Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

New data from the first discovered paleoparadoxiid (Desmostylia) specimen shed light into the morphological variation of the genus Neoparadoxia

Kumiko Matsui (MatsuiK@si.edu)
National Museum of Natural History, Smithsonian Institution
Ana M. Valenzuela-Toro
University of California Santa Cruz
Nicholas D. Pyenson
National Museum of Natural History, Smithsonian Institution

Research Article

Keywords:

Posted Date: July 6th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1094164/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Abstract

Desmostylia is an extinct clade of marine mammals with two major sub-clades, Desmostylidae and Paleoparadoxiidae, known from Oligocene to Miocene strata of the North Pacific coastline. Within Paleoparadoxiidae, three genera have been identified: Archaeoparadoxia, Paleoparadoxia, and Neoparadoxia. The latter taxon is the geochronologically youngest palaeoparadoxiid and characterized by a comparatively larger body size, although it is known only from a few specimens within a short temporal and geographic range. Here we report the discovery of an isolated tooth identified as Neoparadoxia cf. N. cecilialina, constituting only the second individual specimen of Neoparadoxia with preserved dentition yet reported. This specimen was collected near Corona, California, USA, and we attribute it to the "Topanga" Formation, becoming the first record of Neoparadoxia from this unit. While the exact geographic locality was not properly recorded for this specimen when it was collected in 1913, we establish two potential localities based on the associated hand-written museum label and new stratigraphic information. Although this specimen wasinitially identified as Desmostylus hesperus, it was collected 10 years before the first named paleoparadoxiid from Japan. This new occurrence data adds to interpretations of marine mammal assemblages, especially in Southern California where paleoparadoxiids co-occur with desmostylids and sirenians.

Introduction

Desmostylia is an enigmatic extinct group of quadrupedal and herbivorous marine mammals known from Oligocene and the Miocene marine strata of both coasts of the North Pacific Ocean (e.g., [1–3]). Within Desmostylia, Paleoparadoxiidae is a monophyletic family (e.g., [4,5]), comprising four species distributed in three genera (namely *Archaeoparadoxia*, *Paleoparadoxia*, and *Neoparadoxia*; [3,5]). Fossil remains of paleoparadoxiids have been found in marine deposits ranging in age from the latest Oligocene (Chattian) to the earliest late Miocene (Tortonian) of the North Pacific coasts of Japan and the United States (24 to 10 Ma: [3,6,7]).

Paleoparadoxiidae has an extensive and complicated taxonomic history, characterized by several changes in its nomenclature. This family was founded in 1923[8,9] with the discovery of two isolated teeth (likely belonging to two different individuals; see more below) from middle-late Miocene (late Serravallian to early Tortonian) marine strata of the Tsurushi Formation, on Sado Island, Niigata Prefecture, Japan (see [10] for age revisions to the Tsurushi Formation). These specimens (including a left second molar (m2) designated as the type) were originally identified as *Cornwalliustabatai*[8]; however, they were both presumed destroyed in 1945 during the Second World War, with only Tokunaga's original photos and illustrations as reference material. Subsequently, a nearly complete desmostylian skeleton was discovered in 1950, at Izumi (currently Toki City), Gifu Prefecture, Japan. This skeleton from Izumi included forelimbs, cranium, and a mandible (NMNS PV-5601) that was originally recognized as *Desmostylus* sp.[11], but was then reidentified as belonging to *C. tabatai*[12]. Years later, when Reinhart[4] revised desmostylian taxonomy, he founded the new genus *Paleoparadoxia* and recombined

Paleoparadoxia tabatai based on the *C. tabatai* holotype specimens (which Reinhart may not have known were lost) along with specimens from Southern California (UCMP 40862 and UCMP 32076). Later, Shikama[13] designated the Izumi specimen (NMNS PV-5601) as the neotype of *P. tabatai*.

Clark[6] described a second species of *Paleoparadoxia*, *P.weltoni*, based on a smaller but fully adult complete skeleton (UCMP 114285) from the earliest Miocene Schooner Gulch Formation (Aquitanian) in northern California (see [14] for age of the Schooner Gulch Formation). Later, Inuzuka[9] described postcranial material (UCMP 81302) collected during the construction of the Stanford Linear Accelerator Center (now the SLAC National Accelerator Laboratory) near Menlo Park, California, as belonging *Paleoparadoxia* sp. Based on this specimen from the middle Miocene Ladera Sandstone Formation (Langhian-Serravalian), Inuzka[9] proposed that the lost holotype of *Cornwalliustabatai* likely corresponded to the same species represented by UCMP 81302 based on its molar size; yet no further comparisons were conducted.

At the same time Inuzuka[9], proposed yet another new species name, *Paleoparadoxia media*, for the neotype specimen of *P. tabatai* from Izumi. The basis for this decision stems from Inuzuka's apparent rediscovery of one fossil tooth that probably belonged to the same individual of the original holotype specimen of *P. tabatai* from Aikawa Local Museum near the type locality, a left third molar (m3), from the Tsurushi Formation (or Orito Formation) of Sado Island (see[9,15]). Although it is possible that this second specimen belongs to the same individual as the type left m2 of *P. tabatai*, this nomenclatural decision is problematic because it is destabilizing, attributing an older and less complete specimen to the typology of *P. tabatai*. Hasegawa and Kohno[16] petitioned the ICZN (Case 3384) to conserve the name of *P. tabatai* by fixing the Izumi specimen as the lectotype, along with the suppression of *P. media*. The ICZN[17] declined this petition (ICZN Opinion 2232) on the basis of an invalid lectotype designation by Inuzuka[9], which had the effect of maintaining Shikana[13]'s designation of the Izumi specimen as the neotype, consistent with over a half century of desmostylian taxonomic work. We further recommend the suppression of *P. media*, in keeping with this practice.

Domning and Barnes[15] performed a comprehensive morphological assessment of UCMP 81302 and identified it as the new species *Paleoparadoxia repenningi*, until Barnes[3] transferred this species to the new genus *Neoparadoxia*, thereby recombining the species as *N. repenningi*. In this same study, Barnes[3] also transferred the holotype specimen of *Paleoparadoxia weltoni* (UCMP 114285) to a new monotypic genus *Archaeoparadoxia* and described a new species of *Neoparadoxia*, *N. cecilialina* based on a well preserved and complete skeleton including the cranium, mandible, and teeth (LACM 150150) from the early late Miocene Monterey Formation (Tortonian), in Southern California (see below).

Specifically, *Neoparadoxia cecilialina* is the geochronological youngest desmostylian taxon. *N. cecilialina* ranks as the largest paleoparadoxiid, reaching an estimated standard length of 2.73 m as an adult[3], and possessed pectoral limb dimensions 1.5 to 2 times the size of other paleoparadoxiids. Nonetheless, this species is known solely by a single specimen (its holotype), impeding attempts to assess the intra and interspecific variation of the cranial and postcranial morphology and, ultimately, testing any ecomorphological hypotheses among co-occurring desmostylians.

In the summer of 2021, one of the authors (AVT) found a desmostylian specimen (USNM PAL V 11367) in the Department of Paleobiology collections of the National Museum of Natural History, Smithsonian Institution, which corresponds to a complete lower molar with diagnostic features of Paleoparadoxiidae (listed in Systematics) and comparable morphology to *Neoparadoxiacecilialina*. The original museum label with this specimen (Figure 1) indicates that it was originally excavated in the city of Corona, Riverside County, California, USA, in 1913. USNM PAL V 11367 was thus collected ten years before the discovery of the first Paleoparadoxiidae remains (the lost holotype of *P.tabatai*), and 51 years before the discovery of the *Neoparadoxiareppeningi*. Thus, USNM PAL V 11367 represents the historically oldest paleoparadoxiid specimen ever discovered. Finally, this finding provides new information about the morphological variation of paleoparadoxiids.

Systematics

Desmostylia Reinhart 1953 [18]

Desmostyloidea Osborn 1905 [19] *sensu* Matsui and Tsuihiji 2019 [5]

Paleoparadoxiidae Reinhart 1959 [4] *sensu* Matsui, and Tsuihiji 2019 [5]

Diagnosis for Paleoparadoxiidae–Molar tooth with an extra cusp present between the hypoconulid and the protoconid aligned on its posterior side [3]; tooth enamel in occlusal view is thinner than *Cornwallius* and thicker than *Ashoroa, Behemotops,* and *Seuku*; cingulum present on the buccal side.

Neoparadoxia Barnes 2013 [3]

Emeneded diagnosis for *Neoparadoxia*–Molar tooth with a high crown compared to *Archaeoparadoxia* and *Paleoparadoxia*; the extra cusp (EX in Figure 2 and 4) between the hypoconulid and protoconid is high relative to the base of the tooth crown, and enlarged compared to *Archaeoparadoxia* and *Paleoparadoxia*, reaching almost the level of the main cusps of *Archaeoparadoxia* and *Paleoparadoxia*; these latter cusps are more closely appressed to each other than in *Archaeoparadoxia* and *Paleoparadoxia*; thicker tooth enamel than *Archaeoparadoxia* and *Paleoparadoxia* but thinner than *Cornwallius*, *Ounalashkastylus*, and *Desmostylus*; extra cusps (black circles in Figure 4) are higher than *Archaeoparadoxia* and *Paleoparadoxia*; and a weak cingulum compared to *Archaeoparadoxia* and *Paleoparadoxia*.

Neoparadoxia cf. *N. cecilialina*

Material–USNM PAL V 11367 (Figure 2), a right m2? with dental root. Its original label indicates the existence of associated skull material that is presumed lost.

Formation and age–"Topanga" Formation, Upper Burdigalian to lower Langhian (16.5–14.5 Ma)[20]. Details are provided in the discussion section.

Potential localities–City of Corona, Riverside County, California, USA. We propose two potential localities (approximately 33°52'45.7"N 117°40'49.1"W or 33°48'09.5"N 117°29'24.7"W) for USNM PAL V 11367 (Figure 3). Details and comments are provided in the discussion section.

Description and comparisons–USNM PAL V 11367 has a well-worn crown with a dental root. The crown length is 32.22 mm, and its maximum width is 23.02 mm. Its crown has seven cusps. The alignment of the major cusps is consistent with m2 or m3 teeth.

USNM PAL V 11367 has a single and long root that is approximately 52.7 mm long. Only a few paleoparadoxiid molars with roots have been reported before, and little is known about their variability. Nevertheless, the type specimen of *P. tabatai*, lost to the bombing of Tokyo on 25 May 1945 by the United States during the Second World War[13,16], had a long single root comparable to USNM PAL V 11367. Likewise, the neotype of *P. tabatai* has a single root in m3, contrasting with *N. repenningi and N. cecilialina,* which are characterized by having double rooted m2 and m3 alveoli, and m2, respectively ([3]; see Table S1). Similarly, *A. weltoni* has double rooted molars[6]. These observations demonstrate that molar root number in paleoparadoxiids is highly variable, indicating that this trait may not be diagnostic for genera.

The crown of USNM PAL V 11367 has a convex occlusal surface compared to other paleoparadoxiids but broadly is consistent with m2 of *N. cecilialina*. The occlusal surface is inclined in its posterobuccal side. The cingulum of USNM PAL V 11367 is located on its lingual side and is less developed than in *P. tabatai*. The crown in USNM PAL V 11367 is higher of its width than other paleoparadoxiids but similar to *N. cecilialina*. In total, USNM PAL V 11367 displays seven cusps, being consistent with *N. cecilialina* whose m2 also possesses seven cusps, but contrasting with *A. weltoni* and *P. tabatai*, which have five cusps on m3. Nevertheless, USNM PAL V 11367 lacks cuspules, as compared with *N. cecilialina* that shows seven major cusps with one cuspule. All major cusps are high, differing from all other paleoparadoxiid species with cuspules in which major cusps are variable in height. USNM PAL V 11367 has four major cusps and three extra cusps (Figure 2 and 4). Two extra cusps on the posterior side are less developed compared to major cusps. An extra cusp exists between the protoconid and endoconid and has the same height as the major cusps. The types of *A. weltoni* and *P. tabatai* also have the same extra cusp, but these are very small compared to USNM PAL V 11367 and *N. cecilialina*. There is a deep groove between the protoconid-metaconid and entoconid-hypoconulid-extra cusps (dark masked area of Figure 2). This groove is narrower and deeper than other paleoparadoxiids and narrower than in *N. cecilialina.* The arrangement of the major cusps in USNM PAL V 11367 is sub-rhomboidal, contrasting with a more sub-rectangular arrangement displayed by *A. weltoni* and *P. tabatai*. *N. cecilialina* has a trapezoidal arrangement of its major cusps; however, little difference between left and right m2s has been found. In *N. cecilialina*, the entoconid-hypoconulid-extra cusps arrangement of the right side of m2 is straight, but the entoconid-hypoconulid-extra cusps arrangement of the left is bended to posterior side.

The left side of hypoconulid is situated more posterior side than entoconid-extra cusps. In conclusion, based on the number and size of the major cusps, the arrangement of cusps, and the height of the extra cusp, we identify USNM PAL V 11367 as *Neoparadoxia* cf. *N.cecilialina*.

Discussion

Discovery and historiography of USNM PAL V 11357

With basic image enhancement tools (e.g., Adobe Photoshop), we were able to better resolve the original but faded specimen card included with USNM PAL V 11357 (Figure 1). Specifically, we were able to read now-faded handwritten notes (Figure 1A-B), revealing critical information about the specimen. The widespread availability of image enhancement for faded fieldnotes and labels provides a new source of information for uncovering legacy issues in museum collections (e.g. [21–23]), especially in cases where locality data or collecting information cannot be well resolved.

Accession files with this specimen (Supplementary 4) show that it was gifted from Arthur M. Ames to the United States National Museum (now the National Museum of Natural History, Smithsonian Institution) on 15 October 1925, and approved by George P. Merrill, head curator of geology from 1917-1929. Prior to its accession to the museum, an anonymous individual identified the tooth as belonging to *Desmostylus hesperus* by anonymous. Forty years later, on 17 November 1965, Charles A. Repenning reidentified this specimen as *Paleoparadoxia* sp (Figure 1A-B), an assertion that was incorporated into its catalog information. According to the label, USNM PAL V 11367 was collected in the city of Corona, Riverside County, California, yet no precise information of its geological provenance was recorded. On the backside of the label, there are notes (Figure 1B) referring to the US Geologic Survey Corona South 7.5' quadrangle map for Riverside and Orange counties, California[24]. However, no exact horizon or lithology was stated, and the specimen's collector, A. M. Ames, lived in Santa Barbara, California but who died on 25 August 1939[21–23]

In a century after its discovery, the only mention of USNM PAL V 11367 was by Panofsky[25], who listed it in a catalog of desmostylian tooth specimens used as a comparative basis for a mandible restoration of the Stanford specimen *N. repenningi*. Panofsky[25] identified USNM PAL V 11367 as a left m2 with six main cusps, with no additional cusps (Table 1 in [25]), while also stating that this specimen has "an open lake in the center of each of the seven cusps" ([25]: p. 103). The inconsistency of this description differs from our own, which we attribute to differences in morphological criteria during the identification process or a typing error.

Geological horizon and age of USNM PAL V 11367

In this paper, we refer to the "Topanga" Formation following recent recent studies[20,26,27]. The Topanga Formation was originally based on a sequence of marine sandstones exposed in an anticline just west of

Old Topanga Canyon in the central Santa Monica Mountains, California[28]. It has yielded abundant early to middle Miocene marine invertebrates and a few land mammals that are as old as early late Hemingfordian in age[29]. After the initial naming, the name of the formation was applied to a much thicker and heterogeneous sequence of sedimentary and volcanic rocks[30]. Cambell et al. [31] compiled the history and chronology of changes in usage of “Topanga” in the Miocene stratigraphic nomenclature in Southern California,showing that continuous deposition and shared provenance were not demonstrated in every instance. Here we follow i recent studies[20,26,27] and use the name of “Topanga” Formation for the early to middle Miocene rocks bearing fossil marine mammals.

According to the original museum records (Figure 1), USNM PAL V 11367 was collected in the city of Corona, Riverside County, California, USA. This city is in the western part of Riverside County, comprising an approximate area of 100 km^2 [32]. Previously, Panofsky[25] suggested that USNM PAL V 11367 would have derived from the Temblor Formation (14.8 to 15.8 Ma; [33]), likely as a guess based on the prevalence of desmostylian teeth recovered from this unit. . However, there are no Temblor Formation outcrops mapped near Corona[24,34]; the closest outcrops are in Fresno and Kern counties[35], approximately 200 km away.

Geologic maps of Riverside County[24,34,36] indicates that the city limits of Corona encompass a wide variety of sedimentary rocks from the Jurassic to the Holocene in age, although there are no previous fossil records from the “Topanga” Formation in Corona, California. In Corona, only a few marine deposits such as the Jurassic Bedford Canyon Formation and the middle Miocene “Topanga” Formation are exposed[24]. Specifically, the marine sandstones of the “Topanga” Formation occur within the fault zone at the southeast and northwest of Corona. In assessing the age of the “Topanga” Formation, Boessenecker and Churchill[26,37] argued that the lands mammals (late Hemingfordian North American Land Mammal Age, represented by *Aepycamelus*, *Copemys* and *Merychippus*; 17.5–15.9 Ma; [29,33]), benthic foraminifera, fossil mollusks, and K/Ar dating all placed the age range between 17.5–15 Ma for this geological unit[29]. More recently, Velez-Juarbe[20] revised the age of “Topanga” formation to 16.5–14.5 Ma based on Ogg et al. [38].

Outside of Riverside County, the “Topanga” Formation has yielded several remains of fossil marine vertebrates in Southern California, including desmostylians referred to *Desmostylus hesperus*, *Paleoparadoxia* sp., and Desmostylia indet. in Orange County (see [20,26,37,39]; Supplemental 2). USNM PAL V 11367 also represents the second reported fossil marine mammal from Riverside County. Previously, an isolated record of Cetacea indet. was described from the Imperial Formation ([40] and Supplementary 1). The invertebrate assemblage from this unit indicates a late Miocene age (8–6 Ma[41]) , which is younger than the type occurrence of *Neoparadoxia cecilialina*[3]. Furthermore, no outcrops of the Imperial Formation are recognized in or near the city limits of Corona, ruling out a potential origin from Imperial Formation for USNM PAL V 11367.

Based on the correspondence between the estimated age of the “Topanga” Formation and the known range of *Neoparadoxia cecilialina*, combined with the absence of other Miocene marine units in the vicinity of Corona, we propose that USNM PAL V 11367 is from the “Topanga” Formation, implying a middle Miocene age, 16.5–14.5 Ma[20]. Further, considering the reduced distribution of outcrops of the “Topanga” Formation[24,34] in Corona, we identify two potential localities for USNM PAL V 11367 (Figure 3). These two localities are situated in urbanized areas, less than 21 km apart, in the northwest and the southeast corners of Corona’s city limits (see Figure 3B); they are equally less than 40 km apart from the locality of the holotype of *N. cecilialina* in Orange County.

Implications for *Neoparadoxia* age range

The genus *Neoparadoxia* was described by Barnes[3] based on the comparative morphology of two specimens(the holotype of *N. repenningi* and *N. cecilialina*). USNM PAL V 11367 becomes the third known record of *Neoparadoxia*. Fossil remains of *Neoparadoxia* have been only found from the middle-late Miocene of California (Figure 3). [15342]While the estimates of the geochronologic age range of the “Topanga” Formation range from 16.5–14.5 Ma[20], these age ranges fit with the age of *N. repeninngi* or *N. cecilialina: N. repenningi* is 14 Ma from the Ladera Sandstone Formation (e.g., [15]); and Parham et al. [42] recently revised the age of *N. cecilialina* to 14.9–13.1 Ma. Therefore, we revise the age range for the genus *Neoparadoxia* to 16.5-13.1 Ma.

Morphological variation and potential diversity of Paleoparadoxiidae

Our comparisons reveal considerable morphological variation in the arrangement and number of dental cusps across Paleoparadoxiidae (Figure 4). The cusps arrangement for the m2-3 of *Archaeoparadoxia* and *Paleoparadoxia* were previously reported by Inuzuka et al. (1994: Figure 4B), but the addition of another specimen (USNM PAL V11367) shows more morphological variability than previously suspected for the genus *Neoparadoxia* (Figure 4C). Specifically, the holotype of *N. cecilialina* displays slightly different configurations between its right and left m2, driven mainly by the position of the hypoconulid in occlusal view (Figure 4C). USNM PAL V 11367, the second known *Neoparadoxia* m2 (or the first m3) is comparable in size and shape with the same teeth in the type specimen of *N. cecilialina*, especially the right m2. Both the Smithsonian and LACM specimens display a horizontal alignment of the extra cusp, the hypoconulid, and the entoconid; nevertheless, USNM PAL V 11367 shows a tighter configuration, lacking a wide internal spacing between cusps characteristic of the type specimen of *N. cecilialina* (Figure 4C).

The identification of USNM PAL V 11367 from “Topanga” Formation of Corona also suggests that at least members of three genera of Desmostylia co-existed in this geological unit. The “Topanga” Formation holds the greatest richness of desmostylian taxonomic diversity for any geological unit in the world. Previously, *Desmostylus* spp. and paleoparadoxiids rarely co-occurred from the same formation[43,44] based on taphonomic and faunal assemblage comparisons. There are some localities in California and Japan where *Desmostylus* and paleoparadoxiids co-occurred (e.g., Santa Margarita

Formation[45,46], Rosarito Beach Formation[47], Tortugas Formation[47], Temblor Formation[3,4], and Rawan conglomerate sandstone member[48,49]), but such specimens were found from the horizons where fossils were likely reworked or concentrated in high energy depositional settings, such as coquinas and conglomerates, or represent deposits with long-term (10^{5-6} yrs.) non-deposition and subaqueous weathering, such as phosphoritic deposits, bonebeds, or the deposits just above an unconformity[43,50,51]. In those units, we suspect that co-occurrences of desmostylians may reflect allocthonous assemblages rather than ecological communities[52].

It has been hypothesized that *Desmostylus* spp. only lived in cool marine environments[43,53], whereas paleoparadoxiids inhabited a larger environmental range from tropical to cool marine environments as hinted from co-occurring fossil molluscan assemblages in the northwest Pacific[7]. However, in the "Topanga" Formation, the fossil record indicates that both *Desmostylus* and paleoparadoxiids co-occurred[54,55]. Most desmostylians from the "Topanga" Formation are presented by relatively well-preserved remains (i.e., partial skeletons, teeth with well-preserved roots[55,56]), suggesting some taphonomic control (or depositional specificity), with low transportation from basal conglomerate layers or flushing out from lower formations. "Topanga" Formation does not fit the formations that Chinzei[43] mentioned, and this formation might represent a rare environment where desmostylids and paleoparadoxiids coexisted.

Like other marine mammal lineages, desmostylian body sizes reached their maximum body size late in their evolutionary history[57]. By the middle to late Miocene, desmostylians were the largest herbivorous marine mammals along the North Pacific coastlines[57], although they likely competed ecologically with co-occurring sirenians, which later eclipsed desmostylians in body size and survived until historical times in the North Pacific Ocean[58]. Specifically, in the "Topanga" Formation, desmostylians co-occurred with sirenians such as *Metaxytherium arctodites*[59], an ecological association that likely was repeated elsewhere in the mid-Miocene of California (e.g., coeval deposits of the Round Mountain Silt). Given that the "Topanga" Formation likely represented a warm, shallow marine environment[60], the elevated productivity and high availability of seagrasses during the Middle Miocene Climatic Optimum[61] probably contributed to Southern California's favorability as a location for the highest richness of marine mammal herbivores ever known, with three or four desmostylian taxa (*Desmostylus* sp.: [56]; *Paleoparadoxia tabatai*: [4]; *Neoparadoxia*: this study; Paleoparadoxiidae gen. sp. indet: [55]) and one genus of dugongid sirenian. Similar patterns of high taxonomic richness among co-occurring marine mammal guilds existed in "Topanga" Formation and elsewhere during this time (e.g., [20]), indicating that marine food webs significantly differed from such observed today in the North Pacific.

Methods

We report on a single *Neoparadoxia* cf. *N. cecilialina* specimen from the "Topanga" Formation. This specimen was collected in 1913 without a precise record for its source locality by the collector, who died in 1939. The stratigraphic origin of USNM PAL V 11367 is confirmed by the museum records, which we explain in the Discussion section. USNM PAL V 11367 is permanently housed in the Department of Paleobiology collections at the National Museum of Natural History, Smithsonian Institution, Washington DC., USA.

Comparative Specimens

We used some comparative specimens for USNM PAL V 11367. Comparative materials are listed in Supplementary 3.

Institutional Abbreviations

LACM, Natural History Museum of Los Angeles County, Los Angeles, California, USA; NMNS, National Museum of Nature and Science, Tokyo, Japan; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; USNM PAL, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, USA.

Declarations

Acknowledgments

We are especially grateful to Amanda Millhouse, Jessie Nakano, and David Bohaska (all at the Smithsonian) for their assistance with accession and catalog records, as well as comments from two reviewers that improved this manuscript. We also thank Mark Goodwin, and Patricia Holroyd (UCMP), Jorge Velez-Juarbe, Samuel A. McLeod (LACM), and Vanessa R. Rhue (LACM, currently Yale Peabody Museum, Yale University), Naoki Kohno (NMNS) for allowing us to observe desmostylian specimens under their care.

Funding

KM was funded by the Japan Society for the Promotion of Science (JSPS 19J00741/ 21K14031). AVT was funded by ANID PCHA/Becas Chile, Doctoral Fellowship; Grant No. 2016-72170286, a Peter Buck Predoctoral Fellowship by the National Museum of Natural History (NMNH), Smithsonian Institution, and the University of California Santa Cruz Ecology and Evolutionary Biology Department Summer Funds during the performance of this study. NDP was supported by the Kellogg Fund in the Department of Paleobiology, NMNH

Author contributions

All authors conceived and designed the study, wrote the paper, prepared figures, and reviewed drafts of the paper.

Competing interests

There are no competing interests.

Data availability

All data generated during this study are included in this published article and its supplementary information files.

References

1. Domning, D. P., Ray, C. E. & McKenna, M. C. Two New Oligocene Desmostylians and a Discussion of Tethytherian Systematics. *Smithson. Contrib. to Paleobiol.* 1–56 (1986). doi:10.5479/si.00810266.59.1
2. Inuzuka, N., Domning, D. P. & Ray, C. E. Summary of taxa and morphological adaptations of the Desmostylia. *Isl. Arc***3**, 522–537 (1994).
3. Barnes, L. G. A new genus and species of late Miocene Paleoparadoxiid (Mammalia, Desmostylia) from California. *Contrib. Sci.***521**, 51–114 (2013).
4. Reinhart, R. H. A Review of the Sirenia and Desmostylia. *Univ. Calif. Publ. Geol. Sci.***36**, 254 (1959).
5. Matsui, K. & Tsuihiji, T. The phylogeny of desmostylians revisited: Proposal of new clades based on robust phylogenetic hypotheses. *PeerJ***2019**, 1–17 (2019).
6. Clark, J. M. A new early miocene species of Paleoparadoxia (mammalia: Desmostylia) from California. *J. Vertebr. Paleontol.***11**, 490–508 (1991).
7. Matsui, K. & Kawabe, S. The Oldest Record of Paleoparadoxia from the Northwest Pacific with an Implication on the Early Evolution of Paleoparadoxiinae (Mammalia: Desmostylia). *Paleontol. Res.***19**, 251–265 (2015).
8. Tokunaga, S. A new fossil mammal belonging to the Desmostylidae. in *Jubilee publication commemorating Prof. H. Yabe, M.I.A., sixtieth birthday* 289–299 (Tohoku Imperial University, Institute of Geology and Paleontology, 1939).
9. Inuzuka, N. The Stanford Skeleton of Paleoparadoxia (Mammalia：Desmostylia) The Stanford Skeleton of Paleoparadoxia (Mammalia：Desmostylia). *Bull. Ashoro Museum Paleontol.***3**, 3–110 (2005).
10. Kawatani, A. & Kohno, N. The oldest fossil record of the extant genus Berardius (Odontoceti, Ziphiidae) from the Middle to Late Miocene boundary of the western North Pacific. *R. Soc. Open Sci.***8**, (2021).
11. Desmostylus Research Committee. The second skeleton of Desmostylus in Gifu Prefecture. *J. Geol. Soc. Japan***57**, 414 (1951).
12. Ogose, S. On the Desmostylus-bearing Formation in Izumi-mati Gihu prefecture (Miscellaneous Notes). *J. Geol. Soc. Japan***58**, 400 (1952).
13. Shikama, T. Postcranial Skeltons of Japanese Desmostylia. *Paleontol. Soc. Japan Spec. Pap.***12**, 1–241 (1966).

14. Poust, A. & Boessenecker, R. Expanding the geographic and geochronologic range of early pinnipeds: new specimens of Enaliarctos from Northern California and Oregon. *Acta Palaeontol. Pol.***63**, 26–40 (2018).
15. Domning, D. P. & Barnes, L. G. Journal of Vertebrate Paleontology A new name for the ' Stanford skeleton ' of. *J. Vertebr. Paleontol.***27**, 748–751 (2010).
16. Hasegawa, Y. & Kohno, N. Case 3384 Cornwallius tabatai Tokunaga, 1939 (currently Paleoparadoxia tabatai; Mammalia, Desmostylia): proposed conservation of usage of the specific name by the designation of a neotype. *Bull. Zool. Nomencl.***64**, 113–117 (2007).
17. International Commission on Zoological Nomenclature. Opinion 2232 (Case 3384) Cornwallius tabatai Tokunaga, 1939 (currently Paleoparadoxia tabatai; Mammalia, Desmostylia): proposed designation of a neotype not accepted. *Bull. Zool. Nomencl.***66**, 295–296 (2009).
18. Reinhart, R. Diagnosis of the New Mammalian Order, Desmostylia. *J. Geol.***61**, 187–187 (1953).
19. Osborn, H. F. Ten years' progress in the mammalian palaeontology of North America. *Am. Geol.***36**, 199–229 (1905).
20. Velez-Juarbe, J. Eotaria citrica , sp. nov., a new stem otariid from the "Topanga" formation of Southern California. *PeerJ***5**, e3022 (2017).
21. Chatzimanolis, S. Darwin's legacy to rove beetles (coleoptera, staphylinidae): A new genus and a new species, including materials collected on the Beagle's voyage. *Zookeys***379**, 29–41 (2014).
22. Boersma, A. T. & Pyenson, N. D. Arktocara yakataga, a new fossil odontocete (Mammalia, Cetacea) from the Oligocene of Alaska and the antiquity of Platanistoidea. *PeerJ***2016**, 1–41 (2016).
23. Matsui, K. *et al.* A long-forgotten 'dinosaur' bone from a museum cabinet, uncovered to be a Japan's iconic extinct mammal, Paleoparadoxia (Desmostylia, Mammalia). *R. Soc. Open Sci.***5**, (2018).
24. Gray, C. H. J., Morton, D. M., Weber, F. H. J. & Bovard, K. R. *Geologic map of the Corona South 7.5' quadrangle, Riverside and Orange counties, California*. (2002). doi:https://doi.org/10.3133/ofr0221
25. Panofsky, A. I. Stanford Paleoparadoxia Fossil Skeleton Mounting. 1–154 (1998).
26. Boessenecker, R. W. & Churchill, M. A Reevaluation of the Morphology, Paleoecology, and Phylogenetic Relationships of the Enigmatic Walrus Pelagiarctos. *PLoS One***8**, (2013).
27. Boessenecker, R. W. & Churchill, M. The oldest known fur seal. *Biol. Lett.***11**, 20140835 (2015).
28. William S. W. Kew. Geologic Formations of a Part of Southern California and Their Correlation. *Am. Assoc. Pet. Geol. Bull.***7**, 411–420 (1923).
29. Whistler, D. P. & Lander, E. B. New late Uintan to early Hemingfordian land mammal assemblages from the undifferentiated Sespe and Vaqueros formations, Orange County, and from the Sespe and equivalent marine formations in Los Angeles, Santa Barbara, and Ventura counties, Southern Califo. *Bull. Am. Museum Nat. Hist.* 231–266 (2003). doi:10.1206/0003-0090(2003)279<0231:C>2.0.CO;2
30. Jahns, R. H. *Geology of southern California*. *California Division of Mines and Geology Bulletin***170**, (1954).

31. Gavazzi, L. M., Cooper, L. N., Fish, F. E., Hussain, S. T. & Thewissen, J. G. M. Carpal Morphology and Function in the Earliest Cetaceans. *J. Vertebr. Paleontol.* (2020). doi:10.1080/02724634.2020.1833019
32. The City of Corona. City of Corona. (2021). Available at: https://www.coronaca.gov.
33. Tedford, R. H. *et al.* Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs). in *Late Cretaceous and Cenozoic Mammals of North America: Bio- stratigraphy and Geochronology* 169– 231 (2004).
34. Douglas M. Morton, C.H. Gray Jr., Kelly R. Bovard & Michael Dawson. *Geologic map of the Corona North 7.5' quadrangle, Riverside and San Bernardino counties, California*. (2002).
35. Scheirer, A. H. The Three-Dimensional Geologic Model Used for the 2003 National Oil and Gas Assessment of the San Joaquin Basin Province, California. in *Petroleum Systems and Geologic Assessment of Oil and Gas in the San Joaquin Basin Province, California* (ed. Scheirer, A. H.) 81 (U.S. Geological Survey, 2007). doi:10.3133/pp1713.ch07
36. Dibblee, T. W. & Ehrenspeck, H. E. *Geologic map of the Whittier and La Habra quadrangles (western Puente Hills) Los Angeles and Orange Counties, California*. (2001).
37. Boessenecker, R. W. & Churchill, M. The oldest known fur seal. *Biol. Lett.***11**, 2014–2017 (2015).
38. Ogg, J., Ogg, G. & Gradstein, F. *The Concise Geologic Time Scale*. (Cambridge University Press, 2008).
39. Howard, H. & Barnes, L. G. Middle Miocene marine birds from the foothills of the Santa Ana Mountains, Orange County, California. *Contrib. Sci.***383**, 1–9 (1987).
40. Thomas, H. W. & Barnes, L. G. Discoveries of fossil whales in the Imperial Formation, Riverside County, California. *San Bernardino Cty. Museum Assoc. Spec. Publ.***93**, 34–36 (1993).
41. Powell II, C. L. *Paleontology and significance of the Imperial Formation at Garnet Hill, Riverside County, California*. (1995). doi:https://doi.org/10.3133/ofr95489
42. Parham, J. F., Barron, J. A. & Velez-juarbe, J. Middle and late Miocene marine mammal assemblages fromthe Monterey Formation of Orange County , California. *Geol. Soc. Am. Spec. Pap.***556**, 1–14 (2022).
43. Chinzei, K. Modes of occurrence, geologic ranges and geographic distribution of desmostylians. *Monogr. Assoc. Geol. Collab. Japan***28**, 13–23 (1984).
44. Matsui, K., Sashida, K., Agematsu, S. & Kohno, N. 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. *Palaeogeogr. Palaeoclimatol. Palaeoecol.***471**, 254–265 (2017).
45. Repenning, C. A. & Tedford, R. H. Otarioid Seals of the Neogene. *Geol. Surv. Prof. Pap. 992* 93 (1977).
46. Mitchell, E. D. & Repenning, C. A. The chronologic and geographic range of Desmostylians. *Contrib. Sci.***78**, 3–20 (1963).
47. Barnes, L. G. The sequence of fossil marine mammal assemblages in México. in *Avances en Investigación, Paleontología de Vertebrados: México* (eds. Carranza-Castañeda, O. & Córdoba-

Méndez, D. .) 26–79 (Universidad Autónoma del Estado de Hidalgo, Pachuca, Hidalgo, México, 1998).

48. Watanabe, M. & Kimura, M. Description and taxonomy of desmostylian fossils at 2nd site (4th and 5th excavation) in 1999 and 2000. in *Reports from survey research of Akan Fauna 2* 54–75 (Akan Education Board, 2002).
49. Yoshida, S. & Kimura, M. Description and taxonomy of desmostylian fossils at 2nd site (3rd excavation) in 1998. in *Akan Animal Fossils Research Group, editor. Reports from survey research of Akan Fauna 2* 29–53 (Akan Education Board, 2002).
50. Pyenson, N. D. *et al.* Origin of a widespread marine bonebed deposited during the middle Miocene Climatic Optimum. *Geology* **37**, 519–522 (2009).
51. Rogers, R. R., Eberth, D. A. & Fiorillo, A. R. *Bonebeds: Genesis, Analysis, and Paleobiological Significance*. (University of Chicago Press, 2007). doi:10.7208/chicago/9780226723730.001.0001
52. Velez-Juarbe, J., Domning, D. P. & Pyenson, N. D. Iterative evolution of sympatric seacow (Dugongidae, Sirenia) assemblages during the past ~26 million years. *PLoS One* **7**, (2012).
53. Ogasawara, K. Paleoenvironments of Desmostylid and Cenozoic Events of the Northwestern Pacific. *Bull. Ashoro Museum Paleontol.* **1**, 25–34 (2000).
54. Raschke, R. E., Butler, B., Gant, J. & Stadum, C. Early and middle Miocene vertebrates from the Santa Ana Mountains, California. *Mem. Nat. Hist. Found. Orange Cty.* **1**, 61–67 (1984).
55. Awalt, K. M., Parham, J. F. & Velez-Juarbe, J. Desmostylians from the 'Topanga' Formation of Orange County, California, with comments on tooth ontogeny of paleoparadoxiids. in *Society of Vertebrate Paleontology October 2018 Abstracts of paoers 78th Annual Meeting* 83–84 (2018).
56. Santos, G. P., Parham, J. F. & Beatty, B. L. New data on the ontogeny and senescence of Desmostylus (Desmostylia, Mammalia). *J. Vertebr. Paleontol.* **36**, e1078344 (2016).
57. Pyenson, N. D. & Vermeij, G. J. The rise of ocean giants: Maximum body size in Cenozoic marine mammals as an indicator for productivity in the Pacific and Atlantic oceans. *Biol. Lett.* **12**, (2016).
58. Pyenson, N. D., Parham, J. F. & Velez-Juarbe, J. The dilemma of trade samples and the importance of museum vouchers—caveats from a study on the extinction of Steller's sea cow: a comment on Crerar et al. (2014). *Biol. Lett.* **12**, 20150149 (2016).
59. Aranda-Manteca, F. J., Domning, D. P. & Barnes, L. G. A new middle Miocene sirenian of the genus Metaxytherium from Baja California and California: relationships and palaeobiogeographic implications. *Proc. San Diego Soc. Nat. Hist.* **29**, 191–204 (1994).
60. Stadum, C. J. & Finger, K. L. Paleontology and stratigraphy of the Miocene Saddleback Valley limestone, Orange County, Southern California. *Contrib. Sci.* **524**, 31–49 (2016).
61. Zachos, J., Pagani, H., Sloan, L., Thomas, E. & Billups, K. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science (80-.).* **292**, 686–693 (2001).

Figures

Figure 1

The original label of USNM PAL V 11367. A. a front side; B. a backside. Blue masked areas are old descriptions, and pink areas were presumably added later. In addition, “ACC (accession number) No. 89024” was also written on the label, but we could not identify its meaning. This label is also housed in the National Museum of Natural History, Smithsonian Institution (Washington DC, USA).

Figure 2

USNM PAL V 11367. A. occlusal surface; B. buccal view; C. posterior view; D. lingual side; E. anterior view. All scale bars are 2 cm. prd: protoconid; med: metaconid; hyd: hypoconulid; end: entoconid; ex: extra cusp; crown: dental crown; root: dental root. This figure was created by using Adobe Photoshop and Adobe Illustrator (https://www. adobe.com/). KM took photos in this figure using the EOS M5 camera, and EF-M28mm F3.5 macro IS STM (https://canon.jp/).

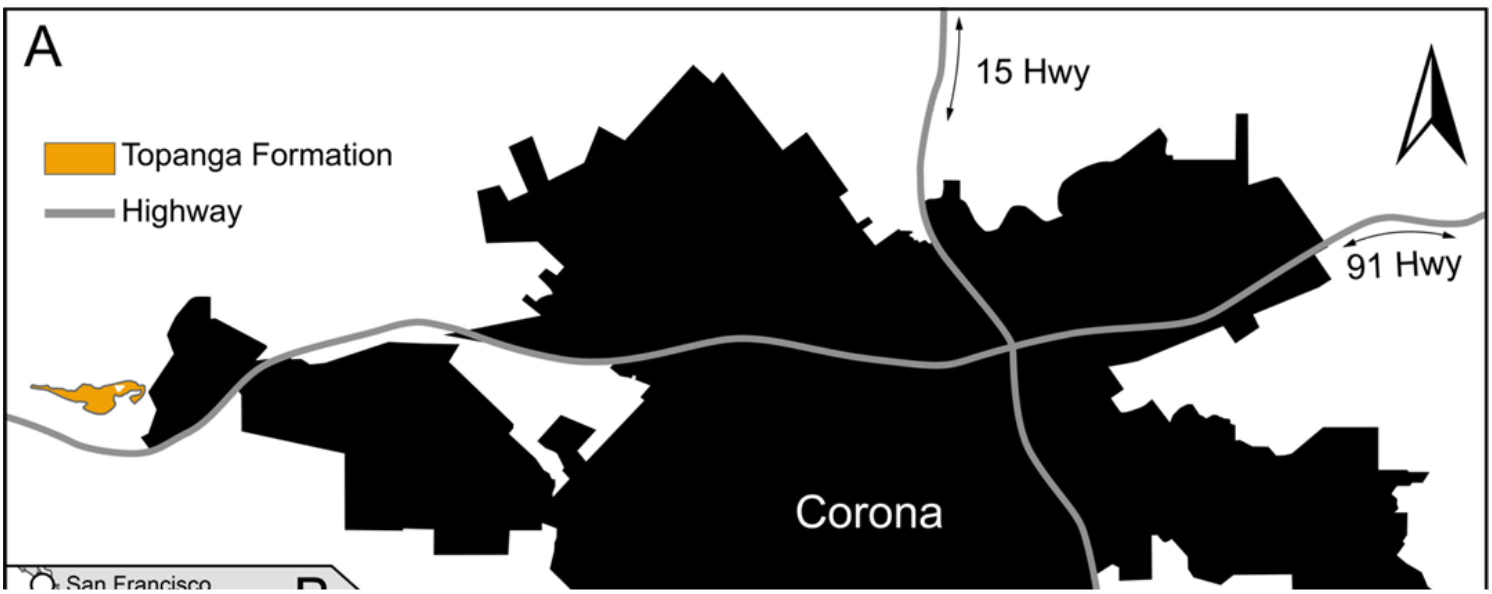

Figure 3

Locality map of *Neoparadoxia*. A. localities of all *Neoparadoxia* previously reported and USNM PAL V 11367. This map is dawned based on geological maps published by Gray et al. [24] and Morton et al. [34]; B. potential localities of USNM PAL V 11367. Orange means distribution area of the "Topanga" Formation in Corona City. The grey line means highways. All figure was created by using Adobe Illustrator (https://www.adobe.com/).

Figure 4

Cusps arrangements of Paleoparadoxiidae. A. simplified cusps arrangement of *Paleoparadoxia* and *Archaeoparadoxia*; B. simplified cusps arrangement of *Neoparadoxia*; C. simple cusps arrangements of *Neoparadoxia* specimens. P: protoconid; M: metaconid; H: hypoconulid; E: entoconid; EX: the extra cusp between H and P; black circle: extra cusps except for EX. All figure was created by using Adobe Illustrator (https://www.adobe.com/).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Supplementary1.csv
- Supplementary2.csv
- TableS1.xlsx