First records of extinct kentriodontid and squalodelphinid dolphins from the Upper Marine Molasse (Burdigalian age) of Switzerland and a reappraisal of the Swiss cetacean fauna (#66097)

First submission

Guidance from your Editor

Please submit by **25 Oct 2021** for the benefit of the authors (and your $200 publishing discount) .

Structure and Criteria
Please read the 'Structure and Criteria' page for general guidance.

Custom checks
Make sure you include the custom checks shown below, in your review.

Raw data check
Review the raw data.

Image check
Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

Files

Download and review all files from the materials page.

1 Latex file(s)
1 Raw data file(s)

Custom checks

Vertebrate animal usage checks

- Have you checked the authors ethical approval statement?
- Were the experiments necessary and ethical?
- Have you checked our animal research policies?

Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

- Clear, unambiguous, professional English language used throughout.
- Intro & background to show context. Literature well referenced & relevant.
- Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- Figures are relevant, high quality, well labelled & described.
- Raw data supplied (see PeerJ policy).

EXPERIMENTAL DESIGN

- Original primary research within Scope of the journal.
- Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- Rigorous investigation performed to a high technical & ethical standard.
- Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- Impact and novelty not assessed. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- All underlying data have been provided; they are robust, statistically sound, & controlled.
- Conclusions are well stated, linked to original research question & limited to supporting results.

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

First records of extinct kentriodontid and squalodelphinid dolphins from the Upper Marine Molasse (Burdigalian age) of Switzerland and a reappraisal of the Swiss cetacean fauna

Gabriel Aguirre-Fernández Corresp., [1], **Jürg Jost** [2], **Sarah Hilfiker** [1]

[1] Paleontological Institute and Museum, University of Zurich, Zurich, Switzerland

[2] Unaffiliated, Zofingen, Switzerland

Corresponding Author: Gabriel Aguirre-Fernández
Email address: gabriel.aguirre@pim.uzh.ch

The Swiss Upper Marine Molasse (OMM) documents a transgression event dated to around 21 to 17 Million years in which dolphin and other vertebrate remains have been reported. We revised the whole cetacean (whales and dolphins) OMM assemblage available in main collections, focusing on the identifica- tion and interpretation of periotics (bone that contains the inner ear). Periotics are rare, but they provide the richest taxonomic information in the sample and hint to environmental associations. Micro-computerized tomography allowed the reconstruction of bony labyrinths for comparisons and environmental interpreta- tions. Three families are represented by periotics: Kentriodontidae, Squalodelphinidae and Physeteridae. The cetacean taxonomic composition of the Swiss OMM reinforces biogeographical patterns reported for the Mediterranean and Paratethys during the Burdigalian at a regional scale and the Calvert cetacean fauna of the northwest Atlantic at oceanic scale.

First records of extinct kentriodontid and squalodelphinid dolphins from the Upper Marine Molasse (Burdigalian age) of Switzerland and a reappraisal of the Swiss cetacean fauna

Gabriel Aguirre-Fernández[1], Jürg Jost[2], and Sarah Hilfiker[1]

[1]**Paleontological Institute and Museum, University of Zurich, Zurich, Switzerland**
[2]**Bärenhubelstrasse 10, Zofingen, Switzerland**

Corresponding author:
Gabriel Aguirre-Fernández[1]

Email address: gabriel.aguirre@pim.uzh.ch

ABSTRACT

The Swiss Upper Marine Molasse (OMM) documents a transgression event dated to around 21 to 17 Million years in which dolphin and other vertebrate remains have been reported. We revised the whole cetacean (whales and dolphins) OMM assemblage available in main collections, focusing on the identification and interpretation of periotics (bone that contains the inner ear). Periotics are rare, but they provide the richest taxonomic information in the sample and hint to environmental associations. Micro-computerized tomography allowed the reconstruction of bony labyrinths for comparisons and environmental interpretations. Three families are represented by periotics: Kentriodontidae, Squalodelphinidae and Physeteridae. The cetacean taxonomic composition of the Swiss OMM reinforces biogeographical patterns reported for the Mediterranean and Paratethys during the Burdigalian at a regional scale and the Calvert cetacean fauna of the northwest Atlantic at oceanic scale.

INTRODUCTION

The Swiss molasse (Fig 1) is a textbook example of a foreland basin (Sissingh, 1998) and includes two marine transgression-regression cycles, spanning from the Rupelian to the Serravalian (Labhart, 1985; Swiss Committee on Stratigraphy, 2020). Among the vertebrate fossils of the molasse, remains of cetaceans (whales and dolphins) are known. Climatic changes and major geographic rearrangements in the Tethys and Parathethys (including the closure of the Tethys Seaway) may have played a significant role in the cetacean composition at regional and global scales (Steeman et al., 2009; Bianucci and Landini, 2002). Cetacean fossils in Swiss localities belong to sediments of the second transgression event, dated 21—17 million years ago (Ma). The Upper Marine Molasse or 'Obere Meeresmolasse' (hereafter referred to as OMM) is an informal lithostratigrahic group composed of two formations; the underlying Lucerne Formation, and the St. Gallen Formation (Jost et al., 2016; Swiss Committee on Stratigraphy, 2020).

The OMM cetacean assemblage is represented by a large, but fragmentary sample. Similar preservation patterns are known for other coeval localities such as the 'Molasse of Baltringen' in Germany and 'Pietra di Cantoni' in northern Italy (Bianucci and Landini, 2002). Here, we focus on the description of six well-preserved periotics and revise all (new and previously reported) cetacean remains in major Swiss collections in order to provide an overview in the context of new taxonomic advances.

The periotic bone contains the inner ear (cochlea and semicircular canals) and has become isolated in many odontocetes (Mead and Fordyce, 2009). This element ~~does~~ not only provide substantial taxonomic information, but also ~~an~~ insight into habitat preferences (Costeur et al., 2018), therefore being extremely valuable in highly-fragmentary assemblages (Aguirre-Fernández et al., 2017; Steeman, 2009).

The Miocene fossil record of cetaceans (whales and dolphins) in the circum-Mediterranean region is

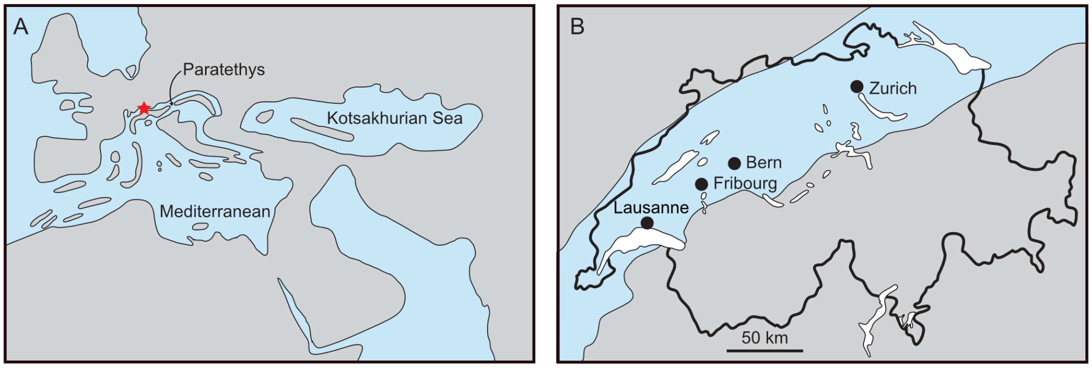

Figure 1. Reconstruction of the Paratethys during the Burdigalian. A) Western Europe with Switzerland marked in red, modified from Rögl (1998) and Berger et al. (2005); B) maximal flooding of the Paratethys over the Swiss Plateau at ca. 18–17.5 Ma, during the deposition of the St. Gallen Fm., based on Schlüchter et al. (2019).

known from localities in Egypt, southern France, southern Germany, Italy, Malta, Spain and Switzerland (Bianucci and Landini, 2002; Dominici et al., 2020). Revisions of several neighbouring faunas prompted this reappraisal ~~on~~ Swiss specimens. The current work builds upon the overview by Pilleri (1986b). We report hitherto unknown kentriodontid and squalodelphinid fossils and we dispute the presence of putative delphinids in the Swiss Marine Molasse. This paper portrays a more conservative view on taxonomic affinities than that in Pilleri (1986b).

MATERIALS AND METHODS

Anatomical descriptions follow the nomenclature of Mead and Fordyce (2009) for external (bone) structures and Ekdale (2013) for internal (bony labyrinth, i.e., cochlea and semicircular canals) structures. External measurements of the periotic were made with a caliper, following Kasuya (1973). Micro-computerized tomography (μct) data of seven periotics were obtained at the University of Zurich using a Nikon XT H 255 ST μct scanner (scanning parameters available in Supplementary Table 2). Segmentation of the earbones and their bony labyrinth endocasts was performed using Mimics Innovation Suite 19.0. Bony labyrinth measurements that serve as correlates for hearing sensitivity are based on the methods des~~rc~~ibed in Racicot and Preucil (2021). The 3D models of all the periotics and their bony labyrinths are available at the MorphoMuseuM repository (https://morphomuseum.com/).

Collection Acronyms

MGL Cantonal Museum of Geology Lausanne, Lausanne, Switzerland.

NHMB Natural History Museum Basel, Basel, Switzerland.

NMBE Natural History Museum Bern, Bern, Switzerland.

PIMUZ Paleontological Institute and Museum, University of Zurich, Zurich, Switzerland.

RESULTS

General Remarks on OMM cetaceans

A total of 290 cetacean elements were observed in the collections described above. All elements were found isolated (i.e., single bones rather than articulated skeletons); almost all were fragmented (i.e., bones were broken and had missing parts) and some were also abraded or polished. The most frequent elements were by far teeth (69%), followed by vertebrae (16%) and ~~periotics~~ periotics (7%). Teeth and vertebrae are of poor taxonomic value and belong to a range of odontocete groups. The few skull elements are also too fragmentary for unambiguous identification. The Supplementary Table S1 includes basic information on all material studied, with previous (i.e., Pilleri, 1986b) and new (this study) taxonomic opinions. We focus below on the periotics and their bony labyrinths because they are the most informative elements for taxonomy and environmental interpretations available in the OMM sample.

SYSTEMATIC PALAEONTOLOGY

Cetacea Brisson, 1762

Odontoceti Flower, 1867

Delphinoidea Flower, 1885

Kentriodontidae Slijper, 1936

Kentriodontidae indet.

(Figs. 2A—L)

Description and remarks

NMBE 5023944 (left periotic), figured in Pilleri (1986b:Plate 5D); NMBE 502345 (right periotic) figured in Pilleri (1986b:Plate 5G); NMBE 5023946 (left periotic) mentioned in Pilleri (1986b: p.29), all three from Brüttelen-Fluh; and NMBE 5036436 (right periotic; figured in Pilleri (1986b:Plate 8K) from Madiswil-Ghürn. All four specimens were identified as delphinidans in Pilleri (1986b). Both localities correspond to sediments of the Lucerne Fm. (Fig 2). The Swiss kentriodontid periotics strongly resemble several species of *Kentriodon*, such as *K. pernix, K. obscurus, K. hoepfneri, K. nakajimai* and *K. sugawarai* in overall shape, dimensions and proportions. Small variation in shape (e.g, in the pinching of the anteroventral angle or the ventral inflexion of the posterior process of the periotic), size and proportions observed among the Swiss kentriodontid periotics (Fig 2) suggest they may represent more than one species, but a systematic study with a larger sample including well-known taxa would be needed to confirm this interpretation. The anterior process of kentriodontids and other delphinoideans is short, thick and with a squared-off (dorsoventral) margin (Kasuya, 1973). The apex of the anterior process is mediolaterally pinched and slightly deflected medially. The length of the anterior process is similar to that of the cochlea (Table 1); the posterior process is relatively short (anteromedially) and directed ventrally; the outline of the pars cochlearis is slighly oval, longer (in anteroposterior axis) than it is wide. The aperture for the cochlear aqueduct is located dorsally and posterior to the aperture for the vestibular aqueduct, both aqueducts are roughly the same size (Fig. 2 i). The mallear fossa is round; the vestibular window is round and relatively large; the fenestra rotunda is teardrop-shaped; the posterior bullar facet is smooth (Fig. 2 j). There is an anterointernal sulcus clearly visible in medial view (Fig. 2 k). The parabullary ridge is ventrally concave (Fig 2 l). The Swiss kentriodontid periotics resemble several species of *Kentriodon*, such as *K. pernix, K. obscurus, K. hoepfneri, K. nakajimai* and *K. sugawarai*.

The bony labyrinths of NMBE 5023944, NMBE 5023946, and NMBE 5036436 (Fig. 3) share features of other odontocetes, such as the small vestibular apparatus as compared to the cochlea, the low number of spiral turns in the cochlea and their loose coiling. Although the comparisons are limited because the bony labyrinth of *Kentriodon pernix* remain undescribed, published cochlear measurements of the bony labyrinth of *Kentriodon pernix* indicate a strong similarity to the Swiss kentriodontids (Table 1).

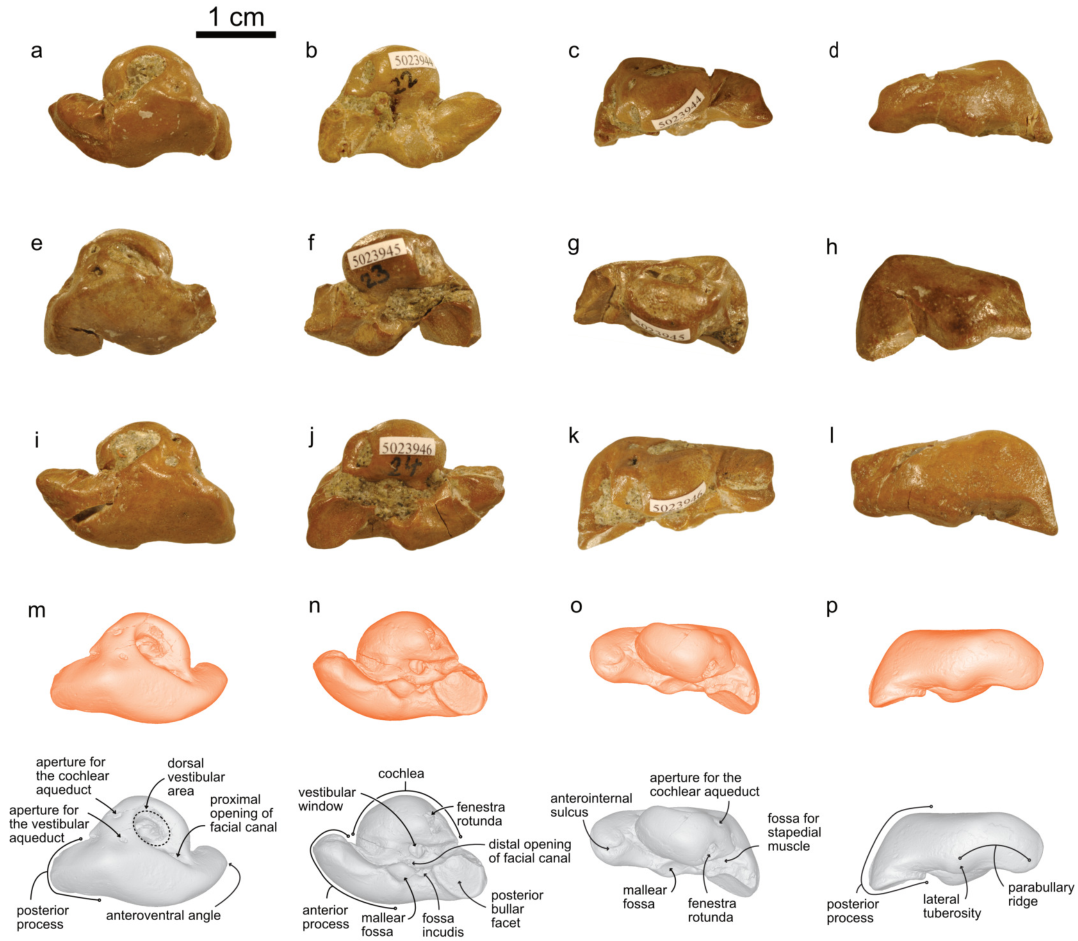

Figure 2. Periotics of Kentriodontidae indet. a–d: NMBE 5023944; e–h: NMBE 5023945; i–l: NMBE 5023946; and m–p: NMBE 5036436 featuring the 3D models (available for download from the MorphoMuseuM repository). The lower row illustrates anatomical landmarks of the periotic as seen in NMBE 5036436. Views: dorsal: a, e, i; ventral: b, f, j; medial: c, g, k; lateral: d, h, l.

Platanistoidea Simpson, 1945

Squalodelphinidae Dal Piaz, 1917

Squalodelphinidae indet.

(Figs. 2 M—T)

Description and remarks

NMBE 5023942 (right periotic), figured in Pilleri (1986b: Plate 5F) and NMBE 5023943 (left periotic), figured in Pilleri (1986b Plate 5E) were both found in Brüttelen-Fluh (Lucerne Fm). Both periotics were identified in Pilleri (1986b) as squalodontids. The earbones are markedly similar in proportions and shape (Fig 4), but they differ in the following features, thus possibly representing two different morphotypes: 1) the shape of their anterior processes (being longer and more slender in NMBE 5023943), 2) the ventral deflection of the anterior process in NMBE 5023942; and 3) the deeper anterior bullar facet in NMBE 5023942. The prominent anterior bullar facet with well-defined medial and lateral boundaries (sensu Lambert et al., 2014, fig. 6) is a diagnostic character also present in other squalodelphinids such as *Squalodelphis fabianii, Notocetus vanbenedeni*, and *Huaridelphis raimondii*. The tuberosity in the posteromedial part of the anterior process is also present in *Huaridelphis raimondii* (see Lambert et al.,

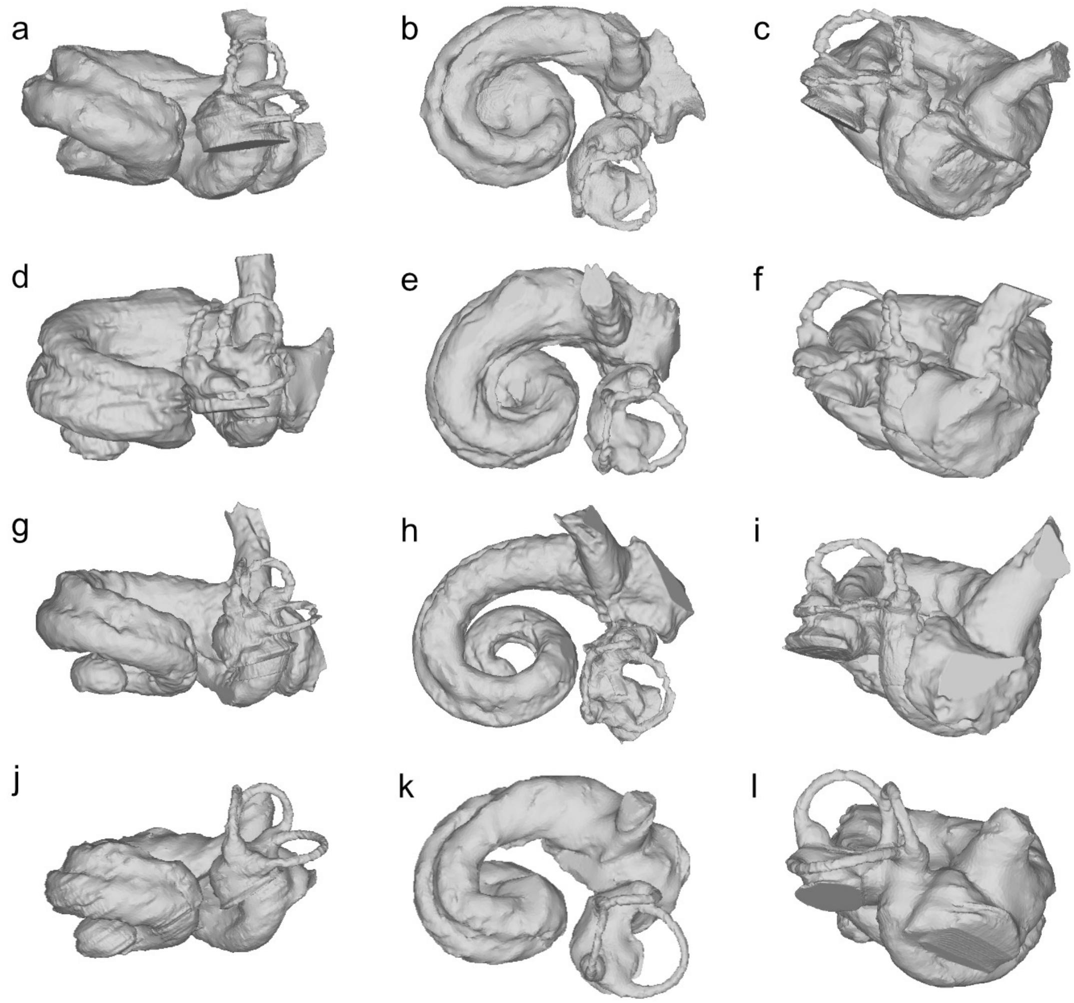

Figure 3. Bony labyrinths of Kentriodontidae indet. a–c: NMBE 5023944 (reflected horizontally); d–f: NMBE 5023945; g–i: NMBE 5023946 (reflected horizontally); j–l: NMBE 5036436. Views: anterior: a, d, g, j; dorsal: b, e, h, k; lateral: c, f, i, l.

2014, figs. 6 A and B) and other squalodelphinids (e.g., *Squalodelphis fabianii* and *Notocetus vanbenedeni*), but is not restricted to this group, as it is also shown in some squalodontids, eurhinodelphinids and xenorophids (Lambert et al., 2014). Some putative family-diagnostic characters such as a square-shaped pars cochlearis and a large and dorsally-oriented aperture for the cochlear aqueduct (sensu Lambert et al., 2014) are absent in NMBE 5023942: the pars cochlearis has a relatively circular outline, the aperture for the cochlear aqueduct is indeed large, but not dorsally-oriented. The Swiss squalodelphinid periotics are smaller than *Phocageneus*, and comparable in size to *Huaridelphis raimondii*, the smallest known member of Squalodelphinidae (Lambert et al., 2014). To our knowledge, there are no models of bony labyrinths of squalodelphinids that could serve for comparisons. The smaller cochlear length and axial height of their bony labyrinths compared to *Phocageneus* (Fig. 5 and Table 2) probably reflects this difference in size.

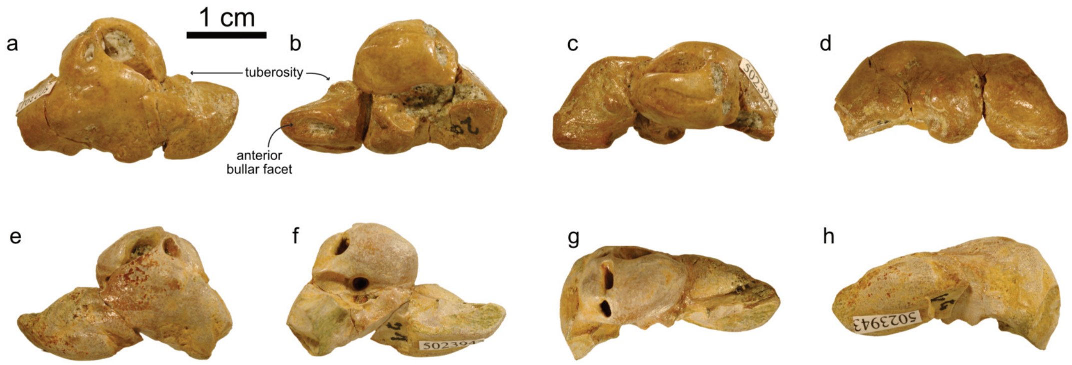

Figure 4. Periotics of Squalodelphinidae indet. a–d: NMBE 5023942; e–h: NMBE 5023943 (reflected horizontally) [*link to be provided*]. Views: anterior: a, e; ventral: b, f; medial: c, g; lateral: d, h.

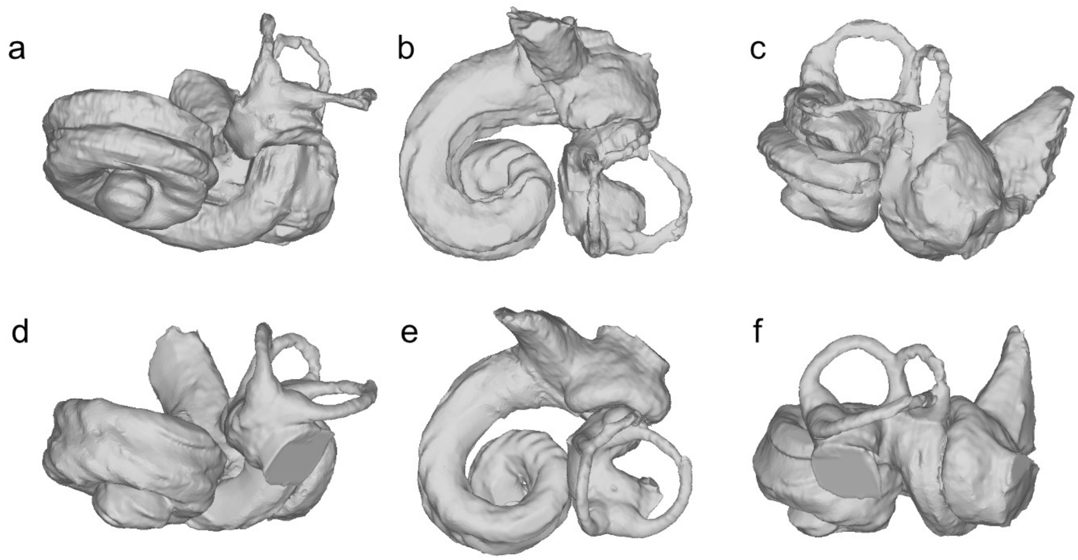

Figure 5. Bony labyrinths of Squalodelphinidae indet. a–c: NMBE 5023942 (reflected horizontally); d–f: NMBE 5023943 (reflected horizontally). Views: anterior: a, d; dorsal: b, e; lateral: c, f.

Physeteroidea Gray, 1821

Physteridae Gray, 1821

Physeteridae indet.

(Figs. 2 U—X)

Description and remarks

NMBE 5036437 (left periotic) was found in Staffelbach-Böl (St. Gallen Formation). The periotic is comparatively large and robust (Fig 6). Of the four characters relevant to the periotic mentioned in the phylogenetic analysis of Lambert et al. (2016), NMBE 5036437 shares with other physeteroids the very small anterior bullar facet and the enlarged accessory ossicle (judged by the size of the fovea epitubaria). The accessory ossicle is fused to the periotic in some physeteroids (e.g., the Gross Pampau physeteroid in Montañez Rivera and Hampe, 2020), but not in NMBE 5036437 (accessory ossicle missing). The posterior part of the posterior process of NMBE 5036437 is directed posteroventrally as in other physeterids and unlike in kogiids. The high and small dorsal crest (lateral to the internal acoustic meatus) of NMBE 5036437 is a feature seen in other physeterids such as *Aulophyseter, Orycterocetus* and *Physeter*. NMBE 5036437 falls in the size range of both *Aulophyseter* and *Orycterocetus*, overall shape and proportions of the cochlea and the anterior and posterior processes resemble *Aulophyseter morricei* Kellogg 1927b, but some features are also comparable to *Orycterocetus crocodilinus* Kellogg 1965 and deserve further comparisons, which were done using photos of the holotypes of *Aulophyseter morricei* and *Orycterocetus crocodilinus*, hereafter referred to by their generic names: In dorsal view, the cochlea of NMBE 5036437 is larger than that of *Aulophyseter* and *Orycterocetus*, but closer in proportions to *Aulophyseter*. The elongated shape of the internal acoustic meatus resembles *Orycterocetus*. The aperture for the cochlear aqueduct is larger than the aperture of the vestibular aqueduct as in *Orycterocetus*. The anterior tip of the anterior process points anteriorly as in *Orycterocetus*. In ventral view, the fenestra rotunda has a "kidney-shaped" outline, which is distinct from both *Aulophyseter* and *Orycterocetus*. The anterior process is square-shaped and facing ventrally as in *Aulophyseter*. The posterior process is more slender than in both *Aulophyseter* and *Orycterocetus*, and the tip of the process is pointing slightly more ventrolaterally. The posterior bullar facet is smooth, unlike in both *Aulophyseter* and *Orycterocetus*. In medial view, the anterior process is more robust (higher), and the dorsal crest is less pronounced than in both *Aulophyseter* and *Orycterocetus*. The dorsal profile of the posterior process is more similar to that of *Orycterocetus*.

Although the external dimensions of the periotic NMBE 5036437 are very similar to those of *Aulophyseter morricei*, there are strong differences in the cochlear length and axial height, also reflected in the axial pitch (Table 3 and Fig. 7).

Figure 6. Periotic of Physeteridae indet. NMBE 5036437 (all periotics and their inner ear labyrinths are available for download from the MorphoMuseuM repository) [*Note: temporary link during review: https://drive.switch.ch/index.php/s/7jWIKHKGUW8HZfT*]. Views: dorsal: a; ventral: b; medial: c; lateral: d.

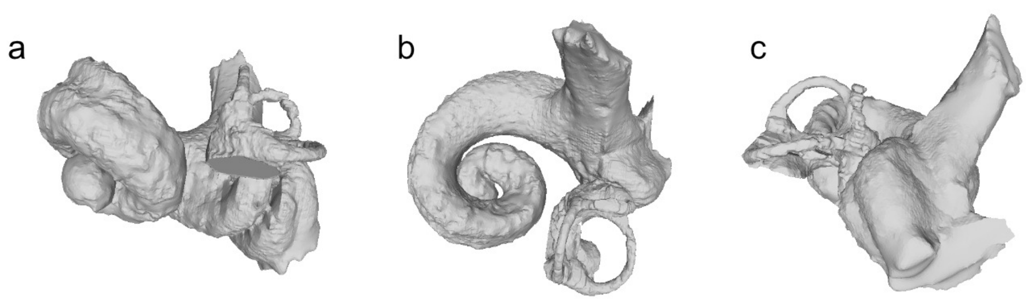

Figure 7. Bony labyrinth of Physeteridae indet. NMBE 5036437. Views: anterior: a; dorsal: b; lateral: c.

DISCUSSION

At a larger scale, the connection of the Paratethys with the Indian Ocean and the Mediterranean during the Aquitanian favoured the distribution of warm-water faunas; these conditions prevailed until the late Burdigalian, when the seaway between the Mediterranean and the Indian Ocean closed, the eastern Parathethys became isolated (forming the so-called Kotsakhurian Sea) and the central/western Paratethys became much reduced (Rögl, 1998). The late Burdigalian is marked by a large diversity of odontocetes and the subsequent demise of many longirostrine forms, possibly linked to climatic changes at the beginning of the Middle Miocene (Bianucci and Landini, 2002). The kentriodontid and squalodelphinid periotics here reported come from localities of the Brüttelen-Muschelnagelfluh Member, right at the base of the Lucerne Formation and therefore from oldest sediments of the OMM. The Brüttelen-Muschelnagelfluh Member is chronologically interpreted at the base of the Burdigalian and environmentally interpreted as shallow marine (Swab, 1960). In contrast, the physeterid periotic was found in sediments of the Staffelbach-Grobsanstein Bed, a local unit at the base of the St. Gallen Fm which is environmentally interpreted as sublittoral (ca. 100 m deep) based on the rich chondrichthyan composition (Jost et al., 2016). Further, the chondrichthyan composition of the Staffelbach-Grobsanstein Bed is extremely similar to that of the Rhone Valley (Jost et al., 2016), a pattern also reported for the mollusc and echinoid faunas, which place Switzerland in a transitional zone between the Central Parathetys faunas (eastwards) and the Rhone Basin and the Mediterranean faunas (westwards) for th Early Burdigalian (Kroh and Menkveld-Gfeller, 2006).

Despite recent efforts to disentangle the relationships of kentriodontids and redefine the group, their monophyly is still a matter of debate (e.g., Guo and Kohno, 2021; Peredo et al., 2018; Lambert et al., 2017). Regardless, the type-bearing genus *Kentriodon* and its closest relatives were cosmopolitan and diverse in the early Miocene Guo and Kohno (2021). Bianucci and Landini (2002) reported the presence of kentriodontids in five Burdigalian-Langhian European localities: Baltringen (southern Germany), Rosignano and Vignale (northern Italy), Cursi-Melpignano quarries of the Salento Peninsula (southern Italy), and Switzerland. The designation of NMBE 502344 and NMBE 502345 (Fig. 2) to Kentriodontidae corroborates the suggestion already made by Bianucci and Varola (1994), contrasting with their previous identification as delphinidan earbones Pilleri (1986b, see plate 5 D & G and plate 8 K). The two skull-based and highly-diagnostic kentriodontid species *Rudicetus squalodontoides* (Burdigalian–Messinian, 18–6 Ma) and *Tagicetus joneti* (late Serravallian, 12.7–11.6 Ma) do not have preserved periotics (Bianucci, 2001; Lambert et al., 2005). Bianucci and Varola (1994) reported kentriodontid periotics from the same area as *R. squalodontoides* (Pietra leccese), contemporaneous with the Swiss localities. Further, Bianucci and Varola (1994) reassigned other earbones (previously recognized as Delphinidae in Pilleri, 1986a; Pilleri et al., 1989) from Piedmont and Baltringen to Kentriodontidae. *Kentriodon hoepfneri* from Gross Pampau, Germany (Kazár and Hampe, 2014) and the kentriodontid remains from Bihor County, Romania (Kazár and Venczel, 2003) are from younger (middle Miocene) sediments. Both the periotic and the bony labyrinth of odontocetes are known to show little intraspecific variation and are therefore representative of a taxon even when the sample size is extremely low, as is usually the case in the fossil record (Kasuya, 1973; Martins et al., 2020). Bony labyrinth measurements that correlate to hearing sensitivity indicate that *Kentriodon pernix* (and possibly other kentriodontids) may have been among the earliest odontocetes to use a narrow-band-high-frequency (NBHF) biosonar (Racicot and Preucil, 2021; Galatius et al., 2018). NBHF may have evolved to avoid predation by large predators such as orcas (Morisaka and Connor, 2007), but their fossil record does not extend into the Miocene. Odontocetes with a similar niche include macroraptorial physeteroids (Racicot and Preucil, 2021; Galatius et al., 2018) and 'squalodontids' (Kellogg, 1923), both abundant in European Miocene localities.

Squalodelphinidae is a monophyletic group sister to Platanistidae (Lambert et al., 2014) with a distribution in both hemispheres of the Pacific and Atlantic coasts (Bianucci et al., 2015). The highest diversity centers in the North Atlantic at around the early Miocene and suggests a close connection between the European and North American faunas (Bianucci et al., 2015). The periotics here described represent the first record of Squalodelphinidae in Switzerland and are contemporaneous with *Medocinia tetragorhina* from the Burdigalian locality Saint-Medard-en-Jalle in France (Muizon, 1988) and *Squalodelphis fabianii* from the Libano Sandstone in northern Italy (Bianucci and Landini, 2002; Dal Piaz, 1917), of which the periotics are unfortunately unknown. Smaller squalodelphinids such as the OMM specimens, about the size of *Huaridelphis raimondii* could be interpreted as having occupied a similar niche to that of the extant *Delphinus delphis*, preying on small fish (Bianucci et al., 2018).

Among the taxa here studied, Physeteridae is also attested by the many teeth from the OMM housed in collections, as already reported in Pilleri (1986b). Here, the physeteroid *Helvicetus rugosus* Pilleri 1986b is regarded as *nomen dubium*. The range of sizes, shapes and degrees of wear of ~~physetorid~~ teeth suggest a high diversity of this group in the OMM, but a revision of the teeth is out of the scope of this paper. Bianucci and Landini (2002) reported the presence of physeterids in many Burdigalian-Langhian localities around the Mediterranean (Baltringen, the Rhone Valley, Rosignano and Vignale, and the Salento Peninsula) ranging all across the Miocene, pointing to a considerable radiation of this group in the area at that time. Several isolated periotics are known from the 'pietra leccese' (Salento Peninsula) and 'pietra di cantoni' (Rosignano and Vignale), possibly representing more than five genera, according to Bianucci and Landini (2002).

Pilleri (1986b) mentioned that Cuvier reported a scapula that can only belong to *Balaenoptera*, reportedly found in Lake Geneva, but such a specimen was not located. Given the age of the sediments and the size of the isolated elements that can only be diagnosed to Cetacea indet., we assume that only odontocetes are represented in the sample. This pattern reflects a global early Miocene 'dark age' for mysticetes, which has been linked to environmental changes at around the Oligocene-Miocene boundary and led to the decline of coastal assemblages. While toothed mysticetes went extinct, filter feeders thrived offshore and recolonized coastal environments in the middle Miocene (Marx et al., 2019).

Overall, the faunal composition of the OMM fits the interpretations outlined in Bianucci and Landini (2002) for the Mediterranean/Paratethys fauna during the Burdigalian. On a broader geographic scale, there is a clear association with the contemporaneous and extremely diverse Calvert fauna by the eastern coast of North America (Bianucci and Landini, 2002; Gottfried et al., 1994).

CONCLUSIONS

There is a prevalence of isolated, fragmented, and sometimes abraded cetacean remains in the OMM. The teeth are the most frequent elements, but their diagnostic potential is very low. Periotics are rare, but extremely diagnostic in comparison. The seven periotics herein described attest the presence of Kentriodontidae (4 morphotypes), Squalodelphinidae (two morphotypes) and Physeteridae (one morphotype). Previous assignations of these periotics to Delphinidae in Pilleri (1986b, plate 5 D & G and plate 8 K) in the OMM (and elsewhere; see Bianucci and Varola, 1994) are indeed kentriodontids. Previous assignations of periotics to Squalodontidae Pilleri (1986b, plate 5 E & F) in the OMM are here identified as Squalodelphinids. Physeteridae is represented by one periotic from the St. Gallen Formation. The faunal composition is similar to that reported for the Burdigalian at a regional scale (Bianucci and Landini, 2002) and reflects similar faunal composition to that of the Calvert Fm on western Atlantic (Gottfried et al., 1994).

SUPPLEMENTAL INFORMATION AND DATA AVAILABILITY

File S1. Overview on all elements studied from main Swiss Collections

Data Availability

The 3D models of periotics and their bony labyrinths are available at the MorphoMuseum repository under the following links:
NMBE 5023942: http://morphomuseum.com/Specimenfiles/sendFile/862/6b30ce
NMBE 5023943: http://morphomuseum.com/Specimenfiles/sendFile/863/cce84d
NMBE 5023944: http://morphomuseum.com/Specimenfiles/sendFile/858/bf74bc
NMBE 5023945: http://morphomuseum.com/Specimenfiles/sendFile/859/37bf6b
NMBE 5023946: http://morphomuseum.com/Specimenfiles/sendFile/860/f63fd9
NMBE 5036436: http://morphomuseum.com/Specimenfiles/sendFile/861/0a96ce
NMBE 5036437: http://morphomuseum.com/Specimenfiles/sendFile/864/5b1778

ACKNOWLEDGMENTS

We thank Loïc Costeur (NHMB), Olivier Lambert (RBINS), Ursula Menkveld (NMBE), Antoine Pictet (GML) and Chrisitan Klug (UZH) for access to material. Beat Lüdi is thanked for allowing the study of and donating the physeterid to the NMBE. Loïc Costeur (NHMB) kindly scanned specimen NMBE 5036436. Christian Meyer, Martin Schneider and Markus Weick are also thanked for their help while at NHMB. Bernhard Hostettler is thanked for help while at NMBE. O. Lambert is thanked for discussions and access to specimen photos for comparisons. Thomas Schmelzle is thanked for discussions on the mammalian ear. Dylan Bastiaans is thanked for advice with segmentation. Marcelo R. Sánchez-Villagra, Rachel Racicot and Aldo Benites are thanked for comments on an earlier draft. Marcelo R. Sánchez-Villagra is thanked for financial support. This project was funded by Fonds für Lehre und Forschung (NHMB) and the Synthesys Programme (BE-TAF project 4644).

REFERENCES

Aguirre-Fernández, G., Mennecart, B., Sánchez-Villagra, M. R., Sánchez, R., and Costeur, L. (2017). A dolphin fossil ear bone from the northern Neotropics—-insights into habitat transitions in iniid evolution. *Journal of Vertebrate Paleontology*, page e1315817.

Berger, J.-P., Reichenbacher, B., Becker, D., Grimm, M., Grimm, K., Picot, L., Storni, A., Pirkenseer, C., Derer, C., and Schaefer, A. (2005). Paleogeography of the Upper Rhine Graben (URG) and the Swiss Molasse Basin (SMB) from Eocene to Pliocene. *International Journal of Earth Sciences*, 94(4):697–710.

Bianucci, G. (2001). A new genus of kentriodontid (Cetacea: Odontoceti) from the Miocene of south Italy. *Journal of Vertebrate Paleontology*, 21(3):573–577.

Bianucci, G., Bosio, G., Malinverno, E., Muizon, C. d., Villa, I. M., Urbina, M., and Lambert, O. (2018). A new large squalodelphinid (Cetacea, Odontoceti) from Peru sheds light on the Early Miocene platanistoid disparity and ecology. *Royal Society Open Science*, 5(4):172302.

Bianucci, G. and Landini, W. (2002). Change in diversity, ecological significance and biogeographical relationships of the Mediterranean Miocene toothed whale fauna. *Geobios*, 24:19–28.

Bianucci, G., Urbina, M., and Lambert, O. (2015). A new record of *notocetus vanbenedeni* (squalodelphinidae, odontoceti, cetacea) from the early miocene of peru. *Comptes Rendus Palevol*, 14(1):5–13.

Bianucci, G. and Varola, A. (1994). Kentriodontidae (Odontoceti, Cetacea) from Miocene sediments of the Pietra Leccese (Apulia, Italy). *Atti della Società toscana di scienze naturali. Memorie, Serie A*, 101:201–212.

Brisson, M. J. (1762). *Regnum animale in classes IX. distributum, sive synopsis methodica sistens generalem animalium distributionem in classes IX, & duarum primarum classium, quadrupedum scilicet & cetaceorum, particularem divisionem in ordines, sectiones, genera & species. Cum brevi cujusque speciei descriptione, citationibus auctorum de iis tractantium, nominibus eis ab ipsis & nationibus impositis, nominibusque vulgaribus*. Theodorum Haak, Lugduni Batavorum [Leiden].

Churchill, M., Martinez-Caceres, M., de Muizon, C., Mnieckowski, J., and Geisler, J. (2016). The origin of high-frequency hearing in whales. *Current Biology*, 26(16):2144–2149.

Costeur, L., Grohé, C., Aguirre-Fernández, G., Ekdale, E., Schulz, G., Müller, B., and Mennecart, B. (2018). The bony labyrinth of toothed whales reflects both phylogeny and habitat preferences. *Scientific reports*, 8(1):1–6.

Dal Piaz, G. (1917). Gli Odontoceti del Miocene Bellunese. Parte Terza, *Squalodephis fabianii*. *Memorie dell'Istituto Geologico della Universitadi Padova*, 5(3):1–28.

Dominici, S., Danise, S., Cau, S., and Freschi, A. (2020). The awkward record of fossil whales. *Earth-Science Reviews*, 205:103057.

Ekdale, E. G. (2013). Comparative anatomy of the bony labyrinth (inner ear) of placental mammals. *PloS one*, 8(6):e66624.

Flower, W. H. (1867). Description of the skeleton of *Inia geoffrensis* and of the skull of *Pontoporia blainvillei*, with remarks on the systematic position of these animals in the order Cetacea. *Transactions of the Zoological Society of London*, 6(3):87–116.

Flower, W. H. (1885). *List of the Specimens of Cetacea in the Zoological Department of the British Museum*. Printed by order of the Trustees.

Galatius, A., Olsen, M. T., Steeman, M. E., Racicot, R. A., Bradshaw, C. D., Kyhn, L. A., and Miller, L. A. (2018). Raising your voice: evolution of narrow-band high-frequency signals in toothed whales (Odontoceti). *Biological Journal of the Linnean Society*, 126(2):213–224.

Gottfried, M. D., Bohaska, D., and Whitmore Jr, F. C. (1994). Miocene cetaceans of the chesapeake group. In *Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr. Proceedings of the San Diego Society of Natural History*, volume 29, pages 229–238.

Gray, J. (1821). On the natural arrangement of vertebrose animals. *London Medical Repository*, 15(1):296–310.

Guo, Z. and Kohno, N. (2021). A new kentriodontid (Cetacea: Odontoceti) from the early to middle Miocene of the western North Pacific and a revision of kentriodontid phylogeny. *PeerJ*, 9:e10945.

Jost, J., Kempf, O., and Kälin, D. (2016). Stratigraphy and palaeoecology of the Upper Marine Molasse (OMM) of the central Swiss Plateau. *Swiss Journal of Geosciences*, 109(2):149–169.
Kasuya, T. (1973). Systematic consideration of recent toothed whales based on the morphology of tympano-periotic bone. *Scientific Reports of the Whales Research Institute*, 25:1–103.
Kazár, E. and Venczel, M. (2003). Kentriodontid remains (Cetacea: Odontoceti) from the Middle Miocene of Bihor County, Romania. *Nymphaea, Folia naturae Bihariae*, 30:39–66.
Kazár, E. and Hampe, O. (2014). A new species of Kentriodon (Mammalia, Odontoceti, Delphinoidea) from the middle/late Miocene of Gross Pampau (Schleswig-Holstein, North Germany). *Journal of Vertebrate Paleontology*, 34(5):1216–1230.
Kellogg, R. (1923). Description of two squalodonts recently discovered in the Calvert Cliffs, Maryland; and notes on the shark-toothed cetaceans. *Proceedings of the United States National Museum*.
Kellogg, R. (1927a). *Kentriodon pernix*, a Miocene porpoise from Maryland. *Proceedings of the United States National Museum*, 69(19):1–55.
Kellogg, R. (1927b). Study of skull of a fossil sperm-whale from the Temblor Miocene of southern California. *Contributions to Palaeontology from the Carnegie Institution of Washington*, pages 1–24.
Kellogg, R. (1957). Two additional Miocene porpoises from the Calvert cliffs of Maryland. *Proceedings of the United States National Museum*, 170(346):279–337.
Kellogg, R. (1965). The Miocene Calvert Sperm Whale *Orycterocetus*. *United States National Museum Bulletin*, 247:47–64.
Kroh, A. and Menkveld-Gfeller, U. (2006). Echinoids from the Belpberg Beds (Obere Meeresmolasse, Middle Burdigalian) in the area of Bern (Switzerland). *Eclogae geologicae Helvetiae*, 99(2):193–203.
Labhart, T. P. (1985). *Geologie der Schweiz.* Hallwag, Bern, 3 edition.
Lambert, O., Bianucci, G., and De Muizon, C. (2016). Macroraptorial sperm whales (Cetacea, Odontoceti, Physeteroidea) from the Miocene of Peru. *Zoological Journal of the Linnean Society*, 0(0).
Lambert, O., Bianucci, G., and Urbina, M. (2014). *Huaridelphis raimondii*, a new early Miocene Squalodelphinidae (Cetacea, Odontoceti) from the Chilcatay Formation, Peru. *Journal of Vertebrate Paleontology*, 34(5):987–1004.
Lambert, O., Bianucci, G., Urbina, M., and Geisler, J. H. (2017). A new inioid (Cetacea, Odontoceti, Delphinida) from the Miocene of Peru and the origin of modern dolphin and porpoise families. *Zoological Journal of the Linnean Society*, 179(4):919–946.
Lambert, O., Estevens, M., and Smith, R. (2005). A new kentriodontine dolphin from the middle Miocene of Portugal. *Acta Palaeontologica Polonica*, 50(2).
Martins, M. C. I., Park, T., Racicot, R., and Cooper, N. (2020). Intraspecific variation in the cochleae of harbour porpoises *(Phocoena phocoena)* and its implications for comparative studies across odontocetes. *PeerJ*, 8:e8916.
Marx, F. G., Fitzgerald, E. M., and Fordyce, R. E. (2019). Like phoenix from the ashes: How modern baleen whales arose from a fossil “dark age”. *Acta Palaeontologica Polonica*, 64(2).
Mead, J. G. and Fordyce, R. E. (2009). *The Therian Skull: a Lexicon With Emphasis on the Odontocetes*. Smithsonian Contributions to Zoology 627. Smithsonian Institution Scholarly Press.
Montañez Rivera, I. and Hampe, O. (2020). An unfamiliar physeteroid periotic (Cetacea: Odontoceti) from the German middle–late Miocene North Sea basin at Gross Pampau. *Fossil Record*, 23(2):151–168.
Morisaka, T. and Connor, R. C. (2007). Predation by killer whales (*Orcinus orca*) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes. *Journal of Evolutionary Biology*, 20(4):1439–1458.
Muizon, C., d. (1988). Le polyphylétisme des Acrodelphidae, odontocètes longisrostres du Miocène européen. *Bulletin du Muséum National d’Histoire Naturelle, Paris, section C, série 4*, 10(1):31–88.
Peredo, C. M., Uhen, M. D., and Nelson, M. D. (2018). A new kentriodontid (Cetacea: Odontoceti) from the early Miocene Astoria Formation and a revision of the stem delphinidan family Kentriodontidae. *Journal of Vertebrate Paleontology*, 38(2):e1411357.
Pilleri, G. (1986a). *The Cetacea of the Western Paratethys: Upper Marine Molasse of Baltringen*. Investigations on Cetacea. Brain Anatomy Institute Bern.
Pilleri, G. (1986b). *The Denticeti of the Western Paratethys (Upper Marine Molasse of Switzerland)*. Investigations on Cetacea 19. Brain Anatomy Institute Bern.
Pilleri, G., Gihr, M., and Kraus, C. (1989). *Odontoceti (Mammalia: Cetacea) from the lower Miocene of Rosignano, Piedmont, North Italy*. Investigations on Cetacea 22. Brain Anatomy Institute Bern.

Racicot, R. A. and Preucil, V. E. (2021). Bony labyrinths of the blackfish (Delphinidae: Globicephalinae). *Marine Mammal Science*.

Rögl, F. (1998). Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). *Annalen des Naturhistorischen Museums in Wien*, 99A:279–310.

Schlüchter, C., Isler, A., Jost, J., Gisler, C., Wanner, J., Murer, R., Strasky, S., Grünig, A., and Hofmann, B. (2019). Erläuterungen Geologischer Atlas der Schweiz 1:25000; 1148 Sumiswald, 1149 Wolhusen und 1168 Langnau i.E. Technical report, Swisstopo.

Simpson, G. G. (1945). The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, 85:1–350.

Sissingh, W. (1998). Comparative Tertiary stratigraphy of the Rhine Graben, Bresse Graben and Molasse Basin: correlation of Alpine foreland events. *Tectonophysics*, 300(1):249–284.

Slijper, E. J. (1936). *Die Cetaceen. Vergleischend-Anatomisch und Systematisch. Ein Beitrag zur vergleichenden Anatomie des Blutgefäss-, Nerven- und Muskelsystems, sowie des Rumpfskelettes der Säugetiere, mit Studien über die Theorie des Aussterbens und der Foetalisation*. A. Asher & Co. B. V., Amsterdam, 2nd (1973) edition.

Steeman, M. E. (2009). A new baleen whale from the late Miocene of Denmark and early mysticete hearing. *Palaeontology*, 52:1169–1190.

Steeman, M. E., Hebsgaard, M. B., Fordyce, R. E., Ho, S. Y. W., Rabosky, D. L., Nielsen, R., Rahbek, C., Glenner, H., Sorensen, M. V., and Willerslev, E. (2009). Radiation of extant cetaceans driven by restructuring of the oceans. *Systematic Biology*, 58:1–13.

Swab, R. F. (1960). Zur stratigraphie und tektonik der molasse der umgebung von biel (kt. bern). *Bulletin der Vereinigung Schweiz. Petroleum-Geologen und -Ingenieure*, 26:21–30.

Swiss Committee on Stratigraphy (2020). Lithostratigraphic Lexicon of Switzerland.

	NMBE 5023944	NMBE 5023945	NMBE 5023946	NMBE 5036436	*Kentriodon pernix*[1]
Periotic					
Greatest length of periotic	25	+ 25	27	23.6	28.8
Width of the periotic	16.6	15.3	15.1	14.5	16.9
Length of pars cochlearis	12	12.6	13.3	13.7	—
Height of pars cochlearis	8.1	9	9.3	7.9	10.5
Width of the pars cochlearis	8	8.3	7.7	8.5	—
Length of anterior process	12	14	11.3	13	13.4
Inner ear endocast					
Cochlear turns (t)	1.5	1.7	1.5	1.7	1.7
Cochlear length	25	29	29	27	27.6
Axial height (h)	4	4	4	3.7	4
Axial pitch (h/t)	2.7	2.3	2.7	2.1	2.3

Table 1. Periotic and inner ear measurements of the fossil kentriodontids (in mm); [1] USNM 8060 as externally measured by Kellogg (1927a) and internally (bony labyrinth) by Churchill et al. (2016); + as preserved

	NMBE 5023942	NMBE 5023943	*Phocageneus*[1]
Periotic			
Greatest length of periotic	33(e)	35(e)	40
Width of the periotic	19.8	15.9	20
Length of pars cochlearis	13.9	14.7	—
Height of pars cochlearis	11.4	10	14.2
Width of the pars cochlearis	8.8	8.2	—
Length of anterior process	15.6	16	21
Inner ear endocast			
Cochlear turns (t)	1.5	1.7	2
Cochlear length	26	30	43.5
Axial height (h)	3.8	4	4.7
Axial pitch (h/t)	2.5	2.3	2.3

Table 2. Periotic and inner ear measurements of fossil squalodelphinids (in mm; e = estimated); [1] as externally measured by Kellogg (1957) for USNM 21039, and internally measured by Churchill et al. (2016) for USNM 182942.

	NMBE 5036437	*Aulophyseter morricei*[1]
Periotic		
Greatest length of periotic	37.3	39
Width of the periotic	25.7	26
Length of pars cochlearis	21.6	—
Height of pars cochlearis	21.3	19
Width of the pars cochlearis	12	—
Length of anterior process	20	20.1
Inner ear endocast		
Cochlear turns (t)	1.7	1.7
Cochlear length	43	32.1
Axial height (h)	7.5	5.7
Axial pitch (h/t)	4.3	3.2

Table 3. Periotic and inner ear measurements of fossil physeterid NMBE 5036437, and *Aulophyseter morricei* (in mm; e = estimated); [1]average of up to 9 periotics, as externally measured in Kellogg (1927b, p.20) and internally (bony labyrinth) by Churchill et al. (2016, TableS2) for SDSNH 55015.