New evidence for the co-occurrence of two genera of Paleoparadoxiidae (Mammalia, Desmostylia) from the Middle Miocene of Japan: insights into taxonomic status and paleodiversity in Desmostylia

Yuma Asai[1], Tatsuro Ando[2], Hiroshi Sawamura[2], and Shoji Hayashi[1,3]

[1] Faculty of Biosphere-Geosphere Science, Okayama University of Science, Okayama, Japan

[2] Ashoro Museum of Paleontology, Hokkaido, Japan

[3] Division of Materials and Manufacturing Science, Graduate School of Engineering, Osaka University, Osaka, Japan

Corresponding Author:

Yuma Asai[1]

Kita-ku Ridaicho 1-1, Okayama, 700-0005, Japan

Email address: yuma.asai.54@gmail.com

ABSTRACT

Desmostylia, an extinct order of marine mammals, includes two major families: Paleoparadoxiidae and Desmostylidae. Within Paleoparadoxiidae, three genera — *Archaeoparadoxia*, *Paleoparadoxia*, and *Neoparadoxia* — have been identified, with *Paleoparadoxia* the only genus found on both coasts of North Pacific Rim. In Akan, Hokkaido, Japan, one of the largest *Paleoparadoxia* fossil assemblage in the world has been discovered from the Middle Miocene Tonokita Formation. Previous studies suggested the presence of two congeneric species of *Paleoparadoxia*, while recent taxonomical revisions raise the possibility that two genera, *Paleoparadoxia* and *Neoparadoxia*, were present in Akan. Here, we describe three paleoparadoxiids specimens from Akan, consisting of two partial crania and a mandible. Based on the morphological comparisons and phylogenetic analysis, we identified these specimens as *Paleoparadoxia* sp. and *Neoparadoxia* sp.. This represents the first record of two genera of Paleoparadoxiidae in the same locality and horizon, with the potential to provide valuable insights into cladogenesis and morphological diversification within this family. In addition, the Akan specimens exhibit mosaic characteristics of *Paleoparadoxia* and *Neoparadoxia*, suggesting that a reassessment of their morphological features for the taxonomic identification and phylogenetic analysis are required. To better understand species-level diversity patterns in Desmostylia, we conducted stage-binned analysis and richness curve analysis. Our analysis revealed three significant points in their diversification history: (1) Desmostylidae reached peak diversity at the

Deleted: is

Deleted: consists

Oligocene-Miocene boundary, coinciding with a glacial event; (2) Paleoparadoxiidae, achieved peak diversity during the Middle Miocene global warming event; (3) Both families declined their diversity and gone out during the Middle to Late Miocene global cooling event. These finding indicate that desmostylian diversity could have been closely linked to climatic events, with the differing peak diversities of Paleoparadoxiidae and Desmostylidae reflecting their respective preferences for warmer and cooler climates. Our analysis provides a valuable baseline for understanding the diversity and evolutionary history of Desmostylia.

INTRODUCTION

Desmostylia is an extinct order of quadrupedal marine mammals from Oligocene and the Miocene deposits of the northern Pacific Rim (*e.g., Domning, Ray & McKenna, 1986*; *Inuzuka, Domning & Ray, 1994*). This group is divided into two major clades, Desmostylidae and Paleoparadoxiidae (*Osborn, 1905*; *Reinhart*, 1959; *Matsui & Tsuihiji, 2019*). Paleoparadoxiidae forms a monophyletic group with three genera and four species: *Archaeoparadoxia weltoni*, *Paleoparadoxia tabatai*, *Neoparadoxia repenningi* and *Neoparadoxia cecilialina*. These species lived from the Late Oligocene to the Late Miocene and were primarily discovered in the United States (*Barnes, 2013*). Among them, only *Paleoparadoxia* is known from both the Japan and North American coasts, with over 30 fossil localities reported in Japan (*Inuzuka, 2005*; *Matsui & Kawabe, 2015*).

In Akan, Hokkaido, Japan, one of the largest *Paleoparadoxia* fossil assemblage in the world has been found from the Middle Miocene Tonokita Formation (*Kimura et al., 1988*). Previous studies suggested the presence of both a large and a small *Paleoparadoxia* species in Akan (*Akan Vertebrate Fossil Assemblage Research Group, 2000 and 2002*; *Inuzuka, 2005*; Fig. 1A). The Akan is the only site where two *Paleoparadoxia* are suggested to co-occurrence in the same stratigraphic horizon, potentially providing a key fossil record for understanding cladogenesis within this group. However, recent studies reidentified the large *Paleoparadoxia* species as *Neoparadoxia*, a newly established genus (*Barnes, 2013*). While this study did not mention the Akan specimens, the most recent taxonomic hypotheses raise the possibility that both *Paleoparadoxia* and *Neoparadoxia* may have been present in Akan (*Matsui & Tsuihiji, 2019*; Fig. 1B).

Repeated taxonomic revisions have hindered comprehensive analyses of desmostylians diversity. Some studies suggest that the body size and morphological diversity of Paleoparadoxiidae had increased from the Middle to Late Miocene (*Inuzuka, 2005*; *Pyenson & Vermeij, 2016*; *Matsui, Valenzuela-Toro & Pyenson, 2022*). However, it remains debated whether these changes represent cladogenesis or intraspecific variation. Additionally, research on the diversification and evolutionary drivers of Desmostylia is limited, with *Berta & Lanzetti (2020)* providing the only comprehensive study to date. The Akan specimens offer significant potential to enhance our understanding of their evolutionary history because they were discovered during the Middle Miocene, when evolutionary changes in Paleoparadoxiidae began.

Here, we describe three paleoparadoxiids specimens from Akan (AMP AK960241, AMP AK970253 and AMP AK000247). Our study represents the first record of the co-occurrence of *Neoparadoxia* and *Paleoparadoxia*, shedding new light on the taxonomic status of Paleoparadoxiidae. In addition, we conducted two types of paleodiversity analyses to clarify the diversification patterns in Desmostylia. Comparing paleodiversity patterns is widely recognized as a valuable approach for examining evolutionary drivers (e.g., *Ando & Fordyce, 2014*; *Boessenecker & Churchill, 2018*; *Berta & Lanzetti, 2020*). In this study, we apply this approach to analyze the diversification dynamics of Desmostylia, assess their potential drivers, and discuss possible biases that should be taken into consideration in future studies.

MATERIAL AND METHODS

Geological setting

The Akan specimens were found on the bank of Chichappupon river in Akan, Kushiro City, Hokkaido, Japan (Fig. 2; 43°11'42''N, 144°05'42''E). The Middle Miocene Tonokita Formation crop out in this region. The Tonokita Formation comprise conglomerate to coarse sandstone containing diatoms, pollen fossil, molluscan shells and marine vertebrates. The marine mammal fossil assemblage was found in pebbly sandstone in the Tonokita Formation, which occur in channel deposits sometimes incised into the under layer. These fossils are mostly fragmented, and the molluscan fossils are disarticulated, suggesting secondarily deposition. The marine mammals include Desmostylia (*Desmostylus* sp. and *Paleoparadoxia* sp.), Pinnipedia and Odontoceti (*Okazaki et al., 1972*; *Kimura et al., 1998*; *Akan vertebrate fossil assemblage research group, 2000 and 2002*). The depositional environment of the Tonokita Formation is interpreted as upper shelf or lower-shoreface (*Urabe & Hoyanagi, 2004*). The paleoclimate was estimated based on marine mollusks and pollen fossil. The molluscan fauna (Atsunai Fauna; e.g. *Glycymeris idensis*, *Swiftopecten swiftii*, *Chlamys cosibensis*, *Masudapecten* sp., *Felaniella usta*, *Serripes groenlandicus*, *Mercenaria yiizukai*, *Spisula onnechiuria*, *Crepidula jimboana*, *Nucella tokudai*) suggests a cool temperate climate (*Suzuki, Kimura & Tanaka, 1999*; S*uzuki, 2000*). Similarly, pollen fossils indicate a temperate climate, characterized by a mixed forest of Taxodiaceae, *Alnus* and *Betula* (*Igarashi, Yahata & Kimura, 2000*; *Yahata, 2000*). Diatom fossils from the Tonokita Formation indicate an age range from 15.9 Ma to 14.9 Ma, corresponding to the *Denticulopsos lauta* zone (*Urabe, Akiha & Hoyanagi, 2003*).

Materials

The Akan specimens were discovered during five excavation surveys conducted between 1996 and 2000. Although the remains are isolated, they include various parts of the body, such as cranial and limb bones, from individuals ranging from juveniles to adults (*Akan vertebrate fossil assemblage research group, 2000 and 2002*). In this study, we focused on three paleoparadoxiids specimens from the Akan, consists of two partial crania and a mandible (AMP AK960241, AMP AK970253, AMP AK000247). AMP AK960241 and AMP AK970253 were excavated in 1996 and 1997, respectively. These specimens were previously identified as *Paleoparadoxia* sp. In contrast, AMP AK000247, discovered in 2000, was assigned to *P. tabatai* (*Akan vertebrate fossil assemblage research group, 2000 and 2002*). All three specimens were collected from the same site and stratigraphic horizon. These

Deleted: In

specimens are currently housed at the Ashoro Museum of Paleontology (AMP).

Phylogenetic analysis

The phylogenetic position of the Akan specimens described here was analyzed based on the data matrix of *Matsui & Tsuihiji (2019)*, adding the three Akan specimens and four new characters. These newly added characters are as follows: character 109, parietal inclined to cranial (0), slightly inclined to cranial (1), not inclined (2); character 110, paraoccipital process of ventral side: inclined medially (0), not inclined or expand laterally (1), not elongate (2); character 111, a few small foramina and sulci in supraorbital process: present (0), only foramina present (1), absent (2); character 112, mandibular fossa or mandibular condyle): long axis is oriented medio-laterally (0),oriented anterolaterally (1). All 112 characters were given equal weight in the analysis. The dataset included 19 operational taxonomic units (OTUs). Outgroups were selected to reflect the three major phylogenetic hypotheses regarding the affinities of Desmostylia, following *Matsui & Tsuihiji (2019)*: the Perissodactylamorpha hypothesis (*Cooper et al., 2014*; *Rose et al., 2014*; *Rose et al., 2020*), the Afrotheria hypothesis (*Domning, Ray & McKenna, 1986*) and the Paenugulatomorpha hypothesis (*Gheerbrant, Filippo & Schmitt A, 2016*). The outgroups used were *Anthracobune* spp. (a primitive perissodactyl, coding based on *Cooper et al. (2014)*), *Pezosiren portelli* (a primitive sirenian, with coding based on *Andrews (1904 and 1906)*), and *Moeritherium* spp. (a primitive proboscidean, with coding based on *Holroyd et al. (1996),* and *Delmer et al. (2006)*). The ingroup taxa include all 13 known species of Desmostylia, as well as the three desmostylids specimens from Akan (AMP AK960241; AMP AK970253; AMP AK000246).

Phylogenetic analysis was performed using PAUP Version 4.0a10 for Windows (*Swofford, 2002*) with a heuristic search option, optimized by the accelerated transformation criterion (ACCTRAN) using the tree-bisection-reconnection (TBR) branch swapping and a simple addition sequence. Bootstrap analysis was conducted after a full heuristic search with 10,000 replications. To incorporate time constrains into the phylogenetic tree, we applied the geoscalePhylo function in the paleotree package (*Bapst, 2012*) for the R version 4.4.1 (*R Core Team, 2024*).

Estimation of Desmostylian diversity

In this study, we conducted two analyses—Stage-binned analysis and Richness curve analysis—to elucidate the diversity changes within two major desmostylian families, Paleoparadoxiidae and Desmostylidae. These analyses are based on the desmostylian fossil occurrence (Supplemental information 1) and our phylogenetic analysis, which suggests that *Paleoparadoxia* sp. and *Neoparadoxia* sp. in Akan represent distinct species from those currently recognized.

For the stage-binned analysis, we followed the methods of *Boessenecker & Churchill (2018)* and *Berta & Lanzetti (2020)*. This analysis examined over 200 desmostylian fossil localities and their stratigraphic ages, determined through a comprehensive literature review of chronostratigraphic data (Supplemental information 1). The number of desmostylian species within each chronostratigraphic stage was counted under the assumption that species persisted continuously throughout their confirmed temporal ranges. Diversity plots were obtained by counting the valid species for each time bin.

For the time-constrained richness curve analysis, we employed methods based on *Magallanes et al. (2018)* to illustrate the minimum and maximum counts of known and inferred lineages (richness) of Desmostylidae and Paleoparadoxiidae throughout their evolutionary history. This approach, accounted for chronostratigraphic uncertainty and ghost lineages. For each taxon, we estimated a minimum and maximum possible age of occurrence, building upon estimates presented in recent studies (Supplemental information 1). Using these age ranges, we constructed a time-constrained 50% majority-rule consensus tree to calculate the minimum and maximum lineages counts at 0.1 Ma interval (35.0 Ma to 5.0 Ma, 300 time slices). The maximum lineage count was calculated based on the assumption that each taxon existed from the earliest to the latest possible age of the rock units. For three taxa known from multiple formations (*P. tabatai, Cornwallius sookensis, Desmostylus hesperus*), the combined maximum age ranges of these formations were used to determine the broadest possible temporal span. The minimum lineage count was estimated by assuming originations and extinctions within the possible range that resulted in the minimized the number of lineages at any given time. In most cases, this involved counting ghost lineages, as a taxa within its estimated range could be presumed either extinct or not yet originated at any given time. Maximum and minimum age estimates for each 0.1 Ma bin among the trees was included in the curves.

SYSTEMATIC PALEONTOLOGY

DESMOSTYLIA *Reinhart, 1953*

DESMOSTYLOIDEA *Osborn 1905 (sensu Matsui & Tsuihiji, 2019)*

PALEOPARADIXIIDAE *Reinhart,* 1959 (*sensu Matsui & Tsuihiji, 2019*)

NEOPARADOXIA *Barnes, 2013*

Neoparadoxia **sp.**

(Figs. 3-6, Table 1)

Emended diagnosis of genus: *Neoparadoxia* can be distinguished from other desmostylians by its paraoccipital process, which is massive, elongated, thickened, and extends laterally. It differs from other paleoparadoxiids in possessing following characters: extremely large body size; a proportionally large and deeply concave temporal fossa; a large mandibular fossa.

Materials: AMP AK960241 (cranium, Figs. 3-6, Table 1).

Locality: The riverbank where the Chichappupon river in the Akan, Kushiro city, Hokkaido, Japan (Fig. 2; 43°11'42''N, 144°05'42''E).

Age and horizon: Tonokita Formation, Middle Miocene, Langhian (15.9-14.9Ma; Figs. 2B,C)

Description

AMP AK960241 (posterior part of the cranium): AMP AK960241 preserves supraoccipital, exoccipital, basioccipital, basisphenoid, parietal and squamosal (Figs. 3-6). Although the Parietal and zygomatic arch are heavily damaged, the exoccipital is perfectly preserved. This specimen, consisting of three fragments, is extremely large—significantly larger than *P. tabatai* and comparable in size to *N. cecilialina* (Table 1). This suggests that it is among of the largest paleoparadoxiid cranium ever discovered from Japan.

The occipital region is nearly complete on the right side (Figs. 3,5,6). The external occipital crest is distinct and the connection to the nuchal crest differs from the condition in *Behemotops katsuiei* (*Inuzuka, 2000*), and the external occipital protuberance is slightly developed. The occipital condyle is preserved only at its base. The paraoccipital process is massive, medially inclined, expand laterally and the tip is thickened. The ventral condylar fossa is well-developed. The hypoglossal foramen is partially damaged and can be observed at the boundary between the exoccipital and the basioccipital, at the base of the paraoccipital process. The stylomastoid foramen opens ventrally on the lateral surface of the exoccipital, posterior to the mandibular fossa. The pharyngeal and the muscular tubercles on the basioccipital are prominent.

The basisphenoid is nearly completed (Fig. 4). The lacerate foramen is widely open between the squamosal and basisphenoid, and the oval foramen is also situated between these two bones.

The parietal, preserved in its posterior portion (Figs. 3,5,6), is slightly inclined cranially. The nuchal crest is pronounced and nearly V-shaped, while sagittal crest strongly developed—unlike *Desmostylus* and *Ashoroa laticosta* (*Inuzuka, 1988 and 2000*). The parasagittal crests are extremely narrow and positioned close to each other. The temporal fossa is notably large and the basisphenoid-occipital suture is completely closed.

The squamosal is partially preserved (Figs. 3-6). The squamosal foramina are present the base of zygomatic arch and near the nuchal crest, with the posterior one being the largest. There number of foramen (three to four) is consistent with *P. tabatai* and *N. cecilialina*. The foramina positions are asymmetrical as in other desmostylians. A passage connecting the anterior external auditory meatus to the skull roof is present, unlike in Desmostylidae (*Clark, 1991*). The mandibular fossa is missing anteriorly, but the preserved portion suggests that it was extremely large. The long axis of the mandibular fossa is oriented anterolaterally, a feature shared with other paleoparadoxiids, *Behemotops* and *Seuku emlongi* (*Domning, Ray & McKenna, 1986*; *Inuzuka, 2000 and 2005*; *Barnes, 2013*; *Beatty & Cockburn, 2015*).

The tympanic region is exposed due to damage to the zygomatic arch and lateral squamosal (Figs. 3,5). The external auditory meatus opens posteriorly on lateral surface of the zygomatic arch and is situated posterodorsally to the mandibular fossa. The epitympanic sinus lies slightly dorsally adjacent to the external auditory meatus. This positional relationship is similar to the condition in *D. hesperus* and *C. sookensis*, suggesting that it may be a shared morphological character within Desmostylia (*Clark, 1991*; *Uno & Kimura, 2004*; *Beatty, 2009*). The tympanic bone, which connects to external auditory meatus, forms a rounded equilateral triangle and measuring approximately 2.5cm per side. The cochlea is exposed medially and features a three-tiered spiral structure measuring approximately 14.4 mm dorsoventrally, filled with sediments. The postzygomatic foramen, located adjacent to the epitymapanic sinus, is wide and shallow, consistent with other desmostylians (*Ijiri & Kamei, 1961*; *Inuzuka, 1988*; *Beatty, 2009*).

PALEOPARADIXIIDAE *Reinhart,* 1959 (*sensu Matsui & Tsuihiji, 2019*)
PALEOPARADOXIA *Reinhart, 1959*

***Paleoparadoxia* sp.**
(Figs. 7-12, Tables 2,3)

Emended diagnosis of genus: *Paleoparadoxia* differs from all other desmostylians in possessing the following characters: the zygomatic arch of squamosal inclined to caudally and not broadened dorsoventrally; the coronoid crest of the dentary curved anteriorly. It differs from *Neoparadoxia* in possessing following characters: the supraorbital process is slightly expanded laterally; the dorsal surface of cranium between supraorbital processes is not depressed; the orbit is positioned slightly dorsally; the mandibular symphysis is slightly rotated anteroventrally.

Materials: AMP AK970253 (cranium, Figs. 7-9, Table 2), and AMP AK000247 (mandible, Figs. 10-12, Table 3).

Locality: The riverbank where the Chichappupon river in the Akan, Kushiro city, Hokkaido, Japan (Fig. 2; 43°11'42''N, 144°05'42''E).

Age and horizon: Tonokita Formation, Middle Miocene, Langhian (15.9-14.9Ma; Figs. 2B,C)

Description

AMP AK970253 (posterior part of the cranium): AMP AK970253 preserves the frontal, basisphenoid, parietal, squamosal, and vomer (Figs. 7-9). Its size is comparable to that of the corresponding part in *P. tabatai* (Table 2). The lambdoid suture is detached while the squamosal suture is fused, as seen in adult *P. tabatai*, thus we identified this specimen as a relatively mature one.

The frontal is heavily damaged in its middle section (Figs. 7,9). The orbits projected slightly from the frontal, and the orbital margins are thickened, porous, and rounded. The supraorbital process is weakly developed laterally and dorsally, similar to *P. tabatai*, but less prominent than in *A. weltoni* and *N. cecilialina* (*Clark, 1991*; *Barnes, 2013*). Nutrient foramina and radiating sulci are supraorbital process. The space between the supraorbital processes is heavily damaged but remains flat.

The basisphenoid is preserved (Fig. 8). The left tympanic bulla is partially-intact anteriorly but missing posterior and medial portion. The shape of the tympanic bulla is elliptical, with its long axis is oriented posterior-laterally. The oval foramen is visible posteriorly on both sides of the sphenoid bone. The pterygoid process is preserved only at its base.

The vomer is heavily damaged, but its suture with the basisphenoid is fully fused.

The parietal (Figs. 7,9) is slightly inclined cranially, with a weakly developed sagittal crest and widely spaced parasagittal crests. The nuchal crest is pronounced and nearly V-shape—unlike *Desmostylus* and *A. laticosta* (*Inuzuka, 1988 and 2000*).

The squamosal is preserved (Figs. 7-9). The squamosal foramina are present at the base of zygomatic arch and near the nuchal crest, with the posterior foramen being the largest. The number of foramina (three to four) is consistent with *P. tabatai* and *N. cecilialina*. The positions of these foramen are asymmetrical, a common character among desmostylians (*Ijiri & Kamei, 1966*; *Barnes, 2013*; *Inuzuka, 1988*). A passage connecting the anterior external auditory meatus to the skull roof is observed, unlike in Desmostylidae (*Clark, 1991*). The mandibular fossa is flat and faced outward. The long axis of the mandibular fossa is oriented anterolaterally, a character shared with other paleoparadoxiids, *Behemotops* and *S. emlongi* (*Domning, Ray & McKenna, 1986*; *Inuzuka, 2000 and 2005*; *Barnes, 2013*; *Beatty & Cockburn, 2015*). The zygomatic arch of squamosal is caudally inclined and relatively thin. The posterior end of the jugal is retracted and does not reach the mandibular fossa as seen in *P. tabatai* but not in *A. weltoni* (*Clark, 1991*). The postzygomatic foramen is wide and shallow, consistent with other desmostylians (*Ijiri and Kamei, 1961*; *Inuzuka, 1988*; *Beatty, 2009*). A funnel-shaped external auditory meatus opens posteriorly behind the zygomatic arch and the mandibular fossa.

AMP AK000247 (mandible): AMP AK000247 is mostly preserved, with the exception of anterior portion of the mandible (Figs. 10-12). It is slightly smaller in size compared to the *P. tabatai* and *A. weltoni* (Table 3). The mandibular body is straight in medial and lateral view, with the upper margin curving slightly posteriorly —unlike the sigmoid shape observed in *Desmostylus* (*Inuzuka, 2000 and 2005*). The mental foramina are present on the lateral side of the mandibular body while the interalveolar margin of the mandible is nearly straight, featuring a large depression on the lingual side. The mandibular symphysis is rotated anteroventrally, becoming approximately horizontal and aligning incisors and canines anteriorly, as seen in Paleoparadoxiidae (*Barnes, 2013*). The masseteric fossa is wide and shallow, while the mylohyopid groove is distinct. The mandibular ramus and the mandibular body form a nearly right angle. The mandibular foramen is oval-shaped, measuring 11.9 mm in short diameter and 23.1 mm in long diameter. The mandibular notch is shallow and the mandibular angle is rounded, bending nearly perpendicularly. The long axis of the mandibular condyle is oriented anterolaterally, as observed in Paleoparadoxiidae, *Behemotops* and *S. emlongi* (*Domning, Ray & McKenna, 1986*; *Inuzuka, 2000 and 2005*; *Barnes, 2013*; *Beatty & Cockburn, 2015*). The coronoid crest (anterior margin of coronoid process) curves anteriorly, with a small angle between the anterior and posterior margin of the coronoid process.

The teeth are not preserved but the alveoli for p1, p2, p4, m1, and m2 are preserved. The alveolus of p1 is elongated sagittal direction, with a diastema present between p1 and p2. The p2 and p4 teeth are closely positioned near the distal end of the mandibular symphysis m1 and m2 are slightly compressed laterally, each displaying two distinct roots. m2 is larger in the sagittal direction compared to m1. The absence of the m3 alveolus suggests that this specimen is a large juvenile.

RESULT

Phylogenetic analysis

Our phylogenetic analysis resulted in 136 most parsimonious trees with a tree length 206 after 311,144 rearrangements were attempted. The consistency index (CI) is 0.623, the rescaled consistency index is 0.407, the retention index (RI) is 0.652 and the homoplasy index (HI) is 0.377. Figure 13 shows the 50% majority-rule consensus tree, which indicates the same Desmostylian topology as *Matsui & Tsuihiji (2019)*, except for Paleoparadoxiidae. The Akan specimens are placed as the derived paleoparadoxiids together with *P. tabatai*, *N. repenningi* and *N. cecilialina.* AMP AK960241, *N. repenningi* and *N. cecilialina* form a monophyletic clade. AMP AK970253, AMP AK000247 and *P. tabatai* form a monophyletic clade in which AMP AK970253 is most closely related to *P. tabatai*. This topology of derived paleoparadoxiids is not supported by the bootstrap value.

Identification

The Akan specimens exhibit a mosaic of characters shared with *Paleoparadoxia* and *Neoparadoxia.* AMP AK960241 exhibits a majority of characters that are diagnostic of *Neoparadoxia*: an extremely large body size; the paraoccipital process is massive, thickened and expand laterally; partially large and deeply concave temporal fossa; a large mandibular fossa. In contrast, this specimen shares the following characters with *Paleoparadoxia*: the paraoccipital process extends slightly medially, and the external occipital protuberance is moderately developed. The 50% majority-rule consensus tree shows that AMP AK960241 and *Neoparadoxia* form a monophyletic clade. Based on these results, we identify this specimen as *Neoparadoxia* sp. This is the first record of *Neoparadoxia* from the western Pacific coast. In addition, the morphological features of AMP AK960241 do not entirely correspond to those of the holotype specimens of *N. cecilialina* (LACM150150) and *N. repenningi* (UCMP81302), suggests that it may represent a previously unrecognized species of *Neoparadoxia*. However, their fragmentary condition requires careful assessment prior to species-level identification.

On the other hand, AMP AK970253 and AMP AK000247 exhibits the majority of characters shared with *Paleoparadoxia*: the zygomatic arch inclined cranially and lacks dorsoventral expansion; the supraorbital process is slightly developed; the dorsal surface of cranium between supraorbital processes is not depressed; the orbit is located slightly dorsally; the mandibular fossa is smaller compared to *N. cecilialina*; the coronoid crest of the dentary curved anteriorly; the mandibular symphysis is slightly rotated anteroventrally; the relatively lower position of the mandibular condyle and mandibular foramen; the mandibular body is straight unlike *N. repenningi*; the dorsal side of the mandibular symphysis lacks foramina, distinguishing it from *N. cecilialina.* In contrast, these specimens possess the following characters of *Neoparadoxia*: numerous nutrient foramina with sulci on the dorsal surface of the supraorbital process; the small angle between the anterior and posterior margins of the coronoid process. The 50% majority-rule consensus tree indicates that AMP AK970253, AMP AK000247 and *P. tabatai* form a monophyletic clade. Therefore, we identify these specimens as *Paleoparadoxia* sp. However, as their morphological characters do not fully correspond to those of the holotype of *P. tabatai* (NMS PV-5601), suggesting that they may represent a different species. Given their fragmentary condition, cautious evaluation is necessary before making a species-level identification. These results reveal that two genera of Paleoparadoxiidae coexisted in Akan.

Estimation of desmostylian diversity

The results of the stage-binned analysis are shown in Figs. 14A and 14B. For Paleoparadoxiidae (Fig. 14A), species diversity remained low, with only one or two species (*P. tabatai* and *A. weltoni*) present from the Oligocene Chattian to the Miocene Burdigalian (28.1-16 Ma). However, during the Middle Miocene Langhian (16-13.8 Ma), species diversity increased sharply to five species, coinciding with the appearance of the Akan paleoparadoxiids and *Neoparadoxia*. Subsequently, diversity declined from the Serravallian to the Tortonian (13.8-7.2 Ma), culminating in the complete extinction of Paleoparadoxiidae by the Late Miocene Messinian. In contrast, for Desmostylidae (Fig 14B), species diversity exhibited minimal fluctuation, resulting in a more stable pattern. From the Oligocene Rupelian to the Chattian (33.9–23 Ma), two basal desmostylids species (*A. laticosta* and *C. sookensis*) were present. During the Early Miocene Aquitanian (23-20.4 Ma), *A. laticosta* and *C. sookensis* went extinct, and the emergence of more derived desmsotlyids (*Ounalashkastylus tomidai* and *D. hesperus*) increased the species count to three, marking a peak in diversity. From the Burdigalian to the Serravallian (20.4-11.6 Ma), despite the extinction of *O. tomidai*, the appearance of *D. japonicus* and *D. coalingensis* maintained the number of species at two. By the Late Miocene Tortonian (11.6-7.2 Ma), only a single species of *D. hesperus* remained, and like Paleoparadoxiidae, Desmostylidae became completely extinct by the Messinian (7.2-5.3 Ma).

The results of the richness curve analysis are shown in Figs. 14C and 14D. For Paleoparadoxiidae (Fig. 14C), the maximum and minimum richness curve exhibited similar trends. Both curves gradually increased from the Oligocene Chattian to Aquitanian, with high richness persisting throughout this period (28.1-20.4 Ma). The peak richness was reached during the mid-Burdigalian to Langhian (approximately 18-15 Ma). Since the Langhian, both curves have shown a sharpe decline, with possible extinction suggested by the Late Miocene Tortonian (11.6-7.2 Ma). For Desmostylidae (Fig. 14D), the maximum and minimum richness curves also exhibited similar patterns, particularly from the Late Oligocene to the Miocene. The maximum richness curve indicated a gradual increase in richness during the Oligocene, while the minimum curve showed a decrease in richness from the mid-Rupelian to the Early Chattian in the Late Oligocene (approximately 31-27 Ma). Both curves showed an increase in richness after the mid-Chattian, peaking around the Late Chattian and near the Oligocene-Miocene boundary (approximately 25-23 Ma). While both curves ware relatively stable during the Miocene, a stepwise decline was observed at the Middle to Late Burdigalian (approximately 17 Ma) and at the Serravallian-Tortonian boundary (11.6 Ma). Both curves also indicated the extinction of Desmostylidae by the Tortonian (11.6-7.2 Ma).

DISCUSSION

Taxonomic status within Paleoparadoxiidae

Previous studies suggested that two types of Paleoparadoxiidae were present in Akan (*Akan Vertebrate Fossil Assemblage Research Group, 2000 and 2002; Inuzuka, 2005*). Our results are consistent with previous studies and represent the first record of *Paleoparadoxia* and *Neoparadoxia* occurring at the same locality and stratigraphic horizon. The Middle Miocene was a period of morphological diversification in Paleoparadoxiidae (*Inuzuka, 2005*; *Pyenson & Vermeij, 2016*; *Matsui, Valenzuela-Toro & Pyenson, 2022*), and the morphological analysis of the Akan specimens has the potential to provide valuable insights into the cladogenesis and diversification of this family.

As discussed in the identification section, the Akan specimens exhibit a mosaic of characters shared with both *Paleoparadoxia* and *Neoparadoxia*. In AMP AK960241 (*Neoparadoxia* sp.), two characters resemble those of *P. tabatai*: (1) the paraoccipital process extends slightly medially; (2) the external occipital protuberance is moderately developed (*Barnes, 2013*). Similarly, in AMP AK970253 and AMP AK000247 (*Paleoparadoxia* sp.), exhibit two diagnostic characters of *Neoparadoxia* are present: (1) numerous nutrient foramina with sulci on the dorsal surface of the supraorbital process (*Barnes, 2013*); (2) the small angle between the anterior and posterior margins of the coronoid process (*Inuzuka, 2005*). These findings underscore the need for a comprehensive reexamination of the diagnostic characters of both genera. In addition, Akan specimens do not fully correspond to the morphological characters of the holotype of *P. tabatai* and *Neoparadoxia*, and the topology of derived Paleoparadoxiidae is not supported by the bootstrap value. These results indicate that the Akan specimens are difficult to identify at the species level within the existing taxonomic framework of Paleoparadoxiidae, requiring a reevaluation of their phylogenetic hypothesis and diagnostic characters (*Kohno, 2024*).

Paleodiversity insights of Desmostylia

The stage-binned analysis and the richness curve analysis revealed new insights into the evolutionary history of desmostylian diversification. For Paleoparadoxiidae (Figs. 14A, C), during the Langhian of the Middle Miocene (16-13.8 Ma), the stage-binned analysis shows an increase in the number of species, attributed to the appearance of Akan paleoparadoxiids and *Neoparadoxia*. The richness curve analysis suggests that high richness revel ware level was sustained from the Oligocene Chattian through the Miocene Aquitanian (approximately 28.1-20.4 Ma), and peaked from the Mid-Burdigalian to Langhian (approximately 18-15 Ma). This diversity peak is roughly coinciding with the Middle Miocene Climatic Optimum (MMCO; 16.9-14.7 Ma), a global warming event (e.g., *Zachos, Dickens & Zeebe, 2008*; *Tripati, Roberts & Eagle, 2009*). Several marine mammal lineages diversified during the MMCO, including Cetaceans and Pinnipediamorpha (*Marx & Fordyce, 2015*; *Boessenecker & Churchill, 2018*; *Guo & Kohno, 2023*). Previous studies suggested that *Paleoparadoxia* preferred subtropical to warm-temperate zone (*Chinzei, 1984*; *Itoigawa, 1984*; *Ogasawara, 2000*; *Inuzuka, 2005*), and the rise in sea level associated with global warming may have expanded the shallow water habitats suitable for Paleoparadoxiidae. Therefore, the MMCO

Formatted: Highlight

may have promoted the diversification of Paleoparadoxiidae. Following the MMCO, both analyses indicate a significant decline in species diversity during the mid-Langhian to Serravallian (approximately 14.5-11.6 Ma). This decline coincides with the Middle Miocene Climate Transition (MMCT; -14 Ma), a global cooling event associated with the expansion of the East Antarctic Ice Sheet (EAIS) and accelerated cooling (e.g., *Flower et al., 1994; Hamon et al., 2013; Frigola, Prange & Schulz, 2018)*. This climate shift is considered a contributing factor to extinctions across various taxa (*Lewis et al., 2008*; *Guo & Kohno, 2023*), and may have played a role in the reduced diversity of Paleoparadoxiidae. After the MMCT, the cooling event of the Late Miocene became more severe (e.g., *Herbert et al., 2016*; *Rousselle et al., 2013*: *Wen et al., 2023*), and both analyses suggest that Paleoparadoxiidae may have gone extinct during the Late Miocene Tortonian to Messinian (11.6-5.3 Ma).

Deleted:

For Desmostylidae (Figs. 14B, D), the stage-binned analysis indicates that two basal species, *A. laticosta* and *C. sookensis*, appeared during the Oligocene. Near the Oligocene-Miocene boundary, the emergence of *O. tomidai* and *D. hesperus* led to a peak in species diversity during the Early Miocene Aquitanian (23-20.4 Ma). The richness curve analysis shows a gradual increase in both maximum and minimum richness curves toward the late-Chattian (approximately 26-23 Ma). These results suggest that the diversity of Desmostylidae may have peaked from the Late Oligocene to the Early Miocene. Around the Oligocene-Miocene boundary (approximately 23 Ma), a brief glacial event known as the Oligocene-Miocene Transition (OMT; e.g., *Miller, Wright & Fairbanks, 1991*; *Zachos, Flower & Paul, 1997*; *Greenop et al., 2019*) occurred, coinciding with ocean current changes, including gradual development of the modern Antarctic Circumpolar Current. The OMT had been associated with faunal turnovers (*Marx and Fordyce, 2015*; *Marx, Fitzgerald & Fordyce, 2019*; *Deng et al., 2021*). Previous studies suggest that Desmostylidae preferred cooler environments (*Chinzei, 1984*; *Itoigawa, 1984*; *Ogasawara, 2000*), with some species discovered in cold polar regions (*Ijiri & Kamei, 1961*; *Beatty, 2006*; *Chiba et al., 2016*). Thus, the OMT may have driven an increase in diversity of Desmostylidae. From the Early to Middle Miocene (Burdigalian to Serravallian; 20.4-11.6 Ma), species diversity remained relatively stable in both analyses, showing little impact from the MMCO or MMCT. However, as with Paleoparadoxiidae, their species diversity declined during the Serravallian to the Tortonian (13.8-7.2 Ma) and is suggested to have gone completely extinct by the Messinian.

These results indicate that desmostylian diversity may have been closely linked to climate change. This study identified three major shifts in species diversity: (1) Desmostylidae reached peak diversification at the OMT, coinciding with a glacial event; (2) Paleoparadoxiidae experienced its highest diversity during the MMCO, a global warming event; (3) Both famillies experienced declining diversity and eventual extinction during the Middle to Late Miocene global cooling period. The interaction of desmostylian diversity and these climatic events has not yet been proven to be the direct cause of their rise and fall. Nevertheless, the vicissitudes of desmostylian diversity were obviously influenced by these climatic changes. Interestingly, Desmostylidae and Paleoparadoxiidae exhibited distinct responses to climate change. Desmostylidae diversified during the Oligocene-Miocene boundary event, while

Paleoparadoxiidae diversified during the MMCO. This differences likely reflects ecological distinctions, with Paleoparadoxiidae favoring warmer climates and Desmostylidae colder ones (*Chinzei, 1984*; *Itoigawa, 1984*; *Ogasawara, 2000*; *Inuzuka, 2005*).

However, the reason why Desmostylia exhibited a decline in diversity only during the Middle to Late Miocene cooling event remains uncertain. Previous studies suggested that Desmostylia had successfully adapted to cold environments in other periods (*Chinzei, 1984*; *Matsui & Kawabe, 2015*). One possible explanation is that the Middle to Late Miocene cooling was more severe than previous cooling events (*Herbert et al., 2016*; *Rousselle et al., 2013*: *Wen et al., 2023*), their survival more difficult. Another potential factor is ecological competition with Sirenia for food resources (*Vélez-Juarbe*, *Domning & Pyenson, 2012*; *Pyenson et al., 2014*; *Matsui, Valenzuela-Toro & Pyenson, 2022*). *Berta & Lanzetti (2020)* noted that the appearance of the genus *Hydrodamalis* and other dugongids in the Tortonian (11.6 Ma-) coincides with the decline of desmostylians. While Desmostylia and Sirenia are known to have coexisted in the United States (*Parham, Barron & Vélez-Juarbe, 2022*), the extent of competitive replacement between these groups in the western Pacific remains poorly understood and requires further investigation.

Commented [GP1]: You may want to read https://doi.org/10.1016/j.palaeo.2013.07.013 to further discuss possible reasons for the disappearance pattern of desmostylia. Not saying it is essential for the paper presented here, but could enrich your analysis

These paleodiversity estimates from the fossil record may also be influenced by three factors: (1) The volume of fossiliferous rock (*Crampton et al., 2003*; *Smith & McGowan, 2007)*. Rock volume is strongly correlated with the richness of higher taxa in the Phanerozoic (*Hannisdal & Peters, 2011*). Addressing and correcting this bias is essential for obtaining more accurate estimates of paleodiversity (*Smith & McGowan, 2007*; *Uhen &*

Pyenson, 2007; *McGowan & Smith, 2008*). However, previous studies have suggested that rock volume containing fossils has a limited impact on marine mammal diversity (*Uhen & Pyenson, 2007*; *Marx, 2009*). Since desmostylians are confined to over 200 localities around the North Pacific within a relatively short temporal range, geological biases are likely minimal in these analyses. (2) Taphonomic bias within Desmostylia. Differences in bone microstructure may affect fossil preservation (*Ando & Fordyce, 2014*). *Hayashi et al. (2013)* revealed that *Paleoparadoxia*, *Ashoroa*, and *Behemotops* show increased bone mass, while *Desmostylus* has a spongy inner structure, reflecting secondary aquatic adaptation. Spongy bones may be less likely to be preserved in deposits, which is consistent with the fact that paleoparadoxiids are abundant in Akan while *Desmostylus* are relatively rare. However, in Utanobori, Hokkaido, Japan, *Desmostylus* is the only desmostylian taxon found (*Inuzuka, 1988*; *Uno, Kaneko & Takabatake, 2016*), and *Desmostylus* and paleoparadoxiids rarely co-occur in the same formation (*Matsui, Valenzuela-Toro & Pyenson, 2022*). This suggests that differences in bone microstructure may have less influence on fossil preservation than habitat or ecological factors. While, *Hayashi et al. (2013)* suggest *Paleoparadoxia* inhabited shallow while *Desmostylus* could swim offshore based on bone microanatomical differences, *Matsui et al. (2017)* argued the opposite based on stratigraphic evidence. These conflicting hypotheses make it difficult to assess the ecological impact on paleodiversity estimates. (3) Taxonomic uncertainty of Desmostylia (*Matsui & Pyenson, 2023*; *Kohno, 2024*). Desmostylians have lower species diversity than other marine mammals (*Berta & Lanzetti, 2020*), and in these analyses, the origination or extinction of a single species had a remarkably large impact on the overall results. As previously mentioned, reassessment of the Desmostylian phylogenetic hypothesis is required, and the results derived from phylogenetic topology analyses should be carefully examined and discussed.

However, these analyses using the existing taxonomic framework provides valuable baseline for understanding Desmostylian diversity history. In the future, a taxonomic reassessment of Desmostylia and more comprehensive phylogenetic analysis will be necessary to better elucidate the drivers of their evolutionary patterns.

CONCLUSIONS

We described three paleoparadoxiids specimens from the Middle Miocene Tonokita Formation in Akan, Hokkaido, Japan. Based on the morphological comparisons and phylogenetic analysis, we identified these specimens as *Paleoparadoxia* sp. and *Neoparadoxia* sp. This represents the first record of the co-occurrence of two genera of Paleoparadoxiidae, with the potential to provide valuable insights into cladogenesis and morphological diversification within this family. The Akan specimens exhibit mosaic characteristics of *Paleoparadoxia* and *Neoparadoxia*. This finding indicates that species-level identification is difficult within the current taxonomic framework of Paleoparadoxiidae, highlighting the need for a reassessment of their phylogenetic hypothesis and diagnostic characters. Additionally, our stage-binned analysis and richness curve analysis shed light on the species-level diversity patterns in Desmostylia. These analyses revealed three significant points in their diversification history: (1) Desmostylidae reached peak diversification at the Oligocene-

Miocene boundary, coinciding with a glacial event; (2) Paleoparadoxiidae, achieved peak diversity during the Middle Miocene global warming event; (3) Both families declined their diversity and gone out during the Middle to Late Miocene global cooling event. These finding indicate that desmostylian diversity could have been closely linked to climatic events, with the differing peak diversities of Paleoparadoxiidae and Desmostylidae reflecting their respective preferences for warmer and cooler climates. However, the uncertain taxonomic status of Desmostylia may have influenced diversity estimates. While our analyses provide a valuable baseline for understanding the diversity history of Desmostylia, future efforts should focus on taxonomic reassessment and comprehensive phylogenetic analysis to refine diversity patterns and clarify their evolutionary drivers.

INSTITUTIONAL ABBREVIATIONS

AMP, Ashoro Museum of Paleontology, Hokkaido, Japan; **FMI**, The Folk Museum of Itsukaichi, Tokyo, Japan; **NSM-PV**, Fossil vertebrate collections at the National Museum of Nature and Science, Tsukuba, Japan. **LACM**, Los Angeles County Museum, California, USA; **UCMP**, University of California Museum of Paleontology, California, USA.

ACKNOWLEDGEMENTS

We express our gratitude to Tatsuya Shinmura (AMP) for providing the 3D data of the specimens and granting us access to study them under his care. We are also indebted to the Akan vertebrate fossil investigation team for their dedicated excavation of *Paleoparadoxia* specimens and locality surveys. Special thanks go to the staff of the AMP for their overall support, as well as to the Kushiro City Board of Education, Hokkaido, Japan, for granting access to the specimens.

REFERENCE

Akan vertebrate fossil assemblage research group. 2000. *Research reports of the Akan vertebrate fossil assemblage (1).* Akan: Akan Town Board of Education.

Akan vertebrate fossil assemblage research group. 2002. *Research reports of the Akan vertebrate fossil assemblage (2).* Akan: Akan Town Board of Education.

Ando T, Fordyce RE. 2014. Evolutionary drivers for flightless, wing-propelled divers in the Northern and Southern Hemispheres. *Palaeogeography Palaeoclimatology Palaeoecology* **400**:50–61 DOI 10.1016/j.palaeo.2013.08.002.

Andrews CW. 1906. *A descriptive catalogue of the tertiary vertebrata of the Fayum, Egypt, based on the collection of the Egyptian Government in the Geological Museum, Cairo, and on the collection in the British Museum (Natural History).* London: Trustees of the British Museum (Natural History).

Andrews III CW. 1904. Further notes on the mammals of the Eocene of Egypt. *Geological Magazine* **1**:109-115 DOI 10.1017/S001675680012343X.

Barnes LG. 2013. A new genus and species of Late Miocene Paleoparadoxiid (Mammalia, Desmostylia) from California. *Contributions in Science* **521**:51-114.

Bapst BW. 2012. paleotree: Paleontological and Phylogenetic Analyses of Evolution.

Formatted: Portuguese

Methods in Ecology and Evolution **3**:803-807 DOI 10.1111/j.2041-210X.2012.00223.x.

Beatty BL. 2006. Specimens of *Cornwallius sookensis* (Desmostylia, Mammalia) from Unalaska Island, Alaska. *Journal of Vertebrate Paleontology* **26**:785–787 DOI 10.1671/0272-4634(2006)26[785:SOCSDM]2.0.CO;2.

Beatty BL. 2009. New material of *Cornwallius sookensis* (Mammalia: desmostylia) from the Yaquina Formation of Oregon. *Journal of Vertebrate Paleontology* **29**:894-909 DOI 10.1671/039.029.0320.

Beatty BL, Cockburn TC. 2015. New insights on the most primitive Desmostylian From a partial skeleton of *Behemotops* (Desmostylia, Mammalia) from Vancouver Island, British Columbia. *Journal of Vertebrate Paleontology* **35**:e979939 DOI 10.1080/02724634.2015.979939.

Berta A, Lanzetti A. 2020. Feeding in marine mammals: An integration of evolution and ecology through time. *Palaeontologia Electronica* **23(2)**:a40 DOI 10.26879/951.

Boessenecker RW, Churchill M. 2018. The last of the desmatophocid seals: a new species of *Allodesmus* from the upper Miocene of Washington, USA, and a revision of the taxonomy of Desmatophocidae. *Zoological Journal of the Linnean Society* **184**:211–235 DOI 10.1093/zoolinnean/zlx098.

Chiba K, Fiorillo AR, Jacobs LL, Kimura Y, Kobayashi Y, Kohno N, Nishida Y, Michael PJ, Tanaka K. 2016. A new desmostylian mammal from Unalaska (USA) and the robust

Formatted: Portuguese

Sanjussen jaw from Hokkaido (Japan), with comments on feeding in derived desmostylids. *Historical Biology* **28**:289-303 DOI 10.1080/08912963.2015.1046718.

Chinzei K. 1984. Modes of occurrence, geologic ranges and geographic distribution of desmostylians. *Monograph of the Association for the Geological Collaboration in Japan*, **28**:13-23.

Clark JM. 1991. A new early Miocene species of *Paleoparadoxia* (Mammalia: Desmostylia) from California. *Journal of Vertebrate Paleontology* **11**:490-508 DOI 10.1080/02724634.1991.10011417.

Cooper LN, Seiffert ER, Clementz M, Madar SI, Bajpai S, Hussain ST, Thewissen JGM. 2014. Anthracobunids from the middle Eocene of India and Pakistan are stem perissodactyls. *PLOS ONE* **9**:e109232 DOI 10.1371/journal.pone.0109232.

Crampton JS, Beu AG, Cooper RA, Jones CM, Marshall B, Maxwell PA. 2003. Estimating the rock volume bias in paleobiodiversity studies. *Science* **301**:358-360. DOI 10.1126/science.1085075.

Deng T, Wu F, Wang S, Su T, Zhou Z. 2021. Major turnover of biotas across the Oligocene/Miocene boundary on the Tibetan Plateau. *Palaeogeography Palaeoclimatology Palaeoecology* **567**:110-241 DOI 10.1016/j.palaeo.2021.110241.

Delmer C, Mahboubi M, Tabuce R, Tassy P. 2006. A new species of *Moeritherium* (Proboscidea, Mammalia) from the Eocene of Algeria: new perspectives on the

Formatted: Portuguese

Formatted: Portuguese

Formatted: Portuguese

Field Code Changed

ancestral morphotype of the genus. *Palaeontology* **49**:421-434 DOI 10.1111/j.1475-4983.2006.00548.x.

Domning DP, Ray CE, McKenna MC. 1986. Two new oligocene desmostylians and a discussion of tethytherian systematics. *Smithsonian Contributions to Paleobiology* **59**:1-56 DOI 10.5479/si.00810266.59.1.

Flower BP, Kennett JP. 1994. The middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. *Palaeogeography Palaeoclimatology Palaeoecology* **108**:537–555 DOI 10.1016/0031-0182(94)90251-8.

Frigola A, Prange M, Schulz M. 2018. Boundary conditions for the Middle Miocene Climate Transition (MMCT v1.0). *Geoscientific Model Development* **11**:1607–1626 DOI 10.5194/gmd-11-1607-2018.

Gheerbrant E, Filippo A, Schmitt A. 2016. Convergence of Afrotherian and Laurasiatherian Ungulate-like Mammals: first Morphological Evidence from the Paleocene of Morocco. *PLOS ONE* **11(2016)**:e0157556 DOI 10.1371/journal.pone.0157556.

Greenop R, Sosdian SM, Henehan MJ, Wilson PA, Lear CH, Foster GL. 2019. Orbital forcing, ice volume, and CO2 across the Oligocene-Miocene transition. *Paleoceanography and Paleoclimatology* **34**:316–328 DOI 10.1029/2018PA003420.

Guo Z, Kohno N. 2023. An Early Miocene kentriodontoid (Cetacea: Odontoceti) from the western North Pacific, and its implications for their phylogeny and

Formatted: Portuguese

Formatted: Portuguese

Formatted: Portuguese

Field Code Changed

paleobiogeography. *PLOS ONE* **18(2)**:e0280218 DOI 10.1371/journal. pone.0280218.

Hamon N, Sepulchre P, Lefebvre V, Ramstein G. 2013. The role of eastern Tethys seaway closure in the Middle Miocene Climatic Transition (ca. 14 Ma). *Climate of the Past* **9**:2687–2702 DOI 5194/cp-9-2687-2013.

Hannisdal B, Shanan EP. 2011. Phanerozoic Earth System Evolution and Marine Biodiversity. *Science* **334**:1121-1124 DOI 10.1126/science.1210695.

Hayashi S, Houssaye A, Nakajima Y, Chiba K, Ando T, Sawamura H, Inuzuka N, Kaneko N, Osaki T. 2013. Bone inner structure suggests increasing aquatic adaptations in Desmostylia (Mammalia, Afrotheria). *PLOS ONE* **8**:e59146 DOI 10.1371/journal.pone.0059146.

Herbert T, Lawrence K, Tzanova A, Peterson LC, Caballero-Gill R, Kelly CS. 2016. Late Miocene global cooling and the rise of modern ecosystems. *Nature Geoscience* **9**:843–847 DOI 10.1038/ngeo2813.

Igarashi Y, Yahata M, Kimura M. 2000. Fossil pollen stratigraphy of Miocene Tonokita Formation, Akan-cho, east Hokkaido. *Bulletin of the Ashoro Museum of Paleontology* 1:85–90.

Ijiri S, Kamei T. 1961. On the skulls of *Desmostylus mirabilis* Nagao from South Sakhalin and of *Paleoparadoxia tabatai* (Tokunaga) from Gifu Prefecture, Japan. *Earth Science* **53**:1-27 DOI 10.15080/agcjchikyukagaku.1961.53_1.

Inuzuka N. 1988. The skeleton of *Desmostylus* from Utanobori, Hokkaido, 1. Cranium.

Formatted: Portuguese

Formatted: Portuguese

Formatted: Portuguese

Field Code Changed

Formatted: Portuguese

Bulletin of the Geological Survey of Japan **39**:139-190 DOI 10.9795/bullgsj.60.257.

Inuzuka N. 2000. Primitive Late Oligocene desmostylians from Japan and Phylogeny of the Desmostylia. *Bulletin of the Ashoro Museum of Paleontology* **1**:91-124.

Inuzuka N. 2005. The Stanford skeleton of *Paleoparadoxia* (Mammalia: Desmostylia). *Bulletin of the Ashoro Museum of Paleontology* **3**:3-110.

Inuzuka N, Domning DP, Ray CE. 1994. Summary of taxa and morphological adaptations of the Desmostylia. *Island Arc* **3**:522–537 DOI 10.1111/j.1440-1738.1994.tb00131.x.

Itoigawa J. 1984. Paleoenvironment in which Desmostylia lived reconstructed from fossil molluscan assemblages. *Monograph of the Association for the Geological Collaboration in Japan* **28**:35–43.

Kohno N. 2024. Identification of a nearly complete skeleton of a paleoparadoxiid (Mammalia: Desmostylia) from the Lower to Middle Miocene Shukunohora Formation, Mizunami Group in Kamado Town, Mizunami City, central Japan. *Bulletin of the Mizunami Fossil Museum, Research reports of the "Paleoparadoxiid Mizunami-Kamado specimen"* **50(3)**:43–50 DOI 10.50897/bmfm.50.3_43.

Kimura M, Yahata M, Sawamura H, Segawa I, Suzuki A, Muraishi Y. 1998. The vertebrate fossils and their horizon from Akan-cho, eastern Hokkaido, Japan. *Earth Science* (*Chikyu Kagaku*) **52**:44–50 DOI 10.15080/agcjchikyukagaku.52.1_44.

**Lewis AR, Marchant DR, Ashworth AC, Hedenäs L, Hemming SR, Johnson JV, Leng MJ, Machlus ML, Newton AE, Raine JI, Willenbring JK, Williams

Formatted: Portuguese

M, Wolfe AP. 2008. Mid-Miocene cooling and the extinction of tundra in continental Antarctica. *Proceedings of the National Academy of Sciences* **105(31)**:10676-10680 DOI 10.1073/pnas.0802501105.

Magallanes I, James FP, Santos GP, Juarbe JV. 2018. A new tuskless walrus from the Miocene of Orange County, California, with comments on the diversity and taxonomy of odobenids. *PeerJ* **6**:e5708 DOI 10.7717/peerj.5708.

Matsui K, Kawabe S. 2015. The oldest record of *Paleoparadoxia* from the Northwest Pacific with an implication on the early evolution of Paleoparadoxiinae (Mammalia: Desmostylia). *Paleontological Research* **19**:251-265 DOI 10.2517/2015PR007.

Matsui K, Pyenson ND. 2023. New evidence for the antiquity of *Desmostylus* (Desmostylia) from the Skooner Gulch Formation of California. *Royal Society Open Science* **10**:221648 DOI 10.1098/rsos.221648.

Matsui K, Sashida K, Agematsu S, Kohno N. 2017. Habitat preferences of the enigmatic Miocene tethythere *Desmostylus* and *Paleoparadoxia* (Desmostylia; Mammalia) inferred from the depositional depth of fossil occurrences in the Northwestern Pacific realm. *Palaeogeography Palaeoclimatology Palaeoecology* **471**:254–265 DOI 10.1016/j.palaeo.2017.02.005.

Matsui K, Tsuihiji T. 2019. The phylogeny of desmostylians revisited: proposal of new clades based on robust phylogenetic hypotheses. *PeerJ* **7**:e7430 DOI 10.7717/peerj.7430.

Matsui K, Valenzuela-Toro AM, Pyenson ND. 2022. New data from the first

Formatted: Portuguese

Formatted: Portuguese

Formatted: Portuguese

Field Code Changed

Formatted: Portuguese

Formatted: Portuguese

Formatted: Portuguese

Formatted: Portuguese

Field Code Changed

discovered paleoparadoxiid (Desmostylia) specimen shed light into the morphological variation of the genus *Neoparadoxia*. *Scientific Reports* **12**-1424 DOI 10.1038/s41598-022-18295-5.

Marx FG. 2009. Marine mammals through time: when less is more in studying palaeodiversity. *Proceedings of the Royal Society B: Biological Sciences* **276**:887 892 DOI 10.1098/rspb.2008.1473.

Marx FG, Fitzgerald EMG, Fordyce RE. 2019. Like phoenix from the ashes: How modern baleen whales arose from a fossil "dark age". *Acta Palaeontologica Polonica* **64(2)**:231-238 DOI 10.4202/app.00575.2018.

Marx FG, Fordyce RE. 2015. Baleen boom and bust: a synthesis of mysticete phylogeny, diversity and disparity. *Royal Society Open Science* **2**:140434 DOI 10.1098/rsos.140434.

Miller KG, Wright JD, Fairbanks RG. 1991. Unlocking the ice house Oligocene-Miocene oxygen isotopes, eustasy, and margin erosion. *Journal of Geophysical Research* **96(B4)**:6829-6848. DOI 10.1029/90JB02015.

Okazaki Y, Sasa Y, Suzuki N, Itou T. 1972. On *Desmostylus* Tooth from Chichappu, Kushio, Hokkaido. *Kushiro Ronshu, Reports of Hokkaido University of Education at Kushiro* **3**:75-86.

Ogasawara K. 2000. Paleoenvironments of desmostylid[s] and Cenozoic events of the Northwestern Pacific. *Bulletin of the Ashoro Museum of Paleontology* **1**:25–34.

Osborn HF. 1905. Ten years' progress in the mammalian palaeontology of North

America. *American Geologist* 36:199–229.

Pyenson ND, Vermeij GJ. 2016. The rise of ocean giants: maximum body size in Cenozoic marine mammals as an indicator for productivity in the Pacific and Atlantic Oceans. *Biology Letters* **12**: 20160186 DOI 10.1098/rsbl.2016.0186.

Parham JF, Barron JA. Vélez-Juarbe J. 2022. Middle and late Miocene marine mammal assemblages fromthe Monterey Formation of Orange County, California. *The Geological Society of America Special Paper* **556**:1–14 DOI 10.1130/2021.2556(10).

R Core Team. 2024. R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. *Available at https://www.R-project.org/ .*

Reinhart RH. 1953. Diagnosis of the new mammalian order, Desmostylia. *The Journal of Geology* **61**:187 DOI 10.1086/626067.

Reinhart RH. 1959. A review of the Sirenia and Desmostylia. *University of California Publications in Geological Sciences* **36**:1-146.

Rose KD, Holbrook LT, Kumar K, Rana RS, Ahrens HE, Dunn RH, Folie A, Jones KE, Smith T. 2020. Anatomy, relationships, and paleobiology of *Cambaytherium* (Mammalia, Perissodactylamorpha, Anthracobunia) from the lower Eocene of western India. *Journal of Vertebrate Paleontology* **39**:1-147 DOI 10.1080/02724634.2020.1761370.

Rose KD, Holbrook LT, Rana RS, Kumar K, Jones KE, Ahrens HE, Missiaen P,

Sahni A, Smith T. 2014. Early Eocene fossils suggest that the mammalian order Perissodactyla originated in India. *Nature communications* **5**:Article 5570. DOI 10.1038/ncomms6570.

Rousselle G, Beltran C, Sicre M, Raffi I, De Rafélis M. 2013. Changes in sea-surface conditions in the equatorial Pacific dur ing the middle Miocene-Pliocene as inferred from coccolith geochemistry. *Earth and Planetary Science Letters* **361**:412–421 DOI 10.1016/j.epsl.2012.11.003.

Smith AB, McGowan AJ. 2007. The shape of the Phanerozoic marine palaeodiversity curve: how much can be predicted from the sedimentary rock record of western Europa? *Palaeontology* **50**:765-774 DOI 10.1111/j.1475-4983.2007.00693.x.

Suzuki A. 2000. Paleoenviromental significance of Miocene molluscan faunas in Hokkaido, northern Japan. *Bulletin of the Ashoro Museum of Paleontology* **1**:57–66.

Suzuki A, Kimura M, Tanaka K. 1999. Molluscan fossils associated with Desmostylians from the middle Miocene in the Akan area, southeastern Hokkaido, Japan. *Journal of Environmental Education* **2**:83-92.

Swofford DL. 2002. PAUP* phylogenetic analysis using parsimony (*and Other Methods). Version 4. Sunderland: Sinauer Associates. *Available at https://paup.phylosolutions.com/.*

Tokunaga S. 1939. A new fossil mammal belonging to the Desmostylidae. . *In, Jubilee Publication in Commemorating Professor H. Yabe, M.I.A., Sixtieth Birthday* **1**:289 299 Institute of Geology and Paleontology, Tohoku Imperial University, Sendai.

Formatted: Portuguese

Formatted: Portuguese

Formatted: Portuguese

Field Code Changed

Formatted: Portuguese

Uhen MD, Pyenson ND. 2007. Diversity estimates, biases, and historiographic effects: resolving cetacean diversity in the Tertiary. *Palaeontologia Electronica* **10**:1-22.

Uno H, Kaneko N, Takabatake T. 2016. Description of the rest of previously studied Utanobori specimens of Desmostylus from Esashi Town, Hokkaido, Japan. *Bulletin of Geological Survey of Japan* **67(5)**:137–165 DOI 10.9795/bullgsj.67.137.

Uno H, Kimura M. 2004. Reinterpretation of some cranial structures of *Desmostylus hesperus* (Mammalia: Desmostylia): a new specimen from the Middle Miocene Tachikaraushinai Formation, Hokkaido, Japan. *Paleontological Research* **8**:1-10 DOI 10.2517/prpsj.8.1.

Urabe A, Akiha F, Hoyanagi K. 2003. Diatom biostratigraphy of the Neogene strata in the Akan area, the eastern Hokkaido, northern Japan. *Journal of the Geological Society of Japan* **109(7)**:399-413 DOI 10.5575/geosoc.109.399.

Urabe A, Hoyanagi K. 2004. Stratigraphy of the late Cenozoic strata in the Akan area: with special emphasis on significance of the lower Miocene in the eastern Hokkaido, northern Japan. *Journal of the Geological Society of Japan* **110(1)**:51-64 DOI 10.5575/geosoc.110.51.

Vélez-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.

Tripati AK, Roberts CD, Eagle RA. 2009. Coupling of CO2 and ice sheet stability over major climate transitions of the last 20 million years. *Science* **326**:1394–1397

Formatted: Portuguese

DOI 10.1126/science.1178296.

Wen Y, Zhang L, Holbourn AE, Zhu C, Huntington KW, Jin T, Li Y, Wang C. 2023. CO_2-forced Late Miocene cooling and ecosystem reorganizations in East Asia. *Proceedings of the National Academy of Sciences* **120(5)**:e2214655120 DOI 10.1073/pnas.2214655120.

Yahata M, Kimura M. 2000. Mode of Occurrence of Desmostylian fossils in Hokkaido and Sakhalin, northwestern Pacific Ocean. *Bulletin of the Ashoro Museum of Paleontology* 1:35–56.

Zachos JC, Dickens GR, Zeebe RE. 2008. An Early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**:279–283 DOI 10.1038/nature06588.

Zachos J, Flower B, Paul H. 1997. Orbitally paced climate oscillations across the Oligocene/Miocene boundary. *Nature* **388**:567–570 DOI 10.1038/41528.

Formatted: Portuguese

Formatted: Portuguese