The phylogeny of Desmostylians revisited: proposal of new clades based on robust phylogenetic hypotheses

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Abstract

Background– Desmostylia is ~~one~~ a clade of extinct aquatic mammals with no living members. Today, this clade is considered as belonging to either Afrotheria or Perissodactyla. In the currently-accepted taxonomic scheme, Desmostylia includes two families, 10 to 12 genera, and 13 –14 species. There have been relatively few phylogenetic analyses published on ~~the~~ desmostylian interrelationships compared to other vertebrate taxa, and ~~have been~~ two main, alternative phylogenetic hypotheses have been proposed in previous studies. One major problem with those previous studies is that the numbers of characters and OTUs were small.

Methods– In this study, we analyzed the phylogenetic interrelationships of Desmostylia based on a new data matrix that includes larger numbers of characters and taxa than any previous studies. The new data matrix was compiled based on data matrices of previous studies and included 3 outgroups and 13 desmostylian ingroup taxa. Analyses were carried out using 5 kinds of parsimonious methods.

Results– Strict consensus trees obtained in all analyses supported the monophyly of Desmostylidae and paraphyly of traditional Paleoparadoxiidae. Based on these results, we propose phylogenetic definitions of the clades Desmostylidae and Paleoparadoxiidae based on common ancestry.

Introduction

Desmostylia is ~~one~~ a clade of extinct aquatic mammals with no living members (Repenning, 1965; Inuzuka, 1984a; Inuzuka, 2000a; Inuzuka, 2000b; Domning, 2002; Gingerich, 2005). The phylogenetic affinities of the clade among mammals are still debated, having been hypothesized as belonging to Afrotheria (Domning, Ray and McKenna, 1986), Perissodactyla (Cooper et al., 2014; Rose et al., 2015) or Paenungulatomorpha (Gheerbrant, Filippo, and Schmitt, 2016), due to their specialized morphology (Figure 1).

In the currently-accepted taxonomic scheme, Desmostylia includes two families, 10 to 12 genera, and 13–14 species (Shikama, 1966; Kohno, 2000; Inuzuka, 2005; Domning and Barnes, 2007; Barnes, 2013; Beatty and Cockburn, 2015; Chiba et al., 2016). The two families are Desmostylidae Osborn, 1905, and Paleoparadoxiidae Reinhart, 1959. ~~Traditionally~~Presently, Desmostylidae includes *Ashoroa laticosta*, *Cornwallius sookensis*, *Ounalashkastylus tomidai*, *Kronokotherium brevimaxillare*, *Desmostylus japonicus, D. hesperus* and *D.* (*Va~~o~~nderhoofius*) *coalingensis* (Domning and Barnes, 2007; Inuzuka, 2005; Chiba et al., 2016). Paleoparadoxiidae ~~traditionally~~ has been considered to include~~s~~ two subfamilies, Behemotopsinae ~~that consists of~~comprising *Seuku emlongi*, *Behemotops proteus* and *Behemotops katsuiei* (Domning, Ray and McKenna, 1986; Inuzuka, 2000a; Beatty and Cockburn, 2015) and Paleoparadoxiinae ~~that includes~~comprising *Archaeoparadoxia weltoni*, *Paleoparadoxia tabatai*, *Neoparadoxia repenni~~n~~ngi* and *Neoparadoxia cecilialina* (Barnes, 2013). It is noteworthy, however, that results of some phylogenetic analyses do not support this taxonomic scheme (e.g. Beatty and Cockburn, 2015).

Comment [D1]: "repenningi" and "japonicus" are misspelled in this and following figures. Also, the names should be italicized in all figures and tables.

Previous studies on desmostylian phylogenetic interrelationships

There have been relatively few phylogenetic analyses published on ~~the~~ desmostylian interrelationships compared to other vertebrate taxa. The results of previous studies are summarized here (Figure 2; Table 1). Domning, Ray and McKenna (1986) performed the first phylogenetic analysis that included~~s~~ Desmostylia. Before their study, Osborn (1905) and Reinhart (1953) suggested that Desmostylia is closely related to Sirenia and Proboscidea, and this hypothesis had been widely ~~been~~ accepted. However, it had not been demonstrated to which of these two clades Desmostylia is more closely related. Domning, Ray and McKenna (1986) analyzed phylogenetic relationships among *Prorastomus*, *Protosiren*, crown Sirenia, the primitive tethytherian *Minchenella, Anthracobune, Moeritherium, Barytherium, Prodeinotherium, Deinotherium, Paleomastodon*, crown Proboscidea and Desmostylia including *Behemotops proteus*, *B. emlongi*, *Paleoparadoxia*, *Cornwallius* and *Desmostylus*. As a result, Desmostylia was found to be most closely related to Proboscidea. In addition, Domning, Ray and McKenna (1986) proposed the hypothesis that *Minchen~~l~~ella* was a suitable candidate for the ancestor (or the sister taxon) of the clade consisting of Desmostylia and Proboscidea, suggesting the origin of the latter two clades in Asia.

Clark (1991) performed the first phylogenetic analysis of ~~the~~ desmostylian inter-relationships including the new species of *Paleoparadoxia* that he described. His analysis included~~s~~ *Behemotops emlongi*, *B. proteus*, *Cornwallius*, *Desmostylus*, *Paleoparadoxia tabatai*, *P. weltoni* and two undescribed desmostylian specimens as OTUs. The result corroborated the monophyly of *Paleoparadoxia* and strongly supported a clade consisting of *Desmostylus*, *Cornwallius* and *Paleoparadoxia*. However, the relationship between *Paleoparadoxia* and the clade including *Desmostylus* and *Cornwallius* was unresolved.

Inuzuka (2000a, 2005) proposed a new phylogenetic tree of Desmostylia encompassing all valid desmostylian species including new primitive desmostylid materials described in Inuzuka (2000a). His data matrix includes more post-cranial characters than ~~those~~ were used in previous phylogenetic analyses of desmostylians. However, the methods employed for these phylogenetic analyses were not described in either paper. According to ~~his~~ Inuzuka's results, Desmostylia consists of two clades, Desmostylidae (*A. laticosta*, *C. sookensis*, *K. brevimaxillare*, *D. hesperus*, *D. japonicus* and *D. coalingensis*) and Paleoparadoxiidae (*B. proteus*, *B. katsuiei*, *P. weltoni*, "*P. media*" and "*P. tabatai*").

Beatty (2009) assembled a new matrix based on previous studies and included new data on *Cornwallis sookensis*. He used *Moeritherium* and *Pezosiren portelli*~~i~~ as outgroups of Desmostylia and included nearly all species of Desmostylia. The tree that Beatty (2009) obtained is different in topology from the one in Inuzuka (2000a and 2005) in that *Behemotops* spp. were placed below the node containing other traditional paleoparadoxiids, making the traditional family Paleoparadoxiidae paraphyletic.

Barnes (2009) made a new data matrix for analyzing the phylogenetic position of a new paleoparadoxiid as well as the inter-relationships of Paleoparadoxiinae. His data matrix includes numerous post-cranial skeletal characters. In the cladogram that he obtained, three formerly-known ~~three~~ species of *Paleoparadoxia* (separated into three genera by Barnes, ~~(~~2013~~)~~) formed the clade Paleoparadoxiinae. The problem with his analysis, however, is that it was based on the assumption of the traditional Paleoparadoxiidae including *Behemotops* being monophyletic. This assumption was not rigorously tested and was challenged by Beatty (2009).

A more recent analysis by Chiba et al. (2016) was ~~performed~~ based on a data matrix modified from Beatty (2009). Chiba et al. (2016) added two molar characters to Beatty (2009)'s

matrix and analyzed the phylogenetic position of *Ounalashkastylus*. The ~~obtained~~ resulting tree has a topology similar to the one obtained in Beatty (2009), with *Ounalashkastylus* placed between *Cornwallius* and the clade consisting of *Desmostylus* and *Vanderhoofius* spp.

Purpose of this study

The above review of ~~the~~ past phylogenetic analyses points to problems with these studies. Firstly, not all valid desmostylian species were included in most previous analyses. Secondly, almost all analyses were based on the assumption that Desmostylia is a member of Afrotheria. Recently, however, this assumption was challenged based on a phylogenetic analysis indicating that Desmostylia is a part of Perissodactyla (Cooper et al., 2014; Rose et al., 2015) or Paenungulatomorpha (Gheerbrant, Filippo, and Schmitt, 2016). If this is the case, using afrotherians (e.g., proboscideans and/or sirenians) as outgroups for a phylogenetic analysis ~~on~~ of ~~the~~ desmo~~n~~stylian interrelationships is problematic. It is instead necessary to run phylogenetic analyses using alternative outgroups representing different hypotheses of affinities of Desmostylia to examine effects of outgroup selections. Thirdly, for the numbers of taxa being analyzed, relatively few characters were used in past analyses. To summarize, global phylogeny of Desmostylia still needs to be analyzed by (1) incorporating all currently ~~valid~~ accepted species, (2) using several outgroups reflecting various hypothes~~i~~s of desmostyian affinities, and (3) producing a data matrix with more characters.

In order to rectify these three problems, a new, largest data matrix for ~~the~~ desmostylian interrelationships was assembled in this study and was ~~run by~~analyzed using different outgroups reflecting currently-proposed hypotheses ~~on~~ of desmostylian affinities. The resulting trees were

then used to obtain a robust topology independent of outgroups ~~for~~ in order to propose~~ing~~ new phylogenetic definitions of the clades Desmostylidae and Paleoparadoxiidae.

Materials & Methods

Taxon Sampling

1. Outgroups

In this study, three separate analyses were performed using different outgroups to account for uncertainty of ~~the~~ desmostylian affinities with other mammals. Desmostylia has been hypothesized as belonging to Afrotheria, Perissodactyla or Paenungulatomorpha. In the case of the Afrotherian hypothesis, it is not certain whether Desmostylia is closer to Sirenia or Proboscidea. Herein the following three analyses using different sets of outgroups were conducted. These analyses cover all appropriate outgroups suggested by the three phylogenetic hypotheses above.

(1) Analysis 1. *Anthracobune* spp. as the outgroup (coding based on Cooper et al. (2014)),

(2) Analysis 2. *Pezosiren portelli*~~*rii*~~, a primitive sirenian, and *Moeritherium* spp., a primitive proboscidean, as the outgroups (coding based on NMNS PV-20726, 20970–4, Andrews (1904 and 1906), Holroyd et al. (1996), and Delmer et al. (2006)),

(3) Analysis 3. *Anthracobune* spp., *Pezosiren portelli*~~*rii*~~ and *Moeritherium* spp. as the outgroups.

2. In-group taxa

In this study, 13 species of desmostylians were included as OTUs. All ~~valid~~ presently-accepted desmostylian species were included. A possible exception is *Kronokotherium brevimaxillare*. ~~although this taxon~~which has been considered ~~as~~ a junior synonym of *Desmostylus hesperus*

(Domning, 1996) and is known only from highly fragmentary specimens (Pronina, 1957; Beatty, 2009). The following is the list of OTUs with sources for coding.

1. *Behemotops proteus* (based on USNM 244035; Domning, Ray and McKenna, 1986; Beatty and Cockburn, 2015; Ray, Domning and McKenna, 1994)
2. *Behemotops katsuiei* (based on AMP 22; Inuzuka, 2000a; Inuzuka, 2009)
3. *Seuku emlongi* (based on USNM 244033 and 186889; Domning, Ray, and McKenna, 1986; Beatty and Cockburn, 2015; Ray, Domning, McKenna, 1994)
4. *Archaeoparadoxia weltoni* (based on UCMP 114285; Clark, 1991)
5. *Paleoparadoxia tabatai* (based on NMNS PV-5601; Shikama, 1966; Ijiri and Kamei, 1961)
6. *Neoparadoxia repenningi* (based on UCMP 81302; Inuzuka, 2005)
7. *Neoparadoxia cecilialina* (based on LACM 150150; Barnes, 2013)
8. *Ashoroa laticosta* (based on AMP 21; Inuzuka, 2000a; Inuzuka, 2011)
9. *Cornwallius sookensis* (based on USNM 11073, 11075, 181738, 181740, 181741, and 214740; Beatty, 2006 and 2009)
10. *Ounalashkastylus tomidai* (based on Chiba et al., 2016; Jacobs et al., 2007; Jacobs et al., 2009)
11. *Desmostylus japonicus* (based on NMNS PV-5600; GSJ-F02071; Kohno, 2000; Yoshiwara and Iwasaki, 1902)
12. *Desmostylus hesperus* (based on UHR-18466; GSJ-F7743; UCMP 32742; Ijiri and Kamei, 1961; Inuzuka, 1980a, 1980b, 1981a, 1981b, 1982, 1988, and 2009)
13. *Desmostylus* (*Vanderhoofius*) *coalingensis* (based on USNM 244489; UCMP 39990; Reinhart, 1959; Inuzuka, 2005; Beatty, 2009)

Software and Analysis

The data matrix was assembled in Mesquite v 3.51 (Maddison and Maddison, 2011). Analyses were conducted with equally weighted parsimony with PAUP* (Swofford, 2003) version 4.0a, build 164 for Macintosh using the heuristic search algorithm with Tree Bisection Reconnection (TBR) branch swapping (saving 10 trees per replication). Branch support was estimated with the bootstrap resampling method (10,000 replicates). Phylogenetic trees were illustrated by using the geoscalePhylo function in the Strap package (Gradstein, Ogg, and Schmitz, 2012) for the statistical programming language R (R Core Team, 2017). The divergence time estimation was also calculated by the geoscalePhylo function in the Strap package.

Comment [D2]: Correct ref. ??

Characters and Data Matrices

Firstly, analyses were run based on previously-published character matrices (Inuzuka, 2000a; Barnes, 2013; Chiba et al., 2016; Clark, 1991; Beatty, 2009) to verify the published tree topologies. Secondly, those matrices were compiled, with coding revised and new characters added. Overall, 110 morphological characters were employed in the new matrix (Figure 3). Character descriptions and data matrices are provided in S1 File and S1 Table.

Results

Reproducibility of previous data matrices

Among previously-published data matrices, only the data matrix of Inuzuka (2005) did not produce the original topology presented in the paper (S1 Figure).

Analyses based on a new data matrix

Bootstrap consensus trees obtained in all the analyses showed the identical topology (Figure 4; S3, 6, 9 Figures) whereas strict consensus trees (S2, 5, 8 Figures) of these analyses had partly different topologies. However, all these topologies (Figure 4, S2–3, 5–6, and 8–9 Figure) agree on both traditional Paleoparadoxiinae including *Archaeoparadoxia*, *Paleoparadoxia* and *Neoparadoxia* and traditional Desmostylidae including *Ashoroa*, *Cornwallius*, *Ounalashkastylus* and *Desmostylus* being monophyletic as well as on Desmostylidae + Paleoparadoxiinae forming a clade. On the other hand, Paleoparadoxiidae *sensu* Inuzuka (2000a, 2005) and Barnes (2013) that includes *Paleoparadoxia*, *Archaeoparadoxia*, *Neoparadoxia*, *Seuku* and *Behemotops* spp. was not recovered as a clade. The positions of *Behemotops* spp. and *Seuku* differ~~s~~ among the strict consensus trees obtained in Analyses 1–3. In ~~the~~ all the bootstrap consensus trees of these analyses, *Behemotops* and *Seuku* formed an unresolved polytomy with the clade containing the ~~rest of~~remaining desmostylians. These genera thus diverged before the split between Paleoparadoxiinae and Desmostylidae.

Discussion

Reproducibility of data matrices

The analysis based on Inuzuka's (2005) original data matrix produced a completely unresolved polytomy with no resolution. This matrix includes ~~a~~ relatively few characters for the number of OTU~~T~~s, likely contributing to non-resolution of the tree topology.

Characters supporting each clade in the present analyses

Although not all character distributions were shared among the strict consensus trees of Analyses 1 through 3 (S4, 7, 10 Figures), many common synapomorphies were found for major clades. Such synapomorphies identified in ~~the~~ all the strict consensus trees are described ~~herein~~below.

The monophyly of traditional Desmostylidae consisting of *Ashoroa*, *Cornwallius*, *Ounalashkastylus* and *Desmostylus* was supported by the presence of 6 or more cusps on M2 (Character 28, state 1), ~~a~~ conical and tusk-like lower incisors (Character 32, state 2), ~~the~~ no passage anterior to the external auditory meatus ~~not~~ connecting to the skull roof (Character 37, state 1), ~~the~~ presence of ~~the~~ an anterior orbital groove (Character 46, state 1), ~~the~~ tibia ~~that is~~ medially twisted with the distal articular surface facing ~~medially~~ laterally ~~inclined~~ (Character 88, state 1) and ~~fused~~ radius and ulna fused (Character 98, state 1). The monophyly of traditional Paleoparadoxiinae consisting of *Archaeoparadoxia*, *Paleoparadoxia* and *Neoparadoxia* was supported by the p4 talonid with the hypoconid and entoconid reduced in height (Character 15, state 1), the mandibular symphysis rotated anteroventrally (Character 68, state 1) and a flat femoral shaft (Character 110, state 2). The clade consisting of Paleoparadoxiinae +

Comment [D3]: Use a more economical way of writing this, such as c. 28(1).

Desmostylidae was supported by the absence of the p3 paraconid (Character 12, state 1), fused double roots of p3 and p4 (Character 14, state 2), swollen and appressed molar cusps (Character 17, state 1), enlarged p4-m3 hypoconulid and entoconid (Character 18, state 1) and a large diastema between the canine and cheek teeth (Character 73, state 2). Synapomorphies of Desmostylia are ~~the~~ a tusk root ~~with~~ enlarged in diameter (Character 5, state 1), an enlarged lower canine (Character 6, state 1), a transversely broad hypoconulid shelf of m3 (Character 16, state 1), transversely aligned lower incisors (Character 30, state 1), a flattened or conical and tusk-like lower incisor (Character 32, states 1 & 2) and the presence of the foramen post-zygomaticus (Character 41, state 1). The monophyly of *Desmostylus* (*D. japonicus* + *D. hesperus* + "*Vanderhoofius*" *coalingensis*) was supported by the loss of the upper canine (Character 3, state 1), the presence of one pair of upper incisors (Character 33, state 1) and the laterally ~~expanded~~ convex interalveolar margin in the diastema of the mandible (Character 70, state 1). The monophyly of *Neoparadoxia* was supported by ~~a~~a small angle ~~of~~ between the anterior and posterior margins of the coronoid process (Character 65, state 1), the tibia–fibula articulation enlarged and extended proximally (Character 106, stale 1) and the astragalar facet on the tibia tilted at least ~~at~~ 60 degrees from horizontal (Character 107, state 1).

Comment [Rev4]: I question whether the upper C is really ever lost in any of these species.

Comment [Rev5]: Also change definition in character list to match description of Inuzuka (2005: 64). The abbreviated definition here is not intelligible.

Comparisons with MPTs and synapomorphies for clades obtained in previous studies

In this study, a new data matrix was constructed including more characters and taxa than those used in previous studies ~~was constructed~~. The present MPT topologies are clearly different from the one presented in Inuzuka (2000a, 2005) but are mostly consistent with the one in Beatty (2009). An assumption by Barnes (2013) that both Paleoparadoxiinae and Paleoparadoxiidae were monophyletic was rejected herein. In addition, the relationship among

Archaeoparadoxia, *Paleoparadoxia* and Desmostylidae was unresolved in Chiba et al. (2016). likely because their matrix did not include ~~a large~~ enough ~~number of~~ characters. In this study, the data matrix consisting of more characters successfully resolved the relationship among these three taxa.

The~~se~~ synapomorphies identified in the present study are ~~fairly~~ somewhat different from those proposed by previous studies. Clark (1991) identified 2 synapomorphies for traditional Paleoparadoxiinae and 3 synapomorphies for Desmostylidae + Paleoparadoxiinae. However, the present analyses did not find any of these characters diagnosing these clades except for Clark's (1991) Character 29 (Character 68 in the present data matrix) ~~diagnosing these clades~~. As an OTU, Clark's (1991) matrix included an undescribed specimen (USNM 23895) not included in the present analyses, possibly causing differences in synapomorphies of these clades.

Inuzuka (2005), on the other hand, identified four synapomorphies for Desmostylia, 6 for Desmostylidae, 3 for traditional Paleoparadoxiinae and 2 for *Desmostylus*. None of those synapomorphies identified in Inuzuka (2005; his Characters 1, 3, 8, 12, 14, 15, 31, 32, 34 and 35) supported these clades in the present analyses. The strict consensus topologies obtained in the present analyses are different from the one presented in Inuzuka (2005). Therefore, such differences may be expected.

Taxonomy of Desmostylia

The present results suggest that the previously-proposed taxa Desmostylidae and Paleoparadoxiinae are monophyletic and valid. On the other hand, Paleoparadoxiidae including *Behemotops* (Inuzuka, 2001; Barnes, 2013; Inuzuka, 2009) turned out to be paraphyletic. Therefore, the currently-used taxon Paleoparadoxiidae needs to be re-defined as a clade excluding *Behemotops*, ~~which has~~leaving it with the same taxonomic content as the currently-used Paleoparadoxiinae (Beatty, 2009). *Behemotops* and *Seuku* are not included in either monophyletic Desmostylidae or Paleoparadoxiidae. Additionally, *Vanderhoofius* (=~~"~~*"Desmostylus*") *coalingensis*, *D. hesperus* and *D. japonicus* formed a clade in the strict consensus trees of all present analyses. Therefore, these results support the hypothesis of Kohno (2000) and Santos et al. (2016) that *Vanderhoofius* ~~was~~ is a junior synonym of *Desmostylus*.

New Definition of Desmostylian Clades

In this study, the monophyly of traditional Paleoparadoxiidae was rejected. Desmostylian families have been defined based on a traditional convention of simply enumerating included taxa. Such an approach was regarded as non-evolutionary by de Queiroz and Gauthier (1990, 1992, and 1994). These authors instead proposed phylogenetic definitions of taxon names, i.e., defining taxon names in terms of common ancestry, which has resulted in the proposal of the formal International Code of Phylogenetic Nomenclature (PhyloCode) governing the naming of clades (Cantino and de Queiroz, 2010). Their rationale is followed here and traditional

desmostylian family names are converted to clade names with new definitions following the PhyloCode rules.

DESMOSTYLIDAE OSBORN, 1905 (CONVERTED CLADE NAME)

Definition: Desmostylidae refers to the clade consisting of *Desmostylus hesperus* Marsh, 1888 and all organisms or species that share a more recent common ancestor with *D. hesperus* than with *Paleoparadoxia tabatai* Tokunaga, 1939.

Comments: Because the Order Desmostylia is currently divided into two families, Desmostylidae and Paleoparadoxiidae, it is appropriate to convert these taxa to branch- or stem-based clades so that all desmostylian species except for a few, early-diverging forms (e.g., those regarded as Family indeterminate by Beatty and Cockburn, 2015) are included in one of these clades. All taxa traditionally regarded as ~~comprising~~ constituting Desmostylidae formed a clade in the present analyses (Figure 4). Therefore, the converted clade of Desmostylidae includes the same set of currently valid taxa as the traditional Family Desmostylidae.

Based on the current analyses, Desmostylidae is diagnosed by the following characteristics: the presence of 6 or more cusps on M2, a conical and tusk-like lower incisor, ~~the~~ no passage anterior to the external auditory meatus ~~not~~ connecting to the skull roof, the presence of an anterior orbital groove, ~~the~~ a tibia that is medially twisted with the distal articular surface medially inclined, and the astragalar facet on the tibia tilted at least ~~at~~ 60 degrees from horizontal.

PALEOPARADOXIIDAE REINHART, 1959 (CONVERTED CLADE NAME)

Comment [D6]: Without ranks?

Comment [D7]: Here and below, it would be helpful to the reader to re-state the character and state numbers of each of these diagnostic features.

Comment [Rev8]: OK?

Definition: Paleoparadoxiidae refers to the clade consisting of *Paleoparadoxia tabatai* Tokunaga, 1939 and all organisms or species that share a more recent common ancestor with *P. tabatai* than ~~to~~ with *Desmostylus hesperus* Marsh, 1888.

Comments: Traditionally-recognized paleoparadoxiids formed a paraphyletic group and thus did not form a clade in all present analyses (Figure 4), necessitating a revision of the content of the taxon. Based on the present analyses, the clade Paleoparadoxiidae is diagnosed by the following synapomorphies: the p4 talonid with the hypoconid and entoconid reduced in height, the mandibular symphysis rotated anteroventrally, and a flat femoral shaft.

DESMOSTYL~~I~~OIDEA OSBORN, 1905 (NEW CLADE NAME)

Definition: Desmostyloidea refers to the clade originating with the most recent common ancestor of *Desmostylus hesperus* Marsh, 1888 and *Paleoparadoxia tabatai* Tokunaga, 1939.

Comments: The new clade Desmostyloidea includes Desmostylidae and Paleoparadoxiidae as its subclades. Because these two clades are defined above as branch-based clades ~~above~~, any member of Desmostyloidea belongs to either Desmostylidae or Paleoparadoxiidae.

The following synapomorphies of Desmostyloidea were identified in the present analyses: the absence of the p3 paraconid, fused double roots of p3 and p4, swollen and appressed molar cusps, enlarged p4-m3 hypoconulid and entoconid, and a large diastema between the canine and cheek teeth.

DESMOSTYLIA REINHART, 1953 (CONVERTED CLADE NAME)

Comment [D9]: This name was previously used by Abel (1933) for the desmostylians, considered as an order within Multituberculata; however, in this usage it is a nomen oblitum. But what is the justification for attributing this name to Osborn, 1905?

Note also that Desmostyloidea at present has the same content as Desmostylia, and is therefore redundant (at least for the time being).

Are you proposing to abandon ranks for desmostylians? If so, that should be made explicit (and I don't recommend it); but if not, would you call Desmostyloidea a suborder?

Definition: Desmostylia refers to the clade originating with the first organism or species to possess ~~the~~ as an apomorphy the transversely broad hypoconulid shelf of the third molar, as inherited by *Desmostylus hesperus* Marsh, 1888.

Comments: The Order Desmostylia was established by Reinh~~e~~art (1953) for the genera *Desmostylus* and *Cornwallius*. Since then, ~~many~~ several new genera ~~were~~ have been referred to this order by Reinh~~a~~art (1959), Domning, Ray and McKenna~~,~~ (1986), Inuzuka (2000), Barnes (2013), Beatty and Cockburn (2015) and Chiba et al. (2016). In the present analyses, such genera were all found to be included in one~~a~~ clade and share numerous synapomorphies.

Several alternative phylogenetic definitions of Desmostylia are possible, ~~while~~ but the newly defined clade approximates traditional use of the name. The node-based definition would be "the clade originating with the most recent common ancestor of *Desmostylus hesperus* Marsh, 1888, *Paleoparadoxia tabatai* Tokunaga, 1939, *Seuku emlongi* (Domning, Ray and McKenna, 1986), *Behemotops proteus* (Domning, Ray and McKenna, 1986), and *Behemotops katsuiei* Inuzuka, 2000". This definition, however, would exclude from the clade earlier-diverging or "stem" species on this lineage ~~from the clade~~. The branch-based definition, on the other hand, would be "the clade consisting of *Desmostylus hesperus* Marsh, 1888 and all organisms or species that share a more recent common ancestor with *D. hesperus* than with *Anthracobune pinfoldi* Pilgrim, 1940, *Trichechus manatus* Linnaeus, 1758, or *Elephas maximus* Linnaeus, 1758", considering currently hypothesized sister clades of Desmostylia. However, the exact relationships of Desmostylia with other mammalian clades are still debated and it is possible that other clades will turn out to be more closely related to Desmostylia than those that ~~are~~ have been hypothesized. Considering that such a case would result in a wildly different taxonomic content of Desmostylia than that currently recognized, this branch-based definition also appears

Comment [D10]: Surely other mammals have evolved a "transversely broad hypoconulid shelf". This seems like a weak basis on which to diagnose an order!

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inappropriate. Considering that members of this taxon ~~has~~ have been recognized based on their shared, unique dental morphology, it is most reasonable to adopt the apomorphy-based definition as proposed here.

Comment [D11]: Originally, this referred to the columnar molars of *Desmostylus*, which are NOT shared by all desmostylians now recognized.

Conclusions

In this study, a new data matrix was assembled for analyzing phylogenetic relationships of Desmostylia. The results of the analyses support a monophyletic Paleoparadoxiinae consisting of *Archaeoparadoxia*, *Paleoparadoxia* and *Neoparadoxia*, as well as a Desmostylidae consisting of *Ashoroa*, *Cornwallius*, *Ounalashkastylus*, and *Desmostylus*. In addition, *Behemotops* and *Seuku* turned out to form an unresolved polytomy with the clade of Paleoparadoxiinae + Desmostylidae. Based on these results, the phylogenetic definitions of Desmostylia, Desmostylidae and Paleoparadoxiidae, as well as a new clade Desmostyloidea, are proposed.

Institutional abbreviations

AMP: Ashoro Museum of Paleontology, Hokkaido, Japan; GSJ: Geological Survey of Japan, Ibaraki, Japan; LACM: Natural History Museum of Los Angeles County ~~Museum~~, Los Angeles, California, USA; NMNS: National Museum of Nature and Science, Tokyo, Japan; UCMP: University of California Museum of Paleontology, Berkeley, California, USA; UHR: Hokkaido University Museum, Sapporo, Japan; USNM: Department of Paleobiology, U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

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Character list

Teeth

General dental morphology

1. Tooth column: normal (0), with thickened enamel (1) (after Inuzuka, 2005, character 26).
2. Dental root: relatively short (0), extremely elongated (1) (after Inuzuka, 2005, character 5).

Canines

3. Upper canine: present (0), absent (1) (after character 26; Beatty, 2009).
4. Lower canine tusk: circular in cross section (0), mediolaterally compressed (1) (after character 27; Beatty, 2009).
5. Lower canine root: not enlarged in diameter (0), enlarged in diameter to form a tusk (1) (after character 17; Barnes, 2013).
6. Lower canine crown: small (0), enlarged (tusk-like) (1) (after character 5; Clark, 1991).

Premolars

7. p1: present (0), absent (1) (after character 7; Clark, 1991).
8. p2: present (0), absent (1) (character 8; Clark, 1991).
9. p2: pre-molariform, with a small cusp anterior to the main cusp and a small talonid (0), with a main cusp and a talonid cusp only(1), caniniform (2) (after character 10; Clark, 1991).
10. p2: single-rooted (0), double-rooted (1), with fused double roots (2) (after character 11; Clark, 1991).

Comment [D12]: Do this for all characters (put author & date first).

Comment [D13]: I question whether it is absent in any desmostylian.

Comment [D14]: Is it also open and ever-growing?

Comment [D15]: OK?

11. p3: present (0), absent (1) (after character 18; Barnes, 2013).

12. p3: paraconid present (0), lost (1) (after character 12; Beatty, 2009).

13. p4: paraconid at the anterior end of the tooth small (0), enlarged (1), reduced to a vestige (2), absent (3) (after character 19; Barnes, 2013).

14. Roots of p3 and p4: single-rooted (0), double-rooted (1), with fused double roots (2) (after character 12; Clark, 1991).

15. p4 talonid: two posterior cusps, the hypoconid and entoconid, equal in height to the anterior two cusps, the protoconid and metaconid (0), the hypoconid and entoconid reduced in height (1) (after character 20; Barnes, 2013).

Molars

16. Hypoconulid shelf of m3: not broadened (0), transversely broad (1) (after character 1; Beatty, 2009).

17. Molar cusps: not swollen, separated (0), swollen and appressed (1) (after character 8; Beatty, 2009).

18. p4-m3 hypoconulid and entoconid: not enlarged (0), enlarged, especially entoconid (1) (after character 9; Beatty, 2009).

19. m2: without extra cuspid (0), with incipient extra cuspid between and labial to protoconid and hypoconid (1), with extra cuspid well developed (2) (after character 10; Beatty, 2009).

20. Extra cusps of molars: absent (0), incipient (1), large, approaching size of main cusps (2) (after character 15; Beatty, 2009).

21. Molars: brachydont (0): hypsodont, cusps columnar (1) (after character 21; Beatty, 2009).

Comment [D16]: It is problematical to distinguish this from state 0.

22. Bony swelling medial to lower molars: absent (0): present (1) (after character 24; Beatty, 2009).

23. m3: with hypoconulid present (0), absent (1) (after character 22; Barnes, 2013).

24. m1: as long as, or longer than, p4 (0) smaller than p4 (1), much smaller than p4 (2) (after character 15; Clark, 1991).

25. m2: without cusp labially between the protoconid and hypoconid (0), with cusp (1) (after character 16; Clark, 1991).

26. Cusps on molar: asymmetrical and strongly tapered (0), columnar and gradually tapered with thick enamel (1) (after character 18; Clark, 1991).

27. Cingulum on molariform teeth: forms distinct ridge (0) forms low swelling (1), absent (2) (after character 20; Clark, 1991).

28. Number of major cusps on M2: fewer than 6 (0), 6 or more (1) (after character 38; Chiba et al., 2016).

29. Number of major cusps on M3: fewer than 7 (0), 7 or more (1) (after character 39; Chiba et al., 2016).

Incisors

30. Lower incisors: anteroposteriorly or obliquely aligned (0), transversely aligned (1) (after character 4; Beatty, 2009).

31. Number of lower incisors: three (0), two (1), one (2), zero (3) (after character 16; Beatty, 2009).

32. Shape of lower incisors: simple and small (0), flattened (1), conical and tusk-like (2) (after character 22; Beatty, 2009).

Comment [D17]: These and other definitions need to be quantified (or otherwise clarified) if other people are going to use them.

33. Pairs of upper incisors: zero (0), one (1), two (2) (after character 23; Beatty, 2009).

34. Incisors: with enamel (0), lacking enamel (1) (after character 30; Beatty, 2009).

35. i2 crown: medial and lateral margins parallel-sided (0), expanded transversely to the extent that its lateral margin is curved laterally (1) (after character 15; Barnes, 2013).

Skull

36. Foramen within squamosal passing anterad from external auditory meatus: absent (0), present (1) (after character 21; Clark, 1991).

37. Passage anterior to external auditory meatus: connects with skull roof (0), does not connect (1) (after character 22; Clark, 1991).

38. Posterior part of premaxilla: short (0), elongate (1) (after character 26; Clark, 1991).

Comment [D18]: Quantify!

39. External auditory meatus: low on skull, open ventrally (0), high on skull, closed ventrally (1) (after character 2; Beatty, 2009).

40. Paroccipital process: not elongated (0), elongated (1) (after character 5; Beatty, 2009).

41. Foramen post-zygomaticus: absent (0), present (1) (after character 6; Beatty, 2009).

42. Premaxilla: does not contact the frontal (0), contacts the frontal (1) (after character 18; Beatty, 2009).

43. Sagittal crest: present (0), absent (1) (after character 19; Beatty, 2009).

44. Zygomatic process of the squamosal: not dorsoventrally broadened (0), broadened (1) (after character 25; Beatty, 2009).

45. Inter-premaxillary dorsal tuberosity: absence of a tuberosity anterior to the external nares on the dorsal surface of the symphysis between the premaxillary bones (0), presence of such a tuberosity (1) (after character 34; Beatty, 2009).

46. Anterior orbital groove: absent (0), present (1) (after character 35; Beatty, 2009).

47. Infraorbital foramen placement with respect to the orbit: in the same coronal plane with the orbit (0), in a coronal plane anterior to that of the orbit (1) (after character 36; Beatty, 2009).

48. Post-zygomatic foramen orientation with respect to the epitympanic sinus: foramen lies either directly anterior or antero-superior to the epitympanic sinus (0), foramen lies antero-inferior to the epitympanic sinus (1) (after character 37; Beatty, 2009).

49. Basioccipital bone: elongated (0), shortened (1) (after character 1; Inuzuka, 2000, 2005).

50. Braincase expansion: small (0), large (1) (after character 8; Inuzuka, 2000, 2005).

51. Zygomatic process: lower level (0), caudally inclined (1) (after character 31; Inuzuka, 2000, 2005).

52. Paroccipital process: normal (0), thickened (1) (after character 32; Inuzuka, 2000, 2005).

53. Median nuchal crest: in usual position (0), more cranially projected (1) (after character 34; Inuzuka, 2000, 2005).

54. Skull: normal proportion (0), narrower for its length (1) (after character 37; Inuzuka, 2000, 2005).

55. Nasal part: low (0), high (1) (after character 38; Inuzuka, 2000, 2005).

56. Zygomatic arch: not inclined medially (0), medially inclined (1) (after character 44; Inuzuka, 2000, 2005).

57. Zygomatic arch: normal location (0), lower for its length (1) (after character 45; Inuzuka, 2000, 2005).

58. Dorsal narial opening: restricted to the anterior end of the snout (0), enlarged and extended posteriorly (1) (after character 3; Barnes, 2013).

Comment [D19]: Quantify!

Comment [D20]: Quantify! At least by reference to some other structure.

Comment [D21]: Explain.

Comment [D22]: Again, definitions like these are not very useful to someone who is unfamiliar with this taxonomic group.

Comment [D23]: Ditto. Quantify!

Comment [D24]: Explain better.

Comment [D25]: At dorsal edge??

Comment [D26]: Explain better.

Comment [D27]: How far (e.g., relative to orbit)?

59. Nasal bones: elongate (0), shortened anteroposteriorly (1) (after character 4; Barnes, 2013).

60. Nasal bones: not widened transversely (0), or widened transversely (1) (after character 5; Barnes, 2013).

61. Dorsal surfaces of the supraorbital processes of the frontal: not elevated above the level of the interorbital region of the cranium (0), elevated dorsally above the level of the interorbital region of the cranium (1) (after character 6; Barnes, 2013).

62. Supraorbital processes of the frontals: small and not projecting very far laterally (0), intermediate (1), widened to the extent that the lateral margins of the postorbital processes project laterally beyond the jugal bones of the zygomatic arches (2) (after character 7; Barnes, 2013).

Mandible

63. Posterior end of the jugal bone: extends posteriorly to reach the anterolateral corner of the glenoid fossa (0), retracted anteriorly and does not reach the glenoid fossa (1) (after character 9; Barnes, 2013).

64. Upper margin of mandibular body: slightly curved (0), sigmoid (1) (after character 30; Inuzuka, 2000, 2005).

65. Angle between the anterior and posterior margins of coronoid process: large (0), small (1) (after character 24; Inuzuka, 2000, 2005).

66. Coronoid crest (= anterior margin of ascending ramus) of the dentary: ascending vertically and curving posteriorly (0), curving anteriorly (1) (after character 10; Barnes, 2013).

67. Mandibular body: not flexed behind p2 (0): ventrally flexed behind p2 (1) (after character 23; Inuzuka, 2000, 2005).

Comment [D28]: Ditto.

Comment [D29]: Maybe cite particular taxa or illustrations to show what you mean.

Comment [D30]: Much better!

Comment [D31]: Definitions 0 and 1 are hard to distinguish; 2 is much better!

Comment [D32]: Include this character under Skull, not Mandible.

Comment [D33]: In what direction?

Comment [D34]: OK?

Comment [D35]: Explain better.

68. Mandibular symphysis: inclined anterodorsally (0), or rotated anteroventrally to become approximately horizontal so that incisors and canines are directed anteriorly (1) (after character 11; Barnes, 2013).

69. Length of mandibular symphysis: less than 25% (0), about 30%(1), more than 40%(2) (after character 35; Inuzuka, 2000, 2005).

70. Interalveolar margin in the diastema of the mandible: not convex laterally (0), convex laterally (1) (after character 43; Inuzuka, 2000, 2005).

71. Bony swelling of mandible in adult; absent (0), developed (1).

72. Diastema between canine and cheek teeth: absent (0), present (1) (after character 6; Clark, 1991).

73. Diastema between p2 and p3: absent (0), small (1), large (2) (after character 9; Clark, 1991).

Postcranial Skeleton

Trunk

74. Sternebrae: unpaired (0), paired (1) (after character 32; Beatty, 2009).

75. Femur shaft: round or oval in cross section (0), flattened (1) (after character 33; Beatty, 2009).

76. Bones of limbs: terrestrial type (0), osteosclerotic (1), pachyosteosclerotic (2), cancellous (3) (after character 20; Beatty, 2009)

77. Bone of vertebrae: terrestrial type (0), osteosclerotic (1), pachyosteosclerotic (2), cancellous (3) (after character 20; Beatty, 2009).

78. Rib cross sections: oval (0), flat (1) (modified after character 36; Inuzuka, 2000, 2005).

Comment [D36]: Of what? The total length of the mandible?

Comment [D37]: This sounds like the same structure as in c. 22.

Comment [D38]: Quantify!

Comment [D39]: Same as c. 110 below?

Comment [D40]: This needs to be better defined.

Comment [D41]: Centrum? Neural arch?

79. Ribs: strongly curved (0), almost straight (1)

80. Thoracic vertebrae, number: 13 (0), 14 or 15 (1), 16 (2), 17 or more (3) (after character 23; Barnes, 2013).

81. Thoracic vertebral transverse processes: projecting laterally, directed away from the vertebral centra (0), inclined dorsolaterally relative to the centra (1) (after character 24; Barnes, 2013).

82. Lumbar vertebrae, number: 5-6 (0), 7 (1) (after character 25; Barnes, 2013).

83. Sacral vertebrae, number: five (0), four (1) (after character 26; Barnes, 2013).

84. Mesosterna: four pairs (0), reduction three pairs (1) (after character 27; Barnes, 2013).

85. Centra, epiphysis: not ring-like (0), ring-like (1).

86. Thoracic vertebrae, spinous processes: approximately straight (0), backwardly inclined (after character 12; Inuzuka, 2000, 2005).

87. Body size: small (0), medium (1), large (2).

Forelimb

88. Tibia: straight (0), medially twisted with its distal articular surface facing laterally (1) (after character 3; Inuzuka, 2000, 2005).

89. Subscapular fossa: nearly flattened (0), deep (1) (after character 14; Inuzuka, 2000, 2005).

90. Humerus, trochlea: enlarged or unchanged (0), decreased in diameter (1) (after character 15; Inuzuka, 2000, 2005).

91. Humeral crest: medially bent (0), less medially bent (1) (after character 22; Inuzuka, 2000, 2005).

Comment [D42]: "Reduction" can't be determined from inspecting one specimen,.

Comment [D43]: Quantify!

Comment [D44]: Belongs under Hindlimb.

Comment [D45]: Try to quantify.

Comment [D46]: Relative to what?

Comment [D47]: Would this be helpful to you if you had to score a specimen for the first time, using this description?

92. Third metacarpal base: not projected (0), proximally projected in the middle (1) (after character 25; Inuzuka, 2000, 2005).

93. Scapula, anterior border: nearly straight (0), slightly curved anteriorly (1), strongly curved anteriorly (2) (after character 28; Barnes, 2013).

94. Scapula, area of teres major muscle attachment on posterior border: concave and rugose (0), smooth, rounded, and convex (1) (after character 29; Barnes, 2013).

95. Ulna, olecranon process: narrow both anteroposteriorly and transversely (0), widened anteroposteriorly and expanded medially (1) (after character 30; Barnes, 2013).

96. Ulna, olecranon process: relatively short, not lengthened proximally (0), lengthened proximally (1) (after character 31; Barnes, 2013).

97. Ulna, posterior border of diaphysis: nearly straight (0), bowed anteriorly, creating a concave posterior margin of the diaphysis (1) (after character 32; Barnes, 2013).

98. Radius and ulna: separated (0), fused (1).

99. Humerus, proximal extension of greater tubercle: extends proximal to head (1), extends to almost same level as head (0).

100. Humerus, width of greater tubercle: wide (1), narrow (0).

101. Humerus, lesser tubercule: prominent (0), indistinct (1).

102. Humerus, intertubercular groove location: on cranial side (0), on medial side (1).

103. Humerus, shape of intertubercular groove: deep and wide (0), shallow and narrow (1), shallow and wide (2).

Hindlimb

Comment [D48]: OK?

Comment [D49]: Quantify!

Comment [D50]: I assume you mean the humerus. Character (0) should be listed before (1).

Comment [D51]: Quantify!

104. Metacarpal 5, proximal end: not expanded (0), expanded laterally (1) (after character 33; Barnes, 2013).

105. Capitate bone, orientation of distal articular facet: transverse (0), medially inclined (1) (after character 34; Barnes, 2013).

106. Distal tibia–fibula articulation: relatively small (0), enlarged and extended proximally (1) (after character 35; Barnes, 2013).

107. Tibia, astragalar facet: not very tilted (= nearly perpendicular to shaft of bone) (0), tilted at least 60 degrees from horizontal (1) (after character 36; Barnes, 2013).

108. Phalanges: not flattened, distal ends only gently expanded (0), flattened with greatly expanded distal ends (1) (after character 30; Clark, 1991)

109. Femur, lesser trochanter: represented by only a muscle scar (0), forms a tubercle (1).

110. Femoral shaft, shape of cross section: circular (0), horizontally-elongated elliptical (1), flat (2).

Comment [D52]: Meaning unclear.

Comment [D53]: Define relative to shaft, not to the "horizontal".

Comment [D54]: In which direction?

Comment [D55]: OK? And compared to other mammals, shouldn't the polarity be the opposite?

Comment [D56]: Same as c. 75?