

# On the invalidity of *Halitherium schinzii* Kaup, 1838 (Mammalia, Sirenia), with comments on systematic consequences

Manja Voss<sup>1</sup>

<sup>1</sup> Museum für Naturkunde - Leibniz Institute for Evolution and Biodiversity Science, Invalidenstraße 43, 10115 Berlin, Germany

Corresponding author: Manja Voss (manja.voss@mfn-berlin.de)

## Abstract

Received 25 February 2014

Accepted 4 March 2014

Published 28 March 2014

Academic editor:

Matthias Glaubrecht

## Key Words

Holotype

early Oligocene

taxonomy

nomenclature

*nomen dubium*

paraphyly

The holotype of the sirenian species *Halitherium schinzii* Kaup, 1838 from the Alzey Formation (early Oligocene) of the Mainz Basin, western Germany, is reviewed in detail and revised. It is concluded that the type specimen, an isolated premolar, is non-diagnostic, because it reveals no characters of taxonomic value. Therefore, the taxon name *H. schinzii* is regarded as a *nomen dubium*, thus cannot be applied to any currently proposed sirenian species. The name of the genus “*Halitherium*”, which is based on the type species “*H. schinzii*”, cannot be applied to other species previously assigned to congeneric taxa. Consequently, taxonomic and systematic re-assessment is required. Due to the fact that “*Halitherium*” is the taxonomical basis of the Halitheriinae, conclusions are drawn on the inappropriateness of this subfamily.

## Introduction

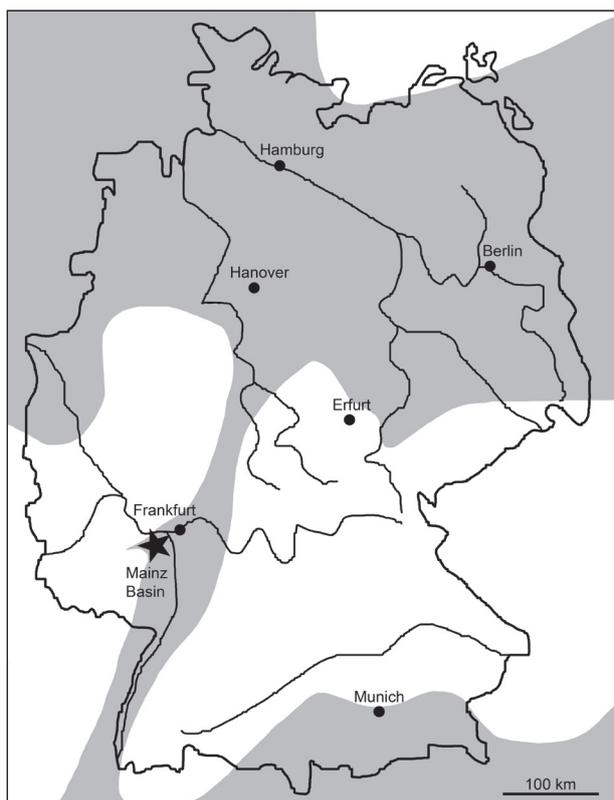
The genus *Halitherium* includes a number of fossil sirenian species, or sea cows, ranging from the late Eocene to early Miocene. Its type species *H. schinzii* Kaup, 1838 is considered as a widespread Central European taxon that inhabited the early Oligocene coastal waters, especially from Germany (e.g., Voss 2008). The morphological basis for the establishment of this species is a single premolar from the Mainz Basin in western Germany (Kaup 1838; Domning 1996). This premolar forms the focus of the present paper as a first step into a revision of the *Halitherium*-species complex.

## Historical Review

In 1834, Kaup and Scholl mentioned a not otherwise specified tooth of an extinct sea cow from the early Oligocene of Germany near Flonheim (Mainz Basin; Fig. 1) as *Pugmeodon schinzii*. As Domning (1996) already recognised, both, the genus and species name, have to be considered

as *nomina nuda*, because Kaup and Scholl (1834) neither provided a description nor a figure of the respective tooth. However, a description and figure of another premolar (HLMD-WT Az 48) under the same species name was given by Kaup (1838), who subsequently transferred it to the genus *Halitherium*, which seemingly is the correct generic name for the species as indicated by later studies (e.g., Kaup 1855; Lepsius 1882; Sickenberg 1934).

Therefore, Domning (1987) opened the nomenclatural case no. 2569 to apply for a proper designation of the holotype of *Pugmeodon schinzii*. By Opinion 1535 of the Bulletin of Zoological Nomenclature Volume 46 (ICZN 1999), all previous designations of type species for the nominal genus *Halitherium* Kaup, 1838 are set aside and *Pugmeodon schinzii* Kaup, 1838 is designated as type species under the plenary powers. Furthermore, the names “*Halitherium*” and “*schinzii*” are ruled to be placed on the official lists and indexes of names and works in Zoology by the International Commission on Zoological Nomenclature (2001).



**Figure 1.** Geographic setting and palaeogeography of the Mainz Basin (black star) in western Germany during the early Oligocene (~ 32 Ma). White areas indicate land, grey areas represent marine conditions (modified after Probst 1986).

In the subsequent decades, early Oligocene sirenian finds from the Mainz Basin comprising cranial and post-cranial elements, and occasionally partial skeletons with nearly complete skulls and mandibles, were generally assigned to *H. schinzii*. Thus, this taxon has become firmly established in the literature as the only sea cow species that had evolved in this specific region to that time (e.g., Krauss 1858; Barthel 1962; Bahlo and Tobien 1982). Apart from its type locality, *H. schinzii* is also known from the Lower Rhine area in western Germany (Voss 2008) and from the Bay of Leipzig in eastern Germany (Fischer and Krumbiegel 1982). Sirenian finds from the Paris Basin (Bizzarini 1995; Bizzarini and Reggiani 2010), the Antwerp and East Flanders Provinces in North Belgium (Sickenberg 1934), Switzerland (Pilleri 1987) and Hungary (pers. obs.) that are referred to *H. schinzii* indicate the widespread distribution of this taxon in Central Europe.

However, considerable intraspecific morphological variations have been postulated for *H. schinzii* since the middle of the 19th century (e.g., Kaup 1855; Lepsius 1882; Sickenberg 1934; Fischer and Krumbiegel 1982). Attempted revisions of *H. schinzii* consequently resulted in the description of numerous specimens forming the basis of new species, as are, respectively, the skull roofs of *H. kaupi* and *H. bronni* (for both taxa see Krauss 1858). However, those are considered to be not valid and synonymous with *H. schinzii* by Domning (1996). Hartlaub (1886) described another species, *Manatherium delheidi*,

based on cranial remains from the lower Oligocene of Antwerp (North Belgium) in comparison with *H. schinzii* from the Mainz Basin (Germany). However, Sickenberg (1934) revised Hartlaub's (1886) species, focussing on aspects of juvenile stages and intraspecific variability. Sickenberg (1934), who already mentioned that a revision of *Halitherium* and *H. schinzii* was necessary, provided a comprehensive and critical review of the Belgian material, but without considering a separation on species level. According to his investigations, all known Belgian records belong exclusively to smaller animals. Therefore, Sickenberg (1934: 271) defined separate morphological groups, "*forma typica*" for the German and "*forma delheidi*" for the Belgian one, and assigned both to *H. schinzii* (see also Domning 1996). The most recent new combination for *H. schinzii* refers to skeletal material from the lower Oligocene of France known as *H. schinzii lareolensis* (Pilleri 1987; Domning 1996).

This review documents that the attempts of different authors to identify morphological distinctions on species level remain ambiguous until today. The debate on splitting and lumping of species currently referred to *H. schinzii* was recently revived by Voss (2012). This author stated that morphological variations within German and Belgian early Oligocene Sirenia might be related to the species level and postulated the presence of an additional species.

The hypothesis of two morphospecies necessitates the examination of the holotype of *H. schinzii* as a target for a revision of this type species. However, the preservation and nature of the holotype material pose major problems. Voss (2010) already postulated that no significant taxonomic definition for *H. schinzii* can be deduced from the premolar HLMD-WT Az 48 and, consequently, this species and the thereon based genus lack a diagnosis.

The present paper aims to clarify this issue by elucidating the morphology and taxonomic value of the premolar and provides perspectives for new taxonomic and systematic approaches.

#### Abbreviations

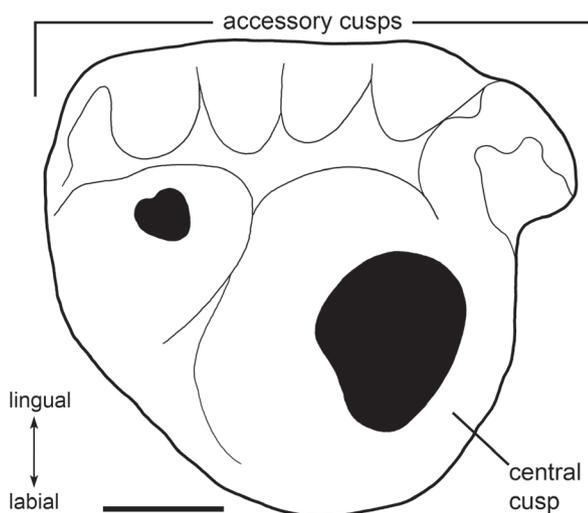
BSPG – Bayerische Staatssammlung für Paläontologie und Geologie München (Germany); HLMD – Hessisches Landesmuseum Darmstadt (Germany); M3 – upper molar 3; P2–4 – upper premolar 2–4.

## The holotype and validity of *Halitherium schinzii*

**Holotype.** Premolar HLMD-WT Az 48.

**Type horizon and locality.** Alzey Formation of the Selztal Group (lower Oligocene) from Flonheim in the Mainz Basin, western Germany.

**Description.** The tooth (Fig. 2) represents a premolar. However, its exact position within the tooth arcade cannot be certainly determined due to incomplete preservation and



**Figure 2.** Isolated premolar and holotype specimen of *Halitherium schinzii* HLMD-WT Az 48 in occlusal view. Scale bar equals 0.25 cm.

wear. A single root was present, but is no more preserved. The crown measures 11 mm in maximum diameters with the lingual side being broader mesiodistally than the labial one. Though worn, the central cusp shows a smooth and convex side facing labially. Lingually, five accessory cusps are present. A further, medium sized cusp being also in wear is present mesially or distally depending on the side and locus the premolar inhabits within the jaw. The overall shape of the crown resembles a clenched fist, which tempted Kaup (1838: 319) to introduce for this specimen the new genus *Pugmeodon* (“Faustzahn”), which he transferred into *Halitherium* (Kaup 1838: 536) in the same volume.

**Remarks.** As it can be inferred from the description above, the taxonomic value of the holotype of *H. schinzii* is doubtful and its assignment to a certain species remains ambiguous. This is additionally corroborated by comparative morphological investigations with species lumped under the genus *Halitherium*.

Compared to *Halitherium taulannense* (Sagne 2001), known by upper and lower premolars, and the *H. schinzii* specimen BSPG 1956 I 540 (see also Barthel 1962), comprising the right P2 and left P3–P4, HLMD-WT Az 48 most likely represents an upper posterior premolar. Using the preserved teeth of both species as reference points, HLMD-WT Az 48 could have occupied either the third or the fourth locus based on its complex cusp pattern. However, a clear assignment of HLMD-WT Az 48 to P3 or P4 of BSPG 1956 I 540 or any upper premolars observable in *H. taulannense* is not possible. On the one hand, this is related to the high degree of wear that precludes comparisons of this tooth with a number of nearly unworn premolars of *H. taulannense* (Sagne 2001), for example. On the other hand, the special crown morphology of HLMD-WT Az 48 described above is considered to hamper a proper identification. The specific arrangement of cusps is found neither in isolated nor associated premolars even of a comparable degree of wear of any known sirenian species.

Apart from BSPG 1956 I 540, complete series of upper premolars are not known in specimens hitherto assigned to *H. schinzii* making further comparative studies difficult. Additionally, other fossil sirenian taxa like *H. cristolii* (Spillmann 1959) have no premolars preserved and only reveal the root alveoli in the bone. Thus, it remains unresolved whether HLMD-WT Az 48 belongs to the left or the right quadrant of the jaw and the identification of its exact position within the tooth arcade is still an open question.

In conclusion, the relation of premolar HLMD-WT Az 48 to the nominal species *H. schinzii* is doubtful or at least cannot be established, because this tooth does not yield any significant characters to diagnose both, the genus and the species. Consequently, the name “*H. schinzii*” is considered a *nomen dubium* as is the genus “*Halitherium*” since “*H. schinzii*” is the type species of that genus. Both terms can be applied to the premolar specimen only and are therefore rejected for further nomenclatural purposes.

Following the principle of priority, article 23.3.5 (ICZN 1999) states that an invalid taxon name must be replaced by the oldest available junior synonym. In this case, three nominal synonyms exist, which however are each considered as inappropriate replacement for “*Halitherium*” due to their poor material basis, uncertain taxonomic assignment and juvenile status or a combination of these factors.

The oldest genus is *Trachytherium* (Gervais 1849; Domning 1996) and is based on a single, isolated lower M3. According to Domning (1988) and Domning and Pervesler (2001) sirenian molars are often characterised by a high degree of intraspecific variation. Beside the fact that this tooth represents the only known specimen, it is therefore emphasised here that the establishment of a new sirenian genus on a molar alone is not sufficient.

The next older genus *Crassitherium* (Van Beneden 1871; Sickenberg 1934; Domning 1996) was established on the basis of a skull fragment and eight vertebrae. While the vertebrae are clearly identified as belonging to a sirenian, there are serious doubts on the taxonomic assignment of the skull fragment, which might be referable to a reptile (Sickenberg 1934: 207). This is also supported by personal investigations of the material in question hence *Crassitherium* is not considered as a useful or valid replacement name.

The third genus *Manatherium* (Hartlaub 1886; Domning 1996) is based on skull fragments of a juvenile. On the basis of personal investigations these fragments are identified as belonging to the frontal, the sphenoid and the right maxilla. Beside the juvenile status of this specimen that already tempted Sickenberg (1934) to declare this genus to be invalid, the preserved material is not considered to reveal diagnostic features for a reliable taxonomic assignment on the species level.

Article 23.3.5 (ICZN 1999) also states that if the rejected name has no valid synonym a new substitute name must be established in its place. Therefore, all taxa originally assigned to “*Halitherium*” require a new designation. A taxonomic and systematic revision of the “*Ha-*

*litherium*”-species complex is in progress to be published and beyond the scope of the present paper.

It is refrained here to designate a neotype, because the conditions specified in article 75.3 (ICZN 1999) do not apply. Most importantly, the name-bearing type specimen of “*H. schinzii*” is neither lost nor destroyed, but still extant and represented by the premolar HLMD-WT Az 48. Additionally, there has never been designated a paratype or paralectotype, which could be chosen as neotype according to recommendation 75A (ICZN 1999). The choice of a neotype originating from the type locality or even the same geological horizon is difficult for several reasons. An obvious potential neotype could be an incomplete skull cap representing the holotype and only specimen of “*Halitherium*” *kaupi* (Krauss 1858), which was assigned as junior synonym of “*H. schinzii*” by Domning (1996). Presenting mainly indistinctive features, which are typical for a juvenile, this specimen is just fragmentarily preserved including only the supraoccipital and parietal in addition to remnants of the frontal. This incompleteness and poor preservation, but mainly the juvenile status prevents a designation of this specimen as a neotype with sufficient diagnostic characters distinguishing this taxon from other sirenian genera. Another reason for the difficulty finding a neotype is the hypothesis by Voss (2012) that a second sirenian species, viz. “*H. bronni*”, might have been present in the early Oligocene of Germany, and therefore the respective type specimen is also not an available choice. Due to the presumed presence of two sympatric species, suitable material deriving from a host species for the potential neotype is not determinable unambiguously. Therefore, the replacement of an unidentifiable name-bearing type by a neotype (article 75.5; ICZN 1999), which would be possible considering “*H. schinzii*” as a *nomen dubium*, is not performed.

## Discussion

### Present systematic framework

The hitherto only cladistic approach with the attempt to consider the entire order Sirenia is represented by Domning’s phylogeny published in 1994. Domning’s (1994, 1996) suprageneric classification maintains the traditional taxonomic concept of Simpson (1945). Accordingly, four sirenian families are distinguished (Fig. 3): the Prorastomidae Cope, 1889, the Protosirenidae Sickenberg, 1934, the Dugongidae Gray, 1821 (including the three subfamilies Halitheriinae, Hydrodamalinae and Dugonginae) and the Trichechidae Gill, 1872 (1821) (comprising the two subfamilies Miosireninae and Trichechinae).

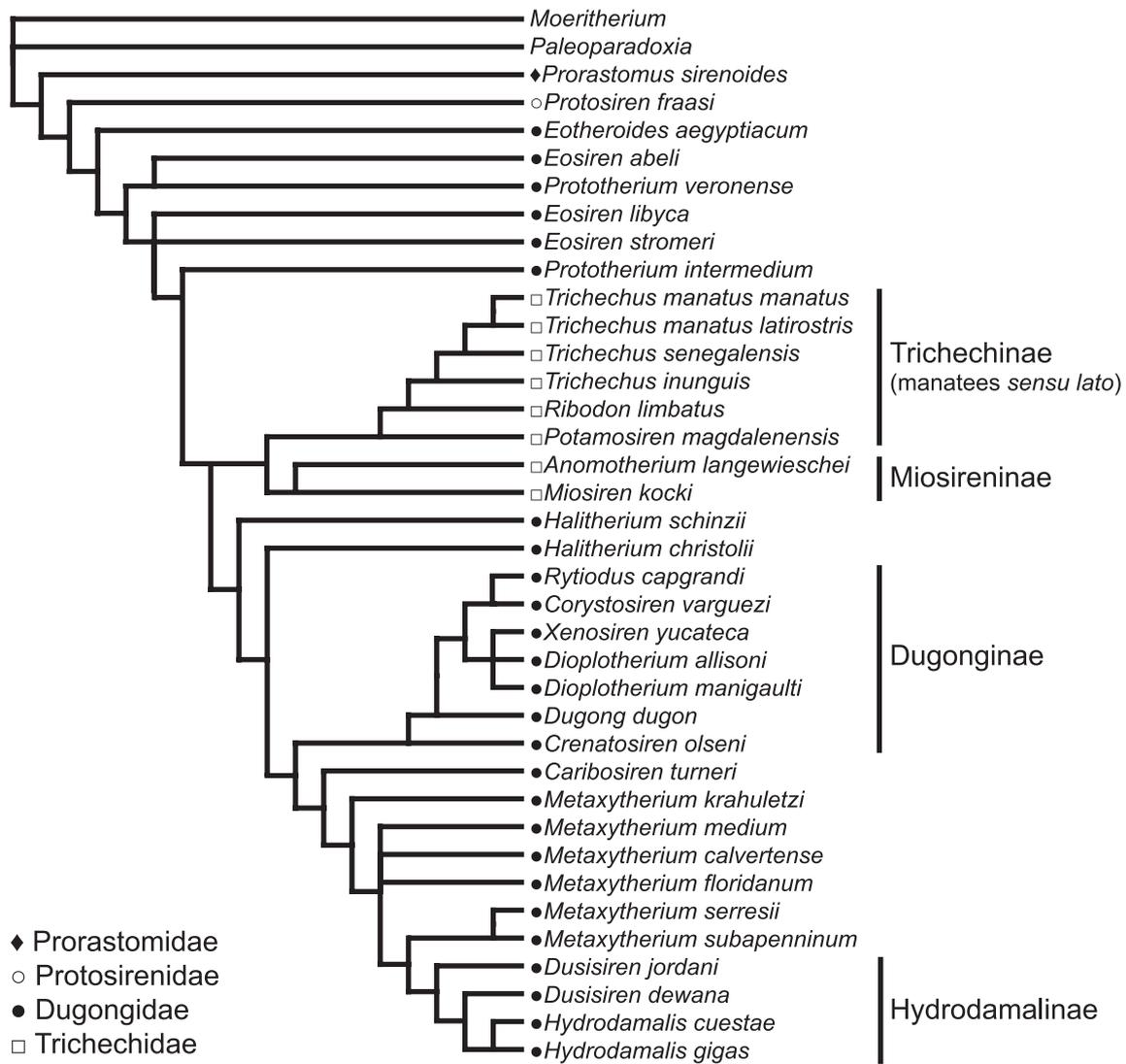
The Prorastomidae and Protosirenidae, both representing semiaquatic quadrupeds, are confined to the Eocene and considered paraphyletic (Domning 1994; 2001a, b). The Dugongidae and Trichechidae represent fully aquatic animals and also include the few extant members belonging to the genera *Dugong* and *Trichechus* (Domning 2001a). According to Domning (1994), trichechids are

monophyletic and nested within the Dugongidae. Consequently, the Dugongidae are paraphyletic. Within dugongids only two monophyletic groups are distinguished, the Dugonginae and Hydrodamalinae (Fig. 3). The most diverse dugongid subfamily and largest group within sirenians at all is represented by the Halitheriinae comprising the genera *Caribosiren* Reinhart, 1959, *Eosiren* Andrews, 1902, *Eotheroides* Palmer, 1899, *Halitherium* Kaup, 1838, *Metaxytherium* De Christol, 1840, and *Prototherium* De Zigno, 1887. However, this exclusively extinct group is paraphyletic indicating that higher-level phylogeny and systematics of the whole order Sirenia is paraphyly-based. Moreover, Domning’s phylogenetic analysis (1994) points out that “halitheriines” itself mainly comprise genera that are invariably paraphyletic and in addition the type genus of this subfamily, “*Halitherium*”, is also not monophyletic (Fig. 3).

Domning (1994: 187) stated that his phylogenetic analysis is a preliminary work and in need of systematic revisions in many parts. Nevertheless, the traditional classification concept of four sirenian families is unrevised subject of systematic studies up to now (e.g., Velez-Juarbe et al. 2012). This causes many systematic problems due to missing diagnoses and hampers a reliable taxonomic assignment of new sirenian finds. According to Domning (1994), the most controversial groups refer to the Eocene dugongids and Eocene sirenian taxa in general, the incompletely resolved clade of the dugongines and the inter- and intrageneric relationships of *Metaxytherium*. The need of revision of these groups is beyond doubt. Additionally, the present study emphasises that the “Halitheriinae”, comprising amongst others the Eocene dugongids and the genus *Metaxytherium*, constitute one of the most questionable sirenian groups, which is the focus of the following discussion.

### The invalidity of *Halitherium* and its effects on sirenian systematics

According to article 11.7.1.1 (ICZN 1999) a family or subfamily, respectively, should be based on a valid genus. However, as outlined above this does not apply here, because the genus “*Halitherium*” is considered a *nomen dubium* and therefore is rejected. Since the “Halitheriinae” comprise a number of genera this problem could be solved by the designation of a new type genus. This taxonomic practise would be reasonable if the group in question represents a clade. However, the subfamily “Halitheriinae” has never been shown to form a monophyletic group in phylogenetic analyses considering Sirenia as a whole (Domning 1994; Fig. 3) as well as on subsets of the order (e.g., Bajpai and Domning 1997; Domning and Pervesler 2001; Domning and Aguilera 2008; Velez-Juarbe et al. 2012). Doubts on the “halitheriine” monophyly are reinforced by the most up to date phylogenetic analysis on Sirenia recently performed by Voss (2013) in her doctoral thesis, which will be published at a later date.



**Figure 3.** Phylogeny of the Sirenia including 36 species and subspecies based on 62 informative cranial and dental characters (modified after Domning 1994). TL = 162, CI = 0.76, RI = 0.91.

In fact, Simpson (1945) and Domning (1996) demonstrate that the “Halitheriinae” rather represent a historically grown assemblage of taxa characterised by morphological features that neither substantiate a monophyletic grouping nor distinguish it from other subfamilies. The latter is amongst others corroborated by the overlap of characters such as “cheek teeth enamelled, closed roots” that were provided by Simpson (1932: 423–424) to define the “Halitheriinae”, Miosireninae and Rytiodontinae. Consequently, the designation of a new type genus is not possible.

Likewise, the type genus “*Halitherium*” is traditionally considered to be monophyletic, because this has never been substantiated with sufficient evidence from any phylogenetic analysis up to now. The “*Halitherium*”-species complex regarded as valid within the European Palaeogene includes “*H. schinzii*” Kaup, 1838 (early Oligocene of Europe), “*H. cristolii*” Fitzinger, 1842 (late Oligocene of Upper Austria) and “*H. taulannense*” Sagne, 2001 (late Eocene of France). As indicated above, none of these taxa form a clade. Instead, each species represents individual

branches in phylogenetic studies (e.g., Domning 1994; Domning and Aguilera 2008).

This paraphyly of “*Halitherium*” is the main reason for the conclusion drawn herein to question the current use of the subfamily “Halitheriinae”. Based on the fact that “*Halitherium*” is the type genus of the “Halitheriinae”, this subfamily is to be reduced to a single species, the type species “*H. schinzii*”, when all hitherto known phylogenies (e.g., Domning 1994; Domning and Aguilera 2008) are considered. Even if a new substitute name would be established for the genus “*Halitherium*” and the respective taxa of the former “*Halitherium*”-species complex receive a new designation, the taxonomic content of this subfamily will still comprise a single species. Therefore, the use of the “Halitheriinae” is not considered essential, because it does not contribute to a better understanding of sirenian diversity, but would rather lead to confusion. Instead, the rejection of the “Halitheriinae” is considered as a target-oriented solution into a more rigid taxonomic framework.

## Conclusions

In the course of the revision of the genus “*Halitherium*”, it is concluded that the premolar holotype of the type species “*H. schinzi*” neither can be clearly identified nor is assignable to a certain species or genus, and therefore it is non-diagnostic. Accordingly, these taxonomic terms are considered as *nomina dubia*. A neotype for “*H. schinzi*” is not designated here due, among other things, to the fact that the presence of two sympatric species in the German early Oligocene is hypothesised (Voss 2012), which makes it difficult to unambiguously define a suitable neotype. As a further consequence, the extinct subfamily “Halitheriinae” is refuted here. On the one hand, this is substantiated by the status of the type genus “*Halitherium*” as *nomen dubium* and, on the other hand, by the paraphyly of “halitheriines” and “*Halitherium*”. Considering all previous phylogenies, especially the order-based analysis by Domning (1994), this subfamily consequently includes a single species only, viz. “*H. schinzi*”. This situation would remain unchanged even though a substitute name would be erected for “*Halitherium*” and “*H. schinzi*”, respectively. Therefore, the use of the “Halitheriinae” is not considered practicable in this study.

As there have been made very few changes to the traditional paraphyly-based classification (see Domning 1994), a first step towards a revised taxonomic concept for the entire sirenian order is suggested here by rejecting the subfamily “Halitheriinae”. Following this recommendation, not only one of the main sources of sirenian paraphyla is resolved, but also new approaches are provided to interpret the taxa originally lumped in this category.

## Acknowledgements

I would like to thank Oliver Hampe (Berlin) for supporting this project. Gabriele Gruber, Norbert Micklich, Eric Milsom and Oliver Sandrock (Darmstadt) are acknowledged for their assistance during my visit to the Hessisches Landesmuseum Darmstadt. Additionally, I am grateful to S. Klug (Bristol), who kindly provided assistance in checking the spelling and grammar, and to Michael Ohl and Matthias Glaubrecht for helpful comments on the manuscript.

## References

Andrews CW (1902) Preliminary note on some recently discovered extinct vertebrates from Egypt. Part III. Geological Magazine 9: 291–295. doi: 10.1017/S0016756800181178

Bahlo E, Tobien H (1982) Bestandsaufnahme der Säugetiere im “prä-aquitane” Tertiär des Mainzer Beckens. Mainzer geowissenschaftliche Mitteilungen 10: 131–137.

Bajpai S, Domning DP (1997) A new dugongine sirenian from the early Miocene of India. Journal of Vertebrate Paleontology 17: 219–228. doi: 10.1080/02724634.1997.10010965

Barthel W (1962) Über ein neues montiertes Skelett von *Halitherium schinzi* Kaup (Sirenia). Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 2: 65–68.

Bizzarini F (1995) Osservazioni sull’*Halitherium schinzi* Kaup, 1838 (Sirenia, Mammalia) conservato presso il Museo Civico di Storia Naturale di Venezia. Bollettino del Museo Civico di Storia Naturale di Venezia 44: 163–171.

Bizzarini F, Reggiani P (2010) *Halitherium schinzi* nel nuovo allestimento del Museo di Storia Naturale di Venezia. Bollettino del Museo Civico di Storia Naturale di Venezia 61: 131–137.

Cope ED (1889) Synopsis of the families of Vertebrata. American Naturalist 23: 849–877. doi: 10.1086/275018

De Christol J (1840) Recherches sur divers ossements fossiles attribués par Cuvier à deux phoques, au lamantin, et à deux espèces d’hippopotames, et rapportés au *Metaxytherium*, nouveau genre de cétacé de la famille des dugongs. L’Institut annaires 8: 322–323.

De Zigno A (1887) Quelques observations sur les siréniens fossiles. Bulletin de la Société Géologique de France 15: 728–732.

Domning DP (1987) *Halianassa studeri* von Meyer, 1838 (Mammalia, Sirenia): proposed designation of a neotype and proposed conservation of *Halitherium* Kaup, 1838 by designation of a type species. The Bulletin of Zoological Nomenclature 44: 122–125.

Domning DP (1988) Fossil Sirenia of the West Atlantic and Caribbean region I. *Metaxytherium floridanum* Hay, 1922. Journal of Vertebrate Paleontology 8: 395–426. doi: 10.1080/02724634.1988.10011728

Domning DP (1994) A phylogenetic analysis of the Sirenia. In: Berta A, Deméré T (Eds) Contributions in marine mammal paleontology honoring Frank C. Whitmore Jr. Proceedings of the San Diego Society of Natural History 29: 177–189.

Domning DP (1996) Bibliography and Index of the Sirenia and Desmostylia. Smithsonian Contributions to Paleobiology 80: 1–611.

Domning DP (2001a) Evolution of the Sirenia and Desmostylia. In: Mazin JM, Buffrénil V de (Eds) Secondary adaptation of tetrapods to life in water. Proceedings of the international meeting Poitiers 1996. Verlag Dr. Friedrich Pfeil, Munich, 151–168.

Domning DP (2001b) The earliest known fully quadrupedal sirenian. Nature 413: 625–627. doi: 10.1038/35098072

Domning DP, Aguilera OA (2008) Fossil Sirenia of the West Atlantic and Caribbean Region. VIII. *Nanosiren garciae*, gen. et sp. nov. and *Nanosiren sanchezi*, sp. nov. Journal of Vertebrate Paleontology 28: 479–500. doi: 10.1671/0272-4634(2008)28[479:FSOTWA]2.0.CO;2

Domning DP, Pervesler P (2001) The Osteology and Relationship of *Metaxytherium krahuletzki* Depéret, 1895 (Mammalia: Sirenia). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft Frankfurt am Main 553: 1–89.

Fischer K, Krumbiegel G (1982) *Halitherium schinzi* Kaup, 1838 (Sirenia, Mammalia) aus dem marinen Mitteloligozän des Weißelsterbeckens (Bezirk Leipzig, DDR). Hallesches Jahrbuch für Geowissenschaften 7: 73–95.

Fitzinger LJ (1842) Bericht über die in den Sandlagern von Linz aufgefundenen fossilen Reste eines urweltlichen Säugers (*Halitherium cristolii*). Bericht über das Museum Francisco-Carolinum Linz 6: 61–72.

Gervais FLP (1849) Sur la repartition des mammifères fossils entre les différents Stages tertiaires qui concourent à former le sol de la France. Académie des Sciences et Lettres de Montpellier. Mémoires de la Section des Sciences 1: 203–219.

- Gill T (1872) Arrangement of the families of mammals. Smithsonian Miscellaneous Collections 230: 1–98.
- Gray JE (1821) On the natural arrangement of vertebrate animals. London Medical Repository 15: 296–310.
- Hartlaub C (1886) Ueber *Manatherium delheidi*, eine Sirene aus dem Oligocän Belgiens. Zoologische Jahrbücher 1: 369–378.
- International Commission on Zoological Nomenclature (ICZN) (1989) Opinion 1535. *Halianassa studeri* von Meyer, 1838 (Mammalia, Sirenia): neotype designated; and *Halitherium* Kaup, 1838 (Mammalia, Sirenia): *Pugmeodon schinzii* Kaup, 1838 designated as the type species. The Bulletin of Zoological Nomenclature 46: 83–84.
- International Commission on Zoological Nomenclature (ICZN) (2001) Official lists and indexes of names and works in zoology. Supplement 1986–2000. The International Trust for Zoological Nomenclature. The Natural History Museum, London.
- International Commission on Zoological Nomenclature (ICZN) (1999) International code of Zoological Nomenclature. Fourth edition. The International Trust for Zoological Nomenclature, The Natural History Museum, London.
- Kaup JJ (1838) *Halitherium* und *Pugmeodon* im Maynzer Becken. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1838: 318–320.
- Kaup JJ (1855) Beiträge zur näheren Kenntnis der urweltlichen Säugethiere. Zweites Heft. Leske, Darmstadt.
- Kaup JJ, Scholl JB (1834) Verzeichnis der Gypsabgüsse von den ausgezeichnetsten urweltlichen Thierresten des Grossherzoglichen Museum zu Darmstadt. Diehl, Darmstadt.
- Krauss CFF (1858) Beiträge zur Kenntnis des Schädel-Baues von *Halitherium*. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1858: 519–531.
- Lepsius GR (1882) *Halitherium Schinzi*, die fossile Sirene des Mainzer Beckens. I. Band. Abhandlungen des Mittelrheinischen geologischen Vereins, Darmstadt.
- Palmer TS (1899) [Review of Dr. E. L. Trouessart's Catalogus Mammalium tam viventium quam fossilium]. Science 10: 491–495. doi: 10.1126/science.10.249.491
- Pilleri G (1987) The Sirenia of the Swiss Molasse. With a descriptive catalogue of the fossil Sirenia preserved in Swiss collections. Brain Anatomy Institute, Ostermundigen, Bern.
- Probst E (1986) Deutschland in der Urzeit. Von der Entstehung des Lebens bis zum Ende der Eiszeit. C. Bertelsmann Verlag, Munich.
- Reinhart RH (1959) A review of the Sirenia and Desmostylia. University of California Publications in Geological Sciences 36: 1–146.
- Sagne C (2001) *Halitherium taulannense*, nouveau sirénien (Sirenia, Mammalia) de l'Éocène supérieur provenant du domaine Nord-Téthysien (Alpes-de-Haute-Provence, France). Comptes rendus de l'Académie des Sciences de la Terre et des Planètes 333: 471–476.
- Sickenberg O (1934) Beiträge zur Kenntnis Tertiärer Sirenen. I. Die Eozänen Sirenen des Mittelmeergebietes. II. Die Sirenen des Belgischen Tertiärs. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 63: 1–352.
- Simpson GG (1932) Fossil Sirenia of Florida and the evolution of the Sirenia. Bulletin of the American Museum of Natural History 59: 419–503.
- Simpson GG (1945) The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History 85: 1–350.
- Spillmann F (1959) Die Sirenen aus dem Oligozän des Linzer Beckens (Oberösterreich) mit Ausführungen über "Osteosklerose" und "Pachyostose". Denkschriften der mathematisch-naturwissenschaftlichen Klasse der Österreichischen Akademie der Wissenschaften 110: 1–68.
- Van Beneden PJ (1871) Un sirénien nouveau du terrain rupélien. Bulletins de l'Académie Royale des Sciences de Belgique (2) 32(9/10): 164–178.
- Velez-Juarbe J, Domning DP, Pyenson ND (2012) Iterative Evolution of Sympatric Seacow (Dugongidae, Sirenia) Assemblages during the Past ~26 Million Years. PLoS ONE 7(2): e31294. doi: 10.1371/journal.pone.0031294
- Voss M (2008) New finds of *Halitherium* (Sirenia, Mammalia) from the lower Oligocene of the Rhine area (Germany). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 249: 257–269. doi: 10.1127/0077-7749/2008/0249-0257
- Voss M (2010) Character evolution, homoplasy and interrelationships of Sirenia. Zitteliana B 29: 103.
- Voss M (2012) A new sea cow record from the lower Oligocene of western Germany: new indications on the skeletal morphology of *Halitherium schinzii* (Mammalia: Sirenia). Paläontologische Zeitschrift 86: 205–217. doi: 10.1007/s12542-011-0125-x
- Voss M (2013) Revision of the *Halitherium*-species complex (Mammalia, Sirenia) from the late Eocene to early Miocene of Central Europe and North America. Unpublished Ph.D. thesis, Humboldt-Universität zu Berlin, Germany, 298 pp. <http://edoc.hu-berlin.de/browsing/dissertationen/>