

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)

1

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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

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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.

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12 ABSTRACT

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23 INTRODUCTION

24 The Swiss molasse (Fig 1) is a textbook example of a foreland basin (Sissingh, 1998) and includes
25 two marine transgression-regression cycles, spanning from the Rupelian to the Serravalian (Labhart,
26 1985; Swiss Committee on Stratigraphy, 2020). Among the vertebrate fossils of the molasse, remains of
27 cetaceans (whales and dolphins) are known. Climatic changes and major geographic rearrangements in
28 the Tethys and Paratethys (including the closure of the Tethys Seaway) may have played a significant
29 role in the cetacean composition at regional and global scales (Steeman et al., 2009; Bianucci and Landini,
30 2002). Cetacean fossils in Swiss localities belong to sediments of the second transgression event, dated
31 21—17 million years ago (Ma). The Upper Marine Molasse or ‘Obere Meeresmolasse’ (hereafter referred
32 to as OMM) is an informal lithostratigraphic group composed of two formations; the underlying Lucerne
33 Formation, and the St. Gallen Formation (Jost et al., 2016; Swiss Committee on Stratigraphy, 2020).

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

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

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

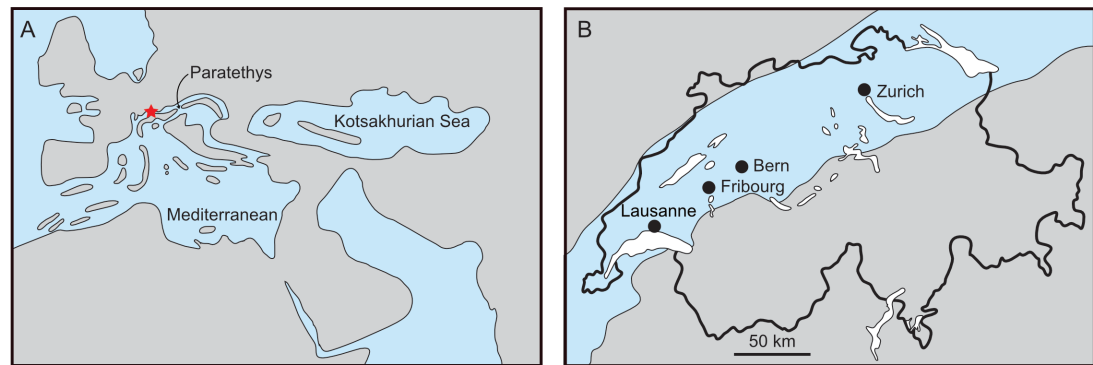


Figure 1. Reconstruction of the Paratethys during the Burdigalian. A) Western Europe with Switzerland marked in red, modified from Rögl (1998) and Berger et al. (2005); B) maximal flooding of the Paratethys over the Swiss Plateau at ca. 18–17.5 Ma, during the deposition of the St. Gallen Fm., based on 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 (μ ct) data of seven periotics were obtained at the University of Zurich using a Nikon XT H 255 ST μ ct 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 described 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 slightly 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 malleolar 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).

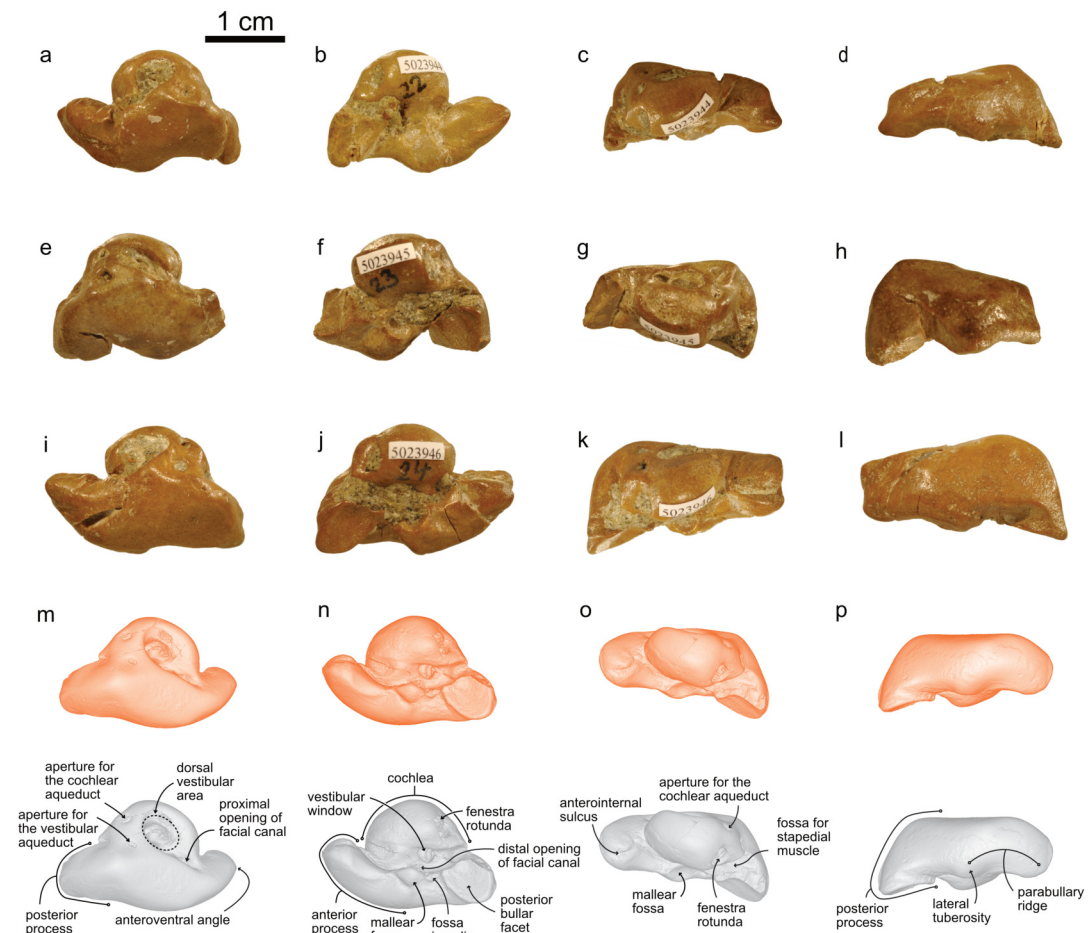


Figure 2. Periotics of Kentriodontidae indet. a–d: NMBE 5023944; e–h: NMBE 5023945; i–l: NMBE 5023946; and m–p: NMBE 5036436 featuring the 3D models (available for download from the MorphoMuseum repository). The lower row illustrates anatomical landmarks of the periotic as seen in NMBE 5036436. Views: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

110 **Platanistoidea** Simpson, 1945

111 **Squalodelphinidae** Dal Piaz, 1917

112 **Squalodelphinidae indet.**

113 (Figs. 2 M—T)

114 **Description and remarks**

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

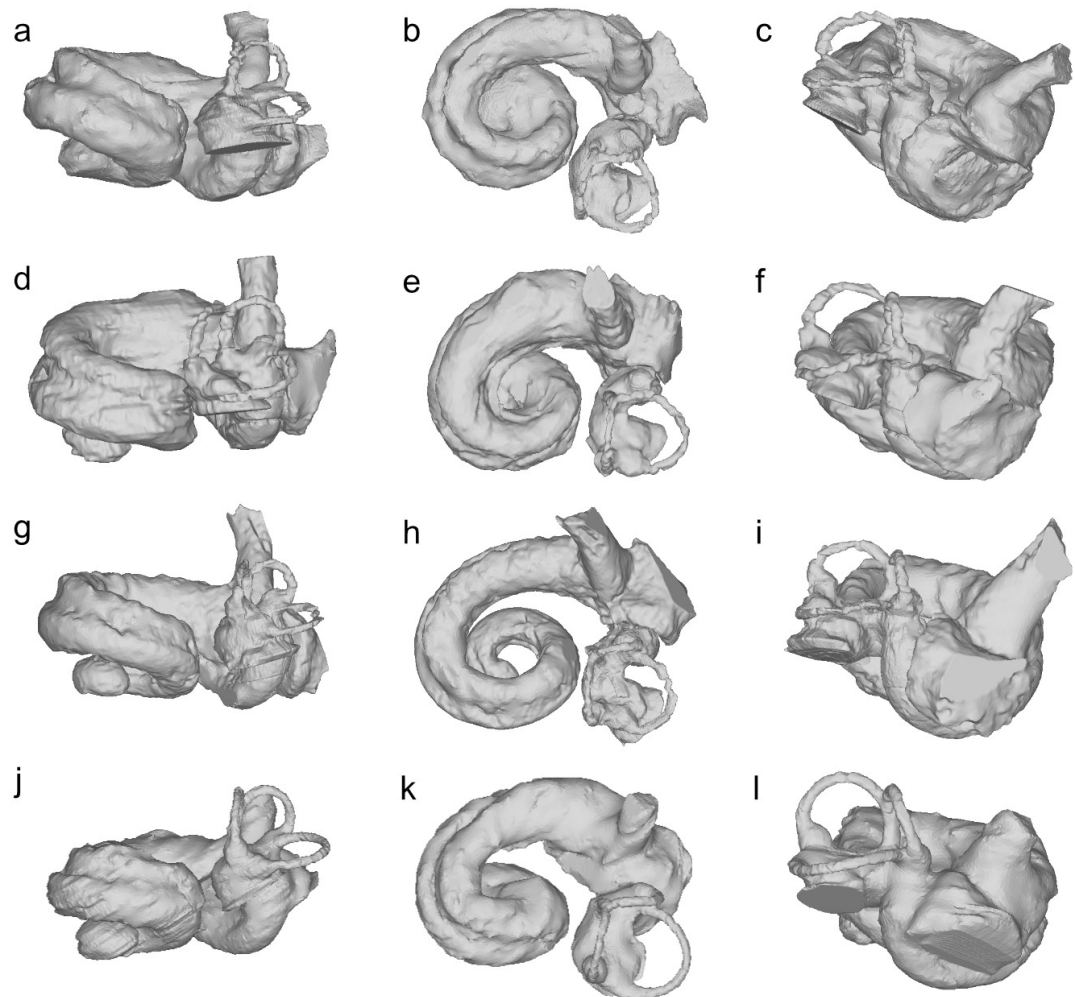


Figure 3. Bony labyrinths of Kentriodontidae indet. a–c: NMBE 5023944 (reflected horizontally); d–f: NMBE 5023945; g–i: NMBE 5023946 (reflected horizontally); j–l: NMBE 5036436. Views: anterior: a, d, g, j; dorsal: b, e, h, k; lateral: c, f, i, l.

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.

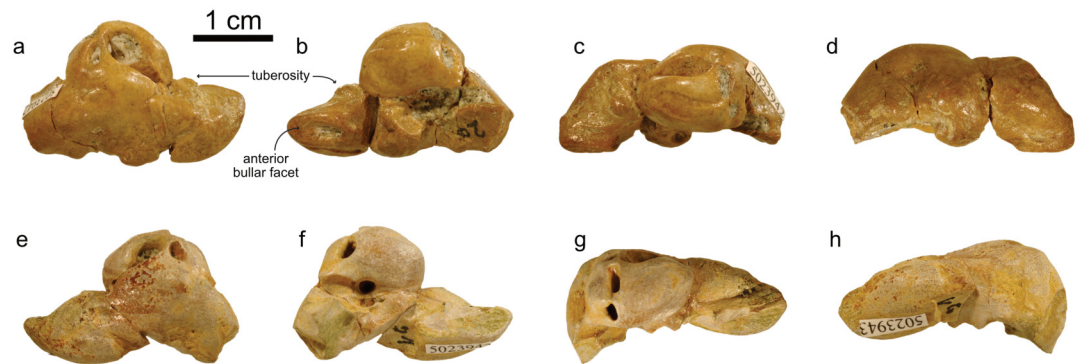


Figure 4. Periotics of *Squalodelphinidae* indet. a–d: NMBE 5023942; e–h: NMBE 5023943 (reflected horizontally) [link to be provided]. Views: anterior: a, e; ventral: b, f; medial: c, g; lateral: d, h.

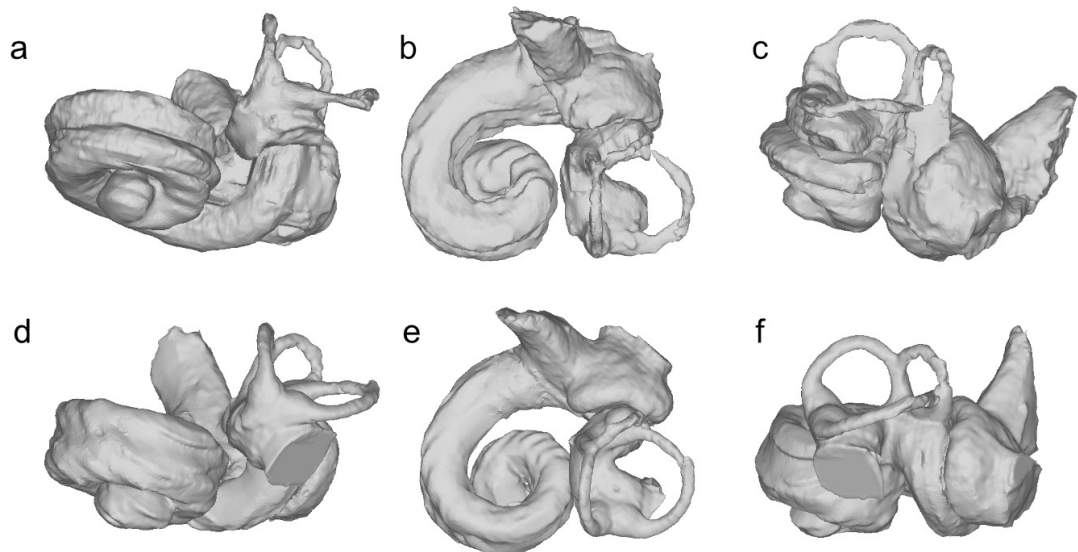


Figure 5. Bony labyrinths of *Squalodelphinidae* indet. a–c: NMBE 5023942 (reflected horizontally); d–f: NMBE 5023943 (reflected horizontally). Views: anterior: a, d; dorsal: b, e; lateral: c, f.

135 **Physeteroidea** Gray, 1821

136 **Physteridae** Gray, 1821

137 **Physeteridae** indet.

138 (Figs. 2 U—X)

139 **Description and remarks**

140 NMBE 5036437 (left periotic) was found in Staffelfach-Böl (St. Gallen Formation). The periotic is
 141 comparatively large and robust (Fig 6). Of the four characters relevant to the periotic mentioned in the
 142 phylogenetic analysis of Lambert et al. (2016), NMBE 5036437 shares with other physeteroids the very
 143 small anterior bullar facet and the enlarged accessory ossicle (judged by the size of the fovea epitubaria).
 144 The accessory ossicle is fused to the periotic in some physeteroids (e.g., the Gross Pampau physeteroid in
 145 Montañez Rivera and Hampe, 2020), but not in NMBE 5036437 (accessory ossicle missing). The posterior
 146 part of the posterior process of NMBE 5036437 is directed posteroventrally as in other physeterids and

147 unlike in kogiids. The high and small dorsal crest (lateral to the internal acoustic meatus) of NMBE
 148 5036437 is a feature seen in other physeterids such as *Aulophyseter*, *Orycterocetus* and *Physeter*. NMBE
 149 5036437 falls in the size range of both *Aulophyseter* and *Orycterocetus*, overall shape and proportions
 150 of the cochlea and the anterior and posterior processes resemble *Aulophyseter morricei* Kellogg 1927b,
 151 but some features are also comparable to *Orycterocetus crocodilinus* Kellogg 1965 and deserve further
 152 comparisons, which were done using photos of the holotypes of *Aulophyseter morricei* and *Orycterocetus*
 153 *crocodilinus*, hereafter referred to by their generic names: In dorsal view, the cochlea of NMBE 5036437
 154 is larger than that of *Aulophyseter* and *Orycterocetus*, but closer in proportions to *Aulophyseter*. The
 155 elongated shape of the internal acoustic meatus resembles *Orycterocetus*. The aperture for the cochlear
 156 aqueduct is larger than the aperture of the vestibular aqueduct as in *Orycterocetus*. The anterior tip of
 157 the anterior process points anteriorly as in *Orycterocetus*. In ventral view, the fenestra rotunda has a
 158 “kidney-shaped” outline, which is distinct from both *Aulophyseter* and *Orycterocetus*. The anterior process
 159 is square-shaped and facing ventrally as in *Aulophyseter*. The posterior process is more slender than in
 160 both *Aulophyseter* and *Orycterocetus*, and the tip of the process is pointing slightly more ventrolaterally.
 161 The posterior bullar facet is smooth, unlike in both *Aulophyseter* and *Orycterocetus*. In medial view, the
 162 anterior process is more robust (higher), and the dorsal crest is less pronounced than in both *Aulophyseter*
 163 and *Orycterocetus*. The dorsal profile of the posterior process is more similar to that of *Orycterocetus*.
 164 Although the external dimensions of the periotic NMBE 5036437 are very similar to those of
 165 *Aulophyseter morricei*, there are strong differences in the cochlear length and axial height, also reflected
 166 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.

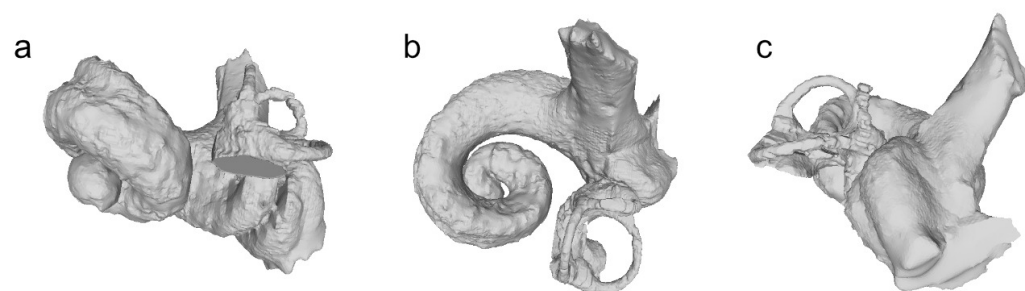


Figure 7. Bony labyrinth of Physeteridae indet. NMBE 5036437. Views: anterior: a; dorsal: b; lateral: c.

DISCUSSION

167 At a larger scale, the connection of the Paratethys with the Indian Ocean and the Mediterranean during
 168 the Aquitanian favoured the distribution of warm-water faunas; these conditions prevailed until the late
 169 Burdigalian, when the seaway between the Mediterranean and the Indian Ocean closed, the eastern
 170 Paratethys 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 Staffebach-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 Staffebach-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 the 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 physeterid 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 assignments 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 assignments 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>

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	NMBE 5023944	NMBE 5023945	NMBE 5023946	NMBE 5036436	<i>Kentriodon pernix</i> ¹
<i>Periotic</i>					
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
<i>Inner ear endocast</i>					
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	<i>Phocageneus</i> ¹
<i>Periotic</i>			
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
<i>Inner ear endocast</i>			
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	<i>Aulophyseter morricei</i> ¹
<i>Periotic</i>		
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
<i>Inner ear endocast</i>		
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.