

Anatomy, Sexual Dimorphism, and Ontogeny of the Tragulid Skull

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Summary

Fossil tragulids are small ruminant artiodactyls characterized by large saber-like upper canines and a stout body. Although they have existed since the late Eocene and display considerable morphological diversity, their evolutionary history and biology remain poorly understood. The genus *Dorcatherium* is particularly affected by taxonomic uncertainty, with many species historically placed in a wastebasket taxonomy. This thesis aims to clarify the taxonomy and paleobiology of the type species of *Dorcatherium*, *D. nauti*. The study is based on complete and partial skulls from the middle to late Miocene locality of Eppelsheim and the earliest late Miocene locality of Hammerschmiede (Germany), complemented by comparative material of the closely related extant tragulid *Hyemoschus aquaticus*. For the first time, the cranial morphology of *D. nauti* is described in detail, allowing the identification of diagnostic autapomorphies independent of dental characters. Comparative analysis reveals a previously unknown sexual dimorphism in cranial ornamentation, with more strongly developed cranial crests in males. Moreover, using 13 skulls from Hammerschmiede, an ontogenetic series based on dental wear stages was established using modern *H. aquaticus* as an analogue, enabling comparisons at similar developmental stages supported further by μ CT data. The results indicate that cranial ornamentation in fossil tragulids was markedly more pronounced and sexually dimorphic than in extant forms, with males of *D. nauti* exhibiting strongly developed cranial crests. In contrast, males and females of the extant *H. aquaticus* display largely similar cranial morphology. Taken together, this pattern suggests a paedomorphic reduction of cranial ornamentation in living tragulids and implies differences in male combat behavior. Comparative ontogenetic analyses further show that the development of cranial ornamentation coincides with the onset of sexual maturity in extant tragulids. By analogy, a similar onset of sexual maturity is inferred for *Dorcatherium nauti*, based on the comparable development of cranial crests observed in similar ontogenetic stages. Beyond cranial morphology, a large comparative dataset of isolated teeth and mandibles from Hammerschmiede was used to investigate body size differences, mortality patterns, and survivorship at the population level. These analyses indicate a survivorship pattern consistent with a litter size of one offspring, comparable to that of the extant *H. aquaticus*. A difference in body size between the fossil and extant tragulid was noticed leading to the conclusion that *D. nauti* might have lived in more open riparian woodlands compared to *H. aquaticus*, who lives in dense undergrowth of the African rainforests. Overall, this thesis provides the first integrative taxonomic and paleobiological framework for *Dorcatherium nauti* and establishes a robust comparative basis for future studies on fossil tragulids, their life-history evolution, and phylogenetic relationships.

Zusammenfassung

Fossile Traguliden sind kleine Wiederkäuer innerhalb der Ordnung der Paarhufer (Artiodactyla) und zeichnen sich durch große, säbelartige obere Eckzähne sowie einen stämmigen Körperbau aus. Erste Fossilnachweise sind aus dem späten Eozän bekannt, und ihre evolutionäre Geschichte ist durch eine ausgeprägte morphologische Vielfalt gekennzeichnet. Trotz ihrer langen geologischen Überlieferung ist bislang nur wenig über die Biologie und Lebensweise fossiler Traguliden bekannt. Die Gattung *Dorcatherium* stellt die häufigste fossile Tragulidengattung Europas dar und umfasst zugleich die größte Anzahl beschriebener Arten. Dennoch ist ihre interne Taxonomie stark umstritten, da zahlreiche Arten historisch im Rahmen einer sogenannten „Wastebasket“-Taxonomie zusammengefasst wurden. Vor diesem Hintergrund widmet sich die vorliegende Arbeit zunächst der Taxonomie der Gattung und in einem zweiten Schritt der paläobiologischen Untersuchung der Typusart *Dorcatherium navi*. Die Studie basiert auf vollständigen und teilerhaltenen Schädeln aus den miozänen Fundstellen von Eppelsheim und Hammerschmiede (Deutschland) und wird durch vergleichendes Material des rezenten nah verwandten Traguliden *Hyemoschus aquaticus* ergänzt. Erstmals wird die Schädelmorphologie von *Dorcatherium navi* detailliert beschrieben, wodurch es möglich war, diagnostische Autapomorphien unabhängig von dentalen Merkmalen zu identifizieren. Vergleichende Analysen belegen eine bislang unbekannte sexuelle Dimorphie der Schädelornamentik, wobei männliche Individuen deutlich stärker ausgeprägte craniale Kämme aufweisen. Auf Grundlage von Zahnabnutzungsstadien wurde unter Verwendung des rezenten Traguliden *Hyemoschus aquaticus* als modernes Analogon eine ontogenetische Serie etabliert, die Vergleiche auf Ebene der Entwicklungsstadien unter Einbeziehung von μ CT-Daten ermöglicht.

Die Ergebnisse zeigen, dass die Schädelornamentik bei fossilen Traguliden deutlich stärker ausgeprägt und sexuell dimorph war als bei rezenten Formen, bei denen Männchen und Weibchen von *H. aquaticus* weitgehend ähnliche craniale Merkmale aufweisen. Dieses Muster deutet insgesamt auf eine paedomorphe Reduktion der Schädelornamentik bei rezenten Traguliden hin und lässt auf Unterschiede im männlichen Kampfverhalten zwischen fossilen und rezenten Vertretern schließen. Ontogenetische Analysen belegen zudem, dass die Ausbildung der Schädelkämme bei rezenten Traguliden mit dem Eintritt der Geschlechtsreife übereinstimmt. In Analogie hierzu wird für *D. navi* basierend auf der Ausbildung der hier vorhandenen Schädelkämme in vergleichbaren ontogenetischen Stadien ein ähnlicher Beginn der Geschlechtsreife und angenommen. Dies deutet auf ähnliche lebensgeschichtliche Entwicklungsverläufe bei fossilen und rezenten Traguliden

hin. Über die Schädelmorphologie hinaus wurde ein umfangreicher Datensatz isolierter Zähne und Mandibeln aus der Hammerschmiede Fundstelle herangezogen, um Körpermassemessungen, Mortalitätsmuster und Überlebensraten auf Populationsebene zu analysieren. Die Ergebnisse zeigen einen Unterschied in der Körpermasse zwischen *D. nauti* und *H. aquaticus* und könnten darauf zurückzuführen sein, dass *D. nauti* in offeneren Habitaten gelebt hat, wie z.B. offenen Uferwäldern im Vergleich zu *H. aquaticus* der im Dickicht des Africanischen Regenwaldes lebt. Weiterhin weisen die Ergebnisse auf eine Überlebensstruktur hin, die mit einer Wurfgröße von einem Jungtier übereinstimmt und damit mit derjenigen des rezenten *H. aquaticus* vergleichbar ist. Zusammenfassend liefert diese Arbeit erstmals einen integrativen taxonomischen und paläobiologischen Rahmen für *D. nauti* und schafft eine vergleichende Grundlage für zukünftige Untersuchungen zur Lebensgeschichte fossiler Traguliden sowie zu deren phylogenetischen Beziehungen.

List of Publications

Publications included in this thesis

The following two articles and one manuscript in submission where published ordered by date of publication.

- I) **Hartung, J.** and M. Böhme. Unexpected cranial sexual dimorphism in the tragulid *Dorcatherium nauti* based on material from the middle to late Miocene localities of Eppelsheim and Hammerschmiede (Germany). *Plos one* 17.5 (2022): e0267951.
- II) **Hartung, J.** and M. Böhme. Cranial ontogenetic development and sexual dimorphism of the extant water chevrotain *Hyemoschus aquaticus*. *Mammalian Biology* 105.2 (2025): 191-200.
- III) **Hartung, J.** and M. Böhme. Ontogenetic skull development and paleobiology of the tragulid *Dorcatherium nauti* (Mammalia: Artiodactyla) from the early Late Miocene hominid locality Hammerschmiede (Germany). Submitted to *Mammalian Evolution* on the 04th of March 2026



Erklärung nach § 5 Abs. 2 Nr. 8 der Promotionsordnung der Math.-Nat. Fakultät

-Anteil an gemeinschaftlichen Veröffentlichungen-

Bei kumulativen Dissertationen erforderlich!

**Declaration according to § 5 Abs. 2 No. 8 of the Doctoral Regulations of the
Faculty of Science**

-Contributions to Collaborative Publications-

Required for Cumulative Theses!

Last Name, First Name: Hartung, Josephina

List of Publications (Please list title, all authors, journal, year)

1. Unexpected cranial sexual dimorphism in the tragulid *Dorcatherium nauti* based on material from the middle to late Miocene localities of Eppelsheim and Hammerschmiede (Germany), Josephina Hartung and Madelaine Böhme, Plos One, 2022
2. Cranial ontogenetic development and sexual dimorphism of the extant water chevrotain *Hyemoschus aquaticus*, Josephina Hartung and Madelaine Böhme, Mammalian Biology, 2024
3. Ontogenetic skull development and paleobiology of the tragulid *Dorcatherium nauti* (Mammalia: Artiodactyla) from the early Late Miocene hominid locality Hammerschmiede (Germany), Josephina Hartung and Madelaine Böhme, Submitted to Mammalian Evolution, date of submission: 04.03.2026

Nr.	Accepted manuscript (peer-reviewed) yes/no	No of authors	Position of candidate in list of authors	Scientific ideas by the candidate (%)	Data generation or/and programming by the candidate (if applicable) (%)	Analysis/ interpretation/ technical work by the candidate (if applicable) (%)	Paper writing done by the candidate (%)
1	yes	2	1	80	90	90	90
2	yes	2	1	90	90	95	90
3	yes	2	1	70	70	80	80

This table can/should be supplemented with suitable continuous text if required.

I confirm that the above-stated is correct.

Date, Signature of the candidate

I/We certify that the above-stated is correct.

Date, Signature of the doctoral committee or at least of one of the supervisors

Publications not included in this thesis that were published during the PhD

The following list includes all articles and book chapters that were published during the PhD but are not included in this thesis ordered by date of publication.

- I) **Hartung, J.**, T. Lechner, and M. Böhme. New cranial material of *Miotragocerus monacensis* (Mammalia: Bovidae) from the late Miocene hominid locality Hammerschmiede (Germany). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 298 (2020): 269-284.
- II) **Hartung, J.**, P.M. Sander, M. Friedman, and T. Wintrich. First record of mawsoniid coelacanths (Actinistia, Sarcopterygii) from the marine Rhaetian (Upper Triassic) of Bonenburg, Germany. *Journal of Vertebrate Paleontology* 41 (2021): e1931258.
- III) **Hartung, J.**, F.J. Augustin, P. Kampouridis, and D. Chure. A unique notostracan trace fossil assemblage from the Upper Triassic Chinle Formation (northeastern Utah, USA) and its paleoecological and paleoenvironmental implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 583 (2021): 110667.
- IV) Kampouridis, P., **J. Hartung**, G.S. Ferreira, and M. Böhme. Reappraisal of the late Miocene elasmotheriine *Parelasmotherium schansiense* from Kutschwan (Shanxi Province, China) and its phylogenetic relationships. *Journal of Vertebrate Paleontology* 41 (2021): e2080556.
- V) Klein, F., L. Costeur, G.S. Ferreira, and **J. Hartung**. The bony labyrinth of the Miocene boselaphin bovid *Miotragocerus pannoniae*: insights into ontogeny. *Journal of Vertebrate Paleontology* 42 (2022): e2153226
- VI) Augustin, F.J., P. Kampouridis, **J. Hartung**, R. Albersdörfer, and A.T. Matzke. The geologically oldest specimen of Pterodactylus: a new exquisitely preserved skeleton from the Upper Jurassic (Kimmeridgian) Plattenkalk deposits of Painten (Bavaria, Germany). *Fossil Record* 25 (2022): 331-343.
- VII) Kampouridis, P., **J. Hartung**, and M. Böhme. Large mammals from the late Middle Miocene of Markt Rettenbach (Bavaria, Germany). *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* (2022): 299-312.
- VIII) Kampouridis, P., **J. Hartung**, F.J. Augustin, H. El Atfy, and G.S. Ferreira. Dental eruption and adult dentition of the enigmatic ptolemaiid *Qarunavus meyeri* from the Oligocene of the Fayum Depression (Egypt) revealed by micro-computed tomography clarifies its phylogenetic position. *Zoological Journal of the Linnean Society* 199 (2023): 1078-1091.

- IX) Augustin, F.J., **J. Hartung**, and P. Kampouridis. Dinosaur faunas of Egypt—the terrestrial late cretaceous vertebrate record. *The phanerozoic geology and natural resources of Egypt*. Cham: Springer International Publishing, 2023. 253-284.
- X) Augustin, F.J., M. Rabi, F. Spindler, P. Kampouridis, **J. Hartung**, R. Alberdörfer, and A.T. Matzke. A new specimen of *Solnhofia parsonsi* from the Upper Jurassic (Kimmeridgian) Plattenkalk deposits of Painten (Bavaria, Germany) and comments on the relationship between limb taphonomy and habitat ecology in fossil turtles. *Plos one* 18 (2023): e0287936.
- XI) Kargopoulos, N., P. Kampouridis, **J. Hartung**, and M. Böhme. Hyaenid remains from the Late Miocene of Kutschwan (Shanxi Province, China). *PalZ* 97 (2023): 653-666.
- XII) Kampouridis, P., M. Ataabadi, **J. Hartung**, and F.J. Augustin. The easternmost occurrence of the Late Miocene schizotheriine chalicothere *Ancylotherium pentelicum* at the classical locality of Maragheh (Iran). *Journal of Mammalian Evolution* 31 (2024): 36.
- XIII) Kampouridis, P., **J. Hartung**, T. Lechner, N. Kargopoulos, and M. Böhme. Disparate occurrences of a chalicotheriine and a schizotheriine chalicothere (Mammalia, Chalicotheriidae) at the Late Miocene hominid locality Hammerschmiede (Germany). *PalZ* 98 (2024): 313-329.
- XIV) Sander, P.M., J. Gravendyck, J. Hack, **J. Hartung**, J. Heijne, R. Kindlimann, D. Konietzko-Meier, T. Lamsfuß, D. Nau, M. Perillo, A. Prino, T. Schaaf, A. H. Schwermann. Late middle Rhaetian vertebrates from Exter Formation bone beds of Bonenburg (Westphalia, Germany): Implications for the end-Triassic extinction event. *Geologie und Paläontologie in Westfalen* 99 (2026) in press

1 Introduction

The Miocene (23.04–5.33 Ma) represents the first epoch of the Neogene and was characterized by a progressive cooling of the global climate toward the Pliocene. During the Miocene, Afro-Arabia collided with the Eurasian continent, leading to the formation of land bridges that facilitated large-scale faunal exchanges, for example among proboscideans. In the Late Miocene, the connection between the Atlantic Ocean and the Mediterranean Sea closed, leading to a drastic desiccation of large parts of the Mediterranean basin. Due to this evaporation, this event is known as the Messinian Salinity Crisis (Jolivet et al. 2006; van der Made et al. 2006; Hou and Li 2017). The collision of the Afro-Arabian plate with Eurasia resulted in the Alpine orogeny and the concurrent development of the Molasse foreland basin, which was infilled with sediments eroded from the growing Alpine chain. The Molasse is classically divided into the Lower Marine Molasse, Lower Freshwater Molasse, Upper Marine Molasse, and Upper Freshwater Molasse, reflecting alternating marine and continental depositional environments (Doppler 1989; Doppler et al. 2005).

The Miocene climate experienced multiple shifts, from the Mid-Miocene Climatic Optimum (~17–15 Ma) with warmer wetter conditions to progressive cooling in the Late Miocene, which influenced the expansion of open woodlands and grasslands in Central Europe (Zachos et al. 2001). Central Europe was likely characterized by a mosaic of forested and more open habitats, although precise reconstructions remain challenging due to regional variations and incomplete fossil records. Pollen and plant macrofossil evidence suggest that subtropical to warm-temperate forests dominated in the Early and Middle Miocene, gradually giving way to more open woodland and mixed environments in the Late Miocene. Climatic conditions appear to have shifted from relatively warm and humid during the Mid-Miocene Climatic Optimum to progressively cooler and drier conditions toward the end of the epoch. These environmental changes likely influenced the distribution and composition of faunal communities, including early tragulids as well as other vertebrate groups, although the exact extent and timing of these shifts in Central Europe remain subject to ongoing research (Kovar-Eder et al. 2001; Worobiec and Worobiec 2019; Böhme et al. 2021; Hofmann and Sachse 2023).

The family Tragulidae was one of the groups that diversified during the Middle to Late Miocene (Rössner 2007; Khan and Akhtar 2013; Rössner and Heissig 2013; Koufos 2020; Guzmán and Rössner 2021; Hartung and Böhme 2022). They originated during the Eocene and have a long fossil history (Métais et al. 2007; Rössner 2007; Hassanin et al. 2012; Sánchez et al. 2018; Mennecart et al. 2021). Despite this long temporal range, the fossil record only reports of few skulls and no articulated skeletons, thus the taxonomy of tragulids

is mainly based on isolated teeth and postcranial material. Consequently, the phylogenetic relationships within Tragulidae remain largely unresolved. In particular, the genus *Dorcatherium* has often functioned as a “wastebasket taxon,” accommodating a variety of fossil species, which has hindered detailed evolutionary and ecological interpretations.

1.1 Aim of study and objectives

Tragulids are an enigmatic group of ruminants and are considered the worlds’ smallest living artiodactyls. However, fossil relatives seem to be quite different e.g. in body size, but also in morphology of the skull and apparently in certain life history traits. In this dissertation I will study several skulls as well as isolated teeth and mandibles of the type species of *Dorcatherium*, *D. naui* from the hominid locality Hammerschmiede in southern Germany and Eppelsheim in south-western Germany and the closely related extant *Hyemoschus aquaticus* from the collection in Tervuren, Brussels. *H. aquaticus* and *D. naui* are frequently recovered as sister taxa in phylogenetic studies (Sánchez et al. 2015; Sánchez et al. 2018) and *H. aquaticus* is frequently used as modern analogue to fossil tragulids. The herein studied fossil skulls will be compared to the other extant taxa of tragulids namely *Tragulus* and *Moschiola* and the closely related fossil *Dorcabune crassum*, which was previously also assigned to *Dorcatherium*, of which also three skulls are published already. The following topics will be examined and discussed in this dissertation:

- (I) Sexual dimorphism in tragulids and reporting and describing the first case of cranial sexual dimorphism in fossil tragulids
- (II) Taxonomic complexity within *Dorcatherium* and the establishment of diagnostic characters for the type species *D. naui*
- (III) Evaluation of the use of *Hyemoschus aquaticus* as a modern analogue for *Dorcatherium naui* by means of comparative cranial and ontogenetic analyses
- (IV) Establishment of a wear stage–based age categorization for *Hyemoschus aquaticus* in order to facilitate direct comparisons of ontogenetic trajectories between fossil and extant tragulids
- (V) Establishment of a cranial ontogenetic series based on skulls of *D. naui* and comparison to data collected for *Hyemoschus aquaticus*
- (VI) Paleoecology of *D. naui* and reconstruction of body size measurements, population analysis, and life history traits of *D. naui* in comparison to *Hyemoschus aquaticus*

Moreover, paleontologists have traditionally distinguished juvenile and adult stages in fossil taxa based on the eruption of the third molar (M3), assuming that individuals reach sexual maturity by the time the M3 erupts. Based on the large data set presented within this thesis, this assumption is tested for *Hyemoschus aquaticus* and *Dorcatherium naui* following the approach of Asher and Lehmann (2008).

1.2 Taxonomy and biology of extant tragulids

Tragulids are ruminants and the sister group to Pecora, who are wearing head gear (Fig. 1). Tragulids don't possess an omasum for water-and nutrient intake (Chen et al. 2019b). Today, tragulids comprise three genera, *Hyemoschus*, who lives in the rainforests of Africa, *Moschiola* in Ceylon, India, and possibly Nepal, and *Tragulus*, who lives in Southeast Asia on the mainland as well as on many islands. The genus *Hyemoschus* is monospecific and contains *H. aquaticus* and *Tragulus* comprises most of the living tragulid species (Smit-van Dort 1989; Meijaard and Groves 2004; Groves and Meijaard 2005; Groves and Grubb 2011; Meijaard 2011; Meijaard et al. 2017; Guzmán and Rössner 2018). *Moschiola* and *Tragulus* share a rather complicated taxonomic history and several species were revised and reassigned in the past years (Meijaard and Groves 2004; Groves and Meijaard 2005). A comprehensive and up-to-date discussion of the taxonomic issues concerning *Tragulus* and *Moschiola* is provided by Guzmán and Rössner (2018). *Tragulus* and *Moschiola* differ from each other in skull morphology, the configuration of the metacarpals and metatarsals, as well as in fur coloration and body size, which clearly supports the validity of their generic distinction. However, the delimitation at the species level has been highly debated throughout the last century, and numerous species have since been erected, reassigned, or revised.

For *Tragulus*, the most comprehensive and recent work by Meijaard and Groves (2004) point at three species groups, *T. napu*, *T. kanchil*, and *T. javanicus* (two Indo-Malayan species and one Indian-Sri Lankan species, e.g. Smit-van Dort 1988, 1989; Corbet and Hill 1992; Endo et al. 2004; Meijaard and Groves 2004; Groves and Meijaard 2005). One group comprises mainly small tragulids and is named *T. javanicus*-group including *T. javanicus* (from Java, Fig. 2), *T. williamsoni* (from northern Thailand and possibly southern China), *T. kanchil* (from southern China (Yunnan) to the Malayan Peninsula and Islands like Sumatra and Borneo, as well as smaller islands), and 16 subspecies. Within the *T. napu*-group mainly large tragulids are included and there are two species comprised such as *T. nigricans* (from Balabac), *T. napu* (from the rest of the range), as well as eight subspecies.

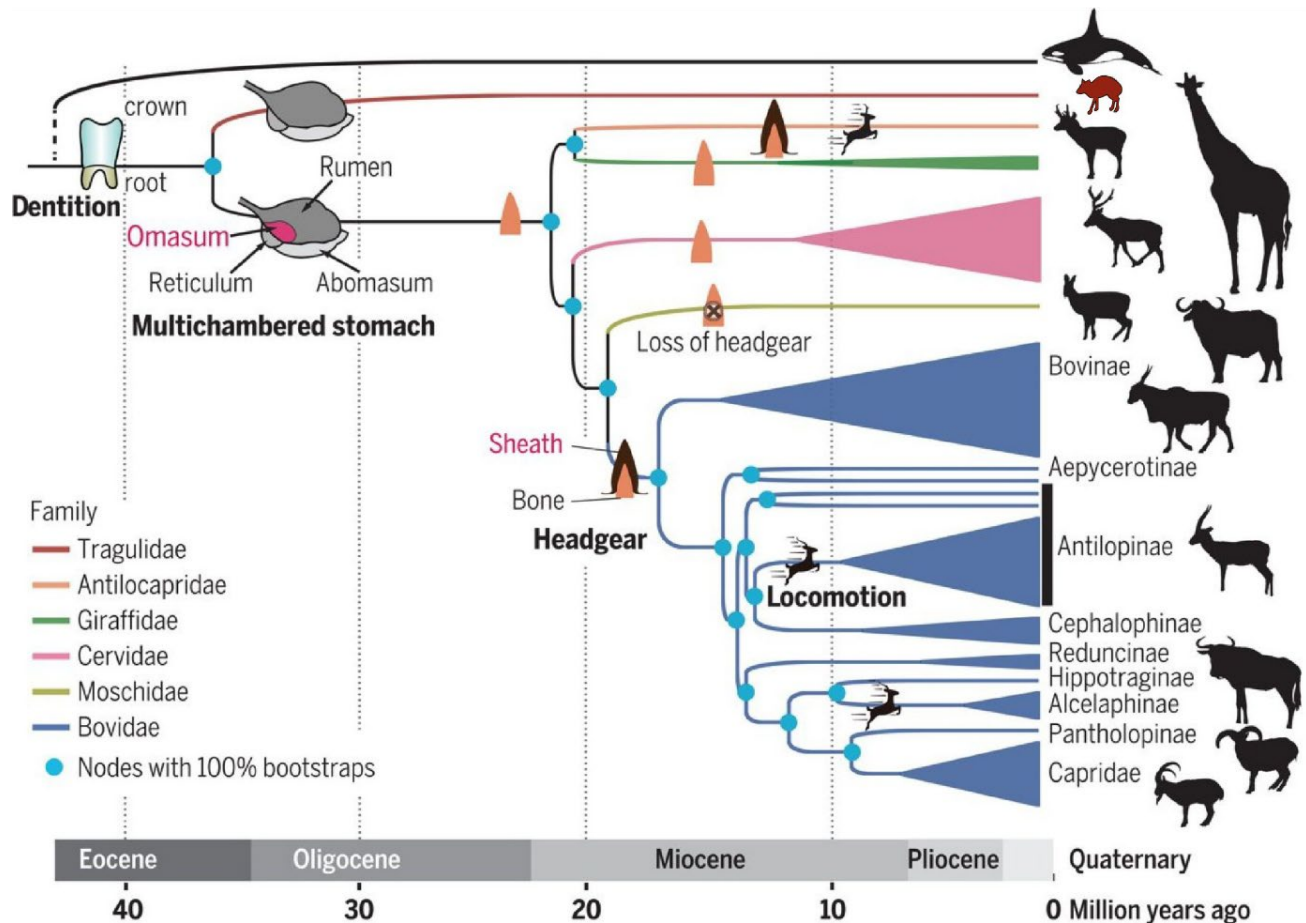


Figure 1: Phylogeny of ruminants modified from Chen et al. (2019b) Large-scale ruminant genome sequencing provides insights into their evolution and distinct traits. Science 364: 1152. Reprinted with permission from AAAS. Tragulidae are marked in red. They don't share the Omasum. They are the sister group to Pecora

At present, there are seven species recognized: *T. javanicus* (only in Java), *T. williamsoni* (Northern Thailand, but also southern China (Meijaard et al. 2017), *T. kanchil* and *T. napu* (both in Southeast Asia but not in Java), *T. nigricans* (Philippines), as well as *T. versicolor* (southern Vietnam); it was, however, until recently unclear whether this species is still extant (Meijaard and Groves 2004), but Chen et al. (2019a) stated that it has a very limited geographical distribution and faces many threats of extinction. In *Moschiola* there are three to four species present, with the fourth species not being entirely described yet. *M. indica*, who lives in southern India, *M. meminna* from the dry zone of Sri Lanka, and *M. kathygre* from the wet zone of Sri Lanka (Meijaard and Groves 2004; Groves and Meijaard 2005).



Figure 2: *Tragulus javanicus* from Java at Wilhelma Zoological and Botanical Garden, Stuttgart. **A)** Male and female; note the enlarged canines of the male **B)** Male in water **C)** Male foraging for food, including vegetables and fruits **D)** Male feeding on vegetables and fruits

Tragulids are considered the worlds' smallest artiodactyls. They are characterized by a comparatively small body size among ruminants and a generally compact, thickset build, arched back with long hind limbs, shorter forelimbs and a short tail. The fur is short and ranges in coloration from uniform brown to mottled patterns with dark markings (Smit-van Dort 1988, 1989; Meijaard and Groves 2004). At present, studies on the biology of tragulids are relatively scarce, and most available information focuses on *Tragulus* and, to a lesser extent, on *Hyemoschus*. Tragulids live nocturnal in the dense undergrowth of forests. Their body form is perfectly adapted for hiding and fleeing beneath dense vegetation. They are common prey for many predators and protect themselves by resting in low tree branches during the day, being active at night, and by the camouflage provided by their fur (Rössner 2007). *Hyemoschus* exhibits a unique behavior: when pursued by a predator, it flees into water and therefore always inhabits areas close to water (Dubost 1978; Meijaard et al. 2010). It hides beneath aquatic vegetation or under overhanging riverbanks and tree roots. Dubost (1978) described *Hyemoschus* as occupying a particularly distinct ecological niche, as it is a forest-dwelling, frugivorous, terrestrial yet aquaphilous, small-sized, and nocturnal species. Compared to *Tragulus* and *Moschiola*, some species of which prefer wetter or drier environments within densely vegetated habitats, *Hyemoschus* shows a remarkably

specialized behavioral ecology. However, Meijaard et al. (2010) reported that some Asian species have also retained aquatic behavior, particularly as a strategy to avoid predators. Hence, certain tragulid species may be more aquaphilous than previously assumed. Tragulids are considered so called “concentrate-selectors”. They eat mainly easily digestible, forage providing food that is high in protein like fruit and seeds, flowers, leaves, shoots, petioles, as well as stems and mushrooms (Dubost 1984). *Hyemoschus* was spotted to even eat fish as it also lives close to the water, but also invertebrates, small mammals, and carrion (Dubost 1964). They are not able to stand on their hindlegs and browse for vegetation, instead they search for food in the ground and eat fruits and leaves that are either fallen down or grow very close to the ground.

Hyemoschus, as well as *Tragulus* live solitary (Rössner 2007; Meijaard et al. 2010). They possess no marking glands, but they mark their home ranges with urine and feces. Only *Tragulus* was observed to mark twigs with a chin gland for communication (Ralls et al. 1975). Males of this family are characterized by large saber-like upper canines, which were used as a display feature, as well as for male-male fights (Dubost and Terrade 1970; Dubost 1975; Ralls et al. 1975; Rössner 2007). Females in contrast have rudimentary upper canines, which are comparably small and cone-like. The fighting behavior among males is described as rather primitive. Males face each other in an antiparallel stance and not in a head-to-head stance. They slash their opponent with their canines at the neck, sides and bellies often causing lethal wounds (Dubost 1975; Ralls et al. 1975). Therefore, males in particular develop a toughened skin on the back and pelvic region to prevent injuries during combats with other tragulids, but probably also as a protective layer against predators and possibly even to shield them when moving through dense undergrowth (Dubost and Terrade 1970).

A comprehensive behavioral study of captive *Hyemoschus aquaticus* was conducted by Dubost (2016). Males of *Hyemoschus* become sexually mature between 5-9 months and 17-27 months based on testicle mass and diameter of the seminiferous tubules, in females sexual maturity starts at 10-16 months and completes at 27 months based on ovary mass and the presence of corpora lutea. The gestation length is very similar in all tragulids ranging from about five to six months (Meijaard 2011). Females normally give birth to one kid. The postpartum oestrus is unknown, but the suckling duration is 5 months or 95 days during gestation. After 9 to 26 months, young disperse from the mother's home range when they reach sexual maturity (Kingdon 1979; Nowak 1999). All tragulids have a similar maximum life span of about 13 to 15 years (Meijaard 2011).

1.3 Taxonomy of fossil tragulids

Tragulids originate during the late Eocene (Métais et al. 2007; Rössner 2007; Hassanin et al. 2012; Sánchez et al. 2018; Menecart et al. 2021) together with several other ruminant taxa like Archaeomerycidae in Asia and the Lophiomerycidae in Eurasia (Menecart et al. 2021). After the Oligocene to Miocene transition, they remain the only surviving ruminant and later diversify during the middle to late Miocene (Rössner 2007; Khan and Akhtar 2013; Rössner and Heissig 2013; Koufos 2020; Guzmán and Rössner 2021; Hartung and Böhme 2022). The oldest fossil tragulid was found in the late Eocene Krabi Basin in southern Thailand and was described by Métais et al. (2001) as *Archaeotragulus krabiensis*. The Oligocene record of tragulids is very scarce, and only little is known about the family's evolutionary history during this period, however, there is *Iberomeryx* considered by several authors (Menecart et al. 2011; Menecart et al. 2018b; Menecart et al. 2021) and *Nalameryx* (Menecart et al. 2022) being the only tragulid genera existing during the Oligocene. During the Oligocene there were two dispersal events from Asia into Europe (Menecart et al. 2021) facilitating the diversification of tragulids during the early Miocene. And thus after the Oligocene/Miocene boundary, *Dorcatherium* becomes widespread in Asia, Africa, and Europe with at least 35 species (e.g. Morales et al. 2003; Farooq et al. 2008; Rössner 2010; Alba et al. 2011; Khan et al. 2012; Khan and Akhtar 2013; Rössner and Heissig 2013; Aiglstorfer et al. 2014b; Alba et al. 2014; Menecart et al. 2018a; Koufos 2020; Guzmán and Rössner 2021; Roussiakis 2021) of which are not all confidently confirmed yet, because the Miocene record of *Dorcatherium* is mainly based on metrics of isolated teeth.

Besides *Dorcatherium*, there are also *Siamotragulus* from Africa, Asia, and Pakistan (Ginsburg et al. 2001; Sánchez et al. 2015; Musalizi et al. 2023), as well as the largest tragulid genus *Dorcabune* from Asia, Pakistan, and China (Farooq et al. 2007a; Farooq et al. 2007b; Koufos 2020; Guzmán and Rössner 2021; Roussiakis 2021; Wei and Weipeng 2021; Musalizi et al. 2023), *Afrotragulus* from East Africa and Asia (Sánchez et al. 2010; Sánchez et al. 2022), and *Yunanotherium* from China (Rössner 2007; Sánchez et al. 2010; Alba et al. 2014). Sánchez et al. (2010) suggested that there were two branches including *Afrotragulus* and *Dorcatherium* as the “African” branch and *Dorcabune* and *Siamotragulus* as the “Asian” branch, however, recent studies disproved that theory, because *Afrotragulus* was found in Asia as well (Sánchez et al. 2022). One species of *Dorcabune*, *Db. liuchengense* is reported from the Pleistocene of the Black Cave (Dark Cave) in Daxin County, Guangxi and represents the youngest find of a fossil tragulid (Liao et al. 2023).

After that, the origin of the extant tragulid genera *Tragulus*, *Moschiola*, and *Hyemoschus* is somewhat not clear. There is a find of *Tragulus sivalensis* (Lydekker 1882, 1884) known from a single molar from the Late Miocene of India, but its taxonomic attribution is still debated (Barry 2025). Tragulid remains morphologically similar to *Moschiola* are known from the Late Miocene Siwalik deposits (e.g. Rössner 2007; Guzmán and Rössner 2018; Barry 2025), although no fossil species has been formally assigned to the genus. The oldest fossil record of *Hyemoschus* is from the Pliocene (5.3 Ma-4.5 Ma) of East Africa Mabaget in the Tugen Hills, Kenia (Pickford 2004). Although this record is based on sparse dental material only, according to Geraads (2010) the upper molar resembles more closely the Late Miocene *Dorcatherium* from southeastern Europe than the extant African water chevrotain. The direct relationship between *Dorcatherium* and *H. aquaticus*, however, is still debated today, but it is very likely that the true *Dorcatherium*-clade' may have been part of dispersal events during the later part of the Late Miocene (see Böhme et al. 2021) facilitating the emergence of *Hyemoschus* in Africa.

The phylogeny of fossil tragulids is mainly based on the morphometric of teeth and isolated or partially articulated postcranial material. A first phylogenetic analysis was established by Sánchez et al. (2015) and focused on the placement of the newly described species *Siamotragulus songhorensis*. They also included *D. nauti* as well as *Dorcabune crassum* and the extant tragulids. A subsequent phylogenetic study was carried out by Sanchez et al. (2018) studying the Tragulidae from Arrisdrift and especially the position of *D. namaquensis* (Fig. 3). The analysis used characters of the teeth and postcranial characters and *Db. crassum* and *D. nauti* were used because of their dental morphological extremes, resulting in the reassignment of *Db. crassum* to *Dorcabune* instead of *Dorcatherium* lately (Musalizi et al. 2023). In these phylogenetic analysis, *Dorcabune crassum* occupies a relatively basal position within the *Dorcatherium* lineage, forming a sister taxon to the more derived clade that includes other *Dorcatherium* species and the lineage leading to *Hyemoschus aquaticus* and *Dorcatherium nauti*. All these analysis place *D. nauti* and *H. aquaticus* close together and *Tragulus* and *Moschiola* closer to *Siamotragulus* and *Afrotragulus*. This observation supports the hypothesis that *Hyemoschus aquaticus* retains a plesiomorphic condition among extant tragulids, as also indicated by its inner ear and petrosal morphology (Mennecart and Costeur 2016; Mennecart et al. 2018a). Therefore, *H. aquaticus* is frequently used as a reference taxon for comparisons between extant and fossil tragulids.

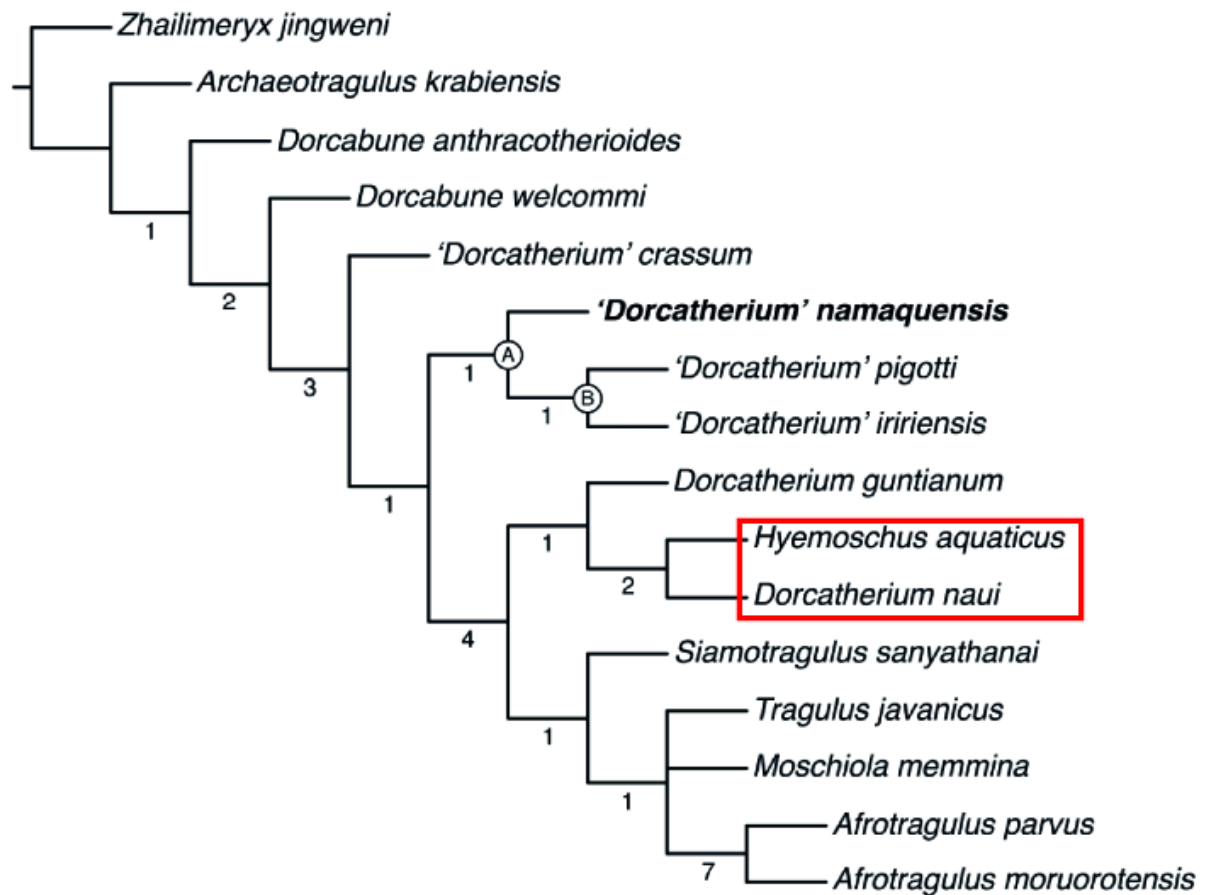


Figure 3: Phylogeny of fossil and extant tragulids based on dental and postcranial characters modified from Sánchez et al. (2018). Visible is the most parsimonious tree. *Db. crassum* is displayed as the sister taxon to *D. nauti* and further derived tragulids and *D. nauti* is the sister taxon to the extant *H. aquaticus*

1.4 History of the holotype of *Dorcatherium*, *D. nauti*

Dorcatherium is the most frequently studied taxon among fossil tragulids. The type species of *Dorcatherium*, *D. nauti*, was first described in Kaup (1833) in a letter to Bronn and was later figured in Kaup (1839a, pl. 23, Fig 1-1b, Fig. 4). The holotype is a mandible from the middle to late Miocene locality of Eppelsheim (Germany) containing p3–m3 and alveoli of p2 and p1. In his letter, Kaup (1833) described the specimen as different from other ruminants, because the mandible contains seven teeth instead of six and he most likely meant the presence of a p1. Furthermore, he described the teeth as similar to a deer. The holotype was later mentioned by Kaup and Scholl (1834) and was finally displayed in 1839 (Kaup 1839a, pl. 23, Fig 1-1b). After that, the holotype was lost, but one cast is stored in the NHMUK under the collection number NHMUK PVM3714 and another one is stored in the SNSB-BSPG under the collection number SNSB-BSPG 1961 XIX 37. A complete male skull with two attached mandibles, NHMUK PV OR 40632, attributed to *D. nauti* was then displayed together with the holotype in Kaup (1839a, pl.23, figs. 1 and 2) and described in

Kaup (1839b). Now this skull is stored in the NHMUK and a cast is available at the GPIT. It represents the only complete *Dorcatherium* skull from the type locality of *D. naui*.

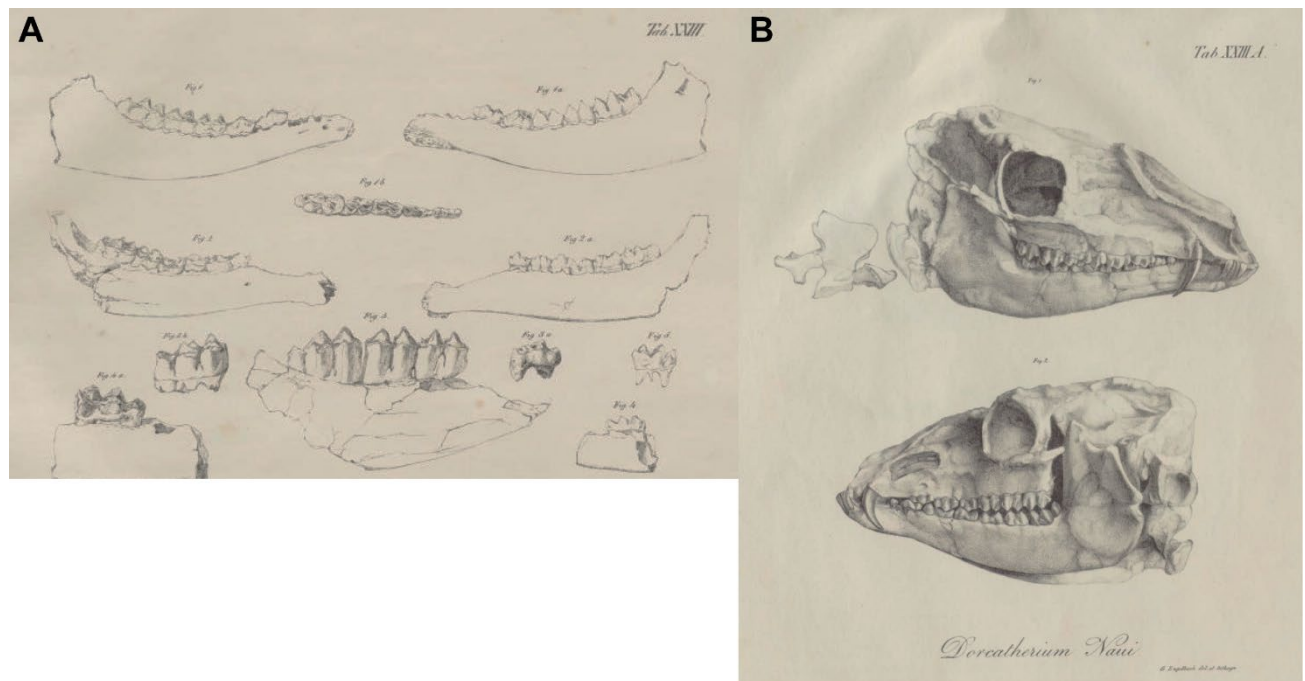


Figure 4: Original drawing of Kaup of *D. naui* from the middle to late Miocene of Eppelsheim, Germany (Kaup 1839a). **A)** Holotype NHMUK PVM3714, which is now lost and **B)** complete skull NHMUK PV OR 40632

1.5 Biology of fossil tragulids

Fossil tragulids are known from several fossil localities across Central Europe, as well as Africa, and Asia. However, only few studies address their overall biology, largely because well-preserved skulls, complete skeletons, and sufficiently large quantitative and qualitative fossil samples haven't been available for study until recently. Studies on the diet of tragulids were conducted by overall tooth morphology with a more selenodont lineage and a bunoselenodont lineage of tragulids, probably indicating two separated dietary adaptations (Rössner and Heissig 2013), as well as on isotopic measurements. According to Rössner and Heissig (2013), the more selenodont lineage includes *D. guntianum*, *D. jourdani*, *D. puyhauberti*, and *D. naui* and the more bunoselenodont lineage contains *D. crassum*, *D. vindebonense*, and *D. penecke*.

Isotopic studies of e.g. *D. guntianum* and *D. chappuisi* indicate mixed-feeding to variably grazing habits (Kaiser and Rössner 2007; Unger et al. 2012; Clauss and Rössner 2014). More recently, according to studies of Mennecart et al. (2022) tooth data of one of the oldest known tragulids revealed that this Oligocene tragulid fed on xeric plants based on $\delta^{13}\text{C}$ values fitting arid environmental conditions or seasonal climate with a dry period. In contrast, the larger tragulid, *D. pigotti*, shows $\delta^{13}\text{C}$ values of the enamel that indicate a more open

wooded habitat (Arney et al. 2024) and has probably a more generalized browsing rather than a frugivorous diet (Guzmán 2018).

Isotopic measurements of *D. nauti* were conducted by Aiglstorfer et al. (2014a) on material from Gratkorn. Aiglstorfer et al. (2014a), as well as Estham et al. (2016) demonstrated that *D. nauti* was likely at least partially frugivorous but overall mixed-feeding, consuming both leaves and grass. Additional fossil material of *D. nauti* from the Hammerschmiede indicates that an exclusively frugivorous diet can be excluded, as the pronounced seasonality of the local paleoenvironment would not have supported such specialization. This interpretation is further supported by the degree of selenodonty in *D. nauti*, which is consistent with mixed feeding and occasional fruit intake. In general, Miocene tragulids were predominantly browsers and did not inhabit exclusively open, grassland-dominated ecosystems (Zachos et al. 2001; Janis 2008).

Modern tragulids reach a maximum body mass of ~15 kg (Rössner 2007), whereas fossil tragulids span a much broader size range—from tiny species such as *Afrotragulus moruorotensis* with a weight of 1.5 kg (Sánchez et al. 2022) to the giant *Dorcabune anthracoides* with more than 100 kg estimated body weight (Guzmán 2018).

1.6 Geological setting of the Hammerschmiede and fossil assemblage

The Hammerschmiede is a late Miocene clay pit that is located in the Allgäu region in Bavaria, southern Germany. The fossil locality is situated in the Northern Alpine Foreland Basin and the sediments comprise fine grained floodplain deposits with interbedded carbonate-rich layers forming fluvial and alluvial deposits from the Middle-to-Late Miocene *Upper Series*, the youngest lithostratigraphic unit of the Upper Freshwater Molasse (Doppler 1989; Doppler et al. 2005). The Hammerschmiede contains two main excavation sites called HAM5 and HAM4 (Fig. 5). Biostratigraphic and magnetostratigraphic age constraints reveal that both levels are dated to the beginning of the late Miocene (Tortonian), with absolute ages of 11.62 Ma for HAM5 and 11.58 Ma for HAM4 respectively (Kirscher et al. 2016). The HAM4 channel represents a larger meandering stream of up to 50 m width, whereas the HAM5 channel is a smaller meandering rivulet or creek with a width of four to five meters (Lechner and Böhme 2025). Excavations are running since 2011 until 2024 and ongoing, about 1.000 metric tons of lower point-bar and channel-lag sediments have been excavated in HAM4 and about 300 metric tons of sediment in HAM5 (Lechner and Böhme 2025: tab. 1). The locality is famous for its rich and diverse faunal content including bivalves and gastropods (Schneider and Prieto 2011), fishes, amphibians, reptiles, small mammals, large mammals (Fuss et al. 2015; Hartung et al. 2020; Kargopoulos et al. 2021a, b; Hartung and

Böhme 2022; Kargopoulos et al. 2022a, b; Lechner and Böhme 2022, 2023; Kampouridis et al. 2024), and birds (Mayr et al. 2020a, b). It furthermore is renowned for the discovery of the associate skeletons of the hominid *Danuvius guggenmosi* (Böhme et al. 2019, 2020) and the second syntopic hominid *Buronijs manfredschmidi* (Böhme et al. 2024).

The palaeoenvironmental conditions during deposition of both channels differ in respect to the openness of the surrounding vegetation (Lechner and Böhme 2025). The larger meandering HAM4 river has been flowing in a relatively open and fire-prone landscape, evidenced by higher abundance of micro- and macro-charcoal, less abundant rodents (dominated by the tree squirrel *Csakvaromys*) and insectivore mammals, more abundant lagomorphs and scincomorph (lizards, scincs) reptiles. In contrast, the small HAM5 rivulet contains less charcoal, more rodents (dominated by the fossorial *Anomalomys*) and insectivores, less abundant lagomorphs and scincomorphs, and is interpreted to be surrounded by more closed forest environment, relative to HAM4. This interpretation is supported by the syntopy of two hominids in HAM5 (Böhme et al. 2019, 2024) and the presence of a chalicotheriine chalicothere, rather than schizotheriine chalicothere in HAM4 (Kampouridis et al. 2024).

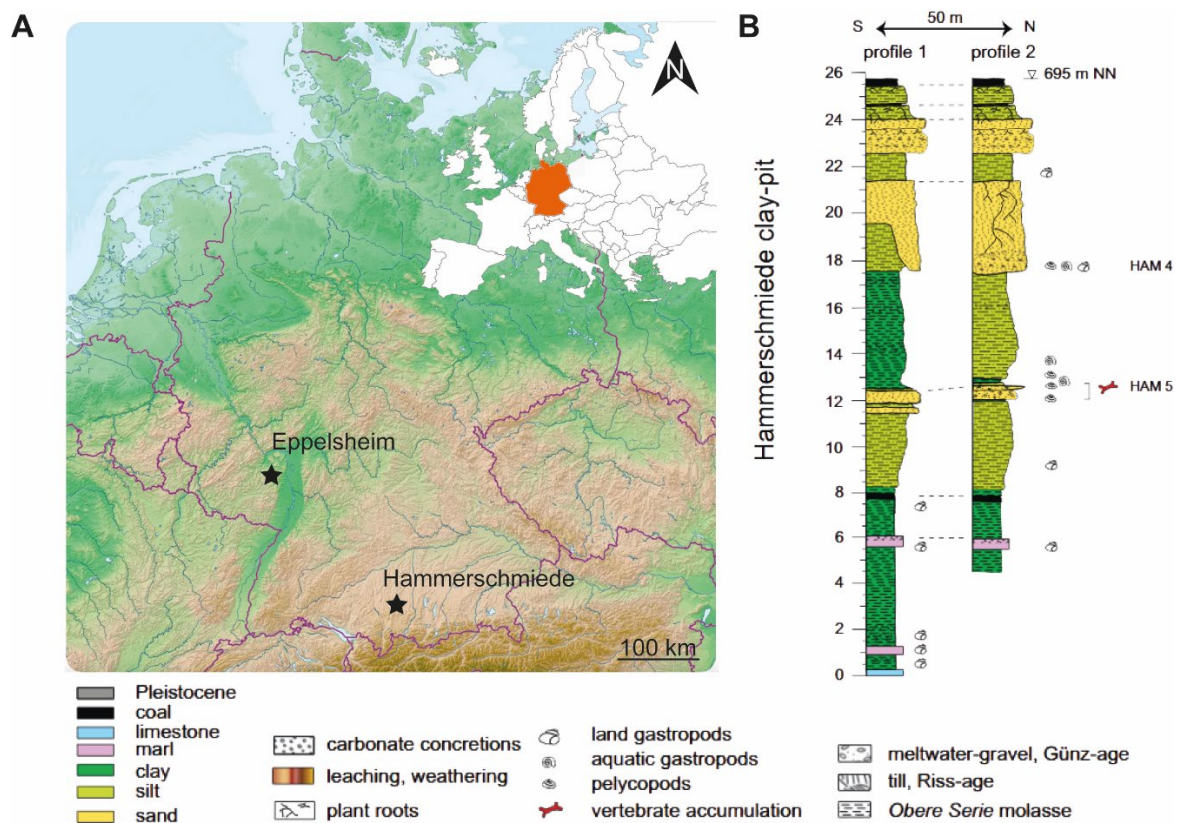


Figure 5: Geography and Stratigraphy of the Hammerschmiede and Eppelsheim localities. **A)** Topographical map of Germany marking the location of the Hammerschmiede fossil locality (early late Miocene) and Eppelsheim (middle to late Miocene). **B)** Stratigraphic profile of the two fossil bearing horizons HAM4 and HAM5 edited from Kirscher et al. (2016)

Eppelsheim is another famous middle to late Miocene fossil locality. It consists of fluvial deposits of the Eppelsheim Formation from the Mainz Basin. The deposits are represented as channel fills and consist of a mixed faunal association of repeatedly reworked paleo-Rhine sediments (Böhme et al. 2012). The Eppelsheim locality contains river sediments of the early Middle Miocene (~15 Ma) reworked during the late Middle Miocene (~12.5 Ma). Therefore, the fauna represent a plethora of different fossil assemblages including e.g. three genera of cervids, deinotheres, represented by one genus, *Deinotherium* and two species, gomphotheres, chalicotheres, carnivores and suids with *Zygodolophodon turicensis*, *Anisodon grande*, and *Palaeomeryx eminens* occurring together throughout the Middle Miocene and *Tetralophodon longirostris* and *Dorcatherium nauti* in the late Middle and early Late Miocene (Böhme et al. 2012).

In this study, I will compare the *D. nauti* skulls from Hammerschmiede and Eppelsheim to fossil skulls of the closely related *Db. crassum* (see chapter 2 Material), previously assigned to *Dorcatherium* (Musalizi et al. 2023). These skulls of *Db. crassum* were published in Seehuber (2015), Guzmán (2018), and Mennecart et al. (2018a) from Miocene fluvial deposits of Walda 2 and Thierhaupten, both also from the Northern Alpine Foreland Basin of southern Germany, as well as one skull from the middle Miocene of Contres in France.

2 Methods

Parameters for the individual scans can be found within the materials and methods section of each paper separately. Scans were conducted at the 3D Imaging Lab of the Senckenberg HEP at the Eberhard Karls University of Tübingen, Germany. The scans were acquired using the Nikon XTH 320 Reflection Target. To successfully compare skulls of fossil, as well as of extant tragulids a categorization according to tooth eruption sequence was established based on nine dental wear stages (Tab. 1). The categories of Dubost (2016) were expanded for a suitable usage in paleontology and three wear stages were added (w0, w2, and w4). This method was used for the upper dentition of *D. nauti* regarding the skulls and isolated teeth. It was similarly used for the lower dentition of *D. nauti*, where it is mainly based on isolated teeth and focuses on the development of the dp4 and m3 (Tab. 1). The age classes were observed for *H. aquarticus* by Dubost (2016) and were also inferred for *D. nauti* (Hartung and Böhme 2024).

Table 1: Wear stages of *H. aquaticus* of the upper dentition and *D. nauti* of the lower dentition compared with individual ages documented by Dubost (2016). Wear stage w0, w2, and w4 were added for more detailed comparison

Wear stage	Dental development of upper teeth (<i>Hyemoschus aquaticus</i>)	Dental development of lower teeth (<i>Dorcatherium nauti</i>)	Age class
8	M3 heavily worn, occlusal pattern abraded	m3 heavily worn, occlusal pattern abraded	>6.5 years: adult (senile)
7	M3 medium worn	all cones of m3 are medium worn and talonid basin shows slight to medium wear	4.5-6.5 years: adult
6	M3 slightly worn, no deciduous teeth present	according to <i>Hyemoschus</i> upper dentition:dp4 is shed, the m3 is worn at metaconid, protoconid, entoconid and hypoconid, talonid basin (entoconulid and hypoconulid) is still unworn	27 months-4.5 years: adult
5	M3 erupted but unworn, dP4 still present	dp4 is still present and the m3 is erupted but unworn	17-27 months: juvenile
4	M3 unerupted but visible in crypt, dP4 present and medium (-heavily) worn	all cones of dp4 are medium (-heavily) worn	10-16 months: juvenile
3	M3 unerupted, M2 erupted but unworn, dP4 worn-slightly worn, permanent, large saber-like upper canines in males erupted	all cones of dp4 show a wear facet	
2	M2 unerupted but visible in crypt, M1 worn to slightly worn, dP4 worn to slightly worn, deciduous upper canine small and rudimentary	metaconid and protoconid of dp4 are slightly worn but the anteriolingual, anteriolabial and entoconid, hypoconid are unworn	
1	M1 erupted but unworn, dP4 unworn, deciduous upper canine small and rudimentary	dp4 is still unworn but the enamel is thicker than in w0 and a root is preserved	5-9 months: juvenile
0	M1 unerupted but visible in crypt, dP4 erupted but unworn, deciduous upper canine small and rudimentary	dp4 erupted but unworn, isolated dp4, have no root preserved, only thin enamel cap is visible	<5 months: juvenile

I refer to the juvenile stage as w0-w5 because deciduous teeth (dp4 and dP4) are still present, an adult stage from w6-w7, and a senile stage at w8. Fossil specimens in wear stage 8 are very rare, as individuals reaching this stage are expected to have exceeded the maximum estimated life span. Consequently, most specimens fall within wear stage 6, which encompasses the largest proportion of the life span. In contrast, wear stages 0 to 5 are subdivided into more finely resolved categories, as tooth formation in tragulids is largely completed within the first 27 months of life, coinciding with dental development and the attainment of sexual maturity. A detailed line drawing of the occlusal abrasion pattern of *Hyemoschus* is displayed in Hartung and Böhme (2024, fig. 1) and of *D. nauti* in Hartung and Böhme (2026, manuscript submitted).

Body size measurements (in kg) on the combined HAM5 and HAM4 sample were conducted using the log-transformed regressions of Janis (1990) for lower molar length (m1-m3) and

length of m2 for “ruminants only”: $[\log(\text{BM}) = 3.337 \times \log(\text{SLML}/10) + 1.118]$, $[\log(\text{BM}) = 3.352 \times \log(\text{LMRL}/10) - 0.604]$; with SLML being the length of the m2 (mm) and LMRL being the length of the m1-m3 (mm). Mortality and survivorship were calculated from the minimum number of individuals (MNI), based on the abundance of left and right M3 and dP4, as well as m3 and dp4, for each wear stage, respectively. The corresponding data are provided in the appendix of Hartung and Böhme (2026, manuscript submitted). Survivorship was derived directly from the MNI per wear stage relative to the total number of individuals.

3 Material

The material for this thesis comprises extant and fossil tragulid skulls, as well as isolated, fossil teeth and mandibles. 39 specimens of the extant water chevrotain *Hyemoschus aquaticus* were studied from the Royal Museum for Central Africa Tervuren, Brussels (Tab. 2). This material includes nine neonate to juvenile specimens of indetermined sex, thirteen subadult to adult males, and seventeen subadult to adult females.

Table 2: Specimens of *Hyemoschus aquaticus* from RMCA, Tervuren (Brussels) studied in Hartung and Böhme (2024). Specimens pictured in Hartung and Böhme (2024) are marked in grey

Collection number	Sex	Wear stage
n.a.	f	7
R.G.2348	f	7
R.G.12514	m	7
R.G.10471	m	7
R.G.574	f	6
R.G.6155	f	6
R.G.3935	f	6
80-36-M-75	m	6
R.G.10332	m	6
83006M 477	m	6
R.G.10767	m	6
R.G.8214	f	5
R.G.4966	f	5
R.G.25448	f	5
83006M 472	f	5
R.G.20080	m	5
83006M 476	m	5
R.G.3366	m	5
R.G.579	m	5
R.G.8333	f	4
R.G.14483	f	4
R.G.13979	f	4
R.G.14748	f	4
R.G.5303	m	4
R.G.26674	m	4
R.G.573	f	3
R.G.9850	f	3
83006M 473	f	3
83006M 474	f	3
R.G.555	m	3
R.G.571	indet.	2
R.G.11211	indet.	2
R.G.14480	indet.	1
R.G.15898	indet.	0
R.G.17283	indet.	0
R.G.17315	indet.	0
R.G.30843	indet.	0
R.G.13369	indet.	0
R.G.17305	indet.	0

For the second paper, fossil material of *Dorcatherium naui* from Hammerschmiede including a complete female skull (GPIT/MA/1800-01) with teeth and a well-preserved male skull (GPIT/MA/17690) without teeth from Hammerschmiede were studied (Hartung and Böhme 2022). Additionally, the complete male skull NHMUK PV OR 40632 including both mandibles from the type series of Kaup (1839 a, b) from Eppelsheim, Germany of which a μ CT scan and a cast were available was used for comparison. Both skulls from Hammerschmiede are well preserved, although GPIT/MA/1800-01 is slightly compressed laterally and GPIT/MA/17690 is missing the snout and teeth. Based on the preservation of NHMUK PV OR 40632, this skull was probably not reworked. Still, the exact age for this skull is not reported, but it occurs within the biostratigraphic distribution of *D. naui* given by (Aiglstorfer et al. 2014b) from the early Sarmatian (~12.5 Ma) to Pannonian (~9 Ma). In the third paper of this thesis 11 additional skulls of *D. naui* from Hammerschmiede were studied, including two complete skulls of males and four female skulls (see Tab. 3). The male skulls are SNSB-BSPG 2020 XCV-474, which is a dorsoventrally flattened skull including teeth and SNSB-BSPG 2020 XCIV-3500, which is preserved similarly but is a juvenile skull. GPIT/MA/17615 and SNSB-BSPG 2020 XCIV-8518 are posterior skull roofs lacking the snout and the teeth. The female skulls comprise GPIT/MA/17841, which is an adult skull being laterally compressed similar to GPIT/MA/18000-01 and SNSB-BSPG 2020 XCV-357, 380, which is a skull from HAM 5 being ventrally flattened, together with SNSB-BSPG 2020 XCIV-8970 from HAM 4, a subadult female skull. SNSB-BSPG 2020 XCIV-18870 is another complete adult female skull, of which only the left side is well preserved. SNSB-BSPG 2020 XCIV-2298, SNSB-BSPG 2020 XCIV-3566, and SNSB-BSPG 2020 XCIV-8793 are partial skull roofs lacking all teeth being probably female. Moreover, 109 age-diagnostic mandibles and isolated teeth from level HAM4 and 17 teeth and mandibles from level HAM5 (all excavated between 2011 and 2024) were measured to investigate the mortality statistics, the survivorship rates, and the body mass distribution of *D. naui*. The studied dental material includes the following numbers of tooth positions: 40 M3, 26 dP4, 28 m3, and 24 dp4 from level HAM4, as well as two dP4, 11 M3, two dp4, and seven m3 from level HAM5 (teeth preserved within skulls and mandibles are included). A list including all tooth measurements can be found in the appendix of Hartung and Böhme (2026, manuscript submitted). Additionally, the length of the m1-m3 and the width of the m2 were measured to calculate the body mass. In total, 13 mandibles from HAM 4 and three mandibles from HAM 5 were used.

Table 3: Specimens of *D. nauti* from Hammerschmiede studied in this thesis, wear stages after Hartung and Böhme (2024)

Collection number	Description	Stratigraphic age	Sex	Wear stage
GPIT/MA/1800-01	Complete skull	HAM4	f	6
GPIT/MA/17690	Complete skull	HAM4	m	/
SNSB-BSPG 2020 XCV-474	Complete skull	HAM5	m	6
SNSB-BSPG 2020 XCIV-3500	Complete skull	HAM4	m	3-4
SNSB-BSPG 2020 XCIV-8518	Partial skull, skull roof	HAM4	m	/
GPIT/MA/17841	Complete skull	HAM4	f	6
SNSB-BSPG 2020 XCIV-18870	Complete skull	HAM4	f	6
SNSB-BSPG 2020 XCV-357, 380	Complete skull	HAM5	f	6
SNSB-BSPG 2020 XCIV-8970	Complete skull	HAM4	f	4
SNSB-BSPG 2020 XCIV-2298	Posterior part of skull, occiput	HAM4	f	/
SNSB-BSPG 2020 XCIV-3566	Posterior part of skull, occiput	HAM4	f	/
SNSB-BSPG 2020 XCIV-8793	Posterior part of skull, occiput	HAM4	f	/
GPIT/MA/17615	Partial skull, posterior part of skull roof	HAM4	m	/

As comparative material, already published skulls of *Db. crassum* from Walda 2 (Guzmán 2018) and Thierhaupten (Seehuber 2015) both from Germany, and one skull from Contres from France (Mennecart et al. 2018a) were used. Another skull from Steinheim am Albuch was first assigned to *D. nauti* (Gentry et al. 1999), but later reassigned to *D. guntianum* (Rössner and Heissig 2013) or *Db. crassum* (Aiglstorfer et al. 2014b), but it was never described. Moreover, skulls of *Moschiola* from the Natural History Museum of Wien and *Tragulus javanicus* from the Geologisch-Paläontologische Sammlung Tübingen were studied.

4 Results

In the following the main results of the two publications and one submitted manuscript are summarized. The full publications and one manuscript in their final and submitted format are attached in the appendix of this thesis.

4.1 Sexual dimorphism in *Dorcatherium*

Previously, sexual dimorphism in fossil tragulids was only known from size-differences in the upper canines, similar to extant chevrotains. Males possess large and saber-like upper canines resembling those of the extant *Moschus*, females in contrast have small, cone-like and rudimentary canines (Rössner 2007). Extant tragulids show little to no sexual size dimorphism depending on genus in body mass or other morphology like e.g. color of the fur (Dubost 1978; Kingdon 1997; Meijaard and Groves 2004). In fossil species it is even more difficult, because of the scarcity of the fossil record with many species based exclusively on the morphometrics of the teeth and size variation in teeth tends to fall within interspecific or ontogenetic variation, not dimorphism. In the following, two skulls from Hammerschmiede (GPIT/MA/18000-01 and GPIT/MA/17690) and one skull from the type locality Eppelsheim (NHMUK PV OR 40632) are examined with respect to differences in cranial morphology related to sexual dimorphism (for a detailed description of these specimens see Hartung and Böhme 2022).

4.1.1 Sexual dimorphism in *D. naui*

The skull GPIT/MA/17690 (Fig. 6) was attributed to *D. naui* based on its overall morphology, although the characteristic teeth were missing (see Hartung and Böhme 2022 for details). However, the detailed description of the specimen from London (NHMUK PV OR 40632) revealed the same features; in addition, this specimen preserved the synapomorphic characters for *D. naui* of the lower mandible and moreover saber-like upper canines typical for male tragulids (Fig. 7).

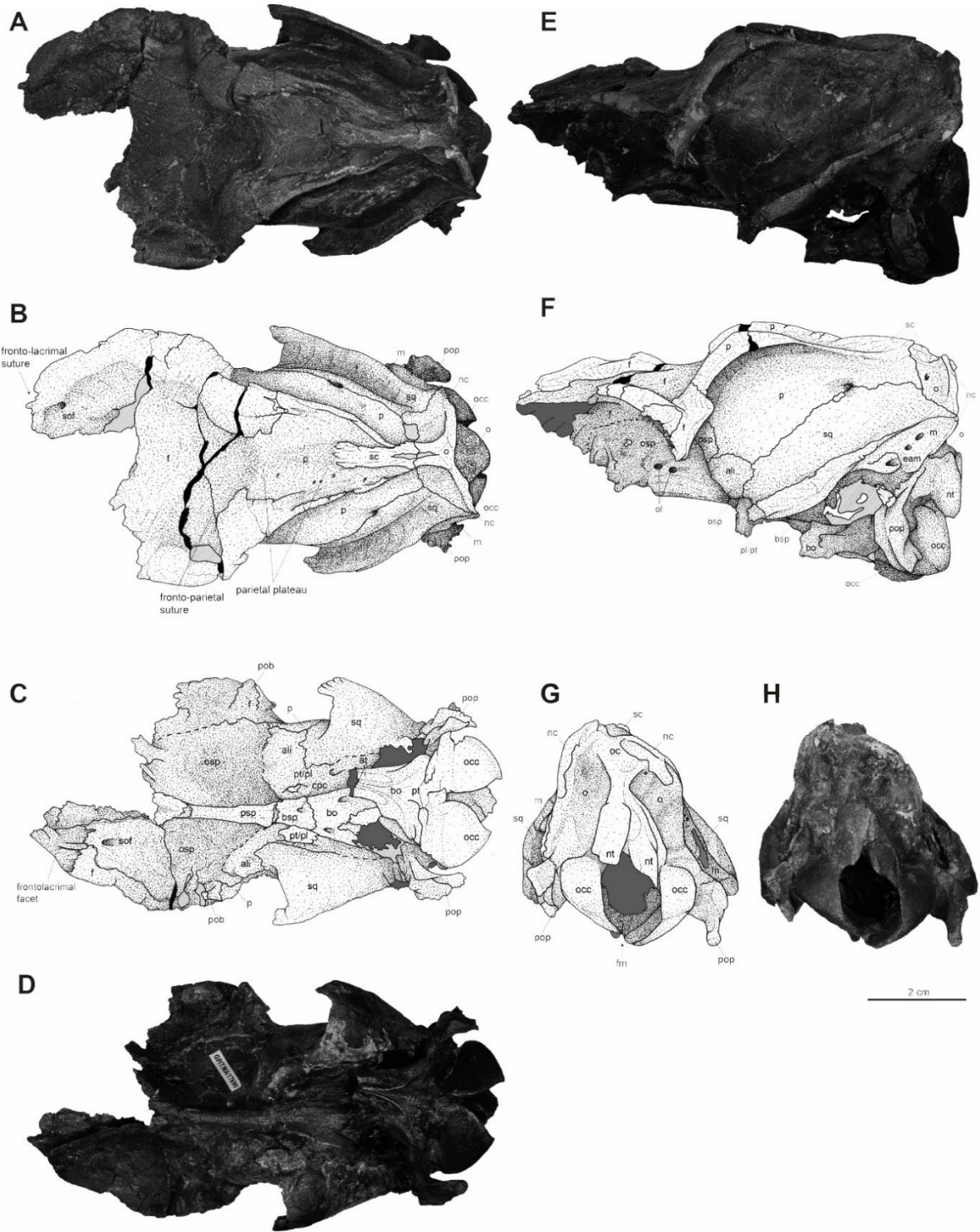


Figure 6: Partial male skull of *Dorcatherium naui* (GPIT/MA/17690) from the Hammerschmiede locality, Germany (HAM 4). **A)** photograph dorsal, **B)** drawing, dorsal, **C)** drawing ventral, **D)** photograph ventral, **E)** photograph lateral, **F)** drawing lateral, **G)** drawing occipital, **H)** photograph occipital. **Abbreviations:** ali, alisphenoid; at, anterior tuberosities; bo, basioccipital; bsp, basisphenoid; cpc, craniopharyngeal canal; eam, external auditory meatus; f, frontal; fm, foramen magnum; m, mastoid process; nc, nuchal crests; nt, nuchal tubercle; o, occipital; of, optic foramen; oc, occipital crest; occ, occipital condyle; osp, orbitosphenoid; p, parietal; pob, postorbital bar; pop, paroccipital process; psp, parasphenoid; pt, posterior tuberosities; pt/pal, pterygoid/palatine; sc, sagittal crest; sq, squamosal; sof, supraorbital foramen; tl, temporal line

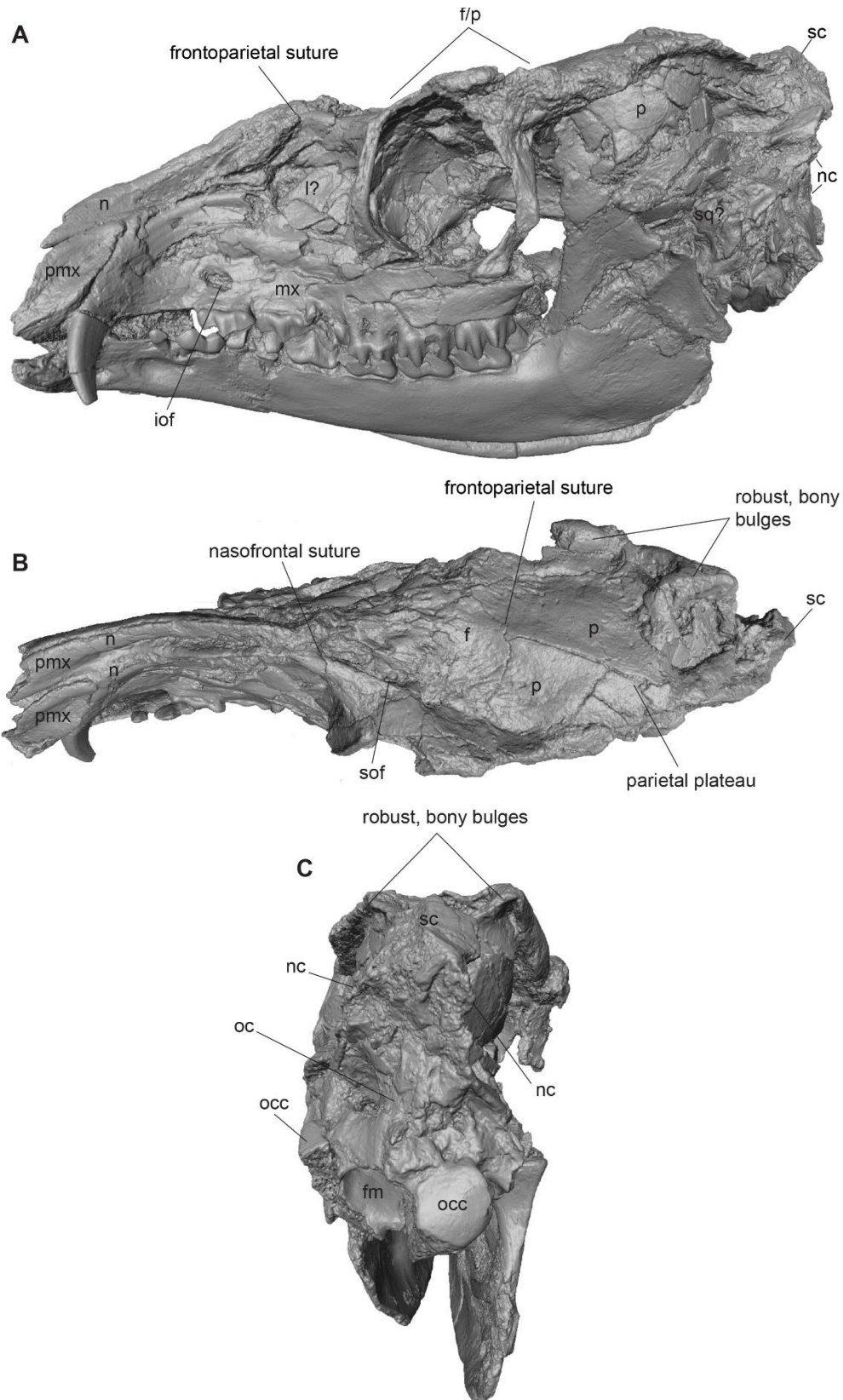


Figure 7: Surface model of the complete skull of *Dorcatherium navi* from Eppelsheim, Germany NHMUK PV OR 40632. **A)** lateral view, left side, **B)** dorsal view, **C)** posterior view. **Abbreviations:** f, frontal; fm, foramen magnum; iof, infraorbital foramen; j?, jugal; l?, lacrimal; mx, maxillary; n, nasal; nc, nuchal crests; oc, occipital crest; occ, occipital condyle; p, parietal; pmx, premaxillary; sc, sagittal crest; sof, supraorbital foramen; sq?, squamosal

More skulls exhibiting this morphology, but also including teeth, were found in the Hammerschmiede during subsequent excavation campaigns, supporting the attribution of GPIT/MA/17690 to *D. nauti* (Hartung and Böhme 2026, manuscript submitted). GPIT/MA/17690 and the other male skulls do not bear large saber-like upper canines as the London specimen, but they contain alveoles for the latter. A very prominent feature visible in GPIT/MA/17690, as well as in NHMUK PV OR 40632 and the other male skulls are robust bony bulges on the frontal and parietal, enclosing a parietal plateau. This feature was previously unknown from fossil tragulids, but the London specimen NHMUK PV OR 40632 shows very well that this is a feature of male *D. nauti*. In addition to that, male skulls are characterized by the presence of (I) a broad, concave and laterally expanding skull roof formed by the anterior frontal (frontal plateau), (II) presence of frontoparietal bulges enclosing a well-developed parietal plateau, (III) a prominent, flat and broad sagittal crest, (IV) large part of occipital participating in the formation of the sagittal crest, (V) strongly-developed nuchal crests, (VI) large and prominent nuchal tubercle, (VII) laterally expanding part of ventral squamosal with only a slight depression, as well as the above mentioned (VIII) large, saber-like upper canines (Fig. 7).

In contrast, females like GPIT/MA/1800-01 exhibit in general a straight and slender outline of the dorsal skull roof and a small canine alveole. The frontal is smaller, only slightly broadened, and the constriction of the parietal plateau is absent. The sagittal crest is less-prominent, slim, and more crest-like. Moreover, the most distinctive sexually dimorphic characters are the absence of robust and prominent frontoparietal bulges on the dorsal skull roof (Fig. 8, 9, and 10). The temporal lines are crest-shaped and encompass a small and slender parietal plateau.

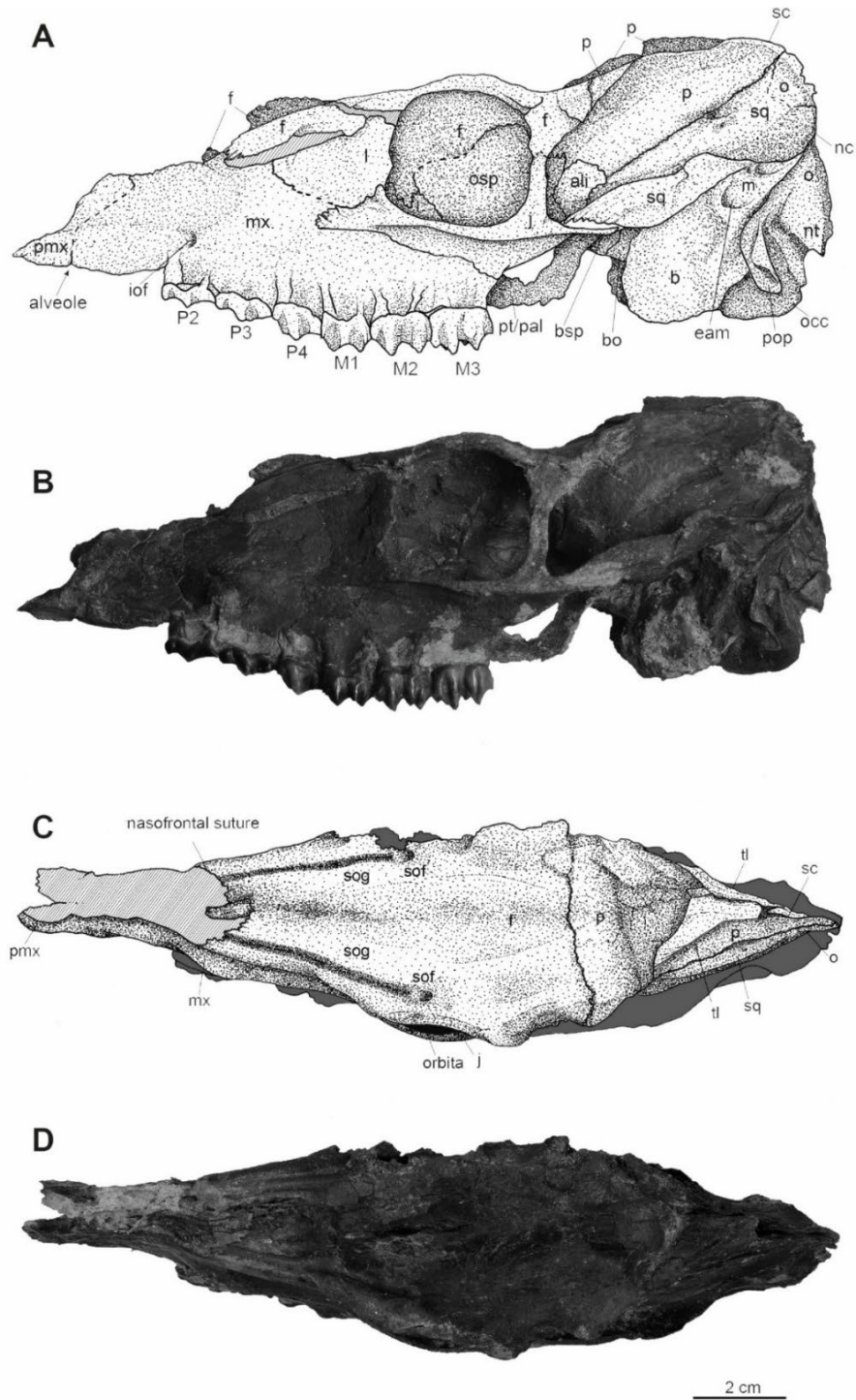


Figure 8: Complete female skull of *Dorcatherium naui* (GPIT/MA/18000-01) in lateral and dorsal view from the Hammerschmiede locality, Germany (HAM4) **A)** drawing lateral, **B)** photograph lateral, **C)** drawing dorsal, **D)** photograph dorsal. **Abbreviations:** ali, alisphenoid; b, bulla tympanica; bsp, basisphenoid; bo, basioccipital; eam, external auditory meatus; f, frontal; io, infraorbital foramen; j, jugal; l, lacrimal; mx, maxillary; nc, nuchal crests; nt, nuchal tubercle; o, occipital; occ, occipital condyle; osp, orbitosphenoid; p, parietal; pmx, premaxillary; pop, paroccipital process; pt/pal, pterygoid/palatine; sc, sagittal crest; sq, squamosal; sof, supraorbital foramen; sog, supraorbital groove; tl, temporal lines

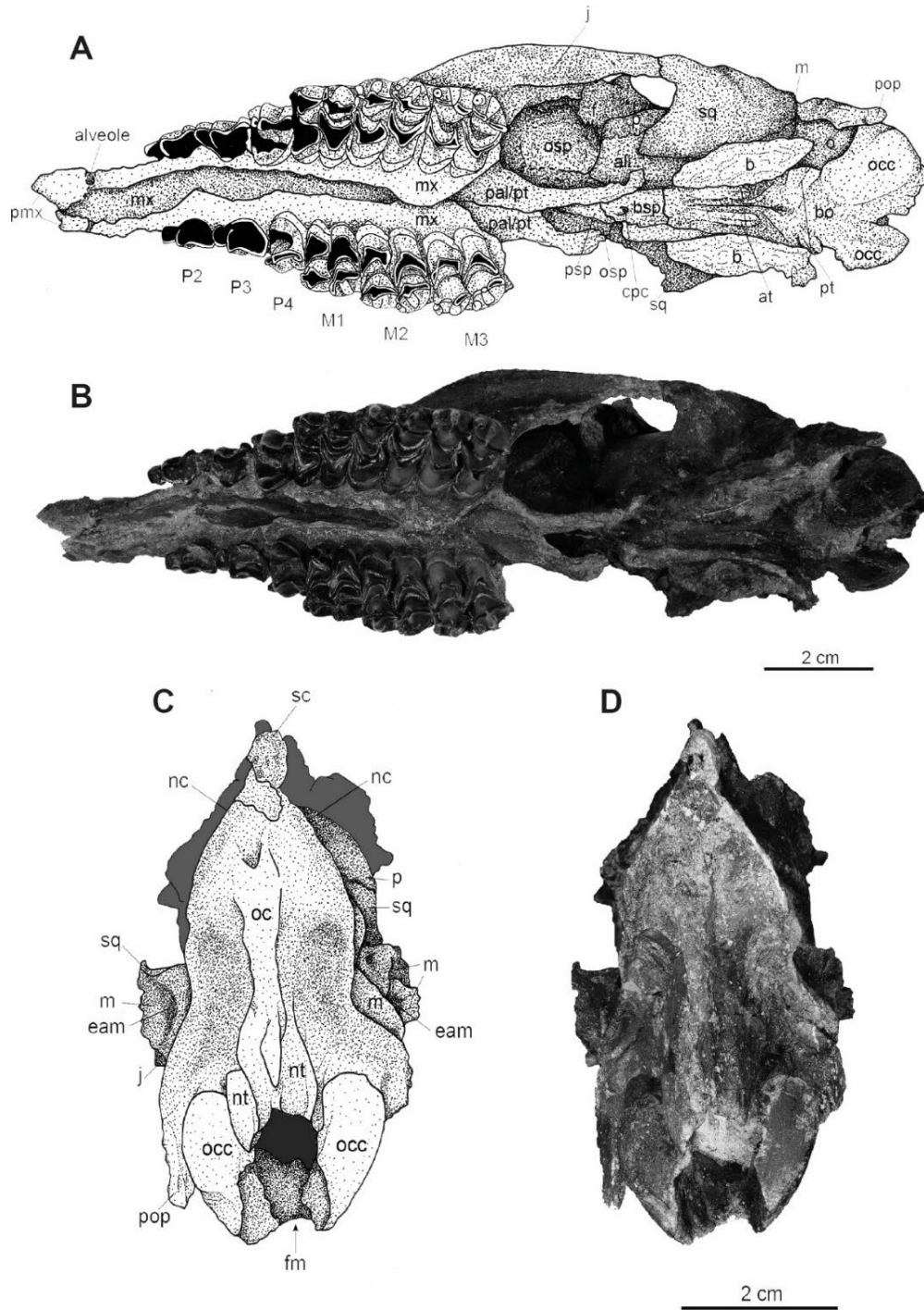


Figure 9: Complete female skull of *Dorcatherium nawi* (GPIT/MA/18000-01) in ventral and occipital view from the Hammerschmiede locality, Germany (HAM4). **A)** drawing ventral, **B)** photograph ventral, **C)** drawing occipital, **D)** photograph occipital. **Abbreviations:** ali, alisphenoid; at, anterior tuberosities; b, bulla tympanica; bsp, basisphenoid; bo, basioccipital; cpc, craniopharyngeal canal; eam, external auditory meatus; f, frontal; fm, foramen magnum; j, jugal; m, mastoid process; mx, maxillary; nc, nuchal crests; nt, nuchal tubercle; o, occipital; oc, occipital crest; occ, occipital condyle; osp, orbitosphenoid; p, parietal; pmx, premaxillary; pop, paroccipital process; psp, presphenoid; pt, posterior tuberosities; pt/pal, pterygoid/palatine; sc, sagittal crest; sq, squamosal

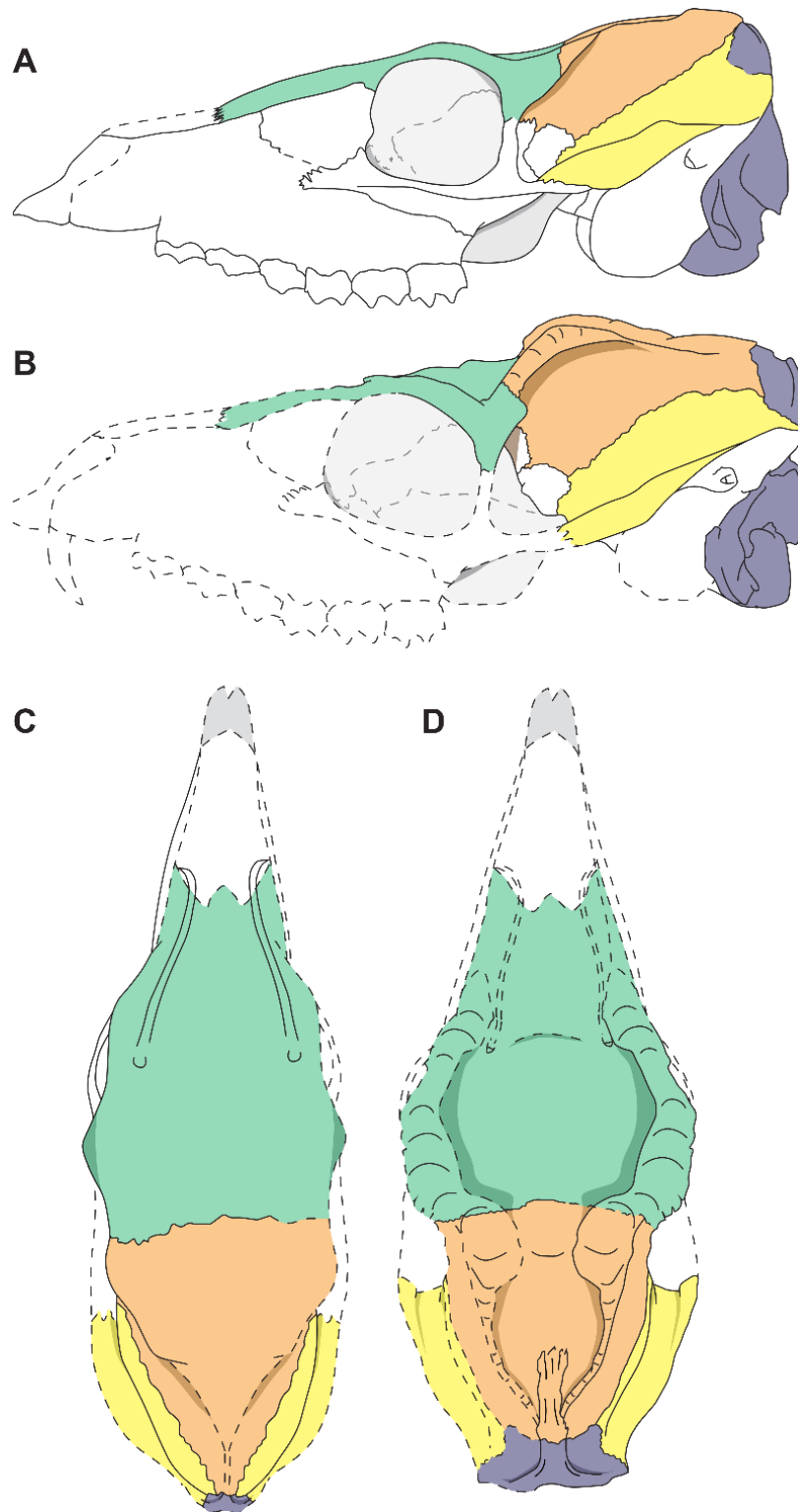


Figure 10: Reconstruction of a male and female skull of *Dorcatherium naui* from the Hammerschmiede locality, Germany. **A)** lateral view of GPIT/MA/18000-01 (female), **B)** lateral view of GPIT/MA/17690 (male), **C)** dorsal view of GPIT/MA/18000-01 (female), **D)** dorsal view of GPIT/MA/17690 (male). Green: frontal; Orange: parietal; Yellow: squamosal; Grey: occipital. Skulls not to scale

4.1.2 Sexual dimorphism in *Db. crassum*

Large saber-like upper canines are also known from males of this species as visible in the skull NMA-Walda 2 described by Guzmán (2018). The skull from Contres, France (Mennecart et al. 2018a) is missing the snout but shares the morphological characters typical for males. In contrast, based on the absence of a large alveolus for the upper canine, the specimen from Thierhaupten NMA-2012-1/2131, described by Seehuber (2015) is a female. In dorsal view, male skulls show broad, flat, and straight temporal lines merging posteriorly into a prominent sagittal crest, forming a Y-shape. Females have rather gracile temporal lines merging into a more crest-like but narrow sagittal crest. In lateral view, the lateral wall of the braincase of the male skull is posteriorly confined by well-developed nuchal crests. These crests are less prominent in females.

4.1.3 Comparison of sexual dimorphism in *Db. crassum* and *D. naui*

Males of *Dorcatherium* are in general more robust with well-developed cranial crests than females, who have a more delicate skull morphology with less-pronounced crests and ridges. Males of *D. naui* possess frontoparietal bulges, which together with the temporal lines enclose the skull roof anteroposteriorly until they merge with the posterior part of the sagittal crest (Fig. 10). In males of *Db. crassum* the frontoparietal bulges are absent, but the temporal lines form two flat ridges, which are only present on the parietals and do not extend onto the frontals forming a Y-shape. Males of both species share a broad and flat sagittal crest. The latter is more crest-like and delicate in females of both species. Moreover, males of *D. naui* expose a well-developed parietal plateau (Fig. 6), which is only less-pronounced in females of this species (Fig. 8). In contrast, in *Db. crassum*, the parietal plateau is absent in both males and females. Moreover, in *D. naui*, the temporal lines proceed posteriorly at the level of the sagittal crest. Here, they run almost parallel to the sagittal crest and merge with the latter slightly anterior to the parietaloccipital suture. In contrast, in males of *Db. crassum* the temporal lines form a Y-structure. Male skulls of *D. naui* contain a concave plateau formed by the frontals anterior to the temporal lines. In contrast, in males of *Db. crassum* the anterior skull roof is flat to convex and forms a straight surface extending the posterior part of the skull (Tab. 4).

Table 4: Cranial differences between males and females of *Dorcatherium nauti* and *Db. crassum*

Cranial characters	Comparative skull morphology (males and females)	
	<i>Dorcatherium nauti</i>	<i>Dorcabune crassum</i>
Orientation of orbitae	lateral facing	dorsolateral facing
Postorbital part of skull (Condylbasal length/postfrontal length)	elongated (ratio=2.9)	shortened (ratio=4.0)
Separation of supraorbital foramen from supraorbital groove	absent	by a bony bridge
Development of nuchal crests	well-developed	strongly-developed and set off
Occipital crest	present	absent
Development of nuchal tubercle	prominent	Weakly-developed
	Comparative skull morphology (males)	
	<i>Dorcatherium nauti</i>	<i>Dorcabune crassum</i>
Frontal plateau	present (concave)	absent
Frontoparietal bulges	present, well-developed	absent
Morphology of temporal lines	thin and crest-like	Broad and flat
Development of parietal plateau	Strongly-developed, domed posterior skull roof	Almost absent, flat skull roof
Morphology of temporal lines and sagittal crest	temporal lines proceed posteriorly, parallel to the level of the sagittal crest, and merge with the sagittal crest	Temporal lines merge with anterior part of sagittal crest and form a Y-structure

4.1.4 Sexual dimorphism of extant tragulids in comparison with fossil *Dorcatherium*

In extant tragulids, sexual dimorphism of the skull is only based on large canines in males and small ones in females. However, Mennecart et al. (2018a) demonstrated that *Db. crassum* and *Hyemoschus* share a “hyper-developed” cranial morphology by the presence of prominent cranial crests and mentioned that females of *Hyemoschus* show less remarkable characters (e.g. weaker crests), a pattern observed similarly in *Dorcatherium* (see above). However, Hartung and Böhme (2024) show that cranial ornamentation in *Hyemoschus* cannot be used as a features to differentiate between males and females and that there are females with well-developed cranial crests, similar to males. I also agree with Guzmán (2018) and Mennecart et al. (2018a) that, based on osteological characters, *Db. crassum* is more similar to *Hyemoschus* than to *Tragulus* and *Moschiola*, which is also the case for *D. nauti*, supporting the plesiomorphic state of *Hyemoschus* among the extant tragulids.

In detail, the temporal lines of male *D. nauti* are more similar to *Hyemoschus* than to *Db. crassum*, but the sagittal crest resembles that of *Db. crassum*. Males of *D. nauti* and

Hyemoschus have similar temporal lines, but the sagittal crest is weaker in extant tragulids and prominent in *Dorcatherium*. In general, males of *Dorcatherium* expose a broad and robust sagittal crest, more developed than in any extant tragulid, whereas in females of *Dorcatherium* the crest is more delicate and less-prominent than in *Hyemoschus*, but somewhat more developed than in *Moschiola* and *Tragulus* (Fig. 11).

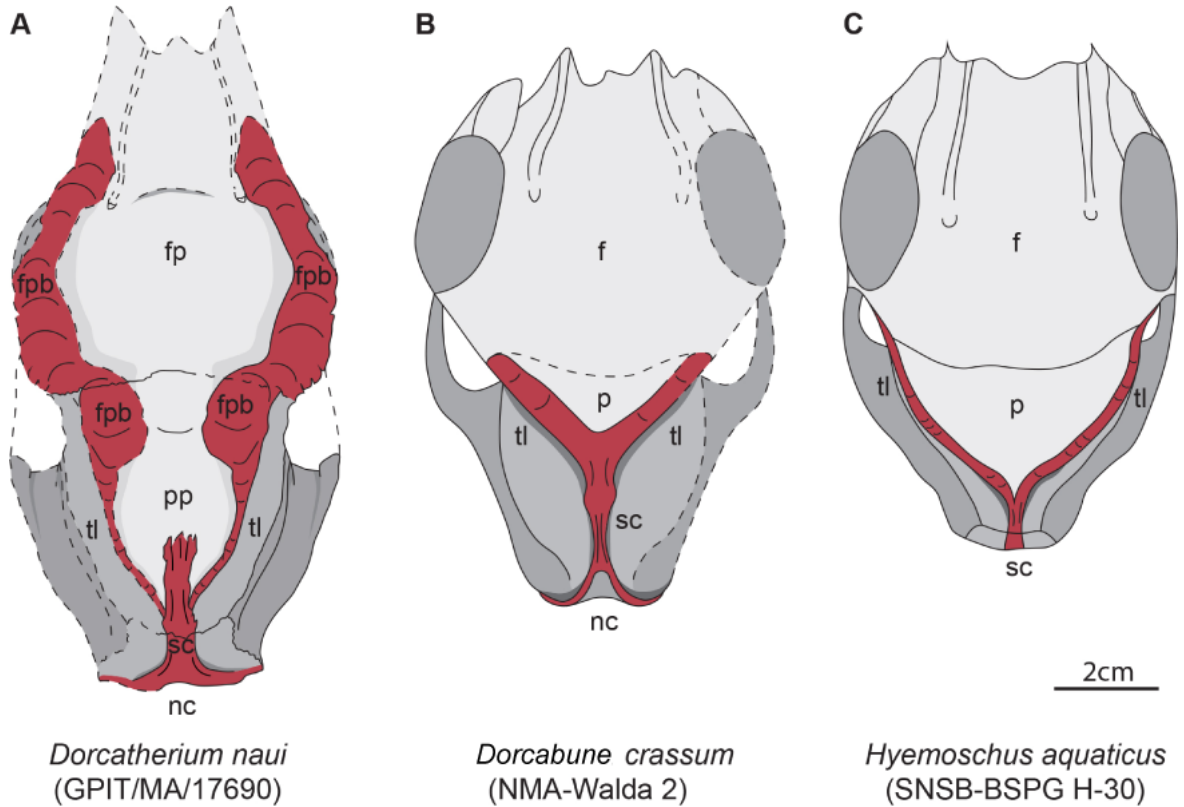


Figure 11: Morphology of the posterior skull roof of males of *Dorcatherium nauti*, *Dorcabune crassum*, and *Hyemoschus aquaticus* showing the morphological similarities and differences among the species. **A)** GPIT/MA/17690, *D. nauti* from Hammerschmiede, Germany (HAM 4), **B)** NMA-Walda 2 (drawn after Guzman-Sandoval, 2018), *Db. crassum* from Walda 2, Germany, **C)** SNSB-BSPG H-30 (redrawn after Guzman-Sandoval, 2018), *Hyemoschus aquaticus*. Red: cranial crests and bulges. **Abbreviations:** f, frontal; fp, frontal plateau; fpb, frontoparietal bulges; nc, nuchal crests; p, parietal; pp, parietal plateau; sc, sagittal crest, tl; temporal lines

4.2 An emended diagnosis for the type species of *Dorcatherium*, *D. nauti*

The detailed description, as well as the herein described sexual dimorphism now allow for an emended and comparative diagnosis of the type species of *Dorcatherium*, *D. nauti*. The family Tragulidae is defined by the presence of the typical Σ -structure (*Tragulus*– and *Dorcatherium*-fold *sensu* Bärmann and Rössner 2011 and Sánchez et al. 2011) in the lower molars (Rössner 2007) and a bunoselenodont to selenodont occlusal pattern (Fig. 12). *Dorcatherium* is the most frequently studied genus, which also includes most of the tragulid fossil species. The genus was conservatively divided into a selenodont lineage including *D. guntianum*, *D. jourdani*, *D. puyhauberti*, and *D. nauti* and a bunoselenodont lineage comprising *Db. crassum*, *D. vindebonense*, and *D. penecke* (Rössner and Heissig 2013). *Dorcatherium* is characterized by a combination of dental characters (see below), and *D. nauti* shares the more selenodont morphology among other tragulids.

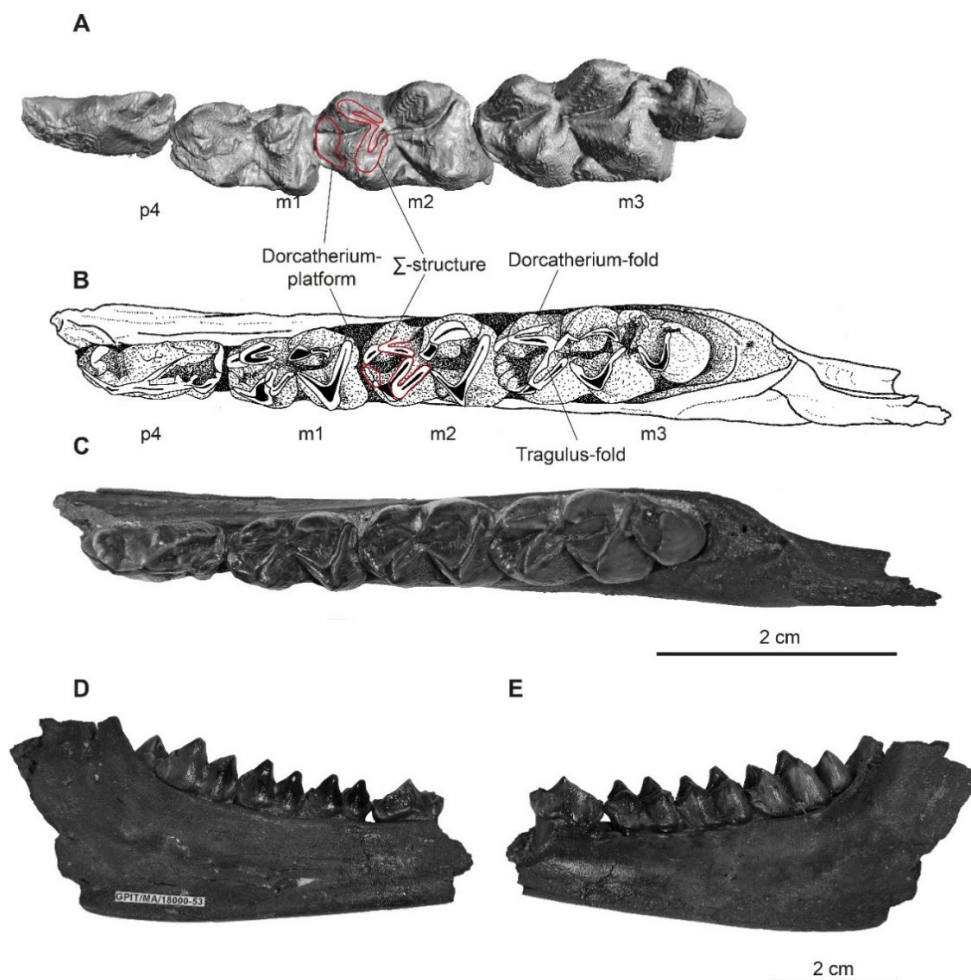


Figure 12: Lower dentition of *Dorcatherium nauti* showing typical features of tragulids, as well as *Dorcatherium*. The mandible GPIT/MA/18000-53 is associated to the skull GPIT/MA/18000-01. **A)** for comparison: virtually isolated, left tooth row of NHMUK PV OR 40632 in occlusal view, **B)** drawing of GPIT/MA/18000-53 in occlusal view, **C)** GPIT/MA/18000-53 in occlusal view, **D)** GPIT/MA/18000-53 in lingual view, **E)** GPIT/MA/18000-53 in buccal view

Dorcatherium nauti was previously exclusively known from the morphology and metrics of the teeth (Bärmann and Rössner 2011; Sánchez et al. 2011; Rössner and Heissig 2013; Aiglstorfer et al. 2014b; Alba et al. 2014; Aiglstorfer and Mayda 2020) and from morphological features at the metatarsals (Sánchez et al. 2011) in comparison to *Db. crassum*, however, the detailed description of the fossil skulls from Hammerschmiede and Eppelsheim revealed the presence of several distinct features exclusively known from this species, such as: lateral facing orbitae, prominent nuchal tubercle, and the presence of an occipital crest (Fig. 11).

Based on the results of the detailed description and comparison of the skull morphology and taking into account the sexual dimorphism of the previously described cranial crests, an emended diagnosis for *D. nauti* is proposed as follows: Mid-sized selenodont tragulid with (I) presence of p1, in combination with (II) the presence of the *Dorcatherium*-platform in the lower molars (*sensu* Alba et al. 2014), and (III) a complex posterior valley of the p4 (*sensu* Aiglstorfer et al. 2014b). Furthermore, the following features are typical for the selenodont lineage: high degree of selenodonta with reduced external postmetacristid (Bärmann and Rössner 2011; Sánchez et al. 2011) in the lower molars and well-developed cristids, flat main cusps (*sensu* Sánchez et al. 2011), and prominent sickle-shaped cones and conids (*sensu* Rössner and Heissig 2013). Among the selenodont lineage, *D. guntianum*, *D. jourdani*, *D. puyhauberti*, and *D. nauti* differ in the size (length and width) of their teeth. The m1 of *D. guntianum* is much smaller in length (maximum length of *D. guntianum* is about 9.8 mm and the minimum length of *D. nauti* is about 11.0 mm). The width of the m1 of *D. jourdani* is smaller, whereas it is larger in *D. puyhauberti* if compared to NHMUK PV OR 40632, the holotype mandible of *D. nauti* (Aiglstorfer et al. 2014b; Aiglstorfer and Mayda 2020; Koufos 2020). *D. nauti* differs from *Db. crassum* in: (A) higher degree of selenodonta, (B) strongly reduced postmetacristid, (C) laterally facing orbitae instead of dorsolaterally oriented orbitae, (D) the separation of supraorbital foramen from supraorbital groove by a bony bridge, (E) well-developed parietal plateau, (F) prominent nuchal tubercle, (G) less-developed nuchal crests, and (H) the presence of an occipital crest.

4.3 Cranial development and sexual dimorphism of the skull of the extant chevrotain *Hyemoschus aquaticus*

Hyemoschus aquaticus, the African water chevrotain, is considered the most “primitive” living tragulid and the sister taxon of all other extant tragulids (Webb and Taylor 1980; Meijaard et al. 2010; Sánchez et al. 2018). In *H. aquaticus*, males and females displays a sexual size dimorphism pattern where males have an average weight of 9.7 kg and females around 12 kg (Robin 1990; Nowak 1999). Skeletal measurements show only minor differences and are often statistically insignificant (Dubost 1978; Kingdon 1997). Males, however, possess enlarged upper canines (used in male–male combat) instead of horns or antlers, as typical for all extant tragulids (Meijaard and Groves 2004). The skull of *H. aquaticus* shows well-developed temporal lines and a sagittal crest and, therefore, due to its phylogenetic position, this species has often been used for comparison with fossil tragulids.

In Hartung and Böhme (2024) we studied 39 skulls of *H. aquaticus* from the RMCA in Tervuren, Brussels including nine neonate to juvenile specimens of indetermined sex, thirteen subadult to adult males, and seventeen subadult to adult females (Fig. 13). We established an ontogenetic series based on wear stages starting at wear stage 0 (neonate) and ending at wear stage 8 (senile). For a detailed description of the wear stages see Hartung and Böhme (2024, tab. 1 and fig. 1). After wear stages 3-4, males and females could be unambiguously identified based on the development of the upper canines. In younger individuals, sex could not be determined (fig. 4 in Hartung and Böhme 2024). The skulls were studied to test the potential of *H. aquaticus* as an analogue for *D. navi* in regards of the morphology and ornamentation of the skull.

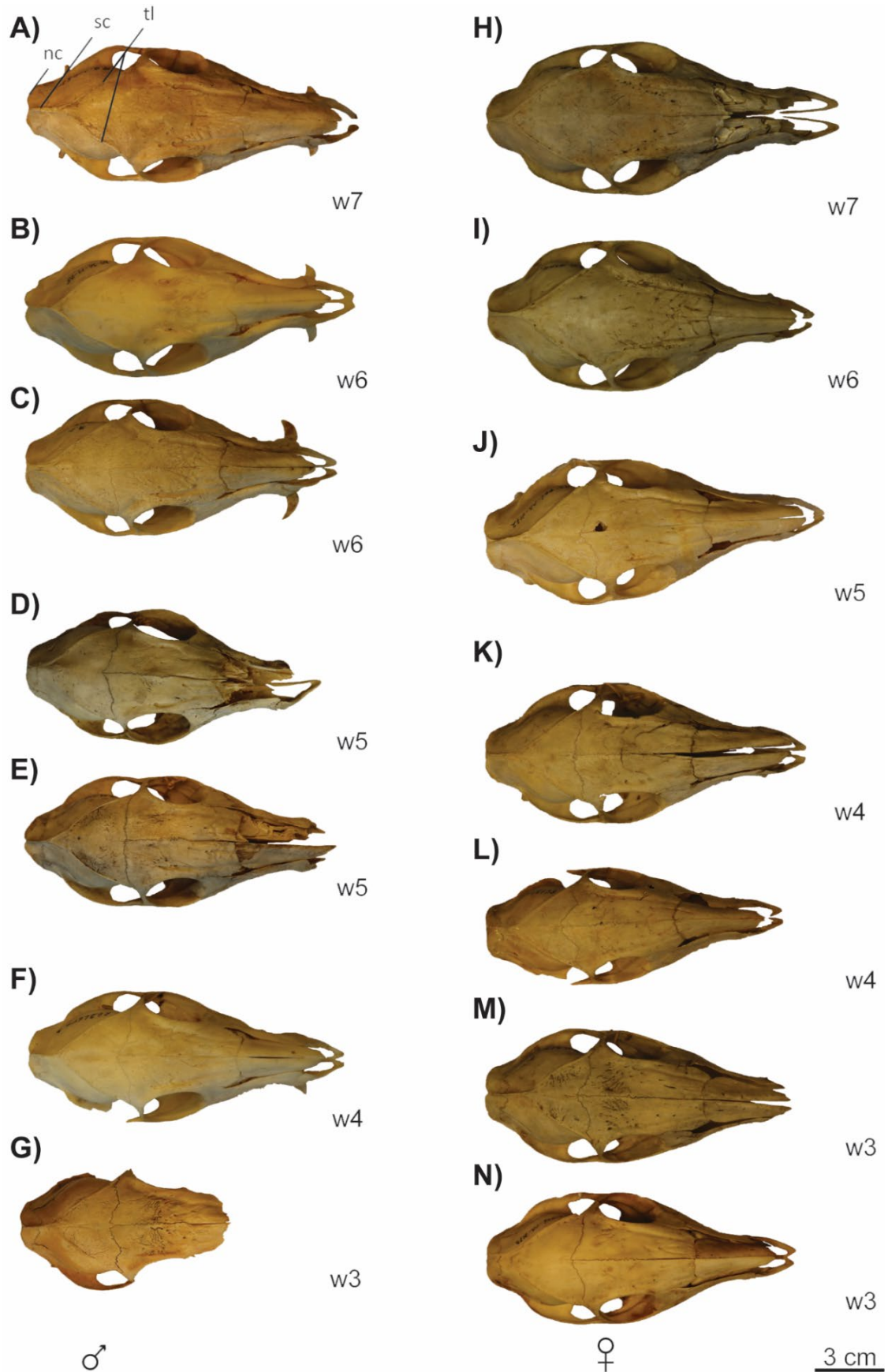


Figure 13: Subadult to adult *Hyemoschus aquaticus* in dorsal view wear stage 3–7. **A)–G)** males, **A)** R.G.10471, **B)** 80–36-M-75, **C)** R.G.10332, **D)** R.G.3366, **E)** R.G.579, **F)** R.G.26674, **G)** R.G.555, **H)–N)** females, **H)** R.G.2348, **I)** R.G.6155, **J)** 83006 M 472, **K)** R.G.8333, **L)** R.G.13979, **M)** R.G.573, **N)** 83006 M 473. **Abbreviations:** w, wear stage; nc, nuchal crests; sc, sagittal crest; tl, temporal lines

4.3.1 Development of cranial ornamentation

During ontogeny, the cranial ornamentation (nuchal crest, sagittal crest, and temporal lines) of males and females of *H. aquaticus* undergoes several morphological changes (Fig. 14). At w0 and w1 (n=7), very fine nuchal crests are already visible, but the sagittal crest and temporal lines are not formed yet. Between w2 (n=2) and w3 (n=5), the temporal lines are crest-like in morphology but do not confine to form the sagittal crest yet and the nuchal crests become stronger. Between wear stage 3 and 4 cranial ornamentation forms in all individuals of this study with the temporal lines merging posteriorly to form the sagittal crest. Albeit, in one female individual of wear stage 3 (83006M 473, Fig. 13N) the sagittal crest is not formed yet, but instead the temporal lines run parallel dorsally. Another female individual (83006M 474, Fig. 13M) at the same wear stage has a well-developed sagittal crest. From w4 to w7 males (n=3) and females (n=17) can show different extends of the development of the cranial ornamentation also within the same wear stage. In this sample, females of wear stage 4 and males at wear stage 5 and 6 represent the strongest variation. Here the sagittal crest in both sexes can be broad and flat, with the temporal lines running parallel dorsally to form a flat plateau between them (R.G. 10332, Fig. 13C; R.G. 3366, Fig. 13D; R.G. 13979, Fig. 13), similar to the condition in one skull described by (Vislobokova 2001), or crest-like, sharp, and high, without the formation of the plateau (80-36-M-75, Fig. 13B; R.G. 579, Fig. 13E; R.G. 8333, Fig. 13K). Obviously, there is a large degree of variation within the development of the cranial ornamentation within subadult and young adult *H. aquaticus* and females of same wear stages can have stronger or similar strong sagittal crests and temporal lines as comparable males (compare Figs. 13B, C, I). The difference in the nuchal crests is not as remarkable as the morphological variability of the sagittal crest and temporal lines.

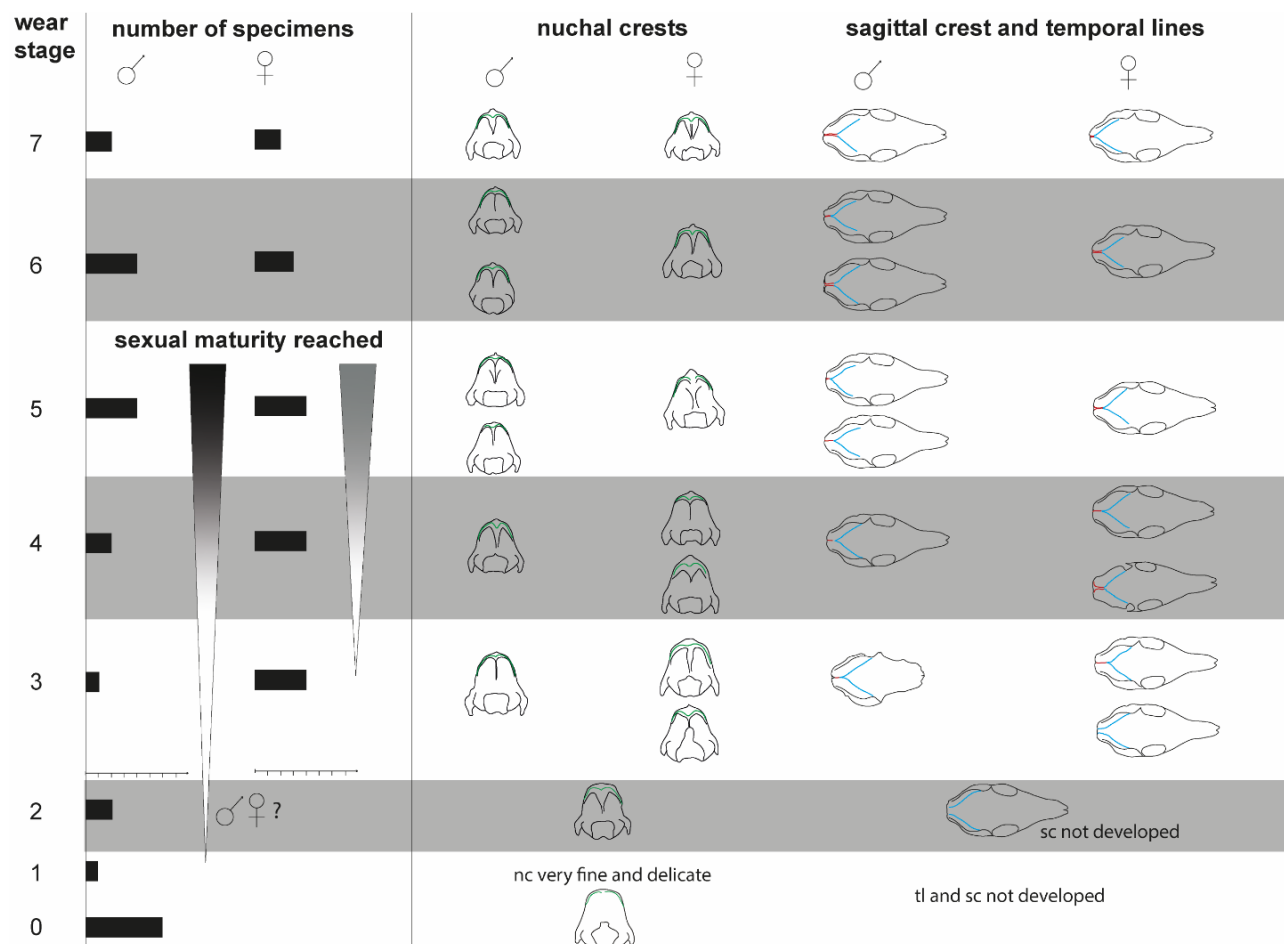


Figure 14: Ontogenetic cranial development of *Hyemoschus aquaticus*. Ontogenetic stages are represented as wear stages. Development of sexual maturity is symbolized by shaded arrows. Incorporated from results of Dubost (2016) males start at 5–9 months (wear stage 1) and complete sexual maturity at 17–27 months (wear stage 5), whereas in females sexual development starts after 10–16 months (wear stage 3) and completes at 27 months (wear stage 5). Right side shows cranial development of nuchal crests (green), sagittal crest (red), as well as temporal lines (blue). Line drawings not to scale. **Abbreviations:** nc, nuchal crests; sc, sagittal crest; tl, temporal lines

4.3.2 Sexual maturity in *H. aquaticus*

The wear stage analysis was based on incorporated results of Dubost (2016), who studied captive African water chevrotain. He studied not only mating behavior, but also the onset of sexual maturity based on testicle mass, diameter of the seminiferous tubules, and production of spermatozoa in males and ovary mass and the presence of corpora lutea in females. The results showed that sexual maturity in males starts at 5–9 months (wear stage 1) and completes at 17–27 months (wear stage 5), whereas in females sexual development starts after 10–16 months (wear stage 3) and completes at 27 months (wear stage 5). The morphological analysis of the skulls from the RMCA revealed that in males the development of cranial crests, such as the nuchal crests and sagittal crest, become stronger at wear stage 3 (Fig. 13 and 14) were the temporal lines confine to form the sagittal crest. Moreover, the

formation of the sagittal crest and the enhancement of the nuchal crests apparently coincides with the eruption of the large upper permanent canine. The cranial development of females at wear stage 3 is similar compared to the male individual regarding the extend of the development of the sagittal and nuchal crests (Fig. 13). The temporal lines, in contrast, are already visible at wear stage 2, but do not confine to form the sagittal crest yet (Fig. 14). However, there is one female specimen at wear stage 3, 83006M 473 (Fig. 13N), not exhibiting the formation of the sagittal crest yet. Instead, the temporal lines are still separated. This might be because this individual is at a very early stage of wear stage 3 compared to the other specimens. This narrows the timing of the development of the sagittal crest, which occurs in this sample at early wear stage 3 at about approximately 13 months in age. Later, between wear stage 4 and wear stage 7, the development of the temporal lines, the sagittal, as well as the nuchal crests is very variable among the sexes and among age classes and shows no tendency towards stronger crests in individuals of late ontogenetic stages. This indicates that the development of these crests begins at wear stage 0, where they are faint and delicate but already visible shortly after birth, and progressively become more pronounced and crest-like, merging posteriorly to contribute to the formation of the sagittal crest by wear stages 3–4.

The ontogenetic series of males and females of *H. aquaticus* shows that females in comparison to males of the same wear stage can have stronger or at least similar developed cranial crests as comparable males and therefore, the degree of cranial ornamentation might not be diagnostic to sex at all. Mennecart et al. (2018a) assumed that females of *H. aquaticus* and juveniles show weaker cranial crests than males, but this argument was based on a limited number of individuals and the analysis of 39 specimens showed that there is no such evidence. The degree of cranial ornamentation is quite similar between males and females of comparable ages and is therefore not suitable as a primary feature of distinction among the sexes and ages from wear stage 3 and onwards. Neonate and juvenile specimens from wear stage 0-2, however, exhibit a different skull morphology as they show very fine nuchal crests, but the sagittal crest and temporal lines are not fully formed yet. Therefore, they can be separated morphologically from the subadult to adult morphotype.

The large dataset of *Hyemoschus aquaticus* skulls also enabled an assessment of the relationship between the eruption of the M3 and the completion of sexual maturity. In *Hyemoschus*, sexual maturity is reached at approximately 27 months in both males and females, corresponding to wear stage 5. The eruption of the upper M3 occurs within a similar time span, between 17 and 27 months (wear stage 5), according to Dubost (2016) and

Hartung and Böhme (2024). Therefore, the hypothesis that the completion of sexual maturity coincides with the eruption of the M3 holds true for *H. aquaticus*.

Asher and Lehmann (2008) examined several mammalian taxa, including *Bos*, *Sus*, *Hippopotamus*, and *Lama*, and found that in the studied artiodactyl taxa sexual maturity is typically reached before the eruption of the M3 and the completion of tooth development. This pattern may differ from that observed in female *Hyemoschus*, where both events occur at approximately the same time (maximum age at completion of dental development/female sexual maturity=1 according to Asher and Lehmann 2008). This difference may be related to dietary adaptations, lifespan, or reproductive strategy. *Hippopotamus* and *Bos* for example show values of 1.8 and 2 respectively, with an age of M3 eruption 16 years in *Hippopotamus* and 3 years in *Bos* and the age of females completing sexual maturity is 9 years and 1.5 years respectively.

4.4 Ontogeny of the skull of *Dorcatherium nauti*

Based on the description of sexual dimorphism in *Dorcatherium nauti* from Hammerschmiede and Eppelsheim and the definition of dental wear stages, a total of 14 skulls of *D. nauti*, including previously described specimens, were assigned to an ontogenetic series (Fig. 15). The assignment can be found in detail in Hartung and Böhme (2026, manuscript submitted).

In males, the cranial ornamentation becomes progressively more pronounced throughout ontogeny, resulting in larger, higher, and more robust frontoparietal bulges as well as the development of a distinct parietal plateau. Specimen SNSB-BSPG 2020 XCIV-8518 (Fig. 15E) represents the youngest individual of this series and exhibits only very faint frontal bulges. The parietal component of the cranial ornamentation is already present and pneumatized, forming a small parietal plateau. This specimen most likely corresponds to an early wear stage 3, but is clearly younger than SNSB-BSPG 2020 XCIV-3500 (wear stage 3-4; Fig. 15D), which displays enlarged parietal bulges, which are strongly pneumatized and merge into already visible frontal bulges. In subsequent specimens, the cranial ornamentation becomes progressively more pronounced and reaches its greatest extent in GPIT/MA/17690 (Fig. 15A). Although this specimen does not preserve any teeth, the degree of cranial ornamentation suggests that it represents the oldest individual of this series. Its exact age, however, cannot be determined. In contrast, females show comparatively little morphological change, with the temporal lines, sagittal crest, and nuchal crest maintaining a largely constant morphology throughout ontogeny (compare Fig. 15F-J).

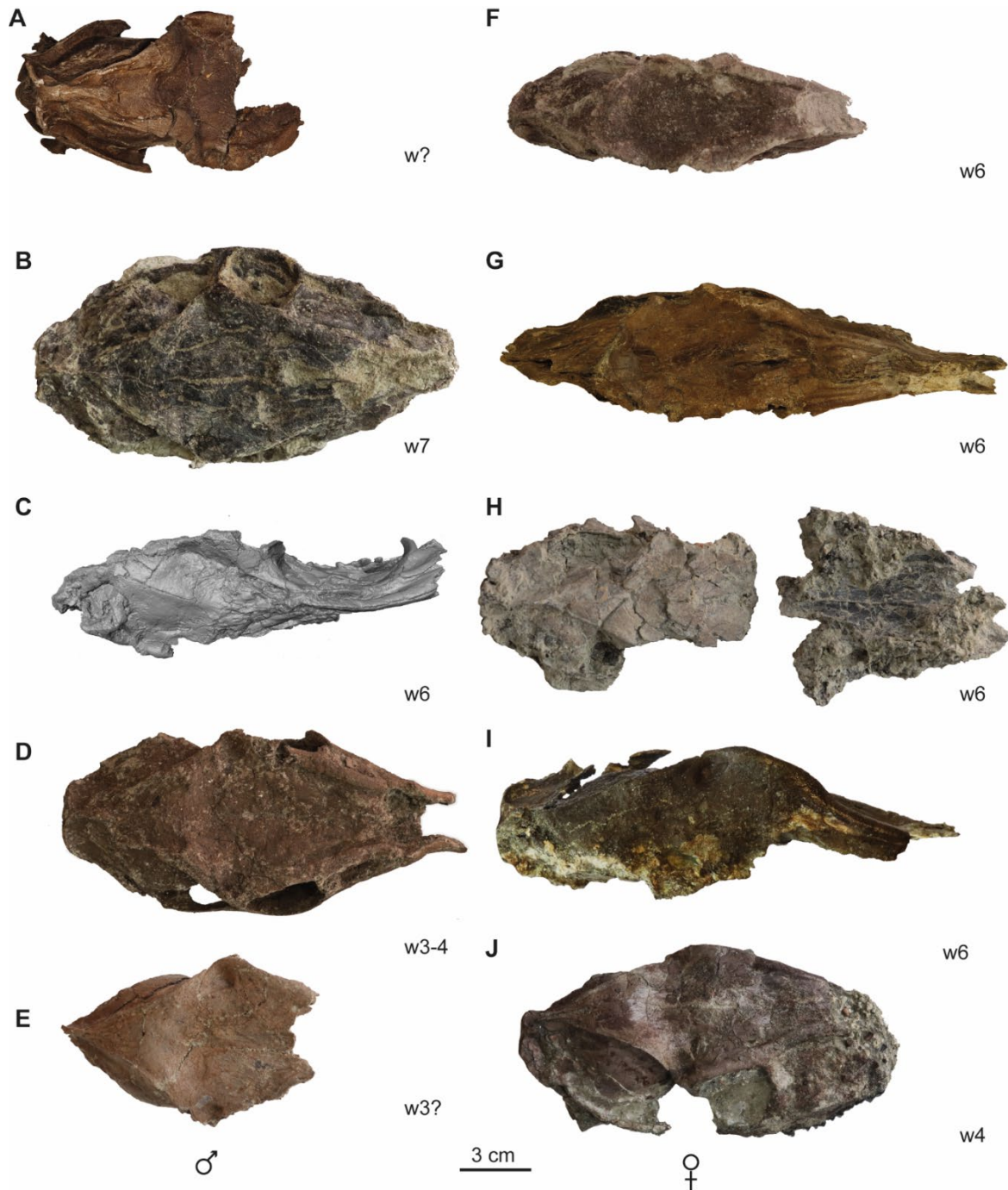


Figure 15: *Dorcatherium naui* from the late Miocene Hammerschmiede locality level HAM4 and HAM5, as well as from the middle to late Miocene locality of Eppelsheim. Adult and juvenile males and females in dorsal view. **A-E** males, **A)** adult without teeth GPIT/MA/17690 from Hammerschmiede level HAM4, **B)** adult SNSB-BSPG 2020 XCV-474 at wear stage 7 from Hammerschmiede level HAM5, **C)** adult NHMUK PV OR 40632 at wear stage 6 from Eppelsheim, **D)** juvenile SNSB-BSPG 2020 XCIV-3500 at wear stage 3-4 from Hammerschmiede level HAM4, **E)** SNSB-BSPG 2020 XCIV-8518 unknown wear stage from Hammerschmiede level HAM4. Based on weak morphology of the cranial crests, the skull is younger than wear stage 3-4, probably early wear stage 3. **F-I** females of determined ontogenetic stage, **F)** adult GPIT/MA/17841 at wear stage 6 from Hammerschmiede level HAM4, **G)** adult GPIT/MA/18000-01 at wear stage 6 from Hammerschmiede level HAM4, **H)** adult SNSB-BSPG 2020 XCV-357, 380 at wear stage 6 from Hammerschmiede level HAM5, **I)** adult SNSB-BSPG 2020 XCIV-18870 at wear stage 6 from Hammerschmiede level HAM4, **J)** SNSB-BSPG 2020 XCIV-8970 at wear stage 4 from Hammerschmiede level HAM4. **Abbreviations:** w, wear stage

In females, the sagittal crests are already visible at wear stage 3-4 as in specimen SNSB-BSPG 2020 XCIV-8970 (Fig. 15J), and these crests are similar in development and morphology with adult specimens of wear stage 6 as in specimen SNSB-BSPG 2020 XCV-357, 380, GPIT/MA/17841, GPIT/MA/18000-01, and SNSB-BSPG XCIV 2020-18870 (Fig. 15F-I). In the virtual cross sections, no pneumatization as in males is visible (Hartung and Böhme 2026, manuscript submitted, fig. 5E-G).

4.4.1 Comparative ontogenetic skull development of *D. nauti* and *H. aquaticus*

In extant tragulids such as *H. aquaticus*, males also show well-developed large, saber-like upper canines in contrast to females, where the upper canines are reduced, similar to fossil tragulids (Rössner 2007). However, cranial ornamentation varies among adult males and females of this species (Hartung and Böhme 2024) and in the other extant tragulid genera, *Moschiola* and *Tragulus*, the cranial crests are reduced (Guzmán 2018; Menecart et al. 2018a and own observations). In contrast, in the fossil tragulid *D. nauti* the cranial ornamentation is much stronger developed than in *H. aquaticus* (compare Fig. 13 and 15). The sagittal crest and the nuchal crests are comparable in their morphology to *H. aquaticus*, but they are much more constricted and offset in *D. nauti*. The largest difference between both species are the remarkable frontoparietal bulges of *D. nauti*, which are formed by the temporal lines on the parietal and an extension of the latter onto the frontal, anterior to the orbit. They are large, bony bulges, and form the parietal part which constricts a parietal plateau. The frontoparietal bulges are not known from any other tragulid so far (Hartung and Böhme 2022). These bulges only develop in males of *D. nauti* and are already present at wear stage 3-4 in SNSB-BSPG 2020 XCIV-3500 (Fig. 15D) if not even earlier as in SNSB-BSPG 2020 XCIV-8518 (Fig. 15E), who might correspond to an early wear stage 3. Cranial ornamentation in *H. aquaticus* are less remarkable at wear stage 3-4 (Hartung and Böhme 2024, fig. 2 and 3, Fig. 13) where only the temporal lines are slightly enhanced and confine to form a sagittal crest.

The present ontogenetic series of *D. nauti* indicates that males of *D. nauti* possess strong sexual dimorphic features already relatively early in life similar to *H. aquaticus*. The bulges show allometric growth if compared to overall body size as typical for male sexual display features (Kodric-Brown et al. 2006). Females in contrast are much more similar to extant *H. aquaticus* by possessing delicate and fine sagittal and nuchal crests and no frontoparietal bulges. From wear stage 4 onwards, the cranial ornamentation of females shows little morphological change throughout ontogeny, similar to the condition observed in *Hyemoschus*. However, no female skulls of *D. nauti* representing younger individuals are

currently known, and the development of cranial crests prior to wear stage 4 therefore remains unknown.

In *D. nauti*, females and males show a different skull morphotype and can be clearly separated even without the presence of an upper canine. This is in contrast to *H. aquaticus*. It is noticeable, that the extend of cranial ornamentation of *H. aquaticus* varies among the sexes in such an extent, that it is not an inclusive feature to distinguish among the sexes and therefore upper canine size remains the most reliable character for sex differentiation in this species. Comparisons of skulls of *D. nauti* and *H. aquaticus* should be taken with care and the pronounced sexual dimorphism of *D. nauti* should be considered when using *H. aquaticus* as a modern analogue.

4.4.2 Comparison of cranial ontogeny of *D. nauti* and *Db. crassum*

In skulls of *Db. crassum* (Seehuber 2015; Guzmán 2018; Mennecart et al. 2018a), males have cranial ornamentation in form of bulges as well, but they differ in their morphology and are in general less developed if compared to *D. nauti*. In *Db. crassum*, the frontal bulges are absent and only the posterior part of the parietal shows flatter bulges that confine to form a Y-structure with the sagittal crest (Guzmán 2018, fig. 4.5 and Mennecart et al. 2018a, fig. 3). This is different from *D. nauti*, where the bulges encompass the entire parietal and continue onto the frontal to encompass a parietal plateau and cover the orbit (Hartung and Böhme 2022). The female of *Db. crassum* in contrast is quite similar in its skull morphology if compared to females of *D. nauti* and both sexes of *H. aquaticus*, because it contains fine and delicate nuchal, temporal, and sagittal crests that follow the same morphology. It can be directly compared to GPIT/MA/17841, GPIT/MA/18000-01, as well as to SNSB-BSPG 2020 XCV-357, 380, and SNSB-BSPG XCIV-18870 as they are all at wear stage 6.

Based on the wear stage of the teeth, the male skull of *Db. crassum* from Walda-2 is already senile, as there is no selenodont pattern visible anymore at the M3 (wear stage 8). It is therefore not directly comparable to any of the present specimens of *D. nauti* and unfortunately the exact individual age of GPIT/MA/16790 is not known, although it can be assumed that this specimen is the ontogenetic oldest from the presented series. However, the difference in the development of the cranial ornamentation is still visible and it is very unlikely that after wear stage 6 a pattern as in *Db. crassum* will be present in senile males of *D. nauti*, because the parietal and frontoparietal bulges are already well-developed and confine with the sagittal crest posteriorly. Therefore, *D. nauti* and *Db. crassum* exhibit clearly distinct ornamentation patterns.

4.4.3 Comparative sexual maturity of *D. nauti* and *H. aquaticus*

In *H. aquaticus*, sexual maturity of males develops between wear stage 3 and 4 (Fig. 13 and chapter 4.3.2) at about 5-9 and at wear stage 5 at 17-27 months and between 10–16 months in females, whereas it completes at 27 months (Dubost 2016). In *D. nauti* well-developed cranial ornamentation in males in form of frontoparietal bulges are already visible at the same ontogenetic age at wear stage 3 to 4, probably even earlier at wear stage 3 similar to *H. aquaticus* (Fig. 15). Because weapons or display features need to be ready as close to adult form as possible by the time they reach sexual maturity to compete successfully for mating (Calamari 2016), I assume that the onset of sexual maturity in *D. nauti* starts at least at wear stage 3-4, if not earlier at an early wear stage 3 (SNSB-BSPG 2020 XCIV-8518, Fig. 15E), similar to *H. aquaticus* (see chapter 4.3.2 and 4.4.1 for more detail). Based on the correlation between age constraints and patterns of tooth eruption and wear, it is suggested that the eruption of the M3 in *Dorcatherium nauti* occurred at approximately the same time as in *H. aquaticus*, namely when the process of sexual maturation is completed (wear stage 5). In contrast, in other artiodactyl taxa studied by Asher and Lehmann (2008), female sexual maturity is reached before the eruption of the M3 and the completion of tooth development.

4.4.4 Interspecific heterochrony

D. nauti is closely related to the extant water chevrotain *H. aquaticus*. The exact relationships were studied last by Sánchez et al. (2015, 2018) where *D. nauti* plotted as the sister taxon to *H. aquaticus*. However, phylogenetic relationships might have been much more complex due to the limit of the fossil record in Africa for example. Both species share similarities in cranial morphology and *H. aquaticus* shows the strongest cranial ornamentation among the extant tragulids, however, *D. nauti* displays a markedly stronger and more intricate cranial ornamentation compared to the extant analogues, suggesting a heterochronic origin of this feature. To test this hypothesis, the heterochrony model of Reilly et al. (1997) was applied, which investigates patterns of morphological change between ancestral and descendant taxa. For this purpose, the morphology of cranial ornamentation in *Dorcatherium nauti* (Hartung and Böhme 2022) is defined as the “ancestral state”, whereas the cranial morphology of *Hyemoschus aquaticus* (Hartung and Böhme 2024) represents the “descendant state”, based on the currently available phylogenetic framework. To incorporate a temporal dimension, the age model established for *H. aquaticus* by Dubost (2016) was applied to *D. nauti* (Hartung and Böhme 2024) and the ontogenetic trajectory of cranial ornamentation was reconstructed by establishing an ontogenetic series based on dental wear stages (Figs. 15). Dental wear stages follow the classification proposed by Hartung and Böhme (2024). We further assume that the onset of sexual maturity in *D. nauti* and *H.*

aquaticus was relatively similar, if not identical (see chapter 4.4.3). This assumption allows a direct comparison of the somatic development of cranial ornamentation throughout ontogeny between both taxa.

After Reilly et al. (1997) a paedomorphic development of the cranial ornamentation (Fig. 17) in *Hyemoschus aquaticus* compared to *D. navi* is present, a truncation of the fossil ontogeny compared to the morphology of the extant analogue caused by a “deceleration” of the development of the morphological character. This was already mentioned for *Db. crassum* (Mennecart et al. 2018), which likewise exhibits pronounced cranial crests that are morphologically similar to those of *D. navi* (Hartung and Böhme 2022 and chapter 4.4.2). In contrast, *H. aquaticus* shows less developed cranial crests and bulges, as well as the absence of a parietal plateau, when compared to *D. navi*. I hypothesize that the onset of cranial ornamentation growth (α) is similar in both taxa, but that a higher developmental rate ($-k$) in *D. navi* results in more complex and developed cranial structures by the time developmental offset (β) is attained.

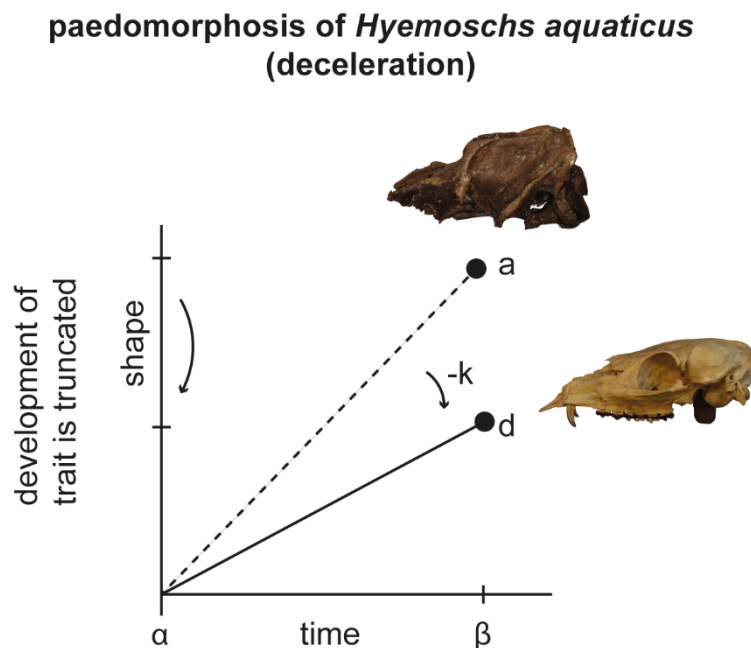


Figure 16: Heterochronic process of *D. navi* (fossil tragulid) and *H. aquaticus* (extant chevrotain) after Reilly et al. (1997). *D. navi* shows a hyperdevelopment of cranial crests and bulges if compared to *H. aquaticus* leading to a paedomorphic state (deceleration and truncation of “ancestral development”) of the cranial ornamentation in *H. aquaticus*. **Abbreviations:** α , age of onset of growth of morphological structure (here cranial ornamentation like e.g. frontoparietal bulges); a, ancestor (here: *Dorcatherium navi*); β , age when offset shape of morphological structure is attained; d, descendent (here: *Hyemoschus aquaticus*); k, rate of shape development

It is also possible to argue for a post-displacement (positive onset, fig. 1 in Reilly et al. 1997) of the shape development, in which a delayed onset in the extant tragulid relative to the fossil one is present. In this scenario, the development of cranial crests starts earlier during ontogeny in *D. nauti* and has therefore more time to develop. Thus, the initiation of cranial-crest growth in *Hyemoschus* would occur at a later time, resulting in a shortened developmental interval and reduced crest elaboration compared to *D. nauti* ($\alpha \rightarrow \alpha_1$). The developmental rate however, would be the same in contrast to a paedomorphosis and the onset time (β) would be similar. Whether this developmental process in *D. nauti* is really beginning earlier if compared to *H. aquaticus*, cannot be conclusively said at the moment, because neonate to juvenile skulls of wear stage 0 to wear stage 2 are so far not present in *D. nauti* or any other fossil tragulid.

When comparing another fossil tragulid with well-known skulls, *Db. crassum*, to *H. aquaticus*, both taxa show greater morphological similarity to each other than to *D. nauti* respectively. In *Db. crassum* and *H. aquaticus*, the frontal component of the cranial bulges as well as the parietal plateau are absent. In addition, *Db. crassum* exhibits broader temporal lines and a more pronounced sagittal crest, forming the characteristic Y-shaped structure. This configuration has been interpreted as a hyperdeveloped condition relative to *H. aquaticus* according to Mennecart et al. (2018), which is consistent with a heterochronic shift involving post-displacement. Consequently, *Db. crassum* may reflect a heterochronic trajectory that differs from the pattern most likely inferred for *H. aquaticus* and *D. nauti*.

The morphological differences in the elaboration of cranial ornamentation and shape of the latter between *D. nauti* and *H. aquaticus* are less-likely to be a result of hypomorphosis, because this would mean that the developmental process ends earlier in *H. aquaticus*, while *D. nauti* extends even further, truncating the fossil ontogeny. Both taxa would have the same onset time, and the pathway of development would be similar, which is clearly not the case, because the cranial morphology in *D. nauti* is different from *H. aquaticus* and even in juvenile male individuals of *D. nauti* (SNSB-BSPG 2020 XCIV-3500 wear stage 3-4 and SNSB-BSPG 2020 XCIV-8518, probably early wear stage 3), the cranial bulges are morphologically clearly distinguishable from the extant tragulid. *D. nauti* exhibits frontoparietal bulges that constrict a parietal plateau and form a strong broad sagittal crest (Hartung and Böhme 2022). In *H. aquaticus*, the temporal lines are enhanced and also the sagittal crest can be broad and strong, but the frontoparietal bulges, as well as the parietal plateau are absent. Moreover, the cranial ornamentation in *H. aquaticus* continues to grow even in senile specimen (fig. 2 in Hartung and Böhme 2022) and the same can be assumed for *D. nauti* based on the morphology of GPIT/MA/17690 (Fig. 15A). Nevertheless, *H. aquaticus* appears

unable to attain the degree of cranial complexity exhibited by *D. naui* and thus no hypomorphosis is present.

Conclusively, *D. naui* already exhibits a strong sexual dimorphism relatively early in life similar to *H. aquaticus*, the only extant tragulid with noticeable cranial ornamentation. The development of these structures has a higher rate in the fossil relative. A comparison to other fossil subadult (wear stage 3-4) tragulids, such as *Db. crassum*, would be very interesting, however, no skulls of that age exist so far. It is noticeable, that the extend of cranial ornamentation of *H. aquaticus* varies among the sexes in such an extent, that it is not an inclusive feature to distinguish among the sexes and therefore upper canine size remains the most reliable character for sex differentiation in this species. This is a contrast to the fossils *D. naui* and *Db. crassum* and therefore comparison of skulls of *Hyemoschus* with *D. naui* as well as with *Db. crassum* need to be taken with care.

4.4.5 Mortality analysis, survivorship rate, and body mass of *D. naui*

The mortality profile of *D. naui* individuals from Hammerschmiede was assessed based on the state of wear of the M3 and dP4, as well as of the lower equivalent m3 and dp4 according to wear stages established by Hartung and Böhme (2024). Based on the upper and lower teeth combined, in HAM4, the total number of individuals that died at a juvenile stage (w0-w5) is 22 and the number of individuals that died at an adult or senile stage (w6-w8) is 22 as well (Fig. 17). At HAM5, the sample size is much smaller and no dP4 of wear stage 0 and wear stage 1 are available. However, the pattern is similar to HAM4, because in HAM5, six individuals died at juvenile stage and seven at an adult stage respectively. The low number of juveniles, combined with the high total number of individuals (MNI=44) at HAM4, indicates that juvenile survivorship reached 50%, meaning that every second individual completes sexual maturity. The same can be attributed to the individuals from HAM5, but has to be taken with some care because of the lower sample size (MNI=13).

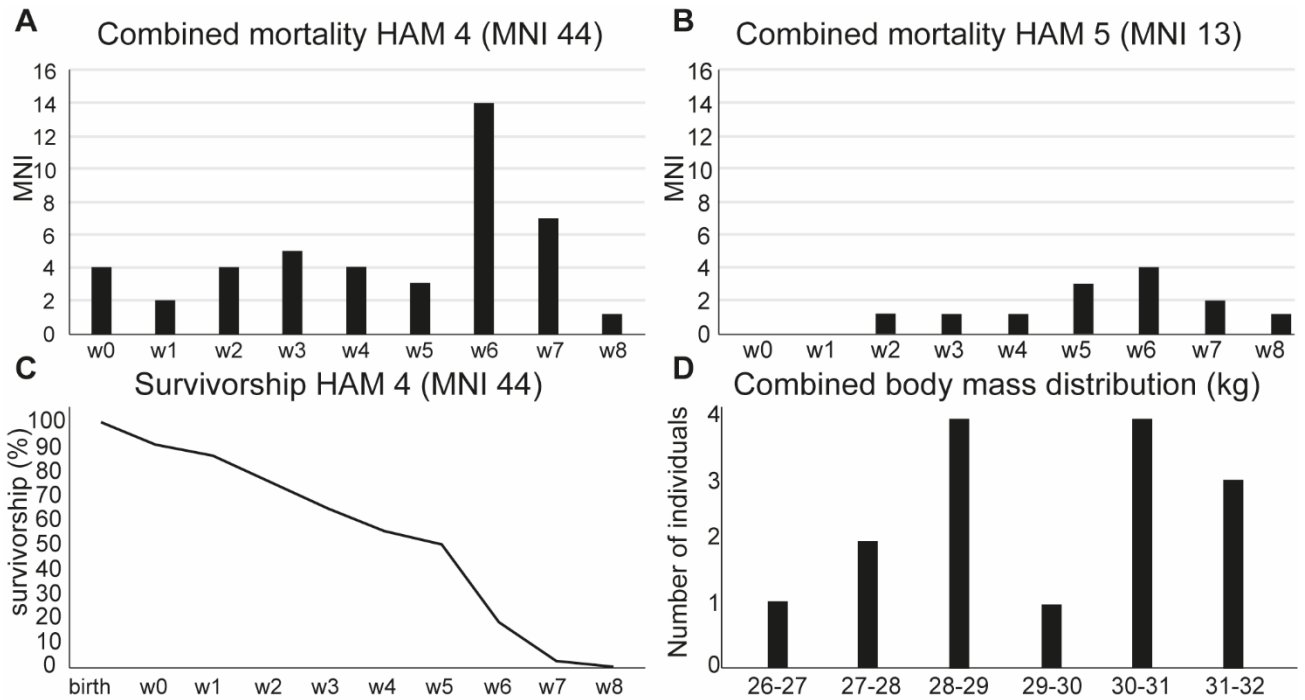


Figure 17: Results of the mortality analysis and body mass estimations for individuals of *D. naui* from Hammerschmiede (HAM4 and HAM5). **A)** Results of the combined mortality study based on the upper M3, dP4, as well as on the lower m3 and dp4 for HAM4 and **B)** for HAM5; **C)** Survivorship for HAM4 based on the combined mortality analysis and **D)** Body mass estimations based on the length of m1-m3 and m2 combined showing a bimodality with skulls attributed to females falling within the heavier range. **Abbreviations:** w, wear stage

For body mass estimates on the combined HAM5 and HAM4 sample we use the log-transformed regressions of Janis (1990) for lower molar length (m1-m3) and length of m2. Body mass according to lower molar length range from 29.1 to 35.4 kg (mean 32 kg, n=15) and for m2 length from 22.2 to 31.2 kg (mean 27.2 kg, n=21). A combined estimate using both regressions on 15 adult mandibles results in body mass between 26.2 and 31.7 kg, with a mean of 29.4 kg. The individual body mass estimates show a bimodal distribution with peaks at 28-29 kg and 30-31 kg (Fig. 17D). The female skull GPIT/MA/18000-01 contains a mandible as well, which was already published in Hartung and Böhme (2022). The estimated body mass of this female was estimated to 31.2 kg (32.6 kg using m1-m3 regression, 29.9 kg using m2 regression), suggesting to attribute the heavier mode to females and the lighter mode to male individuals. This attribution is corroborated by the even larger juvenile female skull SNSB-BSPG 2020 XCIV-08968, which includes both hemimandibles with dp1-m2. The size of their m2s are among the largest in our Hammerschmiede sample and indicate a body mass of 30.7 kg using the m2 regression.

4.5 Behavioral ecology of fossil tragulids

The skulls studied herein represent a valuable window in time, allowing not only the study of overall anatomy and associated sexual dimorphism or ontogeny, but also providing insight into the behavioral ecology of the group.

4.5.1 Interpretation of the function of cranial ornamentation in *Dorcatherium*

Tragulids represent the sister group to Pecora, which are characterized by a remarkable morphological diversity of cranial appendages, giving rise to a wide range of headgear types such as antlers, horns, pronghorns, and ossicones (Davis et al. 2011), used for sexual display and during intra-specific combat (Clutton-Brock 1982; Janis 1982, 1990; Caro et al. 2003; Calamari 2016; Landete-Castillejos et al. 2019). Among living ruminants, tragulids are a non-pecoran group, lacking cranial appendages sensu Davis et al. (2011). The fossil skulls of *D. nauti* from Hammerschmiede and Eppelsheim demonstrate that males of the type species of *Dorcatherium* developed frontoparietal bulges, a form of cranial ornamentation previously unknown among both extant and fossil tragulids. In the closely related *Db. crassum*, cranial ornamentation is visible as well, but it is not as prominent as in *D. nauti* and differs in morphology (see chapter 4.4.2). In *D. nauti*, these bulges are well-developed and markedly set off from the skull roof. They show a rough surface, while the rest of the skull roof has a smooth surface texture similar to some types of headgear known from Pecora (e.g. Davis et al. 2011; Danowitz et al. 2017; Nasoori 2020). Moreover, the results of the μ CT-analysis of the male skulls of *D. nauti* at different ontogenetic ages revealed that the internal structure is quite similar to bovid horn cores or giraffe ossicones, by being porous or cancellous with surrounding compact bone (Hartung and Böhme 2026, manuscript submitted, fig. 5; compare Geist 1966, fig. 2 and Hartung et al. 2020, fig. 4).

These frontoparietal bulges are only present in males of *D. nauti* as in Pecora, where cranial appendages are mainly present and stronger developed in males than in females (Janis 1982, 1990; Caro et al. 2003; Stankowich and Caro 2009; Davis et al. 2011). The bulges in *Dorcatherium* are difficult to interpret, because there is no analogue in tragulids or any other closer related group except Pecora. However, we here interpret that these bulges were probably used in a similar way as in Pecora—most likely for sexual display (Fig. 18).



Figure 18: Life reconstruction of male (left) and female (right) *Dorcatherium nauti*. Illustration by Peter Nickolaus

These bulges, furthermore, cover the dorsal eye-region and could be used in analogy to the frontal bony ridges of extant male *Muntiacus* (Cervidae) which are interpreted to function as a protection against tusk-wounding during male-male combats (Croitor 2001; Croitor and Stefaniak 2009). The fighting behavior of extant tragulids is dominated by slashing and stabbing with the large upper canines (Dubost and Terrade 1970; Rössner 2007) and therefore they develop toughened skin on their backs forming a shield for protection. Hence, an additional protection of the eye region in male *D. nauti* might be useful. However, the interpretation of these structures as display features appears to be the most parsimonious explanation.

4.5.2 Cranial ornamentation and upper canines as display features of *D. nauti*

The present ontogenetic series of *D. nauti* indicates allometric growth pattern of the cranial ornamentation as typical for male display features (Kodric-Brown et al. 2006). During ontogeny, an increase in size and development of frontoparietal bulges occurs in males. The latter possess pronounced and well-developed display features of the skull already at a relatively early ontogenetic stage (wear stage 3-4 or even earlier as in SNSB-BSPG 2020 XCIV-8518 at an early wear stage 3) similar to *H. aquaticus*, where the cranial crests (temporal lines and sagittal crest) start to develop at wear stage 3-4. Thus, the enhancement and strong expression of this cranial trait of *D. nauti* shows that the development of the latter might start relatively early in life and correlates with the process of sexual maturation, similar to the extant *H. aquaticus*, because weapons or display features need to be ready as close to adult form as possible by the time they reach sexual maturity to compete successfully for mating (Calamari 2016).

However, it was stated in Hartung and Böhme (2024) that cranial ornamentation in *H. aquaticus* is not suitable for distinguishing among the sexes and might therefore not even be a display feature at all, instead upper canine size is the most reliable character for differentiation as females only show small rudimentary upper canines in contrast to males, who have saber-like canines. These upper canines erupt at wear stage 3 when the small and cone-like deciduous upper canines are shed. This event happens within the time frame of sexual maturation in male *H. aquaticus*, but is probably not a reliable proxy for the onset of sexual maturity alone. Maturation represents a gradual process extending from wear stage 1 to wear stage 5. In males, two main developmental milestones are observed at approximately 5–9 months (wear stage 1) and 17–27 months (wear stage 5), whereas in females major developmental changes occur between 10–16 months (wear stage 3), with full maturation reached at around 27 months (wear stage 5 according to Dubost 2016 and Hartung and Böhme 2024).

In addition to the beforementioned strong cranial ornamentation, *D. nauti* also possesses saber-like upper canines as visible in NHMUK PV OR 40632. The presence of both structures could, in turn, suggest that the intraspecific competition for females was relatively high and that the social behavior of *D. nauti* differs from *H. aquaticus*, possibly involving a more complex social structure than in the extant species, which lacks any hierarchical organization or strong territorial behavior and lives mainly solitary (Dubost 1975). Although, during mating season, extant males have short combats where they use their upper canines as weapons for stabbing or slashing. It might be possible that *D. nauti* rather used frontoparietal bulges as display features than stabbing each other, leading to less fatal combat outcomes (Hartung and Böhme 2022). This would also be consistent with the theory of Calamari (2016), who states that complex sexual competition structures, like the described cranial ornamentation in *D. nauti*, were used in non-lethal combat or ritualized male-male fights in contrast to simple structures that are commonly used for more violent fighting behavior, like the upper canines.

4.5.3 Reproductive traits, life-history patterns, and habitats

Results of the mortality analysis and the survivorship rate of the HAM4 population of *D. nauti* (Fig. 17A-C) revealed that 50% of newborn tragulids (22 out of MNI=44) survive the juvenile stage (w0-w5) and reach adulthood (w6-w8). Survivorship (mortality) strongly decrease (increase) for prime adults (w6 and w7), and only one individual reached wear stage 8. In HAM5 the MNI is smaller (MNI=13) compared to HAM4, but still most individuals die at wear stage 6 similar to HAM4. The juvenile stage seems to be underrepresented with no individuals of wear stage 0 and wear stage 1. It is not surprising that most individuals die at wear stage 6, because it covers a similar long period (approximately 27 Months to 4.5 years in *Hyemoschus aquaticus*, Dubost 2016) as all juvenile stages (w0-w5) together.

The relatively high survivorship of juveniles suggests that *D. nauti* likely exhibited a low reproductive rate, potentially resulting from small litter sizes and a reduced number of reproductive events over the female life span. The litter size in *Hyemoschus* is very small with only one young per litter (Dubost 2016) and we assume the same for *D. nauti*. Moreover, given the equal number of juveniles compared to adults (Fig. 17), it is possible that females of *D. nauti* had only very few, possibly four, reproductive events throughout their life time resulting in a low reproductive rate. This may indicate that in *D. nauti* senility is reached after an age of six years, which compares well with *H. aquaticus* (wear stage 8 at >6.5 years; Dubost 2016, Hartung and Böhme 2024), and may suggest that the maximum life span of both species was relatively short (maximum age in wild populations of *H. aquaticus* is normally eight years and potentially 11-13 years according to Meijaard 2011).

Body size analysis in form of body mass calculations revealed that females tend to be larger than males, in which females of *D. nauti* are on average approximately 2 kg or 7% heavier than males (Fig. 17D). The mean weight for males lies within a range of 28-29 kg and females reach a mass of 30-31 kg. *Hyemoschus* displays a slightly larger sexual size dimorphism (SSD) pattern where males have an average weight of 9.7 kg and females around 12 kg (Robin 1990; Nowak 1999). However, the most pronounced difference between both species is the absolute body mass, which in *D. nauti* is more than twice as high as in *H. aquaticus*. This important biologic feature may reflect ecological adaptations in more seasonal and open deciduous broadleaf forests during the Miocene of Europe, compared to the thickets of African rainforests where *Hyemoschus* is living. Smaller body size in extant tragulids may facilitate concealment and escape from predators in densely vegetated habitats (Rössner 2007; Meijaard 2011). A preference of *D. nauti* to more open riparian woodlands would be supported by the high numbers of individuals found in HAM4

(MNI=44), making here this species to the most abundant large mammal, whereas in the HAM5 level *D. naui* (MNI=13) is outcompeted by the deer *Euprox furcatus* (MNI=21).

This female-biased SSD is common among mammals and is especially known from smaller mammals as for example Lagomorpha (Darwin 1871; Lindenfors et al. 2007; Tombak et al. 2024). It is explained by a higher fecundity selection in small mammals (Darwin 1871), because of higher energetic demands on females like producing eggs in comparison to sperm, gestation, and lactation, and more space that is used for keeping the eggs. Therefore, female mammals of smaller species develop larger energy stores for high metabolic costs of gestation and lactation, ultimately promoting higher offspring survivorship and reproductive success. However, this theory does not always apply because male sexual selection strategy is often based on a larger body size in males compared to females, which is used for competition with other males (Darwin 1871; Alexander and Borgia 1979; Weckerly 1998; Lindenfors et al. 2007; Cassini 2020a, b, 2022, 2023).

5 Conclusion

The present study demonstrates that fossil tragulids differed substantially from extant representatives with respect to cranial morphology and body dimensions, as exemplified by the type species of the most widely used fossil genus, *Dorcatherium nauti*. The results clearly show that *D. nauti* cannot be regarded as a simple morphological analogue of living tragulids, highlighting the need for a more parsimonious understanding of tragulid evolution.

Despite its frequent use in the literature, the taxonomy of fossil tragulids remains problematic, with *Dorcatherium* historically functioning as a waste-basket taxon. This study attempts to contribute to resolving this issue by providing the first detailed and comprehensive morphological description of the cranial anatomy of *D. nauti*. Based on newly available and well-preserved material, a revised taxonomic framework is proposed, including the identification of cranial autapomorphies that are not restricted to dental characters. In the future it might be useful to establish a lectotype of *Dorcatherium nauti* from the type series of Kaup, e.g. the skull NHMUK PV OR 40632 to reduce taxonomic uncertainties.

Beyond taxonomy, the analysis of cranial morphology and sexual dimorphism yields new insights into the palaeobiology of *D. nauti*. The pronounced cranial ornamentation in males, combined with patterns of sexual dimorphism, suggests that intraspecific competition was likely less fatal and more ritualized than in the extant *Hyemoschus aquaticus*, with cranial ornamentation probably functioning as a visual or structural display feature during sexual selection. This indicates a difference in aspects of social and mating behavior between the fossil and extant taxa.

In contrast, several reproductive and life-history traits were likely shared between *D. nauti* and *H. aquaticus*. The observed biological patterns, including early onset of sexual maturity, sexual size dimorphism with females exceeding males in body size, and a high survivorship of juveniles, are consistent with a low reproductive rate, most likely involving a single offspring per litter and 4 fertile events per lifespan of one female and similar maximum life span compared to *Hyemoschus*.

Taken together, these findings demonstrate that while *D. nauti* and *H. aquaticus* differ in key aspects of cranial morphology, they share fundamental life-history and ecological traits. This supports a close phylogenetic relationship between both taxa and justifies the use of *H. aquaticus* as a comparative modern analogue for *D. nauti*, provided that morphological and behavioral differences are explicitly considered. More broadly, this study highlights the importance of integrating detailed morphological, ontogenetic, and biological data to refine

the taxonomy and evolutionary interpretation of fossil tragulids. Furthermore, it illustrates the complexity and individuality of vertebrate species. The example of tooth development and its correlation with the completion of sexual maturity demonstrates that the biology of fossil vertebrates may be more complex than often assumed and must therefore be interpreted with caution. Consequently, the eruption of the M3 cannot universally be used as a proxy for the completion of sexual maturity or adulthood. This should be taken into particular consideration when isolated teeth are used in population-level analyses of fossil assemblages

6 References

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7 Appendix

First paper of Dissertation

Unexpected cranial sexual dimorphism in the tragulid *Dorcatherium navi* based on material from the middle to late Miocene localities of Eppelsheim and Hammerschmiede (Germany)

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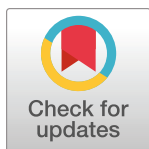
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RESEARCH ARTICLE

Unexpected cranial sexual dimorphism in the tragulid *Dorcatherium nauti* based on material from the middle to late Miocene localities of Eppelsheim and Hammerschmiede (Germany)

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Data Availability Statement: All relevant data are within the paper. Additional three-dimensional data are provided on MorphoSource at www.morphosource.org/concern/media/000374838 and www.morphosource.org/concern/media/000375559.

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Abstract

Tragulids, chevrotains or mouse deer, were common faunal elements during the Miocene. During that time, *Dorcatherium* was the most abundant genus, with *D. nauti* being the first described species. Besides their abundance, until recently only very limited cranial material was available for investigation. Here we present a redescription of the first complete skull of *D. nauti* from the middle to late Miocene locality of Eppelsheim, Germany, based on micro-computed tomography. Furthermore, we present a description and comparison of two additional, new skulls of *D. nauti* from the late Miocene hominid locality Hammerschmiede, Germany. Within *Dorcatherium*, so far, only three other complete skulls are known, all belonging to *D. crassum*. A comparison between the three skulls of *D. nauti* and the already known skulls of *D. crassum* shows that these two species differ in morphological features of the skull, such as laterally facing orbitae, separation of supraorbital foramen from supraorbital groove by a bony bridge, well-developed parietal plateau, prominent nuchal tubercle, less-developed nuchal crests, and the presence of an occipital crest. Moreover, two different osteological morphotypes are present in the skulls of *D. nauti* that can be interpreted as a previously unknown sexual dimorphism. Very similar features are observed in *D. crassum*, which can be likewise related to the same dimorphism. However, males of *D. nauti* differ from males of *D. crassum* by the presence of frontoparietal bulges, which were probably used for sexual display and during male-male combats in males of *D. nauti*. For the first time, sexual dimorphism in *Dorcatherium* is described based on skull characteristics, which are, so far, unknown from any other fossil or extant tragulid.

Introduction

Tragulidae (mouse-deer or chevrotains) are a group of ruminants and the sister group to Pecora. They contain one of the smallest living artiodactyles and survived until today in Asia

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Abbreviations: AP, collection A. de Perthuis, Blois, France; FMNH, Field Museum of Natural History, Chicago, USA; GPIT, Geologisch-Paläontologisches Institut Tübingen, Tübingen, Germany; NHMUK, Natural History Museum, London, UK; NMA, Naturmuseum Augsburg, Augsburg, Germany; SNSB-BSPG, Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.

(*Tragulus* and *Moschiola*) and Africa (*Hyemoschus*) [1]. Tragulidae are characterized by the absence of cranial appendages, bunoselenodont to selenodont dentition, the presence of a Σ -structure in the lower molars, and large, saber-like upper canines in males [2]. The precise evolutionary history of the family is poorly known with the exception that it originated in the late Eocene of Asia [2–5], which was recently confirmed by Mennecart et al. [6], who report the oldest true tragulid from the Eocene of China.

Tragulidae show a high species diversification and distribution during the Miocene with *Dorcatherium* being the most diverse tragulid genus during that time. Rössner and Heissig (Fig 7 in [7]) and Aiglstorfer et al. (Fig 1 in [8]) show that *Dorcatherium* reaches its highest diversity in central Europe during the early middle Miocene with four contemporaneous species around 15 Ma.

Despite their diversity and distribution, the ingroup taxonomy of *Dorcatherium* is in need of revision [9], because complete skulls are rare and most taxonomic studies are based on isolated tooth material only. So far, only few skulls of *Dorcatherium* are described and all belong to *Dorcatherium crassum* [10–12] except for one complete skull of *D. nauti*, described by Kaup [13, 14] from Eppelsheim, Germany. However, no detailed description or illustration of the skull from Eppelsheim was available leading to little attention after its original description and in the recent literature it was only very briefly described [15]. Another skull from Steinheim am Albuch was first assigned to *D. nauti* [16], but later reassigned to *D. guntianum* [7] or *D. crassum* [8].

Here we focus our study on the skull morphology of the type species of *Dorcatherium*, *D. nauti*. The goal of this manuscript is the redescription and comparison of the skull from the type locality of *D. nauti*, Eppelsheim, Germany together with two new skulls from the late Miocene hominid locality Hammerschmiede. For the first time it is possible to show that despite the characteristic dentition, *D. nauti* exposes unique features of the skull.

Geological setting

The Hammerschmiede locality is located in southern Germany (Allgäu, Bavaria) in the Northern Alpine Foreland Basin. The sediments comprise floodplain deposits belonging to the *Upper Series*, the youngest lithostratigraphic part of the Upper Freshwater Molasse [17, 18]. Two fossil bearing levels HAM 5 and HAM 4 represent meandering fluvial channels [19], which contain a rich fauna including bivalves and gastropods [20], fishes, amphibians, reptiles, small mammals, large mammals [21–26], and birds [27, 28]. The locality became famous through the discovery of associated skeletons of the hominid *Danuvius guggenmosi* [22, 23]. Biostratigraphic, as well as magnetostratigraphic age constraints place both levels at the beginning of the late Miocene (Tortonian), with absolute ages of 11.62 Ma for HAM 5 and 11.44 Ma for HAM 4 [19].

The Eppelsheim locality represents fluvial deposits of the Eppelsheim Formation from the Mainz Basin containing a middle to late Miocene mixed faunal association of repeatedly reworked paleo-Rhine sediments [29]. Based on the preservation, the complete skull NHMUK PV OR 40632 of *D. nauti* from Eppelsheim was probably not reworked. An exact age for this skull is not reported, but it occurs within the biostratigraphic distribution of *D. nauti* given by Aiglstorfer et al. [8] from the early Sarmatian (~12.5 Ma) to Pannonian (~9 Ma).

Material and methods

The material used in this study comprises one complete (GPIT/MA/18000-01) skull with an associated mandible (GPIT/MA/18000-53) and one partial skull (GPIT/MA/17690) of *Dorcatherium nauti* from Hammerschmiede; both from level HAM 4. Moreover, we describe

the μ CT scan of NHMUK PV OR 40632, an almost complete skull with attached jaws from Eppelsheim (Germany), that was originally published by Kaup [13, 14], housed at the Natural History Museum of London (NHMUK). A cast (GPIT/MA/03653) of this specimen is also available for study at GPIT. For comparison, we used the three best known and almost complete skulls of *D. crassum* from Thierhaupten [10] and Walda 2, Germany [11], as well as from Contres, France [12]. Additionally, extant artiodactyls from GPIT (unnumbered specimens) including *Tragulus* sp. (GPIT/MA/12997), *T. napu* (GPIT/MA/12998), *T. javanicus* (GPIT/MA/12999), and *Hyemoschus* (FMNH 34294) were used.

The terminology of the dentition follows [30] and the tooth measurements are based on [8, 31] with W being the maximum anterior width and L being the maximum length. The skull terminology follows [32, 33] and the skull measurements of *D. crassum* are provided according to Fig 4.3 in [11] except the postfrontal length and length/height of the sagittal crest, which were done using the surface model provided by [11]. In addition, the postfrontal skull length was measured in dorsal view at the midline between the frontoparietal suture and the maximum posterior extension of the skull. Measurements of *D. naui* from Hammerschmiede and the cast of the specimen from Eppelsheim were taken with a digital caliper with precision of 0.1 mm. The Natural History Museum of London provided a μ CT scan of the skull NHMUK PV OR 40632 for this study. The resolution was equal to 0.095 mm voxelsize.

GPIT/MA/17690 from Hammerschmiede was scanned at the Centre of Visualisation, Digitisation, and Replication (VDR) at the Eberhard Karls University of Tübingen, Germany. The scans were acquired using the Nikon XTH 320 Reflection Target with an acceleration voltage of 190 kV. For specimen GPIT/MA/17690, the resolution was set to 177 μ A. A total of 4476 images were recorded and a 1 mm copper filter was inserted. Images were processed and reconstructed using VG Studio Max 3.4.1.

Systematic paleontology

MAMMALIA Linnaeus, 1758

ARTIODACTYLA Owen, 1848

RUMINANTIA Scopoli, 1777

TRAGULIDAE Milne Edwards, 1864

Genus *Dorcatherium* Kaup, 1833

Type species: *Dorcatherium naui* Kaup, 1833

Dorcatherium naui Kaup, 1833

Emended diagnosis

Mid-sized selenodont tragulid with (I) a high degree of selenodonta having a reduced external postmetacristid (*sensu* [30]) in the lower molars and well-developed cristids and flat main cusps (*sensu* [34]), (II) prominent sickle-shaped cones and conids (*sensu* [7]) in combination with (III) the presence of the *Dorcatherium*-platform in the lower molars (*sensu* [35]), (IV) a complex posterior valley of the p4 (*sensu* [8]), (V) lateral facing orbitae, (VI) prominent nuchal tubercle, and (VII) the presence of an occipital crest.

Differs from *D. crassum* in: (A) higher degree of selenodonta, (B) strongly reduced postmetacristid, (C) laterally facing orbitae instead of dorsolaterally oriented orbitae, (D) the separation of supraorbital foramen from supraorbital groove by a bony bridge, (E) well-developed parietal plateau, (F) prominent nuchal tubercle, (G) less-developed nuchal crests, and (H) the presence of an occipital crest.

Holotype. Mandible with p3–m3 and alveoli of p2 and p1, first described by Kaup [36] and later figured by Kaup (pl. 23, Fig 1–1b in [14]). The holotype is lost, but two casts are

available, one at the NHMUK (NHMUK PV M 3714) and the other one at the SNSB-BSPG (SNSB-BSPG 1961 XIX 37).

Type locality. Eppelsheim, Germany (middle to late Miocene [29]).

Referred material. The complete skull NHMUK PV OR 40632 from Eppelsheim (middle to late Miocene of Germany) (Figs 1 and 2), a complete skull GPIT/MA/18000-01 (Figs 3–6) with associated remains of a mandible (GPIT/MA/18000-53) (Fig 7) found in association to the skull resembling the same wear stage as GPIT/MA/18000-01 and therefore belonging to one individual, as well as a partial skull GPIT/MA/17690 (Figs 8–12), both from the Hammerschmiede locality (late Miocene of Germany) level HAM 4.

Remarks

The holotype of *Dorcatherium nauti* was first described by Kaup [36] in a letter to Bronn. Kaup [36] described the specimen as different from other ruminants, because the mandible contains seven teeth instead of six. Furthermore, he described the teeth as similar to a deer. The holotype was later mentioned by Kaup and Scholl [37] and was finally displayed by Kaup (pl. 23, Fig 1-1b in [14]). After that, the holotype was lost, but one cast is stored in the NHMUK under the collection number NHMUK PV M 3714 and another one is stored in the SNSB-BSPG under the collection number SNSB-BSPG 1961 XIX 37. In the same paper, where the holotype was figured in 1839, Kaup (pl. 23c, Figs 1 and 2 in [14]) also displayed a complete male skull of *D. nauti* (NHMUK PV OR 40632) with attached mandibles and atlas from Eppelsheim, Germany, but this specimen was described later in [13]. Now this skull is stored in the NHMUK and it represents the only other *Dorcatherium* skull from the type locality of *D. nauti*.

Skull morphology of *Dorcatherium nauti*

NHMUK PV OR 40632 is a complete skull with two attached mandibles and two large upper canines (Figs 1 and 2). The skull is laterally compressed with a heavy diagenetic depression of the left preorbital part. This depression is visible in the μ CT scan, the cast housed in the GPIT, and the original drawing of Kaup (pl. 23A, Figs 1 and 2 in [14]). GPIT/MA/17690 and GPIT/MA/18000-01 are both from the Hammerschmiede locality. In GPIT/MA/17690 the preserved parts of the skull are, besides some minor diagenetic anteroposterior and dorsoventral distortion, well-preserved. The preorbital portion of the skull is not preserved (Figs 8 and 9) and therefore the premaxillary, maxillary, nasal, lacrimal, and jugal are not described. In GPIT/MA/18000-01, the left side of the skull is well-preserved, except for some diagenetic alteration (Fig 3), whereas the right side is laterally crushed and the paroccipital process and zygomatic arch with most of the jugal are missing. The premaxillary is partially preserved, while the nasals are missing completely (Fig 4). Furthermore, the teeth P2–M3 of the left and right maxillaries are present. A small alveole for the reduced canine is visible at the anterior most part of the left maxillary (Fig 5).

In general, all skulls are anteroposteriorly elongated and the snout is tapered; the brain cavity is low and prolate. GPIT/MA/18000-01 has a postfrontal length of 53.8 mm and a condylo-basal length of 157.1 mm and GPIT/MA/17690 possesses a slightly larger postfrontal region that is 56.8 mm in length (Table 1). In comparison the skull from Eppelsheim has a postfrontal length of ~65 mm and a condylobasal length of ~149 mm.

Premaxillary

The premaxillary is well preserved in the skull from Eppelsheim (Figs 1 and 2) and partially preserved in GPIT/MA/18000-01 (Fig 3). It forms the anterior part of the snout and continues beneath the anterior extension of the nasal in the skull from Eppelsheim.

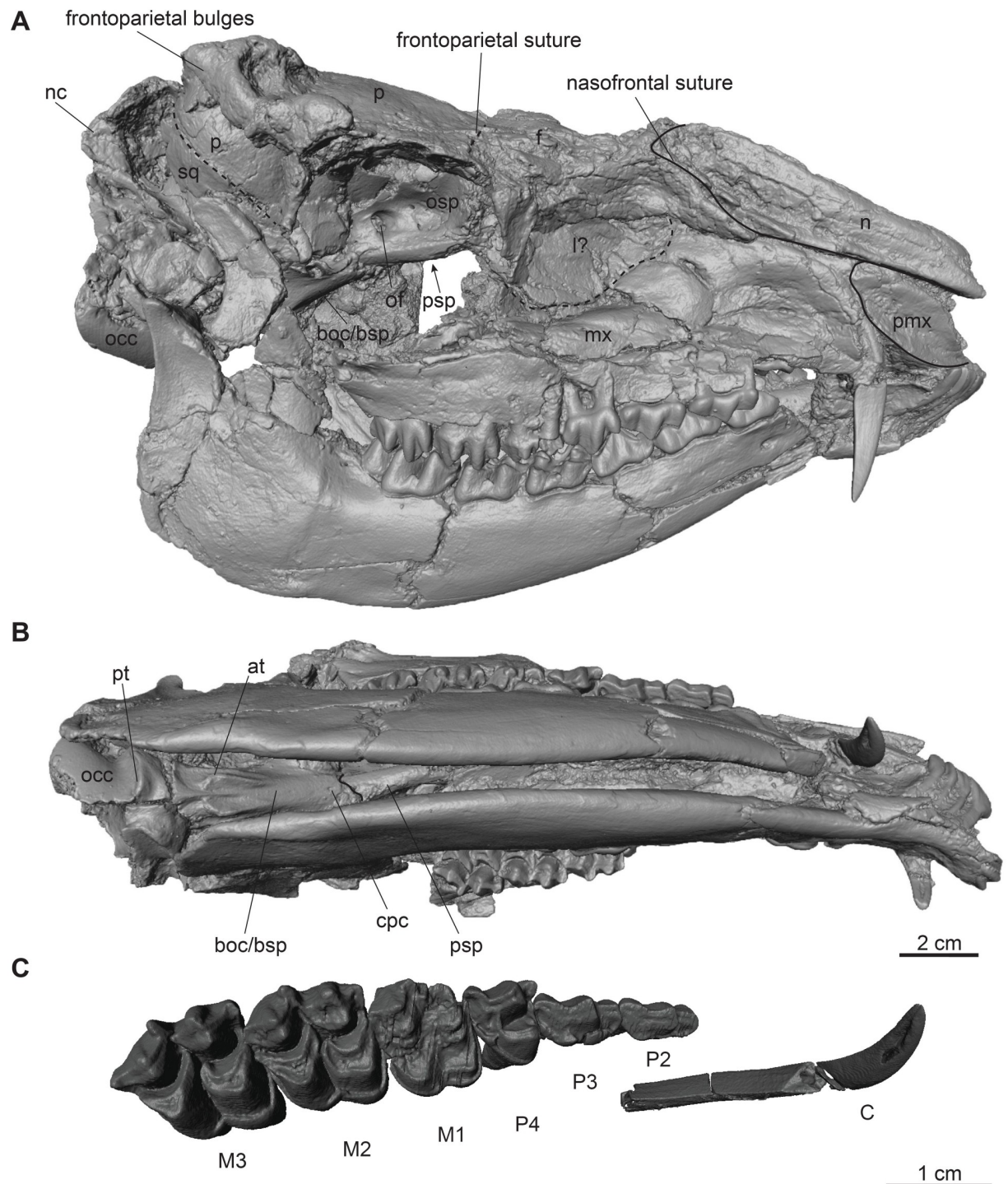


Fig 1. Complete male skull of *Dorcatherium naui* from Eppelsheim, Germany. Surface model of NHMUK PV OR 40632. (A) lateral view, right side, (B) ventral view, (C) close up of right upper tooth row. Abbreviations: at, anterior tuberosities; boc/bsp, basioccipital/basisphenoid; cpc, craniopharyngeal canal; f, frontal; l?, lacrimal; mx, maxillary; n, nasal; nc, nuchal crests; occ, occipital condyle; of, optic foramen; osp, orbitosphenoid; p, parietal; pmx, premaxillary; psp, presphenoid; pt, posterior tuberosities; sq, squamosal.

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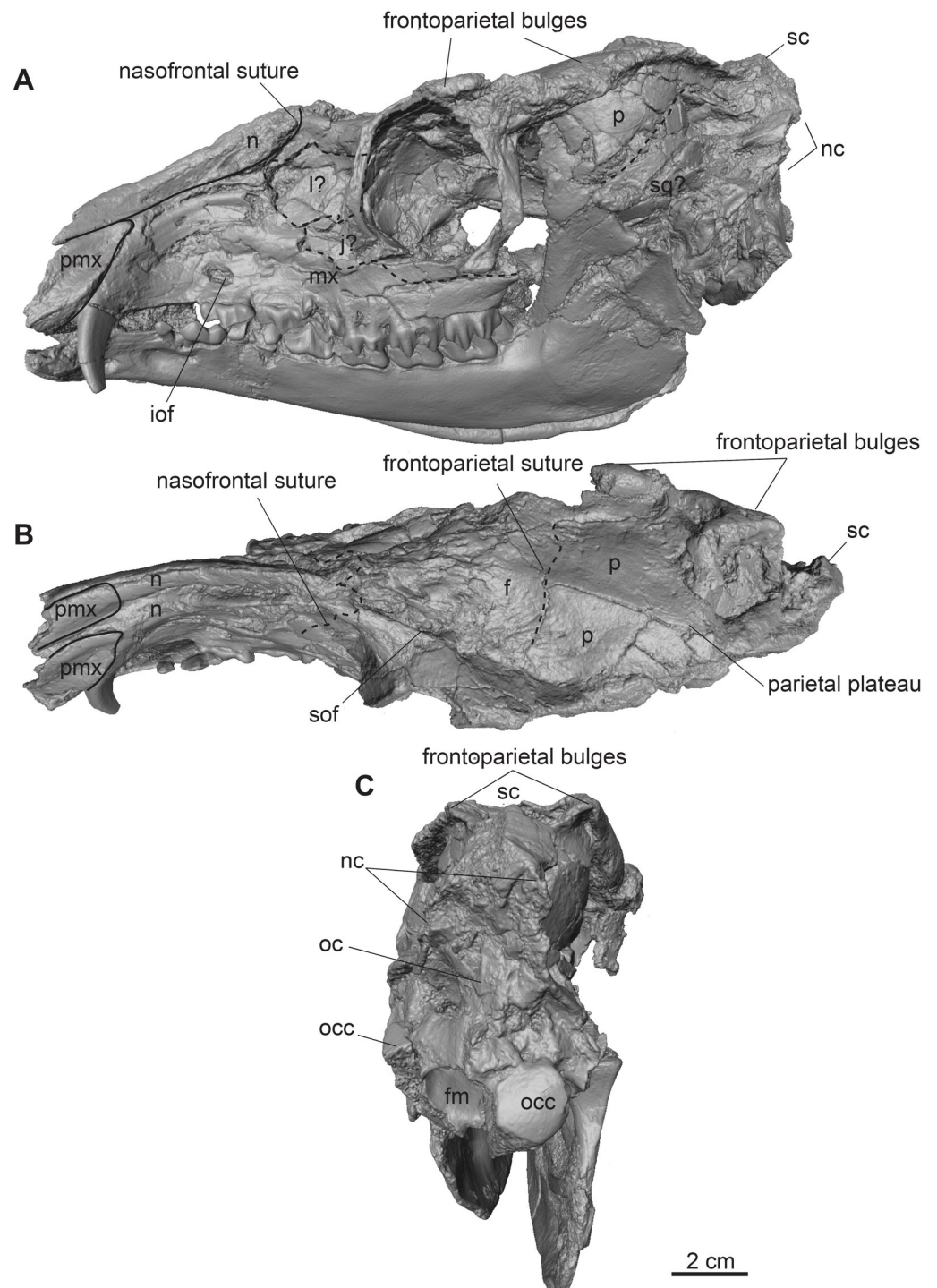


Fig 2. Complete male skull of *Dorcatherium naui* from Eppelsheim, Germany. Surface model of NHMUK PV OR 40632. (A) lateral view, left side, (B) dorsal view, (C) posterior view. Abbreviations: f, frontal; fm, foramen magnum; iof, infraorbital foramen; j?, jugal; l?, lacrimal; mx, maxillary; n, nasal; nc, nuchal crest; oc, occipital crest; occ, occipital condyle; p, parietal; pmx, premaxillary; sc, sagittal crest; sof, supraorbital foramen; sq?, squamosal.

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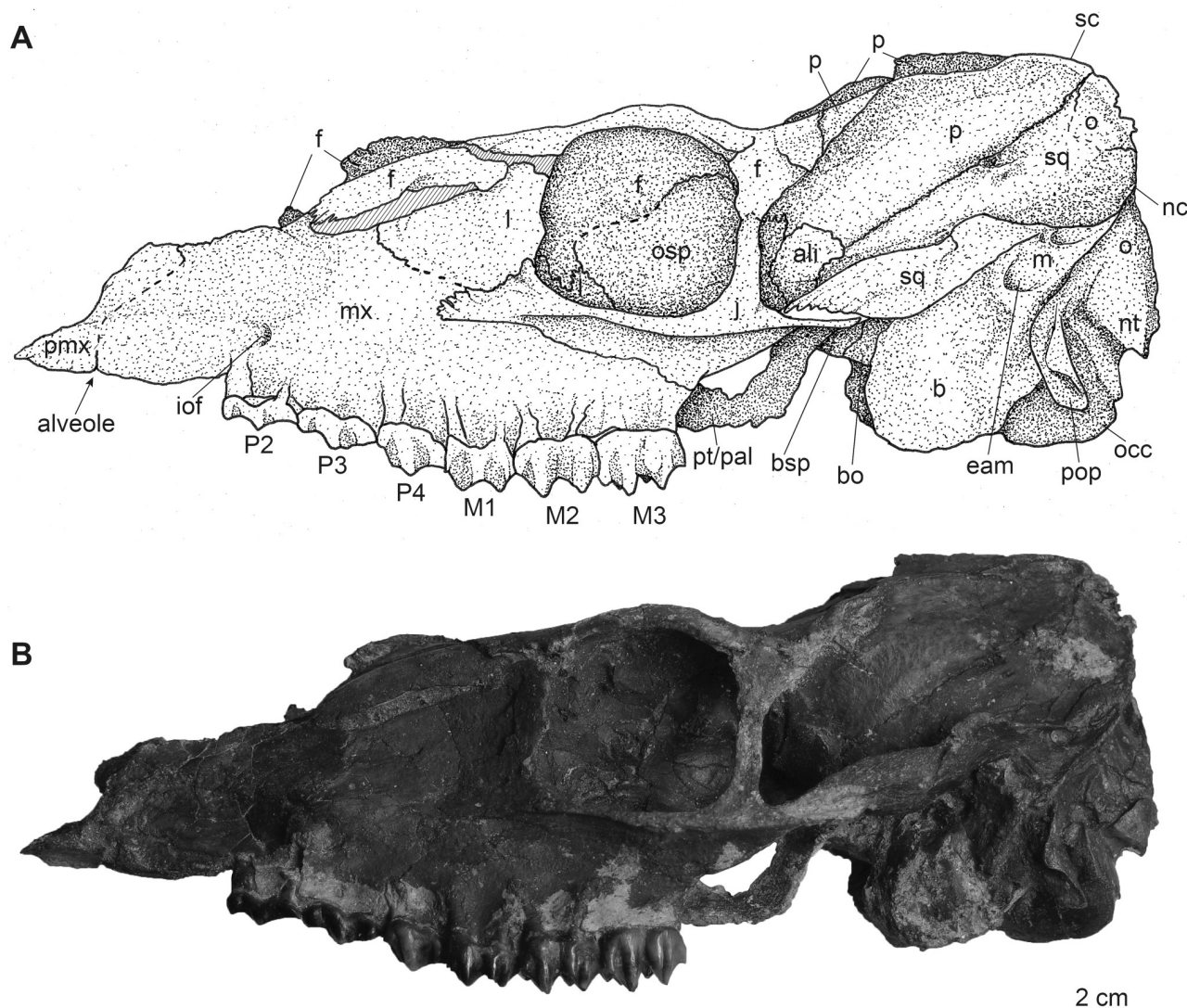


Fig 3. Complete female skull of *Dorcatherium naui* (GPIT/MA/18000-01) in lateral view from the Hammerschmiede locality, Germany (HAM 4). (A) drawing, (B) photograph. Abbreviations: ali, alisphenoid; b, bulla tympanica; bsp, basisphenoid; bo, basioccipital; eam, external auditory meatus; f, frontal; iof, infraorbital foramen; j, jugal; l, lacrimal; mx, maxillary; nc, nuchal crest; nt, nuchal tubercle; o, occipital; occ, occipital condyle; osp, orbitosphenoid; p, parietal; pmx, premaxillary; pop, paroccipital process; pt/pal, pterygoid/palatine; sc, sagittal crest; sq, squamosal.

<https://doi.org/10.1371/journal.pone.0267951.g003>

Maxillary

In GPIT/MA/17690, the maxillaries are not preserved and in the skull from Eppelsheim these bones are heavily distorted due to lateral deformation. In contrast, in GPIT/MA/18000-01, both maxillaries are exposed, but the left one is better preserved (Fig 3). In lateral view, the maxillary is the largest bone of the skull reaching far posteriorly to the level of the posterior part of the closed orbital margin (Fig 3). Anteriorly, where it is sutured to the remains of the premaxillary, it is slightly concave in GPIT/MA/18000-01. Dorsally, the sutural facet for the missing nasal is exposed and posterodorsally, the maxillary is in contact with the frontal, lacrimal and jugal. Above the P2, the infraorbital foramen is visible in GPIT/MA/18000-01 and NHMUK PV OR 40632. In ventral view (Fig 5), the maxillary forms by far the largest part of the snout. Here, the maxillary is crushed in GPIT/MA/18000-01, similar to the specimen from

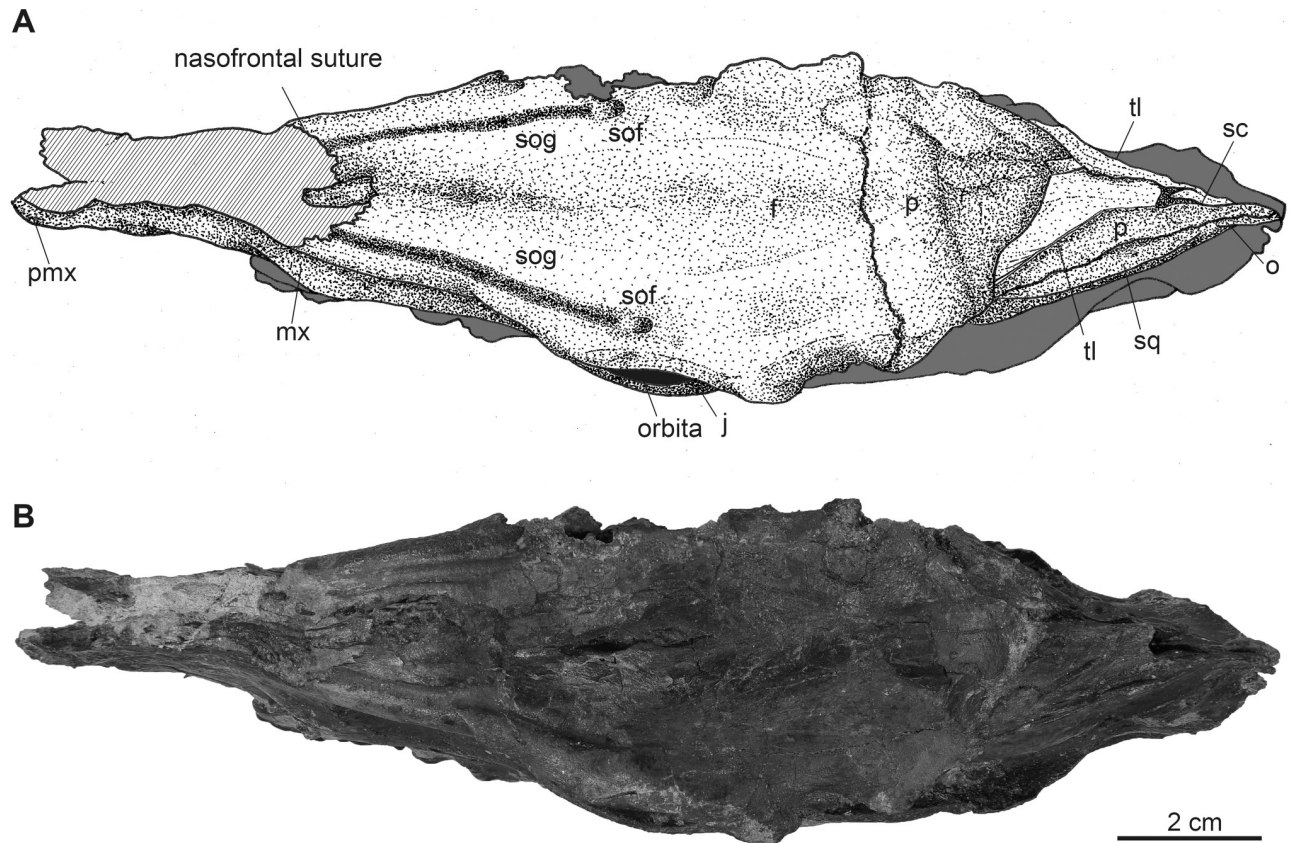


Fig 4. Complete female skull of *Dorcatherium naui* (GPIT/MA/18000-01) in dorsal view from the Hammerschmiede locality, Germany (HAM 4). (A) drawing, (B) photograph. Abbreviations: f, frontal; j, jugal; mx, maxillary; o, occipital; p, parietal; pmx, premaxillary; sc, sagittal crest; sof, supraorbital foramen; sog, supraorbital groove; sq, squamosal; tl, temporal lines.

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Eppelsheim. It is sutured anteriorly with the premaxillary and posteriorly with the palatine. The anterior part of the ventral maxillary contains the alveolus for the canine. This alveolus is very small in GPIT/MA/18000-01 by being only 1.9 mm in diameter compared to the skull from Eppelsheim, where it is 9.2 mm in diameter (Table 1).

Nasal

The skull from Eppelsheim is the only one that preserves the nasal (Figs 1 and 2). In lateral view, the nasal is in contact with the posterodorsal margin of the premaxillary and extends to the anterior end of the latter as already noticed by Rössner [15]. The nasofrontal suture is hardly visible, but seems to be W-shaped with the sagittal process facing anteriorly.

Lacrimal

In lateral view, in the skull from Eppelsheim and GPIT/MA/18000-01 (Figs 1–3), the lacrimal forms the anterior rim of the orbital margin and is anteroposteriorly elongated. It is sutured dorsally with the frontal and inside the orbita with the orbitosphenoid. Ventrally it contacts the maxillary and jugal. A single lacrimal foramen is visible inside the orbita. A lacrimal fossa is absent.

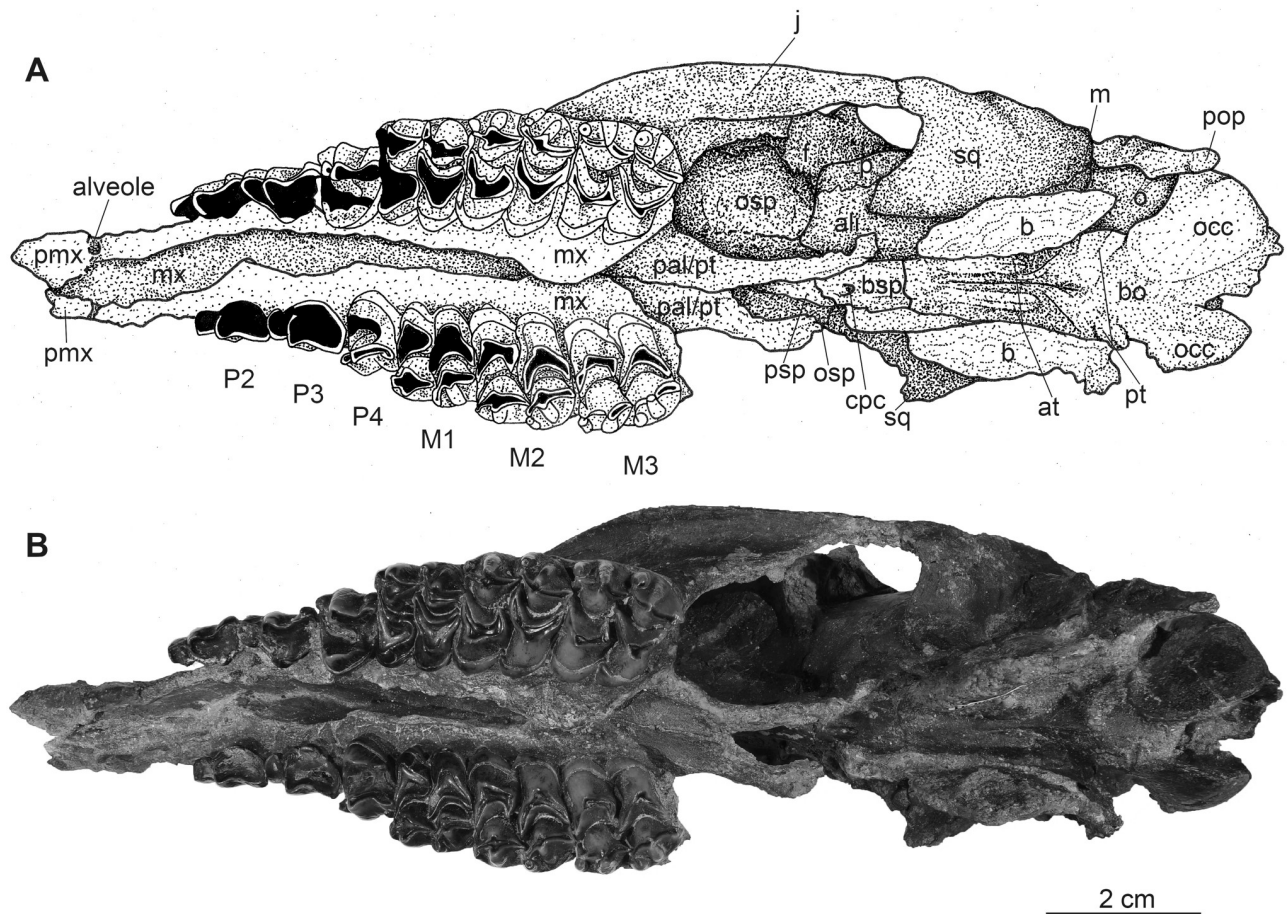


Fig 5. Complete female skull of *Dorcatherium nauti* (GPIT/MA/18000-01) in ventral view from the Hammerschmiede locality, Germany (HAM 4). (A) drawing, (B) photograph. Abbreviations: ali, alisphenoid; at, anterior tuberosities; b, bulla tympanica; bsp, basisphenoid; bo, basioccipital; cpc, craniopharyngeal canal; f, frontal; m, mastoid process; mx, maxillary; o, occipital; occ, occipital condyle; osp, orbitosphenoid; p, parietal; pmx, premaxillary; pop, paroccipital process; psp, presphenoid; pt, posterior tuberosities; pt/pal, pterygoid/palatine; sq, squamosal.

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Skull roof (frontal and parietal)

The fused frontals form a major part of the skull roof in all three specimens (Figs 2, 4 and 9). In dorsal view, they are confined anteriorly by the anterior lacrimomaxillary suture and posteriorly by the frontoparietal suture. Anteriorly, the suture is W-shaped with a prominent anteriorly pointed sagittal prolongation. At the lateral part of the anterior skull roof, the frontals contain the supraorbital foramina originating inside the orbita. Both foramina are situated at the level of the anterior part of the orbita next to the orbital margin (Figs 2, 4 and 9). They continue as parallel supraorbital grooves and run anteriorly towards the nasofrontal suture in the skull from Eppelsheim and the GPIT/MA/18000-01.

While the frontal constitutes the anterior part of the skull roof, the parietal forms the posterior part and is connected posteriorly to the occipital (Fig 4). In GPIT/MA/17690, in dorsal view, the anterior part of the frontals expands laterally, forming a slightly concave plateau encompassed by flat and broad bony bulges above the orbita. These bulges become more prominent, robust, and set off with a rough surface texture at the parietals. Here, they bend medially to constrict the domed anterior parietal, forming the plateau until they merge with

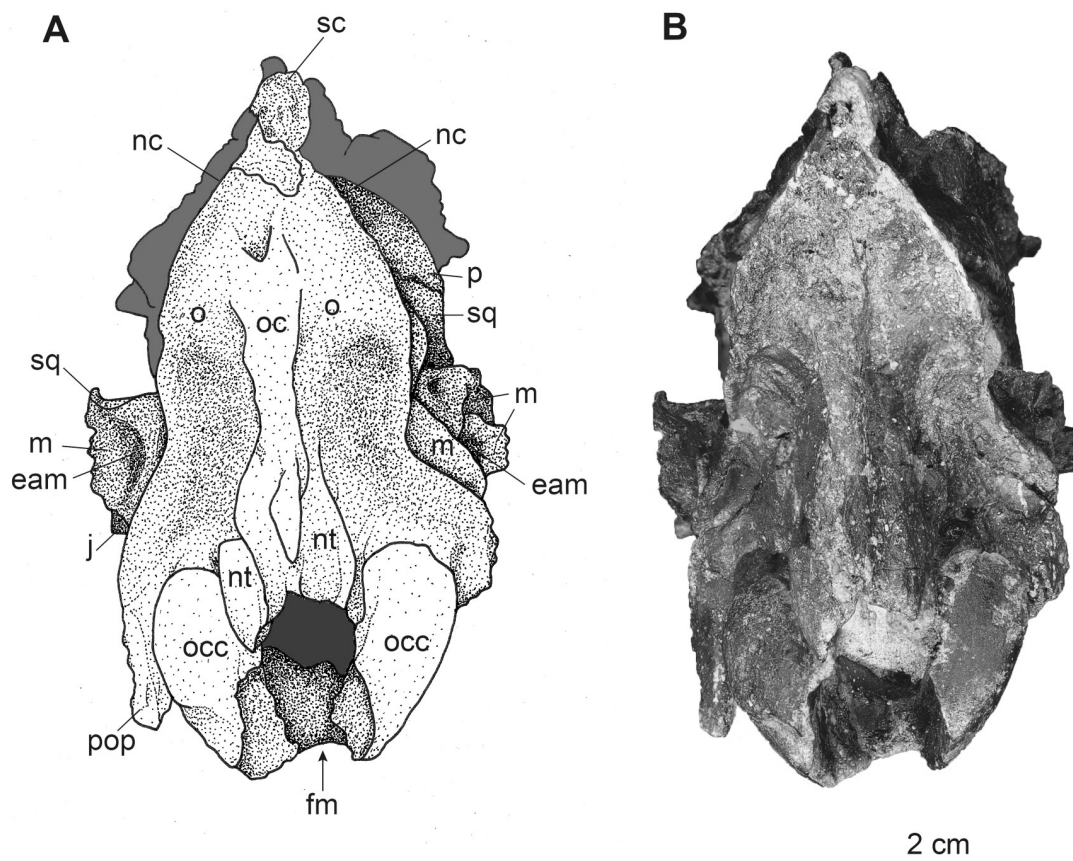


Fig 6. Complete female skull of *Dorcatherium nauti* (GPIT/MA/18000-01) in posterior view from the Hammerschmiede locality, Germany (HAM 4). (A) drawing, (B) photograph. Abbreviations: eam, external auditory meatus; fm, foramen magnum; j, jugal; m, mastoid process; nc, nuchal crest; nt, nuchal tubercle; o, occipital; oc, occipital crest; occ, occipital condyle; p, parietal; pop, paroccipital process; sc, sagittal crest; sq, squamosal.

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the crest-like temporal lines (Figs 8 and 9). Due to the lateral distortion of the skull from Eppelsheim, these structures are poorly preserved. They are deformed on the left side and are broken off at the frontal on the right side (Figs 1 and 2).

Posteriorly, the temporal lines of GPIT/MA/17690 enclose the parietal plateau until they run asymptotic to the well-developed, flat, and broad sagittal crest to merge with the posterior part of the latter. In the skull from Eppelsheim, these structures are well-visible despite the deformation of the skull roof. Fig 2 shows that especially the right side of the skull exposes massive parietal bulges that are set off from the skull roof. In Fig 2C the posterior view of the skull shows two prominent parietal bulges confining towards the center of the skull roof, forming an overhang above the lateral parietal. The internal structure of the bulges is very porous surrounded by compact bone. This is well visible in Fig 10B (cross section 2) at the thickened part above the frontal.

The sagittal crest is best visible in GPIT/MA/17690. Here, its anterior half proceeds onto the well-developed and prominent parietal plateau. The sagittal crest is 26 mm long and 3 mm high. In the specimen from Eppelsheim a sagittal crest is visible, but due to the poor preservation its morphology cannot be accurately described.

In contrast, GPIT/MA/18000-01 exposes no such frontoparietal bulges. Instead, the parietal is enclosed by the crest-like temporal lines surrounding a small plateau at the posterior part of

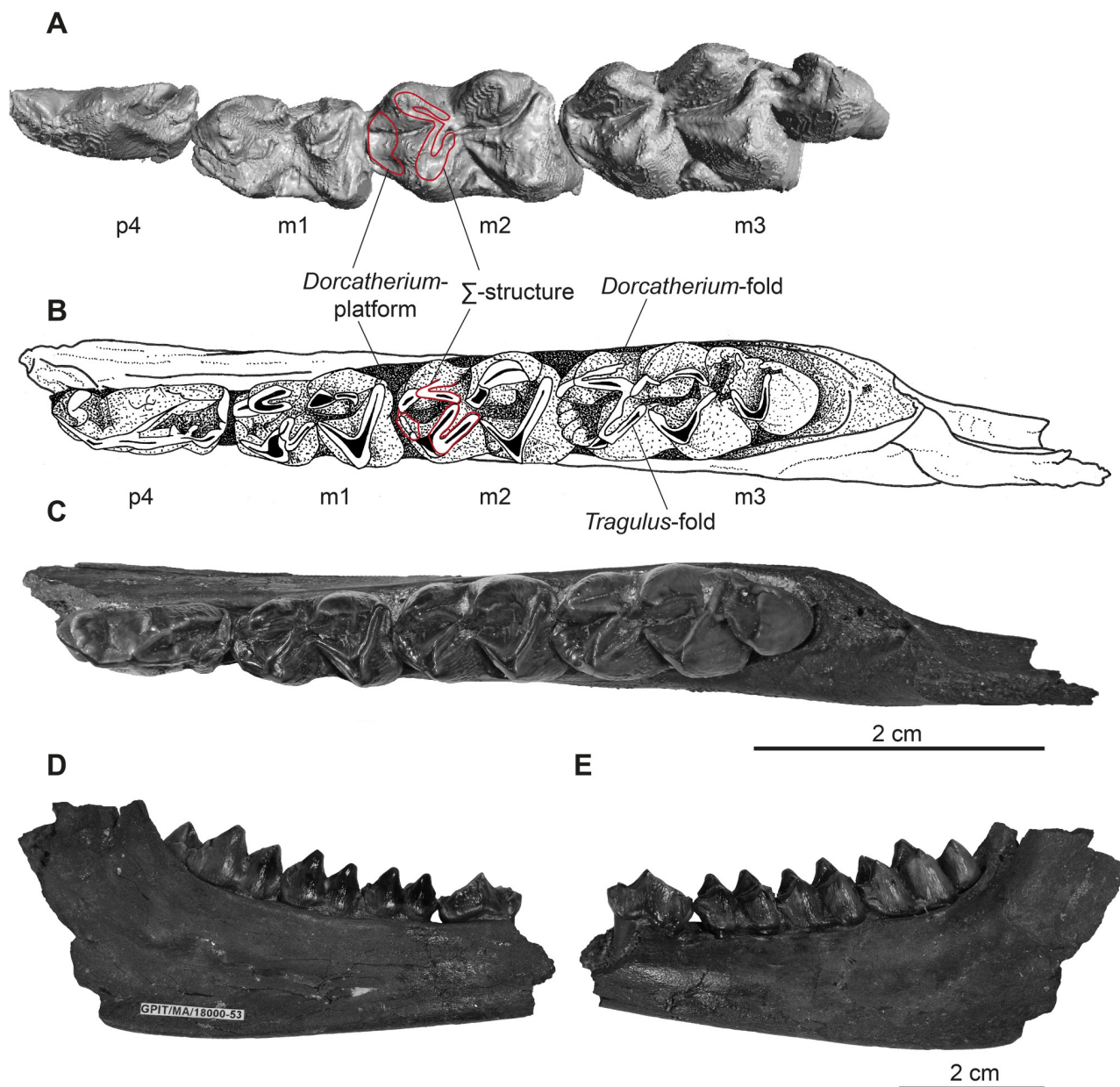


Fig 7. Lower dentition of *Dorcatherium nauti*. The mandible GPIT/MA/18000-53 is associated to the skull GPIT/MA/18000-01. (A) for comparison: virtually isolated, left tooth row of NHMUK PV OR 40632 in occlusal view, (B) drawing of GPIT/MA/18000-53 in occlusal view, (C) GPIT/MA/18000-53 in occlusal view, (D) GPIT/MA/18000-53 in lingual view, (E) GPIT/MA/18000-53 in buccal view.

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the bone. The temporal lines merge posteriorly into a well-developed sagittal crest. The sagittal crest is 14 mm long and 4 mm high at its maximum. The temporal lines form the dorsal margin of the fossa for the temporal muscle.

Squamosal

The parietal and squamosal form the lateral wall of the braincase, with the squamosal forming the ventral part of the lateral wall of the braincase in all three specimens (Figs 2, 3 and 8). Anteriorly, the squamosal is sutured with the alisphenoid, dorsally with the parietal, posteriorly

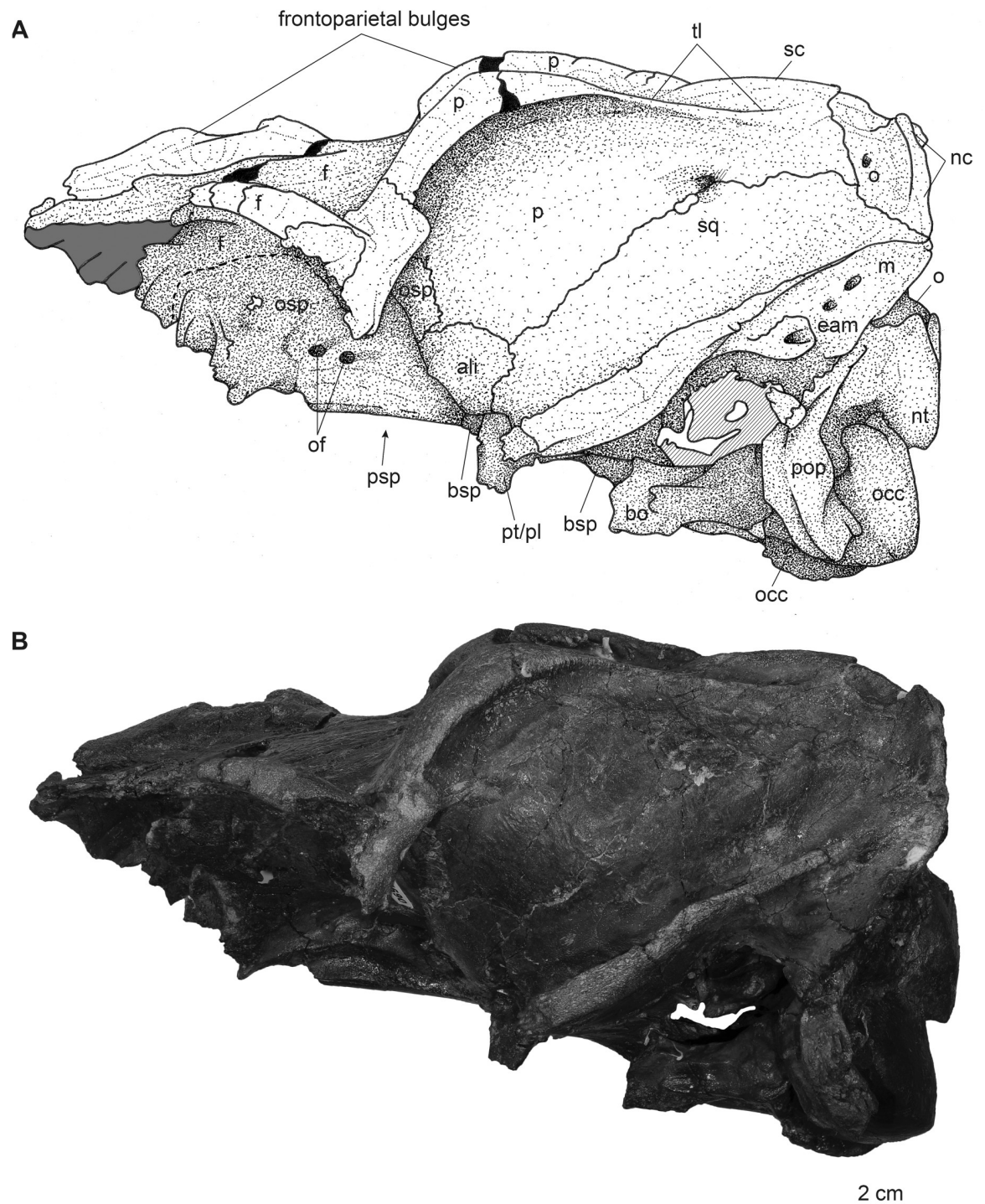


Fig 8. Partial male skull of *Dorcatherium naui* (GPIT/MA/17690) in lateral view from the Hammerschmiede locality, Germany (HAM 4). (A) drawing, (B) photograph. Abbreviations: ali, alisphenoid; bo, basioccipital; bsp, basisphenoid; eam, external auditory meatus; f, frontal; m, mastoid process; nc, nuchal crests; nt, nuchal tubercle; o, occipital; of, optic foramen; occ, occipital condyle; osp, orbitosphenoid; p, parietal; pop, paroccipital process; psp, parasphenoid; pt/pal, pterygoid/palatine; sc, sagittal crest; sq, squamosal; tl, temporal line.

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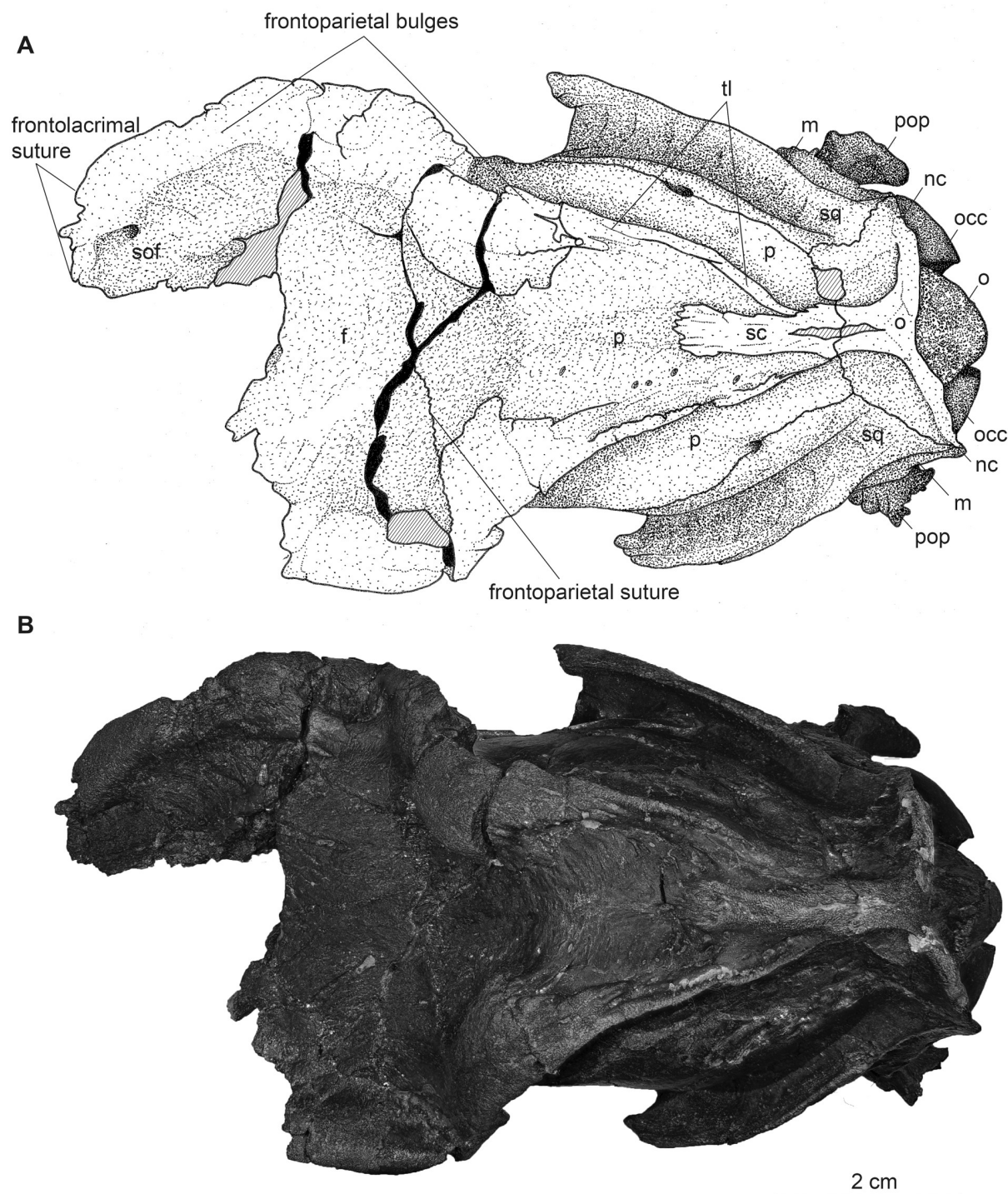


Fig 9. Partial male skull of *Dorcatherium nauti* (GPIT/MA/17690) in dorsal view from the Hammerschmiede locality, Germany (HAM 4). (A) drawing, (B) photograph. Abbreviations: f, frontal; m, mastoid process; nc, nuchal crests; o, occipital; occ, occipital condyle; p, parietal; pop, paroccipital process; sc, sagittal crest; sof, supraorbital foramen; sq, squamosal; tl, temporal line.

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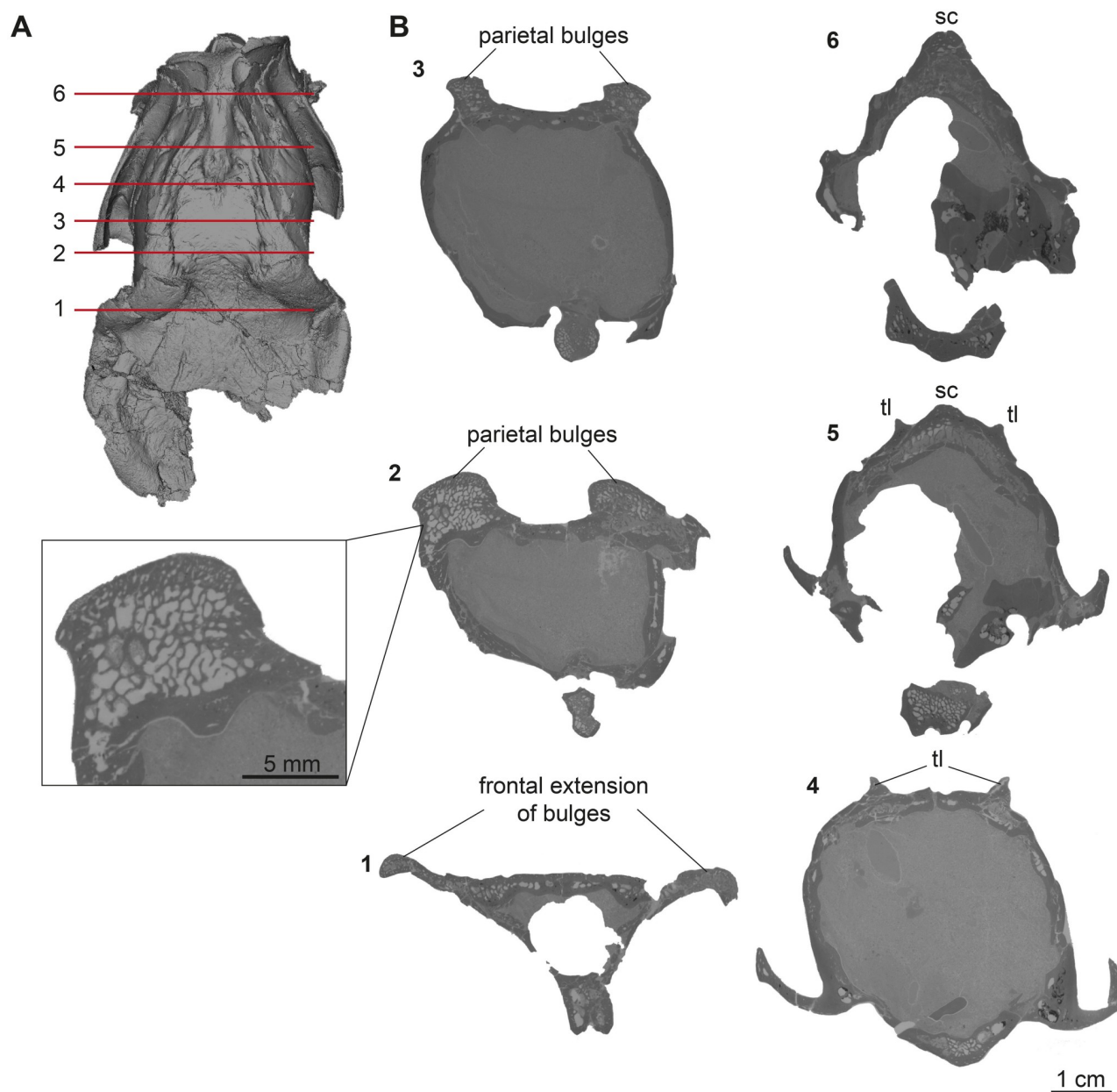


Fig 10. Cranial ornamentation of male *D. naui*. (A) Position of virtual cross section. (B) median plane μ CT-slices of GPIT/MA/17690.

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with the occipital, and ventrally with the mastoid process. At the central level of the squamoso-parietal suture, a foramen is situated. The squamosal expands anterolaterally to contact the jugal at the level of the alisphenoid and together they form the zygomatic arch. The ventrolateral squamosal extension is concave, anteroposteriorly elongated, and furthermore forms the ventral margin of the fossa for the temporal muscle. This ventrolateral squamosal process shows a deep insertion area, formed like a pit in GPIT/MA/18000-01. In GPIT/MA/17690, a small depression is visible instead, while this structure is not visible in the skull from Eppelsheim (Fig 9) due to preservation.

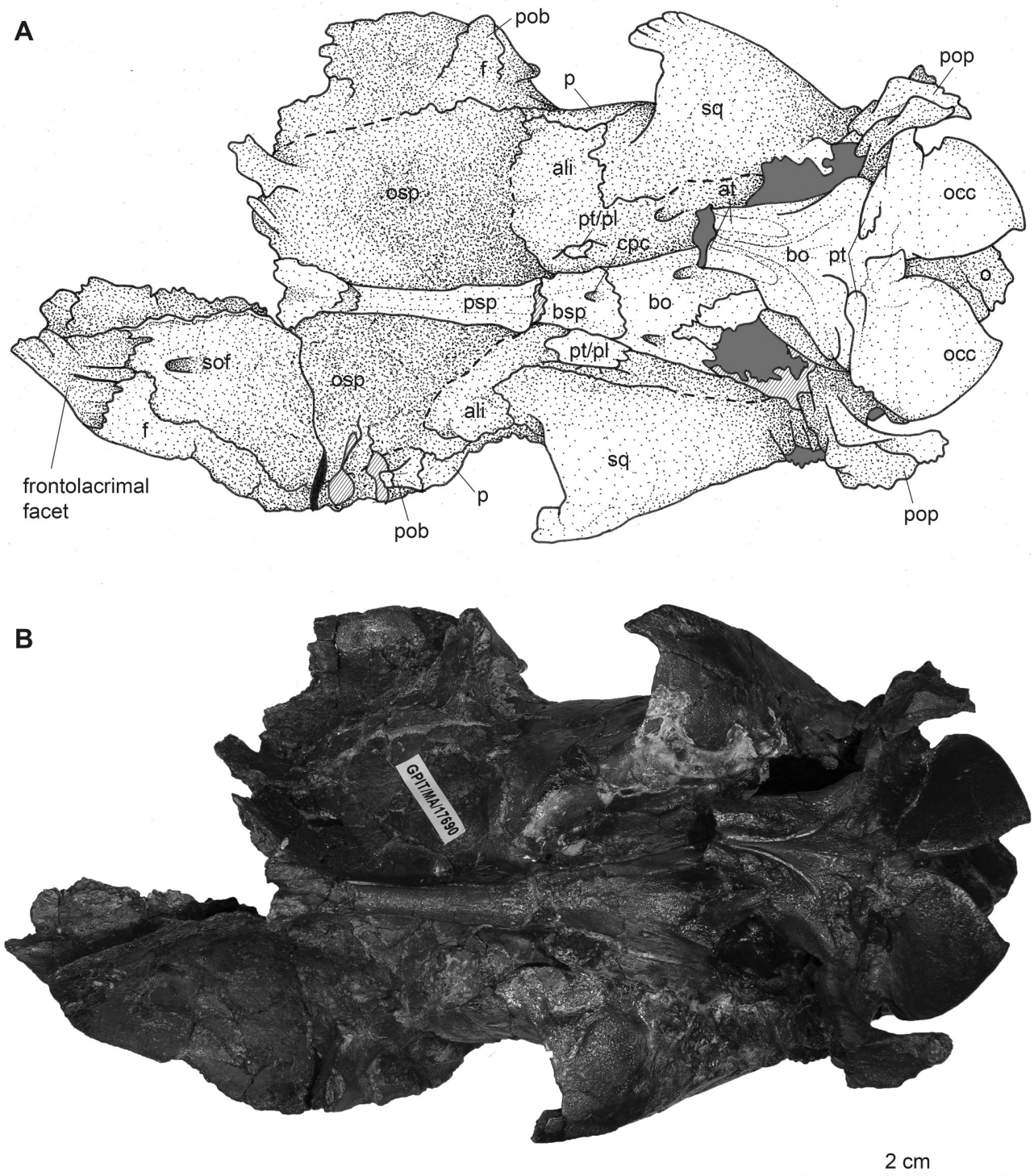


Fig 11. Partial male skull of *Dorcatherium naui* (GPIT/MA/ 17690) in ventral view from the Hammerschmiede locality, Germany (HAM 4). (A) drawing, (B) photograph. Abbreviations: ali, alisphenoid; at, anterior tuberosities; bsp, basisphenoid; bo, basioccipital; cpc, craniopharyngeal canal; f, frontal; o, occipital; occ, occipital condyle; osp, orbitosphenoid; p, parietal; pob, postorbital bar; pop, paroccipital process; psp, presphenoid; pt, posterior tuberosities; pt/pal, pterygoid/palatine; sof, supraorbital foramen; sq, squamosal.

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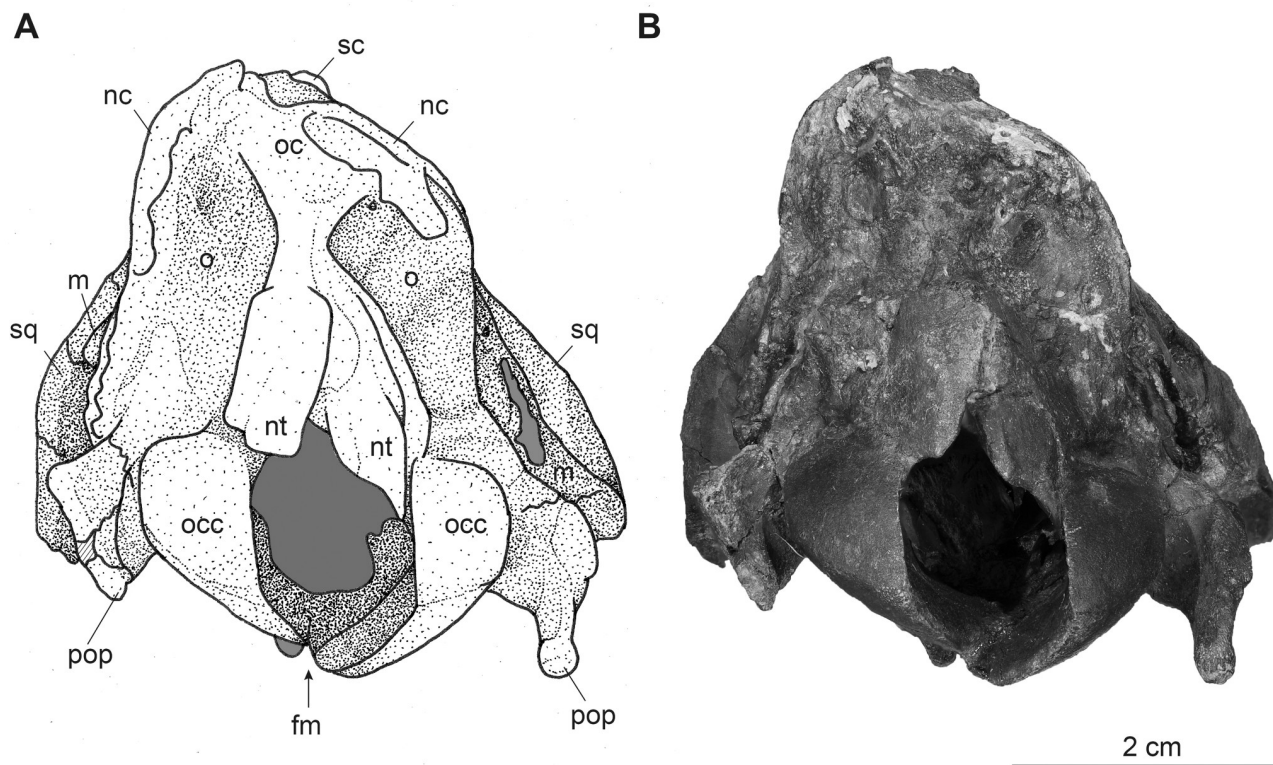


Fig 12. Partial male skull of *Dorcatherium nauti* (GPIT/MA/17690) in posterior view from the Hammerschmiede locality, Germany (HAM 4). (A) drawing, (B) photograph. Abbreviations: fm, foramen magnum; m, mastoid process; nc, nuchal crests; nt, nuchal tubercle; o, occipital; oc, occipital crest; occ, occipital condyle; pop, paroccipital process; sc, sagittal crest; sq, squamosal.

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Nuchal crests

Posteriorly, the squamosal forms a part of the nuchal crests (Figs 2–4, 8 and 9). The latter originate from the sagittal crest, diverge ventrally and represent attachment zones for the neck musculature. Furthermore, the nuchal crests are formed by the occipital and mastoid processes

Table 1. Skull measurements of *Dorcatherium*.

Specimen number	Species and locality	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q
NHMUK PV OR 40632, cast GPIT/MA/03653	<i>D. nauti</i> Eppelsheim	~149	/	/	/	/	/	/	~33	~43	~91	~37	~56	~65	21.1	~65	/	9.2
GPIT/MA/18000-01	<i>D. nauti</i> Hammerschmiede (HAM 4)	157.1	~47	29.8	30.6	~28	~35	~11	~30	~36	~92	~48	~63	72.5	21.4	53.8	14/ ~4	1.9
GPIT/MA/17690	<i>D. nauti</i> Hammerschmiede (HAM 4)	/	53.8	/	/	33.2	45.4	~12	38.5	/	/	36.7	51.9	/	/	56.8	26/3	/
NMA-Walda 2	<i>D. crassum</i> Walda 2	173	80	38.3	36.4	35	44.6	17.9	46.6	52	102.4	37.9	51.9	72.5	21.2	43	29/ 4.2	/
NMA-2012-1/2131 (Thierhaupten)	<i>D. crassum</i> Thierhaupten	153	84.3	27.5	34.1	29.9	38.4	15.2	50	46.9	/	34	45	66.3	/	/	/	/

All measurements are in mm. Parameters and measurements of *D. crassum* (Walda 2 and Thierhaupten) after [11] except (o), (p) and (q); (a) Condylbasal length; (b) Zygomatic width; (c) Largest dorsoventral diameter of orbits; (d) Largest anteroposterior diameter of orbits; (e) Occipital condylar width; (f) Paroccipital 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; (o) postfrontal length; (p) length/height of sagittal crest; (q) diameter of upper canine alveole. Numbers including tilde represent approximations due to the preservation of the specimen.

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and follow the course of the occipital suture until they merge into the paroccipital process. They are more prominent in the GPIT/MA/17690 than in GPIT/MA/18000-01.

Alisphenoid

Anterior to the squamosal, the alisphenoid is situated posteriorly to the orbita and medially to the zygomatic arch (Figs 3 and 8), which is well-visible in both skulls from Hammerschmiede. It forms a part of the lateral wall of the braincase. The alisphenoid is sutured anteriorly with the orbitosphenoid and posteriorly with the parietal and squamosal. In ventral view, the alisphenoid continues beneath the tympanic bulla and is confined by the basioccipital and basisphenoid (Figs 5 and 11).

Jugal

The jugal is preserved in GPIT/MA/18000-01 and the skull from Eppelsheim (Figs 1–3). It is an elongated, slender, tripartite bone. The anterior process is sutured with the maxillary and lacrimal and posteriorly, it forms the flattened ventral margin of the orbita. The dorsal process is sutured to the frontal and together they form the postorbital margin. The posterior process of the jugal is sutured with the squamosal and forms the posterior part of the zygomatic arch. The jugal is characterized by a prominent horizontal edge for the attachment of musculature.

Orbita

The lateral facing orbitae are situated dorsal to the jugal in GPIT/MA/18000-01 and the skull from Eppelsheim. In the latter the left orbita is small and oval if compared to the right one due to compression of the skull. In GPIT/MA/17690 the ventral margin of the orbitae is missing, but the dorsal margins are exposed.

In contrast, the left orbita of GPIT/MA/18000-01 is well-preserved and not compressed. It is large compared to the rest of the skull (Fig 3). The outline of the orbita is round to slightly rectangular. Anteriorly, the orbital margin is formed by the lacrimal, dorsally by the frontal, posteriorly by the postorbital bar, consisting of frontal and jugal, and ventrally by the antero-posteriorly elongated part of the jugal.

Internally, the orbita is formed by the lacrimal, frontal, and orbitosphenoid. In general, inside the orbita, four foramina are visible: the infraorbital foramen, the supraorbital foramen, the optic foramen, and the foramen orbitorotundum. At the anteriormost part, which is not preserved in GPIT/MA/17690, but instead in NHMUK PV OR 40632, the infraorbital foramen is situated along the frontolacrimal suture and connects the internal orbita with the nasal capsule. It contains the maxillary nerve, a branch of nerve (VII) that enters the nasal cavity inside the anterior part of the orbita and exits the nasal cavity at the maxillary. The anterodorsal part of the internal orbita contains the supraorbital foramen pinching through the internal wall of the orbita. It is the connection between the supraorbital foramen at the dorsal skull roof and the eye capsule and contains the ophthalmic branch of the trigeminal nerve (VI) together with the frontal artery and frontal vein.

Inside the posterior orbita the optic foramen is situated at the orbitosphenoid. The optic foramen contains the optic nerve (II). The largest foramen inside the orbita is the foramen orbitorotundum, situated posterior to the optic foramen and ventrally to the alisphenoid, inside the orbitosphenoid. It is a special characteristic of ruminants and the result of fusion of the foramen rotundum and the fissura orbitalis [38]. The foramen contains the ophthalmic nerve (VI), the nerves for the eye musculature consisting of the oculomotor nerve (III), trochlear nerve (IV), and abducent nerve (VI), and the maxillary nerve (VII) [39]. The foramen orbitorotundum connects the brain case with the internal orbita.

Tympanic region

The tympanic region comprises the posterodorsally extending mastoid process. The auditory bullae are poorly preserved in all specimens and are even broken off in GPIT/MA/17690 (Figs 3 and 5). The mastoid is dorsally confined by the squamosal and posteriorly by the occipital. Mastoid and occipital are separated by the nuchal crests and the paroccipital process. Dorsally to the tympanic bullae, the foramen for the external auditory meatus is well-visible on both sides of GPIT/MA/18000-01, as well as GPIT/MA/17690. Posterodorsally to the foramen for the external auditory meatus, two smaller foramina are situated (Figs 3 and 8).

Occipital

In the specimen from Eppelsheim, the occipital is heavily distorted and compressed, so that the foramen magnum is barely visible (Fig 2). In both specimens from Hammerschmiede the occipital is well-preserved and enclosed laterally by the nuchal crests. Dorsally, parts of the occipital extend anteriorly to the nuchal crests onto the lateral side of the skull. This area is larger in GPIT/MA/17690 than in GPIT/MA/18000-01. In posterior view, the occipital is slightly triangular and shows two rugose attachment surfaces for the neck musculature dorsally to the occipital condyles. Although the occipital is laterally compressed, the straight occipital crest is visible in all three specimens of *D. naui* (Figs 2, 6 and 12). The keel proceeds dorsoventrally and merges into two well-developed nuchal tubercles. The occipital condyles are dorsally set off from the occipital ventrally to the well-developed nuchal tubercles. Laterally to the occipital condyles, the elongated, slender paroccipital processes are visible.

Basicranium

In ventral view, the basicranium is well-preserved and comprises the basioccipital and the basisphenoid preserved in all three specimens (Figs 1, 5 and 11). The basioccipital is slender, V-shaped, and laterally confined by the alisphenoid and the tympanic bullae. Anteriorly, the suture between the basioccipital and the basisphenoid is straight. Posteriorly, the occipital condyles merge with the occipital. Anterior to the occipital condyles, two weakly-developed posterior tuberosities are visible that are slightly elevated and form the laterally oriented crests. Slightly anterior, the paired anterior tuberosities form elongated ridges proceeding anteroposteriorly. They have a steep posterior and a flattened anterior part. At the center of the anterior tuberosities, a smooth keel is exposed that vanishes halfway towards the basisphenoid.

The basisphenoid is elongated, rectangular, and extends the basioccipital anteriorly but its size is relatively small compared to the basioccipital. The basisphenoid is bordered laterally by the alisphenoid and the palatine/pterygoid. The basisphenoid contains a prominent foramen for the craniopharyngeal canal in its center [40]. Anterior to the basisphenoid, the presphenoid is slender and anteroposteriorly elongated. The anterior part of the presphenoid becomes thin, narrow, and continues beneath the secondary palate.

Palatine

In ventral view, the palatine is well-visible in GPIT/MA/18000-01. It forms a triangular plateau posterior to the maxillary (Fig 5). The lateral parts are crushed and a suture to the pterygoid is not visible. The palatine/pterygoid forms the lateral wall of the choana and connects with the alisphenoid posteriorly.

Maxillary dentition

GPIT/MA/18000-01 as well as the skull from Eppelsheim preserve the teeth P2–M3 on both sides. In GPIT/MA/18000-01, a small alveolus (1.9 mm in diameter) for the rudimentary upper canine is visible (Figs 3 and 5). In contrast, the skull from Eppelsheim shows large saber-like upper canines with an alveolus size of 9.2 mm (Figs 1 and 2). here, the alveoli extend posteriorly up to the level of the nasomaxillary suture and the anterior margin of the P3. The cross-section of the tooth is drop-shaped.

P2–M3 are bunoselenodont with a well-developed buccal relief. The buccal wall has wrinkled enamel, with straight and parallel folds. The central fold is large compared to the smaller, lateral ones. The lingual wall of P4–M3 is marked by a continuous cingulum reaching from the mesial protocone to the distal metaconule in the molars. The cingulum of P4 surrounds the lingual cone mesiodistally.

In occlusal view, the premolars, P2 and P3 are quite similar to each other but differ from P4 in morphology, as P2 and P3 are longer than wide with well-developed buccal cones. The P4 is wider than long and exposes a deep fossa and a lingual cingulum. The P2 is slightly more elongated than the P3. The P4 contains a broad fossa, its central fold is well-developed, and it connects to the posterobuccal cone. In comparison to P2 and P3, the P4 shows a well-developed lingual cone, encompassing the fossa lingually.

The upper molars are square-shaped and increase in size from M1–M3 (Figs 1 and 5). They contain well-developed styles. The metaconule is V-shaped and the premetaconule crista is longer than the postprotocrista, which reaches the posterolingual wall of the paracone. The postprotocrista is not connected to the premetaconule crista, because the distal postprotocrista folds mesiobuccally. All molars show prominent para— and mesostyles but weak metastyles. The development of the metastyle increases from M1 to M3.

Mandibular dentition

The skull from Eppelsheim preserves remains of the left and right mandible. Both, the mandible ramus, as well as the symphysis are badly preserved (Fig 1). They expose remains of the incisors and the p1–m3. GPIT/MA/18000-53 preserves only the central part of the left mandible, containing the p4–m3 (Fig 7). The teeth p1–m3 are bunoselenodont with a weak lingual relief and wrinkled enamel. In occlusal view, the p1 is monocuspid. The p2 and p3 are generally mesiodistally longer than wide. The p2 is bicuspid with the mesolabial conid being larger than the posterolabial conid. The p3 has a central mesolabial conid, which is the largest cusp. The anterior conid forms a small anterior valley, which is slightly bent anterolingually. The p4 shows a central mesolabial conid, where the posterolingual and posterolabial conid originate. They continue straight and parallel towards the distal part of the p4.

The lower molars show a pair of crests posterior to the metaconid; the internal postmetacristid and well-developed external postmetacristid (*Dorcatherium*-fold, *sensu* [30]). The internal postmetacristid connects to the internal postprotocristid. The internal postprotocristid merges into the external postprotocristid (*Tragulus*-fold, *sensu* [34]) buccally. Together, the postmetacristids and postprotocristids form a Σ -structure. Anterior to the Σ -structure, the well-developed *Dorcatherium*-platform is visible, formed by the well-developed preprotocristid that turns lingually to contact a very small premetacristid.

Anteriorly, the preprotocristid and premetacristid encompass the anterior fossa. The mesostylid and metastylid are absent. The posterior fossa is surrounded by the preentocristid connecting to the internal postmetacristid and the postentocristid forming a slight lingually bent wall, as well as the prehypocristid and posthypocristid buccally. The posthypocristid and postentocristid are not connected, because the posterior postentocristid is bent buccally. The

m3 contains a well-developed back fossa, formed by the hypoconulid. The entoconulid is weakly-developed and therefore the back fossa opens anterolingually.

Taxonomical attribution

Both specimens from Hammerschmiede, as well as the skull from Eppelsheim can be assigned to the family Tragulidae based on the presence of a typical Σ -structure (*Tragulus*- and *Dorcatherium*-fold *sensu* [30, 34]) in the lower molars [2] and a bunoselenodont occlusal pattern (Fig 7), as well as to *Dorcatherium* based on the following combination of characters: (I) presence of p1 in NHMUK PV OR 40632, in combination with (II) the presence of the *Dorcatherium*-platform in the lower molars (*sensu* [35]), and (III) a complex posterior valley of the p4 (*sensu* [8]). Furthermore, GPIT/MA/18000-01 and the skull from Eppelsheim share the following features of the selenodont lineage that includes *D. guntianum*, *D. jourdani*, *D. puyhauberti*, and *D. nauti*: high degree of selenodonty with reduced external postmetacristid [30, 34] in the lower molars and well-developed cristids, flat main cusps (*sensu* [34]), and prominent sickle-shaped cones and conids (*sensu* [7]). Therefore, these skulls are clearly distinguishable from *D. crassum*, *D. vindebonense*, and *D. penecki*.

Among the selenodont lineage *D. guntianum*, *D. jourdani*, *D. puyhauberti*, and *D. nauti* differ in the size (length and width) of their teeth. The m1 of *D. guntianum* is clearly distinct from GPIT/MA/18000-53 and NHMUK PV OR 40632 by its much smaller length (Fig 13, maximum length of *D. guntianum* is about 9.8 mm and the minimum length of *D. nauti* is about 11.0 mm). The width of the m1 of *D. jourdani* is smaller, whereas it is larger in *D. puyhauberti* if compared to GPIT/MA/18000-53 and NHMUK PV OR 40632. Hence, GPIT/MA/18000-53 and NHMUK PV OR 40632 are comparable in size with other known specimens of *D. nauti* [8, 9, 31] and perfectly match the size range of this species. The combination of the metrics of the m1 (Fig 13), as well as the selenodont occlusal morphology of GPIT/MA/18000-53 and NHMUK PV OR 40632, support their assignment to *D. nauti*.

Although GPIT/MA/17690 preserves no teeth, the specimen can still be assigned to Tragulidae based on the morphology of the posterior part of the skull and the morphology of the basicranium. In lateral view, the posterior part of the skull is low, prolate, and elongated posterodorsally, marked by well-developed nuchal, as well as sagittal crests typical for tragulids. Furthermore, a large temporal fossa compared to the rest of the skull is encompassed by the temporal lines and sagittal crest dorsally, the well-developed ventral process of the squamosal ventrally, as well as by the prominent nuchal crests posteriorly. This condition is not present in suids (*Sus scrofa*), cervids (*Capreolus capreolus*, *Muntiacus muntjak*), moschids (*Moschus* sp.), and bovids (*Bos taurus*, *Capra aegagrus*, and *Ovis gmelini*; all GPIT unnumbered). Morphologically similar conditions are visible in the moschid and suid specimens mentioned above; however, in suids the sagittal crest and temporal lines are weaker developed and in moschids, the braincase is more globular, rounded, and the posterior skull roof tapers posteriorly.

Furthermore, the morphology of the basicranium supports the allocation of GPIT/MA/17690 into Tragulidae, because of the presence of a large craniopharyngeal foramen, a slender basicranium with prominent, anteroposteriorly elongated anterior tubercles, and a smooth, central keel. This condition is visible in all three specimens described herein, as well as in the extant *Tragulus* (GPIT/MA/12997) and *D. crassum* from Thierhaupten [10].

Comparison

Distinguishing *D. nauti* from *D. crassum*

In general, the only three available skulls of *D. nauti* from Hammerschmiede and Eppelsheim, as well as the three known skulls of *D. crassum* from Thierhaupten, Walda 2, and Contres are

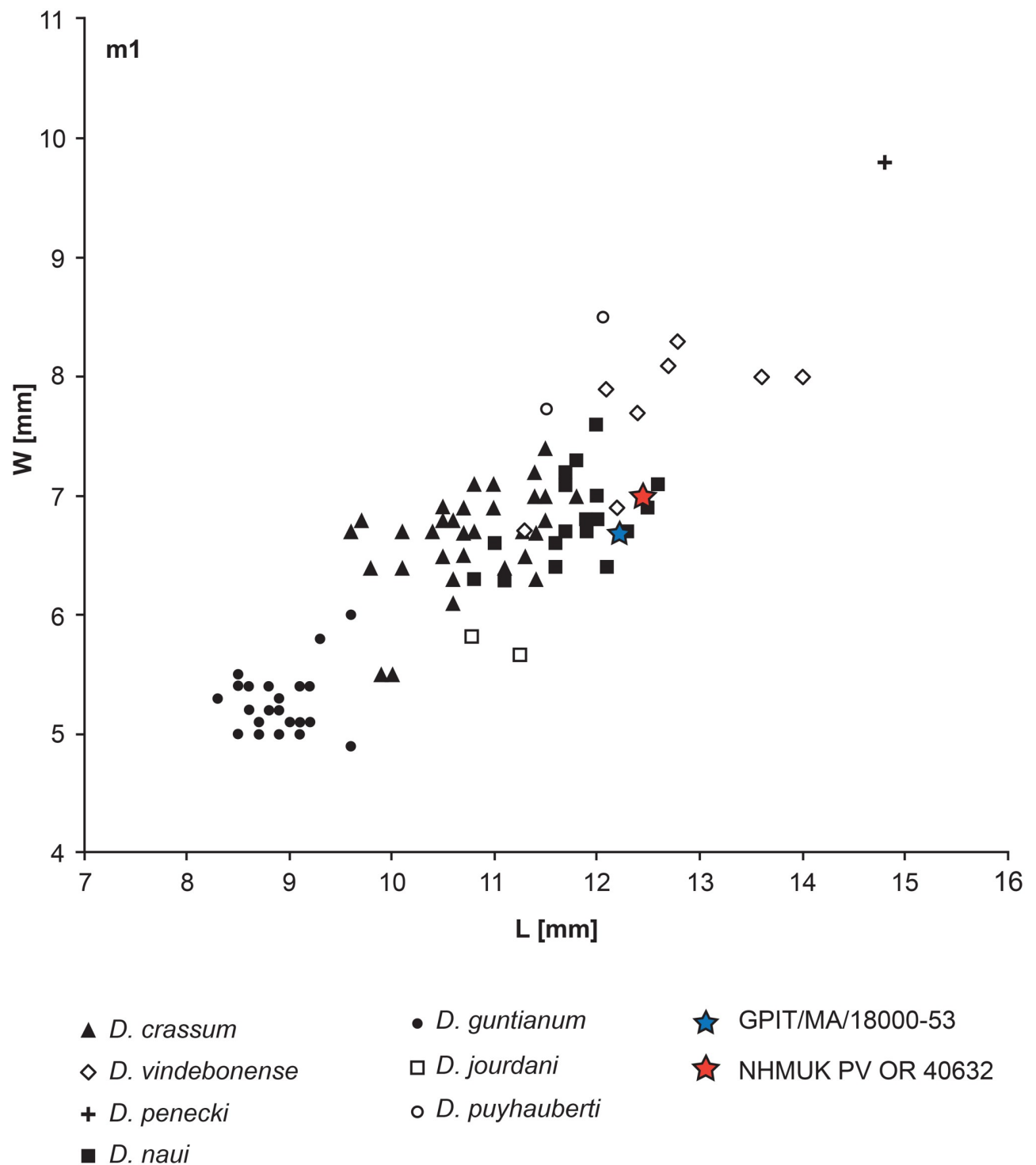


Fig 13. m1 tooth metrics of *Dorcatherium*. Data based on [31]. Position of GPIT/MA/18000-53 and NHMUK PV OR 4632 indicated with a colored star. W = maximum anterior width and L = maximum length.

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Table 2. Cranial differences between males and females of *Dorcatherium nauti* and *Dorcatherium crassum*.

Cranial characters	Comparative skull morphology (males and females)	
	<i>Dorcatherium nauti</i>	<i>Dorcatherium crassum</i>
Orientation of orbitae	lateral facing	dorsolateral facing
Postorbital part of skull (Condylbasal length/postfrontal length)	elongated (ratio = 2.9)	shortened (ratio = 4.0)
Separation of supraorbital foramen from supraorbital groove	absent	by a bony bridge
Development of nuchal crests	well-developed	strongly-developed and set off
Occipital crest	present	absent
Development of nuchal tubercle	prominent	Weakly-developed
Comparative skull morphology (males)		
	<i>Dorcatherium nauti</i>	<i>Dorcatherium crassum</i>
Frontal plateau	present (concave)	absent
Frontoparietal bulges	present, well-developed	absent
Morphology of temporal lines	thin and crest-like	Broad and flat
Development of parietal plateau	Strongly-developed, domed posterior skull roof	Almost absent, flat skull roof
Morphology of temporal lines and sagittal crest	temporal lines proceed posteriorly, parallel to the level of the sagittal crest, and merge with the sagittal crest	Temporal lines merge with anterior part of sagittal crest and form a Y-structure

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all elongated anteroposteriorly with a brain capsule that is prolate and low (Figs 1 and 3; fig. 4.4 in [11]). Only *D. nauti* exposes an elongated posterior region of the skull relative to the condylbasal length (Tables 1 and 2). The orbita of both species are generally large in relation to the rest of the skull. The orientation of the orbita, however, is different in both species. In *D. nauti* the orbita is facing laterally, whereas into *D. crassum* the orbita is laterodorsally oriented.

In dorsal view, a W-shaped nasofrontal suture is exposed in both species. In GPIT/MA/17690, the nasofrontal suture is assumed to have the same position as in the specimen from Walda 2 and GPIT/MA/18000-01; however, as GPIT/MA/17690 is broken off at the center of the orbita, the position of the nasofrontal suture is uncertain. At the frontals, supraorbital foramina and the associated deep supraorbital grooves are present in both, *D. nauti* and *D. crassum*. The supraorbital foramina are situated at the level of the anterior orbita margins in all specimens of *D. nauti*. In *D. crassum* from Contres [12] those foramina lie more posteriorly at the posterior margin of the orbita. In contrast, the specimen from Walda 2 shows the same position as *D. nauti*. As already mentioned by Guzman-Sandoval [11] the position of the supraorbital foramen is highly variable among extant tragulids; similar variations are present in *Dorcatherium*. Only in *D. crassum*, a robust bony bridge is separating the supraorbital foramen.

Posterior to the frontoparietal suture, a parietal plateau is only visible in *D. nauti*, especially in GPIT/MA/17690, but it is almost absent in *D. crassum*. Guzman-Sandoval [11] described the skull roof of *D. crassum* from Walda 2 as “almost flat surface” resulting in an almost absent parietal plateau. In contrast, in *D. nauti*, the plateau extends to the posterior end of the skull roof, enclosed by the temporal lines laterally and the medially bending frontoparietal bulges anteriorly. The temporal lines proceed posteriorly to approximate the sagittal crest asymptotic and merge with the posterior part of the latter. In contrast, in *D. crassum* from Walda 2 the temporal lines merge at the center of the posterior skull roof and blend into the anterior part of the sagittal crest. Together they form a Y-structure.

In lateral and posterior view, both species expose similar, well-developed nuchal crests. They are more prominent and set off in *D. crassum*, especially in NMA-Walda 2 (Figs 4.6 and 4.8 in [11]), than in *D. nauti*. In all specimens of *D. nauti*, an occipital crest is present, but this

crest is absent in *D. crassum* (Figs 2, 6 and 12). Ventrally, the occipital crest merges into well-developed and prominent nuchal tubercles in *D. naui*, whereas in *D. crassum* the nuchal tubercles are less-developed.

In ventral view, *D. crassum* and *D. naui* exhibit similar features of the basicranium, in which the latter is slim and elongated with prominent anteroposteriorly elongated anterior tubercles that are divided by a smooth central keel and a large craniopharyngeal foramen ([10]; pl. 2).

Accounting the differences in skull morphology in addition to the well-known differences in dentition (high degree of selenodonty in *D. naui* and bunoselenodonty in *D. crassum*), the affiliation of *D. crassum* to the genus *Dorcatherium*, with *D. naui* being the type species of the genus, could be questionable. The evidence provided could be strong enough to support an allocation of *D. crassum* into another genus as already suggested by Rössner [2] and Aiglstorfer et al. [8]. However, this has to await future investigations when more fossil tragulid skulls are available.

Comparison of the known skulls of *Dorcatherium* to extant tragulids

Fossil tragulids, as *D. crassum*, have in general a robust morphological appearance as already reported by Guzman-Sandoval [11] and Mennecart et al. [12]. This robustness is characterized by strongly developed neurocranial crests and zygomatic arches, and well-developed sagittal and nuchal crests. The position of the nasofrontal suture is similar in extant tragulids and the known skulls of *Dorcatherium*. The nasofrontal suture of *Dorcatherium* is W-shaped (Fig 4) as in *Tragulus*, but in *Moschiola* ([11]; fig. 4.7) it is V-shaped with the open end pointing anteriorly and in *Hyemoschus* it is almost straight with slight undulations (FMNH 34294).

The supraorbital foramen in extant tragulids is located at the dorsal skull roof at the center of the orbita. The same applies for *Dorcatherium*. The supraorbital grooves are in general larger in *Dorcatherium* and can be separated from the prominent supraorbital grooves by a bony ridge, as visible in *D. crassum* [12].

The sagittal crest in *Dorcatherium* is almost in confluence with the nuchal crests as in *Hyemoschus*. However, in *D. crassum* and *Hyemoschus* the sagittal crest runs posteroventrally, whereas in *D. naui* the sagittal crest and the nuchal crests are at the same level as the parietal plateau (Figs 3 and 8).

D. naui and *D. crassum* show well-developed nuchal crests, much stronger than in *Hyemoschus*. In *Tragulus* and *Moschiola*, the nuchal crests are weak or almost absent [2, 11, 12]. However, in posterior view, the nuchal crests in *D. naui* are more slender dorsally than in *D. crassum* and *Hyemoschus*, resembling the condition of *Moschiola*.

In posterior view, an occipital crest is present in *D. naui* (Figs 6 and 12) and *Hyemoschus* (FMNH 34294) but is absent in *D. crassum* (fig 4.8 in [11] and Fig 3 in [12]). Similar to *Hyemoschus*, the dorsal part of the occipital condyles is set off in *Dorcatherium*. The two nuchal tubercles are well-developed and prominent in *D. naui*, while they are less-developed in *D. crassum* and absent in extant tragulids.

The basicranium of extant tragulids is similar to *Dorcatherium*. They possess a smooth central keel, encompassed by well-developed anteroposteriorly elongated anterior tuberosities and a large craniopharyngeal foramen is visible.

Discussion

Intraspecific variability of *Dorcatherium naui*

Both skulls from the Hammerschmiede as well as the skull from Eppelsheim expose differences in the skull roof, in which GPIT/MA/18000-01 possesses delicate temporal lines and sagittal

crest, whereas GPIT/MA/17690 and NHMUK PV OR 40632 show prominent frontoparietal bulges and a robust sagittal crest. Both skulls, GPIT/MA/17690 and HMUK PV OR 40632 share similar skulls roof, but the latter additionally possesses large saber-like upper canines (diameter of alveolus 9.2 mm). In contrast, in GPIT/MA/18000-01, only a small alveolus for the upper canine (diameter of alveolus 1.9 mm) is visible. Therefore, GPIT/MA/17690 and NHMUK PV OR 40632 are quite similar in skull morphology (see taxonomic assessment) and differ significantly from GPIT/MA/18000-01 leading to the fact that two morphotypes of *D. naui* are present.

Interpretation of the different skull morphotypes of *D. naui*. As discussed above, there are two different morphotypes in the three skulls of *D. naui*. It is evident, that these morphotypes do not represent different species (see systematic Paleontology and taxonomic assessment), but rather represent some kind of intraspecific variation of *D. naui*.

It is possible that this intraspecific variation is a result of ontogeny. For juveniles of *Hyemoschus* [12] it is known that the cranial crests are only weakly developed and that they are clearly smaller than the adults. However, the cranial crests in GPIT/MA/17690 and NHMUK PV OR 40632 are very prominent and furthermore these specimens show well-developed frontoparietal bulges. Additionally, all skulls of *D. naui* are very similar in size (Table 1) and NHMUK PV OR 40632, as well as GPIT/MA/18000-01 possess adult dentition (Figs 1 and 5). Therefore, it is highly unlikely that the variation found in the two different morphotypes can be explained with juvenile and ontogenetic differences.

The only remaining hypothesis is that both morphotypes are a result of sexual dimorphism as already indicated by the strong difference in size of the upper canine alveoli. Mennecart et al. [12] reported a sexual dimorphism in extant tragulids (*Hyemoschus*) in which the males show stronger-developed cranial crests than females, similar to the skulls of *D. naui* described herein, but in general weaker developed. Moreover, male tragulids possess large, saber-like upper canines, which are reduced in females [2]. Based on the canine size, NHMUK PV OR 40632 is a male and GPIT/MA/18000-01 is a female. Because GPIT/MA/17690 is very similar to NHMUK PV OR 40632, although it lacks the anterior part of the snout containing the upper canines, the cranial bulges shared by both specimens indicate that GPIT/MA/17690 is a male and that these bulges are male characters of *D. naui* (Fig 14).

Sexual dimorphism in *Dorcatherium naui*. Given sexual dimorphism as the most possible hypothesis explaining intraspecific morphological variability in crania of *D. naui*, from Hammerschmiede and Eppelsheim, other observed morphological differences could also be related to the same phenomenon of bimodality. Thus, in addition to I) the large saber-like upper canines [2], male skulls of *D. naui* are characterized by: (I) a broad, concave and laterally expanding skull roof formed by the anterior frontal (frontal plateau), (II) presence of frontoparietal bulges enclosing a well-developed parietal plateau, (III) a prominent, flat and broad sagittal crest, (IV) large part of occipital participating in the formation of the sagittal crest, (V) strongly-developed nuchal crests, (VI) large and prominent nuchal tubercle, (VII) laterally expanding part of ventral squamosal with only a slight depression, as well as the above mentioned (VIII) large, saber-like upper canines (Fig 14).

In contrast, females exhibit in general a straight and slender outline of the dorsal skull roof (Fig 14A and 14C). Hence, the frontal is smaller, only slightly broadened, and the constriction of the parietal plateau is absent. The sagittal crest is less-prominent and more crest-like (Fig 14C and 14D). Moreover, the most distinctive sexually dimorphic characters are the absence of robust and prominent frontoparietal bulges on the dorsal skull roof (Figs 9 and 14) and the much smaller upper canines (Figs 3 and 5).

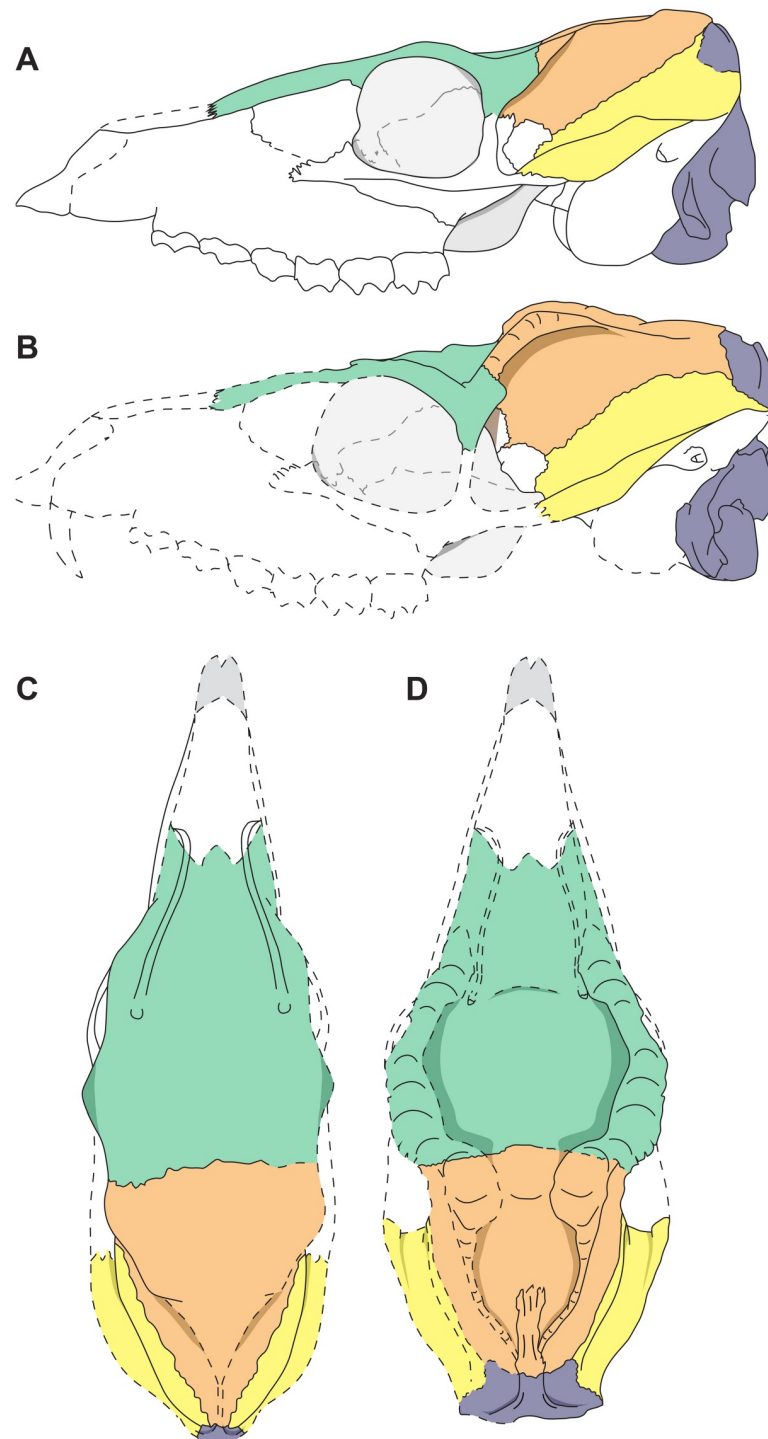


Fig 14. Reconstruction of the male and female skull of *Dorcatherium nauti* from the Hammerschmiede locality, Germany. (A) lateral view of GPIT/MA/18000-01 (female), (B) lateral view of GPIT/MA/17690 (male), (C) dorsal view of GPIT/MA/18000-01 (female), (D) dorsal view of GPIT/MA/17690 (male). Green: frontal; Orange: parietal; Yellow: squamosal; Grey: occipital. Skulls not to scale.

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Sexual dimorphism in *Dorcatherium*

Sexual dimorphism in *Dorcatherium crassum*. In *D. crassum*, large saber-like upper canines are also known from males and therefore, the skull NMA-Walda 2 described by Guzman-Sandoval [11] clearly represents a male. Based on the absence of a large alveolus for the upper canine, the specimen from Thierhaupten NMA-2012-1/2131, described by Seehuber [10], should be a female.

Therefore, the male and the female skull of *D. crassum* can be characterized as follows: In dorsal view, the male skull shows broad and flat temporal lines merging posteriorly into a prominent sagittal crest, but in the female skull the gracile temporal lines merge into a more crest-like but narrow sagittal crest. In lateral view, the lateral wall of the braincase of the male skull is posteriorly confined by well-developed nuchal crests, whereas the crests are less prominent in the female.

In the *D. crassum* specimen from Contres, the anterior part of the snout is missing and therefore, the canines are not preserved. But based on similarities in the skull morphology such as the broad and flat sagittal crest, the prominent temporal lines, and the dorsally broad nuchal crests that are present in the male specimen NMA-Walda 2 and the *D. crassum* specimen from Contres [12] we are confident that both skulls represent males.

Comparison of sexual dimorphism in *D. crassum* and *D. naui*. As discussed above, it is now possible to identify male and female individuals of *Dorcatherium* based not only on the size of the upper canine, but also on characteristics of the skull osteology. In total there are two male skulls and one female skull of both, *D. naui* and *D. crassum*.

The main difference in skull morphology between both species related to sexual dimorphism is that males of *Dorcatherium* are in general more robust with well-developed cranial crests and females have a more delicate skull morphology with less-pronounced crests and ridges.

In detail, males of both species differ in the presence or absence of lateral bulges at the frontoparietal. In males of *D. naui* these bulges, together with the temporal lines enclose the skull roof anteroposteriorly until they merge with the posterior part of the sagittal crest (Figs 14 and 15; Table 2). In males of *D. crassum* the frontoparietal bulges are absent, but the temporal lines form two flat ridges, which are only present on the parietals and do not extend onto the frontals.

Males of both species share a broad and flat sagittal crest. The latter is more crest-like and delicate in females of both species. Moreover, males of *D. naui* expose a well-developed parietal plateau (Figs 9 and 15), which is only less-pronounced in females of this species (Fig 14). In contrast, in *D. crassum*, the parietal plateau is absent in both males and females. Moreover, in *D. naui*, the temporal lines proceed posteriorly at the level of the sagittal crest. Here, they run almost parallel to the sagittal crest and merge with the latter slightly anterior to the parietal-occipital suture. In contrast, in males of *D. crassum* the temporal lines form a Y-structure (Fig 15).

Moreover, the male skull of *D. naui* from the Hammerschmiede contains a concave plateau formed by the frontals anterior to the temporal lines. In contrast, in the male skulls of *D. crassum* the anterior skull roof is flat to convex and forms a straight surface extending the posterior part of the skull.

Sexual dimorphism in extant tragulids in comparison with *Dorcatherium*. In extant tragulids, sexual dimorphism is long known, but only based on large canines in males and small ones in females. Moreover, Mennecart et al. [12] demonstrated that *D. crassum* and *Hymoschus* share a “hyper-developed” cranial morphology and mentioned that females of *Hymoschus* show less remarkable characters (e.g. weaker crests), similar to *Dorcatherium* (see

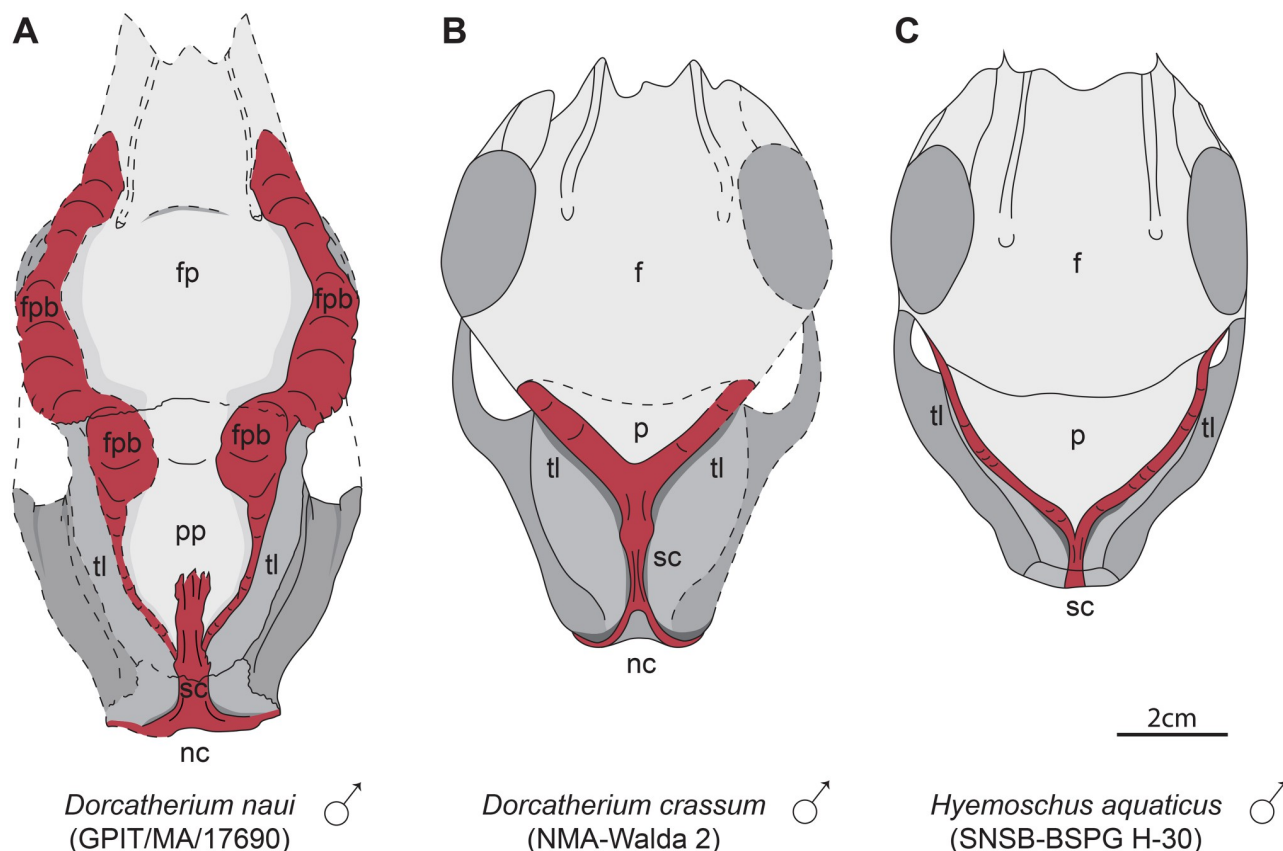


Fig 15. Morphology of the posterior skull roof of males of *Dorcatherium nauti*, *D. crassum*, and *Hyemoschus aquaticus*. (A) GPIT/MA/17690, *D. nauti* from Hammerschmiede, Germany (HAM 4), (B) NMA-Walda 2 (drawn after Guzman-Sandoval, 2018), *D. crassum* from Walda 2, Germany, (C) SNSB-BSPG H-30 (redrawn after Guzman-Sandoval, 2018), *Hyemoschus aquaticus*. Red: cranial crests and bulges. f, frontal; fp, frontal plateau; fpb, frontoparietal bulges; nc, nuchal crests; p, parietal; pp, parietal plateau; sc, sagittal crest; tl, temporal lines.

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above). This is congruent with the herein described features of males and females of *Dorcatherium*, in which males expose well-developed cranial crests (nuchal crests, sagittal crest, and crest-like temporal lines) in contrast to females (Fig 14) and males additionally possess frontoparietal bulges unknown from any other fossil or extant tragulid. Therefore, we agree with Guzman-Sandoval [11] and Mennecart et al. [12] that, based on osteological characters, *D. crassum* is more similar to *Hyemoschus* than to *Tragulus* and *Moschiola* ([11]; fig 4.7). As demonstrated above, this is also the case for *D. nauti*. In detail, the temporal lines of male *D. nauti* are more similar to *Hyemoschus* than to *D. crassum*, but the sagittal crest resembles that of *D. crassum*. Males of *D. nauti* and *Hyemoschus* have similar temporal lines, but the sagittal crest is weaker in extant tragulids and prominent in *Dorcatherium*. In general, males of *Dorcatherium* expose a broad and robust sagittal crest, more developed than in any extant tragulid, whereas in females of *Dorcatherium* the crest is more delicate and less-prominent than in *Hyemoschus*, but somewhat more developed than in *Moschiola* and *Tragulus*.

Interpretation of the function of the frontoparietal bulges in males of *Dorcatherium nauti*

Among land vertebrates, cranial appendages, as well as cranial ornamentation and structures are widely distributed and occur within different vertebrate groups, e.g. [41–47], where they

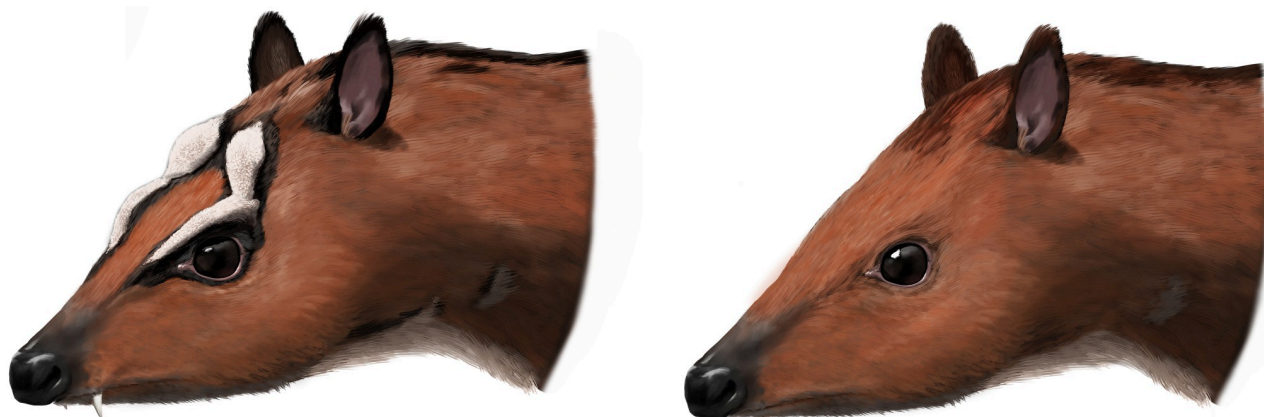


Fig 16. Life reconstruction of male (left) and female (right) *Dorcatherium naui*. Illustration by Peter Nickolaus.

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have many purposes and are often used for sexual display or intra-specific combat [48–52]. Pecora e.g. are known for their morphological variety of cranial appendages that resulted in different types of headgear (antlers, horns, pronghorns, and ossicones [53]), similarly used for sexual display and during intra-specific combat [43, 49, 54–57]. Among living ruminants, tragulids are a non-pecoran group, lacking cranial appendages.

Here we can demonstrate that the frontoparietal bulges in males of *D. naui* represent a cranial ornamentation previously unknown in extant and fossil tragulids. These bulges are well-developed and markedly set off from the skull roof. The bulges show a rough surface, while the rest of the skull roof has a smooth surface texture (Fig 9) as in some types of headgear known from Pecora (e.g. [53, 58, 59]). Moreover, the results of the μ CT-analysis of the male *D. naui* from Hammerschmiede revealed that the internal structure is quite similar to bovid horn cores or giraffe ossicones, by being porous or cancellous with surrounding compact bone (Fig 10; compare [41]; fig. 2). Especially, the thickened part of the bulges anterior to the parietal plateau is very porous (Fig 10b cross section 2) and is located on top of the massive and compact frontal bone.

These frontoparietal bulges are only present in males of *D. naui* as in Pecora, where cranial appendages are mainly present and stronger developed in males than in females [49, 53, 54, 60, 61]. The bulges in *Dorcatherium* are difficult to interpret, because there is no analogue in tragulids or any other closer related group. However, we here interpret that these bulges were probably used in a similar way as in Pecora—most likely for sexual display (Fig 16).

These bulges, furthermore, cover the dorsal eye-region and could therefore be used in analogy to the frontal bony ridges of extant male *Muntiacus* (Cervidae) which are interpreted to function as a protection against tusk-wounding during male-male combats [62, 63]. The fighting behavior of extant tragulids is dominated by slashing and stabbing with the large upper canines [2, 64] and therefore they develop toughened skin on their backs forming a shield for protection. Hence, an additional protection of the eye region in male *D. naui* might be useful.

Conclusion

For the first time, a detailed description of the skull morphology of the type species of *Dorcatherium*, *D. naui*, is provided using three skulls of this species, from the localities of Hammerschmiede (level HAM 4, 11.44 Ma) and Eppelsheim (middle to late Miocene). A comprehensive redescription since Kaups original description in 1839 of the complete skull of

D. naui, NHMUK PV OR 40632 from Eppelsheim, is provided based on a μ CT scan. Therefore, an emended diagnosis for *D. naui* is presented, which includes for the first time, besides dental features, also characters of the skull such as (I) lateral facing orbitae, (II) prominent nuchal tubercle, and (III) the presence of an occipital crest.

A comparison between the three skulls of *D. naui* and the known skulls of *D. crassum* shows that these species differ in morphological features of the skull and not only in their dentition. This study revealed that *D. naui* differs significantly from *D. crassum* in (A) a higher degree of selenodonty, (B) strongly reduced postmetacristid, (C) lateral facing orbitae, (D) separation of supraorbital foramen from supraorbital groove by a bony bridge, (E) well-developed parietal plateau, (F) prominent nuchal tubercle, (G) less-developed nuchal crests, and (H) the presence of an occipital crest. These significant osteological differences between *D. naui* and *D. crassum*, as well as the close resemblance of other bunoselenodont species with *D. crassum* may indicate that they belong to a different genus. This was already suggested by Rössner and Aiglstorfer et al.

This study also showed that unlike other fossil or extant tragulids, *D. naui* exhibited significant sexual dimorphism on several cranial features, apart the well-known canine size. The first female skull of this species is described in detail and based on the morphological comparison with the two available male skulls, it is possible to distinguish them by a, more complex and robust skull roof with well-developed crests and bulges in addition to large upper canines in males in contrast to delicate cranial crests and rudimentary upper canines in females. Similar differences between males and the female skull are described here for *D. crassum*. Moreover, male skulls of *D. naui* differ from males of *D. crassum* by the presence of prominent frontoparietal bulges. These bulges were probably used for sexual display and may have functioned as eye protection in male-male combats. In the future, if more skulls of *Dorcatherium* are available, it will be possible to further understand and identify the sexual dimorphism in tragulids.

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Second paper of Dissertation

Cranial ontogenetic development and sexual dimorphism of the extant water chevrotain
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Cranial ontogenetic development and sexual dimorphism of the extant water chevrotain *Hyemoschus aquaticus*

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Abstract

Tragulids or mouse-deer live in tropical Asia and Africa. They are the sister group of Pecora and have a long fossil record dating back into the Eocene. The extant African species, *Hyemoschus aquaticus*, is the sister taxon of all other extant tragulids and is therefore often used for comparison with fossil mouse deer. However, although many fossil tragulid skulls were found and studied within the last years, no attempt has been made for a comprehensive and comparative study of the ontogenetic development of cranial sexual dimorphism of *H. aquaticus*. Based on 39 extant skulls we establish an ontogenetic categorization of this species, comprising nine stages of tooth wear. We show that (I) in *H. aquaticus* upper canine development remains the main character for distinction of male and female, (II) that the eruption of the permanent upper canines and the development of sagittal crests starts before sexual maturity after the eruption of the second upper molar, and (III) that the development of further cranial crests (nuchal crests, temporal lines) varies greatly within the same age class and among the sexes. Thus cranial ornamentation is not useful as a primary distinction feature between the sexes and of limited importance in identifying ontogenetic age. The newly established categories of wear stages and the observed sexual similarity in cranial crest development can be used in future comparative studies with the other extant mouse-deer and especially with their fossil representatives.

Keywords Tragulidae · Cranial ornamentation · Sagittal crest · Intraspecific variety · Tooth eruption sequence · Artiodactyla

Abbreviations

GPIT	Geologisch-Paläontologisches Institut, Tübingen
NHM Vienna	Naturhistorisches Museum, Wien
R.G.	Register general (RMCA)
RMCA	Royal Museum for Central Africa Tervuren, Brussels

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Introduction

Tragulids are considered the world's smallest artiodactyls. This family of ruminant evolved during the late Eocene (Métais 2006; Rössner 2007; Hassanin et al. 2012; Sánchez et al. 2018; Mennecart et al. 2021) and diversified during the Middle to Late Miocene (e.g. Rössner 2007; Khan and Akhtar 2013; Rössner and Heissig 2013; Koufos 2021; Guzmán and Rössner 2021; Hartung and Böhme 2022). Today, tragulids comprise three genera, *Hyemoschus*, who lives in the rainforests of Africa, *Moschiola* in Ceylon, India, and possibly Nepal, and *Tragulus*, who lives in Southeast Asia. The genus *Hyemoschus* is monospecific and contains *H. aquaticus* and *Tragulus* comprises most of the living tragulid species (Smit-van Dort 1989; Meijaard and Groves 2004; Groves and Meijaard 2005; Meijaard et al. 2017; Guzmán and Rössner 2018). Males of this family are characterized by large saber-like upper canines, which were used as a display feature, as well as for male-male fights (Dubost and Terrade 1970; Dubost 1975; Ralls et al. 1975), whereas small, rudimentary upper canines are present in females. The

dimorphism of the canines is commonly understood to be the main feature to distinguish between the sexes (e.g. Janis 1984, 1990; Rössner 2007). However, among the extant tragulids, *H. aquaticus* was also thought to show the largest sexual dimorphism regarding the skull, in which adult males have a tendency towards stronger cranial crests such as the nuchal crests, sagittal crests, and temporal lines (Mennecart et al. 2018). In contrast, in *Moschiola* and *Tragulus* the development of cranial crests are less significant (Mennecart and Costeur 2016).

So far, detailed studies about the skull morphology of *H. aquaticus* are very rare and mainly based on few individuals (Smit-van Dort 1989; Rössner 2007; Mennecart et al. 2018; Hartung and Böhme 2022) and there is so far no study about the configuration of the skull roof regarding the development of cranial ornamentation of this species. Most studies focus on the general configuration of the skull and the difference between the genera and species as for example Gray (1845), Vislobokova (2001), Rössner (2007), O'Brien (2015), Guzmán and Rössner (2018), and Hartung and Böhme (2022).

During the last years, more fossil tragulid skulls were studied and skulls of *H. aquaticus* were often used for comparison (e.g. Rössner 2007; Mennecart et al. 2018; Hartung and Böhme 2022), because this species is considered to be the “most primitive” living tragulid and the sister taxon of all other extant tragulid (Webb and Taylor 1980; Meijaard et al. 2010). However, comparisons were mainly based on a very limited number of specimens, because zoological collections usually contain only few skulls of this species and a comparison between individuals of the same age class and sex was not always possible. Hence, a detailed age classification for comparison of those skulls is urgently needed.

There have been studies about age estimation using cranial suture closure patterns in ruminants (Jaslow 1989; Kim et al. 2013a, b; Oh et al. 2017a, b, 2019), especially cervids and bovids, which is a useful method to determine age and sex as well. This might be another approach in future studies on this group once more skulls and also comparative data of the other tragulids are available. One example by Oh et al. (2017a) studied the skulls of the Korean water deer (*Hydropotini*), who also possess large saber-like upper canines. They showed that there might be evidence for a difference of suture closure and overall skull allometry between the sexes induced by a large upper canine in males or maybe an ecological adaptation like unique parental care of females (Kim et al. 2013a).

In order to provide a comprehensive framework for future studies of fossil as well as extant tragulids, we study 39 skulls of the species *H. aquaticus* from museum collections and establish an ontogenetic series based on a comprehensive and detailed wear stage classification. We establish our new dental wear categories on initial work of Dubost (2016), who defined six categories on the base of dental eruption sequence, which he correlated with the development of sexual maturity, using testicle mass, diameter of the seminiferous tubules, and production of spermatozoa (at 5–9 months and 17–27 months) for males and ovary mass, as well as the presence of corpora lutea for females (sexual maturity occurs after 10–16 months and reaches its maximum at 27 months).

Our expanded classification, adapted to paleontological requirements, can be used for future studies on extant tragulids and mainly as a base for the comparison with fossil representatives connecting the dental and ontogenetic development and the sexual development and morphology of the skull. The data of *Hyemoschus* as well as the wear

Table 1 Wear stages of *H. aquaticus* compared with Dubost (2016). Wear stage w0, w2, and w4 were added for more detailed comparison

Wear stage	Sample size (male and female)	Dental development	Age class
8	0	M3 heavily worn, occlusal pattern abraded	> 6.5 years: senile individuals
7	4	M3 medium worn	4.5–6.5 years
6	7	M3 slightly worn, no deciduous teeth present	27 months–4.5 years
5	8	M3 erupted but unworn, DP4 still present	17–27 months
4	6	M3 unerupted but visible in crypt, DP4 present and heavily worn	
3	5	M3 unerupted, M2 erupted but unworn, DP4 worn-slightly worn, permanent, large saber-like upper canines in males erupted	10–16 months
2	2	M2 unerupted but visible in crypt, M1 worn to slightly worn, DP4 worn to slightly worn, deciduous upper canine small and rudimentary	
1	1	M1 erupted but unworn, DP4 unworn, deciduous upper canine small and rudimen- tary	5–9 months
0	6	M1 unerupted but visible in crypt, DP4 erupted but unworn, deciduous upper canine small and rudimentary	< 5 months

Age classes are defined and referenced to wear stages by Dubost (2016), based on living animals of known age

wear stage	M3	M2	M1	DP4
8	no specimen available			
7				
6				DP4 shed
5				
4	M3 not fully erupted but visible in crypt			
3	M3 unerupted			
2		M2 not fully erupted but visible in crypt		
1		M2 unerupted		
0			M1 not fully erupted but visible in crypt	

Fig. 1 Occlusal line drawing of *Hyemoschus aquaticus* showing the abrasion pattern of w0–w7 of all important tooth positions used to establish the wear stage series. No specimens of w8 are available

stage classification itself now allow a much more detailed age determination and comparison of incomplete fossil specimens as they are often found in the field, as well as direct comparison to a large and well documented data base of *Hyemoschus* skulls which was lacking in the past. This allows consistent comparison among fossil species as well as between single individuals.

Material and methods

The study comprises 39 specimens of *H. aquaticus* including nine neonate to juvenile, thirteen subadult to adult males, and seventeen subadult to adult females. No senile individual was available. The skulls are housed at the Royal Museum of Central Africa in Tervuren, Belgium and represent one of the largest collections of skulls of *H. aquaticus*. The collection houses more skulls of this species, but for comparative reasons we chose the most complete ones of

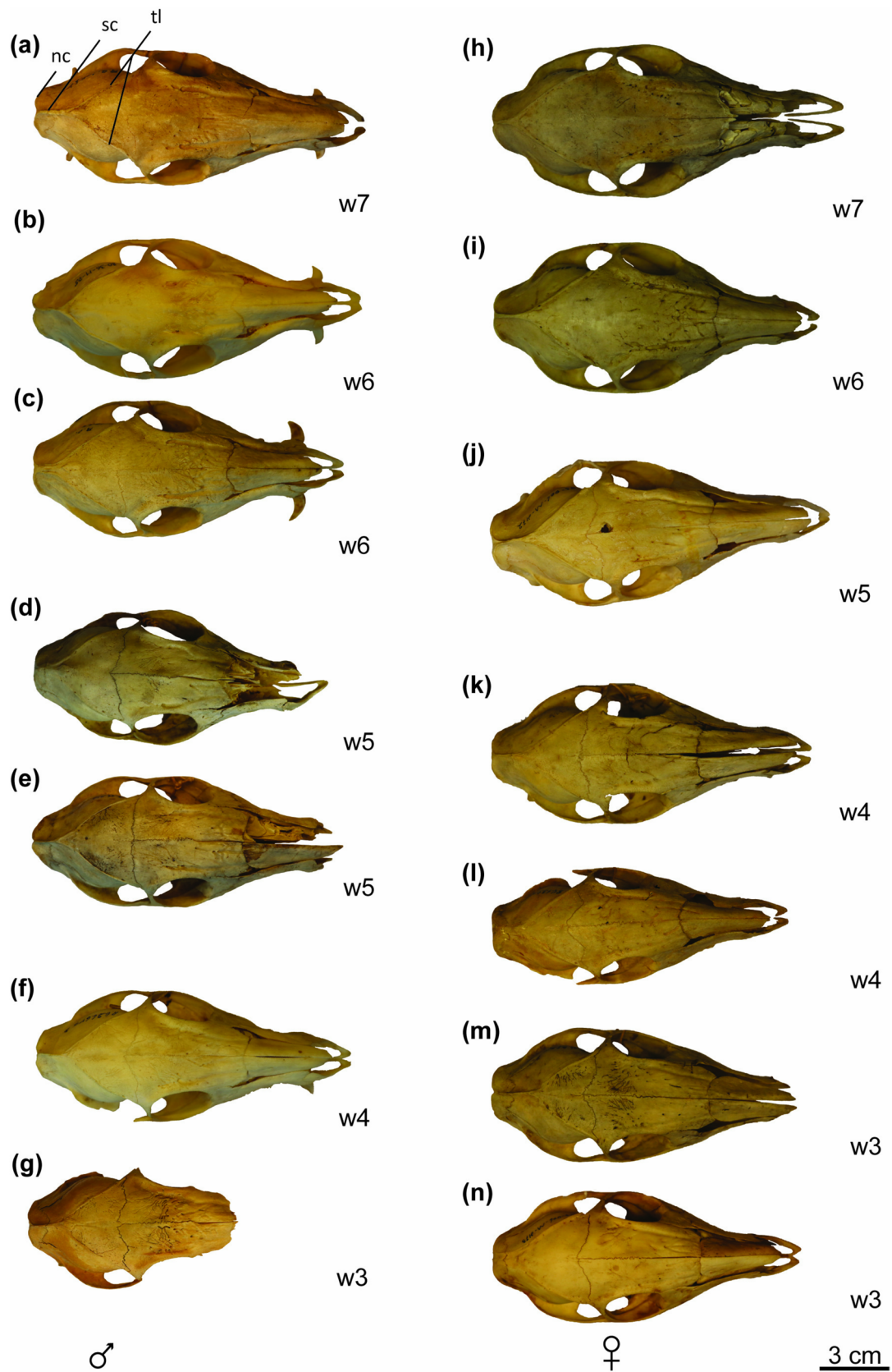


Fig. 2 Subadult to adult *Hyemoschus aquaticus* in dorsal view wear stage 3–7. **a–g** males, **a** R.G.10471, **b** 80–36-M-75, **c** R.G.10332, **d** R.G.3366, **e** R.G.579, **f** R.G.26674, **g** R.G.555, **h–n** females, **h** R.G.2348, **i** R.G.6155, **j** 83006 M 472, **k** R.G.8333, **l** R.G.13979, **m** R.G.573, **n** 83006 M 473. Abbreviations w = wear stage, nc = nuchal crests, sc = sagittal crest, tl = temporal lines

each ontogenetic stage including also variations, which are displayed in the figures. We also compared the skulls morphologically with available skulls of *Tragulus* from GPIT and *Moschiola* from NHM Vienna. The skull terminology follows Whitmore (1953) and Zietzschmann et al. (1943) and the definition of cranial ornamentation follows Hartung and Böhme (2022). All data generated or analysed during this study are included in this published article.

Results

Definition of wear stages

Skulls of *H. aquaticus* were categorized according to the tooth eruption sequence into nine dental wear stages (Table 1 and Fig. 1). We expanded the categories of Dubost (2016) for a suitable usage in paleontology and added three wear stages for more detailed comparative results in future studies especially targeting subadult and juvenile individuals. The new wear stage categorization now includes w0, where the DP4 is erupted but unworn, w2 with the M2 being unerupted and the M1 and DP4 being worn to slightly worn, and w4 where the M3 is unerupted and DP4 is heavily worn.

Sexual dimorphism of the skull

Based on the large sample of skulls, we can show that the osteological determination of sex in *H. aquaticus* is possible from wear stage 3 onwards, when the large saber-like upper canines become fully erupted in males (Figs. 2 and 3). Specimen R.G.555 (Fig. 3g) is the only available male individual at wear stage 3 showing a large alveole for the permanent upper canine. In contrast, females from wear stage 3 and onwards show small and rudimentary permanent upper canines with a small alveole (Fig. 2h–n) as for example in R.G.573 (Fig. 3m) and 83006M 473 (Fig. 3n). In neonate and juvenile individuals between w0 and w2 (Fig. 4) sex remains indetermined, because the deciduous upper canines are not sexually dimorphic. Instead, they are very small and cone-like in all nine individuals (w0–w2).

Development of cranial ornamentation

During ontogeny, the cranial ornamentation (nuchal crest, sagittal crest, and temporal lines) of males and females of *H. aquaticus* undergoes several morphological changes (Fig. 5). At w0 and w1 (n = 7), very fine nuchal crests are already visible, but the sagittal crest and temporal lines are not formed yet. Between w2 (n = 2) and w3 (n = 5), cranial ornamentation forms in all individuals, in which the temporal lines converge to form the sagittal crest and the nuchal crests become stronger. Albeit, in one female individual of wear stage 3 (83006M 473, Fig. 2n) the sagittal crest is not formed yet, but instead the temporal lines run parallel dorsally. Another female individual (83006M 474, Fig. 2m) at the same wear stage has a well-developed sagittal crest (see discussion).

From w4 to w7 males (n = 13) and females (n = 17) can show different extends of the development of the cranial ornamentation also within the same wear stage. In this sample, females of wear stage 4 and males at wear stage 5 and 6 represent the strongest variation (Figs. 1, 2, and 4). Here the sagittal crest in both sexes can be broad and flat, with the temporal lines running parallel dorsally to form a flat plateau between them (R.G. 10332, Fig. 2c; R.G. 3366, Fig. 2d; R.G. 13979, Fig. 2), similar to the condition in one skull described by (Vislobokova 2001), or crest-like, sharp, and high, without the formation of the plateau (80–36-M-75, Fig. 2b; R.G. 579, Fig. 2e; R.G. 8333, Fig. 2k). Obviously, there is a large degree of variation within the development of the cranial ornamentation within subadult and young-adult *H. aquaticus* and females of same wear stages can have stronger or similar strong sagittal crests and temporal lines as comparable males (compare Figs. 2b, c, i, and 5). The difference in the nuchal crests is not as remarkable as the development of the sagittal crest and temporal lines.

Correlation of ontogenetic cranial morphology and development of sexual maturity

At wear stage 3, the only available male shows temporal lines that confine to form the sagittal crest. Nuchal crests become stronger (Fig. 2g). Thus, the formation of the sagittal crest and the enhancement of the nuchal crests apparently happens at the same time as the eruption of the large upper permanent canine (wear stage 3), but more specimens will be needed to confirm this result. The cranial development of females at wear stage 3 is based on four individuals and is similar compared to the male individual regarding the extend of the development of the sagittal and nuchal crests. The temporal lines, in contrast, are already visible at wear stage 2, but do not confine to form the sagittal crest (Fig. 4a) yet. However, there is one female specimen at wear stage 3, 83006M 473 (Fig. 2n), not exhibiting the formation of the sagittal crest yet. Instead, the temporal

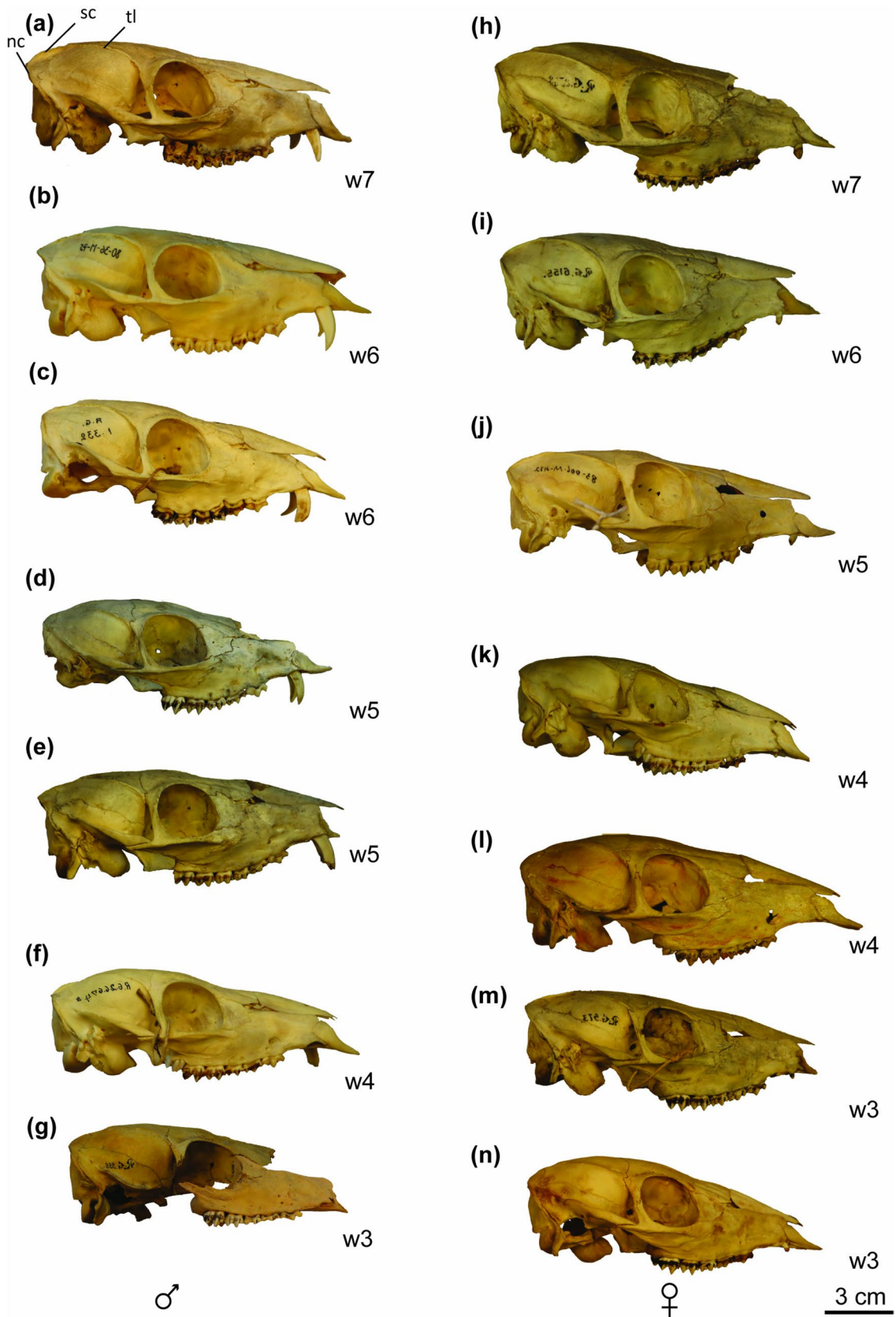


Fig. 3 Subadult to Adult *Hyemoschus aquaticus* in lateral view wear stage (w) 3–7. **a–g** males, **a** R.G.10471, **b** 80–36-M-75, **c** R.G.10332, **d** R.G.3366, **e** R.G.579, **f** R.G.26674, **g** R.G.555, notice the large alveole for the upper canine, which has fallen out in contrast to a very small rudimentary canine in the comparable females **h–n** females, **h** R.G.2348, **i** R.G.6155, **j** 83006 M 472, **k** R.G.8333, **l** R.G.13979, **m** R.G.573, **n** 83006 M 473. *Abbreviations* w = wear stage, nc = nuchal crests, sc = sagittal crest, tl = temporal lines

lines are still separated. This might be because the formation of the latter happens during the eruption of M2 and in this specimen the M2 is not completely erupted. So, this individual might be at a very early stage of wear stage 3 compared to the other specimens. This also narrows the timing of the development of the sagittal crest, which occurs in this sample at early wear stage 3 at about approximately 13 months. Later, between wear stage 4 and wear stage 7, the development of the temporal lines, the sagittal, as well as the nuchal crests is very variable among the sexes and among age classes and shows no tendency towards stronger crests in individuals of late ontogenetic stages. This means that the development of these crests mainly happens between wear stage 0 and wear stage 3.

Discussion

Ontogeny and cranial development in *Moschiola* and *Tragulus* based on the herein established wear stage system

In general, the cranial ornamentation of the other tragulid genera *Tragulus* and *Moschiola* is less-developed and less significant than in *H. aquaticus*, meaning that the sagittal crests, nuchal crests, and temporal lines are generally weaker developed. *T. kanchil* seems to show the lowest degree of development of cranial crests in comparison to *T. napu*, *Moschiola*, and *Hyemoschus* (Mennecart and Costeur 2016; Guzmán and Rössner 2018). Mennecart and Costeur (2016) studied one fetus, three juvenile, and six adult individuals of *T. kanchil* with unknown wear stages. Similar to *H. aquaticus*, the cranial crests become stronger during ontogeny, are visible at a subadult stage, and grow until adulthood. Based on their study, there seems to be no visible difference between males and females except the upper-canine development, similar to *H. aquaticus*. But a similar ontogenetic series including wear stages would be needed to perform a direct comparison to *H. aquaticus*. Guzmán and Rössner (2018, Fig. 6) show a specimen of *T. kanchil* at wear stage 4. Here the sagittal crest is short and low and the temporal lines are less marked compared to *H. aquaticus*. They also study an individual of *T. napu* at wear stage 6, which has a much stronger sagittal crest and temporal lines than the individual of *Moschiola* at wear

stage 6, and an almost similar degree of development of cranial ornamentation as *H. aquaticus*. In *T. javanicus*, the cranial development during ontogeny might be very limited as well, meaning that there is not much difference in the degree of cranial ornamentation between juvenile and subadult to adult specimens (Terai et al. 1998), however this is based on very few specimens and no comparative ontogenetic series is available of these genera and species so far.

The role of cranial ornamentation for identification of sex in extant tragulids

It is possible to identify male *Hyemoschus* skulls before sexual maturity from wear stage 3 onwards based on upper canine development. In males, the canines are large and saber-like, whereas in females the permanent canines and their alveoli are very small compared to the male specimens.

Regarding cranial ornamentation, which was thought to be diagnostic as well, females in comparison to males of the same wear stage can have stronger or at least similar developed cranial crests as comparable males and therefore, the degree of cranial ornamentation might be not diagnostic to sex at all. Interestingly, this might be completely different to fossil tragulids and there is already evidence that there are fossil species who exhibit a “hyper development” of this cranial ornamentation (Mennecart et al. 2018; Hartung and Böhme 2022).

This observation has profound implications for the widespread fossil tragulid *Dorcatherium*, where Hartung and Böhme (2022) showed substantial sexual dimorphism in cranial ornamentation for *D. naui*. The same was assumed for the extant *H. aquaticus* by Mennecart et al. (2018), based on a limited number of individuals. However, based on our large sample size the cranial ornamentation in *Hyemoschus* is quite similar between males and females of comparable ages and is therefore not suitable as a primary feature of distinction among the sexes and ages.

Conclusions

Using the large number of skulls presented in this study, it was possible to establish an ontogenetic series of wear stages of the African water chevrotain *Hyemoschus aquaticus* for the first time. We show that in *H. aquaticus* upper canine development remains the main character for distinction of male and female. We observe substantial variation in the development and extend of cranial crests (nuchal crests, temporal lines, and sagittal crest) within the same age class and

Fig. 4 Neonate to juvenile *Hyemoschus aquaticus* in **a–c** dorsal view and **d–f** lateral view wear stage w0–w2 with indetermined sex. **a** R.G.11211 in dorsal view, **b** R.G.14480 in dorsal view, **c** R.G.17283 in dorsal view, **d** R.G.11211 in lateral view, **e** R.G.14480 in lateral view, **f** R.G.17283 in lateral view. Abbreviations w = wear stage, tl = temporal lines

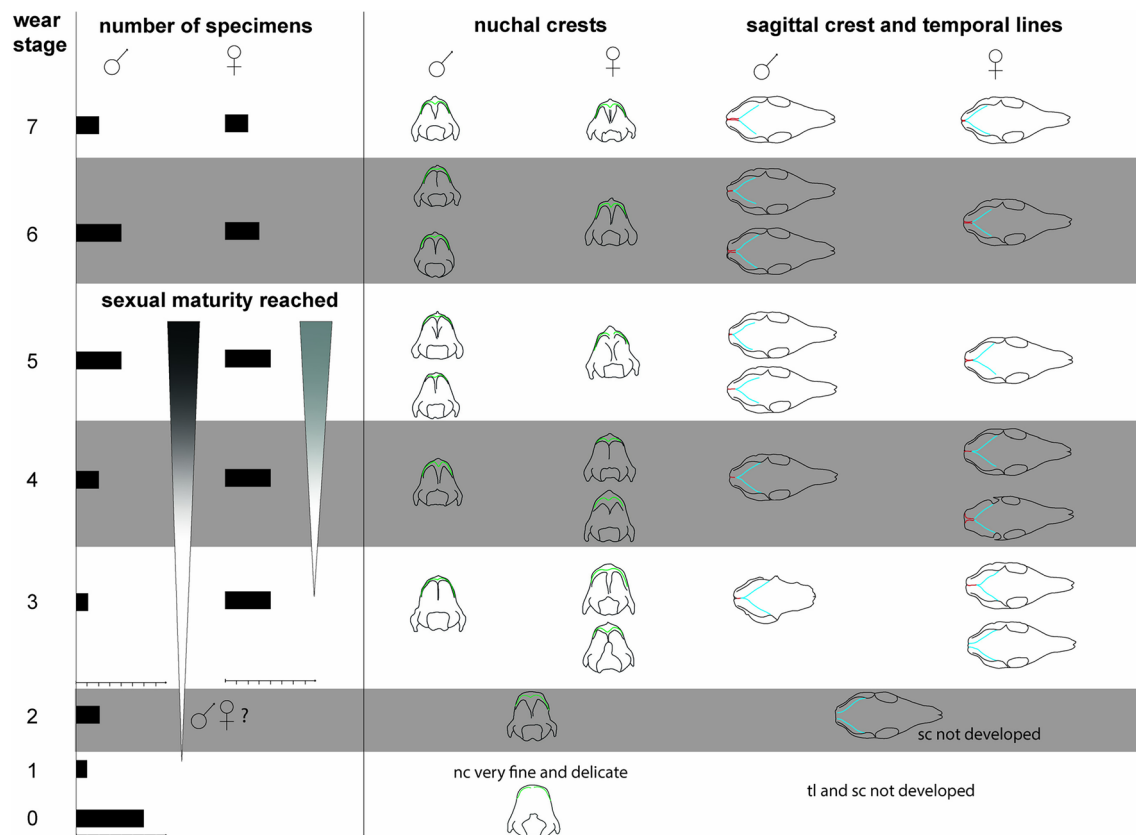
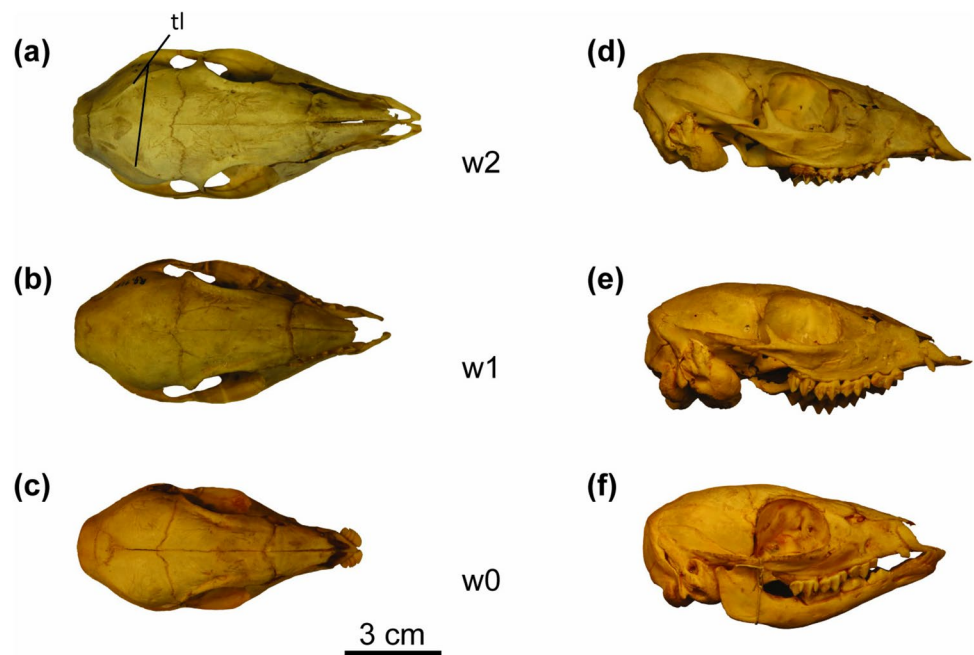


Fig. 5 Ontogenetic cranial development of *Hyemoschus aquaticus*. Ontogenetic stages are represented as wear stages. No individuals of wear stage 8 were available. Determination of sex from collection specimens is possible from wear stage 3 onwards based on eruption of permanent upper canine. Development of sexual maturity is symbolized by shaded arrows. Incorporated from results of Dubost (2016) based on male testicle mass, diameter of the seminiferous tubules, and production of spermatozoa, which starts at 5–9 months (wear

stage 1) and completes at 17–27 months (wear stage 5), whereas in females sexual development starts after 10–16 months (wear stage 3) and reaches its maximum at 27 months (wear stage 5) based on ovary mass and the presence of corpora lutea. Right side shows cranial development of nuchal crests (green), sagittal crest (red), as well as temporal lines (blue). Line drawings not to scale. Abbreviations nc = nuchal crests, sc = sagittal crest, tl = temporal lines

among the sexes, which is comparable to so far published observations on remaining extant Asian tragulids, however, the data on the other tragulid species is very incomplete and detailed comparisons need to await future studies. The eruption of the permanent upper canines and the developments of sagittal crests starts well before sexual maturity, after the eruption of the second upper molar, whereas delicate nuchal crests are already expressed at neonatal ages.

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Declarations

Conflict of interest All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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Third paper of Dissertation

Ontogenetic skull development and paleobiology of the tragulid *Dorcatherium navi*
(Mammalia: Artiodactyla) from the early Late Miocene hominid locality Hammerschmiede
(Germany)

Authors: Josephina Hartung, Madelaine Böhme

Journal: Mammalian Evolution

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**Ontogenetic skull development and paleobiology of the tragulid *Dorcatherium*
naii (Mammalia: Artiodactyla) from the early Late Miocene hominid locality
Hammerschmiede (Germany)**

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Abstract

Ontogeny describes the individual developmental history of an organism across its lifetime. Comparative ontogenetic approaches can be applied to closely related taxa and provide a powerful framework for investigating evolutionary changes in morphology, life history, and developmental timing between fossil and extant relatives. This approach is particularly informative for the fossil chevrotain *Dorcatherium nauti* and the extant African water chevrotain *Hyemoschus aquaticus*, which are consistently recovered as sister taxa in phylogenetic analyses. Until recently, the fossil record of *D. nauti* was sparse, despite the fact that this species represents the type species of one of the most frequently cited fossil tragulid genera. Here we demonstrate that the life history and ecological characteristics, as sexual maturity, sexual size dimorphism, reproduction rate and maximum life span, inferred for fossil *D. nauti* share numerous similarities with those of extant *H. aquaticus*, supporting a close phylogenetic relationship between both taxa. However, we find that *D. nauti* might have lived in more open riparian woodlands, compared to its extant relative. In addition, our results provide evidence for a paedomorphic condition of cranial ornamentation in *H. aquaticus* relative to *D. nauti*. Together, these findings support the use of *H. aquaticus* as a suitable modern analogue for fossil tragulids in general, and for *Dorcatherium* in particular. Moreover, the observed similarities between both taxa are consistent with a paleobiogeographic scenario involving a dispersal event of an ancestral form morphologically similar to *D. nauti* from Eurasia into Africa during the Late Miocene, followed by independent evolution culminating in the emergence of *H. aquaticus* during the Pliocene.

Keywords: skull morphology, population studies, Artiodactyla, life history, habitat analysis

Introduction

Tragulids are a peculiar group of small ruminants and the sister group to Pecora. The group originated in Asia during the Late Eocene (Métais et al. 2001; Rössner 2007; Hassanin et al. 2012; Sánchez et al. 2018; Mennecart et al. 2021) and survived until today, where they live in Asia and Africa. The extant taxa comprise three genera *Moschiola*, *Tragulus* (both from Asia), and *Hyemoschus* (from Africa). The fossil record shows, that tragulids were much more diverse during the Miocene (Rössner 2007; Khan and Akhtar 2013; Rössner and Heissig 2013; Sanchez et al. 2018; Koufos 2020; Guzmán and Rössner 2021; Musalizi et al. 2023) than today, with *Dorcatherium* and the type species *D. nauti* being the most frequently studied genus and species; mainly known from central and southwestern Europe (e.g. Alba et al. 2011; Rössner and Heissig 2013; Aiglstorfer et al. 2014; Mennecart et al. 2018). However, the quality of the fossil record of *D. nauti* was relatively limited comprising primarily teeth and isolated postcranial material, preventing detailed ontogenetic

investigations. This situation has changed with the discovery of the Hammerschmiede hominid site (Böhme et al. 2019), yielding abundant skulls, partial skeletons, and a plethora of mandibles and postcranial bones (Hartung and Böhme 2022; Lechner and Böhme 2025), allowing now a detailed assessment of the paleobiology of this species.

Fossil skulls represent a key source of information for understanding growth trajectories and sexual variation. The development of the artiodactyl skull follows a general vertebrate pattern (Whitmore 1953; Moyano et al. 2019), but in Pecora, the cranial morphology is strongly influenced by the development of headgear and can differ greatly among the sexes (Davis et al. 2011; Nasoori 2020) depending on body size (Calamari 2016) or whether females wear head gear at all (e.g. Bovidae Lundrigan 1996; Stankowich and Caro 2009). However, tragulids do not wear any type of head gear, but a strong ornamentation of the skull is visible in males of *D. nauti* (Hartung and Böhme 2022).

D. nauti and the extant African water chevrotain *H. aquaticus* are recovered as sister taxa in phylogenetic parsimony analyses (Sánchez et al. 2015; 2018). Based on this close relationship, we investigate similarities between these two species regarding the overall biology and ecology.

Recently, the cranial development of *D. nauti* and the fossil tragulid *Dorcabune crassum* (genus affiliation according Musalizi et al. 2023), regarding the ornamentation of the skull with respect to sexual dimorphism was studied in Hartung and Böhme (2022). The study includes in total three skulls of males and females from Hammerschmiede and Eppelsheim (Germany). Here we study 10 additional well-preserved complete and partial skulls of *D. nauti* from the Hammerschmiede locality and establish an ontogenetic series respecting males and females for the first time. We will test the hypothesis whether the ornamentation of the skull of male *D. nauti* undergoes ontogenetic changes and we will discuss the correlation of the development of cranial ornamentation with the onset of sexual maturity. We then compare the data to the already known series of *H. aquaticus* studied in Hartung and Böhme (2024).

Moreover, we analyze a set of isolated teeth and mandibles to conduct a mortality analysis and estimate the survivorship of *D. nauti* from Hammerschmiede. Using this data set, we also calculate the mean body mass for males and females to test whether a sexual size dimorphism is present in *D. nauti*. We use this data to give a comprehensive overview of the paleobiology and life history patterns.

Geological and paleoenvironmental setting of the Hammerschmiede

The Hammerschmiede is a clay pit belonging to the municipality of Pforzen. It is located in the southern part of the Northern Alpine Foreland Basin close to the town of Kaufbeuren (Allgäu, Bavaria). The locality contains fluvial and alluvial deposits from the Middle-to-Late Miocene *Upper Series*, the youngest lithostratigraphic unit of the Upper Freshwater Molasse (Doppler 1989; Doppler et al. 2005). Vertebrate finds

are mainly restricted to the two fluvial channels HAM4 and HAM5 (Kirscher et al. 2016). The 11.58 Ma old HAM4 channel represents a larger meandering stream of up to 50 m width, whereas the 11.62 Ma old HAM5 channel is a smaller meandering rivulet or creek with a width of four to five meters (Lechner and Böhme 2025). Excavations are running since 2011 and until 2024 about 1.000 metric tons of lower point-bar and channel-lag sediments have been excavated in HAM4 and about 300 metric tons of sediment in HAM5 (Lechner and Böhme 2025: tab. 1). The locality is famous for its rich and diverse faunal content including bivalves and gastropods (Schneider and Prieto 2011), fishes, amphibians, reptiles, small mammals, large mammals (Fuss et al. 2015; Hartung et al. 2020; Kargopoulos et al. 2021a, b; Hartung and Böhme 2022; Kargopoulos et al. 2022a, b; Lechner and Böhme 2022, 2023; Kampouridis et al. 2024; Kargopoulos et al. 2024; Böhme and Prieto 2025; Kargopoulos et al. 2025), and birds (Mayr et al. 2020a, b, 2023). It furthermore is renowned for the discovery of the associate skeletons of the hominid *Danuvius guggenmosi* (Böhme et al. 2019, 2020) and the second syntopic hominid *Buroniuss manfredschmidti* (Böhme et al. 2024). The palaeoenvironmental conditions during deposition of both channels differ in respect to the openness of the surrounding vegetation (Lechner and Böhme 2025). The larger meandering HAM4 river has been flowing in a relatively open and fire-prone landscape, evidenced by higher abundance of micro- and macro-charcoal, less abundant rodents (dominated by the tree squirrel *Csakvaromys*) and insectivore mammals, more abundant lagomorphs and scincomorph (lizards, scincs) reptiles. In contrast, the small HAM5 rivulet contains less charcoal, more rodents (dominated by the fossorial *Anomalomys*) and insectivores, less abundant lagomorphs and scincomorphs, and is interpreted to be surrounded by more closed forest environment, relative to HAM4 (Lechner and Böhme 2025). This interpretation is supported by the syntopy of two hominids in HAM5 (Böhme et al. 2019, 2024) and the presence of a chalicotheriine chalicothere, rather than schizotheriine chalicothere in HAM4 (Kampouridis et al. 2024).

Material and methods

The investigated material comprises 14 partial and complete skulls of *D. navi*. 13 are from the earliest Late Miocene Hammerschmiede locality (Tab. 1) and one is from the Middle to Late Miocene locality of Eppelsheim (both from Germany). The skulls GPIT/MA/17690, GPIT/MA/18000-01, SNSB-BSPG 2020 XCIV-3500, SNSB-BSPG 2020 XCIV-8518, SNSB-BSPG 2020 XCIV-2298, SNSB-BSPG 2020 XCIV-3566, SNSB-BSPG 2020 XCIV-8793, SNSB-BSPG 2020 XCIV-8970, GPIT/MA/17615, GPIT/MA/17841, and SNSB-BSPG 2020 XCIV-18870 were excavated from level HAM4. The level HAM5 produce the skull SNSB-BSPG 2020 XCV-474, as well as the skull fragments SNSB-BSPG 2020 XCV-380 and SNSB-BSPG 2020 XCV-357, which belong to one individuum and were excavated in close association. All Hammerschmiede specimens are presently housed in the Palaeontological collection of the University of Tuebingen (GPIT). GPIT/MA/17690 and GPIT/MA/18000-01 were already published in Hartung and Böhme (2022) and μ CT scans of both specimens are available for study. Another complete skull with attached mandibles NHMUK PV

OR 40632 from the type locality of *D. nauti*, Eppelsheim, is housed at the NHMUK in London and was published in Kaup (1839b, a) and described in detail in Hartung and Böhme (2022). The skull terminology follows Whitmore (1953) and Zietzschmann et al. (1943) and the dental nomenclature follows Bärmann and Rössner (2011).

Table 1: Skulls of *Dorcatherium nauti* from the late Miocene locality of Hammerschmiede used for this study.

Collection number	Description	Stratigraphic age	Sex	Wear stage
SNSB-BSPG 2020 XCV-474	Complete skull	HAM5	m	6
SNSB-BSPG 2020 XCV-357, 380	Complete skull	HAM5	f	6
SNSB-BSPG 2020 XCIV-18870	Complete skull	HAM4	m	6
SNSB-BSPG 2020 XCIV-3500	Complete skull	HAM4	m	3-4
GPIT/MA/17690	Complete skull	HAM4	m	/
GPIT/MA/17615	Partial skull, posterior part of skull roof	HAM4	m	/
SNSB-BSPG 2020 XCIV-8518	Partial skull, skull roof	HAM4	m	/
GPIT/MA/17841	Complete skull	HAM4	f	6
GPIT/MA/1800-01	Complete skull	HAM4	f	6
SNSB-BSPG 2020 XCIV-8970	Complete skull	HAM4	f	4
SNSB-BSPG 2020 XCIV-2298	Posterior part of skull, occiput	HAM4	f	/
SNSB-BSPG 2020 XCIV-3566	Posterior part of skull, occiput	HAM4	f	/
SNSB-BSPG 2020 XCIV-8793	Posterior part of skull, occiput	HAM4	f	/

In addition to the Hammerschmiede skulls 109 age-diagnostic mandibles and isolated teeth from level HAM4 and 17 teeth and mandibles from level HAM5 (all excavated between 2011 and 2024) were measured to investigate the mortality statistics, the survivorship rates, and the body mass distribution of *D. nauti*. The studied dental material includes the following numbers of tooth positions: 40 M3, 26 dP4, 28 m3, and 24 dp4 from level HAM4, as well as two dP4, 11 M3, two dp4, and seven m3 from level HAM5 (teeth preserved within skulls and mandibles are included). Additionally, the length of the m1-m3 and of the m2 were measured to calculate the body mass (see below). In total, 13 mandibles from HAM4 and three mandibles from HAM5 were used.

The assignment of the upper teeth into nine wear stages follows Hartung and Böhme (2024) with wear stage 0 being neonate, right after birth, wear stage 1 to wear stage 5 representing the juvenile stage, wear stage 6 and 7 representing the adult stage, and wear stage 8 including senile specimens (Fig. 1). The classification of the lower teeth into wear stages follows the same principle of the upper teeth and is based on the wear of the m3 and dp4 as well. At wear stage 0 the dp4 is erupted but unworn. In isolated dp4, the root is not preserved and only the thin enamel cap is visible. At wear stage 1, the dp4 is still unworn but the enamel is thicker than in w0 and a root is preserved. Wear stage 2 is characterized by the metaconid and the protoconid being slightly worn but the anteriolingual and anteriolabial as well as the entoconid and hypoconid being unworn. At wear stage 3 all cones show a wear facet and at wear stage 4 these cones are medium worn. At wear stage 5 the dp4 is heavily worn and the m3 is erupted but unworn. According to Hartung and Böhme (2024) we assume that the dp4 is shed at wear stage 6 and the m3 is worn at the metaconid, protoconid, as well as at the entoconid and hypoconid. The talonid basin (entoconulid and hypoconulid) is still unworn. At wear stage 7 all cones are medium worn and the talonid basin shows slight to medium wear facets. Wear stage 8 represents senile individuals with the m3 being highly worn so that in some specimens the selenodont pattern is almost not recognizable.

For body mass estimates (in kg) on the combined HAM5 and HAM4 sample of mandibles we use the log-transformed regressions of Janis (1990) for lower molar length (m1-m3) and length of m2 for “ruminants only”: $[\log(\text{BM}) = 3.337 \times \log(\text{SLML}/10) + 1.118]$, $[\log(\text{BM}) = 3.352 \times \log(\text{LMRL}/10) - 0.604]$; with SLML being the length of the m2 (mm) and LMRL being the length of the m1-m3 (mm).

Mortality and survivorship were calculated from the minimum number of individuals (MNI), based on the abundance of left and right M3 and dP4, as well as m3 and dp4, for each wear stage, respectively. Survivorship was derived directly from the MNI per wear stage relative to the total number of individuals. A table including the exact measurements is provided in the appendix (SF1).

The skulls GPIT/MA/17690, GPIT/MA/18000-01, SNSB-BSPG 2020 XCIV-3500, SNSB-BSPG 2020 XCIV-8970, SNSB-BSPG XCIV 2020-8518, SNSB-BSPG 2020 XCV-474, as well as GPIT/MA/17841 were scanned at the 3D Imaging Lab of the Senckenberg HEP at the Eberhard Karls University of Tübingen, Germany. The scans were acquired using the Nikon XTH 320 Reflection Target. For GPIT/MA/17690, the acceleration voltage was set to 190 kV and the resolution was 177 μA . A total of 4476 images were recorded and a 1 mm copper filter was inserted. For GPIT/MA/18000-01, a helical scan was acquired. The acceleration voltage was 195 kV and the resolution was set to 70 μA with a total of 7932 images. SNSB-BSPG 2020 XCIV-3500 and SNSB-BSPG 2020 XCIV-8970 were scanned with an acceleration voltage of 210 kV and a resolution of 90 μA . The number of total images was 4476 and a 0.1 mm copper filter was used for both specimen each. SNSB-BSPG XCIV 2020-8518 was scanned at 215 kV and 75 μA and SNSB-BSPG 2020 XCV-474, as well as GPIT/MA/17841 were scanned at 210 kV and 78 and 80 μA .

respectively. The scans were acquired using a 0.1 mm copper filter as for the other scans and a total number of 4476 images were taken. Images were processed using VG Studio Max 3.4.1. All scans are available at www.morphosource.org/projects/000810219?locale=en.

Abbreviations

GPIT: Geologisch-Paläontologisches Institut Tübingen; NHMUK: Natural History Museum of London; SNSB-BSPG: Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie

Systematic Paleontology

MAMMALIA (Linnaeus 1758)
ARTIODACTYLA (Owen 1848)
RUMINANTIA (Scopoli 1777)
TRAGULIDAE (Milne-Edwards 1864)
Genus *Dorcatherium* (Kaup 1833)
Type species: *Dorcatherium nauti* Kaup, 1833 (Kaup 1833)
Dorcatherium nauti Kaup, 1833 (Kaup 1833)

Locality and age of studied specimens: early Late Miocene locality of Hammerschmiede level HAM5 (11.62 Ma) and HAM4 (11.58 Ma) and middle to late Miocene locality of Eppelsheim in Germany.

Referred Material: Partial and complete skulls from Hammerschmiede: GPIT/MA/17690 (HAM4), SNSB-BSPG 2020 XCV-474 (HAM5), SNSB-BSPG 2020 XCIV-3500 (HAM4), SNSB-BSPG 2020 XCIV-8518 (HAM4), GPIT/MA/17841 (HAM4), GPIT/MA/18000-01 (HAM4), SNSB-BSPG 2020 XCV-357, 380 (HAM5), SNSB-BSPG 2020 XCIV-8970 (HAM4), SNSB-BSPG 2020 XCIV-2298 (HAM4), SNSB-BSPG 2020 XCIV-3566 (HAM4), SNSB-BSPG 2020 XCIV-8793 (HAM4), SNSB-BSPG 2020 XCIV-18870 (HAM4) GPIT/MA/17615 (HAM4), as well as the complete skull NHMUK PV OR 40632 from Eppelsheim. 117 teeth from level HAM4 and 22 teeth from level HAM5 including teeth preserved within skulls as well as in mandibles (for details see SF1 in the appendix).

Remarks: The skulls and teeth can be attributed to *D. nauti* based on characters of the dentition if applicable, such as (I) a high degree of selenodonty having a reduced external postmetacristid (sensu Bärmann and Rössner 2011) in the lower molars and well-developed cristids and flat main cusps (sensu Sánchez et al. 2011), (II) prominent sickle-shaped cones and conids (sensu Rössner and Heissig 2013) in combination with (III) the presence of the *Dorcatherium*-platform in the lower molars (sensu Alba et al. 2014), (IV) a complex posterior valley of the p4 (sensu Aiglstorfer et al. 2014), (V) lateral facing orbitae, (VI) prominent nuchal tubercle, and (VII) the presence of an occipital crest (Hartung and Böhme 2022). In addition to dental characters or if no teeth are preserved, the following characters apply, such as (A) well-developed parietal plateau, (B) well-developed frontoparietal bulges in males,

(C) prominent nuchal tubercle, and (D) less-developed nuchal crests (Hartung and Böhme 2022).

Description and comparison

Sexual dimorphism in *D. nauti*

To investigate the ontogenetic skull development of *D. nauti*, the specimens were separated into males and females based on characters published by Hartung and Böhme (2022). Males possess a unique skull morphology characterized by (I) a broad, concave and laterally expanding skull roof formed by the anterior frontal called the frontal plateau, (II) presence of frontoparietal bulges enclosing a well-developed parietal plateau, (III) a prominent, flat, and broad sagittal crest, (IV) large part of occipital participating in the formation of the sagittal crest, (V) strongly developed nuchal crests, (VI) large and prominent nuchal tubercle, (VII) laterally expanding part of ventral squamosal with only a slight depression, and (VIII) large saber-like upper canines. Females in contrast show delicate and fine cranial crests, no parietal plateau, and rudimentary, small upper canines (Hartung and Böhme 2022).

GPIT/MA/17690 shows well-developed frontoparietal bulges enclosing a clearly constricted parietal plateau and a well-marked sagittal crest (Fig. 2A and 3A) and was already described in Hartung and Böhme (2022) as male. The same applies for NHMUK PV OR 40632 (Fig. 2C and 3C) which furthermore possesses large saber-like upper canines. SNSB-BSPG 2020 XCIV-3500 and SNSB-BSPG 2020 XCV-474 are comparable in their features with NHMUK PV OR 40632 and GPIT/MA/17690 but they are much more compressed dorsoventrally so that the bulges and crests appear more flattened (Fig. 2B, 2D and 3B, 3D). The frontal plateau is still enclosed by the frontoparietal bulges. The sagittal crests, as well as the nuchal crests are well-developed. Therefore, SNSB-BSPG 2020 XCIV-3500 and SNSB-BSPG 2020 XCV-474 are male specimens as well. GPIT/MA/17615 and SNSB-BSPG 2020 XCIV-8518 are morphologically very similar by possessing very fine and flat parietal bulges as typical for males (Fig. 2E and 3E). They appear much flatter than in SNSB-BSPG 2020 XCIV-3500 and SNSB-BSPG 2020 XCV-474. The frontal bulges are delicate but still visible in GPIT/MA/17615 as well as in SNSB-BSPG 2020 XCIV-8518 (Fig. 2E and 3E).

GPIT/MA/18000-01 was published as female (Hartung and Böhme 2022) based on fine and delicate temporal lines, sagittal crests, and nuchal crests (Fig. 2G and 3G). Moreover, a small canine alveolus supported this statement. Like this specimen, the complete skull SNSB-BSPG 2020 XCIV-8970 (Fig. 2J and 3J), SNSB-BSPG 2020 XCIV-18870 (Fig. 2I and 3I), and GPIT/MA/17841 (Fig. 2F and 3F) are females as well. SNSB-BSPG 2020 XCV-357 and SNSB-BSPG 2020 XCV-380 (Fig. 2H) from level HAM5, are compressed dorsoventrally but the features of the skull are still visible. The temporal lines are fine confining in a narrow sagittal crest. The sagittal crest appears very high in lateral view (Fig. 3H); however, this is probably caused by compression. Therefore, this individual is also a female. The partial skulls SNSB-BSPG 2020 XCIV-2298 and SNSB-BSPG 2020 XCIV-8793 preserve the posterior

part of the skull roof with a fine sagittal crest and temporal lines, typical for females. SNSB-BSPG 2020 XCIV-3566 preserves the left part of the parietal above the orbit and shows no bulges, but instead a flat parietal plateau and a fine temporal line are present. Therefore, this specimen is a female as well.

Remarks on the dentition and ontogenetic stage of the complete skulls of *D. nauti*

The two ontogenetic youngest skulls containing teeth are the complete skulls SNSB-BSPG 2020 XCIV-3500 and SNSB-BSPG 2020 XCIV-8970 of wear stage 3-4 and wear stage 4 respectively. SNSB-BSPG 2020 XCIV-3500 exposes teeth from dP2–M2 on both sides (Fig. 4C). SNSB-BSPG 2020 XCIV-8970 (Fig. 4H) contains the right upper tooth row from dP2 to the partially preserved M1. The teeth are brachyselenodont and contain a strong buccal relief. In SNSB-BSPG 2020 XCIV-3500, the part of the maxillary containing the canine is not preserved and the M3 is not formed yet, but a pocket is visible. In SNSB-BSPG 2020 XCIV-8970, the part lying mesial to the dP2 is missing and the distal half of the M1 and further teeth are not preserved. In occlusal view, the dP2 and dP3 are longer than wide containing three cones, which increase in size from mesial to distal. The dP2 is much more elongated than the dP3. The cones are oriented slightly buccodistally and especially the metacone and metaconule are pointing into buccodistal direction. In the dP2, the styles are weakly developed and in the dP3 the mesostyle is well-developed. The protocone and the metaconule are larger in the dP3 than in the dP2 and the dP3 contains a faint posterior cingulum that continues beneath the protocone. The dP4 is molariform and medium-worn in SNSB-BSPG 2020 XCIV-3500 and heavily-worn in SNSB-BSPG 2020 XCIV-8970. It contains strong para- and mesostyles. A strong lingual cingulum is visible and the postprotocrista does not reach the premetaconulecrista. It is smaller than the M1 and M2. The M1 of SNSB-BSPG 2020 XCIV-3500 is medium-worn and the M1 of SNSB-BSPG 2020 XCIV-8970 is heavily-worn. The M2 of SNSB-BSPG 2020 XCIV-3500 is slightly worn. The molars are almost as long as wide. They contain strong para- and mesostyles and have a well-developed, continuous lingual cingulum reaching from the distal side of the metaconule to the mesial side of the protocone. The postprotocrista is bent mesially and does not reach the premetaconulecrista. Based on the characteristics of the dentition and the cranial morphology, SNSB-BSPG 2020 XCIV-3500 represents a juvenile male between wear stage 3 and 4. SNSB-BSPG 2020 XCIV-8970 is a female skull of almost the same age representing wear stage 4.

A detailed description of the permanent dentition of NHMUK PV OR 40632 and GPIT/MA/18000-01 was already published in Hartung and Böhme (2022). In NHMUK PV OR 40632, as well as in GPIT/MA/18000-01 and SNSB-BSPG 2020 XCIV-18870 the M3 is moderately worn representing wear stage 6, indicating that these specimens were about the same age (Fig. 4). In SNSB-BSPG 2020 XCV-357 from level HAM5 the M3 is slightly worn, fitting into wear stage 6 as well but being slightly younger than the skull from London and the adult female from level HAM4 of Hammerschmiede similar to SNSB-BSPG 2020 XCIV-18870. SNSB-BSPG 2020

XCV-474 and GPIT/MA/17841 are also adult specimens at wear stage 7 and 6 respectively, but in both of them the M3 is more worn (heavily worn in SNSB-BSPG 2020 XCV-474) than in the skull from London and GPIT/MA/18000-01, representing thus the oldest individuals of this ontogenetic series. In contrast, GPIT/MA/17690 preserves no teeth to determine the age, however the strong ossification, closed sutures, and the well-developed frontoparietal bulges indicate that the individual was adult. Accordingly, in SNSB-BSPG XCIV-2020 8518 the open midline suture between the parietals and the flat and faint frontoparietal bulges show, that this specimen was juvenile and compared to the still markable parietal bulges of SNSB-BSPG 2020 XCIV-3500 is even younger than the latter, probably corresponding to an early wear stage 3. In females of *D. nauti*, the development of cranial crests is thus not as strongly correlated with ontogeny as in males.

Comparative ontogenetic skull development of *D. nauti* and the extant *H. aquaticus*

In extant tragulids such as *H. aquaticus*, which is often used as a comparison to fossil tragulids, males also show well-developed large, saber-like upper canines in contrast to females, where the upper canines are reduced, similar to fossil tragulids (Rössner 2007). However, cranial ornamentation varies among adult males and females of this species (Hartung and Böhme 2024) and in the other extant tragulid genera, *Moschiola* and *Tragulus*, the cranial crests are reduced (Guzmán 2018; Mennecart et al. 2018 and own observations). Therefore, in the fossil tragulid *D. nauti* the cranial ornamentation is much stronger developed than in *H. aquaticus* (fig. 1 and 2 in Hartung and Böhme 2024). The sagittal crest and the nuchal crests are comparable in their morphology to *H. aquaticus*, but they are much more constricted and offset in *D. nauti*. The largest difference regarding cranial morphology of both species are the remarkable frontoparietal bulges of *D. nauti*, which are formed by the temporal lines on the parietal and an extension of the latter onto the frontal, anterior to the orbit. They are large, bony bulges, and form the parietal part which constricts a parietal plateau. These bulges only develop in males of *D. nauti* and are already present at wear stage 3-4 in SNSB-BSPG 2020 XCIV-3500 (Fig. 2D and 3D) or even earlier at an early wear stage 3 (SNSB-BSPG 2020 XCIV-8518, Fig. 2E and 3E). Cranial ornamentation in *H. aquaticus* are less remarkable at wear stage 3-4 (Hartung and Böhme 2024, fig. 1 and 2) where only the temporal lines are slightly enhanced and confine to form a sagittal crest.

Fig. 5 shows that parietal bulges are pneumatized at wear stage 3-4 (SNSB-BSPG 2020 XCIV-3500, Fig. 5C) up to wear stage 6 (SNSB-BSPG 2020 XCV-474, Fig. 5B) showing a spongiöse bone matrix surrounded by the external parietal bone dorsally and the internal wall of the latter (Fig. 5A, C, and D). These bulges are probably well-developed and pneumatized even in younger individuals, but adequate specimens preserving teeth are missing. SNSB-BSPG XCIV 2020-8518 preserves no teeth but might be younger than SNSB-BSPG 2020 XCIV-3500 based on flatter parietal and frontal bulges. It is noticeable that these structures are visible despite the dorsoventral compression of the specimen (compare Fig. 2D and 2E). Subadult, male

D. nauti, SNSB-BSPG 2020 XCIV-3500 and SNSB-BSPG 2020 XCIV- 8518, seem to have flatter parietal bulges and a less-developed frontal part of the bulges than the adult individuals, GPIT/MA/17690, SNSB-BSPG 2020 XCV-474, and NHMUK PV OR 40632 (Fig. 2A-C). However, these observations need to be taken with care, because of the different degrees of preservation of the fossil specimens. The parietal part of the bulges is especially visible throughout all ontogenetic stages, but the frontal part is very faint, probably due to compression. In the subadult specimens like SNSB-BSPG XCIV-2020 8518 and SNSB-BSPG 2020 XCIV-3500, a rugose surface is visible that forms the lateral part of the frontal in dorsal view (Fig. 2D and E). In contrast in females of *D. nauti* of the same wear stage (Fig. 2J) this rugose surface is absent.

The present ontogenetic series of *D. nauti* indicates that during ontogeny an increase in size and progressive enhancement of frontoparietal bulges occurs in males of *D. nauti* and that the latter possess strong sexual dimorphic features of the skull already relatively early in life if comparable to *H. aquaticus*. The bulges show allometric growth if compared to overall body size as typical for male sexual display features (Kodric-Brown et al. 2006). Females in contrast are much more similar to extant *H. aquaticus* by possessing delicate and fine sagittal and nuchal crests and no frontoparietal bulges. In females, the sagittal crest and crest-like temporal lines are already visible at wear stage 4 as in specimen SNSB-BSPG 2020 XCIV-8970 (Fig. 2J and 3J), and these crests are similar in development and morphology with adult specimens of wear stage 6 as in specimen SNSB-BSPG 2020 XCV-357, 380, GPIT/MA/17841, SNSB-BSPG 2020 XCIV-18870, and GPIT/MA/18000-01 (Fig. 2F-I and 3F-I). In the virtual cross sections, no pneumatization as in males is visible (Fig. 5E-G), although in specimen SNSB-BSPG 2020 XCIV-8970 (Fig. 5G) the temporal lines that form delicate crests appear like that, but the latter is caused by the lateral compression of the skull with the bone structure being distorted.

This means that in contrast to males of *D. nauti*, the cranial ornamentation of females does not develop or change in morphology during ontogeny and remarkable features like frontoparietal bulges are absent.

Comparison of cranial ontogeny of *Dorcatherium nauti* and *Dorcabune crassum*

At present, there are only two other complete skulls known of another fossil tragulid, *Dorcabune crassum*. Guzmán (2018) describes a male skull of *Db. crassum* from Walda-2 in Germany and furthermore mentions another skull of the same species from the Upper Freshwater Molasse of Thierhaupten in Germany published by Seehuber (2015). Guzmán (2018), as well as Hartung and Böhme (2022) assign the skull from Thierhaupten to a female individual and describe a sexual dimorphism in *Db. crassum* that is comparable to *D. nauti*. However, in *Db. crassum*, males have cranial ornamentation in form of bulges as well, but they differ in their morphology and are in general less markable if compared to *D. nauti*. In *Db. crassum*, the frontal bulges are absent and only the posterior part of the parietal shows flatter bulges that confine to form a Y-structure with the sagittal crest (Guzmán 2018, fig. 4.5;

Mennecart et al. 2018). This is different from *D. nauti*, where the bulges encompass the entire parietal and continue onto the frontal to encompass a parietal plateau and cover the orbit (Hartung and Böhme 2022 and Fig. 2). In contrast, the female skull morphology of *Db. crassum* is rather similar to that of females of *D. nauti* and both sexes of *H. aquaticus*, because it contains fine and delicate nuchal, temporal, and sagittal crests that follow the same morphology as in GPIT/MA/17841, GPIT/MA/18000-01, SNSB-BSPG 2020 XCIV-18870, as well as to SNSB-BSPG 2020 XCV-357 and SNSB-BSPG 2020 XCV-380 (all wear stage 6).

Based on the wear stage of the teeth, the male skull of *Db. crassum* from Walda-2 is already senile, as there is no selenedont pattern visible anymore at the M3 (wear stage 8). It is therefore not directly comparable to any of the present specimens of *D. nauti* and unfortunately the exact individual age of GPIT/MA/16790 is not known, although it can be assumed that this specimen is the ontogenetic oldest from the presented series. However, the difference in the development of the cranial ornamentation is still visible and it is very unlikely that after wear stage 6 a pattern as in *Db. crassum* will be present in senile males of *D. nauti*, because the parietal and frontoparietal bulges are already well-developed and confine with the sagittal crest posteriorly.

Interspecific heterochrony

D. nauti is closely related to the extant water chevrotain *H. aquaticus*. The exact relationships were studied last by Sánchez et al. (2015, 2018) where *D. nauti* plotted as the sister taxon to *H. aquaticus*. However, phylogenetic relationships might have been much more complex due to the limit of the fossil record in Africa for example. Both species share similarities in cranial morphology and *H. aquaticus* shows the strongest cranial ornamentation among the extant tragulids, however, *D. nauti* displays a markedly stronger and more intricate cranial ornamentation compared to the extant analogues, suggesting a heterochronic origin of this feature. To test this hypothesis, we apply the heterochrony model of Reilly et al. (1997), which investigates patterns of morphological change between ancestral and descendant taxa. For this purpose, the morphology of cranial ornamentation in *Dorcatherium nauti* (Hartung and Böhme 2022) is defined as the “ancestral state”, whereas the cranial morphology of *Hyemoschus aquaticus* (Hartung and Böhme 2024) represents the “descendant state”, based on the currently available phylogenetic framework (see above). To incorporate a temporal dimension, we apply the age model established for *H. aquaticus* by Dubost (2016) to *D. nauti* (Hartung and Böhme 2024) and reconstruct the ontogenetic trajectory of cranial ornamentation by establishing an ontogenetic series based on dental wear stages (Figs. 1 and 2). Dental wear stages follow the classification proposed by Hartung and Böhme (2024). We further assume that the onset of sexual maturity in *D. nauti* and *H. aquaticus* was relatively similar, if not identical. This assumption allows a direct comparison of the somatic development of cranial ornamentation throughout ontogeny between both taxa.

After Reilly et al. (1997) we observe a paedomorphic development of the cranial ornamentation (Fig. 6) in *Hyemoschus aquaticus* compared to *D. nauti*, a truncation of the fossil ontogeny compared to the morphology of the extant analogue caused by a “deceleration” (after Reilly et al. 1997) of the development of the morphological character. This was already mentioned for *Db. crassum* (Mennecart et al. 2018), which likewise exhibits pronounced cranial crests that are morphologically similar to those of *D. nauti* (Hartung and Böhme 2022). In contrast, *H. aquaticus* shows less developed cranial crests and bulges, as well as the absence of a parietal plateau, when compared to *D. nauti*. We hypothesize that the onset of cranial ornamentation growth (α) is similar in both taxa, but that a higher developmental rate ($-k$) in *D. nauti* results in more complex and developed cranial structures by the time developmental offset (β) is attained.

It is also possible to argue for a post-displacement (positive onset, fig. 1 in Reilly et al. 1997) of the shape development, in which a delayed onset in the extant tragulid relative to the fossil one is present. In this scenario, the development of cranial crests starts earlier during ontogeny in *D. nauti* and has therefore more time to develop. Thus, the initiation of cranial-crest growth in *Hyemoschus* would occur at a later time, resulting in a shortened developmental interval and reduced crest elaboration compared to *D. nauti* ($\alpha > \alpha_1$). The developmental rate however, would be the same in contrast to a paedomorphosis and the onset time (β) would be similar. Whether this developmental process in *D. nauti* is really beginning earlier if compared to *H. aquaticus*, cannot be conclusively said at the moment, because neonate to juvenile skulls of wear stage 0 to wear stage 2 are so far not present in *D. nauti* or any other fossil tragulid.

When comparing another fossil tragulid with well-known skulls, *Db. crassum*, to *H. aquaticus*, both taxa show greater morphological similarity to each other than to *D. nauti*. In *Db. crassum* and *H. aquaticus*, the frontal component of the cranial bulges as well as the parietal plateau are absent. In addition, *Db. crassum* exhibits broader temporal lines and a more pronounced sagittal crest, forming the characteristic Y-shaped structure. This configuration has been interpreted as a hyperdeveloped condition relative to *H. aquaticus* according to Mennecart et al. (2018), which is consistent with a heterochronic shift involving post-displacement. Consequently, *Db. crassum* may reflect a heterochronic trajectory that differs from the pattern most likely inferred for *H. aquaticus* and *D. nauti*.

The morphological differences in the elaboration of cranial ornamentation and shape of the latter between *D. nauti* and *H. aquaticus* are less-likely to be a result of hypomorphosis, because this would mean that the developmental process ends earlier in *H. aquaticus*, while *D. nauti* extends even further, truncating the fossil ontogeny. Both taxa would have the same onset time, and the pathway of development would be similar, which is clearly not the case, because the cranial morphology in *D. nauti* is different from *H. aquaticus* and even in juvenile male individuals of *D. nauti* (SNSB-BSPG 2020 XCIV-3500 wear stage 3-4 and SNSB-

BSPG 2020 XCIV-8518), the cranial bulges are morphologically clearly distinguishable from the extant tragulid. *D. nauti* exhibits frontoparietal bulges that constrict a parietal plateau and form a strong broad sagittal crest (Hartung and Böhme 2022). In *H. aquaticus*, the temporal lines are enhanced and also the sagittal crest can be broad and strong, but the frontoparietal bulges, as well as the parietal plateau are absent. Moreover, the cranial ornamentation in *H. aquaticus* continues to grow even in senile specimen (fig. 2 in Hartung and Böhme 2022) and the same can be assumed for *D. nauti* based on the morphology of GPIT/MA/17690 (Fig. 2A and 3A). Nevertheless, *H. aquaticus* appears unable to attain the degree of cranial complexity exhibited by *D. nauti* and thus no hypomorphosis is present.

Conclusively, *D. nauti* already exhibits a strong sexual dimorphism relatively early in life similar to *H. aquaticus*, the only extant tragulid with noticeable cranial ornamentation. The development of these structures has a higher rate in the fossil relative. A comparison to other fossil subadult (wear stage 3-4) tragulids, such as *Db. crassum*, would be very interesting, however, no skulls of that age exist so far. It is noticeable, that the extend of cranial ornamentation of *H. aquaticus* varies among the sexes in such an extent, that it is not an inclusive feature to distinguish among the sexes and therefore upper canine size remains the most reliable character for sex differentiation in this species. This is a contrast to the fossils *D. nauti* and *Db. crassum* and therefore comparison of skulls of *Hyemoschus* with *D. nauti* as well as with *Db. crassum* need to be taken with care.

Mortality analysis and survivorship rate of *D. nauti*

The mortality profile of *D. nauti* individuals from Hammerschmiede was assessed based on the state of wear of the M3 and dP4, as well as of the lower equivalent m3 and dp4 according to wear stages established by Hartung and Böhme (2024). Based on the upper and lower teeth combined, in HAM4, the total number of individuals that died at a juvenile stage (w0-w5) is 22 and the number of individuals that died at an adult or senile stage (w6-w8) is 22 as well (Fig. 7). At HAM5, the sample size is much smaller and no dP4 of wear stage 0 and wear stage 1 are available. However, the pattern is similar to HAM4, because in HAM5, six individuals died at juvenile stage and seven at an adult stage respectively. The low number of juveniles, combined with the high total number of individuals (MNI=44) at HAM4, indicates that juvenile survivorship reached 50%, meaning that every second individual completes sexual maturity. The same can be attributed to the individuals from HAM5, but has to be taken with some care because of the lower sample size (MNI=13; Fig. 7).

Body mass of *D. nauti*

For body mass estimates on the combined HAM5 and HAM4 sample we use the log-transformed regressions of Janis (1990) for lower molar length (m1-m3) and length of m2. Body mass according to lower molar length range from 29.1 to 35.4 kg (mean 32 kg, n=15) and for m2 length from 22.2 to 31.2 kg (mean 27.2 kg, n=21). A combined

estimate using both regressions on 15 adult mandibles results in body mass between 26.2 and 31.7 kg, with a mean of 29.4 kg. The individual body mass estimates show a bimodal distribution with peaks at 28-29 kg and 30-31 kg (Fig. 7D). The female skull GPIT/MA/18000-01 contains a mandible as well, which was already published in Hartung and Böhme (2022). The estimated body mass of this female was estimated to 31.2 kg (32.6 kg using m1-m3 regression, 29.9 kg using m2 regression), suggesting to attribute the heavier mode to females and the lighter mode to male individuals. This attribution is corroborated by the even larger juvenile female skull SNSB-BSPG 2020 XCIV-08968, which includes both hemimandibles with dp1-m2. The size of their m2s are among the largest in our Hammerschmiede sample and indicate a body mass of 30.7 kg using the m2 regression (see appendix SF1).

Discussion

Influence of sexual dimorphism and intraspecific variability on skull ontogeny in *D. nauti* and *H. aquaticus*

Sexual cranial features develop in *H. aquaticus* within wear stage 3 between an age of 10-16 month (Hartung and Böhme 2024 and Dubost 2016). In males, development of testicle mass starts at 5-9 month (wear stage 1) and production of spermatozoa at 17-27 months during wear stage 5 (Dubost 2016). In *D. nauti*, cranial sexual dimorphism is visible at wear stage 3-4 and it is likely that this morphology of the skull develops even earlier at early wear stage 3 as visible in the skull SNSB-BSPG 2020 XCIV-8518 (Fig. 2E) similar to *H. aquaticus*. The morphology of the cranial bulges in *D. nauti*, however, is unique among both extant and fossil tragulids and differs markedly from that of *H. aquaticus*, even at comparable wear stages. This supports the hypothesis that the cranial structures in *Hyemoschus* are paedomorphic if compared to *D. nauti* rather than being a result of post-displacement, where the development of cranial crests and bulges starts earlier but follows the same morphological trajectories (Reilly et al. 1997, Dubost 2016). However, the age of sexual maturity in *H. aquaticus* cannot be directly related to *D. nauti*, but it might be possible that, following the pattern of Hartung and Böhme (2024, tab. 1 and Fig. 5), the sexual maturation starts when the cranial features develop. If this is the case, the onset of sexual maturation of *D. nauti* could start at early wear stage 3 (or even earlier), similar to *H. aquaticus*, although the development of adult male sexual display features is much stronger in males of *D. nauti* than in male *H. aquaticus*. In *D. nauti* the characteristics of cranial crests are as important as the development of upper canines, as for example in specimen GPIT/MA/17690, where canines are not preserved, but the sex is unambiguous. However, the degree of variation within these crests is still unknown and needs to be evaluated in the future when more skulls are available.

Limits of this study

This model still leaves open questions, such as the morphology of the cranial features of fossil tragulids at wear stage 0-2, because no neonate or early juvenile skulls are available so far and it is questionable whether preservation of those

specimens is even possible. Based on the strong development of cranial features in *D. naui*, it might be possible that some degree of ornamentation is already visible at wear stage 2, which is not the case in *H. aquaticus*.

Moreover, the preservation of fossils, especially of juvenile individuals, is often deficient and can alter the identification of cranial structures and also makes comparison of any measurements difficult. For example, the virtual cross-sections of the fossil skulls (Fig. 5) show that bulges are present in all males: They show bone surface surrounding these structures, with pneumatized inner part. The strongest bulges are visible in GPIT/MA/17690, which is the oldest individual of the series (see description). However, in SNSB-BSPG 2020 XCV-474 from HAM5, the bulges are flattened and the inner structure is altered due to compression. Therefore, the spongiose part of the bone is barely visible, but the bony overhang is preserved, which is not the case in females, and the bulges are best visible in that specimen from external view (Fig. 2B). In GPIT/MA/18000-01, the skull roof shows longitudinal cracks due to the lateral compression, which alters the cranial morphology. However, it is clearly visible in Hartung and Böhme (2022), as well as in figure 2G that there are no such bulges visible as in males.

Furthermore, age determination for extant and fossil individuals in this study follows the stages established by Dubost (2016) and subsequently adapted for fossil tragulids by Hartung and Böhme (2024). For the fossil specimens in particular, absolute individual ages are yet unknown, and the onset of sexual maturation remains uncertain and can only be inferred.

Cranial ornamentation and upper canines as display features of *D. naui*

The present ontogenetic series of *D. naui* indicates allometric growth pattern of the cranial ornamentation as typical for male display features (Kodric-Brown et al. 2006). Males of *D. naui* possess pronounced and well-developed display features of the skull already before the M3/m3 molar eruption at a relatively early ontogenetic stage at wear stage 3-4 (or even at an early wear stage 3 as in SNSB-BSPG 2020 XCIV-8518; Fig. 3E). In *H. aquaticus* the cranial crests (temporal lines and sagittal crest) are only fine and delicate and start to develop at wear stage 3-4, when the large upper canines already erupt. Thus, the enhancement and strong expression of this cranial trait in *D. naui* shows that the development of the trait might start relatively early in life, similar to the *H. aquaticus*. This may be because weapons or display features need to be ready as close to adult form as possible by the time they reach sexual maturity to compete successfully for mating (Calamari 2016). In *H. aquaticus*, sexual maturation in males starts at 5–9 months (wear stage 1) and completes at 17–27 months (wear stage 5), whereas in females sexual development starts after 10–16 months (wear stage 3) and reaches its maximum at 27 months (wear stage 5) (Dubost 2016; Hartung and Böhme 2024). The cranial features of males, however, develop at wear stage 3-4.

However, it was stated in Hartung and Böhme (2024) that cranial ornamentation in *H. aquaticus* is not suitable for distinguishing among the sexes and might therefore not

even be a display feature at all. Instead, upper permanent canines erupt at wear stage 3 when the small and cone-like deciduous upper canines are shed. This event occurs within the general time frame of sexual maturation in male *H. aquaticus*; however, it cannot be considered a reliable proxy for the onset of sexual maturity alone. Maturation represents a gradual process extending from wear stage 1 to wear stage 5. In males, two main developmental milestones are observed at approximately 5–9 months (wear stage 1) and 17–27 months (wear stage 5), whereas in females major developmental changes occur between 10–16 months (wear stage 3), with full maturation reached at around 27 months (wear stage 5 according to Dubost 2016 and Hartung and Böhme 2024).

In addition to the beforementioned strong cranial ornamentation, *D. nauti* also possesses saber-like upper canines as visible in NHMUK PV OR 40632. This observation could, in turn, suggest that the intraspecific competition for females was relatively high and that the ecology of *D. nauti* differs from *H. aquaticus*, possibly involving a more complex social structure than in the extant species, which lacks any hierarchical organization or strong territorial behavior and lives mainly solitary (Dubost 1975). Although, during mating season, extant males have short combats where they use their upper canines as weapons for stabbing or slashing. It might be possible that *D. nauti* rather used frontoparietal bulges as display features than stabbing each other, leading to less fatal combat outcomes (Hartung & Böhme 2022). This would also be consistent with the theory of Calamari (2016), who states that complex sexual competition structures, like the described cranial ornamentation in *D. nauti*, were used in non-lethal combat or ritualized male-male fights in contrast to simple structures that are commonly used for more violent fighting behavior, like the upper canines.

Reproductive traits, life-history patterns, and habitats

Results of the mortality analysis and the survivorship rate of the HAM4 population of *D. nauti* (Fig. 7A, C) revealed that 50% of newborn tragulids (22 out of MNI=44) survive the juvenile stage (wear stage 0-5) and reach adulthood (wear stage 6-8). Survivorship (mortality) strongly decrease (increase) for prime adults (wear stage 6 and 7), and only one individual reached wear stage 8. In HAM5 the MNI is smaller (MNI=13) compared to HAM4, but still most individuals die at wear stage 6 similar to HAM4. The juvenile stage seems to be underrepresented in HAM5 with no individuals of wear stage 0 and wear stage 1. It is not surprising that most individuals in both horizons die at wear stage 6, because it covers a similar long period (approximately 27 Months to 4.5 years in *Hyemoschus aquaticus*, Dubost 2016) as all juvenile stages (wear stages 0-5) together.

The relatively high survivorship of juveniles suggests that *D. nauti* likely exhibited a low reproductive rate, potentially resulting from small litter sizes and a reduced number of reproductive events over the female life span. The litter size in *Hyemoschus* is very small with only one young per litter (Dubost 2016) and we assume the same for *D. nauti*. Moreover, given the equal number of juveniles

compared to adults (Fig. 7), it is possible that females of *D. nauti* had only very few, possibly four, reproductive events throughout their life time resulting in a low reproductive rate. This may indicate that in *D. nauti* senility is reached after an age of six years, which compares well with *H. aquaticus* (wear stage 8 at >6.5 years; Dubost 2016, Hartung & Böhme 2024), and may suggest that the maximum life span of both species was relatively short (maximum age in wild populations of *H. aquaticus* is normally eight years and potentially 11-13 years according to Meijaard (2011)).

Body size analysis in form of body mass calculations revealed that females tend to be larger than males, in which females of *D. nauti* are on average approximately 2 kg or 7% heavier than males. The mean weight for males lies within a range of 28-29 kg and females reach a mass of 30-31 kg. *Hyemoschus* displays an even larger sexual size dimorphism (SSD) pattern where males have an average weight of 9.7 kg and females around 12 kg (Robin 1990; Nowak 1999). However, the most pronounced difference between both species is the absolute body mass, which in *D. nauti* is more than twice as high as in *H. aquaticus*. This important biologic feature may reflect ecological adaptations in more seasonal and open deciduous broadleaf forests during the Miocene of Europe, compared to the thickets of African rainforests where *Hyemoschus* is living. Smaller body size in extant tragulids may facilitate concealment and escape from predators in densely vegetated habitats (Rössner 2007; Meijaard 2011). A preference of *D. nauti* to more open riparian woodlands would be supported by the high numbers of individuals found in HAM4 (MNI=44), making here this species to the most abundant large mammal, whereas in the HAM5 level *D. nauti* (MNI=13) is outcompeted by the deer *Euprox furcatus* (MNI=21).

This female-biased SSD is common among mammals and is especially known from smaller mammals as for example Lagomorpha (Darwin 1871; Lindenfors et al. 2007; Tombak et al. 2024). This SSD is explained by a higher fecundity selection in small mammals (Darwin 1871), because of higher energetic demands on females like producing eggs in comparison to sperm, gestation, and lactation, and more space that is used for keeping the eggs. Therefore, female mammals of smaller species develop larger energy stores for high metabolic costs of gestation and lactation, ultimately promoting higher offspring survivorship and reproductive success. However, this theory does not always apply because male sexual selection strategy is often based on a larger body size in males compared to females, which is used for competition with other males (Darwin 1871; Alexander and Borgia 1979; Weckerly 1998; Lindenfors et al. 2007; Cassini 2020a, b, 2022, 2023).

Potential paleobiogeographic scenario for *Hyemoschus*

Several recent publications suggest a close phylogenetic relationship between the fossil Eurasian species *Dorcatherium nauti* and the extant African *Hyemoschus aquaticus* (Geraads 2010; Sanchez et al. 2015, 2018), designated as 'true *Dorcatherium*-clade' by Sanchez et al. (2018). *Dorcatherium nauti* is known from Western and Central Europe from the late Middle Miocene till the early Late Miocene, between 12.4 and ~9.5 Ma (Aiglstorfer et al. 2014), whereas the species occurs in

Pakistan in the Chinji Formation in the late Middle Miocene (Guzman and Rössner 2021). Several potential, but badly known, European descendants of *D. navi* are known from later parts of the Late Miocene in southeastern Europe (e.g. Kostopoulos & Sen 2016), but after ~7.5 Ma the selenodont lineage of *Dorcatherium*, and the family Tragulidae at all, has disappeared from Western Eurasia and shortly after from Pakistan.

In Africa, tragulids are common and diverse during the Early and Middle Miocene (e.g. Pickford 2001; Sanchez et al. 2015, 2018; Musalizi et al. 2023), but known from only one Late Miocene site (the 9 Ma old Ngeringerowa site in Kenya; Pickford 1991). After a four million years long gap for fossil tragulids in Africa, the family reappeared with the oldest fossil record of *H. aquaticus*, which dates to the early Pliocene of the Mabaget Member at Tugen Hills in Kenya, Africa (5-4.5 Ma Pickford et al. 2004). Although this record is based on sparse dental material only, according to Geraads (2010) the upper molar resembles more closely the Late Miocene *Dorcatherium* from southeastern Europe than the extant water African chevrotain.

The later part of the Late Miocene (Messinian) was a time of massive mammalian dispersals from Eurasia into Africa, triggered by transient hyperaridity events in Western Asia (Böhme et al. 2021). The dispersing genera have both a southern Asian and southeast European origin and we speculate that the ‘true *Dorcatherium*-clade’ may have been part of these dispersals as well.

Conclusion

In this study, we present the first ontogenetic series of a fossil tragulid based on 13 skulls from Hammerschmiede and one from Eppelsheim. The examined fossil sample of *Dorcatherium navi*, in comparison with the phylogenetically related extant African water chevrotain *Hyemoschus aquaticus*, reveals that (I) *D. navi* exhibits more pronounced cranial ornamentation than extant tragulids, allowing reliable distinction between males and females, particularly when upper canines are absent; (II) the development of distinct cranial crests in male *D. navi* begins relatively early in life (at least by wear stage 3-4, if not earlier), similar to *H. aquaticus*, indicating a comparable onset of sexual maturity; and (III) heterochronic changes in the development of cranial crests and bulges occurred in *D. navi* relative to *Hyemoschus*, resulting in paedomorphic traits of the latter. These findings suggest that *D. navi* likely exhibited a unique mating behavior compared to extant chevrotains, with males relying more on ritualized displays. Moreover, the pronounced body size difference between *D. navi* and *H. aquaticus*, with *D. navi* being more than twice as large, suggests that *D. navi* may have been adapted to more open habitats compared to the extant species.

Additionally, a large dataset of isolated teeth and mandibles was used for a mortality analysis and body mass estimations. We observe very similar biological patterns in the fossil *D. navi* as in the extant *H. aquaticus*. Incorporating the early onset of sexual maturity, sexual size dimorphism in which females are larger than males, and large

survivorship of juveniles, we conclude that *D. nauti* probably had a low reproductive rate (one young per litter) and similar maximum life span compared to *Hyemoschus*.

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Statement of competing interests

All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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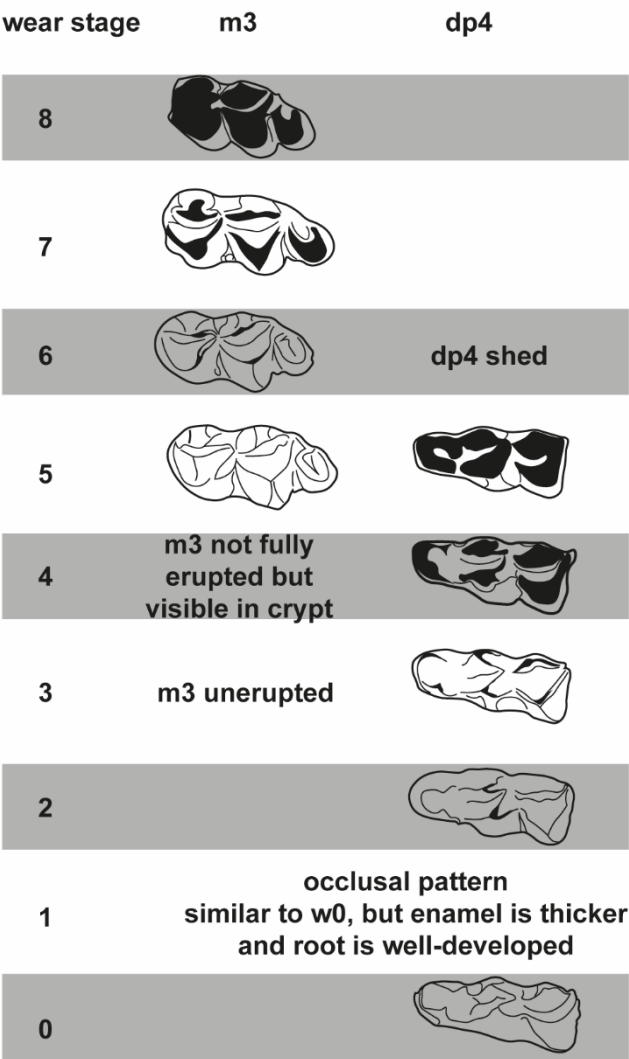
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1027

1028 **Figures**



1029

1030 **Figure 1** Occlusal pattern of the lower dp4 and m3 showing wear stages from w0 to

1031 w8 according to (Hartung and Böhme 2024) of *Dorcatherium naui* from the

1032 Hammerschmiede locality (Germany). Wear stages 0-5 represent the juvenile stage,

1033 wear stage 6 to 7 are the adult stage, and wear stage 8 represents the senile age

1034 category. Size of the teeth are not to scale

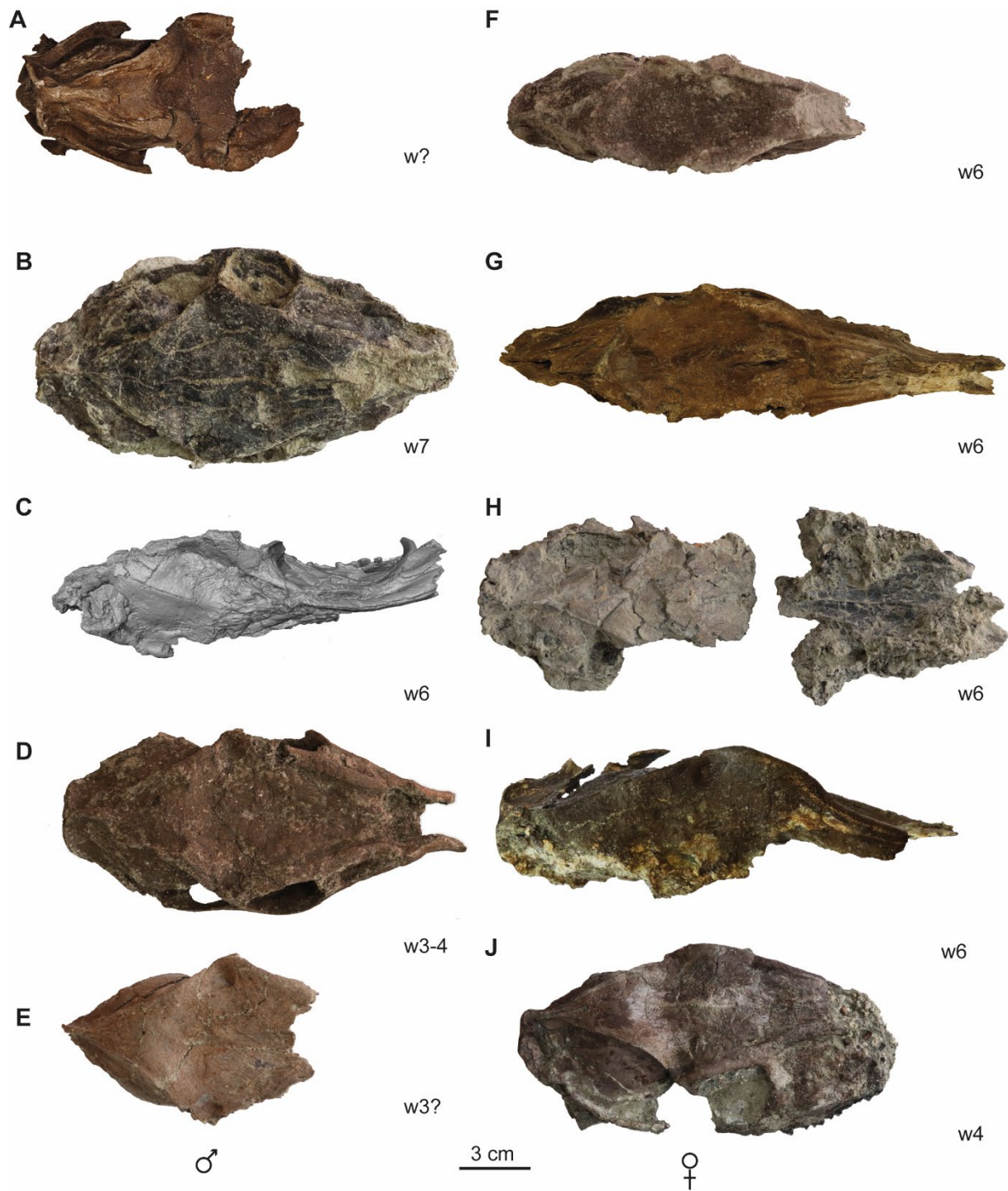


Figure 2 *Dorcatherium naui* from the late Miocene Hammerschmiede locality level HAM4 and HAM5, as well as from the middle to late Miocene locality of Eppelsheim. Adult and juvenile males and females in dorsal view. **A-E** males, **A)** adult without teeth GPIT/MA/17690 from Hammerschmiede level HAM4, **B)** adult SNSB-BSPG 2020 XCV-474 at wear stage 7 from Hammerschmiede level HAM5, **C)** adult NHMUK PV OR 40632 at wear stage 6 from Eppelsheim, **D)** juvenile SNSB-BSPG 2020 XCIV-3500 at wear stage 3-4 from Hammerschmiede level HAM4, **E)** SNSB-BSPG 2020 XCIV-8518 unknown wear stage from Hammerschmiede level HAM4. Based on weak morphology of the cranial crests, the skull is younger than wear stage 3-4, probably early wear stage 3, **F-I** females of determined age, **F)** adult GPIT/MA/17841

at wear stage 6 from Hammerschmiede level HAM4, **G)** adult GPIT/MA/18000-01 at wear stage 6 from Hammerschmiede level HAM4, **H)** adult SNSB-BSPG 2020 XCV-357 at wear stage 6 from Hammerschmiede level HAM5, **I)** adult SNSB-BSPG 2020 XCIV-18870 at wear stage 6 from Hammerschmiede level HAM4, **J)** SNSB-BSPG 2020 XCIV-8970 at wear stage 4 from Hammerschmiede level HAM4.

Abbreviations: w=wear stage

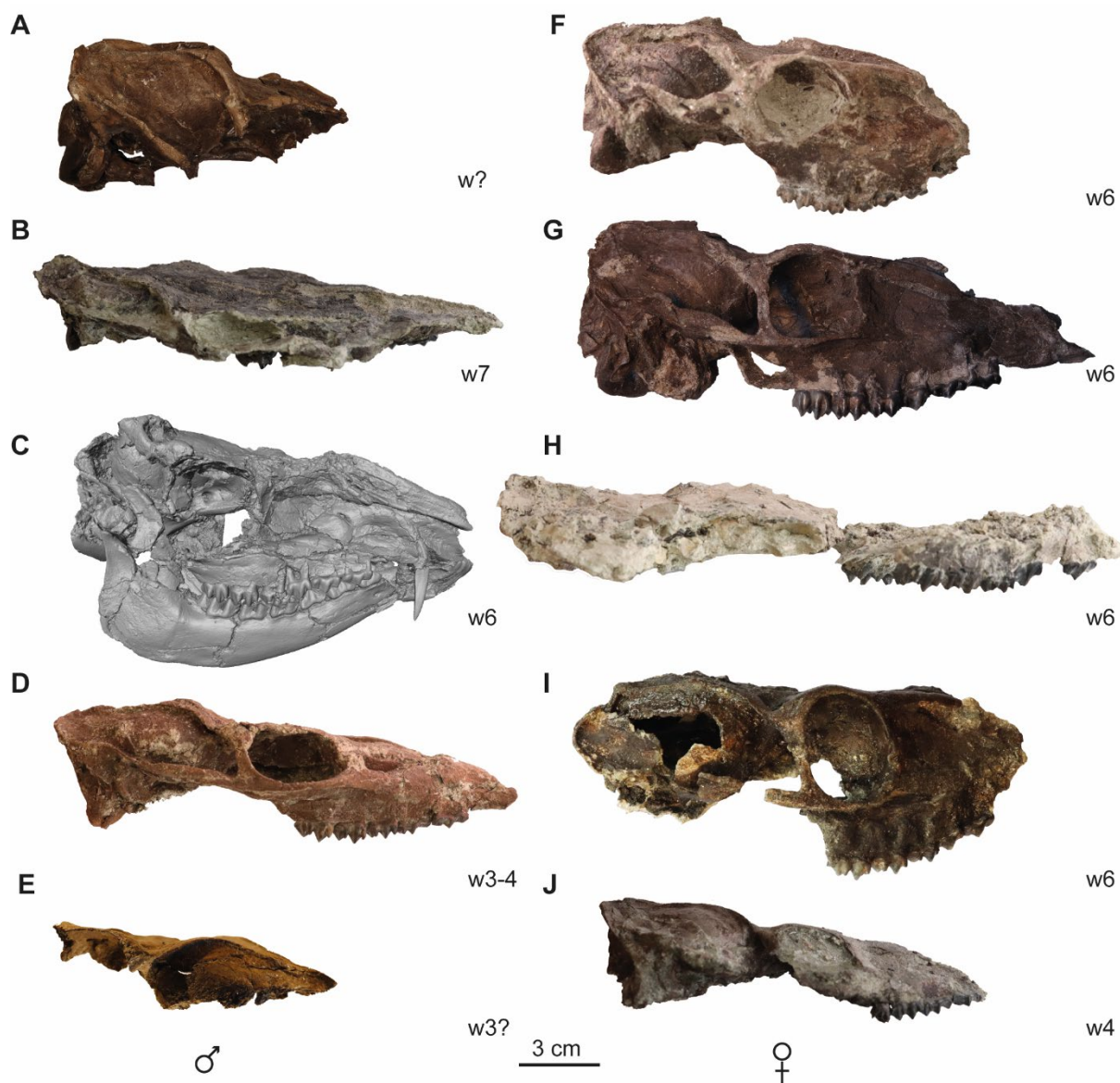
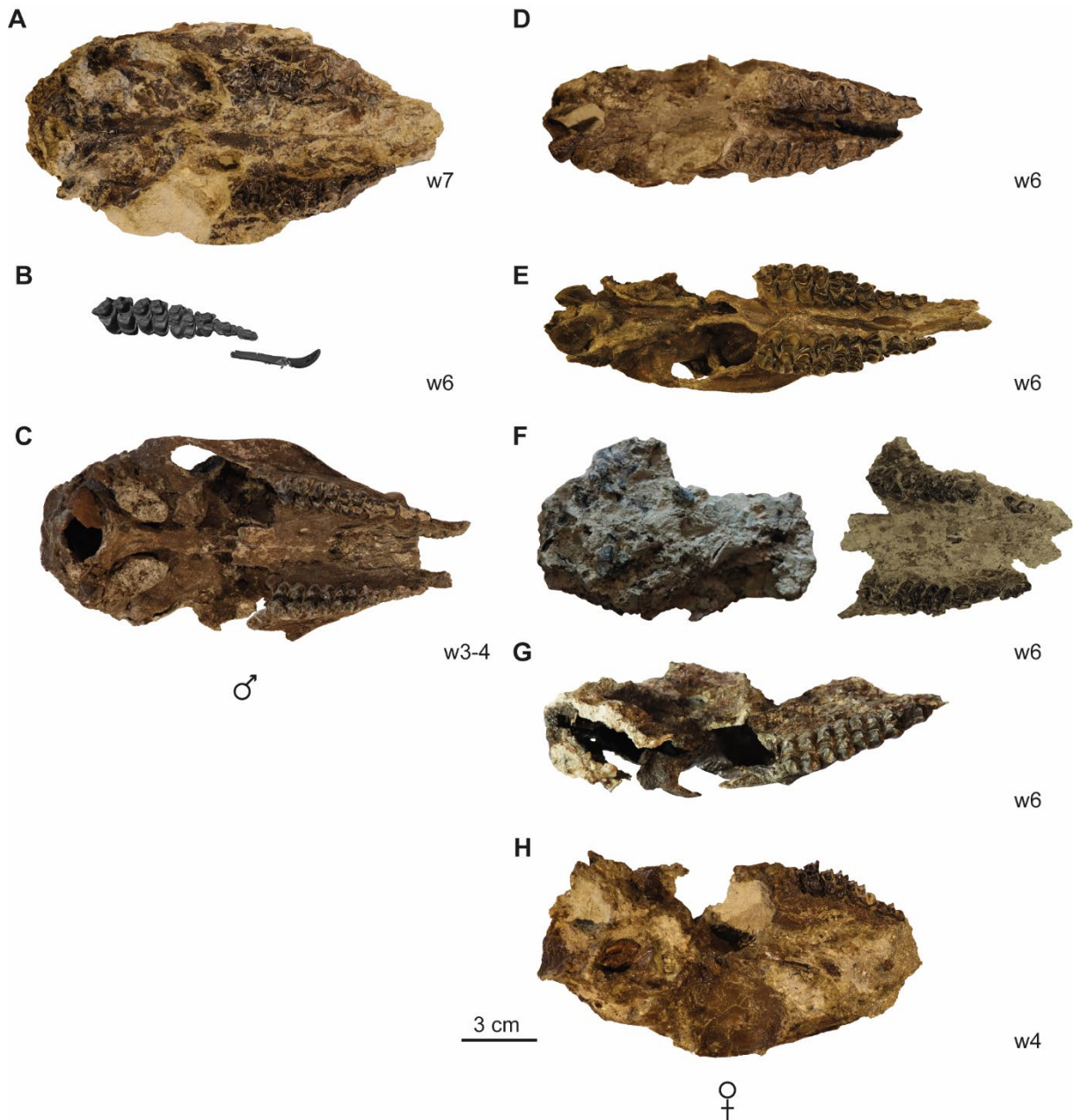


Figure 3 *Dorcatherium naui* from the late Miocene Hammerschmiede locality level HAM4 and HAM5, as well as from the middle to late Miocene locality of Eppelsheim. Adult and juvenile males and females in lateral view. **A-E** males, **A)** adult without teeth GPIT/MA/17690 from Hammerschmiede level HAM 4, **B)** adult SNSB-BSPG 2020 XCV-474 mirrored at wear stage 7 from Hammerschmiede level HAM5, **C)** adult NHMUK PV OR 40632 at wear stage 6 from Eppelsheim, **D)** juvenile SNSB-BSPG 2020 XCIV-3500 at wear stage 3-4 from Hammerschmiede level HAM4, **E)** SNSB-BSPG 2020 XCIV-8518 unknown wear stage from Hammerschmiede level HAM4. Based on weak morphology of the cranial crests, the skull is younger than wear stage 3-4, probably early wear stage 3, **F-I** females with determined age, **F)** adult

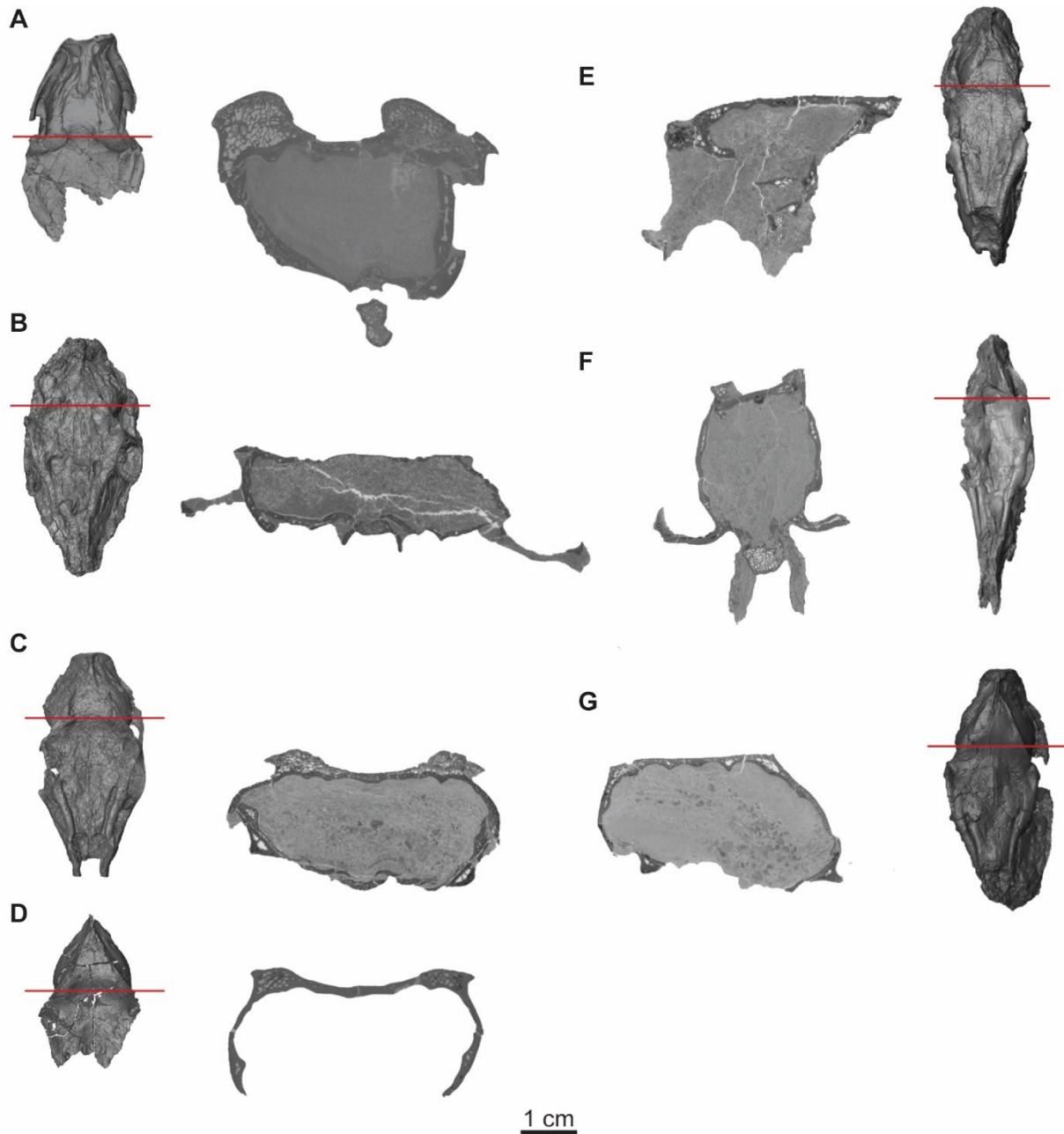
1063 GPIT/MA/17841 mirrored at wear stage 6 from Hammerschmiede level HAM4, **G)**
 1064 adult GPIT/MA/18000-01 mirrored at wear stage 6 from Hammerschmiede level
 1065 HAM4, **H)** adult SNSB-BSPG 2020 XCV-357 and SNSB-BSPG 2020 XCV-380
 1066 mirrored at wear stage 6 from Hammerschmiede level HAM5, **I)** adult SNSB-BSPG
 1067 2020 XCIV-18870 at wear stage 6 from Hammerschmiede level HAM4, **J)** SNSB-
 1068 BSPG 2020 XCIV-8970 mirrored at wear stage 4 from Hammerschmiede level
 1069 HAM4. **Abbreviations:** w=wear stage



1070

1071 **Figure 4** *Dorcatherium naui* from the late Miocene Hammerschmiede locality level
 1072 HAM4 and HAM5, as well as from the middle to late Miocene locality of Eppelsheim.
 1073 Adult and juvenile males and females in ventral view. **A-C** males, **A)** adult SNSB-
 1074 BSPG 2020 XCV-474 at wear stage 7 from Hammerschmiede level HAM5, **B)** adult
 1075 NHMUK PV OR 40632 at wear stage 6 from Eppelsheim, upper right tooth row
 1076 virtually isolated based from μ CT scan, **C)** juvenile SNSB-BSPG 2020 XCIV-3500 at

1077 wear stage 3-4 from Hammerschmiede level HAM4. **D-G** females, **D)** adult
 1078 GPIT/MA/17841 at wear stage 6 from Hammerschmiede level HAM4, **E)** adult
 1079 GPIT/MA/18000-01 at wear stage 6 from Hammerschmiede level HAM4, **F)** adult
 1080 SNSB-BSPG 2020 XCV-357 and 380 at wear stage 6 from Hammerschmiede level
 1081 HAM5, **G)** adult SNSB-BSPG 2020 XCIV-18870 at wear stage 6 from
 1082 Hammerschmiede level HAM 4, **H)** SNSB-BSPG 2020 XCIV-8970 at wear stage 4
 1083 from Hammerschmiede level HAM4. **Abbreviations:** w=wear stage



1084 **Figure 5** Virtual cross sections of *Dorcatherium naui* from Hammerschmiede level
 1085 HAM4 showing the pneumatized inner morphology of frontoparietal bulges in males
 1086 **A-D**. These structures are absent in females **E-G**. **A)** adult GPIT/MA/17690, **B)** adult
 1087 SNSB-BSPG 2020 XCV-474, **C)** subadult SNSB-BSPG 2020 XCIV-3500, **D)** SNSB-
 1088 BSPG XCIV 2020-8518, **E)** adult GPIT/MA/17841, **F)** adult female GPIT/MA/18000-
 1089

01, **G**) subadult female SNSB-BSPG 2020 XCIV-8970. Colors are inverted and contrast was adjusted for better visibility. Surface models are not to scale

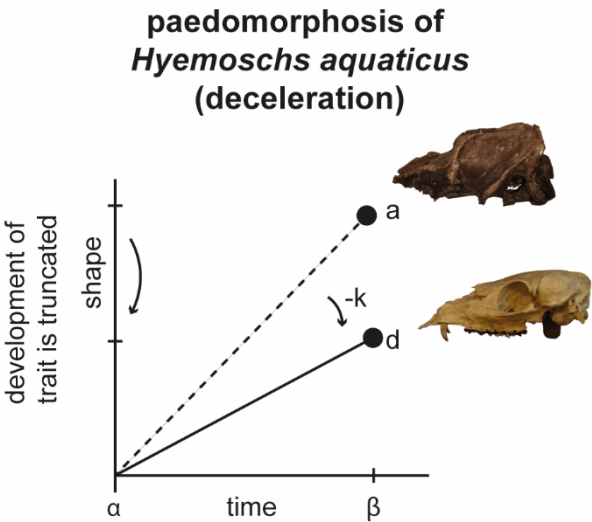


Figure 6 Heterochronic process of *D. nauti* (ancestor) and *H. aquaticus* (descendent) after (Reilly et al. 1997). *D. nauti* shows a hyperdevelopment of cranial crests and bulges if compared to the descendent leading to a paedomorphic state (deceleration and truncation of ancestral development) of the cranial ornamentation in *H. aquaticus*. **Abbreviations:** α =age of onset of growth of morphological structure (here cranial ornamentation like e.g. frontoparietal bulges), a =ancestor (here: *Dorcatherium nauti*), β =age when offset shape of morphological structure is attained, d =descendent (here: *Hyemoschus aquaticus*), k =rate of shape development

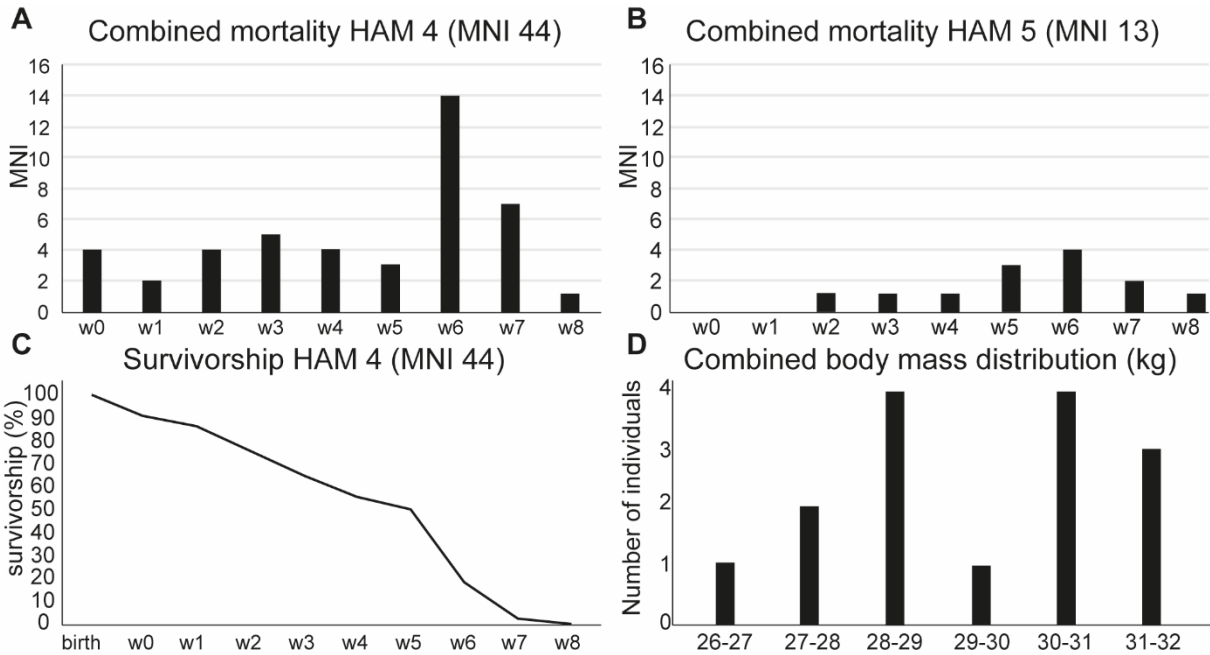


Figure 7 Results of the mortality analysis and body mass estimations for individuals of *D. nauti* from Hammerschmiede (HAM4 and HAM5). **A**) Results of the combined mortality study based on the upper M3, dP4, as well as on the lower m3 and dp4 for HAM4 and **B**) for HAM5; **C**) Survivorship for HAM4 based on the combined mortality

1106 analysis and **D)** Body mass estimations based on the length of m1-m3 and m2
1107 combined showing a bimodality with skulls attributed to females falling within the
1108 heavier range. **Abbreviations:** w=wear stage
1109