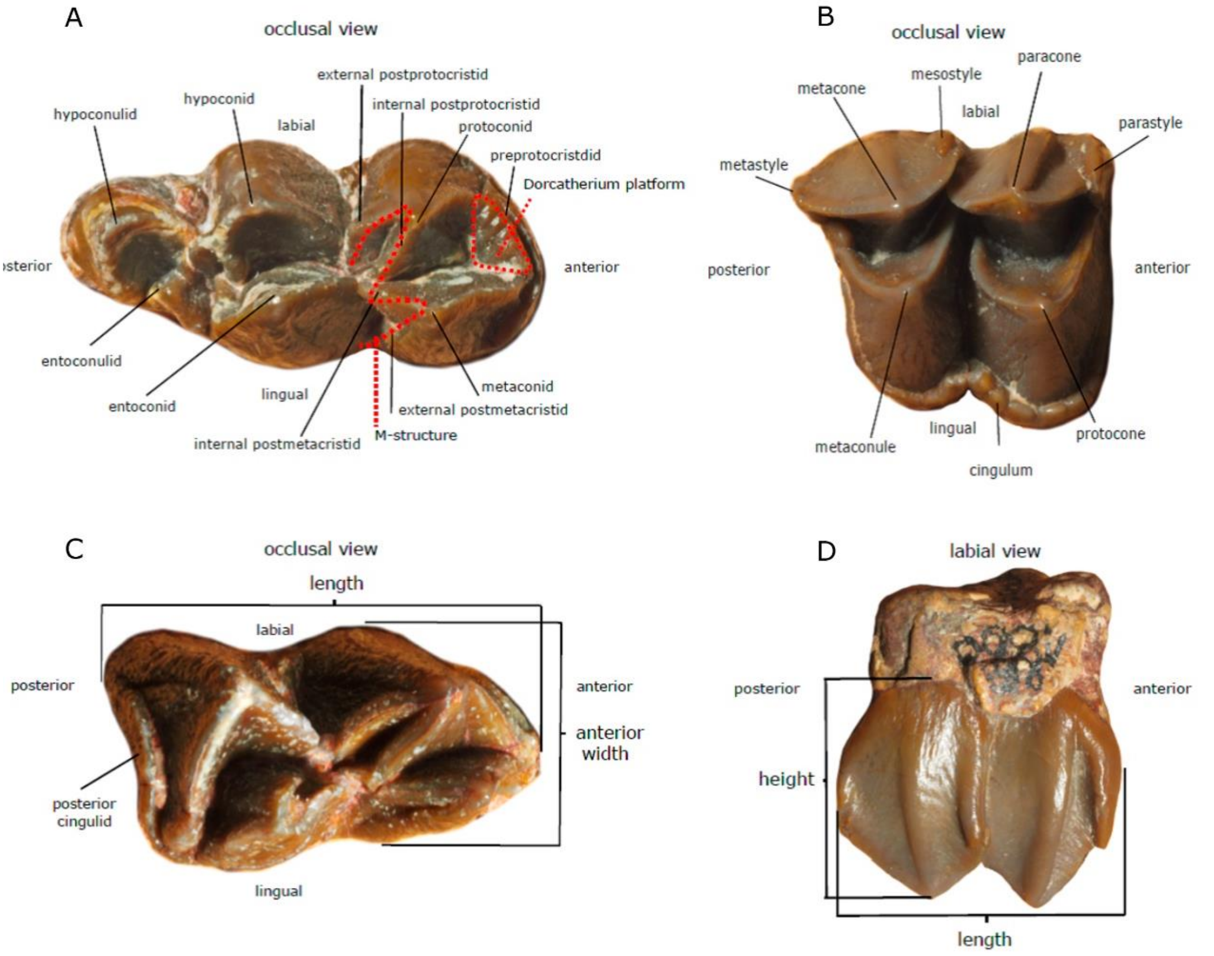


Figure 5.2. Main anatomical elements and measured dimensions (length, width and height) for lower and upper molars discussed in the text. **A**, occlusal view of lower molar with *Dorcatherium* platform and M-structure highlighted in red. **B**, occlusal view of upper molar. **C**, occlusal view of lower molar. **D**, labial view for upper molar.

Analysis: for each tooth position (deciduous teeth [2, 3, 4], premolars [2, 3, 4] and molars [1, 2, 3], we measured l, aw, w, and h, the latter only of unworn teeth, with a digital caliper (precision of 0.1 mm), according to Rössner (1995) (Figure 5.2C, D). For upper and lower molars as well as deciduous teeth, we considered "aw" as "w" (Rössner 1995). Also hi was calculated via the ratio of height to length (Fortelius et al. 2002). Fortelius et al. (2002) grouped dentition into different height classes of lower and upper second molars based on hi, being brachyodont < 0.8, mesodont 0.8-1.2, and hypsodont > 1.2. In order to visualize length vs. width, we generated bivariate plots for each tooth position described above and each species, including available type material (Figure 5.15). In addition, width and length variation of upper and lower dentitions is depicted in univariate plots (Figure 5.16). Through presenting the measurement data in this way, visual and metric access to proportional differences is provided that exist between the different tooth positions (Pickford and Laurent 2014).

Through box plots of length and anterior width of molars, we document intraspecific variability represented by Pakistani tragulid specimens originally identified in the present paper. In addition, we generated box plots based on literature data of the same species for comparison (Figures 5.21 and 5.22). The respective literature is cited: Lydekker (1876), Pilgrim (1915), Colbert (1935), Prasad (1970), West (1980), Sankhyan (1981), Vasishat et al. (1985), Gaur (1992), Farooq et al. (2007a, b, c; 2008), Khan et al. (2005, 2010, 2012, 2017), Iqbal et al. (2011), Khan and Akhtar (2005, 2011, 2013), Batool et al. (2014), Samiullah et al. (2015), Sehgal (2015).

5.3 Results

Systematic palaeontology

Class **Mammalia** Linnaeus, 1758

Order **Artiodactyla** Owen, 1848

Suborder **Ruminantia** Scopoli, 1777

Family **Tragulidae** Milne-Edwards, 1864

Genus ***Dorcabune*** Pilgrim, 1910

Type species *Dorcabune anthracotheroides* Pilgrim, 1910.

Further *Dorcabune* species. *Db. nagrii* Pilgrim, 1915, *Db. sindiense* Pilgrim, 1915, *Db. liuchengense* Han, 1974, *Db. progressus* (Yan 1978), and *Db. welcommi* Ginsburg, Morales and Soria 2001.

Stratigraphic range. From Lower to Middle Siwalik Subgroup (Khan et al. 2010, 2012; Barry 2014; Khan et al. 2017). *Db. anthracotheroides* has a stratigraphic range from Chinji to Nagri Formation (14.2 – 11.2 Ma), while *Db. nagrii* from Nagri and Dhok Pathan Formations (11.3 and 8.2 Ma). In the Sind area of the Indian Subcontinent, *Db. sindiense* is present in the upper most Gaj Formation and lower third of Manchar-Formation, as well as on the Potwar where specimens have been found in the Kamlial and lowest Chinji Formations (14.2 – 11.2 Ma). The Potwar occurrences establish a minimum range of 16.8 Ma to 13.6 Ma, but the Manchar and Gaj localities might be considerably older (Barry 2014; Khan et al. 2017) (Figure 5.4).

Remarks. *Dorcabune* was established by Pilgrim (Pilgrim 1910: 68 - 69), who briefly described *Db. anthracotheroides* on the basis of upper molars and a m3, but without giving specimen numbers or establishing type specimens. In a later study, Pilgrim (1915: 227) established five *Dorcabune* species and described them in detail: *Db*. *sindiense*, *Db*. *anthracotheroides*, *Db*. *hyaemoschoides*, *Db*. *nagrii* and *Db*. *latidens*. Colbert (1935: 302) designated a lectotype and paratypes from the *Db*. *anthracotherioides* type series. In 1935, Colbert revised the genus and only retained *Db*. *sindiense, Db*. *anthracotheroides* (synonymous with *Db*. *hyaemoschoides*) and *Db*. *nagrii* (synonymous with *Db*. *latidens*). The genus *Dorcabune* has a bunoselenodont dentition with a "M-structure" and "*Dorcatherium* platform" on lower molars. Parastyle and mesostyle of upper molars are prominent and isolated. There is a prominent cingulum in the upper molars and strong rugose enamel (Pilgrim 1915; Colbert 1935; Faroq et al. 2007; Khan and Akthar 2013). There is yet no record of a cranium of this genus, but postcranial remains (Barry 2014).

Dorcabune anthracotheroides Pilgrim 1910

(Figure 5.3)

1915 *Dorcabune hyaemoschoides* Pilgrim, page 231, pl. 21 fig. 6 pl. 22, figs. 2, 3.

Differential diagnosis. Largest bunoselenodont / brachyodont tragulid known with wrinkled enamel and pronounced *Dorcatherium*-platform.

Holotype. GSI B 580, a left maxilla with M1 to M3 (Pilgrim 1915: pl. 21, figs. 1 and 1a).

Paratypes. GSI B 581 sin. M2 (Pilgrim 1915, pl. 21, fig. 2), GSI B 582 sin. m3 (Pilgrim 1915: pl. 22, figs 4 and 4a), GSI B 583 fragment of dex. mandible with m1 to m2 (Pilgrim 1915, pl. 21, figs 7 and 7a), GSI B 584 sin. m2 (Pilgrim 1915, pl. 22, fig. 5), GSI B 588 fragmentary dex. P4 (Pilgrim 1915, pl. 21, fig. 8).

Type locality. Chinji, Chakwal, Punjab Province of Pakistan, Lower Siwalik Subgroup, Siwalik Group.

Stratigraphic range. Chinji Formation (Lower Siwalik Subgroup) in the Middle Miocene (Pilgrim 1910, 1915; Colbert 1935; Khan and Akhtar 2013; this study), Nagri and Dhok Pathan Formation (Middle Siwalik Subgroup) in the Upper Miocene (Farooq et al. 2007c; Khan et al. 2010; Khan et al. 2012) (Figure 5.4).

Geographic distribution. *Db. anthracotheroides* has been described from the following localities from north of Pakistan: Chinji (Pilgrim 1915; Colbert 1935; Khan and Akhtar 2013), Phadial (Colbert 1935), Nathot (Colbert 1935), Hasnot (Farooq et al. 2007c; Khan et al. 2012), Dhok Pathan Type Locality (Khan et al. 2010), Kali Nala, NW Kanatti Chak (this study).

Referred material. SNSB-BSPG 1956 II 2595 fragment of dex. mandible with m2 to m3 (Figure 5.3)

Description. m2 and m3 are medium worn (Figure 5.3). They are bunoselenodont and have marked wrinkled enamel. Metaconid and entoconid are higher than the labial conids and have a convex lingual morphology. The “M-structure” is apparent. External postmetacristid and preentocristid meet in one point, as do internal postmetacristid and internal postprotocristid, as well as external postprotocristid and prehypocristid. Preprotocristid runs in a wide curve around the anterior end and fuses with the short premetacristid. Although the tooth is too worn to show the *Dorcatherium* platform, the morphology preserved indicates that there once was one. The prehypocristid does not fuse with the preentocristid, as postentocristid and posthypocristid do not. The hypoconulid of the m3 is large and aligned towards the labial conids. Posthypoconulidcristid and prehypoconulidcristid connect with the posthypocristid, accordingly the third lobus is shallow and closed. There is no entoconulid. There is a clear, but low ectostylid. A cingulid runs from anterior to posterior. Both, the ectostylid and the cingulid are clearer in m2 than in m3. The m3 has a small posterior ectostylid and the cingulid fully surrounds the hypoconulid (Figure 5.3).

Remarks. Bunoselenodonty, size “M-structure”, and marked wrinkled enamel are well in accordance with features described for the type material of *Dorcabune anthracotheroides* (Pilgrim 1915) (Figure 5.3 and Appendix 5, Table 5.1).

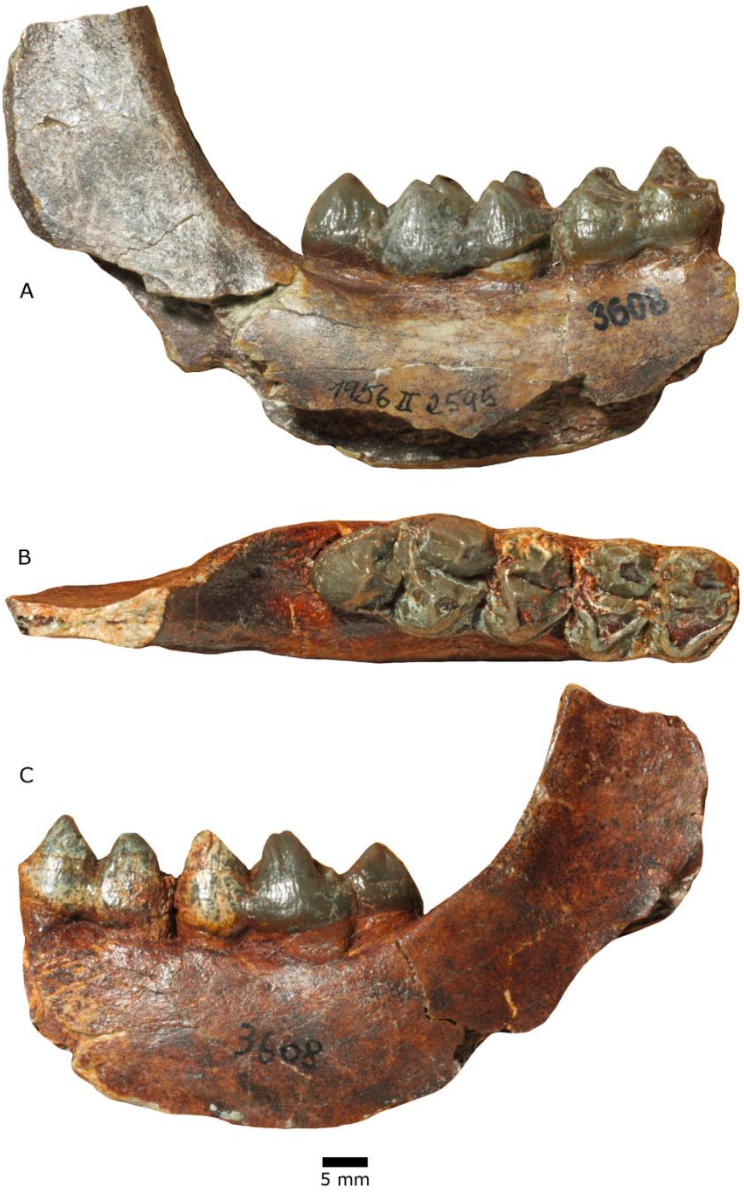


Figure 5.3. *Dorcabune anthracotheroides* Pilgrim, 1910. SNSB-BSPG 1956 II 2595 fragment of dex. mandible with m2 to m3 **A)** labial view; **B)** occlusal view; **C)** lingual view.

Genus ***Dorcatherium*** Kaup, 1833

Type species. *Dorcatherium naui* Kaup & Scholl, 1834

Further Asian *Dorcatherium* species: *Dt. majus* Lydekker, 1876; *Dt. minus* Lydekker, 1876; *Dt. nagrii* Prasad, 1970; *Dt. minimus* West, 1980; and *Dt. orientale* Qiu and Gu 1991.

Stratigraphic range in Asia. It is recorded from the uppermost Oligocene to Early Pliocene of South Asia (Barry 2014; Figure 5.4).

Remarks. The genus *Dorcatherium* was erected by Kaup (1833) on the basis of a right lower jaw with m3 to p3 and alveoli of p2 and p1 (Kaup 1839a, b: plate. 23 figs. 1, 1a, 1b) now lost, but from which casts were made and are stored at the BMNH (M. 3714; Lydekker 1887; Rössner 2010). Five species are generally accepted from the Miocene of Asia (Rössner 2007), but differential diagnoses so far were given for tooth size only. Most information for Asian representatives of *Dorcatherium* comes from teeth and mandibles of the large *Dt. majus,* medium-sized *Dt. minus,* and small-sized *Dt. nagrii* (Lydekker 1876; Colbert 1935; Prasad 1970; Gaur 1992). Information about *Dt. minimus* West 1980 and *Dt. orientale* Qui Zhanxiang and Gu Yumin, 1991 is scarce and available only from their original descriptions. Information on the skull is not available yet for the Asian species, but a few data of postcranial tragulid material from Siwalik species were recently provided by Barry (2014). Thus so far only partial skulls of *Dt. naui* from Eppelsheim in Germany (MN9; Kaup 1839a, b), of *Dt. crassum* from Contres (Loir-et-Cher) in France (MN5b; Mennecart et al. 2018a), *Dt. crassum* from Thierhaupten (Bavaria) in Germany (Seehuber 2015), and of *Dt.* sp. from the island of Chios (Aegean Sea) in Greece (MN5; de Bonis et al. 1998) are described. In Asia, *Dorcatherium* comprises selenodont species only, with more or less strong cingula and cingulids and mostly strong styli and stylids at the molars. The upper molars increase in size from M1 to M3. The lower molars present the "M-structure" and "*Dorcatherium* platform" (Figure 5.2 A). The premolars are long and slender and consist mainly of the labial cones and crests, whereas lingual crown elements are underrepresented. On the lower p4 the entoconid fuses with the postprotocristid. The p3 has only a short lingual entocristid originating at the hypoconid. The upper P4 is shorter and has a triangular shape. Lower p1 and d1 are optional and variable in length and cuspid number (one or two), upper P2 is variable in length too (Rössner 2007, 2010).

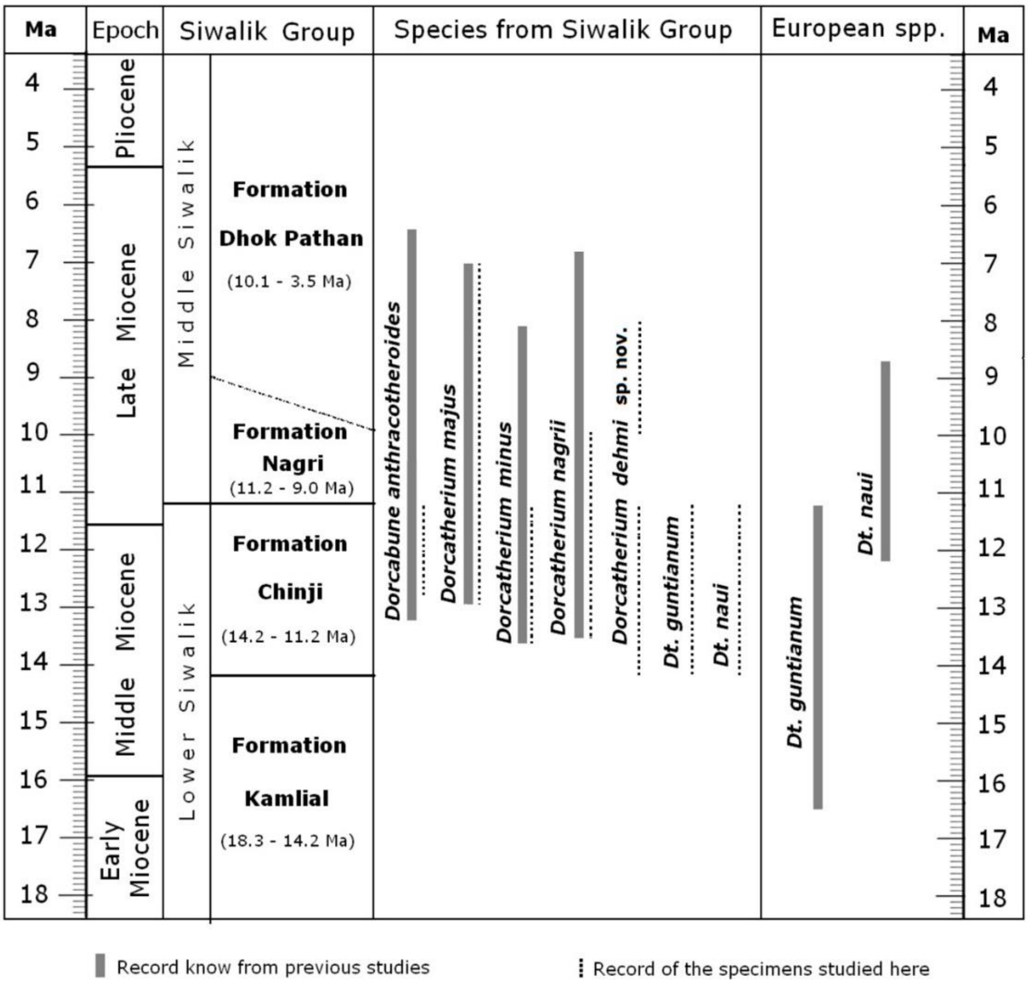


Figure 5.4: Chart depicting the summarized stratigraphic occurrence of the Siwalik and European tragulid species recorded in this study. Correlation of formation boundaries with chronostratigraphy and geochronology was obtained from Barry et al. (2002), Flynn et al. (2014) and Patnaik (2016). The epoch boundaries were obtained from Hilgen et al. (2012). The occurence ranges of the European records of *Dorcatherium naui* and *Dt. guntianum* were obtained from Aiglstorfer et al. (2014) and Rössner (2017) and of Siwalik species from Patnaik (2013).

Dorcatherium majus Lydekker, 1876

(Figure 5.5)

1876 *Dorcatherium majus*, n. sp., nobis. – Lydekker, Pal. Indica,. p. 44ff, pl. VII, figs 4, 6, 9, 10.

1915 *Dorcatherium majus*. – Pilgrim, Rec. Geol. Surv. India, p. 235f, pl.23 figs 2, 2a.

.1935 *Dorcatherium majus* Lydekker. – Colbert, Trans. Am. Phil. Soc., p. 307ff (AMNH 19302, 19304, 19359, 19520, 19524, 19939), figs 138-140.

Differential diagnosis: *Dorcatherium majus* is selenodont and the dentition is morphologically like the other selenedont tragulids except for features related to tooth crown height. The latter is clearly higher than in the type species *Dt. naui* and higher than in all other Asian and European tragulid species and comes with slender styliform mesostyles and higher ectostylids. The Hypsodonty Index for m2 is 0.86. On the d4, the anterior cristids of anterolingual and anterolabial conid are not fused anteriorly, the labial cingulid is weak and the ectostylid is strong. The external enamel texture fluctuates from wrinkled to weakly wrinkled.

Lectotype: GSI B 198, fragment of left maxilla with M2 and M3 (1307) (Lydekker 1876: p 46, pl. VII, figs 4, 6).

Paralectotype: GSI No. B 197, (502) right upper molar (Lydekker 1876: p. 45 ff, pl. VII, figs 9, 10)

Type locality: Kushalghar near Attock, Potwar District, Pakistan, probably Middle Siwalik Subgroup, Siwalik Group.

Stratigraphic range: Chinji Formation (Lower Siwalik Subgroup) in the Middle Miocene (Colbert 1935; Khan and Akhtar 2013; this study), Nagri Formation in the Upper Miocene (this study), and Dhok Pathan-Formation (Middle Siwalik Subgroup) in the Upper Miocene (Khan et al. 2010, 2012; Batool et al. 2014; this study, (Figure 5.4).

Geographical distribution: *Dorcatherium majus* has been described from the following localities in Pakistan: Hasnot (Colbert 1935; Farooq et al. 2007a; Farooq et al. 2008; Khan et al. 2012; Batool et al. 2014), Nagri (Farooq et al. 2007a; this study), Chinji (Colbert 1935; Farooq et al. 2007a; Farooq et al. 2008; Khan and Akhtar 2013; this study), Dhokpathan (Farooq et al. 2007a; Farooq et al. 2008; Khan et al. 2010; this study), Markhal (Farooq et al. 2008; this study), Kanatti (Khan and Akhtar 2013) and Dhok Bun Ameer Khantoon (Samiullah et al. 2015).

Referred material. 1956 II 2519 fragment of sin. maxillary with M1-M2 (Figure 5.5 A, B, C); 1956 II 2535 dex. M2 to M3 (Figure 5.5 D, E, F); AMNH 19304 fragment of sin. maxillary with M1-M2, Siwalik Collection B. Brown 1922; GSI 9909 fragment of dex. maxillary with M1-M2; 1956 II 2508 dex. p4 (Figure 5.5 G, H); 1956 II 2512 isolated sin. m3; 1956 II 2521 sin p4; 1956 II 2603 fragment of sin. mandible with p3-m1 (Figure 5.5 I, J, K); 1956 II 2604 sin. p4 (Figure 5.5 L, M, N); 1956 II 2616 fragment of dex. mandible with d4-m3 (Figure 5.5 O, P, Q); 1956 II 2617 fragment of sin. mandible with p3-m1(Figure 5.6 R, S, T); 1956 II 2618 fragment of dex. mandible with m2 and fragment of m1; 1956 II 2620 fragment of sin. mandible with p4 and posterior fragment of p3; 1956 II 2621 fragment of dex. mandible with d4-m2 and m3 in eruption (Figure 5.6 U V, W);1956 II 2623 fragment of sin. mandible with m3 (Figure 5.7 X, Y, Z); 1968 XVIII 10 fragment of dex. mandible with p4 in eruption, m1, m2, and m3 in eruption (Figure 5.7 A’, B’, C’); 1968 XVIII 56 fragment of dex. mandible with m2 and m3 without back fossa; AMNH 19369 fragment of dex. mandible with m2-m3, Siwalik Collection B. Brown 1922; AMNH 19517 fragment of dex. mandible with m1-m2; AMNH 19520 fragment of dex. mandible with m1-m2, Siwalik Collection B. Brown 1922; AMNH 19524 fragment of dex. mandible with p4-m2, Siwalik Collection B. Brown 1922, studied by Colbert (1935: 307, fig. 139); AMNH 19939 fragment of sin. dental with m3, Siwalik Collection B. Brown 1922; AMNH 39254 sin. m3, Siwalik Collection B. Brown 1922 (Figure 5.7 D', E', F'); GSI 9909 fragment of sin. mandible with m1-m2, GSI 9909 dex. M3.

Description. Molars are selenodont and still preserved *in situ* in fragments of the maxillary bone (Figures 5.5, 5.6 and 5.7). Their tooth crown height (hi m2: 0.86, see appendix 5, Table 5.2) is greater than in the type species of *Dt. naui*. The enamel is wrinkled. In occlusal view they are square with M1 being the smallest and M3 the largest tooth in the upper molar row. The protocone complex has a "v" shape. The postprotocrista is shorter than the preprotocrista. The latter fuses with the parastyle, whereas the postmetaconulecrista does not fuse with the mesostyle. Postprotocrista and premetaconulecrista are not fused. Labial walls of paracone and metacone complex are slightly convex. Parastyle and mesostyle are prominent, but slender. The labial rib of the paracone is prominent, slightly folded towards anterior, and is fused at its base with the parastyle. The labial rib of the metacone is only prominent towards the tip, but less than that of the paracone. The metastyle is usually weak, but strongest in M3. The paracone-complex is arranged anteroposteriorly, whereas the metacone-complex is slightly oblique to the latter. There is a strong cingulum running around the lingual base of the molars (Figure 5.5 A-F). The lower dentition sample records several tooth replacement stages.

Figure 5.5. *Dorcatherium majus* Lydekker, 1876. SNSB-BSPG 1956 II: 2519 fragment of sin. maxillary with M1-M2; **A)** labial view; **B)** occlusal view; **C)** lingual view. SNSB-BSPG 1956 II 2535 dex. M2 and M3; **D)** labial view, **E)** occlusal view, **F)** lingual view. SNSB-BSPG 1956 II 2508 dex. p4; **G)** labial view, **H)** lingual view. SNSB-BSPG 1956 II 2603 fragment of sin. mandible with p3-m1; **I)** labial view, **J)** occlusal view, **K)** lingual view. SNSB-BSPG 1956 II 2604 sin. p4; **L)** labial view, **M)** occlusal view, **N)** lingual view. SNSB-BSPG 1956 II 2616 fragment of dex. mandible with d4-m3; **O)** labial view, **P)** occlusal view, **Q)** lingual view.

Two mandible fragments exhibit heavily or medium worn d4s and m1s, unworn or slightly worn m2s, and m3s in eruption (1956 II: 2616 and 2621). Further, specimen 1956 II 2617 has a p3 in eruption, a strongly worn d4, and a medium worn m1, and specimen 1968 XVIII 10 shows an erupting p4, a medium worn m1, a slightly worn m2, and an m3 in a late eruption stage. The **d4** is triradiculate. It has an elongate shape that is wider posteriorly than anteriorly. The postmetacristid and postprotocristid are split into external and internal cristids, forming the "M-structure". Anterior cristids of anterolingual and anterolabial conids are not fused anteriorly. The preentocristid is short and basally fused with the internal postmetacristid and postprotocristid. The posthypocristid is long and fused to the posterior side of the entoconid. The postentocristid is short and is not fused to the posthypocristid. Anterior and posterior cingulids are present as well as a very strong ectostylid. The labial cingulid and the anterior ectostylid are weak. In occlusal view the hypoconid complex has a "v" shape. The **p3** is slender. The overall morphology is tricuspid, with a clearly dominant mesolabial conid and without lingual elements (Figure 5.5 I-J). Anterior conid and anterior stylid are very small in specimen 1956 II 2617, but clearly developed in 1956 II 2603 (Figure 5.5 I-J), similar to p4 (Figure 5.5 G-H). Two short cristids split from posterior of the posterolabial conid and diverge towards posterolingual and posterolabial by delimiting a wide posterior valley. There are no anterior and posterior cingulids. The **p4** is shorter and wider than the p3 with three cuspids; the mesolabial conid is the dominant one. Lingual cuspids are absent, but anterior and posterior cingulids are present. From the tip of the mesolabial conid, a single anterolabial cristid descends anteriorly and fuses with the anterior conid. The anterior stylid is long. The anterolabial cristid and the anterior stylid are not in-line, but meet in an obtuse angle at the anterior conid. The former delimit the anterior valley. From the posterior face of the mesolabial conid, posterolingual and posterolabial cristids descend. The former differs in length from specimen to specimen but never contacts the posterior crest.

Figure 5.6. *Dorcatherium majus* Lydekker, 1876. SNSB-BSPG 1956 II 2617 fragment of sin. mandible with p3, d4, m1; **R)** labial view, **S)** occlusal view, **T)** lingual view. SNSB-BSPG 1956 II 2621 fragment of dex. mandible with d4-m2 and m3 in eruption; **U)** labial view, **V)** occlusal view, **W)** lingual view.

The posterolabial cristid runs along the labial edge and curves around the posterior edge. It includes an additional small conid, with different morphology from specimen to specimen, in the middle of its length. Both posterior cristids delimit a relatively deep and narrow valley (Figure 5.5G-H). Sometimes the additional small conid performs as a transverse element within this valley (1956 II 2604: Figure 5.5 L, M, N).The lower molars are preserved *in situ* in several mandible fragments and have relatively high crowns in comparison with the type species *Dt. naui* from Europe. The **m1** is shorter and more slender than m2 and m3 and has a more trapezoidal occlusal shape due to a clearly wider posterior lobe. In all lower molar positions, the lingual walls of the lingual conids are convex and the enamel fluctuates from wrinkled to weakly wrinkled The lingual column of the metaconid is prominent. The preprotocristid runs in a wide curve towards anterolingually, forming the "*Dorcatherium* platform", and fuses with the short premetacristid. The "M-structure" is always present with a long external postprotocristid and a short external postmetacristid (Figure 5.5 O-Q). Internal postprotocristid, internal postmetacristid, and preentocristid are in contact as are external postprotocristid and prehypocristid. In m1 and m2 the posthypocristid extends almost to the labial margin of the crown, but ends with a little distance to the postentocristid. On the m1, the ectostylid is mostly strong and more closely with the protoconid. Anterior and posterior cingulid are well developed. The morphology of **m3** is like that of m1 and m2 with rectangular shape in occlusal view. The lingual end of the posthypocristid split into two very short crests, one directed towards the postentocristid and one directed towards the tiny entoconulid. There is a pronounced hypoconulid in a posterolabial position that basically forms the back fossa. The prehypoconulidcristid connects with the posthypocristid, but is not fused to it. The posthypoconulid is very short and touches the entoconulid close to the base only; hence the back fossa is open lingually.

Figure 5.7. *Dorcatherium majus* Lydekker, 1876. SNSB-BSPG 1956 II 2623 fragment of sin. mandible with m3; **X)** labial view, **Z)** occlusal view, **Z)** lingual view. SNSB-BSPG 1968 XVIII 10 fragment of dex. mandible, p4, m1, m2, and m3 in eruption; **A')** labial view, **B')** occlusal view, **C')** lingual view. AMNH 39254 sin. m3, Siwalik Collection B. Brown 1922; **D')** labial view, **E')** occlusal view, **F')** lingual view.

There is a clear entoconulid, but smaller and lower than the hypoconulid. The measurements for the upper and lower dentition here studied, are provided in the Appendix 5 (Table 5.2).

Remarks. When Lydekker (1876) erected *Dorcatheriumt majus* he gave inconsistent information. He designated "*Dorcatherium majus,* n. sp., nobis, Variety a" based on a well-preserved, diagnostic dex. M3 (No. 502; G.S.I. B 197: pl. 7, figs. 9, 10) and a very worn upper molar with no identified position (No. 502-6, G.S.I. B 197: pl. 7, fig. 11). He also described "*Variety b*" based on an M2 and M3 in good state (No. 1307, G.S.I. B 198; pl. 7, figs. 4, 6). According to him, the two teeth of "Variety a" differ chiefly in size, which "perhaps not be more than an individual variety". However, he labeled specimen 502-6 (G.S.I. B 197) on plate 7, fig. 11, as "*Dorcatherium* sp.". He also gave measurements for 502-6 (G.S.I. B 197) (length = 15.2 mm; width = 20.3 mm)

Lydekker (1876) did not provide their dimensions of "*Variety b*" (No. 1307; pl. 7, figs. 4, 6) in spite of good preservation, indicating only a similar size with "*Variety a*". It was Pilgrim (1915) who provided dimensions of these specimens under number "G.S.I. B 198" (page 235) and ratified similar size for both varieties (except specimen No 502-6) (appendix 5, Table 5.2). In his revision, Colbert (1935) designated the two upper molars of "*Variety a"* (G.S.I. B197) the lectotype. However, as there is considerable difference in wear, they did not belong to the same individual and have to be considered as two separate individuals. This violates ICZN (Ride et al. 1999), article 74.5, which says that a particular syntype has to be unambiguously selected, and makes Colbert's designation invalid. Moreover, ICZN, (Ride et al. 1999), article 45.6.4 indicates that (if name before 1961) a variety should be taken to be a subspecies. In consequence, we discard specimen 502-6 (G.S.I. B 197), as its poor preservation does not provide enough information, and designate specimen 1307 (G.S.I. B 198) the lectotype of *Dorcatherium majus.*

Our specimens are congruent with both, the morphology described by Lydekker (1876) and the dimensions of the type material provided by Lydekker (1876) for M3 (No. 502; G.S.I. B 197) and by Pilgrim (1915) for the here newly designated lectotype M2 and M3 (No. 1307: G.S.I. B 198). Consequently, we assigned them to *Dt. majus*. Furthermore, our data are coincident with the previous studies of Colbert (1935), Khan et al. (2010), Khan et al. (2012), Khan and Akhtar (2013), Samiullah et al. (2015), Batool et al. (2015), but do not fit well metrically with Farooq et al. (2007a). The latter classified specimen PUPC No. 67/191 as M3, but with 13.6 mm length and 15.2 mm width. These values fit neither with the *Dt. majus* type material nor is the morphology sufficiently preserved for reliable species assignment (measurements match M1 of *Dt. majus* or M3 of *Dt. naui*).

Since the type material does not comprise lower teeth (Lydekker 1876), our assignments of lower teeth are based on correlation of the largest size classes (with the greatest hi) among lower and upper molars of our *Dorcatherium* sample. The later accord with descriptions and classifications of Pilgrim (1915: pl. 23 fig. 2, tab. page 235-236) and Colbert (1935: page 307-309, figs 138-140), who allocated specimens of lower teeth to *Dt. majus*. Length, width, and height are provided in the appendix 5, Table 5.2 as well as the hypsodonty index, if height is fully preserved.

Dorcatherium minus Lydekker, 1876

(Figures 5.8 and 5.9)

*1876 *Dorcatherium minus*, Nov. Sp. nobis, Siwaliks, – Lydekker, Pal. Indica,. p. 46, pl. VII, figs 3, 7.

.1935 *Dorcatherium minus* Lydekker, – Colbert, Trans. Am. Phil. Soc., p. 309ff (AMNH 19313, 19365, 19517, 19609), fig. 142 (AMNH 119365).

.1992 *Dorcatherium majus* Lydekker 1876, – Gaur, Riv. It. Paleont. Strat., p. 366 (AMNH 19517).

Differential diagnosis. *Dorcatherium minus* is a medium-sized species of the genus, intermediate between the larger *Dt. naui* and *Dt. maliki* (Kostopoulos and Sen 2016) and the smaller *Dt. dehmi* sp. nov. Premolar and molar dentition is morphologically similar to other Miocene selenodont tragulids, except for the ectostylids. The Hypsodonty Index in lower molars ranges from 0.59 to 0.74, and in M1 from 0.84 to 0.85 and is smaller than in *Dt. majus* and *Dt. dehmi* sp. nov. (based on m2 data), but larger than in *Dt. guntianum* (based on m2 data), *Dt. naui*, and *Dt. nagrii* (for the latter two based on m3 data). The d4 coincides morphologically with *Dt. majus* in its anteriorly unfused anterior cristid of anterolingual and anterolabial conids. The enamel of *Dt. minus* is less wrinkled than that of *Dt. majus*.

Holotype. GSI B 195 dex. M2 and M3 according to Lydekker (1876: 46, pl. VII figs. 3 and 7) (No. 1301 in Lydekker), dex. M1 and M2 according to Colbert (1935: 309).

Type locality. Kushalghar near Attock, Potwar District, Pakistan, probably Middle Siwalik Subgroup, Siwalik Group.

Stratigraphic range. Chinji Formation (Lower Siwalik Subgroup) in the Middle Miocene (Khan et al. 2005; Khan and Akhtar 2013; Samiullah et al. 2015; Khan et al. 2017; this study), Nagri Formation (Middle Siwalik Subgroup) in the Upper Miocene (Iqbal et al. 2011), Dhok

Pathan Formation (Middle Siwalik Subgroup) in the Upper Miocene (Khan et al. 2012; Batool et al. 2014; Khan and Akhtar 2005; Sehgal 2015) (Figure 5.4).

Geographical distribution. *Dorcatherium minus* has been described from the following localities in Pakistan exclusively: Hasnot (Khan and Akhtar 2005; Farooq et al. 2007b); Bhandar (Farooq et al. 2007b), Nagri (Farooq et al. 2007b; Iqbal et al. 2011), Chinji (Colbert 1935; Farooq et al. 2007b; this study), Dhok Bun Amir Khatoon (Khan et al. 2017), Rati Dheri (Farooq et al. 2007b), Dhulian (Khan et al. 2005), Vasnal (Farooq et al. 2007b), Bhilomar (Farooq et al. 2007b; this study), Nurpur (Sehgal 2015), Paridarwaza, Jhelum Tehsil (this study), Kanatti Chak (this study).

Referred material. 1956 II 2456 fragment of sin. maxillary with M1-M2; 1956 II 2469 fragment of dex. maxillary with M2-M3; 1956 II 2480 fragment of sin. maxillary with M1-M2 (Figure 5.8 A, B, C); 1956 II 2484 sin. P4; 1956 II 2485 sin. P3 (Figure 5.8 D, E, F); 1956 II 2497 fragment of sin. maxillary with P4-M2 (Figure 5.8 G, H, I); 1956 II 2498 fragment of dex. maxillary with D4-M1 (Figure 5.8 J, K); 1956 II 2536 cranium partially preserved with the dex. P2-M3 and sin. P2, P4, M2-M3 tooth row; AMNH 29856 fragments of dex. and sin. maxillaries each with M1-M3 each, studied by Colbert (1935: 310: fig. 141) (Figure 5.8 L, M, N); AMNH 39303 fragment of sin. maxillary with D3-M1; BM 19043, fragment of sin. maxillary with D3-M1; BM 19043, and fragment of dex. maxillary with D3-D4; 1956 II 2465 dex. M3; 1956 II 2489 fragment of sin. mandible with p3-m2 (Figure 5.8 O, P, Q); 1956 II 2490 fragment of sin. mandible with m3; 1956 II 2496 fragment of sin. mandible with m3; 1956 II 2503 sin. m3; 1956 II 2548 fragment of sin. mandible with m1-m3; 1956 II 2561 fragment of sin. mandible with d4 (posterior portion) and m1; 1956 II 2580 fragment of dex. mandible with m2-m3; 1956 II 2581 fragment of sin. mandible with m1-m2; 1956 II 2588 fragment of sin. mandible with m1 (posterior lobe) and m2; 1956 II 2601 fragment of sin. mandible with m1-m3 (Figure 5.9 R, S, T); 1956 II 2629 fragment of sin. mandible with p4-m3 (Figure 5.9 U, V, W); 1956 II 2655 fragment of dex. mandible with m3; AMNH 19307, fragment of sin. mandible with m2-m3, studied by Colbert (1935: 309); AMNH 19366, fragment of sin. mandible with m2-m3, studied by Colbert (1935: 309); AMNH 39253, fragment of sin. mandible with m3, AMNH 39302 fragment of sin. mandible with m1-m2; AMNH 39306 fragment of sin. mandible with p4-m3; AMNH 39510 fragment of sin. mandible with m1-m2; GSI 234 fragment of dex. mandible with p4 (Figure 5.9 X, Y, Z).

Description. The upper (Figure 5.8 A-N) and lower dentitions (Figures 5.8 O, P, Q and Figure 5.9 R-Z) are preserved in situ of various fragments of maxillary bone Specimen AMNH 39303 represents a tooth replacement stage with slightly to medium worn D3 and D4 and a not yet fully erupted, unworn M1. Only casts of teeth in good condition represent the D3. It is longish, much wider posterior than anterior. It has three labial cones; the paracone is the highest and the anterior cone the smallest. Lingually, only two cones, the larger metaconule and the small protocone, are existent. The posterior lobus and adjacent elements have typical molariform morphology. The posterior cingulum is clear. There is a delicate, but clear labial rib at the anterior conus on specimen 1981 XVII 13. The parastyle is tiny and the mesostyle is delicate and slender, but clear. There is no metastyle. Pre- and postprotocrista are not existent, but there is a lingual cingulum. The **D4** is molariform with a protruding parastyle, which contributes to the typical trapezoidal form in occlusal view (Figure 5.8 K). There is a well-developed cingulum running from anterior via lingual to posterior. The paracone rib is strong. The mesostyle is slender, but also strong. The **P3** is basically composed of labial elements and is lacking lingual elements apart from a small lingual cone and a lingual cingulum. The labial cone is the dominant and central element of the tooth flanked by the short anterolabial and slightly longer posterolabial crista. Its labial rib is prominent (Figure 5.8 D, E, F).

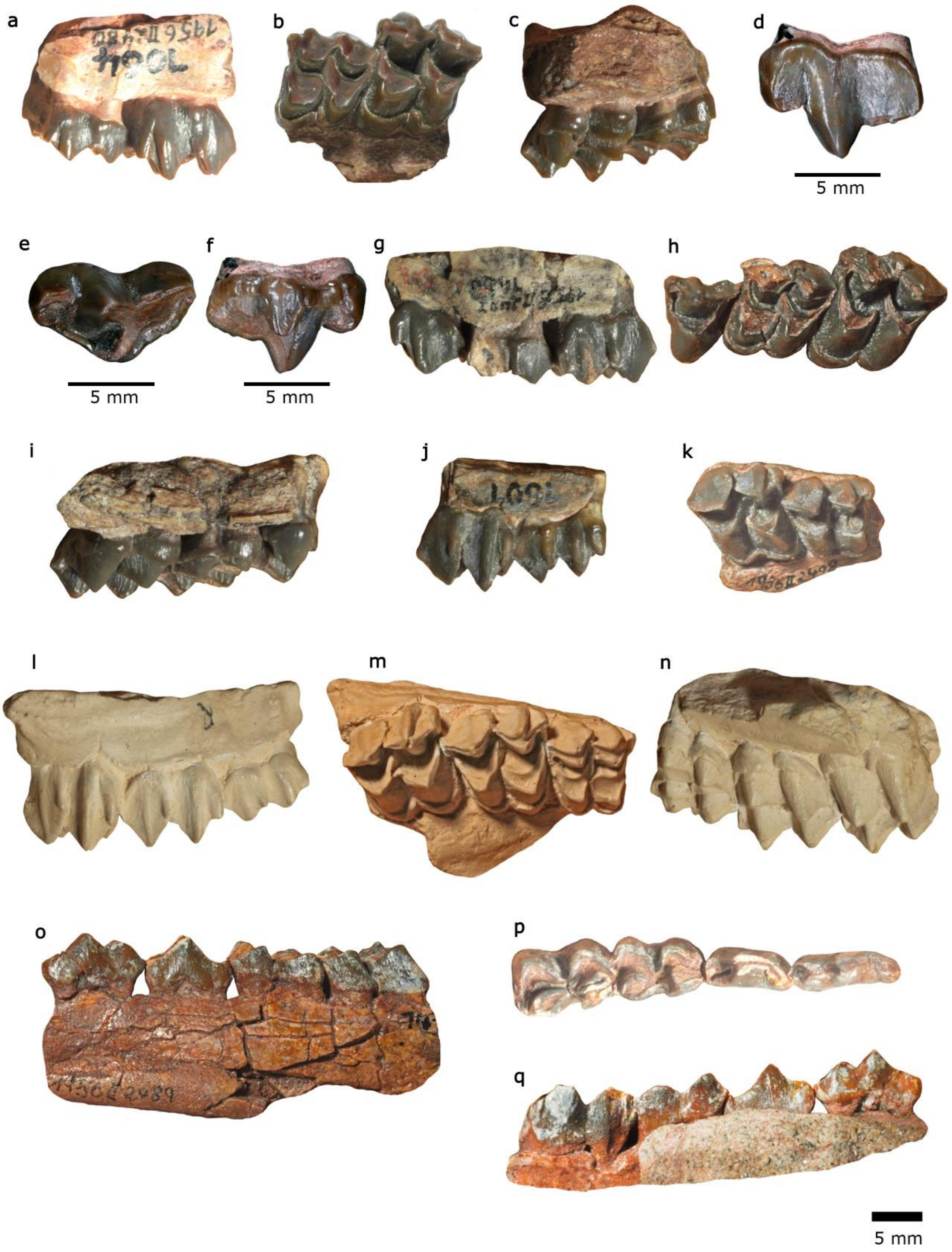


Figure 5.8. *Dorcatherium minus* Lydekker, 1876. SNSB-BSPG 1956 II 2480 fragment of sin. maxillary with M1-M2: **A)** labial view; **B)** occlusal view; **C)** lingual view. SNSB-BSPG 1956 II 2485 sin. P3: **D)** labial view; **E)** occlusal view; **F)** lingual view. SNSB-BSPG 1956 II 2497 fragment of sin. maxillary with P4-M2. **G)** labial view; **H)** occlusal view; **I)** lingual view. SNSB-BSPG 1956 II 2498 fragment of dex. maxillary with D4-M1. **J)** labial view; **K)** occlusal view. AMNH 29856 fragments of dex. and sin. maxillaries with M1-M3 each, studied by Colbert (1935: 310: fig. 141). **L)** labial view of dex.; **M)** occlusal view of dex.; **N)** lingual view of dex. SNSB-BSPG 1956 II 2489 fragment of sin. mandible with p3-m2. **O)** labial view; **P)** occlusal view; **Q)** lingual view.

The anterior and posterior styles are well developed. The lingual cone is attached to the lingual wall of the posterolingual crista. The enamel is finely wrinkled. The **P4** is triangular in occlusal view, similar to the P3 in the labial elements, but with shorter cristae. Lingual elements are clearly developed with a large lingual cone and an anterolingual and a bifurcated posterolingual crista. The anterolabial crista fuses to the anterior style. The internal posterolingual crista fuses to the middle of the posterolabial crista. The external postprotocrista is short and connects to the distinct posterior cingulum (Figure 5.8 G, H, I). The lower premolars and molars coincide in their morphological features (Figure 5.9 R-Z; appendix 5, Table 5.3) with the respective teeth in *Dt. majus* except in the lesser crown height and related features, e.g., lower ectostylids (Figure 5.20).

Remarks. Lydekker (1876) described *Dorcatherium minus* on the basis of a dex. maxillary fragment with M2 and M3 (No 1301). He gave the length and width of M3 only, and length of both teeth, but no dimensions for M2 alone. In 1915, Pilgrim used the latter teeth for comparison with *Dorcabune*, and provided the length and width of No. 1301 under the number G.S.I. B 195. Then, Colbert (1935) established G.S.I B 195 (page 309) as the type specimens of *Dorcatherium minus*. However, Colbert labeled it as "two upper molars, namely right M1 and M2. We could not study the holotype, on which Lydekker (1876) and Colbert (1935) disagreed, which tooth positions are represented (see above). Yet, Lydekker's figures are not informative enough to decide who is right. Length and width given by Lydekker (1876), which do not coincide with Colbert's (1935) measurements. However, the morphology and dimensions in our sample are closest to the type of *Dorcatherium minus* than to any other Pakistani species. In his description, Lydekker wrote: "*this species chiefly differs from the preceding* (*Dt. majus*) *by the much smaller size of the teeth"* and we agree with this statement.

Figure 5.9. *Dorcatherium minus* Lydekker, 1876. SNSB-BSPG 1956 II 2601 fragment of sin. mandible with m1-m3. **R)** labial view; **S)** occlusal view; **T)** lingual view. SNSB-BSPG 1956 II 2629 fragment of sin. mandible with p4-m3. **U)** labial view; **V)** occlusal view; **W)** lingual view. GSI 234 fragment of dex. mandible with p4. **X)** lingual view; **Y)** occlusal view; **Z)** labial view.

Our revision of some *Dorcatherium minus* material studied by Colbert (1935) (appendix 5, Table 5.3) yielded a greater variability than reported by him. Specimens AMNH 19313 (M1-M3), 19365 (m2-m3), 19517 (D4-M1), and 19609 (m2-m3) are clearly larger than *Dt. minus* type specimens and associated lower dentition, and match better with *Dt. naui* specimens (see below), while AMNH 19310 (m1-m3), 19367 (m2-m3), 19368 (m1-m3), and 29855 (M2-M3) fit well with *Dorcatherium dehmi* n. sp. (see below). Similarly, AMNH 29887 (D4-M1) assigned as *Dorcatherium* sp. by Colbert (1935) and AMNH 19306 (M1-M3) assigned as *Dorcatherium* sp. by Colbert (1935), but as *Dt. minus* by Gaur (1992), also were attributed by us to *Dorcatherium dehmi* sp. nov. Additionally, in the last decade studies on tooth specimens associated with *Dt. minus* became available. For example, Farooq et al. (2007b) reported on *Dt. minus* from the Lower and Middle Siwaliks of Pakistan. However, the latter authors referred to specimens AMNH 19517 (D4-M1), AMNH 29856 (M1-M3: Figure 5.8 L, M, N), AMNH 19365, and AMNH 19366 as "type specimens" (page 88) of *Dt. minus* and built their assignment on them, although these specimens do not belong to Lydekker's (1876) type series, but were listed and figured in Colbert (1935) only. Moreover, among these specimens, only AMNH 19366 and 29856 (Figure 5.8 L, M, N) can be associated with *Dt. minus* (see Table XIII) and hence, we recommend reexamination of the specimens described in Farooq et al. (2007b).

Since the type material does not comprise lower teeth (Lydekker 1876), our association of lower teeth with *Dt. minus* is based on size class correlation between upper and lower teeth within our sample. The respective teeth coincide with descriptions and classifications of Pilgrim (1915: tab. page 235) and Colbert (1935: tab. page 311).

Table XIII. History of used dental measurements for *Dorcatherium minus* reference materials from Lydekker (1876), Pilgrim (1915) and Colbert (1935) in later studies. This simbol + was used to indicate data referred to. Measurement for the upper M1 of GSI B195 never has been provided by Pilgrim (1915), but some values are assigned to this tooth, and used by some later studies-authors. Rotuled values are indicating: data or tooth positions became confused (e.g. length given as width and vice versa). In Colbert (1935) the asterisk (*) is indicating individuals revised and determined by us as *Dorcatherium naui*. ^{L} = length. ^{W}= width. ^{H}= Height. nd = no data

Studies and respective measurements used as sources for later authors

	Lydekker (1876)		Pilgrim (1915)							Colbert (1935)								
	No 1301		Lectotype GSI B195 (=No. 1301)			GSI B594				AMNH 29856 (Figure 5.8 L ,M, N)			AMNH 19517*		AMNH 19365*		AMNH 19366	
	M2	**M3**	**M1**	**M2**	**M3**	**p4**	**m1**	**m2**	**m3**	**M1**	**M2**	**M3**	**D4**	**M1**	**m2**	**m3**	**m2**	**m3**
Length mm	nd	11.0	nd	10.6	11.4	10.0	10.8	12.5	16.7	9.8	11.3	11.5	11.0	12.0	13.0	18.0	12.0	16.0
Width mm	nd	10.0	nd	12.3	11.6	4.8	6.8	7.5	8.3	10.0	12.0	13.0	10.0	11.0	7.5	8.0	7.5	8.0
Height mm	nd	nd	nd	nd	9.9	nd	nd	nd	9.0	7.0	8.5	10.0	6.0	7.5	nd	10.0	9.0	10.0

Later authors using the studies from Lydekker (1876), Pilgrim (1915) and Colbert (1935) as sources

	M2	**M3**	**M1**	**M2**	**M3**	**p4**	**m1**	**m2**	**m3**	**M1**	**M2**	**M3**	**D4**	**M1**	**m2**	**m3**	**m2**	**m3**
Sankhyan (1981)				+	+		+	+	8.8^{W}	+	+	+			+	+		
Vasishat et al. (1985)															+	+		
West (1980)												+						
Gaur (1992)										+	+	+		+	+	+	+	+
Khan et al. (2005)															+	+	+	+
Khan and Akhtar (2005)											+	+		+				
Farooq et al. (2007b)			10.0^{L} 10.0^{W} 8.0^{H}	$11.0^{L}12.0^{W}$			Indicated as upperM1	9.0^{W}	10.0^{L} 10.0^{W} 9.0^{H}	+	+	+		+	12.0^{W}	16.0^{W}	7.5^{L}	8.0^{L} 8.0^{W} 8.3^{H}
Khan et al. (2010)				$11.0^{L}12.0^{W}$			12.5^{L} 7.5^{W}				+				12.0^{W}			
Khan and Akhtar (2011)							+	+	+						+	+	+	+
Iqbal et al. (2011)			10.0^{L} 10.0^{W} 8.0^{H}							+					12.0^{W}			
Khan et al. (2012)			10.0^{L} 10.0^{W} 8.0^{H}	$11.0^{L}12.0^{W}$			+	+	+	+	+	+		+	+	+	+	+
Khan and Akhtar (2013)			10.0^{L} 10.0^{W} 8.0^{H}	$11.0^{L}12.0^{W}$			+	+	+	+	+	+		+	+	+	+	+
Batool et al. (2014)															12.0^{W}			
Sehgal (2015)								+							+		+	
Samiullah et al. (2015)			10.0^{L} 10.0^{W} 8.0^{H}							+				+				
Khan et al. (2017)							+	+		+	+	+			+		+	

Dorcatherium nagrii Prasad, 1970

(Figure 5.10)

.1935 *Dorcatherium* sp. – Colbert, Pal. Indica, p. 311f, fig. 144 (AMNH 19613, see below).

*1970 *Dorcatherium nagrii* sp. nov. – Prasad, Pal. Indica, p. 38f, pl. XII, figs 4-10, pl. XIII, figs 5-7.

1981 *Dorcatherium nagrii* Prasad 1970. – Sankhyan, Himal. Geol., p. 91ff, figs 2a-e.

1985 *Dorcatherium nagrii* Prasad, 1970. – Vasishat *et al*. J. Pal. Soc. India, p.59ff, pl. I, figs a - f.

1992 *Dorcatherium nagrii*. – Gaur, Riv. It Paleont. Strat., p. 354, pl. 24 figs a-k.

Differential diagnosis. *Dorcatherium nagrii* is a selenodont smaller-sized tragulid and intermediate in size between the lesser *Dt. minimus* and the larger *Dt. guntianum* as well as *Dt. dehmi* nov. sp. Postcanine dentition is morphologically similar to the other selenodont tragulids. Hypsodonty Index is smaller than in *Dt. naui, Dt. guntianum, Dt. minus* and *Dt. majus* (Figure 5.20)

The lower premolars are extremely slender as compared with other *Dorcatherium* species from the Siwaliks.

Lectotype. GSI 18079, fragment of mandible with m1 to m3 (Prasad 1970, pl. XII, figs 4 and 8).

Paralectotype. GSI 18081, fragment of maxilla with M1 to M3 (Prasad 1970, pl. XIII, fig. 6).

Type locality. 0.5 km northeast of Talyangar Village, Bilaspur District, Himachal Pradesch, India.

Stratigraphic range. Chinji-Formation (Lower Siwalik Subgroup) in the Middle Miocene (Vasishat et al. 1985; this study), Nagri Formation (Middle Siwalik Subgroup) in the Upper

Miocene (Prasad 1970; Gaur 1992; Sankhyan 1981; this study), Dhok Pathan Formation (Middle Siwalik Subgroup) in the Upper Miocene (Sankhyan 1981) (Figure 5.4).

Geographic distribution. *Dorcatherium nagrii* has been described from the following localities in Pakistan: Chinji (Colbert 1935; this study), Hasnot (Colbert 1935), Kanatti Chak (this sudy). In India: Haritalyangar (Prasad 1970), Hari Scarp and Bhapral (Sankhyan 1981), Ramnagar (Vasishat et al. 1985), Talyangar, Udhampur, Nurpur and Kalagarh (Gaur 1992).

Referred material. 1956 II 2455 sin. p4 (Figure 5.10 A, B, C); 1956 II 2577 fragment of sin. m1 (Figure 5.10 D, E, F); 1956 II 2569 fragment of sin. mandible with p3, m1, and m3 (Figure 5.10 G, H, I); AMNH 19613 fragment of dex. mandible with m2-m3, studied by Colbert 1935: 312 (fig. 144); AMNH 39508b, fragment of dex. mandible with m1-m2; AMNH 39508c fragment of sin. mandible with m1-m3; AMNH 39512 dex. m3 (appendix 5, Table 5.4).

Description. The lower permanent dentition is preserved *in situ* in some mandible fragments (Figure 5.10). The only **p3** (1956 II 2569; Figure 5.10 G, H, I) is in a very advanced state of wear and without the anterior part, hence yielding little information. However, the shape is slender. The **p4** (Figure 5.10 G, H) is extremely slender, but with the general tragulid morphology as described above for *Dorcatherium majus* (Figures 5.5 and 5.6). The lower molars coincide with the morphology of *Dt. majus* as well apart from a clearly lesser crown height (appendix 5, Table 5.4; Figure 5.20).

Remarks. When Prasad (1970) established *Dt. nagrii*, he designated upper dentition (M1, M2, M3) (specimen G.S.I. 18079) and lower teeth (m1, m2, m3) (specimen G.S.I. 18081) the holotype. However, it is not clear, if upper and lower dentition belonged to the same individual. This violates ICZN, (Ride et al. 1999), article 74.5, which says that a particular syntype has to be unambigously selected, and makes Prasad's designation invalid.

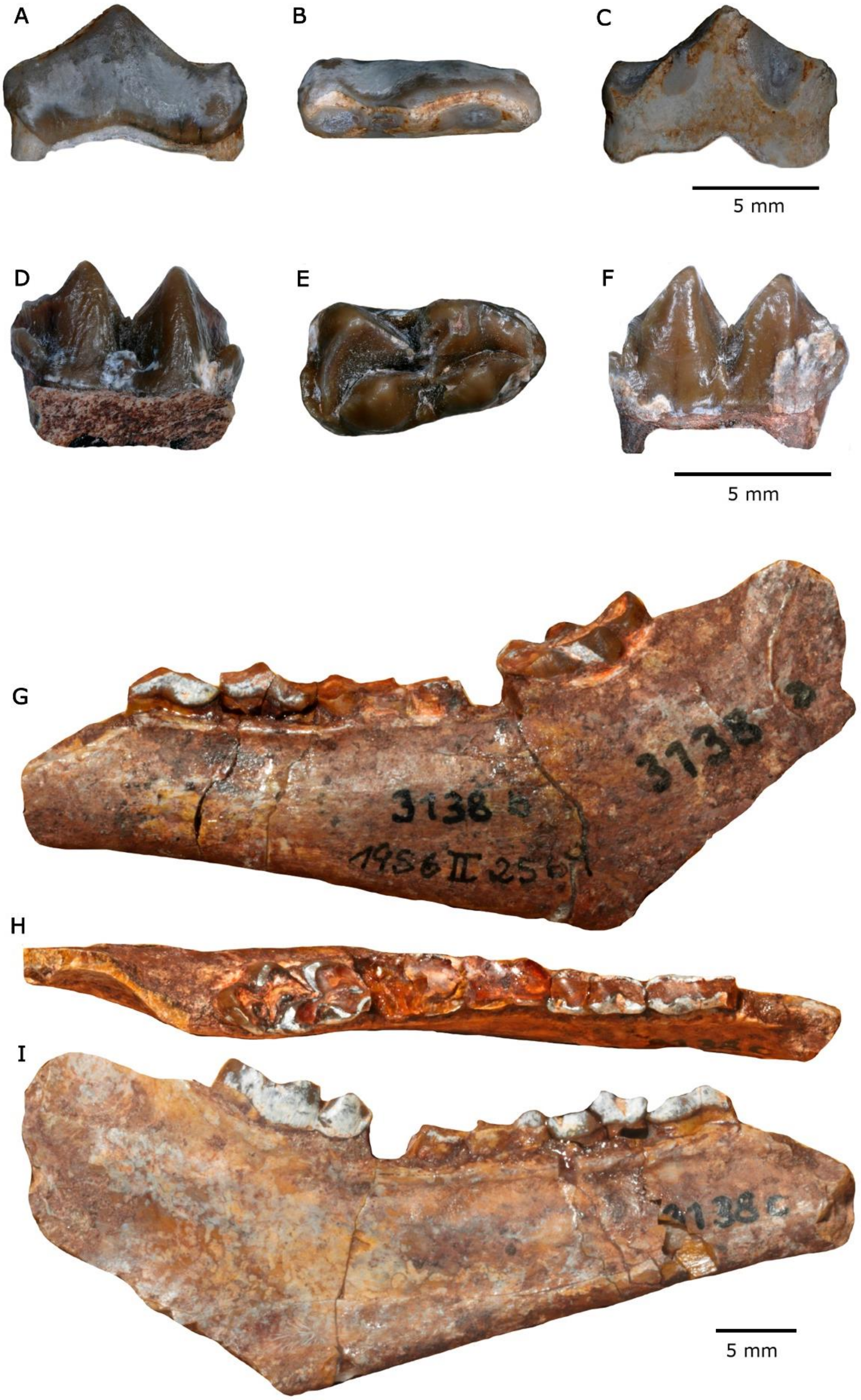


Figure 5.10. *Dorcatherium nagrii* Prasad, 1970. SNSB-BSPG 1956 II 2455 sin. p4 **A)** labial view; **B)** occlusal view; **C)** lingual view. SNSB-BSPG 1956 II 2577 sin. m1; **D)** labial view; **E)** occlusal view; **F)** lingual view. SNSB-BSPG 1956 II 2569 fragment of sin. mandible with p3-m1 and m3; **G)** labial view, **H)** occlusal view, **I)** lingual view.

In consequence, we designate specimen GSI 18079 the lectotype of *Dorcatherium nagrii* and specimen GSI 18081 the paralectotype.

Our studied material matches morphologically and metrically with Prasad's (1970) descriptions of *Dt. nagrii,* and with that from Ramnagar area (Vasishat et al. 1985), and Haytalyangar (Sankhyan 1981; Gaur 1992). When Sankhyan (1981) described new material of *Dt. nagrii* from the Dhok Pathan Formation, he noted that specimen MN-11/76 A (p. 96) described as *Dorcatherium* sp. by Gaur (1980), fits better with *Dt. minus*. Subsequently, this view was confirmed by Vasishat et al. (1985, p. 62). Also, regarding specimen AMNH 19306, initially classified as *Dorcatherium* sp. by Colbert (1935, p. 311), and then included in *Dt. nagrii* by Prasad (1970, p. 39), was finally classified *Dt. minus* by Gaur (1992, p. 366), because of its larger size as compared to the mean of *Dt. nagrii*. Our specimens assigned to *Dt. nagrii* match metrically with the holotypes of *Siamotragulus sanyathanai* (Thomas et al. 1990) and *S. bugtiensis* (Ginsburg et al. 2001) as well as with material of *S. songhorensis* (Sánchez et al. 2014). In the original description of *Siamotragulus sanyathanai*, Thomas et al. (1990) pointed out that the premolars are long, trenchant and strongly compressed and clearly differ from those of *Dorcatherium* and *Dorcabune*. Sánchez et al. (2014) pointed out that the *Dorcatherium* platform in the lower molars is the key to separating *Dorcatherium* specimens from those of *Siamotragulus*. However, in our sample this feature is not clear because of the advanced state of wear. Yet, considering the similarity in dental features and size of *Dt. nagrii* and *Siamotragulus*, a future reexamination based on more material may reveal its possible affiliation to *Siamotragulus*. Barry (2014) considered *Siamotragulus* to be represented among postcrania from the Siwalik Group.

Dorcatherium aff. *majus*

(Figure 5.11)

Locality. Rakh Datwal, WNW Dhok Pathan, Attock District, Punjab Region, Dhok Pathan Formation, Middle Siwalik Subgroup, Siwalik Group, Pakistan.

Referred material. SNSB-BSPG 1956 II 2622 dex. fragment of maxillary with M1-M3 (Figure 5.11).

Description. The teeth are identical in size and qualitative characters of the upper molars of *Dorcatherium majus* described above (Figure 5.5 A-F). However, the specimen we are here referring to differs from *Dt*. *majus* by the almost absent cingulum, which is weak on M1 and lacking on M2 and M3, but, in *Dt*. *majus* it is present without exception in an at least marked development. In order to consider that peculiarity, but also with respect to some probability that the cingula were lost during the preparation process, we classify it provisionally under *Dt*. aff. *majus* (Figure 5.11; appendix 5, Table 5.5).

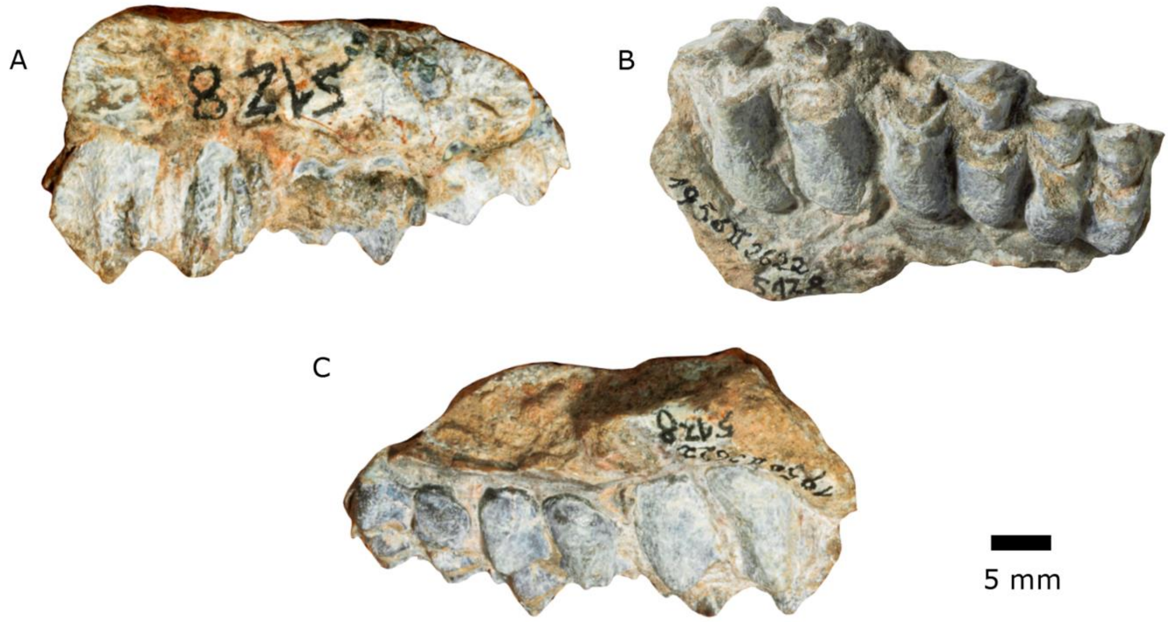


Figure 5.11. *Dorcatherium aff. majus*. SNSB-BSPG 1956 II 2622 dex. fragment of maxillary with M1-M3. **A**) labial view; **B**) occlusal view; **C**) lingual view.

Dorcatherium dehmi sp. nov.

(Figure 5.12)

.1935 *Dorcatherium minus* (in part). – Colbert, Trans. Am Phil. Soc., p. 309ff (AMNH 19310, 19367, 19368, 29855).

.1935 *Dorcatherium* sp. (in part). – Colbert, p. Trans. Am Phil. Soc., 311f (AMNH 19306, 29887).

Differential diagnosis. *Dorcatherium dehmi* sp. nov. is a selenodont small tragulid, intermediate in size between the larger *Dt. minus* and the smaller *Dt. nagrii*, but similar to *Dt. guntianum*. Its postcanine dentition is morphologically like those of other selenodont tragulids. Its tooth crown height is lower (hi in m2 is 0.82 and in M3 it is 0.83) than in *Dt. majus*, and *Dt. minus*, but higher than in *Dt. guntianum*, and *Dt. nagrii* and similar to *Dt. naui*.

Derivatio nominis. In honour of Richard Dehm (1907-1996), a German palaeontologist, former chair of the Institut für Paläontologie und Historische Geologie at the Ludwig-Maximilians-Universität München and director of the Bayerische Staatssammlung für Paläontologie und historische Geologie, who initiated expeditions to Pakistan in 1939 and 1955/56 dedicated to the exploration of the Siwalik fauna.

Holotype. SNSB-BSPG 1956 II 2615 (Figure 5.12 A, B, C) fragment of sin. maxillary with P4 (in eruption), M1, M2, and M3 (only anterior part).

Type locality. Parlewala 3, Dhok Pathan, Dhok Pathan Formation, Middle Siwalik Subgroup, Upper Miocene.

Stratigraphic range. Chinji Formation (Lower Siwalik Subgroup) in the Middle Miocene (Colbert 1935; this study), Dhok Pathan Formation (Middle Siwalik) in the Upper Miocene (Colbert 1935; this study) (Figure 5.4).

Geographical distribution. Hasnot and Chinji (Colbert 1935), Danyar Yill, II Kanatti, Chinji, Parlewala 3, Kadirpur, Rokh Patwal, Kannowali, Marianwala, Palliwala, Kundalnala, Kandalnala 1 (this study).

Referred material. SNSB-BSPG 1956 II 2470 fragment of dex. maxillary with M1-M3; SNSB-BSPG 1956 II 2600 fragment of sin. maxillary with M2-M3; SNSB-BSPG 1956 II 2615 fragment of sin. maxillary with with P4 in eruption, M1-M3 (Figure 5.12 A, B, C); AMNH 19306 fragment of dex. maxillary with M1-M3, original studied by Colbert (1935: 311); AMNH 29855, fragment of sin. maxillary with M2-M3, studied by Colbert (1935: 310) (Figure 5.12 D, E, F); 1956 II 2460 fragment of sin. mandible with d4-m2 or m1-m3; 1956 II 2461 fragment of dex. mandible with m2-m3; 1956 II 2479 fragment of sin. mandible with m2-m3 (Figure 5.12 G, H, Y); 1956 II 2502 fragment of dex. mandible with m2-m3; 1956 II 2597 fragment of sin. mandible with m1-m2; 1956 II 2633 fragment of sin. mandible with posterior part of d3, d-m2 (Figure 5.12 J, K, L), and unerupted m3 as well as fragmet of dex. mandible with m1-m2 and unerupted m3; 1968 XVIII 52 dex. M3 (Figure 5.12 M, N, O); AMNH 19310 fragment of sin. mandible with m1-m3 studied by Colbert (1935: 309) (Figure 5.12 P, Q, R); AMNH 19367 dex. m2-m3 (Figure 5.13 S, T, U); AMNH 19368 fragment of sin. mandible with m1-m3, studied by Colbert 1935: 310) (Figure 5.13 V, W, X) AMNH 20043 dex. M3; AMNH 29887 fragment of sin. mandible with d4-m1, studied by Colbert (1935: 311) (Figure 5.13 Y, Z, A'); AMNH 32588 dex. M3; AMNH 39304 fragment of sin. mandible with m1-m3; AMNH 39509 fragment of sin. mandible with p4-m3 (appendix 5, Table 5.6).

Figure 5.12. *Dorcatherium dehmi* sp. nov. SNSB-BSPG 1956 II 2615 fragment of sin. maxillary with P4 in eruption, M1-M3, **A)** labial view; **B)** occlusal view; **C)** lingual view. AMNH 29855, fragment of sin. maxillary with M2-M3, studied by Colbert (1935: 310), **D)** labial view; **E)** occlusal view; **F)** lingual view. SNSB-BSPG 1956 II 2479 fragment of sin. mandible with m2-m3, **G)** labial view; **H)** occlusal view; **I)** lingual view. SNSB-BSPG 1956 II 2633 fragment of sin. mandible with posterior part of d3, d4-m2, **J)** labial view; **K)** occlusal view; **L)** lingual view. SNSB-BSPG 1968 XVIII 52 dex. m3 **M)** labial view; **N)** occlusal view; **O)** lingual view. AMNH 19310 fragment of sin. mandible with m1-m3 studied by Colbert (1935: 309) **P)** labial view; **Q)** occlusal view; **R)** lingual view.

Description. The teeth studied accord morphologically with *Dt. majus* (see description) except for a lesser tooth crown height (Figure 5.20). Specimen 1956 II 2615 documents a tooth replacement stage with *in situ* M1 (medium worn), M2 (slightly to medium worn) and M3 (hardly worn) and a P4 in eruption (Figure 5.12 A, B, C). Tooth metrics are intermediate between dimensions of the smaller *Dt. nagrii* and the larger *Dt. minus* and similar with *Dt. guntianum* (appendix 5, table 5.6). Specimens AMNH 29855 (Figure 5.12 D, E, F), 19310 (Figure 5.12 P, Q, R), 19367 (Figure 5.13 S, T, U), 19368 (Figure 5.13 V, W, X), were studied and assigned to *Dt. minus* by Colbert (1935). However, they coincide morphometrically with the specimens we identify as *Dorcatherium dehmi* sp. nov. Similarly, AMNH 19306 and 29887 (Figure 5.13 Y, Z, A’) were studied and assigned to *Dorcatherium* sp. by Colbert (1935) and can now be attributed to *Dt. dehmi* sp. nov. The lower teeth of *Dorcatherium dehmi* sp. nov. are morphologically like those of *Dt. majus* with the exception of a lesser tooth crown height (Figure 5.20).

Remarks. Specimens AMNH 19306 and AMNH 29887 (Figure 5.13 Y, Z, A’) identified here as *Dt. dehmi* sp. nov. were studied by Colbert (1935) who attributed them to *Dt.* sp. because *“The teeth are, on the whole, very much like those od* Dorcatherium minus, *but are relatively less hypsodont*” (Colbert 1935, page 311). Prasad (1970, page 39) considered them to belong to his newly established *Dt. nagrii*, which is evidently smaller than *Dt. minus*. Gaur (1992, page 366) classified specimen AMNH 19306 again as *Dt. minus* supported by three figures (M1 Figure 2; M2 Figure 3 and M3, Figure 4), which demonstrate that dimesions are larger than in *Dt. nagrii*. Nevertheless, we can demonstrate that specimen AMNH 19306 is smaller than *Dt. minus* specimens and has a lower tooth crown height what coincides best with *Dt. dehmi* sp. nov.

Figure 5.13. *Dorcatherium dehmi* sp. nov. AMNH 19367 dex. m2-m3, **S)** labial view; **T)** occlusal view; **U)** lingual view. AMNH 19368 fragment of sin. mandible with m1-m3, studied by Colbert (1935: 310) **V)** labial view; **W)** occlusal view; **X)** lingual view. AMNH 29887 fragment of sin. mandible with d4-m1, studied by Colbert (1935: 311) **Y)** labial view; **Z)** occlusal view; **A')** lingual view.

Dorcatherium guntianum von Meyer, 1846

(Figure 5.14)

*1846 Dorcatherium Guntianum. – Von Meyer, N. Jb. Min. Geol. Geogn. Petref., p. 472.

v.1886 Hyaemoschus guntianus H. v. Meyer. – Schlosser, p.134f, pl. VI, figs 22,23

v.1935 *Dorcatherium* sp. (in part). – Colbert, Pal. Indica., p. 311f (AMNH 29854).

v.2013 *D. guntianum* von Meyer, 1846. – Rössner and Heissig, Suisse J. Geosc., p. 341ff, figs 3, 4.

v.2017 *Dorcatherium guntianum* (von Meyer, 1846). – Rössner, Zitteliana, p. 353ff, figs 2, 4-3, 4-4.

(for more complete synonymy list see Rössner and Heissig 2013)

Differential diagnosis. *Dorcatherium guntianum* is a selenodont small Miocene tragulid, intermediate in size between the larger *Dt. minus* and the smaller *Dt. nagrii* and similar with *Dt. dehmi* sp. nov. (Figures 5.21 and 5.22) Postcanine dentition is morphologically similar to that of other selenodont tragulids. Its tooth crown height (hi m2 0.63, hi m3 0.48) is less than in *Dt. majus, Dt. naui, Dt. minus* and *Dt. dehmi* sp. nov. (Figure 5.20) but it is greater than in *Dt. nagrii* and the bunoselenodont *Dorcatherium* species from Europe *Dt. crassum, Dt. vindebonense,* and *Dt. peneckei*.

Syntypes. von Meyer (1846:472) made the species name available by stating ‘In der Nähe von Günzburg an der Donau...Apotheker Wetzler in Günzburg, durch den diese Gegenstände fleissig gesammelt werden...als eine neue Spezies, die ich Dorcatherium Guntianum genannt habe, und welche kleiner ist als Dorcatherium Naui von Eppelsheim...’.[Close to Günzburg an der Donau...pharmacist Wetzler in Günzburg, who studiously collects those specimens...as a new species, which I have named Dorcatherium Guntianum and which is smaller than

Dorcatherium Naui from Eppelsheim…]. According to the given information and later work with figures (Schlosser 1886; Dehm 1984) and collection labels (*Dorcatherium* / *Hyaemoschus guntianum*; Wetzler Collection; Günzburg); the type series can be clearly identified at SNSB-BSPG (appendix 5, Table 5.7) with catalogue number 1881 IX and consists of upper and lower permanent and deciduous teeth as well as postcranial bones (see also Rössner and Heissig 2013).

Type locality. Reisensburg (Günzburg, Bavaria, Germany), Upper Freshwater Molasse, European Land Mammal Unit MN4, Karpatian, Burdigalian, see Rössner and Heissig (2013).

Stratigraphic range. From the Lower (MN4, Karpatian, Burdigalian) to Middle Miocene (MN8, Badenian, Langhian) of Europe (Rössner and Heissig 2013; Rössner 2017) and in the Middle Miocene of the Lower Siwalik Subgroup (Colbert 1935; Chinji this study) (Figure 5.4).

Geographic distribution. *Dorcatherium guntianum* has been recorded from lots of different locations in Central and Western Europe (for detailed location list see online resources of Rössner and Heissig 2013): Austria, France, Germany, and Switzerland. In Pakistan the species is recorded only from Chinji area (Colbert 1935; this study)

Referred material. SNSB-BSPG 1956 II 2554 fragment of dex. mandible with m1-m3 (Figure 5.14 A, B, C); AMNH 29854 fragment of dex. mandible with m2-m3 (Figure 5.14 D, E, F).

Description. The lower molars are selenodont and preserved *in situ* in two mandible fragments (Figure 5.14). Whereas teeth of 1956 II 2554 (Figure 5.14 A, B, C) are well preserved and unworn to only sightly worn, teeth of AMNH 29854 (Figure 5.14 D, E, F) are medium to heavy wear. However, size (appendix 5, Table 5.7) and lingual morphology are indicative. Apart from a low-crowned morphology (Figure 5.20), features are not different from all the other selenodont tragulids describe in the present paper. The m3 of 1956 II 2554 has a third lobe, which is still filled with sediment and hence does not expose details such as bifurcation of the posthypocristid or unfused entoconulid (Figure 5.14 A, B, C).

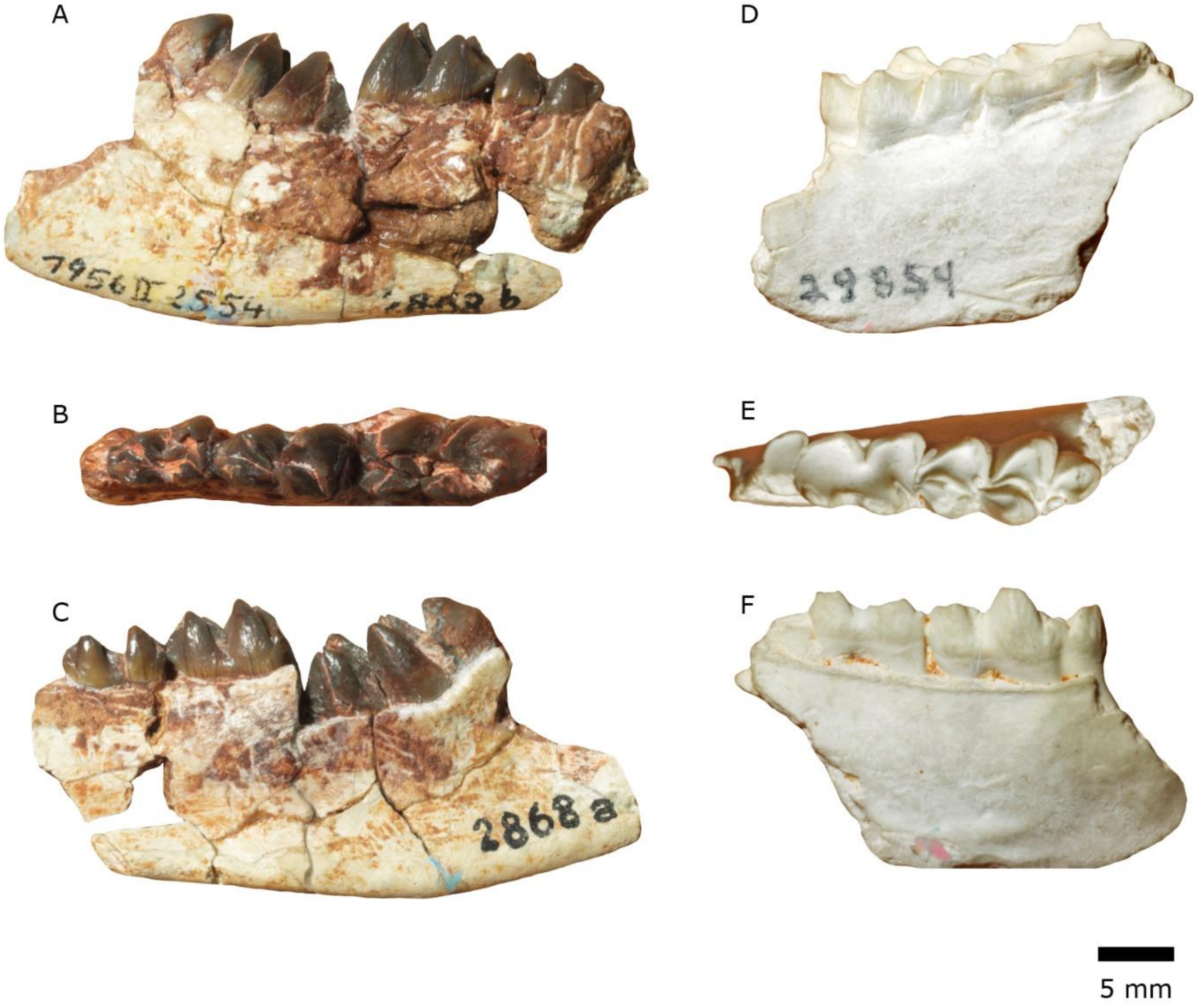


Figure 5.14. *Dorcatherium guntianum* von Meyer, 1846. SNSB-BSPG 1956 II 2454 fragment of dex. mandible with m1-m3, **A**) labial view; **B**) occlusal view; **C**) lingual view. AMNH 29854 fragment of dex. mandible with m2-m3, **D**) labial view; **E**) occlusal view; **F**) lingual view.

Remarks. The described specimens match in size and morphology with *Dorcatherium guntianum* from the Lower and Middle Miocene of Europe (see Rössner 2017 and references therein). *Dorcatherium guntianum* was established by von Meyer (1846: 472) on the basis of material (deciduous and permanet upper and lower dentition and postcrania) from Reisensburg (Bavaria, Germany) of the Wetzler collection, who recognized that it is morphologically equal, but smaller than the type species *Dt. naui*. However, a holotype has not be designated yet nor has the type material been described so far. The type material is stored at SNSB-BSPG (appendix 5, Table 5.7), and hence was available for comparison and some specimens are figured in Schlosser (1886) and measurements are given in Rössner and Heissig (2013) and Rössner (2017). *Dorcatherium guntianum* is a widely-distributed species in Europe (Fortelius 2012), but finding *Dt. guntianum* in Asia is quite unexpected and shakes previous hypotheses on relationships of European and Asian tragulids (e.g. Rössner 2017). Recently revised *Dt. minus* remains from the earliest Miocene in Vietnam (Prieto et al. 2018) were considered to be most similar to *Dt. guntianum* with the exception of having a '...bifurcated protocrista on the [upper] molars...' for what the authors could not find an equivalent in known *Dorcatherium* species and, therefore, could not be specific on species affiliation (*Dorcatherium* sp.). Indeed, a bifurcated protocrista is a feature indicating members of stem Pecora but not Tragulidae. Future studies may reveal a much broader distribution of *Dt. guntianum* in Asia. In Europe *Dt. guntianum* is the smallest species and one of the higher crowned brachyodont tragulid species.

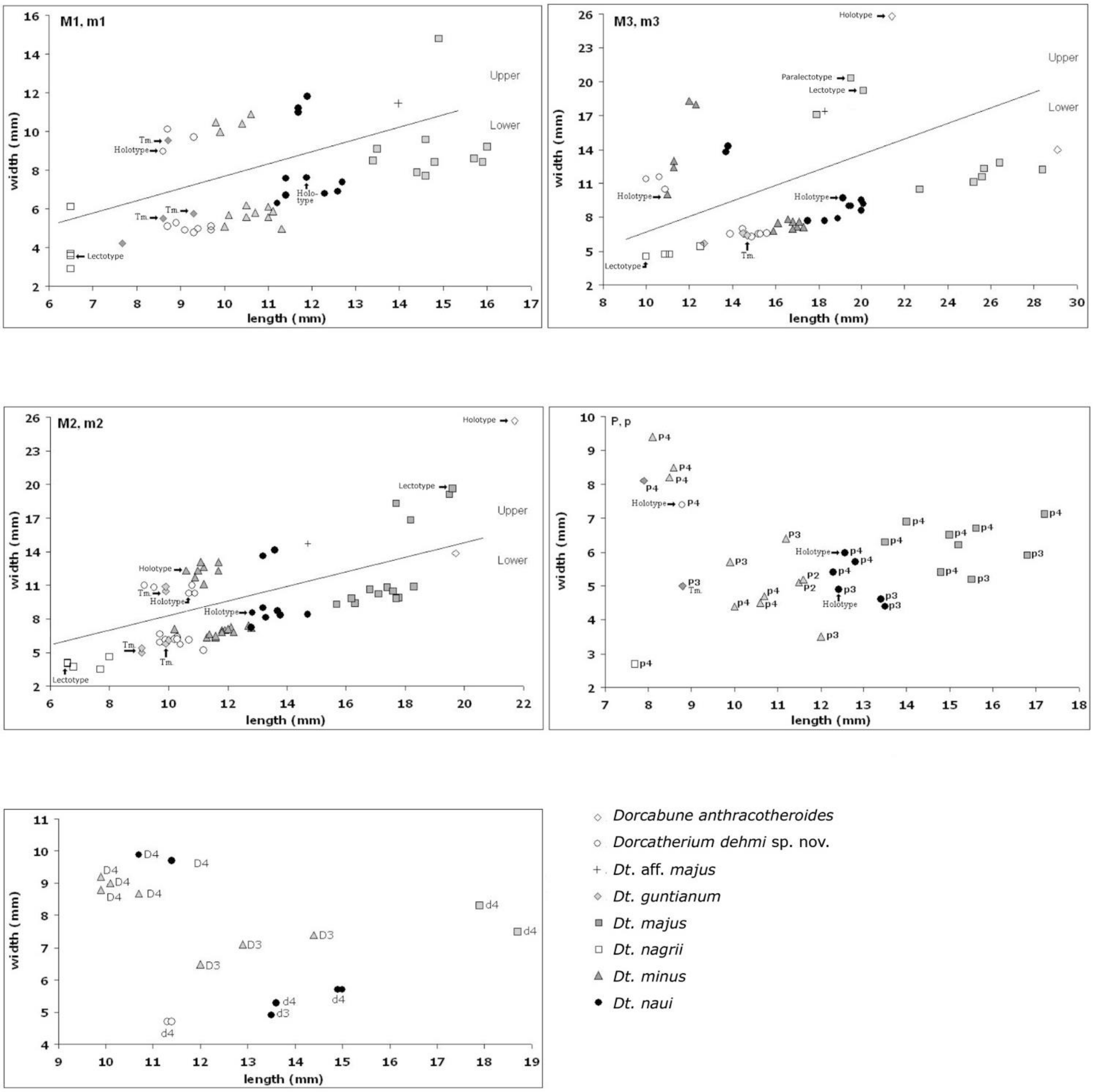


Figure 5.15. Bivariate plots of width v/s length for lower and upper postcanine teeth of species from Siwalik Group studied here, and additional holotype, lectotype, paratype and type material data (Tm).

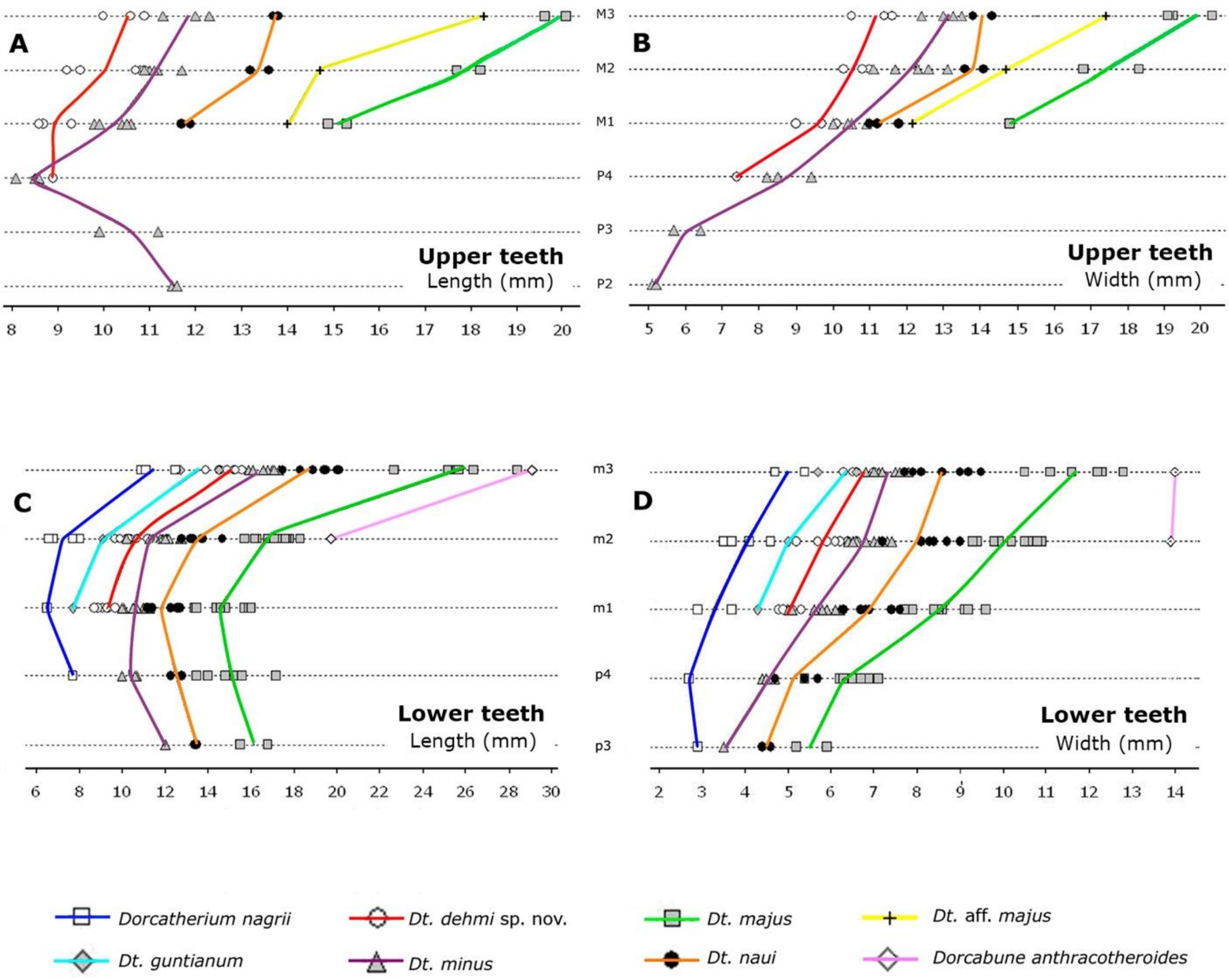


Figure 5.16. Dimension variation in dentitions of tragulid species from Siwalik Group studied here. **A)** length variation for upper dentition, **B)** width variation for upper dentition, **C)** length variation for lower dentition, **D)** width variation for lower dentition. The line joining tooth positions is only referential for the entire variation recorded, and does not represent a statistic mean.

Dorcatherium naui Kaup & Scholl, 1834

(Figure 5.17, 5.18 and 5.19)

*1834 Dorcatherium Naui. – Kaup & Scholl.

v.1839a *Dorcatherium Naui*. – Kaup, p. 91ff.

v.1839b *Dorcatherium Naui*. – Kaup, pl. XXIII fig. 1, pl. XXIII A figs 1-2, pl. XXIII B figs 1-4, pl. XXIII C figs 1-7.

1935 *Dorcatherium minus* Lydekker 1876. – Colbert, Pal. Indica, p. 309ff (AMNH 19313. 19365. 19517. 19609), fig. 142.

v.2009 *Dorcatherium naui* Kaup & Scholl, 1834. – Hillenbrand *et al*. Ann. Naturhist. Mus. Wien, p. 522ff, pl. 1 figs 1-13, pl. 2 fig. 9.

2011 *Dorcatherium naui* Kaup & Scholl, 1834. – Alba *et al*. Geobios, p. 138ff, figs 1,2.

v.2014 *Dorcatherium naui* Kaup, 1833. – Aiglstorfer *et al*. Palaeobio. Palaeoenv., p. 88ff, figs 2, 4a, 5 in part.

Differential diagnosis. *Dorcatherium naui* is a selenodont medium-sized Miocene tragulid species, intermediate in size between the smaller *Dt. minus* and the larger *Dt. majus*. It is similar in size with the European bunoselenodont *Dt. crassum*. Postcanine dentition is morphologically like that of other selenodont tragulids described here, and have more slender lower molars and less bulky upper molar styles than *Dt. crassum*. The tooth crown height (hi m3 0.52 to 0.56, hi M3 0.78, appendix 5, Table 5.8) is less than in *Dt. majus* and *Dt. minus*, but higher than in *Dt. guntianum*, *Dt. nagrii*, *Dt. crassum*, *Dt. vindebonense*, and *Dt. peneckei*, and similar to *Dt. dehmi* sp. nov. Contrary to *Dt. majus*, in *Dt. naui* anterior cristids of anterolingual and anterolabial conids on d4 are fused anteriorly, labial cingulids are absent, and there is a clear anterior ectostylid. *Dorcatherium naui* can be separated from *Dt. mailiki* due to a more complex distal fossete in p4.

Holotype. Right half of a mandible with p3 to m3 and alveoli of p2 and p1 described by Kaup (1839a) and figured in Kaup (1839b. pl. XXIII. figs. 1. 1a and 1b). The mandible is lost, but casts are available at the BM (M. 3714) and SNSB-BSPG (1961 XIX 37, appendix 5, Table 5.8) (Lydekker 1887; Rössner 2010).

Syntypes. BM cranium and mandible with full dentition and axis (Kaup 1839a, p. 92ff; Kaup 1839b, pl. XXIII A figs 1-2, pl. XXIII B figs 1-4, pl. XXIII C fig. 1).

Type locality. Eppelsheim, Deinotherien-Sand, early Late Miocene, early Tortorian, Vallesian, MN9, Germany.

Stratigraphic range. From the late Middle Miocene, late Serravallian, Sarmatian, Astaracian, MN7/8 (Alba et al. 2011; Aiglstorfer et al. 2014) to the Late Miocene, Tortorian / Messinian, Vallesian / Turolian, MN12 (Clauss and Rössner 2014, Hillenbrand et al. 2009; Rössner 2007, Rössner and Heissig 2013) of Europe, and in the Chinji Formation (Lower Siwaliks Subgroup, Siwalik Group) in the Middle Miocene of Pakistan (Colbert 1935; this study) (Figure 5.4).

Geographic distribution of species. See Aiglstorfer et al. (2014) for a detailed list of sites, which yielded *Dorcatherium naui* in Spain, Austria, Germany, Poland, and Hungary. In Pakistan, it has been recorded from Chinji and Nathot (Colbert 1935; this study), Kanatti (this study), Kanatti Chak (this sudy), S Bhilomar, Kagalawala (this study).

Referred material. 1956 II 2568 dex. maxillary with M1-M3 (Figure 5.17 A, B, C); AMNH 19313 fragment of sin maxillary with M1-M3, studied by Colbert (1935: 309) (Figure 5.17 D, E, F); AMNH 19517 fragment of sin. maxillary with D4-M1, studied by Colbert (1935: 310) (Figure 5.17 G, H, I); AMNH 39308 fragment of sin. maxillary with D4-M1 (Figure 5.17 J, K, L); 1956 II 2463 sin. M3; 1956 II 2468 dex. M3; 1956 II 2656 sin. p4 (Figure 5.17 M, N, O); 1956 II 2486 fragment of sin. mandible with m1; 1956 II 2570 fragment of dex. mandible with m1-m2 and m3 (Figure 5.18 P, Q, R); 1956 II 2572 dex. M3; 1956 II 2582 fragment of sin. mandible with m3; 1956 II 2584 fragment of sin. mandible with d3-d4 (Figure 5.18 S, T, U); 1956 II 2585 fragment of dex. mandible with m2 (Figure 5.18 V, W, X); 1956 II 2587 sin. m3 (Figure 5.18 Y, Z, A'); AMNH 19365 sin. m2-m3 (Figure 5.18 B', C', D'); AMNH 19609 fragment of dex. mandible with p3-m3, studied by Colbert (1935: 310) (Figure 5.19 E', F', G'); AMNH 32742. sin. M3; AMNH 39262 fragment of dex. mandible with m2-m3; AMNH 39305 fragment of sin. mandible with p3-m2 and fragment of m3; AMNH 39307 fragment of sin. mandible with d4-m1 (appendix 5, Table 5.8); GSI 235 fragment of sin mandible with d4-m1 (Figure 5.19 H', I', J').

Description. Basically, the tooth morphology is like that of *Dorcaherium minus* and *Dt. majus*, except for the crown height (Figure 5.20), which is less and overall size is intermediate. Measurements are provided in the Table 5.8 as well as the hypsodonty index (appendix 5). The only **d3** (1956 II 2584) is in perfect condition (Figure 5.18 S, T, U). It is biradiculate and has a longish shape, with an anterior mesolabial and a posterolabial conid. The mesolabial conid is the dominant cuspid. A short but clear crest splits from its tip to posterior. The tooth does not have an anterior, but a posterior cingulid. At the posterior aspect of the posterolabial conid three cristids split from the apex to posterolabial and posterolingual. The posterior one bends towards the posterolingual corner and eventually bifurcates into two small cristids at the posterolingual corner close to the posterior end of the posterolingual cristid. The **d4** (Figure 5.18 S, T, U) is similar in morphology with *Dt. majus*, except the lesser tooth crown height, fused anterior cristids of anterolingual and anterolabial conids, a lacking labial cingulid and a clear anterior ectostylid in *Dt. naui*. Lower premolars and molars resemble morphologically those in *Dt. majus* but with a lesser crown height (Figures 5.18 and 5.19).

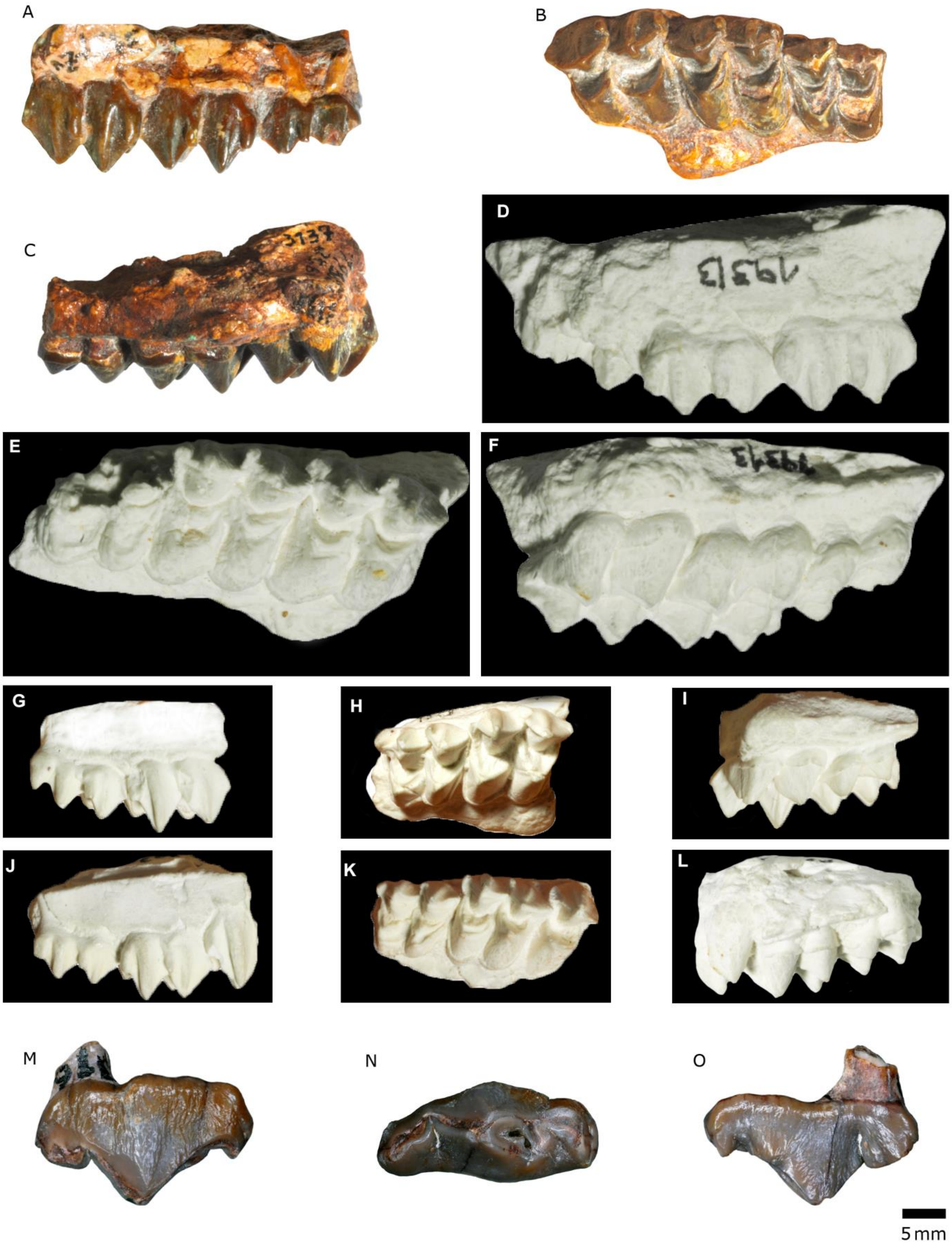


Figure 5.17. *Dorcatherium naui* Kaup, 1833. SNSB-BSPG 1956 II 2568 dex. maxillary with M1-M3: **A**) labial view; **B**) occlusal view; **C**) lingual view. AMNH 19313 fragment of sin maxillary with M1-M3, studied by Colbert (1935: 309): **D**) labial view; **E**) occlusal view; **F**) lingual view. AMNH 19517 fragment of sin. maxillary with D4-M1, studied by Colbert (1935: 310): **G**) labial view; **H**) occlusal view; **I**) lingual view. AMNH 39308 fragment of dex. maxillary with D4-M1: **J**) labial view; **K**) occlusal view; **L**) lingual view. SNSB-BSPG 1956 II 2656 dex. p4: **M**) labial view, **N**) occlusal view, **O**) lingual view.

Remarks. The specimens from the Siwaliks associated by us with *Dorcatherium naui*, nest well within dimensions given by Hillenbrand et al. (2009), Rössner (2010), Alba et al. (2014), and Aiglstorfer et al. (2014) for the medium-sized species *Dt. naui* and *Dt. crassum*. They are larger than those of *Dt. minimus* (West 1980), *Dt. nagrii* (Prasad 1970; Vasishat et al. 1985; Gaur 1992), *Dt. minus* (Lydekker 1876; Pilgrim 1915) and *Dt. dehmi* nov. sp. and are smaller than *Dt. majus* (Pilgrim 1915; Colbert 1935). In morphology, *Dorcatherium naui* from the Siwaliks is in accordance with *Dt. naui* from Europe (Hillenbrand et al. 2009, Alba et al. 2011, Aiglstorfer et al. 2014). Additional critical features are listed in the "Differential diagnosis" above.

Recently, Kostopoulos and Sen (2016) established *Dorcatherium maliki* from western Turkey, a species very similar to *Dt. naui*. The occlusal length for the lower molar row and the premolar and molar size for *Dt. mailiki* match that of the holotype of *Dt. naui*. The values also overlap with the values taken from other *Dt. naui* material reported from Europe and with those of the Pakistani material (Appendix 5, Table 5.8). This is specially significant by the high degree of correspondence of morphology and morphometric variables between *Dt. maliki* and *Dt. naui*, which indicate a close phylogenetic relationship between both species. However, *Dt. maliki* differs from *Dt. naui* in the longer hypoconid on dp2 and p3 compared to the protoconid, the strong protoconulid of dp2, the simple distal fossette of p4, and the frequent presence of a distinct lingual protocristid on the lower molars. Moreover, *Dt. maliki* is stated is stated to be have a tricuspid d2, which is bicuspid in *Dt. naui* (Aiglstorfer et al. 2014). However, we could not study the original material of *Dt. maliki* what makes it impossible to asses the relevant morphological features in comparison with *Dt. naui* and othe tragulids, except that in *Dt. naui* from Pakistan simple and complex p4 morphologies (Figures 5.17 M, N, O and 5.19 E´, F´, G´) of the posterior valley are recorded. A complex p4 morphology has been described for *Dt. naui* from Europe by Aiglstorfer et al. (2014: fig. 5).

Figure 5.18. *Dorcatherium naui* Kaup, 1833. SNSB-BSPG 1956 II 2570 fragment of dex. mandible with m1- m3: **P**) labial view, **Q**) occlusal view, **R**) lingual view. SNSB-BSPG 1956 II 2584 fragment of sin. mandible with d3-d4: **S**) labial view, **T**) occlusal view, **U**) lingual view. SNSB-BSPG 1956 II 2585 fragment of dex. mandible with m2-m3 (in part): **V**) labial view, **W**) occlusal view, **X**) lingual view. SNSB-BSPG 1956 II 2587 sin. m3: **Y**) labial view, **Z**) occlusal view, **A'**) lingual view. AMNH 19365 sin. m2-m3: **B'**) labial view, **C'**) occlusal view, **D'**) lingual view.

Hence, for the time being the respective specimens from Pakistan are best classified with *Dt. naui* due to a better material basis. The validity of *Dt. maliki* remains questionable. Rather than representing a new species, it may represent another population or subspecies of *Dt. naui*. Yet, more evidence is needed to answer the question. In European *Dt. naui* populations, p1 or its alveolus(i) are occasionally recorded along with mandibles without it (Moyá-Solá1981; Hillenbrand et al. 2009; Morales et al. 2012; Alba et al. 2014; Aiglstorfer et al. 2014). However, due to insufficient material, we cannot provide information about this feature for *Dt. naui* from Siwaliks. Future studies may reveal a much wieder distribution of *Dt. naui* in Asia.

Identifications of *Dt. minus* from Pakistan and India by various authors based on specimens described by Colbert (1935) (AMNH 19517: Figure 5.17 G, H, I) and AMNH 19365 Figure 5.19 B´, C´, D´), which in turn were revised here as *Dt. naui*, makes it highly probable that *Dt. naui* is also present in Dhulian (Khan et al. 2005), Hasnot (Khan and Akhtar 2005; Khan et al. 2012; Batool et al. 2014), Nagri (Farooq et al. 2007; Iqbal et al. 2011), Rati Dheri, Bhandar, Vasnal (Farooq et al. 2007; Iqbal et al. 2011), Dhok Bun Amir Khatoon village (Khan and Akhtar 2013; Khan et al. 2017), Dhok Bun Ameer Khatoon (Samiullah et al. 2015) and Nurpur (Sehgal 2015).

Figure 5.19. *Dorcatherium naui* Kaup, 1833. AMNH 19609 fragment of dex. mandible with p3-m3, studied by Colbert (1935: 310): **E’**) labial view, **F’**) occlusal view, **G’**) lingual view. GSI 235 fragment of sin. mandible with d4-m1: **H’**) labial view, **I’**) occlusal view, **J’**) lingual view.

5.4 Discussion

Fossil remains of Miocene tragulids are abundant and stored in various public collections around the world (Geraads 2010; Barry 2014), including the SNSB - BSPG in Munich, Germany (Gentry *et al*. 1999; Rössner 2017). Most of this material was collected from the Siwalik Group in southern Asia and is represented by teeth and postcrania, which, so far, have been scarcely studied. A large portion of the specimens was assigned to *Dorcatherium* sp., without further determination to the species level (e.g., Lydekker 1876; Colbert 1935; Antoine *et al*. 2013; Barry 2014; Flynn *et al*. 2014; Khan *et al*. 2017). The specimens investigated and identified here are characterized by features that are indicative of Miocene tragulid representatives (e.g., Lydekker 1876; Pilgrim 1915; Colbert 1935; Mottl 1961; Fahlbusch 1985; Rössner 2007). These features comprise a strong cingulum on upper molars (Figure 5.2B), brachyodonty with different degrees of tooth crown height (according to hi) (Figure 5.20), the absence of a mesostylid, the presence of a M-structure in lower molars and fourth lower deciduous premolar, the length and width increase from M1 to M3, as well as the slender morphology of lower and upper premolars (except in P4) due to hardly or no lingual crown elements. Moreover, the presence of a *Dorcatherium* platform (Sánchez *et al*. 2010, 2014, Figure 5.2A and C) indicates that the studied teeth belong to *Dorcatherium* Kaup, 1833 or *Dorcabune* Pilgrim, 1910. *Dorcabune* is distinguished from *Dorcatherium* by a buno-selenodont dentition and markedly wrinkled enamel, while *Dorcatherium* species are exclusively selenodont with different degrees of tooth crown height (according to hi, mostly brachyodont), but *Dt. majus* is slightly above the limit to mesodonty according to the definition in Fortelius *et al*. (2002) (Figure 5.20). The Asian *Dorcatherium* species differ from the African *Dorcatherium pigotti, Dt. chappuisi* and *Dt. iririensis* by a higher tooth crown height and a more selenodont dentition (Whitworth 1958; Pickford 2002).

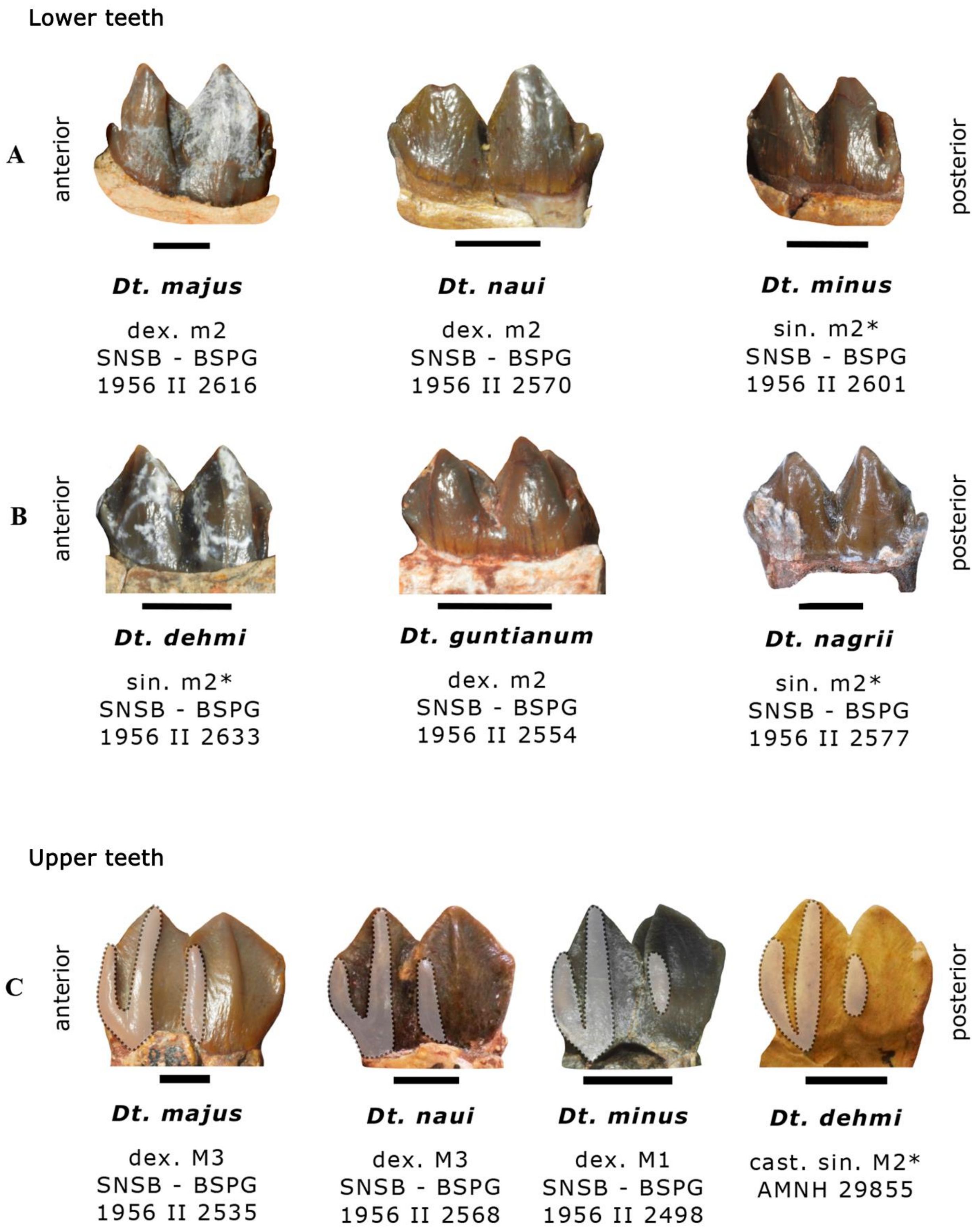


Figure 5.20. Lingual and labial views of lower and upper molars of *Dorcatherium* species recorded in the Siwalik Group of Pakistan in order to visualize different tooth crown heights. Row **A**, lingual views of lower molars for larger (*Dt. majus*) and medium-sized species (*Dt. naui* and *Dt. minus*. Row **B**, lingual views of lower molars for small-sized species. Row **C**, labial views of upper molars. Scale bar 5 mm.

The tooth morphometric of the specimens studied here match with type material of the classically described Siwaliks species *Dorcatherium nagrii*, *Dt. minus, Dt. majus*, and *Dorcabune anthracotheroides* (Figure 5.15). The species identity of one *Dorcatherium* specimen, primarily determined as *Dorcatherium* aff. *majus* (Figure 5.11), still remains unclear, but might be resolved in the future, when more tragulid material from the Siwaliks is described. We could identify a new species, erecting *Dorcatherium dehmi* sp. nov., (Figure 5.12 and 5.13) and assigned some Pakistan specimens to the previously exclusively European *Dt. guntianum* (Figure 5.14) and *Dt. naui* (Figures 5.17, 5.18 and 5.19), thus recording these two species for the first time in Asian fossil material. This finding points to more extensive tragulid affinities between Europe and Asia than previously thought (see also Made 1996).

Recently, Barry (2014) concluded that potentially as many as sixteen species, belonging to *Dorcabune*, *Dorcatherium* and *Siamotragulus,* could be recorded in the fossils from the Siwalik Hills, which differ in size and, in some instances, skeletal proportions. Apart from that, distinctive interspecific morphological traits were not stated (see Colbert 1935; Flynn et al. 1995; Khan et al. 2012; Flynn et al. 2014; Barry 2014; Khan et al. 2017). However, detailed morphological studies of dentition and postcrania have proven to be a successful tool to distinguish between tragulid species, for example, in the case of European *Dorcatherium crassum* and *Dt. naui* (Moyà-Solà 1981; Hillebrand et al. 2009; Rössner 2010; Alba et al. 2011; Sánchez et al. 2011; Morales et al. 2012; Aiglstorfer et al. 2014), the African *Afrotragulus* (Sánchez et al. 2010), and the Afro-Eurasian *Siamotragulus* (Thomas et al. 1990; Ginsburg et al. 2001; Sánchez et al. 2014). In our study, the consideration of tooth morphology, related to tooth crown height (Figure 5.20), apart from size, allowed us to identify the specimens and assess species richness, which would have been otherwise partially obscured by overlapping size ranges as evidenced by figures 5.21 and 5.22.

In Asian tragulid species, the constant use of exclusively metric variables for species determination (e.g. Khan et al. 2012; Khan and Akhtar 2013; Khan et al. 2017 and references therein) has produced wide intraspecific metric variation at the expense of the underestimation of species diversity (see Figures 5.21 and 5.22).

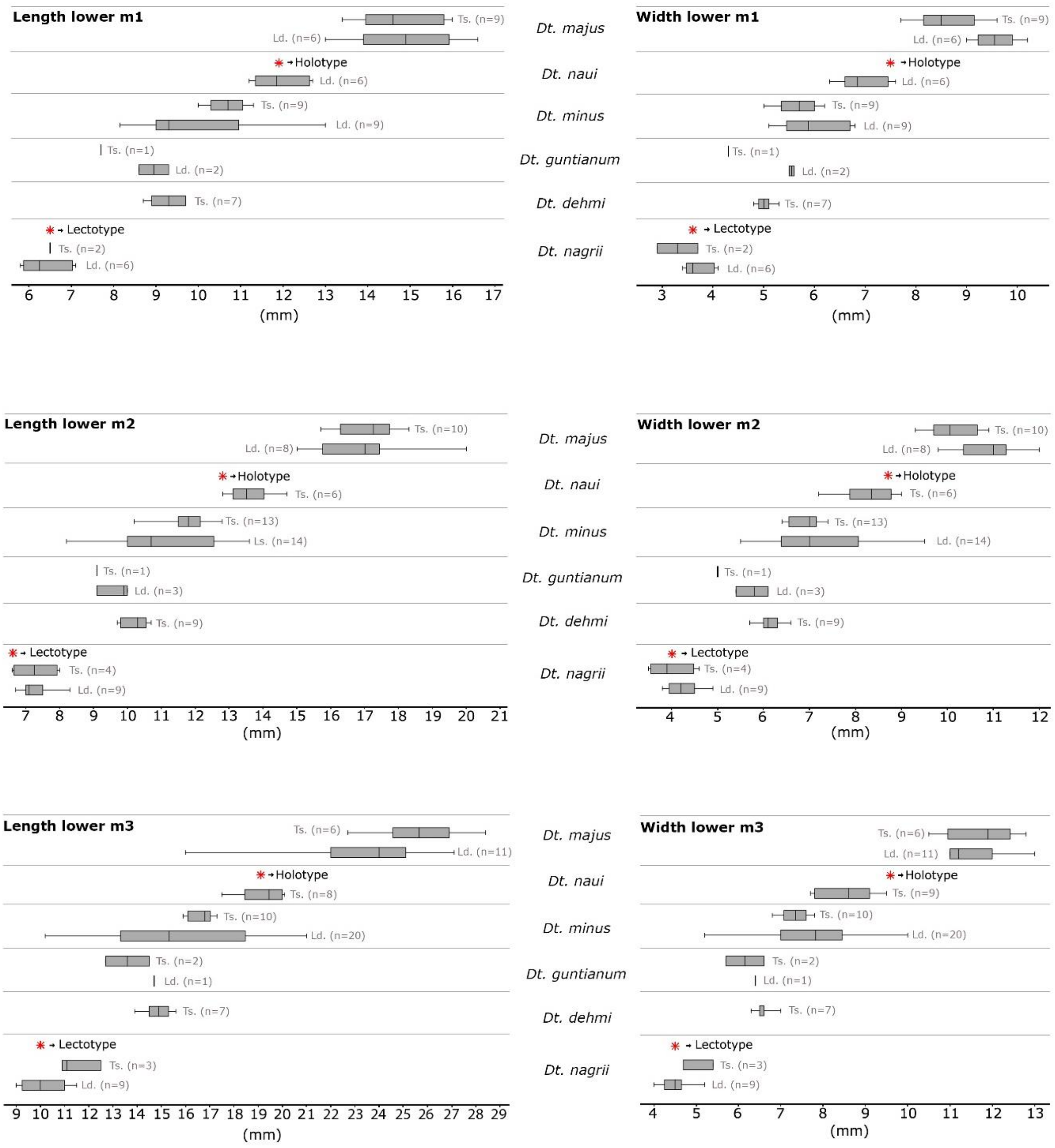


Figure 5.21. Box plot of length and width of lower molars of *Dorcatherium* species from the Siwalik Group. Ts.: data of this study. LD: Literature data.

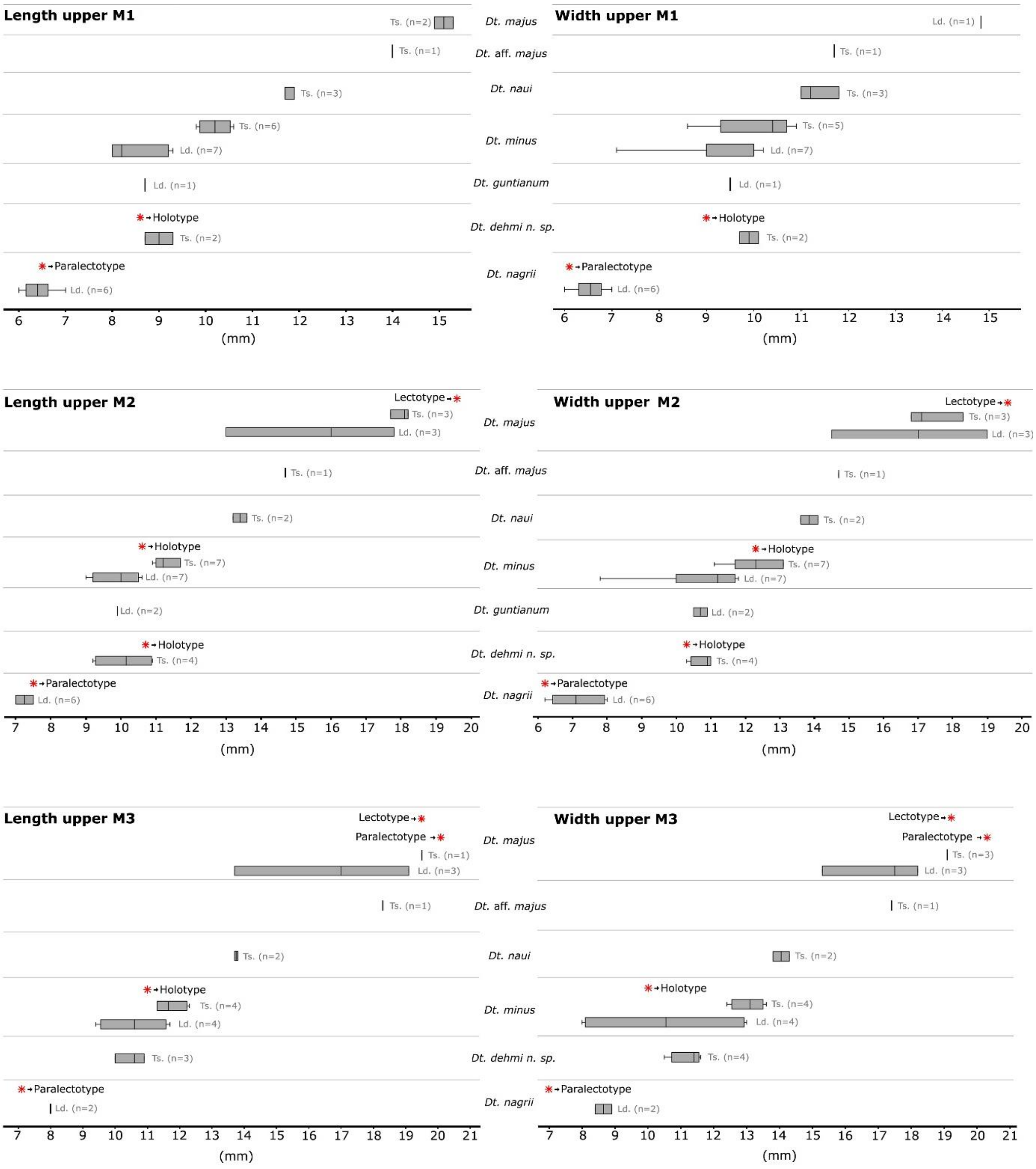


Figure 5.22. Box plot of length and width of upper molars of *Dorcatherium* species from the Siwalik Group. Ts.: data of this study. LD: Literature data.

Yet, Asian *Dorcatherium* dentition is morphologically uniform as long as it does not concern tooth crown height and related morphological features (split level of styles above crown base, shape of styles) (Figure 5.20). There may be more potential in premolar and deciduous cheek tooth morphology as distinguishing characters (see Aiglstorfer et al. 2014), but more material needs is to be found before this can be proven. Accordingly, future studies on fossil tragulids from the Siwaliks should keep the potential of tooth morphology for taxonomic purposes in mind. At this point, we want to kindly make aware of recent mistakes in morphological assessments, i.e. 1) confused tooth position, highlighting a supposedly unique lower molar feature, instead of an anterior fragment of a lower fourth deciduous tooth (e.g. Khan et al. 2017: table 1, page 886, also see Table XIII in this study), and 2) mix up of *Dorcabune* and *Dorcatherium* (Singh et al. 2018: Figure 4t) as well as *Dorcabune* and a bovid (Singh et al. 2018: Figure 4u).

According to Antoine et al. (2013) and Barry et al. (2013), *Dorcatherium* ([sic] or perhaps *Siamotragulus*) records are older than those of *Dorcabune* and come from the latest Oligocene (at least 28.1 Ma - 23.0 Ma) and early Miocene of the Chitarwata (at least 22.0 Ma and perhaps as old as 26.0 Ma) and Vihowa Formations in Pakistan (at least 19.1 mya - 11.2 Ma). However, the age of the lower Chitarwata Formation is still controversial (for discussion, see Lindsay et al. 2005; Antoine et al. 2013; Métais et al. 2017). Undoubtedly, the Miocene represents the time of highest diversity and widest geographical distribution of tragulids (Rössner 2007; Clauss and Rössner 2014; Barry 2014). However, the synchronous existence of *Dorcatherium* in the Early Miocene of Africa (ca. 22.5 Ma, Whitworth 1958, Pickford 2001, Geraads 2010) and Pakistan (at least 22.0 Ma, Antoine et al. 2013) represents an enigma, as occurring prior to the *Gomphotherium* land bridge (19.0 to 16.0 Ma; Rögl 1998, 1999). This terrestrial corridor was reconstructed based on a faunal exchange and is considered to have emerged in the context of tectonical collision between Africa and Arabia (Madden and van

Couvering 1976; Made 1999; Harzhauser et al. 2007). The latter refers to land connections between Africa and the Indian Subcontinent as well as between Europe and these two areas that allowed faunal exchange and are considered to have emerged in the context of tectonic collision between Africa and Arabia (Madden and van Couvering 1976; Made 1999; Harzhauser *et al*. 2007). However, Made (2014 and references therein) pointed out that the fossil evidence documents several migration events over an even longer period of time (21.0 to 12.5 mya). This coincides much better, if still not satisfying, with the given tragulid record and hints to first African tragulid migrations coming from Asia. Future evidence may help to solve this paleobiogeographic riddle (see also Grossman *et al*. 2019).

In Europe, *Dorcatherium* is recorded from the Early Miocene (minimum appearance date ca. 17.8 Ma), probably through successive heterochronous dispersal events from the East/Southeast to the West/Southwest of Europe, rather than a synchronous appearance (Rössner 2017). Mennecart et al. (2018b) proposed that Bachitheriidae migration linked western to southeastern Europe in the “*Bachiterium* dispersal event”, where the tragulid *Iberomeryx* from the earliest Oligocene of Georgia would have participated in this dispersal event, because it appeared simultaneously in western and southeastern Europe. The recently described *Dorcatherium maliki* from the late Miocene of West European Turkey (Kostopoulos and Sen 2016) and our discovery of the previously exclusively European species *Dt. naui* and *Dt. guntianum* among the material of the Pakistani Siwaliks also points in the direction (Figures 5.15, 5.16, 5.20, 5.21 and 5.22). This is especially significant by the high degree of correspondence of morphology and morphometric variables between *Dt. maliki* and *Dt. naui* (see remarks section regarding *Dorcatherium naui*), which indicate a close phylogenetic relationships between both both species. Besides reports on early Early Miocene *Dorcatherium pigotti* from Africa (Geraads 2010) and the Eastern Mediterranean (Tchernov et al. 1987), all

Dorcatherium, *Dorcabune*, and *Siamotragulus* representatives were considered to be endemic, continent-restricted species.

With the emergence of the “*Gomphotherium* land bridge”, the probable dispersal of tragulids between Asia and Africa or vice versa was enabled. In addition, the presence of similar vegetation types on both continents might have facilitated the exchange of browsing mammals between them, as has been shown for other groups (e.g. Rhinos, Chalicotheres, Suids and Carnivores or creodonts, Barry 1988; Patnaik 2016 and references therein). During the Middle Miocene, the Chinji Formation was deposited in an environment holding vegetation composed predominantly evergreen plants with additional moist- deciduous elements (Srivastava et al. 2014). Under these conditions, tragulid species would have occupied a relatively stable ecological niche, dominated by C3 plants and more or less warm global temperatures (Zachos et al. 2001; Flynn et al. 2016). However, it is unclear how tragulids could cross a belt of dry habitats or open enviromentn in northern Africa, the Middle East and Central Asia (Made and Mateos 2010) that possibly existed for as much as 20 Ma. Indeed, Mayda and Rössner (2007) reported on remains of tragulids from Sabuncubeli near Izmir (Turkey) in MN3, early Early Miocene (Bruijn et al 2006) predating the minimum appearance datum of European *Dorcatherium* records in MN4a (17.8 Ma, C5Dr2r, Burdigalian, late Early Miocene (Rössner 2017). This implies that, tragulids were detained for some time in Asia minor from continuing their dispersal, what may have been due to the dry or open environments (Jan van der Made, pers. Com.) impossible to live in for wetland adapted animals like the tragulids (Rössner and Heissig 2013, Rössner 2017).

When tragulids entered Africa and Europe they immediately attained species diversity, what dropped after the Middle Miocene (Made 1992, Pickford 2001, Clauss and Rössner 2014). After MN12 tragulids disappeared in Europe, but lived on in Pakistan and other places in Asia as well as in Africa. In Asia, tragulids represented quite some diversity as well during the

Middle Miocene, however a clear diversity drop has not been documented so far for the Late Miocene.

Overall spatiotemporal dispersal patterns of tragulids (and other taxa) may be correlated with gradual global cooling, especially in higher latitudes, superimposed on a relatively stable humid climate during the Neogene (Made 1992). In Asia, palynological evidence from the Lower Siwalik suggests the existence of vast forests with subtropical to temperate broad-leafed tree taxa (e.g., *Quercus*, *Lithocarpus*/*Castanopsis*, *Alnus*), and tropical evergreen forest taxa (Hoorn et al. 2000). In contrast the lower Middle Siwalik yielded evidence of invasive grassland dispersal (Hoorn et al. 2000, Patnaik 2016). There is no indication yet, that tragulids where severely affected by that vegetation change in the Siwalik deposition area. Recent ecological studies revealed the habitat use to be the most common dimension along which sympatric species partition resources to reduce competition (e.g. Davis et al. 2018). In this respect, the different tooth crown heights in the mostly contemporaneous tragulid species documented in our study (Figure 5.20) are likely to represent adaptations to different feeding habits. The extant tragulids, of which data on feeding habits are available, are the frugivorous *Hyemoschus aquaticus* of Africa and two *Tragulus* species of Asia, respectively (Dubost 1978; Heydon and Bulloh 1997), while frugivory has not been confirmed for fossil species so far. In fact, it has been found that fossil species with more or less the same body mass as living species were adapted to either intermediate diet (*Afrotragulus parvus,* 2.7 kg, Ungar et al. 2012; *Dorcatherium guntianum* 12.4 kg, Kaiser and Rössner 2007), or graze (*Siamotragulus songhorensis,* 5.6 kg, Ungar et al. 2012). In the future, detailed analyses of teeth may reveal feeding habits of fossil tragulids and their relatedness with tooth crown height.

In the future, the feeding habits of sympatric living tragulids should be analyzed in detail, and how they are related to tooth crown height. Explorations in that direction may be applied to fossil representatives, in order to improve our knowledge also on their diet.

5.5 Conclusions

Although there is a general consensus on the high tragulid diversity from the Siwalik Hills (Barry 2014; Khan et al. 2017), we recorded only three clasically *Dorcatherium* and one *Dorcabune* species from the Siwaliks, in contrast to the sixteen species reported by Barry (2014). Since their original establishment and also in subsequent studies, the differentiation within the genera of Tragulidae was based on tooth size only (e.g. Pilgrim 1915; Colbert 1935; Gaur 1992; Khan et al. 2012; Barry 2014 and references therein). In this context, a striking feature of previous quantitative analysis is for example, the poor completely missing reference to the data of type material for the asian species of *Dorcatherium* (Lydekker 1876) and *Dorcabune* (Pilgrim 1915) and/or the erroneous assignments of tooth position (see Table 5.4). On the basis of size, tooth crown height and related morphological features, here we identified the following species from the Siwaliks: *Dorcatherium nagrii*, *Dt. minus*, *Dt. majus* and *Dorcabune anthracotheroides*. In accordance with Barry (2014), we also agree that *Dt. nagrii* and the species of the genus *Siamotragulus* are very similar in tooth morphology and the analysis of post-cranial material and unworn teeth from Siwalik is required. We also classified one specimen as *Dt.* aff. *majus*, while another one, here recognized as *Dorcatherium dehmi* sp. nov. had remained undescribed so far because tooth size overlapped with that of other species and morphological details were not considered (Figures 5.15, 5.20, 5.21 and 5.22). Unexpectedly, we were able to recognize *Dt. naui* and *Dt. guntianum* and thus report for the first time, their occurrence outside of Europe. This discovery is also the first record of tragulid species with a distribution range spanning more than one continent, in this case, Europe and the Indian subcontinent.

Our results reveal the taxonomic potential of tooth morphology, especially of premolars and deciduous cheek teeth which, in future studies should be considered keeping in mind not only size variation.

Our results also show that among the Siwalik layers, the Middle Miocene Chinji Formation harboured the highest tragulid diversity, with seven species, followed by the Late Miocene Nagri and Dhok Pathan Formations with two and three species, respectively. Here, the *Dorcatherium guntianum* recored from the Chinji Formation (14.2 mya - 11.2 mya) is not older than that known from Europe (16.5 mya - 12.2 mya). By contrast, the *Dorcatherium naui* record from the Chinji Formation (14.2 mya - 11.2 mya) is older than the European one (8.7 mya - 12.2 mya) (Figure 5.5). It is expected that future discoveries in the fossil-rich Siwalik area should extend the knowledge on the systematics, biostratigraphy, and biogeography of tragulids.

CHAPTER 6

Conclusions

Conclusions

This thesis analyzed palaeobiology of Tragulidae. In doing so, I quantified the degree of similarity between fossil and living species through time. The results demonstrate that there was great morphological diversity from the past to the present, reflected in body size, dentition and skull morphology.

From the upper Eocene to the present, with a peak during the Middle Miocene, the tragulids were represented by a number of over 30 species that covered a broad range of body sizes from 1.0 kg to more than 100.0 kg (Chapter 2). Today, all extant tragulids are of small body size only. In an independent multivariate analysis I tested support based on skull morphometrics of living species for the recently revised taxonomy of crown Tragulidae (Chapter 3). This study also showed hitherto undocumented evidence of two different neurocranium shapes in living species: a globose shape in the Asian *Tragulus javanicus* and *T. kanchil* and a somewhat flattened geometry in *T. napu* and *Moschiola* spp. This skull study on the living tragulids was used as a reference when studying the skull of the well-preserved *Dorcatherium crassum* from the Middle Miocene of Germany. It was described based on analog and digital data and virtuell 3D reconstruction (Chapter 4). Comparative morphometric analysis of *Dt. crassum* was done for the first time at a multivariate basis in the context of the extant variability. The results show clear segregation from extant relatives and is closest in morphometric variables to the living *Hyaemoschus aquaticus* from Africa, suggesting that the two species most probably had a similar biology. Both species have even a more flattened skull geometry than *T. napu* and *Moschiola* spp. In detail, hyper-development of some elements such as the sagittal and nuchal crest, the neurocranium and the canine characterises *Dt. crassum*. My analysis of postcanine dental proportions revealed a similar intra- and inter-specific general pattern in all species studied (Chapter 2). There is an increase of size (width and length) in premolars and molars more pronounced in large species and similar in fossil and living species of the same body size. Based on Miocene tragulids from Pakistan (Chapter 4), I quantified a previously not reported variation in the tooth crown height and related morphological features. Accordingly, I provide an improved species delimitation for four of so far seven species from that spatiotemporal unit, found morphological evidence to establish the new species *Dorcatherium dehmi*, and unexpectedly discovered the hitherto only European *Dorcatherium naui* and *Dt. guntianum*.

Living tragulids were previously described as ‘living fossils’, but this has been recently questioned (see Chapter 2). My results show significant variation for these ruminants and coincide as in other groups (e.g. *Gynko* spp, *Latimeria* sp. etc, see chapter 2) previously misinterpreted as ‘living fossils’, which were shown to be part of a greater morphological diversity than previously thought (Chapter 2). Considering that ancient diversity of tragulids was greater than the current representatives, it is difficult to assess with these data, which are plesiomorphic or derived characters.

Finally, the outcomes presented in this Ph.D. thesis clearly enhance the understanding of morphological diversity and palaeobiology of these mammals, and highlight the importance of studies on tragulids in order to improve the understanding on their origin and evolution.

Future prospects

In spite of the large numbers of Tragulidae specimens in diverse collection worldwide – some of them only recently gathered, some lying there for more than century – our knowledge about the systematics, origin, and diversification of these ruminants remains poor. This lack of knowledge also applies to the recent members of Tragulidae. Apart from physiological studies on captive individuals and efforts to determine the systematics of recent Tragulidae, there are hardly any studies on their biology, ecology, and evolution. Even in the 21th century there are no comprehensive phylogenetic and population genetic studies available. Accordingly, I suggest the following important next steps in Tragulidae research.

- The complete description of fossil genera and species of Tragulidae is needed urgently. There are studies that mention a great number of taxa, however these are not determined at the species level, creating large lists of "Tragulidae sp.".
- Together with the species level determination, the geographical and stratigraphical origin of the specimens must be given.
- The knowledge about the biology, ecology and distribution of the recent members of Tragulidae must be enhanced considerably.
- Our understanding of the paleobiology of Tragulidae must be improved by the joint analysis of fossil and recent data.

Methods as for example *computed tomography* for the analysis of form and function or for the reconstruction of taxonomic characters for species delimitation, as well as the *tooth microwear* method for the investigation of paleodiet, are now at our disposal. We only have to get down to work and bring together all the data and results.

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Appendix

Palaeobiology of tragulids (Mammalia: Artiodactyla: Ruminantia)

Appendix Chapter 2

Table 2.1. List of tragulid specimens as compiled for this study and from literature.

						Measurements (mm)	
Category	**Genera**	**Species**	**Specimen**	**Literature source**	**Tooth**	**Length**	**Width / Anterior width**
Fossil	*Afrotragulus*	*moruorotensis*	Mor 1'2000	Pickford (2001a)	m1	4.4	2.5
Fossil	*Afrotragulus*	*moruorotensis*	Mor 1'2000	Pickford (2001a)	m2	4.6	2.9
Fossil	*Afrotragulus*	*moruorotensis*	Mor 1'2000	Pickford (2001a)	m3	6.7	2.9
Fossil	*Afrotragulus*	*moruorotensis*	Mt 86'51	Pickford (2001a)	m3	7.5	2.9
Fossil	*Afrotragulus*	*parvus*	846.48 R.106	Whitworth (1958)	p3	7.0	2.5
Fossil	*Afrotragulus*	*parvus*	801.47 R.3	Whitworth (1958)	p4	4.9	1.9
Fossil	*Afrotragulus*	*parvus*	846.48 R.106	Whitworth (1958)	p4	6.8	2.7
Fossil	*Afrotragulus*	*parvus*	56.51 R.3A	Whitworth (1958)	p4	5.2	2.0
Fossil	*Afrotragulus*	*parvus*	308.51 R.3	Whitworth (1958)	p4	7.2	3.6
Fossil	*Afrotragulus*	*parvus*	612.51	Whitworth (1958)	p4	5.2	2.3
Fossil	*Afrotragulus*	*parvus*	BMNH-M82689	Sánchez et al. (2010)	m1	4.9	2.6
Fossil	*Afrotragulus*	*parvus*	665.47 R.3.	Whitworth (1958)	m1	5.5	2.8
Fossil	*Afrotragulus*	*parvus*	801.47 R.3.	Whitworth (1958)	m1	5.1	2.8
Fossil	*Afrotragulus*	*parvus*	1171.50	Whitworth (1958)	m1	5.3	3.6
Fossil	*Afrotragulus*	*parvus*	612.51	Whitworth (1958)	m1	5.8	3.1
Fossil	*Afrotragulus*	*parvus*	750.52 R.39	Whitworth (1958)	m1	5.2	2.3
Fossil	*Afrotragulus*	*parvus*	795.52 R.110	Whitworth (1958)	m1	5.0	2.8
Fossil	*Afrotragulus*	*parvus*	BMNH-M82689	Sánchez et al. (2010)	m2	6.0	3.2
Fossil	*Afrotragulus*	*parvus*	BMNH-M82690	Sánchez et al. (2010)	m2	6.5	3.2
Fossil	*Afrotragulus*	*parvus*	801.47 R.3.	Whitworth (1958)	m2	6.1	3.3
Fossil	*Afrotragulus*	*parvus*	485.49 R.3A	Whitworth (1958)	m2	5.8	3.4
Fossil	*Afrotragulus*	*parvus*	1171.50	Whitworth (1958)	m2	7.1	4.6
Fossil	*Afrotragulus*	*parvus*	750.52 R.39	Whitworth (1958)	m2	5.7	3.3
Fossil	*Afrotragulus*	*parvus*	795.52 R.110	Whitworth (1958)	m2	6.3	3.6
Fossil	*Afrotragulus*	*parvus*	485.49 R.3A	Whitworth (1958)	m3	7.8	3.6
Fossil	*Afrotragulus*	*parvus*	1171.50	Whitworth (1958)	m3	9.9	4.4
Fossil	*Afrotragulus*	*parvus*	750.52 R.39	Whitworth (1958)	m3	8.0	3.6
Fossil	*Afrotragulus*	*parvus*	795.52 R.110	Whitworth (1958)	m3	8.0	3.7
Fossil	*Archaeotragulus*	*krabiensis*	TF-2997	Métais et al. (2001)	p2	5.6	2.6
Fossil	*Archaeotragulus*	*krabiensis*	TF-2997	Métais et al. (2001)	p3	7.2	3.5
Fossil	*Archaeotragulus*	*krabiensis*	TF-2997	Métais et al. (2001)	p4	7.0	3.9
Fossil	*Archaeotragulus*	*krabiensis*	TF-2989	Métais et al. (2001)	m1	7.2	4.0
Fossil	*Archaeotragulus*	*krabiensis*	TF-2997	Métais et al. (2001)	m1	6.8	4.0
Fossil	*Archaeotragulus*	*krabiensis*	TF-2989	Métais et al. (2001)	m2	7.5	4.9
Fossil	*Archaeotragulus*	*krabiensis*	TF-2997	Métais et al. (2001)	m2	7.3	5.1

Fossil	*Archaeotragulus*	*krabiensis*	TF-2989	Métais et al. (2001)	m3	10.5	5.0
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	p2	6.9	2.7
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	p2	7.3	2.5
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/40/1927	This study	p2	7.4	2.7
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	p2	7.8	2.7
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/22/1927	This study	p2	8.1	3.0
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/23/1927	This study	p2	8.6	2.9
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	p3	9.5	3.4
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	p3	9.7	3.3
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/22/1927	This study	p3	9.8	3.6
Fossil	*Dorcatherium*	*guntianum*	NMA-1495	This study	p3	9.9	3.4
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	p3	9.9	3.6
Fossil	*Dorcatherium*	*guntianum*	NMA-85.25	This study	p3	10.0	3.6
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	p4	7.6	4.0
Fossil	*Dorcatherium*	*guntianum*	NMA-85.45	This study	p4	8.6	4.3
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	p4	8.6	4.0
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	p4	8.8	4.0
Fossil	*Dorcatherium*	*guntianum*	NMA-740	This study	p4	9.0	4.0
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	p4	9.0	3.7
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	p4	9.0	4.2
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/22/1927	This study	p4	9.2	4.0
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	p4	9.3	4.2
Fossil	*Dorcatherium*	*guntianum*	NMA-86-302/333	This study	p4	9.4	4.0
Fossil	*Dorcatherium*	*guntianum*	NMA-Col. Selner 64	This study	m1	8.5	5.8
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	m1	8.6	6.0
Fossil	*Dorcatherium*	*guntianum*	NMA-1995	This study	m1	8.7	6.4
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/24/1927	This study	m1	8.9	5.7
Fossil	*Dorcatherium*	*guntianum*	NMA-1747	This study	m1	9.0	6.4
Fossil	*Dorcatherium*	*guntianum*	NMA-85.25	This study	m1	9.0	6.6
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	m1	9.1	6.4
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	m1	9.3	5.7
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/22/1927	This study	m1	9.6	5.9
Fossil	*Dorcatherium*	*guntianum*	SO-614	This study	m1	8.3	5.5
Fossil	*Dorcatherium*	*guntianum*	SNSB-BSPG 1881 IX 737	This study	m1	8.6	5.5
Fossil	*Dorcatherium*	*guntianum*	SNSB-BSPG 1881 IX 735	This study	m1	9.3	5.6
Fossil	*Dorcatherium*	*guntianum*	SNSB-BSPG 1956 II 2554	This study	m1	7.7	4.3
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/23/1927	This study	m2	9.9	6.1
Fossil	*Dorcatherium*	*guntianum*	SNSB-BSPG 1881 IX 731	This study	m2	9.9	5.8
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/24/1927	This study	m2	10.0	6.7
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/25/1927	This study	m2	10.1	6.7
Fossil	*Dorcatherium*	*guntianum*	NMA-1995	This study	m2	10.3	7.1
Fossil	*Dorcatherium*	*guntianum*	SNSB-BSPG 1881 IX 736	This study	m2	9.1	5.4
Fossil	*Dorcatherium*	*guntianum*	SNSB-BSPG 1881 IX 737	This study	m2	10.0	6.1
Fossil	*Dorcatherium*	*guntianum*	SNSB-BSPG 1956 II 2554	This study	m2	9.1	5.0
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	m3	13.7	6.8

Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	m3	14.0	6.8
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/24/1927	This study	m3	14.0	6.7
Fossil	*Dorcatherium*	*guntianum*	NMA-86-292/333	This study	m3	14.0	6.3
Fossil	*Dorcatherium*	*guntianum*	NMA-85.24	This study	m3	14.1	6.7
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	m3	14.2	6.6
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/25/1927	This study	m3	14.3	7.1
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/38/1927	This study	m3	14.3	6.6
Fossil	*Dorcatherium*	*guntianum*	NMA-1747	This study	m3	14.4	7.3
Fossil	*Dorcatherium*	*guntianum*	NMA-740	This study	m3	14.4	6.6
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/22/1927	This study	m3	14.6	6.6
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	m3	14.6	6.7
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	m3	14.7	7.4
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	m3	15.0	6.6
Fossil	*Dorcatherium*	*guntianum*	NMA-85.31	This study	m3	15.0	7.3
Fossil	*Dorcatherium*	*guntianum*	NMA-85.28	This study	m3	15.1	7.2
Fossil	*Dorcatherium*	*guntianum*	NMA-85.27	This study	m3	15.1	6.7
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	m3	15.2	7.0
Fossil	*Dorcatherium*	*guntianum*	NMA-86-291/333	This study	m3	15.2	7.0
Fossil	*Dorcatherium*	*guntianum*	NMA-85.30	This study	m3	15.2	7.1
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	m3	15.3	7.0
Fossil	*Dorcatherium*	*guntianum*	NMA-411	This study	m3	15.4	6.8
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	m3	15.5	6.5
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	m3	15.5	7.0
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	m3	15.5	7.2
Fossil	*Dorcatherium*	*guntianum*	NMA-85.32	This study	m3	15.8	7.4
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	m3	15.8	7.0
Fossil	*Dorcatherium*	*guntianum*	NMA-85.29	This study	m3	15.8	7.0
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/39/1927	This study	m3	16.0	7.5
Fossil	*Dorcatherium*	*guntianum*	NMA-740	This study	m3	16.1	8.3
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/29/1927	This study	m3	16.1	7.3
Fossil	*Dorcatherium*	*guntianum*	NMA-1417	This study	m3	16.6	7.1
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	m3	16.7	7.8
Fossil	*Dorcatherium*	*guntianum*	SNSP-BSPG 1881 IX 737	This study	m3	14.7	6.4
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/101	Gaur (1992)	p2	5.2	2.3
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/101	Gaur (1992)	p3	7.0	2.6
Fossil	*Dorcatherium*	*nagrii*	SNSB-BSPG 1956 II 2569	This study	p3	nd	2.9
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/102	Gaur (1992)	p4	8.2	3.3
Fossil	*Dorcatherium*	*nagrii*	SNSB-BSPG 1956 II 2455	This study	p4	7.7	2.7
Fossil	*Dorcatherium*	*nagrii*	GSI-18079	Prasad (1970)	m1	6.5	3.6
Fossil	*Dorcatherium*	*nagrii*	GSI-K21.658	Prasad (1970)	m1	7.0	4.0
Fossil	*Dorcatherium*	*nagrii*	HT-34-81	Sankhyan (1982)	m1	6.0	3.5
Fossil	*Dorcatherium*	*nagrii*	PUA-89/76 RN	Vasishat et al. (1985)	m1	7.1	4.1
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/102	Gaur (1992)	m1	5.8	3.4
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/106	Gaur (1992)	m1	5.9	3.6
Fossil	*Dorcatherium*	*nagrii*	SNSB-BSPG 1956 II 2569	This study	m1	6.5	3.7

Fossil	*Dorcatherium*	*nagrii*	AMNH-39508b (1981 XVII 71)	This study	m1	6.5	2.9
Fossil	*Dorcatherium*	*nagrii*	GSI-18079	Prasad (1970)	m2	6.6	4.0
Fossil	*Dorcatherium*	*nagrii*	GSI-K21.658	Prasad (1970)	m2	7.5	4.5
Fossil	*Dorcatherium*	*nagrii*	GSI-K21.744	Prasad (1970)	m2	7.5	4.0
Fossil	*Dorcatherium*	*nagrii*	GSI-K47.768	Prasad (1970)	m2	7.1	4.5
Fossil	*Dorcatherium*	*nagrii*	HT-34-81	Sankhyan (1982)	m2	7.0	4.2
Fossil	*Dorcatherium*	*nagrii*	HT-37-81	Sankhyan (1982)	m2	7.0	4.0
Fossil	*Dorcatherium*	*nagrii*	PUA-89/76 RN	Vasishat et al. (1985)	m2	8.3	4.9
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/102	Gaur (1992)	m2	7.1	4.2
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/105	Gaur (1992)	m2	7.4	3.8
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/106	Gaur (1992)	m2	6.7	3.9
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/107	Gaur (1992)	m2	7.0	4.5
Fossil	*Dorcatherium*	*nagrii*	SNSB-BSPG 1956 II 2577	This study	m2	7.7	3.5
Fossil	*Dorcatherium*	*nagrii*	AMNH-39508b (1981 XVII 71)	This study	m2	6.8	3.7
Fossil	*Dorcatherium*	*nagrii*	AMNH-19613 (1981 XVII 68)	This study	m2	8.0	4.6
Fossil	*Dorcatherium*	*nagrii*	AMNH-39508c (1981 XVII 70)	This study	m2	6.6	4.1
Fossil	*Dorcatherium*	*nagrii*	GSI-18079	Prasad (1970)	m3	10.0	4.5
Fossil	*Dorcatherium*	*nagrii*	GSI-K21.744	Prasad (1970)	m3	9.0	4.5
Fossil	*Dorcatherium*	*nagrii*	GSI-K47.768	Prasad (1970)	m3	9.0	4.6
Fossil	*Dorcatherium*	*nagrii*	HT-34-81	Sankhyan (1982)	m3	11.0	4.5
Fossil	*Dorcatherium*	*nagrii*	HT-36-81	Sankhyan (1982)	m3	9.5	4.0
Fossil	*Dorcatherium*	*nagrii*	HT-37-81	Sankhyan (1982)	m3	10.0	4.2
Fossil	*Dorcatherium*	*nagrii*	PUA-89/76 RN	Vasishat et al. (1985)	m3	10.5	5.2
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/102	Gaur (1992)	m3	11.0	4.3
Fossil	*Dorcatherium*	*nagrii*	SNSB-BSPG 1956 II 2569	This study	m3	11.1	4.7
Fossil	*Dorcatherium*	*nagrii*	AMNH-39512 (1981 XVII 75)	This study	m3	12.5	5.4
Fossil	*Dorcatherium*	*nagrii*	AMNH-19613 (1981 XVII 68)	This study	m3	10.9	4.7
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/105	Gaur (1992)	m3	11.5	4.7
Fossil	*Dorcatherium*	*pigotti*	737.52	Whitworth (1958)	p2	7.1	2.5
Fossil	*Dorcatherium*	*pigotti*	M. 26684	Hamilton (1973)	p3	10.0	3.6
Fossil	*Dorcatherium*	*pigotti*	737.52	Whitworth (1958)	p3	8.5	3.1
Fossil	*Dorcatherium*	*pigotti*	M. 26684	Hamilton (1973)	p4	9.6	4.0
Fossil	*Dorcatherium*	*pigotti*	737.52	Whitworth (1958)	p4	7.9	3.8
Fossil	*Dorcatherium*	*pigotti*	M. 26684	Hamilton (1973)	m1	9.3	5.8
Fossil	*Dorcatherium*	*pigotti*	737.52	Whitworth (1958)	m1	8.2	4.8
Fossil	*Dorcatherium*	*pigotti*	M. 26684	Hamilton (1973)	m2	11.0	6.6
Fossil	*Dorcatherium*	*pigotti*	837.47 R.75	Whitworth (1958)	m2	10.0	6.0
Fossil	*Dorcatherium*	*pigotti*	737.52	Whitworth (1958)	m2	8.9	5.3
Fossil	*Dorcatherium*	*pigotti*	790.52 R.38	Whitworth (1958)	m2	8.2	5.6
Fossil	*Dorcatherium*	*pigotti*	791.52	Whitworth (1958)	m2	9.5	5.7
Fossil	*Dorcatherium*	*pigotti*	837.47 R.75	Whitworth (1958)	m3	14.0	6.0
Fossil	*Dorcatherium*	*pigotti*	790.52 R.38	Whitworth (1958)	m3	13.8	6.0
Fossil	*Dorcatherium*	*pigotti*	791.52	Whitworth (1958)	m3	14.0	5.9
Extant	*Hyemoschus*	*aquaticus*	NHMW-5407	This study	p2	7.7	2.9
Extant	*Hyemoschus*	*aquaticus*	NHMW-40827/Gr.290	This study	p2	8.5	2.8

Extant	*Hyemoschus*	*aquaticus*	SMNS-1842	This study	p2	7.6	2.8
Extant	*Hyemoschus*	*aquaticus*	NHMB-2692	This study	p2	8.5	3.0
Extant	*Hyemoschus*	*aquaticus*	NHMB-8699	This study	p2	7.5	2.7
Extant	*Hyemoschus*	*aquaticus*	NHMB-LXX4	This study	p2	8.3	2.7
Extant	*Hyemoschus*	*aquaticus*	NHMW-5407	This study	p3	8.9	3.4
Extant	*Hyemoschus*	*aquaticus*	NHMW-40827/Gr.290	This study	p3	8.4	3.1
Extant	*Hyemoschus*	*aquaticus*	SMNS-1842	This study	p3	8.4	3.3
Extant	*Hyemoschus*	*aquaticus*	NHMB-2692	This study	p3	9.5	3.4
Extant	*Hyemoschus*	*aquaticus*	NHMB-LXX4	This study	p3	9.0	3.1
Extant	*Hyemoschus*	*aquaticus*	NHMW-5407	This study	p4	9.1	4.1
Extant	*Hyemoschus*	*aquaticus*	NHMW-40827/Gr.290	This study	p4	8.6	3.9
Extant	*Hyemoschus*	*aquaticus*	NHMB-2692	This study	p4	8.8	4.1
Extant	*Hyemoschus*	*aquaticus*	NHMB-8699	This study	p4	9.3	4.1
Extant	*Hyemoschus*	*aquaticus*	UMZC-H.14.933	This study	m1	10.0	6.0
Extant	*Hyemoschus*	*aquaticus*	UMZC-H.14.933	This study	m1	10.3	5.9
Extant	*Hyemoschus*	*aquaticus*	NHMW-5407	This study	m1	9.4	6.1
Extant	*Hyemoschus*	*aquaticus*	NHMW-40827/Gr.290	This study	m1	8.9	5.2
Extant	*Hyemoschus*	*aquaticus*	SMNS-1842	This study	m1	8.3	5.6
Extant	*Hyemoschus*	*aquaticus*	NHMB-2692	This study	m1	9.9	6.4
Extant	*Hyemoschus*	*aquaticus*	NHMB-8699	This study	m1	8.0	5.3
Extant	*Hyemoschus*	*aquaticus*	NHMB-LXX4	This study	m1	9.1	6.5
Extant	*Hyemoschus*	*aquaticus*	NHMW-5407	This study	m2	9.2	6.9
Extant	*Hyemoschus*	*aquaticus*	NHMW-40827/Gr.290	This study	m2	9.5	6.2
Extant	*Hyemoschus*	*aquaticus*	SMNS-1842	This study	m2	10.0	6.7
Extant	*Hyemoschus*	*aquaticus*	NHMB-2692	This study	m2	9.2	7.1
Extant	*Hyemoschus*	*aquaticus*	NHMB-8699	This study	m2	9.1	7.1
Extant	*Hyemoschus*	*aquaticus*	NHMB-LXX4	This study	m2	10.2	7.4
Extant	*Hyemoschus*	*aquaticus*	NHMW-5407	This study	m3	13.2	7.1
Extant	*Hyemoschus*	*aquaticus*	NHMW-40827/Gr.290	This study	m3	12.9	6.2
Extant	*Hyemoschus*	*aquaticus*	NHMB-2692	This study	m3	12.7	6.9
Extant	*Hyemoschus*	*aquaticus*	NHMB-LXX4	This study	m3	14.3	7.1
Fossil	*Iberomeryx*	*minor*	Sc. 118	Sudre (1984)	p2	3.8	nd
Fossil	*Iberomeryx*	*minor*	ITD-908	Sudre (1984)	p3	6.6	3.0
Fossil	*Iberomeryx*	*minor*	QB 32	Sudre (1984)	p3	5.5	1.5
Fossil	*Iberomeryx*	*minor*	Sc. 118	Sudre (1984)	p3	4.2	nd
Fossil	*Iberomeryx*	*minor*	nn	Sudre (1984)	p4	4.0	2.0
Fossil	*Iberomeryx*	*minor*	QB 29	Sudre (1984)	p4	4.0	1.8
Fossil	*Iberomeryx*	*minor*	QB 32	Sudre (1984)	p4	5.0	1.9
Fossil	*Iberomeryx*	*minor*	Sc. 118	Sudre (1984)	p4	3.9	nd
Fossil	*Iberomeryx*	*minor*	Schlosser 1886	Sudre (1984)	p4	4.4	nd
Fossil	*Iberomeryx*	*minor*	MJSN-BEU001-410	Mennecart et al. (2011)	p4	4.7	nd
Fossil	*Iberomeryx*	*minor*	MJSN-PRC004-159	Mennecart et al. (2011)	p4	4,0	nd
Fossil	*Iberomeryx*	*minor*	nn	Sudre (1984)	m1	4.5	2.5
Fossil	*Iberomeryx*	*minor*	Schlosser 1886	Sudre (1984)	m1	4.8	nd
Fossil	*Iberomeryx*	*minor*	QB 29	Sudre (1984)	m1	4.4	2.5

Fossil	*Iberomeryx*	*minor*	QB 32	Sudre (1984)	m1	5.5	3.0
Fossil	*Iberomeryx*	*minor*	Sc. 118	Sudre (1984)	m1	4.6	2.9
Fossil	*Iberomeryx*	*minor*	NMB-Sc. 118	Mennecart et al. (2011)	m1	4.4	nd
Fossil	*Iberomeryx*	*minor*	MJSN-PRC004-159	Mennecart et al. (2011)	m1	5.1	nd
Fossil	*Iberomeryx*	*minor*	nn	Sudre (1984)	m2	5.0	3.0
Fossil	*Iberomeryx*	*minor*	QB 29	Sudre (1984)	m2	5.1	3.1
Fossil	*Iberomeryx*	*minor*	QB 32	Sudre (1984)	m2	5.5	3.1
Fossil	*Iberomeryx*	*minor*	Sc. 118	Sudre (1984)	m2	5.0	3.5
Fossil	*Iberomeryx*	*minor*	Schlosser 1886	Sudre (1984)	m2	5.0	nd
Fossil	*Iberomeryx*	*minor*	NMB-Sc. 118 dext.	Mennecart et al. (2011)	m2	5.8	nd
Fossil	*Iberomeryx*	*minor*	MJSN-BEU001-411	Mennecart et al. (2011)	m2	4.9	nd
Fossil	*Iberomeryx*	*minor*	MJSN-BEU001-409	Mennecart et al. (2011)	m2	4.9	nd
Fossil	*Iberomeryx*	*minor*	MJSN-PRC004-159	Mennecart et al. (2011)	m2	5.3	nd
Fossil	*Iberomeryx*	*minor*	NMB-Q.W.540	Mennecart et al. (2011)	m2	6.1	nd
Fossil	*Iberomeryx*	*minor*	NMB-Qu.B.30	Mennecart et al. (2011)	m2	5.5	nd
Fossil	*Iberomeryx*	*minor*	NMB-Qu.B.31	Mennecart et al. (2011)	m2	5.4	nd
Fossil	*Iberomeryx*	*minor*	USTL-ITD28	Sudre (1984)	m3	8.1	3.5
Fossil	*Iberomeryx*	*minor*	USTL-ITD29	Sudre (1984)	m3	8.5	4.4
Fossil	*Iberomeryx*	*minor*	nn	Sudre (1984)	m3	7.0	3.0
Fossil	*Iberomeryx*	*minor*	QB 29	Sudre (1984)	m3	7.7	3.5
Fossil	*Iberomeryx*	*minor*	QB 32	Sudre (1984)	m3	8.	3.7
Fossil	*Iberomeryx*	*minor*	Sc. 118	Sudre (1984)	m3	8.1	3.4
Fossil	*Iberomeryx*	*minor*	Schlosser 1886	Sudre (1984)	m3	7.5	nd
Fossil	*Iberomeryx*	*minor*	NMB-Sc. 118 dext.	Mennecart et al. (2011)	m3	8.2	nd
Fossil	*Iberomeryx*	*minor*	MJSN-PRC004-159	Mennecart et al. (2011)	m3	8.1	nd
Fossil	*Iberomeryx*	*minor*	NMB-Q.W.540	Mennecart et al. (2011)	m3	8.2	nd
Fossil	*Iberomeryx*	*minor*	NMB-Qu.B.30	Mennecart et al. (2011)	m3	7.8	nd
Fossil	*Iberomeryx*	*minor*	NMB-Qu.B.31	Mennecart et al. (2011)	m3	7.6	nd
Fossil	*Iberomeryx*	*parvus*	GK3-11	Métais et al. (2016)	p3	3.0	1.2
Fossil	*Iberomeryx*	*parvus*	GK3-36	Métais et al. (2016)	p4	4.4	1.9
Fossil	*Iberomeryx*	*parvus*	GK3-8	Métais et al. (2016)	m1	5.3	2.2
Fossil	*Iberomeryx*	*parvus*	641-5	Métais et al. (2016)	m1	5.5	2.6
Fossil	*Iberomeryx*	*parvus*	641-4	Métais et al. (2016)	m1	5.4	2.5
Fossil	*Iberomeryx*	*parvus*	GK3-3	Métais et al. (2016)	m1	5.6	2.6
Fossil	*Iberomeryx*	*parvus*	GK3-42	Métais et al. (2016)	m2	6.1	2.9
Fossil	*Iberomeryx*	*parvus*	641-7	Métais et al. (2016)	m2	6.3	2.6
Fossil	*Iberomeryx*	*parvus*	641-3	Métais et al. (2016)	m2	6.8	3.0
Fossil	*Iberomeryx*	*parvus*	GK3-34	Métais et al. (2016)	m2	7.2	3.4
Fossil	*Iberomeryx*	*parvus*	GK3-33	Métais et al. (2016)	m2	6.0	2.9
Fossil	*Iberomeryx*	*parvus*	641-6	Métais et al. (2016)	m2	7.1	3.1
Fossil	*Iberomeryx*	*parvus*	641-2	Métais et al. (2016)	m3	7.8	2.9
Fossil	*Iberomeryx*	*parvus*	GK3-2	Métais et al. (2016)	m3	7.9	2.7
Extant	*Moschiola*	*indica*	NHMW-B6016	This study	p2	5.4	2,0
Extant	*Moschiola*	*indica*	NHMW-B6016	This study	p3	6.1	2.1
Extant	*Moschiola*	*indica*	ZMH-4771	This study	p4	8.2	3.3

Extant	*Moschiola*	*indica*	NHMW-B6016	This study	p4	6.6	2.7
Extant	*Moschiola*	*indica*	ZMH-4793	This study	m1	6.0	4.0
Extant	*Moschiola*	*indica*	ZMH-4793	This study	m1	6.1	4.0
Extant	*Moschiola*	*indica*	ZMH-4771	This study	m1	7.0	3.7
Extant	*Moschiola*	*indica*	ZMH-4773	This study	m1	7.0	4.2
Extant	*Moschiola*	*indica*	ZMH-4770	This study	m1	7.0	4.1
Extant	*Moschiola*	*indica*	ZMH-4770	This study	m1	7.3	4.5
Extant	*Moschiola*	*indica*	ZMH-4773	This study	m1	7.9	4.1
Extant	*Moschiola*	*indica*	ZMH-4771	This study	m1	8.0	3.9
Extant	*Moschiola*	*indica*	ZMH-4791	This study	m1	6.5	4.3
Extant	*Moschiola*	*indica*	ZMH-4791	This study	m1	7.0	4.3
Extant	*Moschiola*	*indica*	NHMW-B6016	This study	m1	6.2	4.4
Extant	*Moschiola*	*indica*	ZMH-4771	This study	m2	7.1	4.6
Extant	*Moschiola*	*indica*	ZMH-4793	This study	m2	7.4	4.2
Extant	*Moschiola*	*indica*	ZMH-4770	This study	m2	7.5	4.8
Extant	*Moschiola*	*indica*	ZMH-4771	This study	m2	7.6	4.4
Extant	*Moschiola*	*indica*	ZMH-4793	This study	m2	7.6	4.3
Extant	*Moschiola*	*indica*	ZMH-4770	This study	m2	7.9	4.7
Extant	*Moschiola*	*indica*	ZMH-4791	This study	m2	7.7	4.7
Extant	*Moschiola*	*indica*	ZMH-4791	This study	m2	8.0	4.9
Extant	*Moschiola*	*indica*	NHMW-B6016	This study	m2	7.6	4.8
Extant	*Moschiola*	*indica*	ZMH-4771	This study	m3	10.7	4.6
Extant	*Moschiola*	*indica*	ZMH-4771	This study	m3	11.1	4.8
Extant	*Moschiola*	*indica*	NHMW-B6016	This study	m3	9.7	4.7
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	p2	49	1.9
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	p2	5.0	2.0
Extant	*Moschiola*	*meminna*	NHMB-C1366	This study	p2	5.6	2.1
Extant	*Moschiola*	*meminna*	NHMB-C2453	This study	p2	6.4	2.3
Extant	*Moschiola*	*meminna*	NHMB-C2588	This study	p2	5.5	2.0
Extant	*Moschiola*	*meminna*	NHMB-2328	This study	p2	5.9	1.9
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	p3	6.7	2.8
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	p3	7.0	2.7
Extant	*Moschiola*	*meminna*	NHMB-C1366	This study	p3	6.1	2.7
Extant	*Moschiola*	*meminna*	NHMB-C2453	This study	p3	7.4	2.9
Extant	*Moschiola*	*meminna*	NHMB-C2588	This study	p3	6.9	2.8
Extant	*Moschiola*	*meminna*	NHMB-C1429	This study	p3	6.5	2.7
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	p4	7.4	2.7
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	p4	7.4	3.0
Extant	*Moschiola*	*meminna*	NHMB-C1366	This study	p4	6.9	3.2
Extant	*Moschiola*	*meminna*	NHMB-C2453	This study	p4	7.3	3.0
Extant	*Moschiola*	*meminna*	NHMB-C2588	This study	p4	6.4	2.9
Extant	*Moschiola*	*meminna*	NHMB-C1429	This study	p4	6.5	2.9
Extant	*Moschiola*	*meminna*	NHMB-2328	This study	p4	8.0	3.1
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	m1	7.0	4.7
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	m1	7.2	4.5

Extant	*Moschiola*	*meminna*	NHMB-C1366	This study	m1	6.6	3.8
Extant	*Moschiola*	*meminna*	NHMB-C2453	This study	m1	6.7	3.9
Extant	*Moschiola*	*meminna*	NHMB-C2588	This study	m1	5.9	4.0
Extant	*Moschiola*	*meminna*	NHMB-C1429	This study	m1	6.3	4.3
Extant	*Moschiola*	*meminna*	NHMB-2328	This study	m1	6.3	3.7
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	m2	7.9	5.0
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	m2	8.1	4.5
Extant	*Moschiola*	*meminna*	NHMB-C1366	This study	m2	7.2	4.2
Extant	*Moschiola*	*meminna*	NHMB-C2453	This study	m2	6.9	4.6
Extant	*Moschiola*	*meminna*	NHMB-C2588	This study	m2	6.6	4.5
Extant	*Moschiola*	*meminna*	NHMB-C1429	This study	m2	7.1	4.6
Extant	*Moschiola*	*meminna*	NHMB-2328	This study	m2	6.3	4.1
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	m3	10.9	4.6
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	m3	11.0	4.7
Extant	*Moschiola*	*meminna*	NHMB-C1366	This study	m3	9.0	4.1
Extant	*Moschiola*	*meminna*	NHMB-C2453	This study	m3	10.0	4.7
Extant	*Moschiola*	*meminna*	NHMB-C2588	This study	m3	82	4.3
Extant	*Moschiola*	*meminna*	NHMB-C1429	This study	m3	9.1	4.5
Extant	*Moschiola*	*meminna*	NHMB-2328	This study	m3	9.3	3.8
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2505	Ginsburg et al. (2001)	p4	8.1	3.0
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2485	Ginsburg et al. (2001)	m2	8.2	6.0
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2503	Ginsburg et al. (2001)	m2	8.3	5.2
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2485	Ginsburg et al. (2001)	m3	12.2	5.5
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2491	Ginsburg et al. (2001)	m3	13.3	5.3
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2493	Ginsburg et al. (2001)	m3	13.4	6.0
Fossil	*Siamotragulus*	*sanyathanai*	PG1	Thomas et al. (1990)	p3	9.0	nd
Fossil	*Siamotragulus*	*sanyathanai*	PG1	Thomas et al. (1990)	p4	8.0	nd
Fossil	*Siamotragulus*	*sanyathanai*	PG1	Thomas et al. (1990)	m1	6.7	nd
Fossil	*Siamotragulus*	*sanyathanai*	PG1	Thomas et al. (1990)	m2	8.0	nd
Fossil	*Siamotragulus*	*sanyathanai*	PG1	Thomas et al. (1990)	m3	11.7	nd
Fossil	*Siamotragulus*	*songhorensis*	448.48	Whitworth (1958)	p3	7.8	2.5
Fossil	*Siamotragulus*	*songhorensis*	F. 3193	Whitworth (1958)	p4	6.8	2.7
Fossil	*Siamotragulus*	*songhorensis*	448.48	Whitworth (1958)	p4	7.6	3.0
Fossil	*Siamotragulus*	*songhorensis*	Nap IV'785	Pickford (2002)	p4	6.7	2.7
Fossil	*Siamotragulus*	*songhorensis*	Nap V	Pickford (2002)	p4	6.9	2.8
Fossil	*Siamotragulus*	*songhorensis*	Nap V 64	Pickford (2002)	p4	7.0	4.0
Fossil	*Siamotragulus*	*songhorensis*	Nap V 64	Pickford (2002)	p4	7.1	3.0
Fossil	*Siamotragulus*	*songhorensis*	F. 3205	Whitworth (1958)	m1	6.4	4.0
Fossil	*Siamotragulus*	*songhorensis*	F. 3207	Whitworth (1958)	m1	7.0	4.4
Fossil	*Siamotragulus*	*songhorensis*	754.52	Whitworth (1958)	m1	6.2	3.7
Fossil	*Siamotragulus*	*songhorensis*	756.52	Whitworth (1958)	m1	6.6	4.0
Fossil	*Siamotragulus*	*songhorensis*	NAP XXI 10J'08	Sánchez et al. (2014)	m1	7.1	4.2
Fossil	*Siamotragulus*	*songhorensis*	LT 120´07	Quiralte et al. (2008)	m1	6.7	3.6
Fossil	*Siamotragulus*	*songhorensis*	Nap IXC 64	Pickford (2002)	m1	6.4	3.4
Fossil	*Siamotragulus*	*songhorensis*	Nap I 91'99	Pickford (2002)	m1	6.7	3.8

Fossil	*Siamotragulus*	*songhorensis*	Nap I Peg 2 64	Pickford (2002)	m1	6.7	3.6
Fossil	*Siamotragulus*	*songhorensis*	Nap I 64	Pickford (2002)	m1	6.8	3.5
Fossil	*Siamotragulus*	*songhorensis*	Nap I 88' 98	Pickford (2002)	m1	7.2	3.7
Fossil	*Siamotragulus*	*songhorensis*	F. 3205	Whitworth (1958)	m2	7.6	4.6
Fossil	*Siamotragulus*	*songhorensis*	36.49	Whitworth (1958)	m2	8.0	4.2
Fossil	*Siamotragulus*	*songhorensis*	519.49	Whitworth (1958)	m2	6.8	3.7
Fossil	*Siamotragulus*	*songhorensis*	754.52	Whitworth (1958)	m2	7.4	4.5
Fossil	*Siamotragulus*	*songhorensis*	756.52	Whitworth (1958)	m2	7.2	4.5
Fossil	*Siamotragulus*	*songhorensis*	nn	Pickford (2002)	m2	7.1	4.2
Fossil	*Siamotragulus*	*songhorensis*	Nap IXC 64	Pickford (2002)	m2	7.4	4.1
Fossil	*Siamotragulus*	*songhorensis*	Nap I 88´98	Pickford (2002)	m2	7.5	4.
Fossil	*Siamotragulus*	*songhorensis*	Nap IV 64 P67-07	Pickford (2002)	m2	7.6	4.8
Fossil	*Siamotragulus*	*songhorensis*	Nap V Aug 62	Pickford (2002)	m2	7.6	4.6
Fossil	*Siamotragulus*	*songhorensis*	N I 64	Pickford (2002)	m2	7.7	3.5
Fossil	*Siamotragulus*	*songhorensis*	Nap IV 13´99	Pickford (2002)	m2	7.8	4.6
Fossil	*Siamotragulus*	*songhorensis*	Nap I 94´99	Pickford (2002)	m2	8.0	4.3
Fossil	*Siamotragulus*	*songhorensis*	Nap V 61	Pickford (2002)	m2	8.0	4.9
Fossil	*Siamotragulus*	*songhorensis*	Nap V 61 6	Pickford (2002)	m2	8.0	4.2
Fossil	*Siamotragulus*	*songhorensis*	Nap IV 61	Pickford (2002)	m2	8.2	5.4
Fossil	*Siamotragulus*	*songhorensis*	Nap V 12´02	Pickford (2002)	m2	8.3	4.6
Fossil	*Siamotragulus*	*songhorensis*	Nap V 13´02	Pickford (2002)	m2	8.2	4.8
Fossil	*Siamotragulus*	*songhorensis*	Nap V 92´02	Pickford (2002)	m2	7.9	4.3
Fossil	*Siamotragulus*	*songhorensis*	Nap V 62	Pickford (2002)	m2	8.2	4.6
Fossil	*Siamotragulus*	*songhorensis*	F. 3205	Whitworth (1958)	m3	10.5	5.0
Fossil	*Siamotragulus*	*songhorensis*	518.49	Whitworth (1958)	m3	12.1	5.1
Fossil	*Siamotragulus*	*songhorensis*	754.52	Whitworth (1958)	m3	10.5	4.7
Fossil	*Siamotragulus*	*songhorensis*	758.52	Whitworth (1958)	m3	10.1	4.2
Fossil	*Siamotragulus*	*songhorensis*	SAM-PQ.N.21	Quiralte et al. (2008)	m3	7.2	4.0
Fossil	*Siamotragulus*	*songhorensis*	Nap V 61	Pickford (2002)	m3	9.6	4.3
Fossil	*Siamotragulus*	*songhorensis*	Nap	Pickford (2002)	m3	10.0	4.6
Fossil	*Siamotragulus*	*songhorensis*	Nap Iv 64 P67-07	Pickford (2002)	m3	10.6	4.5
Fossil	*Siamotragulus*	*songhorensis*	Nap I 139´99	Pickford (2002)	m3	11.0	4.5
Fossil	*Siamotragulus*	*songhorensis*	Nap Iv 64 P67-07	Pickford (2002)	m3	11.0	4.7
Fossil	*Siamotragulus*	*songhorensis*	Nap I 61	Pickford (2002)	m3	11.0	4.9
Fossil	*Siamotragulus*	*songhorensis*	Nap	Pickford (2002)	m3	11.2	4.7
Fossil	*Siamotragulus*	*songhorensis*	Nap Iv 64 P67-07	Pickford (2002)	m3	11.3	4.8
Fossil	*Siamotragulus*	*songhorensis*	Nap	Pickford (2002)	m3	11.4	4.3
Fossil	*Siamotragulus*	*songhorensis*	Nap I 94´99	Pickford (2002)	m3	11.4	4.7
Fossil	*Siamotragulus*	*songhorensis*	Nap V 19´98	Pickford (2002)	m3	11.8	5.0
Fossil	*Siamotragulus*	*songhorensis*	Nap V 59´02	Pickford (2002)	m3	10.7	4.3
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	p2	6.2	2.1
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	p2	6.2	2.0
Extant	*Tragulus*	*javanicus*	NHMW-40818	This study	p2	5.3	2.1
Extant	*Tragulus*	*javanicus*	SMNS-16874	This study	p2	5.3	1.8
Extant	*Tragulus*	*javanicus*	SMNS-16875	This study	p2	5.2	2.1

Extant	*Tragulus*	*javanicus*	NMW-7595	This study	p3	6.3	2.3
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	p3	6.8	2.6
Extant	*Tragulus*	*javanicus*	NHMW-40818	This study	p3	6.1	2.3
Extant	*Tragulus*	*javanicus*	SMNS-16874	This study	p3	5.5	2.1
Extant	*Tragulus*	*javanicus*	SMNS-16875	This study	p3	5.7	2.1
Extant	*Tragulus*	*javanicus*	SMNS-16873	This study	p3	5.9	1.9
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	p4	6.0	2.8
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	p4	6.2	2.6
Extant	*Tragulus*	*javanicus*	NHMW-40818	This study	p4	5.5	3.0
Extant	*Tragulus*	*javanicus*	SMNS-16874	This study	p4	5.3	2.4
Extant	*Tragulus*	*javanicus*	SMNS-16875	This study	p4	4.9	2.7
Extant	*Tragulus*	*javanicus*	SMNS-16873	This study	p4	6.5	2.9
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	m1	6.4	3.1
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	m1	6.7	3.0
Extant	*Tragulus*	*javanicus*	NHMW-40818	This study	m1	5.4	3,.8
Extant	*Tragulus*	*javanicus*	SMNS-16874	This study	m1	4.7	3.2
Extant	*Tragulus*	*javanicus*	SMNS-16875	This study	m1	4.7	3.3
Extant	*Tragulus*	*javanicus*	SMNS-16873	This study	m1	5.0	3.6
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	m2	6.2	3.8
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	m2	6.4	3.7
Extant	*Tragulus*	*javanicus*	NHMW-40818	This study	m2	6.6	5.1
Extant	*Tragulus*	*javanicus*	SMNS-16874	This study	m2	6.2	3.8
Extant	*Tragulus*	*javanicus*	SMNS-16875	This study	m2	6.4	4.2
Extant	*Tragulus*	*javanicus*	SMNS-16873	This study	m2	5.8	3.9
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	m3	8.6	3.9
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	m3	8.7	4.0
Extant	*Tragulus*	*javanicus*	NHMW-40818	This study	m3	9.6	5.3
Extant	*Tragulus*	*javanicus*	SMNS-16875	This study	m3	8.9	4.2
Extant	*Tragulus*	*javanicus*	SMNS-16876	This study	m3	8.7	3.5
Extant	*Tragulus*	*javanicus*	SMNS-16873	This study	m3	7.9	4.2
Extant	*Tragulus*	*kanchil*	NHMB-C3795	This study	p2	5.3	1.7
Extant	*Tragulus*	*kanchil*	NHMB-C3735	This study	p2	4.6	2.0
Extant	*Tragulus*	*kanchil*	NHMB-3002	This study	p2	5.1	1.9
Extant	*Tragulus*	*kanchil*	NHMB-C1891	This study	p2	5.5	2.1
Extant	*Tragulus*	*kanchil*	NHMB-C3808	This study	p2	4.4	1.7
Extant	*Tragulus*	*kanchil*	NHMB-C3802	This study	p2	5.2	1.9
Extant	*Tragulus*	*kanchil*	NHMB-C3803	This study	p2	4.7	1.8
Extant	*Tragulus*	*kanchil*	NHMB-C3798	This study	p2	5.0	1.9
Extant	*Tragulus*	*kanchil*	NHMB-C3791	This study	p2	5.3	1.9
Extant	*Tragulus*	*kanchil*	NHMB-C3804	This study	p2	4.1	1.8
Extant	*Tragulus*	*kanchil*	NHMB-C3797	This study	p2	5.6	2.0
Extant	*Tragulus*	*kanchil*	SNSB-BSPG 1977 I 185	This study	p2	4.4	1.7
Extant	*Tragulus*	*kanchil*	SNSB-BSPG 1977 I 185	This study	p2	4.3	1.7
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	p2	5.3	2.1
Extant	*Tragulus*	*kanchil*	NHMB-C3795	This study	p3	6.4	2.3

Extant	*Tragulus*	*kanchil*	NHMB-C3735	This study	p3	5.3	2.3
Extant	*Tragulus*	*kanchil*	NHMB-3002	This study	p3	6.0	2.3
Extant	*Tragulus*	*kanchil*	NHMB-C1891	This study	p3	6.1	2.5
Extant	*Tragulus*	*kanchil*	NHMB-C3808	This study	p3	5.2	2.0
Extant	*Tragulus*	*kanchil*	NHMB-C3802	This study	p3	6.2	2.4
Extant	*Tragulus*	*kanchil*	NHMB-C3803	This study	p3	5.6	2.1
Extant	*Tragulus*	*kanchil*	NHMB-C3798	This study	p3	5.6	2.2
Extant	*Tragulus*	*kanchil*	NHMB-C3791	This study	p3	6.4	2.4
Extant	*Tragulus*	*kanchil*	NHMB-C3804	This study	p3	5.5	2.2
Extant	*Tragulus*	*kanchil*	NHMB-C3797	This study	p3	6.2	2.4
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	p3	6.4	2.3
Extant	*Tragulus*	*kanchil*	SNSB-BSPG 1977 I 185	This study	p3	5.2	2.0
Extant	*Tragulus*	*kanchil*	SNSB-BSPG 1977 I 185	This study	p3	5.2	2.0
Extant	*Tragulus*	*kanchil*	NHMB-C3806	This study	p3	5.7	1.9
Extant	*Tragulus*	*kanchil*	NHMB-C3809	This study	p3	6.0	2.1
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	p3	6.5	2.2
Extant	*Tragulus*	*kanchil*	NHMB-C3795	This study	p4	5.0	2.6
Extant	*Tragulus*	*kanchil*	NHMB-C3735	This study	p4	5.5	2.6
Extant	*Tragulus*	*kanchil*	NHMB-3002	This study	p4	5.4	2.5
Extant	*Tragulus*	*kanchil*	NHMB-C1891	This study	p4	5.4	2.7
Extant	*Tragulus*	*kanchil*	NHMB-C3818	This study	p4	6.3	2.8
Extant	*Tragulus*	*kanchil*	NHMB-C3808	This study	p4	5.3	2.5
Extant	*Tragulus*	*kanchil*	NHMB-C3809	This study	p4	7.0	2.4
Extant	*Tragulus*	*kanchil*	NHMB-C3802	This study	p4	4.9	2.8
Extant	*Tragulus*	*kanchil*	NHMB-C3803	This study	p4	5.3	2.5
Extant	*Tragulus*	*kanchil*	NHMB-C3798	This study	p4	4.6	2.5
Extant	*Tragulus*	*kanchil*	NHMB-C3791	This study	p4	4.9	3.0
Extant	*Tragulus*	*kanchil*	NHMB-C3804	This study	p4	5.2	2.5
Extant	*Tragulus*	*kanchil*	NHMB-C3797	This study	p4	5.6	2.6
Extant	*Tragulus*	*kanchil*	SNSB-BSPG 1977 I 185	This study	p4	5.3	2.4
Extant	*Tragulus*	*kanchil*	SNSB-BSPG 1977 I 185	This study	p4	5.3	2.6
Extant	*Tragulus*	*kanchil*	NHMB-C3806	This study	p4	6.4	2.8
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	p4	5.5	2.7
Extant	*Tragulus*	*kanchil*	NHMB-C3795	This study	m1	5.5	3.3
Extant	*Tragulus*	*kanchil*	NHMB-C3735	This study	m1	4.4	3.0
Extant	*Tragulus*	*kanchil*	NHMB-3002	This study	m1	4.9	3.3
Extant	*Tragulus*	*kanchil*	NHMB-C1891	This study	m1	5.4	3.9
Extant	*Tragulus*	*kanchil*	NHMB-C3818	This study	m1	5.1	3.3
Extant	*Tragulus*	*kanchil*	NHMB-C3808	This study	m1	4.5	3.3
Extant	*Tragulus*	*kanchil*	NHMB-C3809	This study	m1	5.4	3.5
Extant	*Tragulus*	*kanchil*	NHMB-C3802	This study	m1	4.8	3.4
Extant	*Tragulus*	*kanchil*	NHMB-C3803	This study	m1	4.8	3.3
Extant	*Tragulus*	*kanchil*	NHMB-C3791	This study	m1	5.6	3.4
Extant	*Tragulus*	*kanchil*	NHMB-C3804	This study	m1	4.1	2.8
Extant	*Tragulus*	*kanchil*	NHMB-C3797	This study	m1	4.9	3.4

Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	m1	5.3	3.0
Extant	*Tragulus*	*kanchil*	SNSB-BSPG 1977 I 185	This study	m1	4.5	2.7
Extant	*Tragulus*	*kanchil*	SNSB-BSPG 1977 I 185	This study	m1	4.7	2.8
Extant	*Tragulus*	*kanchil*	NHMB-C3806	This study	m1	5.8	3.7
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	m1	6.0	3.1
Extant	*Tragulus*	*kanchil*	NHMB-C3795	This study	m2	5.7	4.2
Extant	*Tragulus*	*kanchil*	NHMB-C3735	This study	m2	5.4	4.0
Extant	*Tragulus*	*kanchil*	NHMB-3002	This study	m2	5.1	4.4
Extant	*Tragulus*	*kanchil*	NHMB-C1891	This study	m2	5.9	4.9
Extant	*Tragulus*	*kanchil*	NHMB-C3818	This study	m2	6.2	4.0
Extant	*Tragulus*	*kanchil*	NHMB-C3808	This study	m2	6.2	4.0
Extant	*Tragulus*	*kanchil*	NHMB-C3809	This study	m2	6.6	4.0
Extant	*Tragulus*	*kanchil*	NHMB-C3802	This study	m2	5.4	4.3
Extant	*Tragulus*	*kanchil*	NHMB-C3803	This study	m2	6.2	4.4
Extant	*Tragulus*	*kanchil*	NHMB-C3798	This study	m2	5.3	4.3
Extant	*Tragulus*	*kanchil*	NHMB-C3791	This study	m2	6.1	4.4
Extant	*Tragulus*	*kanchil*	NHMB-C3804	This study	m2	5.8	4.6
Extant	*Tragulus*	*kanchil*	NHMB-C3797	This study	m2	6.1	4.1
Extant	*Tragulus*	*kanchil*	SNSB-BSPG 1977 I 185	This study	m2	6.3	3.6
Extant	*Tragulus*	*kanchil*	SNSB-BSPG 1977 I 185	This study	m2	6.3	3.4
Extant	*Tragulus*	*kanchil*	NHMB-C3806	This study	m2	6.3	3.8
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	m2	7.0	4.0
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	m2	7.0	4.0
Extant	*Tragulus*	*kanchil*	NHMB-C3795	This study	m3	8.6	4.2
Extant	*Tragulus*	*kanchil*	NHMB-C3735	This study	m3	9.1	4.2
Extant	*Tragulus*	*kanchil*	NHMB-3002	This study	m3	8.3	4.1
Extant	*Tragulus*	*kanchil*	NHMB-C1891	This study	m3	8.9	4.6
Extant	*Tragulus*	*kanchil*	NHMB-C3818	This study	m3	7.8	3.9
Extant	*Tragulus*	*kanchil*	NHMB-C3802	This study	m3	8.5	4.4
Extant	*Tragulus*	*kanchil*	NHMB-C3803	This study	m3	8.7	4.5
Extant	*Tragulus*	*kanchil*	NHMB-C3798	This study	m3	8.7	4.3
Extant	*Tragulus*	*kanchil*	NHMB-C3791	This study	m3	8.1	4.1
Extant	*Tragulus*	*kanchil*	NHMB-C3804	This study	m3	8.7	4.6
Extant	*Tragulus*	*kanchil*	NHMB-C3809	This study	m3	8.4	4.2
Extant	*Tragulus*	*kanchil*	NHMB-C3797	This study	m3	8.4	4.5
Extant	*Tragulus*	*kanchil*	SNSB-BSPG 1977 I 185	This study	m3	8.5	4.1
Extant	*Tragulus*	*kanchil*	SNSB-BSPG 1977 I 185	This study	m3	8.4	4.1
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	m3	9.7	4.3
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	m3	10.2	4.1
Extant	*Tragulus*	*napu*	NHMB-10085	This study	p2	6.1	2.2
Extant	*Tragulus*	*napu*	NHMW-40378	This study	p2	6.3	2.2
Extant	*Tragulus*	*napu*	NHMW-5001	This study	p2	6.7	2.2
Extant	*Tragulus*	*napu*	NHMW-1923	This study	p2	6.2	2.1
Extant	*Tragulus*	*napu*	NHMB-i 0007	This study	p2	6.7	2.3
Extant	*Tragulus*	*napu*	NHMW-40378	This study	p2	6.3	2.2

Extant	*Tragulus*	*napu*	NHMB-10085	This study	p3	6.3	2.6
Extant	*Tragulus*	*napu*	NHMB-C2950	This study	p3	7.3	3.0
Extant	*Tragulus*	*napu*	UMZC-H. 14.976	This study	p3	7.3	3.0
Extant	*Tragulus*	*napu*	NHMW-5001	This study	p3	7.2	2.5
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	p3	7.1	2.8
Extant	*Tragulus*	*napu*	NHMW-1923	This study	p3	7.1	2.4
Extant	*Tragulus*	*napu*	NHMB-i 0007	This study	p3	7.2	2.8
Extant	*Tragulus*	*napu*	NHMW-40826	This study	p3	6.4	2.6
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	p3	7.1	2.8
Extant	*Tragulus*	*napu*	NHMB-10085	This study	p4	5.7	3.2
Extant	*Tragulus*	*napu*	NHMB-C2950	This study	p4	6.5	3.5
Extant	*Tragulus*	*napu*	NHMW-5001	This study	p4	6.0	3.4
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	p4	6.1	3.2
Extant	*Tragulus*	*napu*	NHMW-1923	This study	p4	6.4	3.2
Extant	*Tragulus*	*napu*	NHMW-40826	This study	p4	6.3	3.1
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	p4	6.1	3.2
Extant	*Tragulus*	*napu*	NHMB-10085	This study	m1	5.4	3.9
Extant	*Tragulus*	*napu*	NHMB-C2950	This study	m1	6.1	3.9
Extant	*Tragulus*	*napu*	UMZC-H. 14.976	This study	m1	7.3	4.3
Extant	*Tragulus*	*napu*	UMZC-H. 14.976	This study	m1	7.4	4.2
Extant	*Tragulus*	*napu*	NHMW-40378	This study	m1	6.3	4.6
Extant	*Tragulus*	*napu*	NHMW-5001	This study	m1	5.9	4.1
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	m1	6.5	4.1
Extant	*Tragulus*	*napu*	NHMW-1923	This study	m1	6.3	4.4
Extant	*Tragulus*	*napu*	NHMB-i 0007	This study	m1	6.3	4.1
Extant	*Tragulus*	*napu*	NHMW-40826	This study	m1	6.9	3.8
Extant	*Tragulus*	*napu*	NHMW 40378	This study	m1	6.3	4.5
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	m1	6.5	4.0
Extant	*Tragulus*	*napu*	NHMB-10085	This study	m2	6.7	5.0
Extant	*Tragulus*	*napu*	NHMB-C2950	This study	m2	6.6	4.7
Extant	*Tragulus*	*napu*	UMZC-H. 14.976	This study	m2	7.9	5.6
Extant	*Tragulus*	*napu*	UMZC-H. 14.976	This study	m2	7.9	5.5
Extant	*Tragulus*	*napu*	NHMW-5001	This study	m2	7.3	4.7
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	m2	6.5	4.9
Extant	*Tragulus*	*napu*	NHMW-1923	This study	m2	6.9	5.3
Extant	*Tragulus*	*napu*	NHMB-i 0007	This study	m2	6.9	5.3
Extant	*Tragulus*	*napu*	NHMW-40826	This study	m2	7.1	4.5
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	m2	6.5	4.5
Extant	*Tragulus*	*napu*	NHMB-10085	This study	m3	9.2	4.9
Extant	*Tragulus*	*napu*	NHMB-C2950	This study	m3	9.4	5.0
Extant	*Tragulus*	*napu*	UMZC-H. 14.976	This study	m3	1.,0	5.5
Extant	*Tragulus*	*napu*	UMZC-H. 14.976	This study	m3	1.,4	5.6
Extant	*Tragulus*	*napu*	NHMW-5001	This study	m3	9.8	4.7
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	m3	9.9	4.9
Extant	*Tragulus*	*napu*	NHMW-1923	This study	m3	9.9	5.0

Extant	*Tragulus*	*napu*	NHMW-40826	This study	m3	9.8	5.2
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	m3	9.9	4.8
Extant	*Tragulus*	*napu*	NHMB-i 0007	This study	m3	10.3	5.5
Extant	*Tragulus*	*nigricans*	NHMB-8672	This study	p2	5.7	1.9
Extant	*Tragulus*	*nigricans*	NHMB-8672	This study	p3	6.5	2.3
Extant	*Tragulus*	*nigricans*	NHMB-8672	This study	m1	5.7	3.9
Extant	*Tragulus*	*nigricans*	NHMB-8672	This study	m2	6.3	5.0
Fossil	*Yunannotherium*	*simplex*	V 8134.1	Han Defen (1986)	p2	7.0	2.6
Fossil	*Yunannotherium*	*simplex*	V 8134.2	Han Defen (1986)	p2	6.6	2.4
Fossil	*Yunannotherium*	*simplex*	V 8134.1	Han Defen (1986)	p3	7.6	2.8
Fossil	*Yunannotherium*	*simplex*	V 8134.2	Han Defen (1986)	p3	7.7	2.8
Fossil	*Yunannotherium*	*simplex*	V 8134.3	Han Defen (1986)	p3	6.7	2.8
Fossil	*Yunannotherium*	*simplex*	V 8134.1	Han Defen (1986)	p4	6.5	3.0
Fossil	*Yunannotherium*	*simplex*	V 8134.2	Han Defen (1986)	p4	5.3	3.0
Fossil	*Yunannotherium*	*simplex*	V 8134.3	Han Defen (1986)	p4	6.7	2.8
Fossil	*Yunannotherium*	*simplex*	V 8134.15	Han Defen (1986)	m1	7.0	4.2
Fossil	*Yunannotherium*	*simplex*	V 8134.16	Han Defen (1986)	m2	7.2	4.1
Fossil	*Yunannotherium*	*simplex*	V 8134.17	Han Defen (1986)	m2	7.8	4.3
Fossil	*Yunannotherium*	*simplex*	V 8134.2	Han Defen (1986)	m3	10.0	4.8
Fossil	*Yunannotherium*	*simplex*	V 8134.7	Han Defen (1986)	m3	9.9	5.0
Fossil	*Yunannotherium*	*simplex*	V 8134.8	Han Defen (1986)	m3	10.0	5.0
Fossil	*Yunannotherium*	*simplex*	V 8134.9	Han Defen (1986)	m3	9.0	4.3
Fossil	*Yunannotherium*	*simplex*	V 8134.10	Han Defen (1986)	m3	10.9	4.9
Fossil	*Yunannotherium*	*simplex*	V 8134.11	Han Defen (1986)	m3	9.9	4.8
Fossil	*Yunannotherium*	*simplex*	V 8134.12	Han Defen (1986)	m3	10.0	4.6
Fossil	*Yunannotherium*	*simplex*	V 8134.13	Han Defen (1986)	m3	10.2	5,0
Fossil	*Afrotragulus*	*moruorotensis*	Mor 1'2000	Pickford (2001a)	M2	4.0	4,3
Fossil	*Afrotragulus*	*moruorotensis*	Mor 1'2000	Pickford (2001a)	M3	4.6	4,0
Fossil	*Afrotragulus*	*parvus*	1164.50 R.I.	Whitworth (1958)	P2	5.5	2.5
Fossil	*Afrotragulus*	*parvus*	1164.50 R.I.	Whitworth (1958)	P3	5.5	3.2
Fossil	*Afrotragulus*	*parvus*	694.51	Whitworth (1958)	P4	5.6	5.4
Fossil	*Afrotragulus*	*parvus*	BMNH-M82686	Sánchez et al. (2010)	M1	5.1	4.5
Fossil	*Afrotragulus*	*parvus*	490.49 R.3A	Whitworth (1958)	M1	5.2	5.2
Fossil	*Afrotragulus*	*parvus*	996.50 R.I.	Whitworth (1958)	M1	5.6	5.6
Fossil	*Afrotragulus*	*parvus*	1164.50 R.I.	Whitworth (1958)	M1	5.1	5.2
Fossil	*Afrotragulus*	*parvus*	1658.50	Whitworth (1958)	M1	5.7	6.0
Fossil	*Afrotragulus*	*parvus*	751.52	Whitworth (1958)	M1	6.0	6.8
Fossil	*Afrotragulus*	*parvus*	BMNH-M82686	Sánchez et al. (2010)	M2	5.6	5.6
Fossil	*Afrotragulus*	*parvus*	505.47 R.I.A	Whitworth (1958)	M2	6.1	7.0
Fossil	*Afrotragulus*	*parvus*	490.49 R.3A	Whitworth (1958)	M2	5.5	6.0
Fossil	*Afrotragulus*	*parvus*	891.50 R.I.	Whitworth (1958)	M2	7.0	6.7
Fossil	*Afrotragulus*	*parvus*	996.50 R.I.	Whitworth (1958)	M2	6.7	6.2
Fossil	*Afrotragulus*	*parvus*	1164.50 R.I.	Whitworth (1958)	M2	7.0	6.1
Fossil	*Afrotragulus*	*parvus*	1658.50	Whitworth (1958)	M2	6.0	7.1
Fossil	*Afrotragulus*	*parvus*	751.52	Whitworth (1958)	M2	7.4	8.0

Fossil	*Afrotragulus*	*parvus*	505.47 R.I.A	Whitworth (1958)	M3	6.1	6.8
Fossil	*Afrotragulus*	*parvus*	891.50 R.I.	Whitworth (1958)	M3	6.1	6.8
Fossil	*Afrotragulus*	*parvus*	996.50 R.I.	Whitworth (1958)	M3	6.1	6.5
Fossil	*Afrotragulus*	*parvus*	1164.50 R.I.	Whitworth (1958)	M3	7.1	6.1
Fossil	*Afrotragulus*	*parvus*	1658.50	Whitworth (1958)	M3	6.1	7.3
Fossil	*Afrotragulus*	*parvus*	751.52	Whitworth (1958)	M3	7.3	8.0
Fossil	*Dorcatherium*	*guntianum*	SNSB-BSPG 1956 II 2554	This study	m3	14.5	6.6
Fossil	*Dorcatherium*	*guntianum*	AMNH-29854 (1981 XVII 26)	This study	m3	12.7	5.7
Fossil	*Dorcatherium*	*guntianum*	NMA-411	This study	P2	9.7	4.4
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	P2	10.4	4.9
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	P2	10.5	4.3
Fossil	*Dorcatherium*	*guntianum*	SNSP-BSPG 1881 IX 648b	This study	P3	8.8	5.0
Fossil	*Dorcatherium*	*guntianum*	NMA-800	This study	P3	10.0	6.5
Fossil	*Dorcatherium*	*guntianum*	NMA-1995	This study	P3	10.8	4.8
Fossil	*Dorcatherium*	*guntianum*	NMA-2005/67/1633	This study	P4	8.2	9.7
Fossil	*Dorcatherium*	*guntianum*	NMA-1415	This study	P4	8.3	8.9
Fossil	*Dorcatherium*	*guntianum*	SNSP-BSPG 1881 IX 648a	This study	P4	7.9	8.1
Fossil	*Dorcatherium*	*guntianum*	MNA-1747	This study	M1	8.0	9.5
Fossil	*Dorcatherium*	*guntianum*	NMA-1995	This study	M1	8.5	9.1
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	M1	8.6	9.7
Fossil	*Dorcatherium*	*guntianum*	NMA-1995	This study	M1	8.7	9.2
Fossil	*Dorcatherium*	*guntianum*	SNSP-BSPG 1881 IX 647	This study	M1	8.7	9.5
Fossil	*Dorcatherium*	*guntianum*	GB-1407	This study	M1	8.6	9.4
Fossil	*Dorcatherium*	*guntianum*	MNA-85.46	This study	M2	8.4	9.0
Fossil	*Dorcatherium*	*guntianum*	NMA-1/148	This study	M2	9.0	11.4
Fossil	*Dorcatherium*	*guntianum*	NMA-1995	This study	M2	9.4	10.7
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	M2	9.5	10.7
Fossil	*Dorcatherium*	*guntianum*	SNSP-BSPG 1881 IX 47i	This study	M2	9.8	10.9
Fossil	*Dorcatherium*	*guntianum*	NMA-1995	This study	M2	9.9	10.0
Fossil	*Dorcatherium*	*guntianum*	MNA-1747	This study	M2	9.9	10.9
Fossil	*Dorcatherium*	*guntianum*	SNSP-BSPG 1881 IX 732	This study	M2	9.9	10.5
Fossil	*Dorcatherium*	*guntianum*	MNA-85.46	This study	M3	8.8	9.6
Fossil	*Dorcatherium*	*guntianum*	NMA-1633	This study	M3	10.0	11.8
Fossil	*Dorcatherium*	*guntianum*	NMA-1995	This study	M3	10.2	11.5
Fossil	*Dorcatherium*	*guntianum*	NMA-1995	This study	M3	10.3	11.2
Fossil	*Dorcatherium*	*guntianum*	MNA-1747	This study	M3	10.3	11.8
Fossil	*Dorcatherium*	*guntianum*	NMA-1/148	This study	M3	10.6	12.3
Fossil	*Dorcatherium*	*minimus*	H-GSP-1983	West (1980)	M3	5.1	5.5
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/100	Gaur (1992)	P4	6.0	5.8
Fossil	*Dorcatherium*	*nagrii*	GSI-18081	Prasad (1970)	M1	6.5	6.1
Fossil	*Dorcatherium*	*nagrii*	GSI-K47.759	Prasad (1970)	M1	6.5	6.4
Fossil	*Dorcatherium*	*nagrii*	GSI-K47.794	Prasad (1970)	M1	7.0	7.0
Fossil	*Dorcatherium*	*nagrii*	GSI-K50.981	Prasad (1970)	M1	6.5	6.5
Fossil	*Dorcatherium*	*nagrii*	HT-64-81	Sankhyan (1982)	M1	6.0	6.0
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/100	Gaur (1992)	M1	6.3	6.7

Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/103	Gaur (1992)	M1	6.2	6.6
Fossil	*Dorcatherium*	*nagrii*	GSI-18081	Prasad (1970)	M2	7.5	6.2
Fossil	*Dorcatherium*	*nagrii*	GSI-K47.759	Prasad (1970)	M2	7.0	7.0
Fossil	*Dorcatherium*	*nagrii*	GSI-K47.794	Prasad (1970)	M2	7.5	7.2
Fossil	*Dorcatherium*	*nagrii*	GSI-K50.981	Prasad (1970)	M2	7.0	6.2
Fossil	*Dorcatherium*	*nagrii*	HT-39-81	Sankhyan (1982)	M2	7.0	6.0
Fossil	*Dorcatherium*	*nagrii*	HT-64-81	Sankhyan (1982)	M2	7.0	6.5
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/100	Gaur (1992)	M2	7.5	8.0
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/103	Gaur (1992)	M2	7.5	7.9
Fossil	*Dorcatherium*	*nagrii*	GSI-18081	Prasad (1970)	M3	7.1	7.0
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/100	Gaur (1992)	M3	8.0	8.4
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/103	Gaur (1992)	M3	8.0	8.9
Fossil	*Dorcatherium*	*nagrii*	VPL/AS/H/104	Gaur (1992)	M3	8.0	8.9
Fossil	*Dorcatherium*	*pigotti*	1897.50 R.3A	Whitworth (1958)	P3	8.0	5.1
Fossil	*Dorcatherium*	*pigotti*	Mb. 210	Whitworth (1958)	P3	7.3	5.5
Fossil	*Dorcatherium*	*pigotti*	791.50 R.104	Whitworth (1958)	P4	7.0	7.5
Fossil	*Dorcatherium*	*pigotti*	1897.50 R.3A	Whitworth (1958)	P4	6.7	7.8
Fossil	*Dorcatherium*	*pigotti*	302.51 R.3	Whitworth (1958)	P4	7.0	8.0
Fossil	*Dorcatherium*	*pigotti*	747.52 R12	Whitworth (1958)	P4	6.5	7.5
Fossil	*Dorcatherium*	*pigotti*	Mb. 210	Whitworth (1958)	P4	6.2	6.8
Fossil	*Dorcatherium*	*pigotti*	331.47 R.IA	Whitworth (1958)	M1	8.1	9.6
Fossil	*Dorcatherium*	*pigotti*	791.50 R.104	Whitworth (1958)	M1	8.0	9.0
Fossil	*Dorcatherium*	*pigotti*	1895.50 R.3A	Whitworth (1958)	M1	7.5	8.7
Fossil	*Dorcatherium*	*pigotti*	302.51 R.3	Whitworth (1958)	M1	7.8	9.0
Fossil	*Dorcatherium*	*pigotti*	747.52 R12	Whitworth (1958)	M1	7.9	8.6
Fossil	*Dorcatherium*	*pigotti*	331.47 R.IA	Whitworth (1958)	M2	9.0	10.8
Fossil	*Dorcatherium*	*pigotti*	791.50 R.104	Whitworth (1958)	M2	9.0	11.0
Fossil	*Dorcatherium*	*pigotti*	1895.50 R.3A	Whitworth (1958)	M2	8.8	10.0
Fossil	*Dorcatherium*	*pigotti*	302.51 R.3	Whitworth (1958)	M2	9.0	10.0
Fossil	*Dorcatherium*	*pigotti*	747.52 R12	Whitworth (1958)	M2	9.0	10.0
Fossil	*Dorcatherium*	*pigotti*	Mb. 210	Whitworth (1958)	M2	7.6	9.4
Fossil	*Dorcatherium*	*pigotti*	331.47 R.IA	Whitworth (1958)	M3	9.6	11.5
Fossil	*Dorcatherium*	*pigotti*	1895.50 R.3A	Whitworth (1958)	M3	9.0	10.2
Fossil	*Dorcatherium*	*pigotti*	302.51 R.3	Whitworth (1958)	M3	10.0	10.8
Fossil	*Dorcatherium*	*pigotti*	747.52 R12	Whitworth (1958)	M3	9.1	11.0
Fossil	*Dorcatherium*	*pigotti*	Mb. 210	Whitworth (1958)	M3	8.0	9.0
Extant	*Hyemoschus*	*aquaticus*	NHMW-5407	This study	P2	9.5	4.4
Extant	*Hyemoschus*	*aquaticus*	NHMW-40827/Gr.290	This study	P2	9.9	4.1
Extant	*Hyemoschus*	*aquaticus*	SMNS-1842	This study	P2	9.8	3.8
Extant	*Hyemoschus*	*aquaticus*	NHMB-8699	This study	P2	8.8	4.1
Extant	*Hyemoschus*	*aquaticus*	NHMW-5407	This study	P3	8.2	4.9
Extant	*Hyemoschus*	*aquaticus*	NHMW-40827/Gr.290	This study	P3	8.0	4.8
Extant	*Hyemoschus*	*aquaticus*	SMNS-1842	This study	P3	9.5	5.6
Extant	*Hyemoschus*	*aquaticus*	NHMB-2692	This study	P3	8.6	5.8
Extant	*Hyemoschus*	*aquaticus*	NHMB-8699	This study	P3	8.9	7.6

Extant	*Hyemoschus*	*aquaticus*	NHMB-LXX4	This study	P3	10.0	7.2
Extant	*Hyemoschus*	*aquaticus*	NHMW-5407	This study	P4	6.8	7.3
Extant	*Hyemoschus*	*aquaticus*	NHMW-40827/Gr.290	This study	P4	7.1	7.0
Extant	*Hyemoschus*	*aquaticus*	SMNS-1842	This study	P4	8.0	7.9
Extant	*Hyemoschus*	*aquaticus*	NHMB-8699	This study	P4	6.8	6.8
Extant	*Hyemoschus*	*aquaticus*	NHMB-LXX4	This study	P4	8.8	8.4
Extant	*Hyemoschus*	*aquaticus*	NHMW-5407	This study	M1	8.5	9.4
Extant	*Hyemoschus*	*aquaticus*	NHMW-40827/Gr.290	This study	M1	8.4	8.8
Extant	*Hyemoschus*	*aquaticus*	SMNS-1842	This study	M1	8.8	9.9
Extant	*Hyemoschus*	*aquaticus*	NHMB-2692	This study	M1	8.3	9.4
Extant	*Hyemoschus*	*aquaticus*	NHMB-8699	This study	M1	7.5	9.3
Extant	*Hyemoschus*	*aquaticus*	NHMB-LXX4	This study	M1	8.8	9.6
Extant	*Hyemoschus*	*aquaticus*	NHMW-5407	This study	M2	9.7	10.7
Extant	*Hyemoschus*	*aquaticus*	NHMW-40827/Gr.290	This study	M2	9.7	10.6
Extant	*Hyemoschus*	*aquaticus*	SMNS-1842	This study	M2	10.0	10.8
Extant	*Hyemoschus*	*aquaticus*	NHMB-2692	This study	M2	9.6	11.0
Extant	*Hyemoschus*	*aquaticus*	NHMB-8699	This study	M2	9.2	11.2
Extant	*Hyemoschus*	*aquaticus*	NHMW-5407	This study	M3	10.0	11.0
Extant	*Hyemoschus*	*aquaticus*	NHMW-40827/Gr.290	This study	M3	10.2	10.5
Extant	*Hyemoschus*	*aquaticus*	NHMB-2692	This study	M3	10.0	12.0
Extant	*Hyemoschus*	*aquaticus*	NHMB-8699	This study	M3	10.0	10.9
Extant	*Hyemoschus*	*aquaticus*	NHMB-LXX4	This study	M3	10.2	11.2
Fossil	*Iberomeryx*	*minor*	ITD-912	Sudre (1984)	P2	4.3	2.0
Fossil	*Iberomeryx*	*minor*	ITD-912	Sudre (1984)	P3	4.2	3.0
Fossil	*Iberomeryx*	*minor*	MGB-1182	Sudre (1984)	P4	4.0	4.8
Fossil	*Iberomeryx*	*minor*	ITD-907	Sudre (1984)	M1	4.5	5.2
Fossil	*Iberomeryx*	*minor*	ITD-910	Sudre (1984)	M1	4.7	5.4
Fossil	*Iberomeryx*	*minor*	ITD-911	Sudre (1984)	M1	5.2	6.1
Fossil	*Iberomeryx*	*minor*	ROQ 2-333	Sudre (1984)	M1	4.8	5.0
Fossil	*Iberomeryx*	*minor*	PLA 2-1160	Sudre (1984)	M1	5.5	6.0
Fossil	*Iberomeryx*	*minor*	MGB-1182	Sudre (1984)	M1	5.0	5.6
Fossil	*Iberomeryx*	*minor*	ITD-910	Sudre (1984)	M2	5.5	6.2
Fossil	*Iberomeryx*	*minor*	ITD-911	Sudre (1984)	M2	6.0	6.1
Fossil	*Iberomeryx*	*minor*	QB 296	Sudre (1984)	M2	5.8	6.4
Fossil	*Iberomeryx*	*minor*	ROQ 2-331	Sudre (1984)	M2	6.0	6.9
Fossil	*Iberomeryx*	*minor*	ROQ 2-333	Sudre (1984)	M2	5.9	6.0
Fossil	*Iberomeryx*	*minor*	MGB-1182	Sudre (1984)	M2	5.3	6.6
Fossil	*Iberomeryx*	*minor*	ITD-910	Sudre (1984)	M3	5.7	6.7
Fossil	*Iberomeryx*	*minor*	ITD-911	Sudre (1984)	M3	6.1	6.8
Fossil	*Iberomeryx*	*minor*	ROQ 2-333	Sudre (1984)	M3	6.2	6.3
Fossil	*Iberomeryx*	*minor*	MGB-1182	Sudre (1984)	M3	5.8	6.6
Fossil	*Iberomeryx*	*parvus*	GK3-4	Métais et al. (2016)	P2	6.3	3.7
Fossil	*Iberomeryx*	*parvus*	GK3-5	Métais et al. (2016)	P4	3.8	4.4
Fossil	*Iberomeryx*	*parvus*	GK2-4	Métais et al. (2016)	M1	5.3	5.2
Fossil	*Iberomeryx*	*parvus*	KZ-7	Métais et al. (2016)	M1	5.4	5.1

Fossil	*Iberomeryx*	*parvus*	641-13	Métais et al. (2016)	M1	5.3	5.5
Fossil	*Iberomeryx*	*parvus*	GK3-31	Métais et al. (2016)	M2	6.4	6.8
Fossil	*Iberomeryx*	*parvus*	641-12	Métais et al. (2016)	M2	6.3	6.2
Extant	*Moschiola*	*indica*	ZMH-4772	This study	P2	9.0	3.9
Extant	*Moschiola*	*indica*	ZMH-4771	This study	P3	6.9	4.1
Extant	*Moschiola*	*indica*	ZMH-4771	This study	P3	7.3	4.2
Extant	*Moschiola*	*indica*	ZMH-4772	This study	P3	8.0	4.6
Extant	*Moschiola*	*indica*	ZMH-4771	This study	P4	5.5	6.0
Extant	*Moschiola*	*indica*	ZMH-4771	This study	P4	6.0	6.0
Extant	*Moschiola*	*indica*	ZMH-4772	This study	P4	6.8	6.6
Extant	*Moschiola*	*indica*	ZMH-4793	This study	M1	6.7	6.5
Extant	*Moschiola*	*indica*	ZMH-4793	This study	M1	6.9	6.5
Extant	*Moschiola*	*indica*	ZMH-4773	This study	M1	6.9	6.8
Extant	*Moschiola*	*indica*	ZMH-4773	This study	M1	7.0	7.0
Extant	*Moschiola*	*indica*	ZMH-4771	This study	M1	7.9	7.3
Extant	*Moschiola*	*indica*	ZMH-4771	This study	M1	7.3	7.2
Extant	*Moschiola*	*indica*	ZMH-4770	This study	M1	7.3	6.9
Extant	*Moschiola*	*indica*	ZMH-4770	This study	M1	7.5	6.7
Extant	*Moschiola*	*indica*	ZMH-4772	This study	M1	7.7	7.6
Extant	*Moschiola*	*indica*	ZMH-4793	This study	M2	7.2	7.6
Extant	*Moschiola*	*indica*	ZMH-4771	This study	M2	7.5	7.3
Extant	*Moschiola*	*indica*	ZMH-4793	This study	M2	7.6	7.7
Extant	*Moschiola*	*indica*	ZMH-4771	This study	M2	8.0	7.5
Extant	*Moschiola*	*indica*	ZMH-4770	This study	M2	8.0	7.5
Extant	*Moschiola*	*indica*	ZMH-4772	This study	M2	8.4	8.9
Extant	*Moschiola*	*indica*	ZMH-4771	This study	M3	7.1	7.9
Extant	*Moschiola*	*indica*	ZMH-4771	This study	M3	7.1	8.0
Extant	*Moschiola*	*indica*	ZMH-4772	This study	M3	7.8	8.3
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	P2	7.0	2.5
Extant	*Moschiola*	*meminna*	NHMW-B6016	This study	P2	6.3	2.3
Extant	*Moschiola*	*meminna*	NHMB-C1366	This study	P2	7.4	2.7
Extant	*Moschiola*	*meminna*	NHMB-C2453	This study	P2	7.2	2.7
Extant	*Moschiola*	*meminna*	NHMB-C2588	This study	P2	7.2	3.1
Extant	*Moschiola*	*meminna*	NHMB-C1429	This study	P2	7.1	2.9
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	P3	6.3	3.6
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	P3	7.0	4.1
Extant	*Moschiola*	*meminna*	NHMW-B6016	This study	P3	6.0	3.4
Extant	*Moschiola*	*meminna*	NHMB-C1366	This study	P3	7.1	3.6
Extant	*Moschiola*	*meminna*	NHMB-C2453	This study	P3	6.7	4.1
Extant	*Moschiola*	*meminna*	NHMB-C2588	This study	P3	5.9	3.9
Extant	*Moschiola*	*meminna*	NHMB-C1429	This study	P3	6.4	3.7
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	P4	5.4	6.3
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	P4	6.9	6.1
Extant	*Moschiola*	*meminna*	NHMW-B6016	This study	P4	4.8	6.0
Extant	*Moschiola*	*meminna*	NHMB-C1366	This study	P4	5.4	6.0

Extant	*Moschiola*	*meminna*	NHMB-C2453	This study	P4	5.1	5.4
Extant	*Moschiola*	*meminna*	NHMB-C2588	This study	P4	4.7	5.4
Extant	*Moschiola*	*meminna*	NHMB-C1429	This study	P4	5.4	5.6
Extant	*Moschiola*	*meminna*	NHMB-2328	This study	P4	5.7	5.6
Extant	*Moschiola*	*meminna*	ZMH-4791	This study	M1	7.4	7.0
Extant	*Moschiola*	*meminna*	ZMH-4791	This study	M1	8.0	7.2
Extant	*Moschiola*	*meminna*	NHMB-C1366	This study	M1	6.2	6.6
Extant	*Moschiola*	*meminna*	NHMB-C2453	This study	M1	6.0	6.7
Extant	*Moschiola*	*meminna*	NHMB-C2588	This study	M1	6.5	6.9
Extant	*Moschiola*	*meminna*	NHMB-C1429	This study	M1	6.1	6.7
Extant	*Moschiola*	*meminna*	NHMB-2328	This study	M1	6.7	7.1
Extant	*Moschiola*	*meminna*	ZMH-4791	This study	M2	7.6	7.6
Extant	*Moschiola*	*meminna*	ZMH-4791	This study	M2	7.7	7.7
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	M2	8.1	8.2
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	M2	8.3	8.4
Extant	*Moschiola*	*meminna*	NHMW-B6016	This study	M2	6.6	8.0
Extant	*Moschiola*	*meminna*	NHMB-C1366	This study	M2	7.3	7.0
Extant	*Moschiola*	*meminna*	NHMB-C2453	This study	M2	7.1	7.8
Extant	*Moschiola*	*meminna*	NHMB-C2588	This study	M2	7.2	7.1
Extant	*Moschiola*	*meminna*	NHMB-C1429	This study	M2	6.5	7.4
Extant	*Moschiola*	*meminna*	NHMB-2328	This study	M2	7.1	6.6
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	M3	7.8	8.5
Extant	*Moschiola*	*meminna*	MCNM-nn	This study	M3	7.8	8.2
Extant	*Moschiola*	*meminna*	NHMW-B6016	This study	M3	7.3	8.6
Extant	*Moschiola*	*meminna*	NHMB-C1366	This study	M3	7.0	6.0
Extant	*Moschiola*	*meminna*	NHMB-C2453	This study	M3	7.4	8.1
Extant	*Moschiola*	*meminna*	NHMB-C2588	This study	M3	6.6	7.8
Extant	*Moschiola*	*meminna*	NHMB-C1429	This study	M3	6.8	7.0
Extant	*Moschiola*	*meminna*	NHMB-2328	This study	M3	5.6	5.6
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2498	Ginsburg et al. (2001)	M2	9.3	10.0
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2497	Ginsburg et al. (2001)	M2	9.7	10.3
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2499	Ginsburg et al. (2001)	M3	9.0	9.8
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2498	Ginsburg et al. (2001)	M3	8.9	10.6
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2495	Ginsburg et al. (2001)	M3	8.6	10.1
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2500	Ginsburg et al. (2001)	M3	9.0	10.0
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2484	Ginsburg et al. (2001)	M3	9.0	9.8
Fossil	*Siamotragulus*	*bugtiensis*	PAK-2492	Ginsburg et al. (2001)	M3	9.0	10.0
Fossil	*Siamotragulus*	*sanyathanai*	PG2	Thomas et al. (1990)	P2	9.0	nd
Fossil	*Siamotragulus*	*sanyathanai*	PG2	Thomas et al. (1990)	P3	9.1	nd
Fossil	*Siamotragulus*	*sanyathanai*	PG2	Thomas et al. (1990)	P4	6.2	nd
Fossil	*Siamotragulus*	*sanyathanai*	PG2	Thomas et al. (1990)	M1	7.2	nd
Fossil	*Siamotragulus*	*sanyathanai*	PG2	Thomas et al. (1990)	M2	9.2	nd
Fossil	*Siamotragulus*	*sanyathanai*	PG2	Thomas et al. (1990)	M3	9.7	nd
Fossil	*Siamotragulus*	*songhorensis*	763.52	Whitworth (1958)	P3	8.7	5.0
Fossil	*Siamotragulus*	*songhorensis*	Nap V 64	Pickford (2002)	P3	6.5	5.0

Fossil	*Siamotragulus*	*songhorensis*	107.48	Whitworth (1958)	M1	7.1	6.5
Fossil	*Siamotragulus*	*songhorensis*	761.52	Whitworth (1958)	M1	6.0	6.2
Fossil	*Siamotragulus*	*songhorensis*	762.52	Whitworth (1958)	M1	7.5	7.6
Fossil	*Siamotragulus*	*songhorensis*	Nap IV 64	Pickford (2002)	M1	7.0	7.0
Fossil	*Siamotragulus*	*songhorensis*	Nap V 62	Pickford (2002)	M1	7.2	7.7
Fossil	*Siamotragulus*	*songhorensis*	107.48	Whitworth (1958)	M2	7.7	7.7
Fossil	*Siamotragulus*	*songhorensis*	316.49	Whitworth (1958)	M2	7.1	7.6
Fossil	*Siamotragulus*	*songhorensis*	761.52	Whitworth (1958)	M2	7.3	8.1
Fossil	*Siamotragulus*	*songhorensis*	762.52	Whitworth (1958)	M2	8.1	8.1
Fossil	*Siamotragulus*	*songhorensis*	Nap V 15	Pickford (2002)	M2	7.6	8.1
Fossil	*Siamotragulus*	*songhorensis*	nn	Pickford (2002)	M2	7.7	7.9
Fossil	*Siamotragulus*	*songhorensis*	Nap IV 64	Pickford (2002)	M2	7.7	8.6
Fossil	*Siamotragulus*	*songhorensis*	Nap I 58	Pickford (2002)	M2	7.9	7.6
Fossil	*Siamotragulus*	*songhorensis*	Nap V 64	Pickford (2002)	M2	7.9	8.2
Fossil	*Siamotragulus*	*songhorensis*	Nap V 61 16	Pickford (2002)	M2	7.9	7.8
Fossil	*Siamotragulus*	*songhorensis*	nn	Pickford (2002)	M2	8.0	7.7
Fossil	*Siamotragulus*	*songhorensis*	Nap V Aug 62	Pickford (2002)	M2	8.2	7.8
Fossil	*Siamotragulus*	*songhorensis*	Nap V 64	Pickford (2002)	M2	8.3	8.4
Fossil	*Siamotragulus*	*songhorensis*	107.48	Whitworth (1958)	M3	8.1	8.0
Fossil	*Siamotragulus*	*songhorensis*	316.49	Whitworth (1958)	M3	7.1	7.3
Fossil	*Siamotragulus*	*songhorensis*	761.52	Whitworth (1958)	M3	8.3	9.0
Fossil	*Siamotragulus*	*songhorensis*	Nap I 58	Pickford (2002)	M3	8.2	8.7
Fossil	*Siamotragulus*	*songhorensis*	Nap V 64	Pickford (2002)	M3	8.2	8.8
Fossil	*Siamotragulus*	*songhorensis*	Nap V Aug 62	Pickford (2002)	M3	8.2	8.9
Fossil	*Siamotragulus*	*songhorensis*	Nap I 61 16	Pickford (2002)	M3	8.2	8.5
Fossil	*Siamotragulus*	*songhorensis*	nn	Pickford (2002)	M3	8.4	8.2
Extant	*Tragulus*	*javanicus*	UMZC-H.15.014	This study	P2	5.6	2.2
Extant	*Tragulus*	*javanicus*	UMZC-H.15.014	This study	P2	5.6	2.5
Extant	*Tragulus*	*javanicus*	NHMW-40818	This study	P2	6.4	2.6
Extant	*Tragulus*	*javanicus*	SMNS-16874	This study	P2	5.6	2.4
Extant	*Tragulus*	*javanicus*	SMNS-16875	This study	P2	6.2	2.5
Extant	*Tragulus*	*javanicus*	SMNS-16876	This study	P2	6.4	3.1
Extant	*Tragulus*	*javanicus*	UMZC-H.15.014	This study	P3	5.3	3.1
Extant	*Tragulus*	*javanicus*	UMZC-H.15.014	This study	P3	5.7	2.8
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	P3	6.0	2.8
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	P3	6.1	3.2
Extant	*Tragulus*	*javanicus*	NHMW-40818	This study	P3	5.8	3.8
Extant	*Tragulus*	*javanicus*	SMNS-16874	This study	P3	5.2	3.2
Extant	*Tragulus*	*javanicus*	SMNS-16875	This study	P3	6.1	2.8
Extant	*Tragulus*	*javanicus*	SMNS-16876	This study	P3	6.5	4.1
Extant	*Tragulus*	*javanicus*	SMNS-16873	This study	P3	5.6	3.7
Extant	*Tragulus*	*javanicus*	UMZC-H.15.014	This study	P4	4.0	4.1
Extant	*Tragulus*	*javanicus*	UMZC-H.15.014	This study	P4	4.2	4.2
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	P4	4.6	4.4
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	P4	4.7	4.7

Extant	*Tragulus*	*javanicus*	NHMW-40818	This study	P4	4.7	5.1
Extant	*Tragulus*	*javanicus*	SMNS-16874	This study	P4	4.1	4.9
Extant	*Tragulus*	*javanicus*	SMNS-16875	This study	P4	5.0	4.5
Extant	*Tragulus*	*javanicus*	SMNS-16876	This study	P4	4.8	5.0
Extant	*Tragulus*	*javanicus*	SMNS-16873	This study	P4	4.7	4.4
Extant	*Tragulus*	*javanicus*	UMZC-H.15.014	This study	M1	5.0	4.7
Extant	*Tragulus*	*javanicus*	MCNM-nn	This study	M1	5.2	4.8
Extant	*Tragulus*	*javanicus*	UMZC-H.15.014	This study	M1	5.3	4.5
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	M1	5.3	4.8
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	M1	5.4	4.6
Extant	*Tragulus*	*javanicus*	MCNM-nn	This study	M1	5.6	4.7
Extant	*Tragulus*	*javanicus*	SMNS-16874	This study	M1	4.4	5.1
Extant	*Tragulus*	*javanicus*	SMNS-16875	This study	M1	5.5	5.5
Extant	*Tragulus*	*javanicus*	SMNS-16876	This study	M1	6.2	5.6
Extant	*Tragulus*	*javanicus*	SMNS-16873	This study	M1	5.0	5.7
Extant	*Tragulus*	*javanicus*	UMZC-H.15.014	This study	M2	5.7	5.2
Extant	*Tragulus*	*javanicus*	MCNM-nn	This study	M2	5.8	5.6
Extant	*Tragulus*	*javanicus*	MCNM-nn	This study	M2	5.9	5.6
Extant	*Tragulus*	*javanicus*	UMZC-H.15.014	This study	M2	6.0	6.8
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	M2	6.6	6.0
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	M2	6.6	6.2
Extant	*Tragulus*	*javanicus*	NHMW-40818	This study	M2	6.0	7.3
Extant	*Tragulus*	*javanicus*	SMNS-16874	This study	M2	5.7	6.6
Extant	*Tragulus*	*javanicus*	SMNS-16875	This study	M2	5.5	7.0
Extant	*Tragulus*	*javanicus*	SMNS-16876	This study	M2	7.4	7.6
Extant	*Tragulus*	*javanicus*	SMNS-16873	This study	M2	6.3	5.8
Extant	*Tragulus*	*javanicus*	UMZC-H.15.014	This study	M3	5.7	5.5
Extant	*Tragulus*	*javanicus*	UMZC-H.15.014	This study	M3	5.9	5.6
Extant	*Tragulus*	*javanicus*	MCNM-nn	This study	M3	5.9	5.9
Extant	*Tragulus*	*javanicus*	MCNM-nn	This study	M3	6.1	5.9
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	M3	6.2	6.5
Extant	*Tragulus*	*javanicus*	NMW-7595	This study	M3	6.5	6.6
Extant	*Tragulus*	*javanicus*	NHMW-40818	This study	M3	6.7	7.7
Extant	*Tragulus*	*javanicus*	SMNS-16874	This study	M3	6.4	7.3
Extant	*Tragulus*	*javanicus*	SMNS-16875	This study	M3	6.7	7.1
Extant	*Tragulus*	*javanicus*	SMNS-16876	This study	M3	7.4	7.2
Extant	*Tragulus*	*javanicus*	SMNS-16873	This study	M3	6.7	5.4
Extant	*Tragulus*	*kanchil*	NHMB-C3795	This study	P2	6.0	2.7
Extant	*Tragulus*	*kanchil*	NHMB-C3735	This study	P2	5.6	2.4
Extant	*Tragulus*	*kanchil*	NHMB-10085	This study	P2	6.8	2.8
Extant	*Tragulus*	*kanchil*	NHMB-3002	This study	P2	6.2	2.7
Extant	*Tragulus*	*kanchil*	NHMB-C1891	This study	P2	5.8	2.6
Extant	*Tragulus*	*kanchil*	NHMB-C3802	This study	P2	6.1	2.7
Extant	*Tragulus*	*kanchil*	NHMB-C3803	This study	P2	5.9	2.3
Extant	*Tragulus*	*kanchil*	NHMB-C3798	This study	P2	5.8	2.7

Extant	*Tragulus*	*kanchil*	NHMB-C3791	This study	P2	6.4	2.7
Extant	*Tragulus*	*kanchil*	NHMB-C3804	This study	P2	6.0	2.6
Extant	*Tragulus*	*kanchil*	NHMB-C3797	This study	P2	6.9	2.8
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	P2	6.8	2.8
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	P2	7.0	2.5
Extant	*Tragulus*	*kanchil*	NHMB-C3795	This study	P3	4.6	3.0
Extant	*Tragulus*	*kanchil*	NHMB-C3735	This study	P3	5.6	2.8
Extant	*Tragulus*	*kanchil*	NHMB-10085	This study	P3	6.6	3.8
Extant	*Tragulus*	*kanchil*	NHMB-3002	This study	P3	5.4	3.4
Extant	*Tragulus*	*kanchil*	NHMB-C1891	This study	P3	5.9	3.8
Extant	*Tragulus*	*kanchil*	NHMB-C3802	This study	P3	5.4	3.6
Extant	*Tragulus*	*kanchil*	NHMB-C3798	This study	P3	4.9	3.1
Extant	*Tragulus*	*kanchil*	NHMB-C3791	This study	P3	6.3	3.2
Extant	*Tragulus*	*kanchil*	NHMB-C3804	This study	P3	5.8	3.4
Extant	*Tragulus*	*kanchil*	NHMB-C3797	This study	P3	6.2	3.6
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	P3	6.5	3.1
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	P3	6.6	3.1
Extant	*Tragulus*	*kanchil*	NHMB-C3795	This study	P4	4.2	4.4
Extant	*Tragulus*	*kanchil*	NHMB-C3735	This study	P4	4.0	4.8
Extant	*Tragulus*	*kanchil*	NHMB-10085	This study	P4	4.5	5.4
Extant	*Tragulus*	*kanchil*	NHMB-3002	This study	P4	4.3	4.5
Extant	*Tragulus*	*kanchil*	NHMB-C1891	This study	P4	4.8	4.7
Extant	*Tragulus*	*kanchil*	NHMB-C3818	This study	P4	4.4	4.3
Extant	*Tragulus*	*kanchil*	NHMB-C3808	This study	P4	3.7	4.8
Extant	*Tragulus*	*kanchil*	NHMB-C3802	This study	P4	4.1	4.6
Extant	*Tragulus*	*kanchil*	NHMB-C3803	This study	P4	4.0	4.8
Extant	*Tragulus*	*kanchil*	NHMB-C3798	This study	P4	4.4	4.4
Extant	*Tragulus*	*kanchil*	NHMB-C3791	This study	P4	4.7	4.9
Extant	*Tragulus*	*kanchil*	NHMB-C3804	This study	P4	4.0	4.6
Extant	*Tragulus*	*kanchil*	NHMB-C3797	This study	P4	4.7	4.7
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	P4	4.4	4.0
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	P4	4.8	4.1
Extant	*Tragulus*	*kanchil*	NHMB-C3795	This study	M1	4.7	4.9
Extant	*Tragulus*	*kanchil*	NHMB-C3735	This study	M1	4.6	5.2
Extant	*Tragulus*	*kanchil*	NHMB-10085	This study	M1	5.9	6.7
Extant	*Tragulus*	*kanchil*	NHMB-3002	This study	M1	4.9	5.2
Extant	*Tragulus*	*kanchil*	NHMB-C1891	This study	M1	5.4	5.7
Extant	*Tragulus*	*kanchil*	NHMB-C3818	This study	M1	4.7	4.8
Extant	*Tragulus*	*kanchil*	NHMB-C3808	This study	M1	5.3	6.3
Extant	*Tragulus*	*kanchil*	NHMB-C3802	This study	M1	4.6	4.8
Extant	*Tragulus*	*kanchil*	NHMB-C3803	This study	M1	4.1	4.9
Extant	*Tragulus*	*kanchil*	NHMB-C3798	This study	M1	4.0	5.0
Extant	*Tragulus*	*kanchil*	NHMB-C3791	This study	M1	5.2	5.0
Extant	*Tragulus*	*kanchil*	NHMB-C3804	This study	M1	3.9	4.9
Extant	*Tragulus*	*kanchil*	NHMB-C3797	This study	M1	4.9	5.6

Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	M1	5.4	5.0
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	M1	5.4	4.9
Extant	*Tragulus*	*kanchil*	NHMB-C3795	This study	M2	6.0	5.9
Extant	*Tragulus*	*kanchil*	NHMB-C3735	This study	M2	5.8	6.4
Extant	*Tragulus*	*kanchil*	NHMB-10085	This study	M2	7.3	7.5
Extant	*Tragulus*	*kanchil*	NHMB-3002	This study	M2	6.8	6.2
Extant	*Tragulus*	*kanchil*	NHMB-C1891	This study	M2	6.2	7.4
Extant	*Tragulus*	*kanchil*	NHMB-C3818	This study	M2	6.1	5.7
Extant	*Tragulus*	*kanchil*	NHMB-C3808	This study	M2	5.9	7.2
Extant	*Tragulus*	*kanchil*	NHMB-C3802	This study	M2	5.7	5.7
Extant	*Tragulus*	*kanchil*	NHMB-C3803	This study	M2	5.4	6.0
Extant	*Tragulus*	*kanchil*	NHMB-C3798	This study	M2	5.2	6.1
Extant	*Tragulus*	*kanchil*	NHMB-C3791	This study	M2	5.8	5.7
Extant	*Tragulus*	*kanchil*	NHMB-C3804	This study	M2	5.7	6.4
Extant	*Tragulus*	*kanchil*	NHMB-C3797	This study	M2	5.6	6.6
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	M2	6.4	6.1
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	M2	6.6	6.2
Extant	*Tragulus*	*kanchil*	NHMB-C3795	This study	M3	6.7	5.5
Extant	*Tragulus*	*kanchil*	NHMB-C3735	This study	M3	6.4	7.0
Extant	*Tragulus*	*kanchil*	NHMB-10085	This study	M3	7.3	7.0
Extant	*Tragulus*	*kanchil*	NHMB-3002	This study	M3	6.5	6.7
Extant	*Tragulus*	*kanchil*	NHMB-C1891	This study	M3	7.0	7.7
Extant	*Tragulus*	*kanchil*	NHMB-C3818	This study	M3	6.1	5.0
Extant	*Tragulus*	*kanchil*	NHMB-C3802	This study	M3	6.2	5.6
Extant	*Tragulus*	*kanchil*	NHMB-C3803	This study	M3	6.0	6.8
Extant	*Tragulus*	*kanchil*	NHMB-C3798	This study	M3	6.3	6.7
Extant	*Tragulus*	*kanchil*	NHMB-C3791	This study	M3	6.4	5.3
Extant	*Tragulus*	*kanchil*	NHMB-C3804	This study	M3	6.0	7.4
Extant	*Tragulus*	*kanchil*	NHMB-C3797	This study	M3	6.3	6.6
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	M3	6.0	6.3
Extant	*Tragulus*	*kanchil*	NHMW-1473	This study	M3	6.2	5.7
Extant	*Tragulus*	*napu*	NHMB-C2950	This study	P2	6.8	3.3
Extant	*Tragulus*	*napu*	NHMW-5001	This study	P2	7.3	3.1
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	P2	6.8	3.5
Extant	*Tragulus*	*napu*	NHMW-1923	This study	P2	7.5	3.4
Extant	*Tragulus*	*napu*	NHMB-C2950	This study	P3	6.6	4.3
Extant	*Tragulus*	*napu*	NHMW-40378	This study	P3	6.4	4.4
Extant	*Tragulus*	*napu*	NHMW-5001	This study	P3	6.7	3.9
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	P3	6.6	4.2
Extant	*Tragulus*	*napu*	NHMW-1923	This study	P3	7.0	4.3
Extant	*Tragulus*	*napu*	NHMB-i 0007	This study	P3	7.2	4.6
Extant	*Tragulus*	*napu*	NHMB-C2950	This study	P4	5.1	5.4
Extant	*Tragulus*	*napu*	NHMW-40378	This study	P4	5.4	5.9
Extant	*Tragulus*	*napu*	NHMW-5001	This study	P4	5.0	5.6
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	P4	5.5	4.8

Extant	*Tragulus*	*napu*	NHMW-1923	This study	P4	5.5	5.6
Extant	*Tragulus*	*napu*	NHMB-i 0007	This study	P4	5.4	5.9
Extant	*Tragulus*	*napu*	NHMB-C2950	This study	M1	5.6	6.2
Extant	*Tragulus*	*napu*	UMZC-H. 14.976	This study	M1	6.4	6.6
Extant	*Tragulus*	*napu*	UMZC-H. 14.976	This study	M1	6.6	6.6
Extant	*Tragulus*	*napu*	NHMW-5001	This study	M1	5.7	5.9
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	M1	5.8	6.2
Extant	*Tragulus*	*napu*	NHMW-1923	This study	M1	5.8	6.5
Extant	*Tragulus*	*napu*	NHMB-i 0007	This study	M1	6.2	6.9
Extant	*Tragulus*	*napu*	NHMB-C2950	This study	M2	6.4	7.0
Extant	*Tragulus*	*napu*	UMZC-H. 14.976	This study	M2	7.4	8.2
Extant	*Tragulus*	*napu*	UMZC-H. 14.976	This study	M2	8.0	8.4
Extant	*Tragulus*	*napu*	NHMW-40378	This study	M2	7.6	8.0
Extant	*Tragulus*	*napu*	NHMW-5001	This study	M2	6.8	7.5
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	M2	7.2	7.4
Extant	*Tragulus*	*napu*	NHMW-1923	This study	M2	7.1	7.5
Extant	*Tragulus*	*napu*	NHMB-i 0007	This study	M2	7.0	7.8
Extant	*Tragulus*	*napu*	NHMB-C2950	This study	M3	7.0	7.6
Extant	*Tragulus*	*napu*	UMZC-H. 14.976	This study	M3	7.4	8.9
Extant	*Tragulus*	*napu*	UMZC-H. 14.976	This study	M3	8.0	8.9
Extant	*Tragulus*	*napu*	NHMW-40378	This study	M3	8.0	9.0
Extant	*Tragulus*	*napu*	NHMW-5001	This study	M3	7.5	7.9
Extant	*Tragulus*	*napu*	NHMW-B6014	This study	M3	7.2	7.8
Extant	*Tragulus*	*napu*	NHMW-1923	This study	M3	7.2	7.7
Extant	*Tragulus*	*napu*	NHMB-i 0007	This study	M3	7.3	8.1
Extant	*Tragulus*	*nigricans*	NHMB-8672	This study	P2	7.3	2.7
Extant	*Tragulus*	*nigricans*	NHMB-8672	This study	P3	6.6	4.8
Extant	*Tragulus*	*nigricans*	NHMB-8672	This study	P4	5.8	5.5
Extant	*Tragulus*	*nigricans*	NHMB-8672	This study	M1	6.4	5.6
Extant	*Tragulus*	*nigricans*	NHMB-8672	This study	M2	6.8	5.9
Fossil	*Yunannotherium*	*simplex*	V 8134.18	Han Defen (1986)	M2	8.8	9.7
Fossil	*Dorcabune*	*welcommi*	PAK-2464	Ginsburg et al. (2001)	p4	11.1	5.8
Fossil	*Dorcabune*	*welcommi*	PAK-2464	Ginsburg et al. (2001)	m1	10.7	7.2
Fossil	*Dorcabune*	*welcommi*	PAK-2464	Ginsburg et al. (2001)	m2	11.4	8.8
Fossil	*Dorcabune*	*welcommi*	PAK-2464	Ginsburg et al. (2001)	m3	19.7	9.7
Fossil	*Dorcatherium*	*chappuisi*	786.52 Rs.	Whitworth (1958)	p2	13.5	4.6
Fossil	*Dorcatherium*	*chappuisi*	Holotype	Whitworth (1958)	p2	13.5	5.0
Fossil	*Dorcatherium*	*chappuisi*	528.50 R.3	Whitworth (1958)	p3	13.5	5.1
Fossil	*Dorcatherium*	*chappuisi*	Holotype	Whitworth (1958)	p3	13.0	5.5
Fossil	*Dorcatherium*	*chappuisi*	528.50 R.3	Whitworth (1958)	p4	12.3	6.0
Fossil	*Dorcatherium*	*chappuisi*	Holotype	Whitworth (1958)	p4	12.5	6.0
Fossil	*Dorcatherium*	*chappuisi*	352.47 R.1	Whitworth (1958)	m1	11.6	7.6
Fossil	*Dorcatherium*	*chappuisi*	785.52 R. III	Whitworth (1958)	m1	11.7	7.2
Fossil	*Dorcatherium*	*chappuisi*	Holotype	Whitworth (1958)	m1	12.0	8.0
Fossil	*Dorcatherium*	*chappuisi*	352.47 R.1	Whitworth (1958)	m2	12.9	9.0

Fossil	*Dorcatherium*	*chappuisi*	785.52 R. III	Whitworth (1958)	m2	12.5	8.5
Fossil	*Dorcatherium*	*chappuisi*	Holotype	Whitworth (1958)	m2	13.0	9.5
Fossil	*Dorcatherium*	*chappuisi*	352.47 R.1	Whitworth (1958)	m3	18.8	8.7
Fossil	*Dorcatherium*	*chappuisi*	785.52 R. III	Whitworth (1958)	m3	18.0	8.7
Fossil	*Dorcatherium*	*chappuisi*	Holotype	Whitworth (1958)	m3	19.0	9.5
Fossil	*Dorcatherium*	*crassum*	Ss 5229	This study	p2	12.0	4.3
Fossil	*Dorcatherium*	*crassum*	Sa 2307	This study	p2	12.0	4.1
Fossil	*Dorcatherium*	*crassum*	Ss 5235.	This study	p2	12.2	4.8
Fossil	*Dorcatherium*	*crassum*	Ss 5234.	This study	p2	12.5	4.4
Fossil	*Dorcatherium*	*crassum*	Ss 5233.	This study	p2	12.6	4.6
Fossil	*Dorcatherium*	*crassum*	Ss 5237.	This study	p2	12.8	4.9
Fossil	*Dorcatherium*	*crassum*	IPS-24607	Alba et al. (2014)	p2	11.3	4.0
Fossil	*Dorcatherium*	*crassum*	Sa 9950	Morales et al. (2012)	p2	12.4	4.6
Fossil	*Dorcatherium*	*crassum*	So 3629.	This study	p3	12.0	5.0
Fossil	*Dorcatherium*	*crassum*	Sa 2307	This study	p3	12.1	4.4
Fossil	*Dorcatherium*	*crassum*	Sa 13630	This study	p3	12.4	5.1
Fossil	*Dorcatherium*	*crassum*	SS 52190	This study	p3	12.5	4.9
Fossil	*Dorcatherium*	*crassum*	Ss 5232	This study	p3	13.0	5.2
Fossil	*Dorcatherium*	*crassum*	SNSP-BSPG 1969 I 163	This study	p3	13.2	5.2
Fossil	*Dorcatherium*	*crassum*	Ss 5228	This study	p3	13.9	5.2
Fossil	*Dorcatherium*	*crassum*	IPS-24607	Alba et al. (2014)	p3	11.7	4.2
Fossil	*Dorcatherium*	*crassum*	IPS-24753b	Alba et al. (2014)	p3	12.6	4.5
Fossil	*Dorcatherium*	*crassum*	Sa 9950	Morales et al. (2012)	p3	11.9	4.8
Fossil	*Dorcatherium*	*crassum*	Ss 5231	This study	p4	11.9	5.3
Fossil	*Dorcatherium*	*crassum*	SS 52190	This study	p4	11.9	5.5
Fossil	*Dorcatherium*	*crassum*	So 3629	This study	p4	12.0	5.8
Fossil	*Dorcatherium*	*crassum*	Ss 5236	This study	p4	12.0	5.7
Fossil	*Dorcatherium*	*crassum*	SNSP-BSPG 1969 I 163	This study	p4	12.0	5.8
Fossil	*Dorcatherium*	*crassum*	MNHN Sa 2307	This study	p4	12.1	5.0
Fossil	*Dorcatherium*	*crassum*	Ss 5230	This study	p4	12.5	5.7
Fossil	*Dorcatherium*	*crassum*	Sa 13630	This study	p4	12.9	5.7
Fossil	*Dorcatherium*	*crassum*	IPS-24607	Alba et al. (2014)	p4	11.3	5.6
Fossil	*Dorcatherium*	*crassum*	IPS-24753b	Alba et al. (2014)	p4	11.8	5.7
Fossil	*Dorcatherium*	*crassum*	Sa 9950	Morales et al. (2012)	p4	12.0	5.6
Fossil	*Dorcatherium*	*crassum*	Sa 2307	This study	m1	10.2	6.6
Fossil	*Dorcatherium*	*crassum*	SNSP-BSPG 1969 I 163	This study	m1	11.0	7.3
Fossil	*Dorcatherium*	*crassum*	SS 52190	This study	m1	11.0	6.3
Fossil	*Dorcatherium*	*crassum*	Sa 2303	This study	m1	11.0	6.9
Fossil	*Dorcatherium*	*crassum*	SS 5220	This study	m1	11.2	7.0
Fossil	*Dorcatherium*	*crassum*	Sa 13630	This study	m1	11.8	6.8
Fossil	*Dorcatherium*	*crassum*	IPS-57513	Alba et al. (2014)	m1	11.5	7.7
Fossil	*Dorcatherium*	*crassum*	IPS-24106	Alba et al. (2014)	m1	10.8	7.5
Fossil	*Dorcatherium*	*crassum*	IPS-24753c	Alba et al. (2014)	m1	11.7	7.0
Fossil	*Dorcatherium*	*crassum*	IPS-24757	Alba et al. (2014)	m1	11.1	7.6
Fossil	*Dorcatherium*	*crassum*	IPS-24758	Alba et al. (2014)	m1	10.2	7.2

Fossil	*Dorcatherium*	*crassum*	IPS-57512	Alba et al. (2014)	m1	10.6	7.3
Fossil	*Dorcatherium*	*crassum*	Sa 9950	Morales et al. (2012)	m1	11.2	8.0
Fossil	*Dorcatherium*	*crassum*	Sa 2307	This study	m2	11.1	7.9
Fossil	*Dorcatherium*	*crassum*	SS 52190	This study	m2	11.2	8.0
Fossil	*Dorcatherium*	*crassum*	Sa 2303	This study	m2	11.9	8.3
Fossil	*Dorcatherium*	*crassum*	SS 5220	This study	m2	12.1	8.3
Fossil	*Dorcatherium*	*crassum*	SNSP-BSPG 1969 I 163	This study	m2	13.0	9.0
Fossil	*Dorcatherium*	*crassum*	Sa 13630	This study	m2	13.3	8.4
Fossil	*Dorcatherium*	*crassum*	IPS-57513	Alba et al. (2014)	m2	12.1	8.7
Fossil	*Dorcatherium*	*crassum*	IPS-24753c	Alba et al. (2014)	m2	11.8	9.0
Fossil	*Dorcatherium*	*crassum*	IPS-24757	Alba et al. (2014)	m2	12.4	8.6
Fossil	*Dorcatherium*	*crassum*	IPS-24758	Alba et al. (2014)	m2	11.6	8.1
Fossil	*Dorcatherium*	*crassum*	IPS-57512	Alba et al. (2014)	m2	12.1	8.3
Fossil	*Dorcatherium*	*crassum*	Sa 9955	Morales et al. (2012)	m2	12.3	9.5
Fossil	*Dorcatherium*	*crassum*	Sa 2307	This study	m3	18.2	8.8
Fossil	*Dorcatherium*	*crassum*	SS 52190	This study	m3	19.3	8.9
Fossil	*Dorcatherium*	*crassum*	Sa 13630	This study	m3	19.4	8.9
Fossil	*Dorcatherium*	*crassum*	IPS-24607	Alba et al. (2014)	m3	17.9	8.8
Fossil	*Dorcatherium*	*crassum*	dIPS24753c	Alba et al. (2014)	m3	17.5	8.5
Fossil	*Dorcatherium*	*crassum*	Sa 9950	Morales et al. (2012)	m3	18.6	9.3
Fossil	*Dorcatherium*	*iririensis*	Nap V Aug 62	Pickford (2002)	p3	11.7	4.3
Fossil	*Dorcatherium*	*iririensis*	Nap V Aug 62	Pickford (2002)	p4	10.3	5.0
Fossil	*Dorcatherium*	*iririensis*	Nap V 23´85	Pickford (2002)	m1	10.5	6.6
Fossil	*Dorcatherium*	*iririensis*	Nap V Aug 62	Pickford (2002)	m1	10.6	6.5
Fossil	*Dorcatherium*	*iririensis*	Nap V 2´99	Pickford (2002)	m2	12.2	7.5
Fossil	*Dorcatherium*	*iririensis*	Nap V 61 13	Pickford (2002)	m2	11.2	7.5
Fossil	*Dorcatherium*	*jourdani*	MHNL-CR 68	This study	m1	10.9	5.9
Fossil	*Dorcatherium*	*jourdani*	MHNL-CR 65	This study	m1	11.3	5.7
Fossil	*Dorcatherium*	*jourdani*	MHNL-CR 68	This study	m2	11.4	6.6
Fossil	*Dorcatherium*	*jourdani*	MHNL-CR 65	This study	m2	11.6	6.5
Fossil	*Dorcatherium*	*jourdani*	MHNL-CR 68	This study	m3	15.4	7.1
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ779	Kostopoulos and Sen (2016)	p2	11.3	3.7
Fossil	*Dorcatherium*	*maliki*	ITU-371	Kostopoulos and Sen (2016)	p3	14.2	4.7
Fossil	*Dorcatherium*	*maliki*	ITU-371	Kostopoulos and Sen (2016)	p3	14.6	5.0
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ768	Kostopoulos and Sen (2016)	p4	12.7	4.8
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ772	Kostopoulos and Sen (2016)	p4	13.7	5.3
Fossil	*Dorcatherium*	*maliki*	ITU-371	Kostopoulos and Sen (2016)	p4	13.8	5.5
Fossil	*Dorcatherium*	*maliki*	ITU-nn	Kostopoulos and Sen (2016)	p4	12.9	4.8
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ765	Kostopoulos and Sen (2016)	m1	11.4	8.3
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ748	Kostopoulos and Sen (2016)	m1	11.7	7.5
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ783	Kostopoulos and Sen (2016)	m2	13.5	9.3
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ767	Kostopoulos and Sen (2016)	m2	13.2	8.2
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ766	Kostopoulos and Sen (2016)	m2	13.7	9.0
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ782	Kostopoulos and Sen (2016)	m2	13.8	9.3
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQno No	Kostopoulos and Sen (2016)	m2	12.7	8.4

Fossil	*Dorcatherium*	*maliki*	ITU-nn	Kostopoulos and Sen (2016)	m2	12.7	8.0
Fossil	*Dorcatherium*	*maliki*	MNHN.FTRQ784	Kostopoulos and Sen (2016)	m3	20.1	9.3
Fossil	*Dorcatherium*	*maliki*	MNHN.FTRQ748	Kostopoulos and Sen (2016)	m3	18.0	7.7
Fossil	*Dorcatherium*	*maliki*	ITU-nn	Kostopoulos and Sen (2016)	m3	18.6	9.0
Fossil	*Dorcatherium*	*minus*	PUPC 13/11	Khan et al. (2017)	p3	10.5	4.9
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2489	This study	p3	12.0	3.5
Fossil	*Dorcatherium*	*minus*	GSI-B594	Pilgrim (1915)	p4	10.0	4.8
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2489	This study	p4	10.0	4.4
Fossil	*Dorcatherium*	*minus*	GSI-234	This study	p4	10.7	4.7
Fossil	*Dorcatherium*	*minus*	AMNH-39306 (1981 XVII 24)	This study	p4	10.6	4.5
Fossil	*Dorcatherium*	*minus*	GSI-B594	Pilgrim (1915)	m1	10.8	6.8
Fossil	*Dorcatherium*	*minus*	PUPC 02/158	Farooq et al. (2007b)	m1	10.6	6.7
Fossil	*Dorcatherium*	*minus*	PUPC 13/14	Khan et al. (2017)	m1	9.8	5.7
Fossil	*Dorcatherium*	*minus*	PUPC 68/107	Khan and Akhtar (2013)	m1	10.7	5.6
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2561	This study	m1	11.0	5.6
Fossil	*Dorcatherium*	*minus*	AMNH-19594 (1981 XVII 17)	This study	m1	11.3	5.0
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2489	This study	m1	10.5	6.2
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2601	This study	m1	10.1	5.7
Fossil	*Dorcatherium*	*minus*	AMNH-39302 (1981 XVII 19)	This study	m1	11.0	6.1
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2548	This study	m1	10.0	5.1
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2581	This study	m1	11.1	5.9
Fossil	*Dorcatherium*	*minus*	AMNH-39510 (1981 XVII 38)	This study	m1	10.7	5,.
Fossil	*Dorcatherium*	*minus*	AMNH-39306 (1981 XVII 24)	This study	m1	10.5	5.6
Fossil	*Dorcatherium*	*minus*	GCS-09/04	Iqbal et al. (2011)	m2	12.2	7.6
Fossil	*Dorcatherium*	*minus*	GSI-B594	Pilgrim (1915)	m2	12.5	7.5
Fossil	*Dorcatherium*	*minus*	PC-GCUF 10/21	Batool et al. (2015)	m2	11.0	7.0
Fossil	*Dorcatherium*	*minus*	PC-GCUF 12/01	Batool et al. (2015)	m2	11.0	6.9
Fossil	*Dorcatherium*	*minus*	PUPC 02/158	Farooq et al. (2007b)	m2	12.7	8.3
Fossil	*Dorcatherium*	*minus*	PUPC 68/294	Farooq et al. (2007b)	m2	11.0	6.5
Fossil	*Dorcatherium*	*minus*	PUPC 72/10	Khan and Akhtar (2013)	m2	11.2	7.0
Fossil	*Dorcatherium*	*minus*	AMNH-19594 (1981 XVII 17)	This study	m2	11.9	7.0
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2629	This study	m2	10.2	7.1
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2489	This study	m2	11.4	6.6
Fossil	*Dorcatherium*	*minus*	AMNH-39306 (1981 XVII 24)	This study	m2	12.1	7.3
Fossil	*Dorcatherium*	*minus*	AMNH-39302 (1981 XVII 19)	This study	m2	12.7	7.4
Fossil	*Dorcatherium*	*minus*	AMNH-39510 (1981 XVII 38)	This study	m2	11.8	7.0
Fossil	*Dorcatherium*	*minus*	AMNH-19307 (1981 XVII 10)	This study	m2	12.8	7.2
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2580	This study	m2	11.3	6.4
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2581	This study	m2	11.8	6.8
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2548	This study	m2	11.6	6.4
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2588	This study	m2	12.2	6.8
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2601	This study	m2	11.6	6.5
Fossil	*Dorcatherium*	*minus*	AMNH-19366 (1981 XVII 18)	This study	m2	12.0	7.1
Fossil	*Dorcatherium*	*minus*	GSI-B594	Pilgrim (1915)	m3	16.7	8.3
Fossil	*Dorcatherium*	*minus*	PUPC 02/158	Farooq et al. (2007b)	m3	18.6	8.7

Fossil	*Dorcatherium*	*minus*	PUPC 68/294	Farooq et al. (2007b)	m3	16.1	6.8
Fossil	*Dorcatherium*	*naui*	IPS-4422	Alba et al. (2011)	p2	10.1	3.5
Fossil	*Dorcatherium*	*naui*	HLMD-488	This study	p2	10.5	3.5
Fossil	*Dorcatherium*	*naui*	BMNH-40632	This study	p2	10.8	37
Fossil	*Dorcatherium*	*naui*	UMJGP-204661	Aiglstorfer et al. (2014)	p2	10.1	3.6
Fossil	*Dorcatherium*	*naui*	UMJGP-204667	Aiglstorfer et al. (2014)	p2	10.1	3.6
Fossil	*Dorcatherium*	*naui*	UMJGP-210694	Aiglstorfer et al. (2014)	p2	10.2	nd
Fossil	*Dorcatherium*	*naui*	UMJGP-210694	Aiglstorfer et al. (2014)	p2	10.5	3.1
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2741	Aiglstorfer et al. (2014)	p2	9.9	3.3
Fossil	*Dorcatherium*	*naui*	IPS-4422	Alba et al. (2011)	p3	12.2	4.1
Fossil	*Dorcatherium*	*naui*	BMNH-40632	This study	p3	12.5	4.2
Fossil	*Dorcatherium*	*naui*	HLMD-488	This study	p3	13.7	4.7
Fossil	*Dorcatherium*	*naui*	AMNH-39305 (1981 XVII 53)	This study	p3	13.5	4.4
Fossil	*Dorcatherium*	*naui*	AMNH-19609 (1981 XVII 2)	This study	p3	13.4	4.6
Fossil	*Dorcatherium*	*naui*	BMNH-M3714 (1961 XIX 37)	This study	p3	12.4	4.9
Fossil	*Dorcatherium*	*naui*	UMJGP-210694	Aiglstorfer et al. (2014)	p3	13.2	nd
Fossil	*Dorcatherium*	*naui*	UMJGP-204667	Aiglstorfer et al. (2014)	p3	12.8	4.5
Fossil	*Dorcatherium*	*naui*	UMJGP-204661	Aiglstorfer et al. (2014)	p3	12.5	4.5
Fossil	*Dorcatherium*	*naui*	UMJGP-210694	Aiglstorfer et al. (2014)	p3	12.7	4.2
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2741	Aiglstorfer et al. (2014)	p3	13.0	4.4
Fossil	*Dorcatherium*	*naui*	IPS-4422	Alba et al. (2011)	p4	11.7	4.6
Fossil	*Dorcatherium*	*naui*	BMNH-40632	This study	p4	11.6	5.7
Fossil	*Dorcatherium*	*naui*	HLMD-488	This study	p4	11.8	5.1
Fossil	*Dorcatherium*	*naui*	HLMD DIN 1203	This study	p4	12.3	4.9
Fossil	*Dorcatherium*	*naui*	HLMD 489	This study	p4	12.6	4.7
Fossil	*Dorcatherium*	*naui*	AMNH-19609 (1981 XVII 2)	This study	p4	12.3	5.4
Fossil	*Dorcatherium*	*naui*	SNSB-BSPG 1956 II 2656	This study	p4	12.8	5.7
Fossil	*Dorcatherium*	*naui*	AMNH-39305 (1981 XVII 53)	This study	p4	nd	4.7
Fossil	*Dorcatherium*	*naui*	UMJGP-210694	Aiglstorfer et al. (2014)	p4	11.7	5.2
Fossil	*Dorcatherium*	*naui*	UMJGP-210694	Aiglstorfer et al. (2014)	p4	11.3	4.7
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2741	Aiglstorfer et al. (2014)	p4	11.2	5.0
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2734	Aiglstorfer et al. (2014)	p4	10.5	4.7
Fossil	*Dorcatherium*	*naui*	BMNH-M3714 (1961 XIX 37)	This study	p4	12.6	5.9
Fossil	*Dorcatherium*	*naui*	IPS-4422	Alba et al. (2011)	m1	10.3	7.3
Fossil	*Dorcatherium*	*naui*	BMNH-40632	This study	m1	11.1	6.9
Fossil	*Dorcatherium*	*naui*	HLMD 489	This study	m1	11.5	6.5
Fossil	*Dorcatherium*	*naui*	HLMD DIN 1203	This study	m1	12.1	6.7
Fossil	*Dorcatherium*	*naui*	AMNH-19609 (1981 XVII 2)	This study	m1	11.4	7.6
Fossil	*Dorcatherium*	*naui*	GSI-235	This study	m1	12.6	6.9
Fossil	*Dorcatherium*	*naui*	AMNH-39305 (1981 XVII 53)	This study	m1	11.4	6.7
Fossil	*Dorcatherium*	*naui*	SNSB-BSPG 1956 II 2570	This study	m1	12.3	6.8
Fossil	*Dorcatherium*	*naui*	AMNH-39307 (1981 XVII 36)	This study	m1	11.2	6.3
Fossil	*Dorcatherium*	*naui*	SNSB-BSPG 1956 II 2486	This study	m1	12.7	7.4
Fossil	*Dorcatherium*	*naui*	BMNH-M3714 (1961 XIX 37)	This study	m1	11.9	7.5
Fossil	*Dorcatherium*	*naui*	UMJGP-210694	Aiglstorfer et al. (2014)	m1	11.9	6.8

Fossil	*Dorcatherium*	*naui*	UMJGP-204664	Aiglstorfer et al. (2014)	m1	10.8	6.3
Fossil	*Dorcatherium*	*naui*	UMJGP-204663	Aiglstorfer et al. (2014)	m1	11.6	6.4
Fossil	*Dorcatherium*	*naui*	UMJGP-210694	Aiglstorfer et al. (2014)	m1	11.1	6.3
Fossil	*Dorcatherium*	*naui*	UMJGP-210693	Aiglstorfer et al. (2014)	m1	11.9	6.7
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2741	Aiglstorfer et al. (2014)	m1	11.7	6.7
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2734	Aiglstorfer et al. (2014)	m1	11.0	6.6
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2401	Aiglstorfer et al. (2014)	m1	12.0	6.8
Fossil	*Dorcatherium*	*naui*	IPS-4422	Alba et al. (2011)	m2	11.4	7.8
Fossil	*Dorcatherium*	*naui*	IPS-33110	Alba et al. (2011)	m2	12.1	7.8
Fossil	*Dorcatherium*	*naui*	BMNH-40632	This study	m2	11.3	7.9
Fossil	*Dorcatherium*	*naui*	HLMD-488	This study	m2	11.9	7.7
Fossil	*Dorcatherium*	*naui*	HLMD-489	This study	m2	12.6	7.7
Fossil	*Dorcatherium*	*naui*	HLMD DIN 1203	This study	m2	12.8	8.0
Fossil	*Dorcatherium*	*naui*	AMNH-39305 (1981 XVII 53)	This study	m2	13.7	8.7
Fossil	*Dorcatherium*	*naui*	AMNH-19609 (1981 XVII 2)	This study	m2	13.2	9.0
Fossil	*Dorcatherium*	*naui*	AMNH-19365 (1981 XVII 3)	This study	m2	12.8	7.2
Fossil	*Dorcatherium*	*naui*	SNSB-BSPG 1956 II 2570	This study	m2	13.8	8.3
Fossil	*Dorcatherium*	*naui*	AMNH-39262 (1981 XVII 49)	This study	m2	14.7	8.4
Fossil	*Dorcatherium*	*naui*	SNSB-BSPG 1956 II 2585	This study	m2	13.3	8.1
Fossil	*Dorcatherium*	*naui*	UMJGP-204663	Aiglstorfer et al. (2014)	m2	12.6	7.8
Fossil	*Dorcatherium*	*naui*	UMJGP-204662	Aiglstorfer et al. (2014)	m2	12.6	7.5
Fossil	*Dorcatherium*	*naui*	UMJGP-210694	Aiglstorfer et al. (2014)	m2	13.2	7.8
Fossil	*Dorcatherium*	*naui*	UMJGP-210694	Aiglstorfer et al. (2014)	m2	13.1	7.5
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2741	Aiglstorfer et al. (2014)	m2	12.8	7.8
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2734	Aiglstorfer et al. (2014)	m2	12.4	7.4
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2756	Aiglstorfer et al. (2014)	m2	13.0	8.0
Fossil	*Dorcatherium*	*naui*	BMNH-M3714 (1961 XIX 37)	This study	m2	12.8	8.7
Fossil	*Dorcatherium*	*naui*	IPS-4422	Alba et al. (2011)	m3	18.0	8.5
Fossil	*Dorcatherium*	*naui*	IPS-33110	Alba et al. (2011)	m3	17.2	7.7
Fossil	*Dorcatherium*	*naui*	BMNH-40632	This study	m3	16.3	8.7
Fossil	*Dorcatherium*	*naui*	HLMD-488	This study	m3	18.5	8.2
Fossil	*Dorcatherium*	*naui*	HLMD-DIN 1203	This study	m3	18.7	8.7
Fossil	*Dorcatherium*	*chappuisi*	324.47 R.I	Whitworth (1958)	P2	13.0	6.2
Fossil	*Dorcatherium*	*chappuisi*	324.47 R.I	Whitworth (1958)	P3	12.0	7.5
Fossil	*Dorcatherium*	*chappuisi*	324.47 R.I	Whitworth (1958)	P4	9.6	9.2
Fossil	*Dorcatherium*	*chappuisi*	324.47 R.I	Whitworth (1958)	M1	11.1	12.1
Fossil	*Dorcatherium*	*chappuisi*	201.50	Whitworth (1958)	M1	11.3	11.5
Fossil	*Dorcatherium*	*chappuisi*	789.52 Rs.	Whitworth (1958)	M1	11.0	11.0
Fossil	*Dorcatherium*	*chappuisi*	324.47 R.I	Whitworth (1958)	M2	12.4	14.5
Fossil	*Dorcatherium*	*chappuisi*	789.52 Rs.	Whitworth (1958)	M2	12.3	12.9
Fossil	*Dorcatherium*	*chappuisi*	324.47 R.I	Whitworth (1958)	M3	12.2	14.6
Fossil	*Dorcatherium*	*chappuisi*	789.52 Rs.	Whitworth (1958)	M3	12.0	13.7
Fossil	*Dorcatherium*	*crassum*	Ss 5214	This study	P3	11.1	8.5
Fossil	*Dorcatherium*	*crassum*	Ss 5214	This study	P4	8.6	9.0
Fossil	*Dorcatherium*	*crassum*	IPS-24753a	Alba et al. (2014)	P4	9.0	9.6

Fossil	*Dorcatherium*	*crassum*	Sa 2300	This study	M1	9.7	11.0
Fossil	*Dorcatherium*	*crassum*	Ss 5213	This study	M1	10.0	11.9
Fossil	*Dorcatherium*	*crassum*	Sa 1015	This study	M1	10.8	11.4
Fossil	*Dorcatherium*	*crassum*	Ss 5214	This study	M1	11.0	11.2
Fossil	*Dorcatherium*	*crassum*	Sa 10859	This study	M1	11.4	12.6
Fossil	*Dorcatherium*	*crassum*	Sa 10857	This study	M1	11.6	11.2
Fossil	*Dorcatherium*	*crassum*	IPS-24753a	Alba et al. (2014)	M1	10.4	11.4
Fossil	*Dorcatherium*	*crassum*	Sa 10859	This study	M2	11.8	13.7
Fossil	*Dorcatherium*	*crassum*	Sa 2300	This study	M2	11.8	13.0
Fossil	*Dorcatherium*	*crassum*	Ss 5214	This study	M2	12,0	13.5
Fossil	*Dorcatherium*	*crassum*	Sa 1015	This study	M2	12.3	13.5
Fossil	*Dorcatherium*	*crassum*	Ss 5213	This study	M2	12.5	14.3
Fossil	*Dorcatherium*	*crassum*	Sa 10857	This study	M2	12.5	12.9
Fossil	*Dorcatherium*	*crassum*	IPS-24753a	Alba et al. (2014)	M2	12.6	13.5
Fossil	*Dorcatherium*	*crassum*	Ss 5214	This study	M3	12.2	14.6
Fossil	*Dorcatherium*	*crassum*	Sa 2300	This study	M3	12.3	14.0
Fossil	*Dorcatherium*	*crassum*	Sa 10857	This study	M3	12.9	13.3
Fossil	*Dorcatherium*	*crassum*	Sa 1015	This study	M3	12.9	14.1
Fossil	*Dorcatherium*	*crassum*	Ss 5213	This study	M3	13.6	15.0
Fossil	*Dorcatherium*	*crassum*	IPS-63879	Alba et al. (2014)	M3	13.2	15.8
Fossil	*Dorcatherium*	*iririensis*	Nap V	Pickford (2002)	M3	10.7	11.3
Fossil	*Dorcatherium*	*jourdani*	MHNL-CR 70 or 69	This study	P2	11.5	5.6
Fossil	*Dorcatherium*	*jourdani*	MHNL-CR 67	This study	M1	10.4	10.2
Fossil	*Dorcatherium*	*jourdani*	MHNL-CR 66	This study	M1	11.0	105
Fossil	*Dorcatherium*	*jourdani*	MHNL-CR 66	This study	M2	11.4	11.2
Fossil	*Dorcatherium*	*jourdani*	MHNL-CR 67	This study	M2	12.2	11.3
Fossil	*Dorcatherium*	*jourdani*	MHNL-CR 67	This study	M3	12.0	11.4
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ759	Kostopoulos and Sen (2016)	P2	12.8	7.2
Fossil	*Dorcatherium*	*maliki*	ITU-nn	Kostopoulos and Sen (2016)	P4	12.5	12.8
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ754	Kostopoulos and Sen (2016)	M1	11.1	12.5
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ755	Kostopoulos and Sen (2016)	M1	10.4	12.8
Fossil	*Dorcatherium*	*maliki*	ITU-nn	Kostopoulos and Sen (2016)	M1	11.3	13.5
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ753	Kostopoulos and Sen (2016)	M2	12.8	14.3
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ757	Kostopoulos and Sen (2016)	M2	13.4	13.5
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ751	Kostopoulos and Sen (2016)	M2	13.7	14.7
Fossil	*Dorcatherium*	*maliki*	MNHN.F.TRQ752	Kostopoulos and Sen (2016)	M2	13.3	15.1
Fossil	*Dorcatherium*	*maliki*	ITU-379	Kostopoulos and Sen (2016)	M3	15.5	15.1
Fossil	*Dorcatherium*	*maliki*	ITU-nn	Kostopoulos and Sen (2016)	M3	14.7	14.9
Fossil	*Dorcatherium*	*minus*	AMNH-39306 (1981 XVII 24)	This study	m3	17.0	7.2
Fossil	*Dorcatherium*	*minus*	AMNH-19366 (1981 XVII 18)	This study	m3	16.1	7.5
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2465	This study	m3	17.3	7.1
Fossil	*Dorcatherium*	*minus*	AMNH-39253 (1981 XVII 14)	This study	m3	16.8	7.6
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2601	This study	m3	16.1	7.5
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2490	This study	m3	17.0	7.2
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2503	This study	m3	16.8	7.0

Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2496	This study	m3	17.1	7.6
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2629	This study	m3	16.6	7.8
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2655	This study	m3	15.9	6.8
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2536	This study	P2	11.6	5.2
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2536	This study	P2	11.5	5.1
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2485	This study	P3	9.9	5.7
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2536	This study	P3	11.2	6.4
Fossil	*Dorcatherium*	*minus*	PC-GCUF 09/22 (H14)	Khan et al. (2012)	P4	8.5	9.0
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2484	This study	P4	8.5	8.2
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2497	This study	P4	8.1	9.4
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2654	This study	P4	9.6	9.1
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2536	This study	P4	8.6	8,.
Fossil	*Dorcatherium*	*minus*	PC-GCUF 11/178	Batool et al. (2015)	M1	9.7	10.5
Fossil	*Dorcatherium*	*minus*	PUPC 08/90	Samiullah et al. (2015)	M1	9.4	10.0
Fossil	*Dorcatherium*	*minus*	PUPC 87/40	Farooq et al. (2007b)	M1	10.0	117
Fossil	*Dorcatherium*	*minus*	PUPC 87/84	Farooq et al. (2007b)	M1	9.3	10.0
Fossil	*Dorcatherium*	*minus*	AMNH-39303 (1981 XVII 13)	This study	M1	9.9	10.0
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2480	This study	M1	10.4	10.4
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2498	This study	M1	10.6	10.9
Fossil	*Dorcatherium*	*minus*	AMNH-29856 (1981 XVII 32)	This study	M1	9.8	10.5
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2456	This study	M1	10.5	nd
Fossil	*Dorcatherium*	*minus*	GSI-B195	Pilgrim (1915)	M2	10.6	12.3
Fossil	*Dorcatherium*	*minus*	PUPC 02/01	Farooq et al. (2007b)	M2	10.6	11.7
Fossil	*Dorcatherium*	*minus*	PUPC 03/15 (H15)	Khan et al. (2012)	M2	11.0	13.0
Fossil	*Dorcatherium*	*minus*	PUPC 68/08	Khan and Akhtar (2013)	M2	11.0	13.4
Fossil	*Dorcatherium*	*minus*	PUPC 68/355	Farooq et al. (2007b)	M2	10.5	11.8
Fossil	*Dorcatherium*	*minus*	PUPC 68/41	Farooq et al. (2007b)	M2	11.0	13.0
Fossil	*Dorcatherium*	*minus*	PUPC 86/200 (H18)	Khan et al. (2012)	M2	11.0	11.9
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2456	This study	M2	11.2	11.1
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2536	This study	M2	11.2	12.6
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2536	This study	M2	10.9	11.7
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2469	This study	M2	11.0	12.3
Fossil	*Dorcatherium*	*minus*	AMNH-29856 (1981 XVII 32)	This study	M2	11.7	12.3
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2497	This study	M2	11.7	13.1
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2480	This study	M2	11.1	13.1
Fossil	*Dorcatherium*	*minus*	GCS-09/01	Iqbal et al. (2011)	M3	11.2	12.7
Fossil	*Dorcatherium*	*minus*	GCS-09/02	Iqbal et al. (2011)	M3	12.5	13.7
Fossil	*Dorcatherium*	*minus*	GSI-B195	Pilgrim (1915)	M3	11.4	11.6
Fossil	*Dorcatherium*	*minus*	PC-GCUF 11/184	Batool et al. (2015)	M3	12.8	12.8
Fossil	*Dorcatherium*	*minus*	PUPC 01/2002	Farooq et al. (2007b)	M3	11.7	12.4
Fossil	*Dorcatherium*	*minus*	AMNH-29856 (1981 XVII 32)	This study	M3	11.3	13.0
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2536	This study	M3	12.0	13.2
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2536	This study	M3	12.3	13.6
Fossil	*Dorcatherium*	*minus*	SNSB-BSPG 1956 II 2469	This study	M3	11.3	12.4
Fossil	*Dorcatherium*	*minus*	PUPC 68/355	Farooq et al. (2007b)	M3	11.7	13.0

Fossil	*Dorcatherium*	*naui*	AMNH-19365 (1981 XVII 3)	This study	m3	17.5	7.7
Fossil	*Dorcatherium*	*naui*	AMNH-19609 (1981 XVII 2)	This study	m3	20.0	9.5
Fossil	*Dorcatherium*	*naui*	AMNH-39262 (1981 XVII 49)	This study	m3	20.1	9.2
Fossil	*Dorcatherium*	*naui*	SNSB-BSPG 1956 II 2463	This study	m3	18.3	7.7
Fossil	*Dorcatherium*	*naui*	SNSB-BSPG 1956 II 2572	This study	m3	19.5	9.0
Fossil	*Dorcatherium*	*naui*	SNSB-BSPG 1956 II 2582	This study	m3	nd	8.1
Fossil	*Dorcatherium*	*naui*	SNSB-BSPG 1956 II 2587	This study	m3	19.4	9.0
Fossil	*Dorcatherium*	*naui*	SNSB-BSPG 1956 II 2468	This study	m3	20.0	8.6
Fossil	*Dorcatherium*	*naui*	AMNH-32742 (1981 XVII 4)	This study	m3	18.9	7.9
Fossil	*Dorcatherium*	*naui*	UMJGP-204662	Aiglstorfer et al. (2014)	m3	18.3	8.5
Fossil	*Dorcatherium*	*naui*	UMJGP-204665	Aiglstorfer et al. (2014)	m3	18.8	8.4
Fossil	*Dorcatherium*	*naui*	UMJGP-204109	Aiglstorfer et al. (2014)	m3	17.0	8.2
Fossil	*Dorcatherium*	*naui*	UMJGP-210694	Aiglstorfer et al. (2014)	m3	17.2	7.9
Fossil	*Dorcatherium*	*naui*	UMJGP-210694	Aiglstorfer et al. (2014)	m3	17.2	nd
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2741	Aiglstorfer et al. (2014)	m3	18.4	8.3
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2734	Aiglstorfer et al. (2014)	m3	16.8	8.0
Fossil	*Dorcatherium*	*naui*	BMNH-M3714 (1961 XIX 37)	This study	m3	19.1	9.6
Fossil	*Dorcatherium*	*naui*	BMNH-40632	This study	P2	12.2	5.0
Fossil	*Dorcatherium*	*naui*	BMNH-40632	This study	P3	11.4	6.2
Fossil	*Dorcatherium*	*naui*	BMNH-40632	This study	P4	10.0	9.2
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2379	Aiglstorfer et al. (2014)	P4	10.2	10.2
Fossil	*Dorcatherium*	*naui*	IPS-43491	Alba et al. (2011)	M1	13.0	13.8
Fossil	*Dorcatherium*	*naui*	GPIT/MA/2375	Aiglstorfer et al. (2014)	M1	10.8	11.7
Fossil	*Dorcatherium*	*naui*	UMJGP-209952	Aiglstorfer et al. (2014)	M1	11.0	11.7
Fossil	*Dorcatherium*	*naui*	IPS-43491	Alba et al. (2011)	M2	13.2	14.9
Fossil	*Dorcatherium*	*naui*	BMNH-40632	This study	M2	12.3	13.5
Fossil	*Dorcatherium*	*naui*	UMJGP-210698	Aiglstorfer et al. (2014)	M2	12.9	13.8
Fossil	*Dorcatherium*	*naui*	IPS-45288	Alba et al. (2011)	M3	12.8	14.2
Fossil	*Dorcatherium*	*naui*	UMJGP-210697	Aiglstorfer et al. (2014)	M3	13.9	14.4
Fossil	*Dorcatherium*	*naui*	BMNH-40632	This study	M3	13.0	13.8
Fossil	*Dorcatherium*	*puyhauberti*	sd (Vatiluk loc.)	This study	M2	11.6	13.8
Fossil	*Dorcatherium*	*puyhauberti*	sd (Vatiluk loc.)	This study	M3	12.0	12.4
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	p3	14.7	6.0
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	p3	14.9	5.6
Fossil	*Dorcatherium*	*vindebonense*	NHMW-21	This study	m2	14.5	9.7
Fossil	*Dorcatherium*	*vindebonense*	NHMW-23	This study	m2	14.9	10.2
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	m2	15.1	9.9
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	m3	21.1	10.4
Fossil	*Dorcatherium*	*vindebonense*	NHMW-23	This study	m3	22.9	10.7
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	P2	14.9	7.4
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	P2	17.3	7.2
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	P3	15.5	9.7
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	P4	12.7	12.1
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	M1	13.3	14.9
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	M1	13.4	13.7

Fossil	*Dorcatherium*	*vindebonense*	NHMW-N 5	This study	M1	14.0	15.5
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	M2	14.6	16.1
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	M2	15.5	16.8
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	M2	16.0	16.7
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	M2	16.9	17.0
Fossil	*Dorcatherium*	*vindebonense*	NHMW-37 A	This study	M3	16.8	17.7
Fossil	*Dorcabune*	*nagrii*	GSI-B106	Pilgrim (1915)	m1	13.8	10.0
Fossil	*Dorcabune*	*nagrii*	GSI-B106	Pilgrim (1915)	m2	15.1	12.0
Fossil	*Dorcabune*	*nagrii*	GSI-B591	Pilgrim (1915)	m2	15.2	11.0
Fossil	*Dorcabune*	*nagrii*	PUPC 70/13	Farooq et al. (2007a)	m3	22.7	10.4
Fossil	*Dorcabune*	*nagrii*	GSI-B106	Pilgrim (1915)	m3	23.1	12.8
Fossil	*Dorcabune*	*nagrii*	GSI-B591	Pilgrim (1915)	m3	21.7	11.4
Fossil	*Dorcabune*	*nagrii*	PUPC 70/13	Farooq et al. (2007a)	m3	22.7	10.4
Fossil	*Dorcabune*	*nagrii*	PUPC 68/425	Khan et al. (2010)	M1	15.2	17.6
Fossil	*Dorcabune*	*nagrii*	PUPC 96/45	Khan et al. (2010)	M1	14.0	16.0
Fossil	*Dorcabune*	*nagrii*	GSI-B598	Pilgrim (1915)	M2	13.4	14.4
Fossil	*Dorcabune*	*nagrii*	GSI-B598	Pilgrim (1915)	M3	14.8	16.8
Fossil	*Dorcabune*	*nagrii*	GSI-B590	Pilgrim (1915)	M3	14.6	16.7
Fossil	*Dorcatherium*	*majus*	GSI-B593	Pilgrim (1915)	p2	14.3	4.3
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2617	This study	p3	15.5	5.2
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2603	This study	p3	16.8	5.9
Fossil	*Dorcatherium*	*majus*	GSI-B593	Pilgrim (1915)	p3	17.7	nd
Fossil	*Dorcatherium*	*majus*	PC-GCUF 10/49	Batool et al. (2015)	p4	14.2	7.2
Fossil	*Dorcatherium*	*majus*	PUPC 86/2	Farooq et al. (2008)	p4	13.3	6.0
Fossil	*Dorcatherium*	*majus*	PUPC 86/5	Farooq et al. (2008)	p4	13.1	5.7
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2603	This study	p4	14.0	6.9
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1968 XVIII 10	This study	p4	15.0	6.5
Fossil	*Dorcatherium*	*majus*	AMNH-19524 (1981 XVII 52)	This study	p4	14.8	5.4
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2508	This study	p4	15.6	6.7
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2521	This study	p4	17.2	7.1
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2604	This study	p4	15.2	6.2
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2620	This study	p4	13.5	6.3
Fossil	*Dorcatherium*	*majus*	GSI-B593	Pilgrim (1915)	p4	17.3	6.2
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2603	This study	m1	14.6	9.6
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2621	This study	m1	15.7	8.6
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2616	This study	m1	14.6	7.7
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1968 XVIII 10	This study	m1	15.9	8.4
Fossil	*Dorcatherium*	*majus*	AMNH-19524 (1981 XVII 52)	This study	m1	14.4	7.9
Fossil	*Dorcatherium*	*majus*	AMNH-19517 (1968 XVIII 15)	This study	m1	13.4	8.5
Fossil	*Dorcatherium*	*majus*	AMNH-19520 (1981 XVII 48)	This study	m1	14.8	8.4
Fossil	*Dorcatherium*	*majus*	GSI-9909 (1981 XVII 65)	This study	m1	13.5	9.1
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2617	This study	m1	16.0	9.2
Fossil	*Dorcatherium*	*majus*	GSI-B593	Pilgrim (1915)	m1	15.7	9.5
Fossil	*Dorcatherium*	*majus*	PC-GCUF 10/49	Batool et al. (2015)	m1	15.5	10.2
Fossil	*Dorcatherium*	*majus*	PUPC 86/2	Farooq et al. (2008)	m1	14.3	9.0

Fossil	*Dorcatherium*	*majus*	PUPC 86/5	Farooq et al. (2008)	m1	13.0	9.3
Fossil	*Dorcatherium*	*majus*	WIF/A-1476	Sehgal (2015)	m1	14.2	9.8
Fossil	*Dorcatherium*	*majus*	WIF/A-1477	Sehgal (2015)	m1	14.5	9.0
Fossil	*Dorcatherium*	*majus*	GSI-B593	Pilgrim (1915)	m2	17.5	10.9
Fossil	*Dorcatherium*	*majus*	PC-GCUF 10/49	Batool et al. (2015)	m2	17.2	11.2
Fossil	*Dorcatherium*	*majus*	PUPC 63/243	Farooq et al. (2008)	m2	17.0	10.2
Fossil	*Dorcatherium*	*majus*	PUPC 63/243	Farooq et al. (2008)	m2	16.0	12.0
Fossil	*Dorcatherium*	*majus*	PUPC 86/152	Farooq et al. (2008)	m2	16.2	12.0
Fossil	*Dorcatherium*	*majus*	PUPC 98/61	Farooq et al. (2008)	m2	17.0	10.5
Fossil	*Dorcatherium*	*majus*	WIF/A-1476	Sehgal (2015)	m2	17.0	11.3
Fossil	*Dorcatherium*	*majus*	WIF/A 1478	Sehgal (2015)	m2	16.5	10.5
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2616	This study	m2	16.3	9.4
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2618	This study	m2	17.8	9.9
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2621	This study	m2	18.3	10.9
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1968 XVIII 10	This study	m2	17.4	10.8
Fossil	*Dorcatherium*	*majus*	AMNH-19517 (1968 XVIII 15)	This study	m2	16.8	10.6
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1968 XVIII 56	This study	m2	17.1	10.2
Fossil	*Dorcatherium*	*majus*	AMNH-19369 (1981 XVII 42)	This study	m2	17.7	9.8
Fossil	*Dorcatherium*	*majus*	AMNH-19520 (1981 XVII 48)	This study	m2	17.6	10.5
Fossil	*Dorcatherium*	*majus*	AMNH-19524 (1981 XVII 52)	This study	m2	15.7	9.3
Fossil	*Dorcatherium*	*majus*	GSI-9909 (1981 XVII 65)	This study	m2	16.2	9.8
Fossil	*Dorcatherium*	*majus*	GSI-B593	Pilgrim (1915)	m3	25.0	11.4
Fossil	*Dorcatherium*	*majus*	PC-GCUF 10/49	Batool et al. (2015)	m3	23.3	12.0
Fossil	*Dorcatherium*	*majus*	PUPC-84/115	Farooq et al. (2008)	m3	24.0	11.0
Fossil	*Dorcatherium*	*majus*	PUPC-86/152	Farooq et al. (2008)	m3	23.0	11.0
Fossil	*Dorcatherium*	*majus*	PUPC-86/2	Farooq et al. (2008)	m3	25.1	11.0
Fossil	*Dorcatherium*	*majus*	PUPC-86/3	Farooq et al. (2008)	m3	25.0	11.4
Fossil	*Dorcatherium*	*peneckei*	NMA-1415	This study	p3	15.8	5.6
Fossil	*Dorcatherium*	*peneckei*	NMA-86-485	This study	p4	14.2	7.6
Fossil	*Dorcatherium*	*peneckei*	NMA-1415	This study	p4	16.3	9.3
Fossil	*Dorcatherium*	*peneckei*	LMJ-1601	This study	m1	15.0	9.5
Fossil	*Dorcatherium*	*peneckei*	LMJ-1601	This study	m2	16.6	12.3
Fossil	*Dorcatherium*	*peneckei*	NMA-1747	This study	m3	20.0	10.6
Fossil	*Dorcatherium*	*peneckei*	NMA-85.9	This study	m3	20.9	10.9
Fossil	*Dorcatherium*	*peneckei*	NMA-85.6	This study	m3	21.6	11.0
Fossil	*Dorcatherium*	*peneckei*	NMA-85.7	This study	m3	21.9	12.5
Fossil	*Dorcatherium*	*peneckei*	LMJ-1601	This study	m3	23.1	12.8
Fossil	*Dorcatherium*	*peneckei*	Stallhofen	This study	m3	23.1	12.8
Fossil	*Dorcatherium*	*peneckei*	NMA-411	This study	m3	25.7	13.3
Fossil	*Dorcatherium*	*majus*	AMNH-19369 (1981 XVII 42)	This study	m3	25.6	11.6
Fossil	*Dorcatherium*	*majus*	AMNH-19939 (1981 XVII 45)	This study	m3	25.7	12.3
Fossil	*Dorcatherium*	*majus*	AMNH-39254 (1981 XVII 44)	This study	m3	22.7	10.5
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2623	This study	m3	25.2	11.1
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2512	This study	m3	28.4	12.2
Fossil	*Dorcatherium*	*majus*	GSI-9909 (1981 XVII 66)	This study	m3	26.4	12.8

Fossil	*Dorcatherium*	*majus*	PUPC 95/3	Farooq et al. (2007a)	P4	14.0	15.0
Fossil	*Dorcatherium*	*majus*	AMNH-19304 (1981 XVII 47)	This study	M1	15.3	nd
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2519	This study	M1	14.9	14.8
Fossil	*Dorcatherium*	*majus*	PC-GCUF 10/93	Khan and Akhtar (2013)	M1	14.8	14.7
Fossil	*Dorcatherium*	*majus*	AMNH-19302	Colbert (1935)	M2	18.5	21.5
Fossil	*Dorcatherium*	*majus*	GSI-B198	Pilgrim (1915)	M2	19.6	19.6
Fossil	*Dorcatherium*	*majus*	PUPC 03/14	Khan et al. (2010)	M2	19.0	19.0
Fossil	*Dorcatherium*	*majus*	PUPC 05/2 (H12)	Khan et al. (2012)	M2	19.0	22.8
Fossil	*Dorcatherium*	*majus*	PUPC 69/5	Khan and Akhtar (2013)	M2	18.5	17.3
Fossil	*Dorcatherium*	*majus*	PUPC 85/15	Farooq et al. (2007a)	M2	19.0	20.0
Fossil	*Dorcatherium*	*majus*	PUPC 85/21	Farooq et al. (2007a)	M2	18.0	22.0
Fossil	*Dorcatherium*	*majus*	PUPC 87/328	Farooq et al. (2007a)	M2	17.8	19.0
Fossil	*Dorcatherium*	*majus*	AMNH-19304 (1981 XVII 47)	This study	M2	17.7	18.3
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2519	This study	M2	18.2	16.8
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2535	This study	M2	19.5	19.1
Fossil	*Dorcatherium*	*majus*	SNSB-BSPG 1956 II 2535	This study	M3	18.1	17.1
Fossil	*Dorcatherium*	*majus*	GSI-B198	Pilgrim (1915)	M3	20.1	19.2
Fossil	*Dorcatherium*	*majus*	PUPC 69/193	Khan and Akhtar (2013)	M3	20.0	18.5
Fossil	*Dorcatherium*	*majus*	PUPC 69/268	Khan and Akhtar (2013)	M3	19.4	18.6
Fossil	*Dorcatherium*	*majus*	PUPC 86/46	Batool et al. (2015)	M3	20.0	21.6
Fossil	*Dorcatherium*	*majus*	PUPC 87/197	Farooq et al. (2007a)	M3	20.5	22.0
Fossil	*Dorcatherium*	*majus*	PUPC 87/328	Farooq et al. (2007a)	M3	19.1	18.2
Fossil	*Dorcatherium*	*peneckei*	NMA-85.8	This study	M2	16.5	19.1
Fossil	*Dorcatherium*	*peneckei*	NMA-85.8	This study	M3	17.3	20.5
Fossil	*Dorcabune*	*anthracotheroides*	GSI-B585	Pilgrim (1915)	p3	17.8	6.9
Fossil	*Dorcabune*	*anthracotheroides*	GSI-B585	Pilgrim (1915)	p4	16.6	8.4
Fossil	*Dorcabune*	*anthracotheroides*	AMNH-19355	Colbert (1935)	m1	17.0	12.0
Fossil	*Dorcabune*	*anthracotheroides*	GSI-B582 and B583	Pilgrim (1915)	m1	18.6	11.9
Fossil	*Dorcabune*	*anthracotheroides*	GSI-B585	Pilgrim (1915)	m1	16.2	10.6
Fossil	*Dorcabune*	*anthracotheroides*	PUPC 68/44	Khan and Akhtar (2013)	m1	15.4	9.0
Fossil	*Dorcabune*	*anthracotheroides*	PUPC 86/40 (H23)	Khan et al. (2012)	m1	19.3	14.0
Fossil	*Dorcabune*	*anthracotheroides*	SNSB-BSPG 1956 II 2595	This study	m2	19.7	13.9
Fossil	*Dorcabune*	*anthracotheroides*	AMNH-19355	Colbert (1935)	m2	17.5	13.0
Fossil	*Dorcabune*	*anthracotheroides*	GSI-B582 and B583	Pilgrim (1915)	m2	19.5	14.7
Fossil	*Dorcabune*	*anthracotheroides*	GSI-B585	Pilgrim (1915)	m2	16.7	12.6
Fossil	*Dorcabune*	*anthracotheroides*	PUPC 96/65	Farooq et al. (2007c)	m2	20.3	13.3
Fossil	*Dorcabune*	*anthracotheroides*	PUPC 96/66	Farooq et al. (2007c)	m2	19.0	12.0
Fossil	*Dorcabune*	*anthracotheroides*	PUPC 99/89	Farooq et al. (2007c)	m2	19.6	11.5
Fossil	*Dorcabune*	*anthracotheroides*	GSI-B582 and B583	Pilgrim (1915)	m3	30.9	16.0
Fossil	*Dorcabune*	*anthracotheroides*	GSI-B585	Pilgrim (1915)	m3	28.7	14.0
Fossil	*Dorcabune*	*anthracotheroides*	PC-GCUF 10/95	Khan and Akhtar (2013)	m3	28.4	14.0
Fossil	*Dorcabune*	*anthracotheroides*	PUPC 04/01	Khan et al. (2010)	m3	29.5	15.0
Fossil	*Dorcabune*	*anthracotheroides*	PUPC 85/28	Farooq et al. (2007c)	m3	26.0	13.0
Fossil	*Dorcabune*	*anthracotheroides*	SNSB-BSPG 1956 II 2595	This study	m3	29.1	14.0
Fossil	*Dorcabune*	*anthracotheroides*	GSI-B580	Pilgrim (1915)	M1	18.0	23.1

Fossil	*Dorcabune*	*anthracotheroides*	GSI-B580	Pilgrim (1915)	M2	21.7	25.7
Fossil	*Dorcabune*	*anthracotheroides*	PUPC 04/21 (H12)	Khan et al. (2012)	M2	21.0	21.0
Fossil	*Dorcabune*	*anthracotheroides*	PUPC-99/338	Khan et al. (2010)	M2	19.4	22.0
Fossil	*Dorcabune*	*anthracotheroides*	AMNH-19652	Colbert (1935)	M3	19.5	22.5
Fossil	*Dorcabune*	*anthracotheroides*	AMNH-29998	Colbert (1935)	M3	18.8	22.0
Fossil	*Dorcabune*	*anthracotheroides*	GSI-B580	Pilgrim (1915)	M3	21.4	25.8
Fossil	*Dorcabune*	*anthracotheroides*	GSI-B587	Pilgrim (1915)	M3	18.9	21.3

Table 2.2. Raw data of the Occlusal Tooth Area (OTA) and Occlusal Surface Area (OSA) for upper dentition of fossil and living tragulids. (f) = fossils species; (l) = living species.

Species	**Body mass**	**Occlusal Tooth Area (OTA) for upper dentition**						**Occlusal Surface Area (OSA)**		**Total OSA**	**log$_{10}$ Body mass (kg)**	**log$_{10}$ OSA Premolar**	**log$_{10}$ OSA Molar**	**log$_{10}$Total OSA**
	Kg	**P2**	**P3**	**P4**	**M1**	**M2**	**M3**	**Premolars**	**Molars**	**Premolars + Molars**				
Iberomeryx minor (f)	1.6	8.6	12.6	19.2	27.6	36.6	39.3	40.4	103.5	143.9	0.2	1.6	2.0	3.6
Afrotragulus parvus (f)	2.7	13.8	17.6	30.2	30.4	42.5	44.8	61.6	117.7	179.3	0.4	1.8	2.1	3.9
Dorcatherium guntianum (f)	12.7	46.3	53.6	72.5	80.1	99.8	114.4	172.4	294.3	466.7	1.1	2.2	2.5	4.7
Siamotragulus songhorensis (f)	5.6	n.d.	38.0	n.d.	49.0	62.2	68.3	-	179.5	-	0.7	-	2.3	-
Dorcatherium pigotti (f)	11.6	n.d.	40.5	50.3	70.6	89.3	96.5	-	256.4	-	1.1	-	2.4	-
Dorcatherium nagrii (f)	4.5	n.d.	n.d.	34.8	41.7	50.0	64.8	-	156.5	-	0.7	-	2.2	-
Hyemoschus aquaticus (l)	12.0	38.8	53.4	56.8	78.9	104.5	112.0	149.0	295.4	444.4	1.1	2.2	2.5	4.6
Moschiola indica (l)	3.0	35.1	31.9	38.0	50.4	60.5	59.2	105.0	170.1	275.1	0.5	2.0	2.2	4.3
Moschiola meminna (l)	2.5	19.1	24.4	31.5	46.2	55.8	53.1	75.0	155.1	230.1	0.4	1.9	2.2	4.1
Tragulus javanicus (l)	1.9	15.3	19.0	20.9	26.5	39.0	41.3	55.2	106.8	162.0	0.3	1.7	2.0	3.8
Tragulus kanchil (l)	2.0	16.6	19.4	19.9	25.7	38.4	40.6	55.9	104.7	160.6	0.3	1.7	2.0	3.8
Tragulus nigricans (l)	2.9	19.9	31.5	31.8	36.1	40.0	n.d.	83.2	-	-	0.5	1.9	-	-
Tragulus napu (l)	4.0	23.4	28.9	29.3	38.6	55.7	61.5	81.6	155.8	237.4	0.6	1.9	2.2	4.1
Dorcatherium chappuisi (f)	29.9	80.6	90.0	88.3	128.4	169.2	171.3	258.9	468.9	727.8	1.5	2.4	2.7	5.1
Dorcatherium crassum (f)	24.9	n.d.	94.4	81.9	123.4	164.7	186.1	-	474.2	-	1.4	-	2.7	-
Dorcatherium minus (f)	22.8	59.5	54.5	84.1	100.8	134.6	150.8	198.1	386.2	584.3	1.4	2.3	2.6	4.9
Dorcatherium naui (f)	24.4	61.0	70.7	92.0	179.4	181.4	180.6	223.7	541.4	765.1	1.4	2.3	2.7	5.1
Dorcatherium jourdani (f)	20.9	64.4	n.d.	n.d.	110.8	132.8	136.8	-	380.4	-	1.3	-	2.6	-
Dorcatherium maliki (f)	33.8	92.2	n.d.	160.0	142.8	191.5	226.5	-	560.8	-	1.5	-	2.7	-
Dorcatherium vindebonense (f)	49.0	117.4	150.4	153.7	199.6	262.5	297.4	421.5	759.5	1181.0	1.7	2.6	2.9	5.5
Dorcabune nagrii (f)	52.5	n.d.	n.d.	n.d.	245.8	227.3	243.8	-	716.9	-	1.7	-	2.9	-
Dorcatherium majus (f)	77.0	n.d.	n.d.	210.0	225.8	376.2	391.2	-	993.2	-	1.9	-	3.0	-
Dorcabune anthracotheroides (f)	111.5	n.d.	n.d.	n.d.	415.8	475.2	451.8	-	1342.8	-	2.0	-	3.1	-

Table 2.3. Raw data of the Occlusal Tooth Area (OTA) and Occlusal Surface Area (OSA) for the lower dentition of fossil and living tragulids. (f) = fossils species; (l) = living species.

Species	**Body mass**	**Occlusal Tooth Area (OTA) for lower dentition**						**Occlusal Surface Area (OSA)**		**Total OSA Premolars+Molars**	**$\log_{10}$ Body mass (kg)**	**$\log_{10}$ OSA Premolar**	**$\log_{10}$ OSA Molar**	**$\log_{10}$Total OSA**
	Kg	**p2**	**p3**	**p4**	**m1**	**m2**	**m3**	**Premolars**	**Molars**					
Archaeotragulus krabiensis (f)	4.7	14.3	25.0	27.7	27.8	36.4	52.4	67.0	116.6	183.6	0.7	1.8	2.1	3.9
Iberomeryx parvus (f)	3.3	n.d.	3.6	8.4	13.5	19.7	22.0	-	55.2	-	0.5	-	1.7	-
Iberomeryx minor (f)	1.6	n.d.	19.8	8.2	13.0	16.3	28.8	-	58.1	-	0.2	-	1.8	-
Afrotragulus moruorotensis (f)	1.0	n.d.	n.d.	n.d.	11.0	13.3	20.6	-	44.9	-	0.0	-	1.7	-
Dorcatherium pigotti (f)	11.6	17.8	31.2	34.2	46.7	56.0	83.1	83.2	185.8	269.0	1.1	1.9	2.3	4.2
Dorcatherium guntianum (f)	12.4	21.2	34.1	35.8	53.1	62.3	105.3	91.1	220.7	311.8	1.1	2.0	2.3	4.3
Dorcatherium nagrii (f)	4.5	12.0	18.2	27.1	23.7	30.5	45.8	57.3	100.0	157.3	0.7	1.8	2.0	3.8
Siamotragulus songhorensis (f)	5.6	n.d.	19.5	21.3	25.6	34.3	49.4	-	109.3	-	0.7	-	2.0	-
Afrotragulus parvus (f)	2.7	n.d.	17.5	15.2	15.1	22.0	32.5	-	69.6	-	0.4	-	1.8	-
Yunnanotherium simplex (f)	5.1	17.0	20.5	18.1	29.4	31.5	48.0	55.6	108.9	164.5	0.7	1.7	2.0	3.8
Hyemoschus aquaticus (l)	12.0	22.6	29.0	36.3	54.4	65.8	90.7	87.9	210.9	298.8	1.1	1.9	2.3	4.3
Moschiola indica (l)	3.0	10.7	12.7	22.4	28.6	34.9	49.3	45.8	112.8	158.6	0.5	1.7	2.1	3.7
Moschiola meminna (l)	2.5	11.3	18.7	21.2	27.2	32.2	42.4	51.2	101.8	153.0	0.4	1.7	2.0	3.7
Tragulus javanicus (l)	1.9	11.2	13.5	15.6	18.2	25.7	36.7	40.3	80.6	120.9	0.3	1.6	1.9	3.5
Tragulus kanchil (l)	2.0	9.2	12.9	14.3	16.4	24.9	37.1	36.4	78.4	114.8	0.3	1.6	1.9	3.5
Tragulus napu (l)	4.0	14.0	19.2	20.1	26.8	35.3	50.4	53.3	112.5	165.8	0.6	1.7	2.1	3.8
Dorcatherium chappuisi (f)	29.9	64.8	70.2	74.4	89.5	115.3	166.9	209.4	371.7	581.1	1.5	2.3	2.6	4.9
Dorcatherium crassum (f)	24.9	54.7	60.9	67.2	79.1	102.9	164.0	182.8	346.0	528.8	1.4	2.3	2.5	4.8

Dorcatherium minus (f)	22.8	n.d.	51.1	48.0	65.1	85.4	134.4	-	284.9	-	1.4	-	2.5	-
Dorcabune welcommi (f)	20.3	n.d.	n.d.	64.4	77.0	100.3	191.1	-	368.4	-	1.3	-	2.6	-
Dorcatherium naui (f)	24.4	37.4	55.6	59.9	76.9	93.9	148.3	152.9	319.1	472.0	1.4	2.2	2.5	4.7
Dorcatherium jourdani (f)	20.9	n.d.	n.d.	n.d.	64.4	75.3	109.3	-	249.0	-	1.3	-	2.4	-
Dorcatherium maliki (f)	33.8	41.8	69.9	67.8	91.2	115.6	164.3	179.5	371.1	550.6	1.5	2.3	2.6	4.8
Dorcabune nagrii (f)	52.5	n.d.	n.d.	n.d.	138.0	174.2	253.5	-	565.7	-	1.7	-	2.8	-
Dorcatherium peneckei (f)	71.2	n.d.	88.5	129.8	142.5	204.2	269.2	-	615.9	-	1.9	-	2.8	-
Dorcatherium majus (f)	77.0	61.5	n.d.	85.6	134.3	184.2	278.4	-	596.9	-	1.9	-	2.8	-
Dorcabune anthracotheroides (f)	111.5	n.d.	122.8	139.4	201.2	241.3	414.9	-	857.4	-	2.0	-	2.9	-

Appendix Chapter 3

Table 3.1. Stud specimens. In bold, species assignments according to this study, which differ from current assignments in collections. Tj = Tragulus javanicus, Tk = Tragulus kanchil, Tn = Tragulus napu, Tm = Tragulus meminna, Mi = Moschiola indica, Me-i = Meminna indica, Mo-k = Moschus kanchil, Mm = Moschiola meminna, nd = no data. SNSB-BSPG: Bavarian Natural History Collections - Bavarian State Collection of Paleontology and Geology, Munich, Germany; NMB: Natural History Museum Basel, Switzerland; SMNS: Natural History Museum Stuttgart, Germany; NHMW: Natural History Museum Vienna, Austria; SNSB-ZSM: Bavarian Natural History Collections - Zoological State Collection Munich, Germany.

Collection	**Inventory Number**	**Species assignment according to:**			**Sex**	**Geographical provenance**
		Skull label	**Collection catalogue**	**This study (PCA-plot N° in Fig. 3)**		
SNSB-BSPG	1977-I-185	*Tj*	nd	***Tragulus kanchil*** (10)	Female	Sumatra, Lubuk Pakam, Deli, North Sumatra
NMB	2453	*Mm*	*Mm*	*Moschiola meminna* (28)	Female	Sri Lanka
	1366	*Me-i*	*Mm*	*Moschiola meminna* (25)	Male	Sri Lanka
	1429	*Tm*	*Mm*	*Moschiola meminna* (29)	Male	Sri Lanka
	2328	*Tm / Mm*	*Mm*	*Moschiola meminna* (24)	Male	Sri Lanka
	2588	*Tm*	*Mm*	*Moschiola meminna* (30)	Male	Sri Lanka
	3735	*Tj / Tk*	*Tk*	*Tragulus kanchil* (13)	Female	Sumatra
	3002	*Tk*	*Tk*	*Tragulus kanchil* (2)	Female	Sumatra
	1891	*Tj*	*Tk*	*Tragulus kanchil* (17)	Female	Sumatra
	3803	*Tj*	*Tk*	*Tragulus kanchil* (9)	Female	Sumatra, Indagrii
	3797	*Tj / Tk*	*Tk*	*Tragulus kanchil* (14)	Female	Sumatra, Indagrii
	3804	*Tj*	*Tk*	*Tragulus kanchil* (8)	Female	Sumatra
	3802	*Tj*	*Tk*	*Tragulus kanchil* (5)	Female	Sumatra
	3795	*Tj*	*Tk*	*Tragulus kanchil* (7)	Male	Sumatra
	3808	*Tj*	*Tk*	*Tragulus kanchil* (12)	Male	Sumatra
	3809	*Tj*	*Tk*	*Tragulus kanchil* (6)	Male	Sumatra
	3791	*Tk*	*Tk*	*Tragulus kanchil* (4)	Male	Sumatra
	3798	*Tj*	*Tk*	*Tragulus kanchil* (1)	Male	Sumatra
	10085	*Tk*	*Tk*	***Tragulus napu* (36)**	Female	Borneo, Balikpapan
	3806	*Tj*	*Tk*	*Tragulus kanchil* (3)	Female	Sumatra
	I0007	*Tn*	*Tn*	*Tragulus napu* (42)	Female	Sumatra, Deli, North Sumatra
	C2950	*Tk - Tj*	*Tk*	***Tragulus napu* (43)**	Female	Sunda Islands
SMNS	2006	*Tm*	*Mm*	*Moschiola meminna* (27)	Female	Sri Lanka
	16875	*Tj*	*Tj*	*Tragulus javanicus* (19)	Female	Java

	16868	*Tj*	*Tj*	*Tragulus javanicus* (22)	Female	Java
	16874	*Tj*	*Tj*	*Tragulus javanicus* (18)	Male	Java
	16876	*Tj*	*Tj*	*Tragulus javanicus* (23)	Male	Java
NHMW	1923	*Tn*	*Tn*	*Tragulus napu* (39)	Male	Borneo
	40826	*Tn*	*Tn*	*Tragulus napu* (35)	Male	Borneo
	40378	*Tn*	*Tn*	*Tragulus napu* (34)	Male	Sumatra
	B6016	*Mm*	*Mm*	***Moschiola indica* (31)**	Male	India
	40818	*Tj / Tk*	*Tj*	*Tragulus javanicus* (21)	Female	Java
	1473	*Tn*	*Tn*	***Tragulus kanchil* (16)**	Male	Sumatra
	B6014	*Tn*	*Tn*	*Tragulus napu* (32)	Male	Sumatra
SNSB-ZSM	1962/224	*Tj*	*Tj*	***Tragulus kanchil* (11)**	Female	Thailand
	1964/223	*Tj*	-	***Tragulus kanchil* (15)**	Male	Thailand
	09/411	*Tn*	-	*Tragulus napu* (33)	Male	Borneo
	1909/233	*Tn*	-	*Tragulus napu* (41)	Male	Borneo
	1973/271	*Tn*	*Tn-*	*Tragulus napu* (37)	Male	Sumatra
	1903/9443	*Tn*	-	*Tragulus napu* (40)	Male	Sumatra
	1906/6	*Mm*	-	***Moschiola indica* (38)**	Female	India
	1917/2163	*Mm*	-	*Moschiola meminna* (26)	Male	Sri Lanka
	4 (ex 21)	*Mo-k / Tj*	-	***Tragulus javanicus* (20)**	Female	Java

Appendix Chapter 4

Table 4.1. Fossil and living tragulids here studied. SNSB-BSPG: Bavarian Natural History Collections - Bavarian State Collection of Paleontology and Geology, Munich, Germany; NMB: Natural History Museum Basel, Switzerland; SMNS: Natural History Museum Stuttgart, Germany; NHMW: Natural History Museum Vienna, Austria; SNSB-ZSM: Bavarian Natural History Collections - Zoological State Collection Munich, Germany; NMA: Natural History Museum Augsburg, Germany. For NMA-Walda 2 the 3D model is available at: https://data.ub.uni-muenchen.de/

Species	Sex	Collection	Inventory Number	Geographical provenance
Dorcatherium crassum	Male	NMA	Walda 2	Germany, Europe
Dorcatherium crassum	Female	NMA	2012-1/2131	Germany, Europe
Hyemoschus aquaticus	Male	NHMW	5407	Cameroon, Africa
Hyemoschus aquaticus	Male	Currently at SNSB-BSPG	H-30	Kongo, Africa
Hyemoschus aquaticus	Male	NHMW	40827	Gabon, Africa
Moschiola meminna	Male	SNSB-ZSM	1911-2163	Sri Lanka, Asia
Moschiola meminna	Male	NHMB	C-1366	Sri Lanka, Asia
Moschiola meminna	Male	NHMB	1429	Sri Lanka, Asia
Moschiola meminna	Male	NHMB	2328	Sri Lanka, Asia
Tragulus javanicus	Male	SMNS	16874	Java, Asia
Tragulus javanicus	Male	SMNS	16876	Java, Asia
Tragulus napu	Male	SNSB-ZSM	09-411	Borneo, Asia
Tragulus napu	Male	SNSB-ZSM	1909/233	Borneo, Asia
Tragulus napu	Male	NHMW	1923	Borneo, Asia
Tragulus napu	Male	NHMW	40826	Borneo, Asia
Tragulus napu	Male	NHMW	40378	Sumatra, Asia
Tragulus napu	Male	SNSB-ZSM	1903-9443	Sumatra, Asia
Tragulus napu	Male	NHMW	B6014	Sumatra, Asia
Tragulus kanchil	Male	NHMB	C3808	Sumatra, Asia
Tragulus kanchil	Male	NHMB	C3798	Sumatra, Asia
Tragulus kanchil	Male	NHMW	1473	Sumatra, Asia
Tragulus kanchil	Male	SNSB-ZSM	1964-233	Thailand, Asia

Appendix Chapter 5

Table 5.1. Dental measurements of *Dorcabune anthracotheroides* from this study and the lectotype (Pilgrim 1915). n.a.: not applicable.

Tooth	Catalogue number	Length [mm]	Width [mm]	Height [mm]	Hypsodonty Index	Figure 3
dex. m2	SNSB-BSPG 1956 II 2595	19.7	13.9	n.a.	n.a.	A, B, C
dex. m3	SNSB-BSPG 1956 II 2595	29.1	14.0	n.a.	n.a.	A, B, C
sin. M1	Holotype GSI B580	18.0	23.1	n.a.	n.a.	Pilgrim (1915): Pl. 21, fig. 1
sin. M2	Holotype GSI B580	21.7	25.7	n.a.	n.a.	Pilgrim (1915): Pl. 21, fig. 1
sin. M3	Holotype GSI B580	21.4	25.8	n.a.	n.a.	Pilgrim (1915): Pl. 21, fig. 1

Table 5.2 Dental measurements and Hypsodonty Index for specimens of *Dorcatherium majus* studied here. Data of the type specimens are provided. n.a.: not applicable.

Tooth	Catalogue number	SNSB – BSPG catalogue number cast	Length [mm]	Width [mm]	Height [mm]	Hypsodonty Index	Figures 5.5, 5.6, 5.7
sin. d4	SNSB-BSPG 1956 II 2617	n.a.	17.9	8.3	n.a.	n.a.	R, S, T
dex. d4	SNSB-BSPG 1956 II 2621	n.a.	18.7	7.5	n.a.	n.a.	U, V, W
sin. p3	SNSB-BSPG 1956 II 2617	n.a.	15.5	5.2	n.a.	n.a.	R, S, T
sin. p3	SNSB-BSPG 1956 II 2603	n.a.	16.8	5.9	n.a.	n.a.	I, J, K
sin. p4	SNSB-BSPG 1956 II 2603	n.a.	14.0	6.9	n.a.	n.a.	I, J, K
dex. p4	SNSB-BSPG 1968 XVIII 10	n.a.	15.0	6.5	n.a.	n.a.	A´, B´, C´
dex. p4	AMNH 19524	1981 XVII 52	14.8	5.4	n.a.	n.a.	n.a.
sin. p4	SNSB-BSPG 1956 II 2508	n.a.	15.6	6.7	n.a.	n.a.	G, H
sin. p4	SNSB-BSPG 1956 II 2521	n.a.	17.2	7.1	n.a.	n.a.	n.a.
sin. p4	SNSB-BSPG 1956 II 2604	n.a.	15.2	6.2	n.a.	n.a.	L, M, N
sin. p4	SNSB-BSPG 1956 II 2620	n.a.	13.5	6.3	n.a.	n.a.	n.a.
sin. m1	SNSB-BSPG 1956 II 2603	n.a.	14.6	9.6	n.a.	n.a.	I, J, K
dex. m1	SNSB-BSPG 1956 II 2621	n.a.	15.7	8.6	n.a.	n.a.	U, V, W
dex. m1	SNSB-BSPG 1956 II 2616	n.a.	14.6	7.7	n.a.	n.a.	O, P, Q
dex. m1	SNSB-BSPG 1968 XVIII 10	n.a.	15.9	8.4	n.a.	n.a.	A´, B´, C´
dex. m1	AMNH 19524	1981 XVII 52	14.4	7.9	n.a.	n.a.	n.a.
dex. m1	AMNH 19517	1968 XVIII 15	13.4	8.5	n.a.	n.a.	n.a.
dex. m1	AMNH 19520	1981 XVII 48	14.8	8.4	n.a.	n.a.	n.a.
sin. m1	GSI 9909	1981 XVII 65	13.5	9.1	n.a.	n.a.	n.a.
sin. m1	SNSB-BSPG 1956 II 2617	n.a.	16.0	9.2	n.a.	n.a.	R, S, T
dex. m2	SNSB-BSPG 1956 II 2616	n.a.	16.3	9.4	14.0	0.86	O, P, Q
dex. m2	SNSB-BSPG 1956 II 2618	n.a.	17.8	9.9	n.a.	n.a.	n.a.
dex. m2	SNSB-BSPG 1956 II 2621	n.a.	18.3	10.9	n.a.	n.a.	U, V, W
dex. m2	SNSB-BSPG 1968 XVIII 10	n.a.	17.4	10.8	n.a.	n.a.	A´, B´, C´
dex. m2	AMNH 19517	1968 XVIII 15	16.8	10.6	n.a.	n.a.	n.a.
dex. m2	SNSB-BSPG 1968 XVIII 56	n.a.	17.1	10.2	n.a.	n.a.	n.a.
dex. m2	AMNH 19369	1981 XVII 42	17.7	9.8	n.a.	n.a.	n.a.
dex. m2	AMNH 19520	1981 XVII 48	17.6	10.5	n.a.	n.a.	n.a.

dex. m2	AMNH 19524	1981 XVII 52	15.7	9.3	n.a.	n.a.	n.a.
sin. m2	GSI 9909	1981 XVII 65	16.2	9.8	n.a.	n.a.	n.a.
dex. m3	AMNH 19369	1981 XVII 42	25.6	11.6	n.a.	n.a.	n.a.
sin. m3	AMNH 19939	1981 XVII 45	25.7	12.3	n.a.	n.a.	n.a.
sin. m3	AMNH 39254	1981 XVII 44	22.7	10.5	n.a.	n.a.	D´, E´ F´
sin. m3	SNSB-BSPG 1956 II 2623	n.a.	25.2	11.1	n.a.	n.a.	X, Y, Z
sin. m3	SNSB BSPG 1956 II 2512	n.a.	28.4	12.2	n.a.	n.a.	n.a.
dex. m3	GSI 9909	1981 XVII 66	26.4	12.8	n.a.	n.a.	n.a.
dex. M1/2	GSI 9909	1981 XVII 64	14.9	n.a.	n.a.	n.a.	n.a.
sin. M1	AMNH 19304	1981 XVII 47	15.3	n.a.	n.a.	n.a.	n.a.
sin. M1	SNSB-BSPG 1956 II 2519	n.a.	14.9	14.8	n.a.	n.a.	A, B, C
dex. M2/3	GSI 9909	1981 XVII 64	16.3	16.9	n.a.	n.a.	n.a.
sin. M2	AMNH 19304	1981 XVII 47	17.7	18.3	n.a.	n.a.	n.a.
sin. M2	SNSB-BSPG 1956 II 2519	n.a.	18.2	16.8	n.a.	n.a.	A, B, C
dex. M2	SNSB-BSPG 1956 II 2535	n.a.	18.1	17.1	18.3	1.01	D, E, F
dex. M3	SNSB-BSPG 1956 II 2535	n.a.	19.5	19.1	16.0	0.82	D, E, F
sin. M2	Lectotype No: 1307/GSI B198 (Pilgrim 1915)	n.a.	19.6	19.6	n.a.	n.a.	n.a.
sin. M3	Lectotype No: 1307/GSI B198 (Pilgrim 1915)	n.a.	20.1	19.2	n.a.	n.a.	n.a.
dex. M3	Paralectotype No: 502/GSI B197 (Lydekker 1876)	n.a.	19.5	20.3	n.a.	n.a.	n.a.

Table 5.3. Dental measurements and Hypsodonty Index for the specimens of *Dorcatherium minus* studied here. Also, data from type specimens are provided. n.a.: not applicable.

Tooth	Catalogue number	SNSB - BSPG Catalogue number cast	Length [mm]	Width [mm]	Height [mm]	Hypsodonty Index	Figures 5.8, 5.9
sin. d4	SNSB-BSPG 1956 II 2561	n.a.	n.a.	4.7	n.a.	n.a.	n.a.
sin. p3	SNSB-BSPG 1956 II 2489	n.a.	12.0	3.5	n.a.	n.a.	O, P, Q
sin. p4	SNSB-BSPG 1956 II 2489	n.a.	10.0	4.4	n.a.	n.a.	O, P, Q
dex. p4	GSI 234	n.a.	10.7	4.7	n.a.	n.a.	X, Y, Z
sin. p4	AMNH 39306	1981 XVII 24	10.6	4.5	n.a.	n.a.	n.a.
sin. m1	SNSB-BSPG 1956 II 2561	n.a.	11.0	5.6	6.7	0.60	n.a.
sin. m1	AMNH 19594	1981 XVII 17	11.3	5.0	n.a.	n.a.	n.a.
sin. m1	SNSB-BSPG 1956 II 2489	n.a.	10.5	6.2	n.a.	n.a.	O, P, Q
sin. m1	SNSB-BSPG 1956 II 2601	n.a.	10.1	5.7	n.a.	n.a.	R, S, T
sin. m1	AMNH 39302	1981 XVII 19	11.0	6.1	n.a.	n.a.	n.a.
sin. m1	SNSB-BSPG 1956 II 2548	n.a.	10.0	5.1	n.a.	n.a.	n.a.
sin. m1	SNSB-BSPG 1956 II 2581	n.a.	11.1	5.9	n.a.	n.a.	n.a.
sin. m1	AMNH 39510	1981 XVII 38	10.7	5.8	n.a.	n.a.	n.a.
sin. m1	AMNH 39306	1981 XVII 24	10.5	5.6	n.a.	n.a.	n.a.
sin. m2	AMNH 19594	1981 XVII 17	11.9	7.0	n.a.	n.a.	n.a.
sin. m2	SNSB-BSPG 1956 II 2629	n.a.	10.2	7.1	n.a.	n.a.	U, V, W
sin. m2	SNSB-BSPG 1956 II 2489	n.a.	11.4	6.6	n.a.	n.a.	O, P, Q
sin. m2	AMNH 39306	1981 XVII 24	12.1	7.3	n.a.	n.a.	n.a.
sin. m2	AMNH 39302	1981 XVII 19	12.7	7.4	9.5	0.74	n.a.
sin. m2	AMNH 39510	1981 XVII 38	11.8	7.0	n.a.	n.a.	n.a.
sin. m2	AMNH 19307	1981 XVII 10	12.8	7.2	n.a.	n.a.	n.a.
dex. m2	SNSB-BSPG 1956 II 2580	n.a.	11.3	6.4	n.a.	n.a.	n.a.
sin. m2	SNSB-BSPG 1956 II 2581	n.a.	11.8	6.8	n.a.	n.a.	n.a.

sin. m2	SNSB-BSPG 1956 II 2548	n.a.	11.6	6.4	n.a.	n.a.	n.a.
sin. m2	SNSB-BSPG 1956 II 2588	n.a.	12.2	6.8	n.a.	n.a.	n.a.
sin. m2	SNSB-BSPG 1956 II 2601	n.a.	11.6	6.5	n.a.	n.a.	R, S, T
sin. m2	AMNH 19366	1981 XVII 18	12.0	7.1	n.a.	n.a.	n.a.
sin. m3	AMNH 39306	1981 XVII 24	17.0	7.2	n.a.	n.a.	n.a.
sin. m3	AMNH 19366	1981 XVII 18	16.1	7.5	n.a.	n.a.	n.a.
dex. m3	SNSB-BSPG 1956 II 2465	n.a.	17.3	7.1	n.a.	n.a.	n.a.
sin. m3	AMNH 39253	1981 XVII 14	16.8	7.6	n.a.	n.a.	n.a.
sin. m3	SNSB-BSPG 1956 II 2601	n.a.	16.1	7.5	10.3	0.63	R, S, T
sin. m3	SNSB-BSPG 1956 II 2490	n.a.	17.0	7.2	n.a.	n.a.	n.a.
sin. m3	SNSB-BSPG 1956 II 2503	n.a.	16.8	7.0	n.a.	n.a.	n.a.
sin. m3	SNSB-BSPG 1956 II 2496	n.a.	17.1	7.6	10.2	0.59	n.a.
sin. m3	SNSB-BSPG 1956 II 2629	n.a.	16.6	7.8	n.a.	n.a.	U, V, W
dex. m3	SNSB-BSPG 1956 II 2655	n.a.	15.9	6.8	n.a.	n.a.	n.a.
dex. D3	BM 19043	1961 XIX 38	12.9	7.1	n.a.	n.a.	n.a.
sin. D3	BM 19043	1961 XIX 38	14.4	7.4	n.a.	n.a.	n.a.
sin. D3	AMNH 39303	1981 XVII 13	12.0	6.5	n.a.	n.a.	n.a.
sin. D4	AMNH 39303	1981 XVII 13	9.9	8.8	n.a.	n.a.	n.a.
dex. D4	BM 19043	1961 XIX 38	9.9	9.2	n.a.	n.a.	n.a.
sin. D4	BM 19043	1961 XIX 38	10.7	8.7	n.a.	n.a.	n.a.
dex. D4	SNSB-BSPG 1956 II 2498	n.a.	10.1	9.0	n.a.	n.a.	J, K
sin. P2	SNSB-BSPG 1956 II 2536	n.a.	11.6	5.2	n.a.	n.a.	n.a.
dex. P2	SNSB-BSPG 1956 II 2536	n.a.	11.5	5.1	n.a.	n.a.	n.a.
sin. P3	SNSB-BSPG 1956 II 2485	n.a.	9.9	5.7	n.a.	n.a.	D, E, F
sin. P3	SNSB-BSPG 1956 II 2536	n.a.	11.2	6.4	n.a.	n.a.	n.a.
sin. P4	SNSB-BSPG 1956 II 2497	n.a.	8.1	9.4	n.a.	n.a.	G, H, I
sin. P4	SNSB-BSPG 1956 II 2484	n.a.	8.5	8.2	n.a.	n.a.	n.a.
sin. P4	SNSB-BSPG 1956 II 2536	n.a.	8.6	8.5	n.a.	n.a.	n.a.
sin. M1	AMNH 39303	1989 XVII 13	9.9	10.0	n.a.	n.a.	n.a.
sin. M1	BM 19043	1961 XIX 38	10.0	8.6	8.5	0.85	n.a.
sin. M1	SNSB-BSPG 1956 II 2480	n.a.	10.4	10.4	n.a.	n.a.	A, B, C
dex. M1	SNSB-BSPG 1956 II 2498	n.a.	10.6	10.9	8.9	0.84	J, K
dex. M1	AMNH 29856	1981 XVII 32	9.8	10.5	n.a.	n.a.	L, M, N
sin. M1	SNSB-BSPG 1956 II 2456	n.a.	10.5	n.a.	n.a.	n.a.	n.a.
sin. M2	SNSB-BSPG 1956 II 2456	n.a.	11.2	11.1	n.a.	n.a.	n.a.
dex. M2	SNSB-BSPG 1956 II 2536	n.a.	11.2	12.6	11.1	0.99	n.a.
sin. M2	SNSB-BSPG 1956 II 2536	n.a.	10.9	11.7	n.a.	n.a.	n.a.
dex. M2	SNSB-BSPG 1956 II 2469	n.a.	11.0	12.3	n.a.	n.a.	n.a.
dex. M2	AMNH 29856	1981 XVII 32	11.7	12.3	n.a.	n.a.	L, M, N
sin. M2	SNSB-BSPG 1956 II 2497	n.a.	11.7	13.1	n.a.	n.a.	G, H, I
sin. M2	SNSB-BSPG 1956 II 2480	n.a.	11.1	13.1	n.a.	n.a.	A, B, C
dex. M3	AMNH 29856	1981 XVII 32	11.3	13.0	n.a.	n.a.	L, M, N
dex. M3	SNSB-BSPG 1956 II 2536	n.a.	12.0	13.2	11.9	0.99	n.a.
sin. M3	SNSB-BSPG 1956 II 2536	n.a.	12.3	13.6	11.8	0.95	n.a.
dex. M3	SNSB-BSPG 1956 II 2469	n.a.	11.3	12.4	n.a.	n.a.	n.a.
dex. M2	Holotype No: 1301/GSI B195 (Pilgrim 1915)	n.a.	10.6	12.3	n.a.	n.a.	n.a.
dex. M3	Holotype No: 1301/GSI B195 (Lydekker 1876)	n.a.	11.0	10.0	n.a.	n.a.	n.a.

Table 5.4. Dental measurements and Hypsodonty Index for the specimens of *Dorcatherium nagrii* studied and type material. n.a.: not applicable.

Tooth	Catalogue number	SNSB-BSPG catalogue number cast	Length [mm]	Width [mm]	Height [mm]	Hypsodonty Index	Figure 5.10
sin. p3	SNSB-BSPG 1956 II 2569	n.a.	broken	2.9	n.a.	n.a.	G, H, I
sin. p4	SNSB-BSPG 1956 II 2455	n.a.	7.7	2.7	n.a.	n.a.	A, B, C
sin. m1	SNSB-BSPG 1956 II 2569	n.a.	6,5	3.7	n.a.	n.a.	G, H, I
dex. m1	AMNH 39508b	1981 XVII 71	6.5	2.9	n.a.	n.a.	n.a.
sin. m2	SNSB-BSPG 1956 II 2577	n.a.	7.7	3.5	n.a.	n.a.	D, E, F
dex. m2	AMNH 39508b	1981 XVII 71	6.8	3.7	n.a.	n.a.	n.a.
dex. m2	AMNH 19613	1981 XVII 68	8.0	4.6	n.a.	n.a.	n.a.
sin. m2	AMNH 39508c	1981 XVII 70	6.6	4.1	n.a.	n.a.	n.a.
sin. m3	SNSB-BSPG 1956 II 2569	n.a.	11.1	4.7	n.a.	n.a.	G, H, I
dex. m3	AMNH 39512	1981 XVII 75	12.5	5.4	4.7	0.38	n.a.
dex. m3	AMNH 19613	1981 XVII 68	10.9	4.7	n.a.	n.a.	n.a.
m1	Lectotype GSI No. 18079 (Prasad 1970)	n.a.	6.5	3.6	n.a.	n.a.	n.a.
m2	Lectotype GSI No. 18079 (Prasad 1970)	n.a.	6.6	4.0	n.a.	n.a.	n.a.
m3	Lectotype GSI No. 18079 (Prasad 1970)	n.a.	10.0	4.5	n.a.	n.a.	n.a.
M1	Paralectotype GSI No. 1801 (Prasad 1970)	n.a.	6.5	6.1	n.a.	n.a.	n.a.
M2	Paralectotype GSI No. 1801 (Prasad 1970)	n.a.	7.5	6.2	n.a.	n.a.	n.a.
M3	Paralectotype GSI No. 1801 (Prasad 1970)	n.a.	7.1	7.0	n.a.	n.a.	n.a.

Table 5.5. Dental measurements for *Dorcatherium* aff. *majus* studied here. n.a.: not applicable.

Tooth	Catalogue number SNSB - BSPG	Length [mm]	Width [mm]	Height [mm]	Figure 5.11
dex. M1	1956 II 2622	14.0	11.7	n.a.	A, B, C
dex. M2	1956 II 2622	14.7	14.7	n.a.	A, B, C
dex. M3	1956 II 2622	18.3	17.4	n.a.	A, B, C

Table 5.6. Dental dimensions and Hypsodonty Index for specimens of *Dorcatherium dehmi* sp. nov. n.a.: not applicable.

Tooth	Catalogue number	SNSB-BSPG catalogue number cast	Length [mm]	Width [mm]	Height [mm]	Hypsodonty Index	Figures 5.12, 5.13
sin. d4	AMNH 29887	1981 XVII 69	11,3	4.7	n.a.	n.a.	Y, Z, A´
sin. d4	SNSB-BSPG 1956 II 2633	n.a.	11,4	4.7	n.a.	n.a.	J, K, L
sin. m1	AMNH 29887	1981 XVII 69	9,1	4.9	n.a.	n.a.	Y, Z, A´
sin. m1	SNSB-BSPG 1956 II 2633	n.a.	9.3	4.8	n.a.	n.a.	J, K, L
sin. m1	AMNH 39304	1981 I 9	8.9	5.3	n.a.	n.a.	n.a.
sin. m1	AMNH 19368	1981 XVII 20	9.7	4.9	n.a.	n.a.	V, W, X
sin. m1	AMNH 19310	1981 XVII 34	8.7	5.1	n.a.	n.a.	P, Q, R

sin. m1	SNSB-BSPG 1956 II 2597	n.a.	9.7	5.1	n.a.	n.a.	n.a.
dex. m1	SNSB-BSPG 1956 II 2502	n.a.	9.4	5.0	n.a.	n.a.	n.a.
sin. m2	SNSB-BSPG 1956 II 2633	n.a.	10.7	6.1	8.8	0.82	J, K, L
sin. m2	AMNH 39304	1981 XVII 9	9.7	6.6	n.a.	n.a.	n.a.
sin. m2	AMNH 19368	1981 XVII 20	10.2	6.2	n.a.	n.a.	V, W, X
sin. m2	AMNH 19310	1981 XVII 34	10.3	6.2	n.a.	n.a.	P, Q, R
sin. m2	SNSB-BSPG 1956 II 2597	n.a.	10.7	6.1	n.a.	n.a.	n.a.
sin. m2	SNSB-BSPG 1956 II 2460	n.a.	9.9	6.1	n.a.	n.a.	n.a.
dex. m2	AMNH 19367	1981 XVII 35	10.4	5.7	n.a.	n.a.	S, T, U
dex. m2	SNSB-BSPG 1956 II 2461	n.a.	10.3	6.4	n.a.	n.a.	n.a.
dex. m2	SNSB-BSPG 1956 II 2502	n.a.	9.7	5.9	n.a.	n.a.	n.a.
sin. m3	AMNH 19310	1981 XVII 34	13.9	6.5	n.a.	n.a.	P, Q, R
sin. m3	SNSB-BSPG 1956 II 2479	n.a.	14.9	6.3	n.a.	n.a.	G, H, I
dex. m3	SNSB-BSPG 1956 II 2461	n.a.	14.6	6.5	n.a.	n.a.	n.a.
dex. m3	SNSB-BSPG 1968 XVIII 52	n.a.	15.2	6.5	n.a.	n.a.	M, N, O
dex. m3	AMNH 20043	1981 XVII 39	15.6	6.6	n.a.	n.a.	n.a.
dex. m3	AMNH 32588	1981 XVII 30	15.3	6.5	n.a.	n.a.	n.a.
dex. m3	AMNH 39304	n.a.	14.5	7.0	8.2	0.56	n.a.
dex. m3	AMNH 19367	n.a	n.a.	n.a	8.4	n.a.	S, T, U
sin. m3	AMNH 19368	n.a	n.a.	n.a	7.9	n.a.	V, W, X
sin. P4	Holotype SNSB-BSPG 1956 II 2615	n.a.	8.9	7.4	n.a.	n.a.	A, B, C
sin. M1	Holotype SNSB-BSPG 1956 II 2615	n.a.	8.6	9.0	n.a.	n.a.	A, B, C
dex. M1	SNSB-BSPG 1956 II 2470	n.a.	9.3	9.7	n.a.	n.a.	n.a.
sin. M2	Holotype SNSB-BSPG 1956 II 2615	n.a.	10.7	10.3	n.a.	n.a.	A, B, C
dex. M2	SNSB-BSPG 1956 II 2470	n.a.	10.8	11.0	n.a.	n.a.	n.a.
sin. M2	AMNH 29855	1981 XVII 11	10.9	10.3	n.a.	n.a.	D, E, F
dex. M3	SNSB-BSPG 1956 II 2470	n.a.	10.6	11.6	n.a.	n.a.	n.a.
sin. M3	AMNH 29855	1981 XVII 11	10.9	10.5	n.a.	n.a.	D, E, F
dex. M1	AMNH 19306	1981 XVII 12	8.7	10.1	n.a.	n.a.	n.a.
dex. M2	AMNH 19306	1981 XVII 12	9.2	11.0	n.a.	n.a.	n.a.
dex. M3	AMNH 19306	1981 XVII 12	n.a.	11.4	n.a.	n.a.	n.a.
sin. M2	SNSB-BSPG 1956 II 2600	n.a.	9.5	10.8	n.a.	n.a.	n.a.
sin. M3	SNSB-BSPG 1956 II 2600	n.a.	10.0	11.4	n.a.	n.a.	n.a.

Table 5.7. Dental measurements and Hypsodonty Index for the specimens of *Dorcatherium guntianum* from the Siwalik Group studied here and type material. n.a.: not applicable.

Tooth	**Catalogue number**	**SNSB – BSPG catalogue number cast**	**Length [mm]**	**Width [mm]**	**Height [mm]**	**Hypsodonty Index**	**Figure 5.14**
dex. m1	SNSB-BSPG1956 II 2554	n.a.	7.7	4.3	n.a.	n.a.	A, B, C
dex. m2	SNSB-BSPG1956 II 2554	n.a.	9.1	5.0	5.8	0.63	A, B, C
dex. m3	SNSB-BSPG1956 II 2554	n.a.	14.5	6.6	7.0	0.48	A, B, C
dex. m3	AMNH 29854	1981 XVII 26	12.7	5.7	n.a.	n.a.	D, E, F
d2	SNSB-BSPG1881 IX 740	Type series (Wetzler)	8.3	2.6	n.a.	n.a.	n.a.
d4	SNSB-BSPG1881 IX 738	Type series (Wetzler)	11.4	4.5	n.a.	n.a.	n.a.
m1	SNSB-BSPG1881 IX 735	Type series (Wetzler)	9.3	5.6	n.a.	n.a.	n.a.
m1	SNSB-BSPG1881 IX 737	Type series (Wetzler)	8.6	5.5	n.a.	n.a.	n.a.
m2	SNSB-BSPG1881 IX 731	Type series (Wetzler)	9.9	5.8	n.a.	n.a.	n.a.
m2	SNSB-BSPG1881 IX 736	Type series (Wetzler)	9.1	5.4	n.a.	n.a.	n.a.
m2	SNSB-BSPG1881 IX 737	Type series (Wetzler)	10.0	6.1	n.a.	n.a.	n.a.

m3	SNSB-BSPG1881 IX 737	Type series (Wetzler)	14.7	6.4	n.a.	n.a.	n.a.
D4	SNSB-BSPG1881 IX 733	Type series (Wetzler)	8.2	8.9	n.a.	n.a.	n.a.
D4	SNSB-BSPG1881 IX 647	Type series (Wetzler)	8.7	n.a.	n.a.	n.a.	n.a.
P3	SNSB-BSPG1881 IX 648b	Type series (Wetzler)	8.8	5.0	n.a.	n.a.	n.a.
P4	SNSB-BSPG1881 IX 648a	Type series (Wetzler)	7.9	8.1	n.a.	n.a.	n.a.
M1	SNSB-BSPG1881 IX 647	Type series (Wetzler)	8.7	9.5	n.a.	n.a.	n.a.
M2	SNSB-BSPG1881 IX 732	Type series (Wetzler)	9.9	10.5	n.a.	n.a.	n.a.
M2	SNSB-BSPG1881 IX47 i	Type series (Wetzler)	9.9	10.9	n.a.	n.a.	n.a.

Table 5.8. Dental measurements and Hypsodonty Index for the specimens of *Dorcatherium naui* from the Siwalik Group studied here and holotype. n. a.: not applicable.

Tooth	**Catalogue number**	**SNSB – BSPG catalogue number cast**	**Length [mm]**	**Width [mm]**	**Height [mm]**	**Hypsodonty Index**	**Figures 5.17, 5.18, 5.19**
sin. d3	SNSB-BSPG 1956 II 2584	n.a.	13.5	4.9	n.a.	n.a.	S, T, U
sin. d4	AMNH 39307	1981 XVII 36	13.6	5.3	n.a.	n.a.	n.a.
sin. d4	SNSB-BSPG 1956 II 2584	n.a.	14.9	5.7	n.a.	n.a.	S, T, U
sin. d4	GSI 235	n.a.	15.0	5.7	n.a.	n.a.	H´, I´, J´
sin. p3	AMNH 39305	1981 XVII 53	13.5	4.4	n.a.	n.a.	n.a.
dex. p3	AMNH 19609	1981 XVII 2	13.4	4.6	n.a.	n.a.	E´, F´, G´
dex. p4	AMNH 19609	1981 XVII 2	12.3	5.4	n.a.	n.a.	E´, F´, G´
dex. p4	SNSB-BSPG 1956 II 2656	n.a.	12.8	5.7	n.a.	n.a.	M, N, O
sin. p4	AMNH 39305	1981 XVII 53	broken	4.7	n.a.	n.a.	n.a.
dex. m1	AMNH 19609	1981 XVII 2	11.4	7.6	n.a.	n.a.	E´, F´, G´
sin. m1	GSI 235	n.a.	12.6	6.9	n.a.	n.a.	H´, I´, J´
sin. m1	AMNH 39305	1981 XVII 53	11.4	6.7	n.a.	n.a.	n.a.
dex. m1	SNSB-BSPG 1956 II 2570	n.a.	12.3	6.8	n.a.	n.a.	P, Q, R
sin. m1	AMNH 39307	1981 XVII 36	11.2	6.3	n.a.	n.a.	n.a.
sin. m1	SNSB-BSPG 1956 II 2486	n.a.	12.7	7.4	n.a.	n.a.	n.a.
sin. m2	AMNH 39305	1981 XVII 53	13.7	8.7	n.a.	n.a.	n.a.
dex. m2	AMNH 19609	1981 XVII 2	13.2	9.0	n.a.	n.a.	E´, F´, G´
sin. m2	AMNH 19365	1981 XVII 3	12.8	7.2	n.a.	n.a.	B´, C´, D´
dex. m2	SNSB-BSPG 1956 II 2570	n.a.	13.8	8.3	n.a.	n.a.	P, Q, R
dex. m2	AMNH 39262	1981 XVII 49	14.7	8.4	n.a.	n.a.	n.a.
dex. m2	SNSB-BSPG 1956 II 2585	n.a.	13.3	8.1	n.a.	n.a.	V, W, X
sin. m3	AMNH 19365	1981 XVII 3	17.5	7.7	n.a.	n.a.	B´, C´, D´
dex. m3	AMNH 19609	1981 XVII 2	20.0	9.5	n.a.	n.a.	E´, F´, G´
dex. m3	AMNH 39262	1981 XVII 49	20.1	9.2	n.a.	n.a.	n.a.
sin. m3	SNSB-BSPG 1956 II 2463	n.a.	18.3	7.7	n.a.	n.a.	n.a.
dex. m3	SNSB-BSPG 1956 II 2572	n.a.	19.5	9.0	n.a.	n.a.	n.a.
sin. m3	SNSB-BSPG 1956 II 2582	n.a.	n.a.	8.1	9.1	n.a.	n.a.
sin. m3	SNSB-BSPG 1956 II 2587	n.a.	19.4	9.0	11.0	0.56	Y, Z, A´
dex. m3	SNSB-BSPG 1956 II 2468	n.a.	20.0	8.6	n.a.	n.a.	n.a.
sin. m3	AMNH 32742	1981 XVII 4	18.9	7.9	10.0	0.52	n.a.
sin. D4	AMNH 19517	1981 XVII 15	11.4	9.7	n.a.	n.a.	G, H, I
sin. D4	AMNH 39308	1981 I 8	10.7	9.9	n.a.	n.a.	J, K, L
sin. M1	AMNH 19517	1981 XVII 15	11.7	11.2	n.a.	n.a.	G, H, I
sin. M1	AMNH 39308	1981 I 8	11.9	11.8	n.a.	n.a.	J, K, L
dex. M1	SNSB-BSPG 1956 II 2568	n.a.	11.7	11.0	n.a.	n.a.	A, B, C
dex. M2	SNSB-BSPG 1956 II 2568	n.a.	13.2	13.6	n.a.	n.a.	A; B; C

sin. M2	AMNH 19313	1981 XVII 5	13.6	14.1	n.a.	n.a.	D, E; F
dex. M3	SNSB-BSPG 1956 II 2568	n.a.	13.7	13.8	10.7	0.78	A, B, C
sin. M3	AMNH 19313	1981 XVII 5	13.8	14.3	n.a.	n.a.	D, E, F
dex. p3	BM M3714 Holotype	1961 XIX 37	12.4	4.9	n.a.	n.a.	n.a.
dex. p4	BM M3714 Holotype	1961 XIX 37	12.6	5.9	n.a.	n.a.	n.a.
dex. m1	BM M3714 Holotype	1961 XIX 37	11.9	7.5	n.a.	n.a.	n.a.
dex. m2	BM M3714 Holotype	1961 XIX 37	12.8	8.7	n.a.	n.a.	n.a.
dex. m3	BM M3714 Holotype	1961 XIX 37	19.1	9.6	n.a.	n.a.	n.a.

CURRICULUM VITAE

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Education

2001-2004. BSc Biological Sciences, Universidad Arturo Prat, Iquique Chile. Facultad de Recursos Naturales, Departamento de Biología y Biología Marina. Monograph tittle: Habit, distribution and food habit of *Orestias agassi* in the north of Chile (original title in Spanish). Supervisor, Prof. Walter Sielfeld Kowald

2001-2005. Degree in Biological Sciences. Universidad Arturo Prat, Iquique Chile. Facultad de Recursos Naturales, Departamento de Biología y Biología Marina.

2006-2009. MSc Zoology, Universidad de Concepción, Departamento de Zoología, Facultad de Ciencias Naturales y Oceanográficas. Concepción – Chile. Project title: Systematics of the genera *Aconaemys* and *Spalacopus* (Rodentia, Hystricognathi, Octodontidae): Genera and limit of species. Supervisor, Dr Guillermo D’Elía Vargas

Since April 2015 PhD candidate, Ludwig-Maximilians-University, Faculty of Geosciences Department of Earth and Environmental Sciences, Munich Germany.

Since April 2015 researcher at the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany

Academic position:

Since 2008 lecturer for Evolution and Zoology at the Universidad de Concepción, Concepción-Chile.

Grants:

Since 2014 – 2019. Scholar CONICYT – Chile (National Commission for Science and Technology); scholar DAAD-Germany (Deutscher Akademischer Austauschdients) and scholar Universidad de Concepción, Concepción-Chile.

Scientific articles:

Guzmán, J. A. and G. E. Rössner. 2019. Miocene chevrotain (Mammalia, Artiodactyla, Tragulidae) from Pakistan. Historical Biology. https://doi.org/10.1080/08912963.2019.1661405

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Scientific meeting: (Summarized)

Cañón, C. J. A. Guzmán and U. F. J. Pardiñas. 2018. Systematics of an Andean akodontine, *Akodon mimus* (Cricetidae, Sigmodontinae): insights from molecular markers. 6th

International Conference of Rodent Biology and Management & 16th Rodent et Spatium. 3 – 7.09. Postdam, Germany.

Guzmán, J. A. N. Espinoza and N. Verdugo. 2018. Predation by *Rattus rattus* on the hantavirus reservoir *Oligoryzomys longicaudatus* (El Laja National Park, south of Chile.

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Guzmán, J. A. and G. Rössner. 2016. *"*Mouse-deer (mammalia, Artiodactyla, Tragulidae) diversity in the past and the present: lessons from fossils*"*. 17th Annual Meeting of the Gesellschaft für Biologische Systematic (GfBS 2016). Ludwig Maximilians Universität, Munich, 21 to 24.04.2016.

Guzmán, J. A. and G. Rössner. 2016. Taxonomical revision of the chevrotains or mouse-deer (Tragulidae) from collection material". 43. Arbeitskreistreffen Wirbeltierpaläontologie. Urweltmuseum GEOSKOP / Burg Lichtenberg (Pfalz), 11 to 13.03.2016.

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Guzmán, J. A., M. Vidal and J.C. Ortiz. 2009. Skull morphometric differences associated to diet in the Patagonian foxes *Lycalopex culpaeus* and *L. griseus.* 10th International Mammalogical Congress. Mendoza - Argentina, 9-14 August 2009.

Research projects

2013-2015. Principal investigator of the project: The effect of exotic rodent on the native fauna of Laguna del Laja Nacional Park (original title in Spanish). Project of Research Office of the Universidad de Concepcion, Chile

2011-2013. Principal investigator of the project: The genetics legacy of the Last Glacial Maximun (LGM) on the species of *Oligoryzomys longicaudatus* in the southern Patagonia in Chile. Project of Research Office of the Universidad de Concepcion, Chile

2010. Co-investigator of the Project: The *Atelognathus* genus in Chile: an ecophysiological study in the Chilean Patagonia. Project of Research Office of the Concepción University (DIUC N° 20090652).

2008**.** Co-Investigator of the project: Rodents, glaciers and gene trees patterns and processes of diversification of small mammals in southern South America (FONDECYT N°11070157).

Workshop Attended

- 3D Visualization AMIRA Software course. Faculty of Biology, Ludwig_Maximilians-Universität, München. From May to October 2017. Speaker: Timea Neusser. AG: Gerhard Hazsprunar.

- Course Evolution of Mammals. Ludwig-Maximilians-University, Faculty of Geosciences Department of Earth and Environmental Sciences, Munich Germany. 4th to 8th April 2016 (full-time). Speaker: Gertrud Rößner

- Micro-Ct applications on fossil studies. Zoologische Staatssammlung München (ZSM). 25th and 26th June 2015.