A quantitative test of the “Ecomorphotype Hypothesis” for fossil true seals (Family Phocidae) (#96112)

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A quantitative test of the “Ecomorphotype Hypothesis” for fossil true seals (Family Phocidae)

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The fossil record of true seals (Family Phocidae) is mostly made up of isolated bones, some of which are type specimens. Previous studies have sought to increase referral of non-overlapping and unrelated fossils to these taxa using the ‘ecomorphotype hypothesis’, which stipulates that certain differences in morphology between taxa represent adaptations to differing ecology. On this basis, bulk fossil material can be lumped to a specific ecomorphotype, and then referred to species in that ecomorphotype, even if they are different bones. This qualitative and subjective method has been used often to expand the taxonomy of phocid fossils, but has never been quantitatively tested.

We test the proposed ecomorphotypes using morphometric analysis of fossil and extant northern true seal limb bones, specifically principal components analysis and discriminate function analysis. A large amount of morphological overlap between ecomorphotypes, and poor discrimination between them, suggests that the ‘ecomorphotype hypothesis’ is not a valid approach. Further, the analysis failed to assign fossils to ecomorphotypes designated in previous studies, with some fossils from the same taxa being designated as different ecomorphotypes.

The failure of this approach suggests that all fossils referred using this method should be considered to have unknown taxonomic status. In light of this, and previous findings that phocid limb bones have limited utility as type specimens, we revise the status of named fossil phocid species. We conclude that the majority of named fossil phocid taxa should be considered *nomina dubia*.

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Abstract

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Introduction

The taxonomy and systematics of extinct true seals (Family Phocidae) is heavily influenced by their fossil record, which is notoriously incomplete (Berta et al., 2018; Valenzuela-Toro and Pyenson, 2019). The majority of extinct taxa (53%) have been described from isolated postcranial bones (Valenzuela-Toro and Pyenson, 2019; Berta et al., 2022), specifically humeri and femora. These bones have limited taxonomic utility and therefore make comparisons to other fossils and taxa difficult (Churchill and Uhen, 2019).

To assist in the referral of isolated phocid fossils to known or new taxa, an ‘ecomorphotype hypothesis’ was proposed by Koretsky (2001). This hypothesis proposed that phocines (northern true seals) occupied specific ecological niches which were related to the morphology of the mandible, humerus, and femur. These morphologies supposedly enable different seal species (with assumed different ecological niches) to occupy the same region. This technique has subsequently been used to lump isolated fossils into five distinct ecomorphs. Fossils from the same (or sometimes different) formation which are completely isolated and unassociated with one another are purportedly referable to the same species and expand its hypodigm, even if the elements those fossils represent (e.g. a femur) do not overlap at all with the holotype (e.g. a humerus). Since its original description, this ‘ecomorphotype hypothesis’ (Koretsky et al., 2020) has been expanded to devinophocines (extinct stem-phocids), monachines (southern true seals), and cystophorines (an unsupported true seal subfamily, see below).

This technique, which relies on subjective qualitative morphological coding, has been used to refer a multitude of fossils to taxa with otherwise isolated postcranial type specimens (Koretsky & Grigorescu, 2002; Koretsky, 2003; Koretsky & Peters, 2008; Koretsky & Ray, 2008; Koretsky et al., 2012; Koretsky & Rahmat, 2013; Koretsky et al., 2014; Koretsky et al., 2015; Rahmat & Koretsky, 2016; Rahmat et al., 2017; Rahmat & Koretsky, 2018; Hafed et al., 2023). This occasionally includes fossils other than the mandible, humerus, and femur, or fossil elements that are fragmentary and incomplete. While the referral of fossil Phocidae with the ecomorphotype hypothesis represents a substantial body of work, the validity of this hypothesis has recently fallen into question (Dewaele et al., 2017a; Dewaele et al., 2018; Churchill & Uhen, 2019; Valenzuela-Toro & Pyenson, 2019; Rule et al, 2020a). Specifically, there has been no quantitative test of this method, which is concerning considering the taxonomic identity a large portion of the referred phocid fossil record hinges on the validity of this ‘hypothesis’.

We aim to quantitatively test the validity of the “ecomorphotype hypothesis” for the first time, using morphometric analysis of northern true seal (subfamily Phocinae) limb bones. In addition, we provide a review of the taxonomic status of genera and species of fossil true seals.

Materials & Methods

We used a subset of the dataset published in Churchill & Uhen (2019), which was a measurement protocol of the humeri and femora of phocid seals. The definition for measurements used can be found in Churchill & Uhen (2019). As the original ecomorphotype hypothesis was defined for Phocinae (Koretsky, 2001; Koretsky et al., 2020), we only used measurements for fossil and extant Phocinae. We excluded Cystophora cristata as the authors of the ecomorphotype hypothesis consider it to be in a separate subfamily (Cystophorinae; Koretsky et al., 2020), however we note that this assignment contradicts the vast majority of morphological and molecular evidence which supports this taxon as a member of Phocinae (Fulton & Strobeck, 2010; Dewaele et al., 2017b; Berta et al., 2018; Paterson et al., 2020; Rule et al., 2020b; Park et al., 2024). We then expanded on this dataset using 36 specimens from the Natural History Museum in London (NHMUK) and a specimen of *Phoca largha* in the National Science Museum in Tokyo (NMNS). Measurements were taken with digital callipers and were recorded in millimetres, and right and left sides (when both existed) were averaged. The raw data was then transformed so that all other measurements for the humerus were scaled against total humerus length (TLH), and all other measurements for the femur were scaled against maximum length of the femur (MLF). Data was analysed at the specimen level, rather than averaging by species (which would result in few data points). We analysed the data for the humeri and femora both separately and together. Fossils were excluded when humeri and femora were analysed together. For all analyses we used the first four phocine ecomorphotypes defined in Koretsky et al. (2020), but restricted the codings to extant taxa and treated fossil taxa as unknowns; because of this, ecomorphotype group 5 was excluded as it is solely consisted of the fossil taxon *Cryptophoca maeotica*.

We assessed the utility of the ecomorphotypes of Koretsky et al. (2020) for the referral of dissociated fossils to specific taxa using several methods. Analyses were performed in R version 4.2.1 (R Core Team, 2023), and mostly follow those in Churchill & Uhen (2019). To visualise the morphological variation between the ecomorphotypes, we performed a principal components analysis (PCA) on the datasets using the R function ‘prcomp’ from the R Stats package (R Core Team, 2023). We evaluated the first two principal components only. To determine if ecomorphotypes were a good system to discriminate fossils into separate taxonomic bins, we performed a discriminant function analysis (DFA) on the datasets using the ‘lda’ function in the R package MASS (Venables & Ripley, 2002). We assessed the DFA for the three variations of the dataset using jackknife resampling. We plotted Linear Discriminant 1 (LD1), which explained the greatest variation. The accuracy of the assignment of fossils by the DFA to ecomorphotypes was assessed using the posterior probability.

Results

The PCA of phocine limb bones (Figure 1) demonstrated substantial overlap between the four ecomorphotypes along both principal components 1 and 2. The exception is a small amount of separation between ecomorphotypes 1 and 4 on PC2 of the combined dataset (Figure 1C). In all PCA's, ecomorphotype 2 occupied the morphospace the most, likely due to the large amount of taxa assigned to this group by Koretsky et al. (2020). The principal components (PCs) making up 95% of variation were as follows: the first 11 PCs for the humeri dataset, the first 11 PCs for the femora dataset, and the first 17 PCs for the combined dataset.

The DFA of phocine limb bones struggled to assign specimens to ecomorphotype categories. Jackknife validation supported the femora dataset as the most reliable model (0.77), but there was substantial overlap between all categories in LD1 of this model (Figure 2B). In the humeri and combined datasets, there was some separation between ecomorphotypes 1, 3 and 4 along LD1, but no separation for ecomorphotype 2, except between ecomorphotype 2 and 1 in the combined dataset (Figure 2). Humeri and femora specimens of the fossil taxon *Phocanella pumila* were not consistently assigned to the same ecomorphotype, and were assigned to all ecomorphs except ecomorphotype 3 (Table 1). For the fossil specimens assigned an ecomorphotype by Koretsky et al. (2020) (*Leptophoca proxima*, ecomorphotype 3; *Monachopsis pontica*, ecomorphotype 3, *Praepusa pannonica*, ecomorphotype 1; *Praepusa vindobonensis*, ecomorphotype 3; *Pontophoca sarmatica*, ecomorphotype's 3 and 5) none were assigned by the DFA to their 'correct' ecomorphotype, as all were assigned to ecomorphotype 2 with the exception of *Pontophoca sarmatica* (ecomorphotype 4) (Table 1).

Discussion

The 'ecomorphotype hypothesis' is not valid

A large portion of the phocid fossil record has been referred to existing or newly erected taxa using the 'ecomorphotype hypothesis' (Koretsky, 2001; Valenzuela-Toro & Pyenson, 2019; Koretsky et al., 2020), but until now this hypothesis had never been quantitatively assessed. Our results clearly demonstrate that there is no quantitative basis or support for this hypothesis.

Firstly, the results of the PCAs indicate substantial overlap in the morphospaces between ecomorphotypes (Figure 1). At least some degree of separation between groups should be expected along at least one PC axis if ecomorphotypes were morphologically characteristic groups. But this is not the case based on our results (Figure 1).

Secondly, the DFA indicates that ecomorphotypes poorly perform as discriminating morphological/ecological groupings (Figure 2). The best performing model by Jackknife validation (femur only) has the most overlap between the ecomorphotype categories (Figure 2b). For the next best model (humerus only), ecomorphotype 2 overlaps with all other ecomorphotypes (Figure 2a). This is likely due to ecomorphotype 2 possessing the most species compared to the other ecomorphotypes (Koretsky et al., 2020). The combined dataset does seem to demonstrate some discrimination between ecomorphotypes, but is not supported after jackknife validation. In addition, it would not function well as a model, as it would require testing possibly countless combinations of unknown fossil humeri and femora from a given formation. For some formations, such as the Yorktown Formation and Calvert Formation, which have thousands of unassociated phocid fossils (Valenzuela-Toro & Pyenson, 2019) this is not feasible.

Thirdly, the DFA failed to assign any of the fossil taxa (treated as unknowns in our analysis; Table 1) to their previously assigned ecomorphotypes (Koretsky et al., 2020). In the case of *Phocanella pumila*, for which the Churchill & Uhen (2019) dataset contained multiple humeri and femora specimens, the DFAs failed to assign them to a consistent ecomorphotype. This would cast particular doubt on not only the referral of bulk fossil material using the 'ecomorphotype hypothesis', but also on proposed fossil-only ecomorphotypes (e.g. ecomorphotype 5 for Phocinae; Koretsky et al., 2020).

The above results affirm concerns on the ‘ecomorphotype hypothesis’ by recent papers (Dewaele et al., 2017a; Dewaele et al., 2018; Churchill & Uhen, 2019; Valenzuela-Toro & Pyenson, 2019; Rule et al, 2020a). We therefore recommend that, going forward, the ‘ecomorphotype hypothesis’ be abandoned as a method of referring otherwise unassociated fossil material to the same species. Instead, future rigorous taxonomy should employ a more systematic approach which involves demonstrating overlap of bony elements between associated and isolated specimens. This is a much more reliable approach, and has been employed recently as more complete fossil phocid material becomes available (Amson & Muizon, 2014; Valenzuela-Toro et al., 2016; Dewaele et al., 2018; Rule et al, 2020a; Rule et al. 2020b).

Implications for Phylogenetic and Macroevolutionary Inferences

The misidentification of phocid fossil occurrences has important implications for studies that aim at inferring phylogenetic and diversification patterns in this group. Modern methods such as PyRate (Silvestro et al. 2014a, 2014b) rely on the multiple occurrences for each species to properly estimate the preservation rates, and consequently “true” times of speciation and extinction. When fossil specimens are incorrectly assigned to a given species, this would therefore impact all the estimations, and will hence provide incorrect information about the diversification dynamics of the group. Based on our results, it is possible to say that we would not be able to use the fossil record for phocids to estimate the diversification dynamics of phocids, given that apart from very few cases most species have too few occurrences (in most cases only one per species; Valenzuela-Toro & Pyenson 2019; Berta et al. 2022) to be suitable to be used in the analyses. Additionally, a recently developed method that allows for the estimation of phylogenetic trees including both extant and fossil species (metatrees, Lloyd et al. 2016) can be also impacted by this misassignment. This method draws information from the age range of fossil species to estimate the branch lengths related to those lineages. With fossil occurrences wrongly assigned to a given species, it can show a much longer range than what we would get by only considering the correctly assigned ones (or even only the type specimen, using the geological stage in which the specimen was deposited as a surrogate age).

The validity of fossil phocid species

Valenzuela-Toro & Pyenson (2019), in their analysis of the fossil record of pinnipeds, highlighted the need for best taxonomic practices in the field, as these have downstream effects on phylogenetic and macroevolutionary analyses of pinnipeds. Recent reviews of the fossil record of phocids have highlighted the need for revision of problematic taxa, especially phocines (Berta et al., 2018; Berta et al., 2022). Churchill & Uhen (2019) suggested that, based on their morphometric analysis of phocid limb bones, that fossil phocids known described from isolated limb elements should be considered nomina dubia. Whilst one study has so far reviewed two of these taxa (Rule et al., 2020a), the vast majority remain unassessed. The results presented here demonstrate that all fossil phocid species whose hypodigms have been expanded using the ‘ecomorphotype hypothesis’ should instead be restricted to the type specimens only.

Considering the above, we assert that all fossil phocids described using isolated limb bones be considered *nomina dubia* (Table 1), which represents over 50% of previously described extinct phocid taxa (Figure 3). In addition, other taxa described from equally incomplete and isolated material (e.g. *Lobodon vetus* and *Palmidophoca callirhoe*, whose type specimens are isolated dentitions) should also be considered nomina dubia. We also recommend the revision of several taxa. Specifically, *Phocanella pumila* is described from isolated axial postcrania, and the taxonomic utility of these elements has not been tested.

Other more complete taxa might also need revision, such as *Devinophoca emryi*. Despite the type specimen being a skull, this taxon is known from the same formation as the only other member of its genus (*Devinophoca claytoni*), and both are morphologically very similar and usually end up close to each other on phylogenies (e.g. Rule et al., 2020b; Park et al., 2024). Another taxon, *Histriophoca alekseevi*, is likely valid, however the referral to the modern genus *Histriophoca* should be revisited in light of recent work. The genus *Praepusa* also needs to be revised. While the type species *Praepusa pannonica* (which has a holotype consisting of a fragmentary mandible with teeth), might be valid, the referral of *Praepusa procaspica* and *Praepusa trachankutica* to the same genus is questionable as none of the type specimens overlap.

We recommend that in future, any novel method for aiding the referral of phocid fossils (or indeed fossils from any group) be grounded in a rigorous, quantitative, and statistically sound framework. This will help avoid taxonomic ambiguity in the fossil record, and ensure that any subsequent macroevolutionary analyses are based on solid taxonomic foundations.

Conclusions

We tested the proposed ‘ecomorphotype hypothesis’, a qualitative system for the referral of phocid fossils, using quantitative methods. Our analyses do not support the ‘ecomorphotype hypothesis’, and found that ecomorphotype groupings performed poorly for assigning unknown fossils. We therefore find that fossils referred to taxa using this method cannot be linked to isolated and non-overlapping type specimens. As a result of our findings, and those from previous studies, we find that the majority of extinct phocid species should be considered *nomina dubia*.

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Figure 1

Principal Components Analysis

Principal Components Analysis (PCA) of phocine humeri (A), femora (B), and both humeri and femora (C). The first two PC axes are displayed, and convex hulls are grouped by ecomorphotypes and fossil specimens.

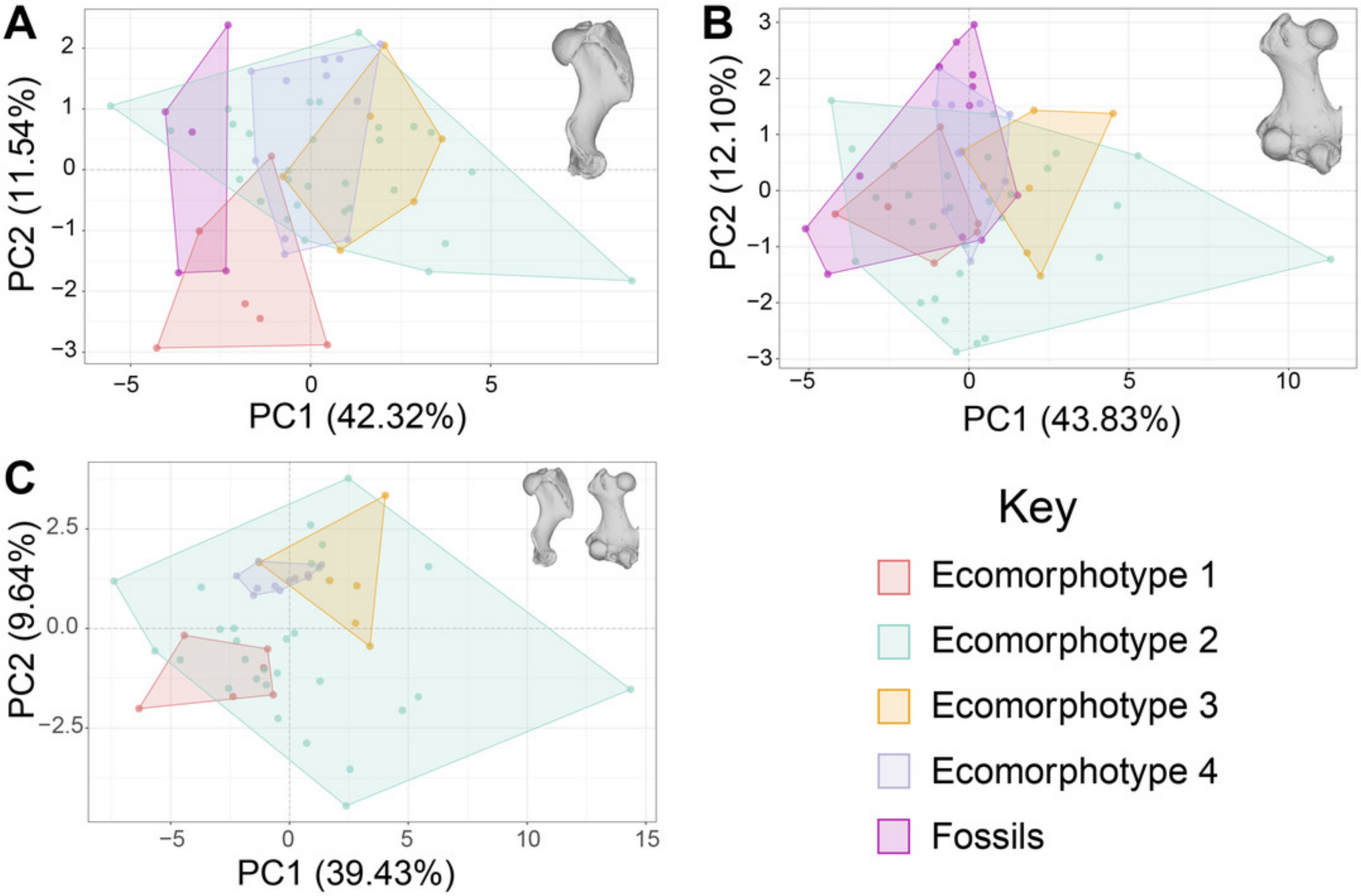

Figure 2

Discriminant Function Analysis

Discriminant Function Analysis (DFA) of phocine humeri (A), femora (B), both humeri and femora (C). Linear Discriminant 1 (LD1) is shown. Proportions of trace by LD1: 67.97% (A), 54.1% (B), 71.08% (C). Jackknife validation: 0.69 (A), 0.77 (B), 0.67 (C).

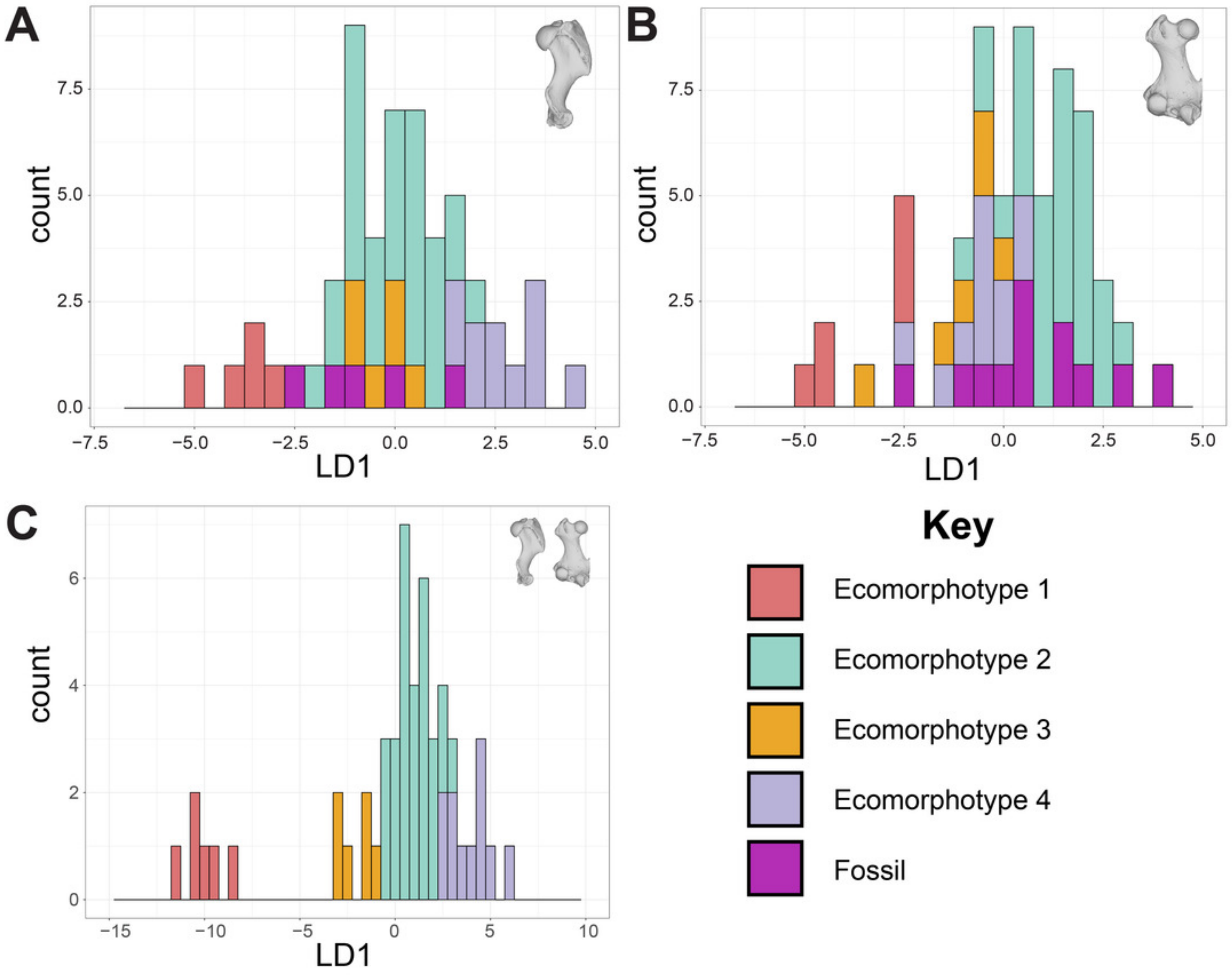

Figure 3

Status of the taxonomic validity of fossil phocid species.

Distribution of data from Table 2. “n” = number.

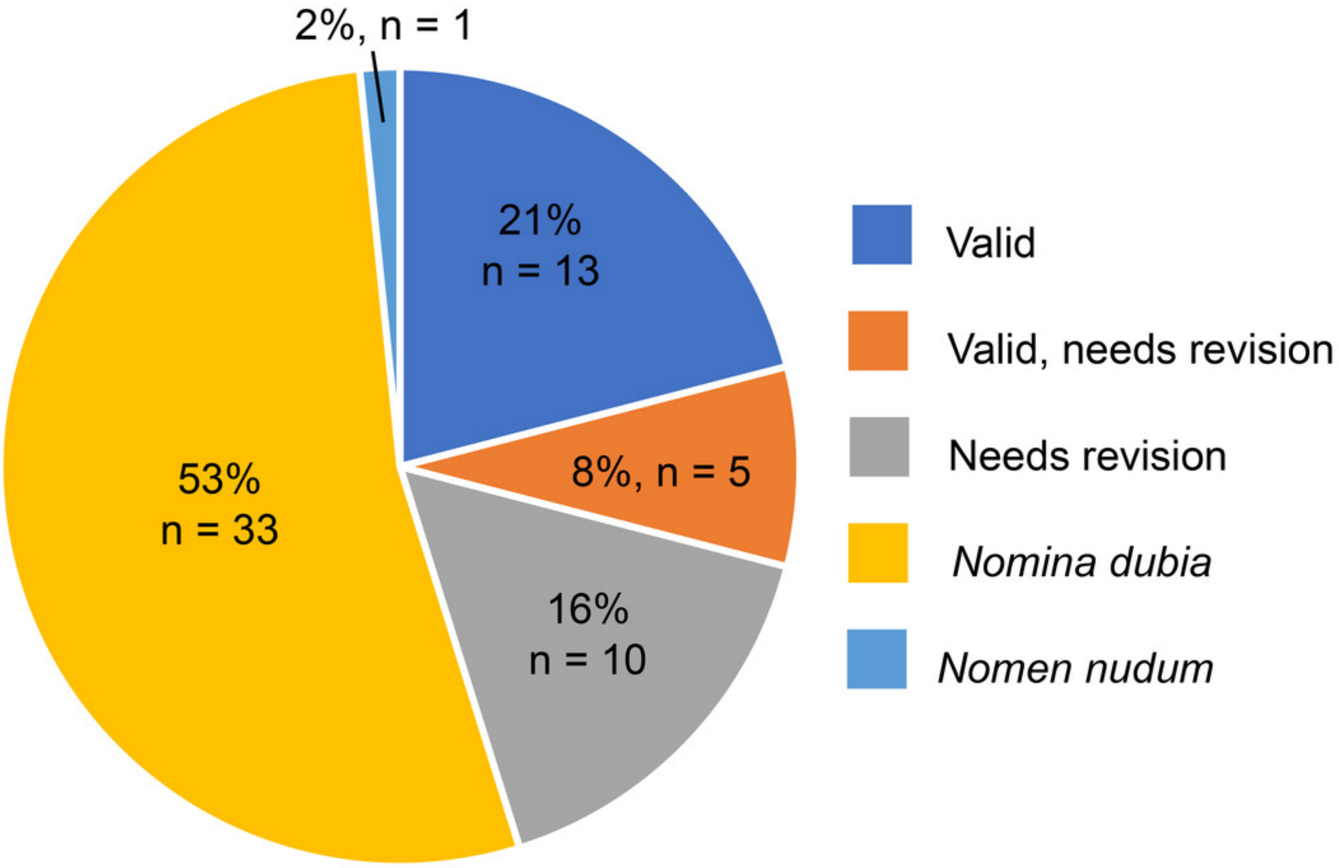

Table 1(on next page)

Posterior probabilities of ecomorphotype categories

Posterior probabilities of ecomorphotype categories by discriminant function analysis of phocine humeri and femora.

Table 1. Posterior probabilities of ecomorphotype categories by discriminant function analysis of phocine humeri and femora.

Taxon	Specimen and element	Ecomorphotype 1	Ecomorphotype 2	Ecomorphotype 3	Ecomorphotype 4
Phocanella pumila	USNM 329059 (humerus)	0.04%	99.16%	0.81%	0.002%
	USNM 171151 (humerus)	99.87%	0.11%	0.02%	0.002%
	NHMUK PV M1199 (cast of IRSNB 1080-M227, humerus)	<0.001%	99.96%	0.03%	0.02%
	NHMUK PV M1206 (cast of IRSNB 1101-M234, humerus)	<0.001%	97.31%	2.69%	<0.001%
	USNM 305283 (femur)	<0.001%	99.63%	<0.001%	0.37%
	USNM 329060 (femur)	1.59%	0.43	<0.001%	55.25%
	USNM 175217	<0.001%	76.11%	<0.001%	23.88%

	(femur)				
	USNM 181649 (femur)	<0.001%	94.27%	0.02%	5.53%
	USNM 481569 (femur)	96.08%	0.55%	<0.001%	3.36%
Nanophoca vitulinoides	NHMUK PV M1212 (cast of IRSNB 1063-M242, humerus)	<0.001%	96.99%	0.14%	2.87%
	NHMUK PV M1216 (cast of IRSNB 1049-M247, femur)	34.15%	23.42%	<0.001%	42.43%
Cryptophoca maeotica	USNM 214979 (femur, cast of LPB 259)	0.004%	88.25%	0.3%	11.45%
Leptophoca "amphiatlantica"	USNM 321926 (femur)	<0.001%	99.99%	<0.001%	<0.001%
Leptophoca proxima	USNM 559330 (femur)	0.01%	97.68%	0.003%	2.31%

Monachopsis pontica	USNM 214967 (femur, cast of LPB 21)	<0.001%	99%	<0.001%	0.99%
Praepusa vindobonensis	USNM 214993 (femur, cast of LPB 158?)	<0.001%	93.03%	<0.001%	6.97%
Praepusa? *pannonica*	USNM 214978 (femur, cast of LPB 5?)	<0.001%	99.7%	<0.001%	0.3%

Table 2(on next page)

Taxonomic review of fossil Phocidae.

Taxa listed do not include any taxa or names that have fallen out of use in the literature. Comments either reflect reasoning for status, or a citation in support of status. List is expanded from Berta et al. (2022).

Table 2. Taxonomic review of fossil Phocidae. Taxa listed do not include any taxa or names that have fallen out of use in the literature. Comments either reflect reasoning for status, or a citation in support of status. List is expanded from Berta et al. (2022).

Taxon	**Status**	**Comments**
Acrophoca longirostris	Valid	Type is a partial skeleton
Afrophoca libyca	Needs revision	Type is a fragmentary mandible
Auroraphoca atlantica	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Australophoca changorum	Valid	Type is a partial skeleton
Batavipusa neerlandica	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Callophoca obscura	*Nomen dubium*	Berta et al., 2015 and Churchill and Uhen, 2019 analysis, supported by Rule et al., 2020a
Cryptophoca maeotica	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Devinophoca claytoni	Valid	Type is a partial skull
Devinophoca emryi	Needs revision	Similar to *D. claytoni*, and from same formation as *D. claytoni*
Eomonachus belegaerensis	Valid	Type is a partial skull
Frisiphoca aberratum	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Frisiphoca affine	*Nomen dubium*	Churchill and Uhen, 2019 analysis

Gryphoca nordica	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Gryphoca similis	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Hadrokirus martini	Valid	Type is a partial skeleton
Hadrokirus novotini	Needs revision	Type is a fragmentary mandible
Histriophoca alekseevi	Valid, needs revision	Type is a partial skull. Needs revision for referral to modern genus *Histriophoca*
Homiphoca capensis	Valid	Type is a skull
Homiphoca murfreesi	Needs revision	Type is a fragmentary mandible
Kawas benegasorum	Valid	Type is a partial skeleton
Leptophoca proxima	Needs revision	Type is a humerus, but undescribed associated fossils exist.
Leptophoca "amphiatlantica"	*Nomen dubium*	Dewaele et al., 2017a
Lobodon vetus	*Nomen dubium*	Type is an isolated postcanine, likely represents a modern specimen
Magnotherium johnsii	Valid, needs revision	Type is a fragmentary skull, but not character rich
Mesotaria ambigua	*Nomen dubium*	Berta et al., 2015 and Churchill and Uhen, 2019 analysis, supported by Rule et al 2020a
Messiphoca mauretanica	Valid, needs revision	Type is a partial skeleton, skull is referred
Miophoca vetusta	*Nomen dubium*	Dewaele et al., 201

Monachopsis pontica	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Monotherium delognii	*Nomen dubium*	Berta et al., 2015
Monotherium? wymani	Needs revision	Type is an ear region
Nanophoca vitulinoides	Valid	Type is a partial skeleton
Noriphoca gaudini	Valid	Type is a partial skull
Pachyphoca chapskii	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Pachyphoca ukrainica	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Pachyphoca volkodavi	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Palmidophoca callirhoe	*Nomen dubium*	Type is a tooth
Phoca bessarabica	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Phoca moori	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Phocanella pumila	Needs revision	Type is an isolated atlas
Piscophoca pacifica	Valid	Type is a partial skeleton
Planopusa semenovi	Valid	Type is partial snout
Platyphoca danica	*Nomen dubium*	Churchill and Uhen, 2019 analysis

Platyphoca nystii	*Nomen dubium*	Berta et al., 2015
Platyphoca vulgaris	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Pliophoca etrusca	Valid	Type is a partial skeleton
Pontophoca jutlandica	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Pontophoca sarmatica	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Pontophoca simionescui	Needs revision	No designated type specimen
Praepusa boeska	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Praepusa magyaricus	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Praepusa pannonica	Needs revision	Type is a mandible
Praepusa procaspica	Valid, needs revision	Type is associated forelimb
Praepusa tarchankutica	Valid, needs revision	Type is a cranium
Praepusa vindobonensis	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Pristiphoca occitana	*Nomen nudum*	Berta et al., 2015
Properiptychus argentinus	Needs revision	Type is a partial maxilla
Prophoca rousseaui	*Nomen*	Churchill and Uhen, 2019 analysis

	dubium	
Sarcodectes magnus	Valid	Type is a partial skeleton
Sarmatonectes sintsovi	*Nomen dubium*	Churchill and Uhen, 2019 analysis
Terranectes magnus	*Nomen dubium*	Dewaele et al., 2018
Terranectes parvus	*Nomen dubium*	Dewaele et al., 2018
Virginiaphoca magurai	*Nomen dubium*	Churchill and Uhen, 2019 analysis

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