

Long bone variability in true seals (Mammalia, Phocidae), with implications for understanding their fossil record

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Abstract

Historically, humeri and femora have been treated as diagnostic elements for fossil phocid (Carnivora, Pinnipedia, Phocidae) identification. This resulted in the naming of a plethora of extinct phocid taxa with isolated humeri and femora as type specimens. However, the documented evidence of sexual dimorphism in pinnipeds, including qualitative and preliminary quantitative studies of long bone shapes, indicates the existence of both intra- and interspecific variation; their respective strengths will help determine whether long bones should or should not be used for taxonomy. The present study quantitatively assesses the morphological variability of phocid long bones, using 3D geometric morphometrics on a large sample ($n = 145$) covering 16 extant taxa. Morphospaces resulting from principal component analyses sort both extant phocid subfamilies (Phocinae and Monachinae) well, for both humeri and femora. Thus, this study suggests that humeri and femora might be diagnostic enough only to differentiate between subfamilies and maybe some genera, but usually lack clear genus- or species-specific shapes when variability is considered. As such, isolated long bones are preferably not to be used as type specimens. A taxonomic reassessment of holotypes of fossil species based on isolated long bones on a taxon-by-taxon basis is therefore warranted.

KEYWORDS

femur, fossils, geometric morphometrics, humerus, Phocidae

1 | INTRODUCTION

The semi-aquatic clade Pinnipedia is currently represented by three extant families: Odobenidae (the walrus), Otariidae (fur seals and sea lions), and Phocidae (true seals) (e.g., Berta et al., 2018; Berta & Wyss, 1994; Paterson et al., 2020). Phocidae form the most diverse family of pinnipeds, with 19 extant species and a near cosmopolitan distribution, inhabiting all major seas and oceans, except for the Indian Ocean (e.g., Berta

et al., 2015, 2018; Jefferson et al., 2008). Extant phocids range from slightly over 1 m (*Pusa* spp.) to over 6 m in length (*Mirounga leonina*) (Jefferson et al., 2008). Some phocids also show marked sexual dimorphism, which is most easily visible in the large size difference between males and females of certain extant species (the hooded seal *Cystophora cristata*, the gray seal *Halichoerus grypus*, the leopard seal *Hydrurga leptonyx*, and the elephant seals of genus *Mirounga*) (e.g., Jefferson et al., 2008). Sexual dimorphism is present in many other phocid species

as well, albeit less profound (e.g., Jefferson et al., 2008; Kienle et al., 2022).

Historically, propodials (the humerus and the femur) have been thought to be diagnostic for phocid species (e.g., Koretsky, 2001; Koretsky & Ray, 2008; Dewaele, Lambert, & Louwye, 2017; Dewaele, Peredo, et al., 2018). This line of reasoning has been expanded to use isolated humeri and femora as type specimens for over 20 extinct phocid taxa (Churchill & Uhen, 2019; Rule et al., 2024). These taxa are primarily described from the Neogene of the North Atlantic realm and the Parathetys; and the state of preservation of these type specimens varies considerably. However, the morphological variability of phocid long bones remains understudied. The morphological differences between the two phocid subfamilies, Phocinae and Monachinae, have long been described qualitatively but have only been tested quantitatively in a few preliminary studies (Churchill & Uhen, 2019; Dewaele, Amson, et al., 2017; Dewaele, Lambert, & Louwye, 2017; Koretsky, 1987, 2001; Rule et al., 2024). In the light of how many fossil species have been named based on isolated long bones, it has been remarkably unclear whether isolated long bones can be used as type specimens or for species identification or not. Is interspecific morphological variation obscured by intraspecific variation, that is, obscured by sexual dimorphism or not? Despite the importance of this question, there is, to date, only one single study addressing this very issue quantitatively: a study by Churchill and Uhen (2019). Using 2D geometric morphometrics, they found that fossil phocid humeri and femora could only be clearly distinguished to the subfamilial level and that intraspecific and interspecific variation overlap. Practically, they also concluded that (isolated) long bones are suboptimal to identify (extinct) phocid species and allow questioning the validity many such extinct species with isolated long bones as type specimens. The present study aims to go further by using 3D morphometry on a larger biological sample, including more taxa and more specimens, to draw more robust conclusions on the problem.

2 | MATERIALS AND METHODS

2.1 | Material

Our sample of phocid humeri and femora (Supplementary Information, Humerus Specimen List, and Femur Specimen List) contains a total of 145 3D models, comprising of 80 humeri and 65 femora, belonging to 14 and 12 phocid taxa, respectively (Table 1). Scans were acquired using a Artec EVA Lite white light 3D scanner from George Mason University's Uhen Lab. These

TABLE 1 Taxon list and list of the number of 3D models of femora and humeri used in this study.

Taxon	No. of femora modeled	No. of humeri modeled
Monachinae		
<i>Hydrurga leptonyx</i>	5	6
<i>Leptonychotes weddellii</i>	6	5
<i>Lobodon carcinophaga</i>	1	5
<i>Mirounga angustirostris</i>	6	5
<i>Monachus monachus</i>	1	1
<i>Neomonachus schauinslandi</i>	3	4
<i>Neomonachus tropicalis</i>	0	1
<i>Ommatophoca rossii</i>	2	3
Phocinae		
<i>Cystophora cristata</i>	6	9
<i>Erignathus barbatus</i>	4	4
<i>Halichoerus grypus</i>	13	12
<i>Histriophoca fasciata</i>	0	2
<i>Pagophilus groenlandicus</i>	14	15
<i>Phoca vitulina</i>	0	1
<i>Phoca vitulina concolor</i>	2	4
<i>Phoca vitulina richardii</i>	2	3

Note: Although the Caribbean monk seal, *Neomonachus tropicalis*, is officially extinct, it went extinct in recent history and is treated as an extant species for the purpose of the present study.

specimens are all housed in the National Museum of Natural History, Washington, DC. Three-dimensional models were post-processed using the software Geomagic Studio (2013 version) to optimize the models for geometric morphometry. Because sex is difficult to assess on humeri and femora of phocids, the sex of the specimens remains often unknown. Only adults and near-adult subadults have been considered for this study, and their propodeal morphology is considered to be 'fixed' at this ontogenetic stage. No clear (skeletal) younger subadults or juveniles were included. Specimens were considered of use for the present study if the epiphyses of their long bones were fused to the diaphysis.

2.2 | Landmarking

Landmarking was performed in Landmark editor (v3.0.0.6) using both semi landmarks and curves to sample the whole morphology. Seventeen fixed landmarks and 24 curves resulting in 117 semi-landmarks were placed on the humeri (Figure 1, Table 2); and 14 fixed

landmarks were coupled with 24 curves composed of 92 semi-landmarks that were placed on the femora (Figure 2, Table 3). Whereas the fixed landmarks were placed manually on all specimens, curves were applied semi-automatically using the landmark transference tool and adjusted manually when needed. Coordinates were exported as individual pts-files and imported in the R statistical environment (R Core Team, 2024) all at once using the “import.pts” function from Chatar et al. (2024). Landmark and semi-landmark coordinates are provided as Supplementary Information (Data_long_bones_phocids_femur.csv, Data_long_bones_phocids_humerus.csv, Semilandmark_Humerus.csv, and Semilandmark_Femur.csv; and pts-files for each specimen).

2.3 | Morphometric and statistical analyses

All the analyses were performed in the R statistical environment version 4.3.3. Landmark coordinates were combined into two arrays: one for humeri and one for

femora. We applied the same analytical protocol to each array: (i) a procrustes superimposition using the gpa-gen function from the geomorph package (Baken et al., 2021); (ii) a principal component analysis (PCA) on the Procrustes coordinates using the gm.prcomp function from the geomorph package (Baken et al., 2021). Subsequently, a canonical variate analysis (CVA) with cross-validation was performed using the CVA function of the Morpho package (Schlager, 2017) to statistically assess shape differences between humeri and femora at the sub-family, tribe and genus levels. We ran the CVA on the PCs, rather than on the Procrustes coordinates, considering the high number of Procrustes coordinates relative to the number of specimens in each group. For each dataset, we retained the minimum number of PCs required to explain 95% of the total morphological variation, resulting in 31 PCs for the humeri and 26 for the femora. From those analyses we extracted the classification accuracy (given in the percentage of specimens properly assigned to a group), the Kappa statistic to give a reliability estimation of the classification, and the number of specimens that could not be classified even with the inbuilt CVA

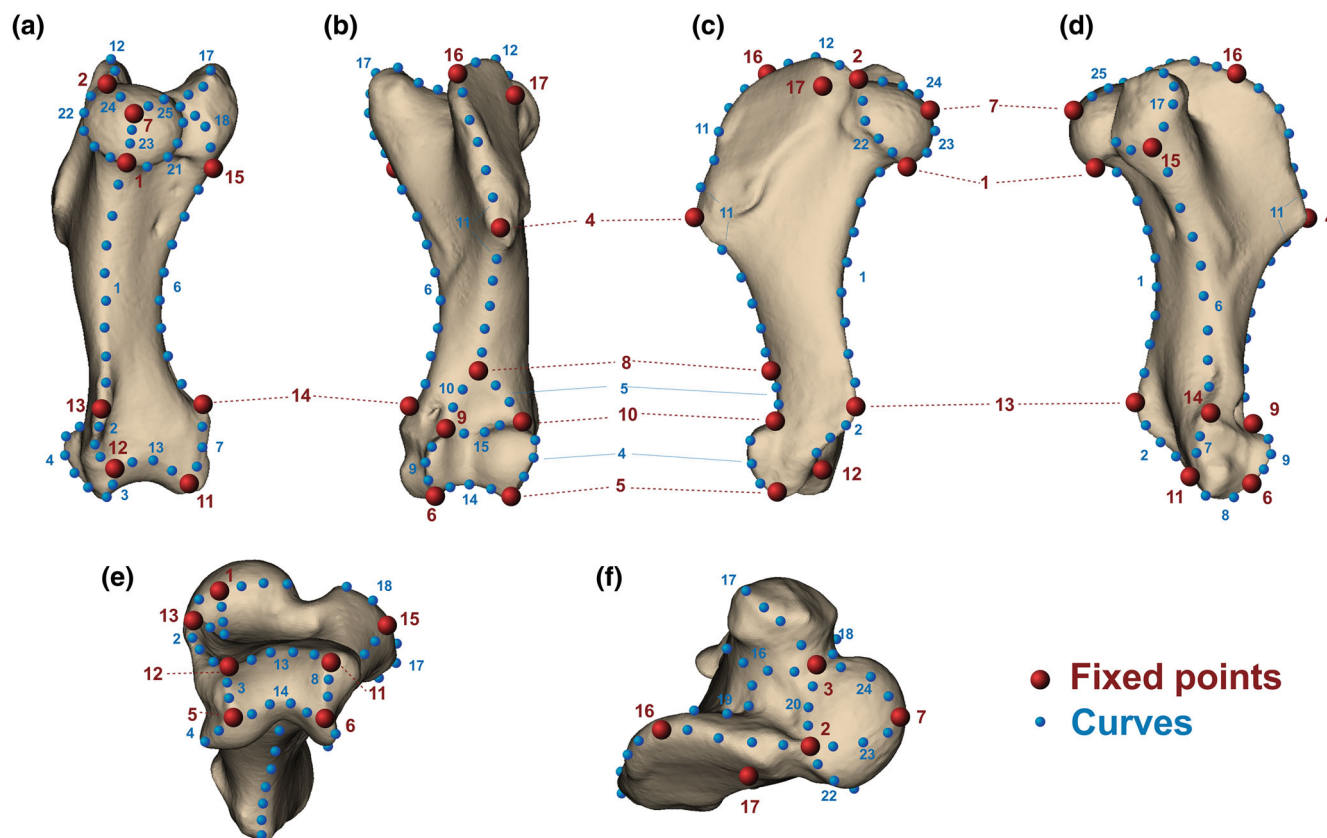


FIGURE 1 Position of the landmarks on the humerus (USNM 188962, *Cystophora cristata*) in posterior (a), anterior (b), lateral (c), medial (d), distal (e) and proximal (f) view. Fixed landmarks are represented by larger red dots and curves by smaller blue dots. Note that some curves are not anchored by single points, however, the first and last point of each of those curves was considered fixed during the sliding. See Table 2 for the definitions of the landmarks.

TABLE 2 Definitions of the landmarks on the humerus (17 fixed landmarks and 117 semi-landmarks).

Fixed landmarks	s0	Most posterodistal point of the ridge of the head.
	s1	Most proximal contact between the head and the lesser tubercle.
	s2	Most proximal contact between the head and the greater tubercle.
	s3	Distal tip of the <i>M. pectoralis</i> muscle scar on the deltopectoral crest.
	s4	Most distal contact between the capitulum and the trochlea.
	s5	Distal pit of the medial crest of the trochlea.
	s6	Center of the head in posteroproximal view.
	s7	Proximal tip of the coronoid fossa.
	s8	Contact with the mediodistal tip of the coronoid fossa and the medial ridge of the trochlea.
	s9	Contact with the laterodistal tip of the coronoid fossa and the lateral ridge of the capitulum.
	s10	Contact between the posteromedial corner of the trochlea and the medial epicondyle.
	s11	Contact between the posterolateral corner of the trochlea and the lateral epicondyle.
	s12	Contact between the lateral epicondyle ridge and the tip of the <i>M. anconeus lateralis</i> muscle scar.
	s13	Edge at the proximal tip of the <i>M. flexor digitorum superficialis</i> muscle scar.
	s14	Most distal point at the base of the greater tubercle.
	s15	Edge at the proximal tip of the <i>M. atlantoscapularis</i> muscle scar.
	s16	Center of the <i>M. supraspinatus</i> muscle scar.
Sliding landmarks	c0	Posterior ridge of the diaphysis.
	c1	Ridge of the lateral epicondyle going to the posterior part of the trochlea.
	c2	Lateral ridge of the trochlea going to the capitulum.
	c3	Lateral ridge of the capitulum.
	c4	Lateral ridge of the coronoid fossa.
	c5	Medial ridge of the diaphysis.
	c6	Ridge of the medial epicondyle going to the posterior part of the trochlea.
	c7	Posteromedial ridge of the trochlea.
	c8	Anteromedial ridge of the trochlea.
	c9	Medial ridge of the coronoid fossa.
	c10	Anterior ridge of the diaphysis.
	c11	Proximal ridge of the deltopectoral crest.
	c12	Posteroproximal ridge of the trochlea.
	c13	Most distal curve of the trochlea.
	c14	Anteroproximal ridge of the trochlea.
	c15	Lateral contact between the base of the greater tubercle and the shaft.
	c16	Curve from s14 to s2 passing by the most proximal point of the greater tubercle.
	c17	Medial contact between the base of the greater tubercle and the shaft.
	c18	Curve going straight from s15 to the middle of c15.
	c19	Ridge of the head between s1 and s2.
	c20	Medial ridge of the head between s2 and s0.
	c21	Lateral ridge of the head between s1 and s0.
	c22	Curve of the head going from s0 to the middle of c19 and passing by s6.
	c23	Curve of the head going straight from s1 to s6.
	c24	Curve of the head going straight from s2 to s6.

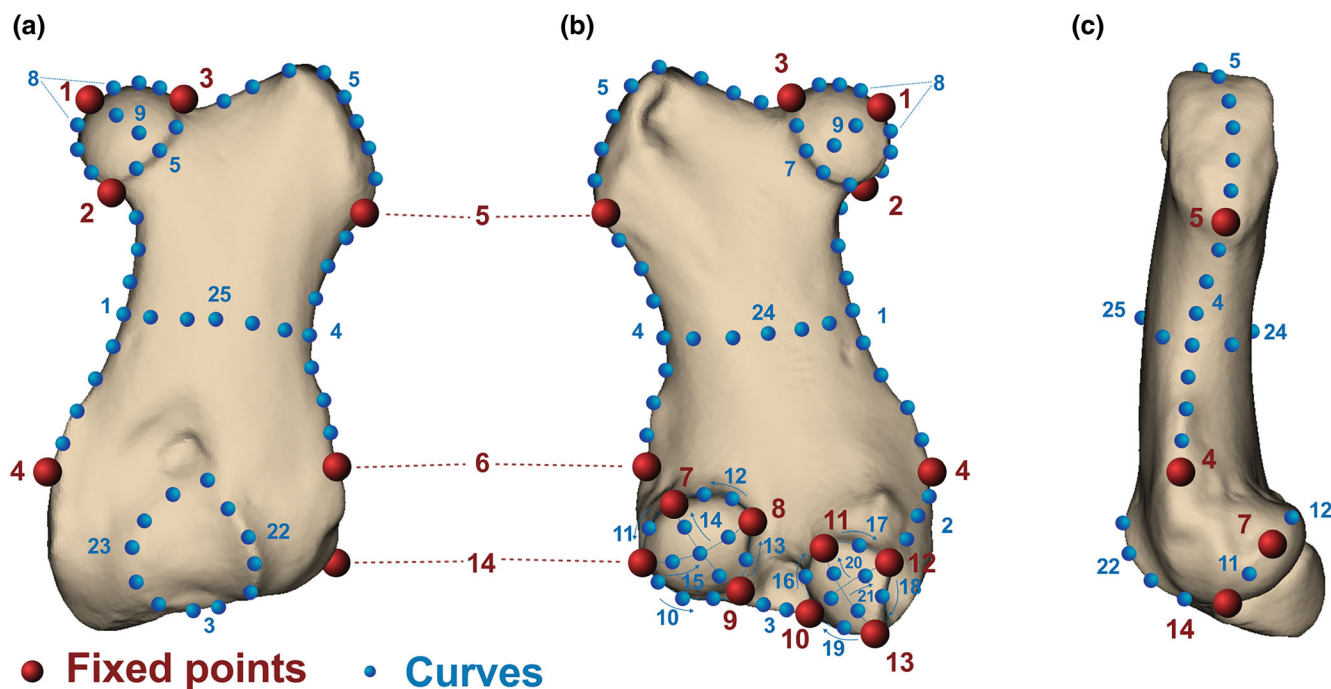


FIGURE 2 Position of the landmarks on the femur (USNM 188962, *Cystophora cristata*) in anterior (a), posterior (b) and lateral (c) view. Fixed landmarks are represented by larger red dots and curves by smaller blue dots. Note that some curves are not anchored by single points, however, the first and last point of each of those curves was considered fixed during the sliding. See Table 3 for the definitions of the landmarks.

Jackknife cross-validation. Finally, we explored the morphological disparity using the `morphol.disparity` function of the `geomorph` package (Baken et al., 2021) to extract the Procrustes variance (disparity) per taxonomic level (family, tribe, genus).

Our R script can be found as Supplementary Information (R Script).

3 | RESULTS

3.1 | Humeral morphospace occupation

The PCA on the humeri coordinates retrieved 80 axes, the first three principal components (PCs) explain a cumulative percentage of 59.93% of the observed morphometric variation: PCs 1, 2, and 3 explain respectively 42.89%, 10.81%, and 6.23% of the variation (Figure 3).

Monachinae and Phocinae are well-separated along the PC1 axis. The notable exception is the recently extinct monachine Caribbean monk seal (*Neomonachus tropicalis*), which is a stark outlier altogether in the PC1 versus PC2 plot (Figure 3a), but lies close to the cluster of phocine scores in the PC1 versus PC3 plot (Figure 3b). Both plots show that monachines (except *N. tropicalis*) and phocines are separated along the PC1 axis, with all Monachinae (except *N. tropicalis*) having positive PC1 scores

and Phocinae (and *N. tropicalis*) having negative PC1 scores. In addition, the variance along PC1 within the subfamilies is larger among Monachinae than among Phocinae. Indeed, Phocinae are roughly clustered in between -0.05 and 0 on PC1 while Monachinae (except *N. tropicalis*) range from 0.01 to more than 0.1 .

Along the PC2 axis, again, the range of variance among Phocinae is notably smaller than the range of Monachinae. However, the distribution of Monachinae along the PC2 axis entirely overlaps with the distribution of Phocinae. The PC3 axis shows a different story, with both subfamilies globally overlapping, except for specimens of *C. cristata* and the bearded seal (*Erignathus barbatus*), conferring a larger range to Phocinae compared to Monachinae.

At lower systematic levels, morphometric variability at the genus level is relatively larger in Monachinae than in Phocinae, although total variability within each of the two subfamilies remains small in absolute numbers. Among Phocinae, only the humerus of *E. barbatus* appears to consistently lie off the group along the PC3 axis, adjoined by one specimen of *C. cristata* (Figure 3b). For Monachinae, the clusters of each species appear well distinct from those of other species, with the exception of the humerus of the Mediterranean monk seal (*Monachus monachus*) overlapping the Hawaiian monk seals (*Neomonachus schauinslandi*) in the PC1 versus PC2 plot

TABLE 3 Definitions of the landmarks on the femur (14 fixed landmarks and 92 semi-landmarks).

Fixed landmarks	s0	Center of the head in lateroproximal view.
	s1	Most medialodistal point of the ridge of the head.
	s2	Most lateraloproximal point of the ridge of the head.
	s3	Proximal tip of the medial epicondyle.
	s4	Lateralodistal tip of the greater trochanter.
	s5	Proximal tip of the <i>M. gastrocnemius lateralis</i> muscle scar on the lateral epicondyle.
	s6	Lateraloproximal corner of the lateral condyle.
	s7	Medialoproximal corner of the lateral condyle.
	s8	Medialodistal corner of the lateral condyle.
	s9	Lateralodistal corner of the medial condyle.
	s10	Lateraloproximal corner of the medial condyle.
	s11	Medialoproximal corner of the medial condyle.
	s12	Medialodistal corner of the medial condyle.
	s13	Lateralodistal corner of the lateral condyle.
Sliding landmarks	c0	Medial ridge of diaphysis between s1 and s3.
	c1	Ridge between s3 and s11.
	c2	Distal ridge of the interchondyloid fossa.
	c3	Lateral ridge of the diaphysis between s4 and s5.
	c4	Curve going from s2 to s4 passing by the proximal tip of the greater trochanter and the proximal ridge of the proximal epiphysis.
	c5	Anterior ridge of the head.
	c6	Posterior ridge of the head.
	c7	Curve going from s2 to s1 passing by s0.
	c8	Curve passing by s0 going from the middle of c5 to the middle of c6.
	c9	Distal ridge of the lateral condyle.
	c10	Lateral ridge of the lateral condyle.
	c11	Proximal ridge of the lateral condyle.
	c12	Medial ridge of the lateral condyle.
	c13	Curve going from s8 to s6 passing by the center of the lateral condyle.
	c14	Curve going from s7 to s13 passing by the center of the lateral condyle.
	c15	Lateral ridge of the medial condyle.
	c16	Proximal ridge of the medial condyle.
	c17	Medial ridge of the medial condyle.
	c18	Distal ridge of the medial condyle.
	c19	Curve going from s12 to s10 passing by the center of the medial condyle.
	c20	Curve going from s11 to s9 passing by the center of the medial condyle.
	c21	Lateral ridge of the patellar surface between the highest point of this ridge to its lowest point when the distal epiphysis lays flat.
	c22	Medial ridge of the patellar surface between the highest point of this ridge to its lowest point when the distal epiphysis lays flat.
	c23	Posterior curve going straight from the middle of c0 to the middle of c3.
	c24	Anterior curve going straight from the middle of c0 to the middle of c3.

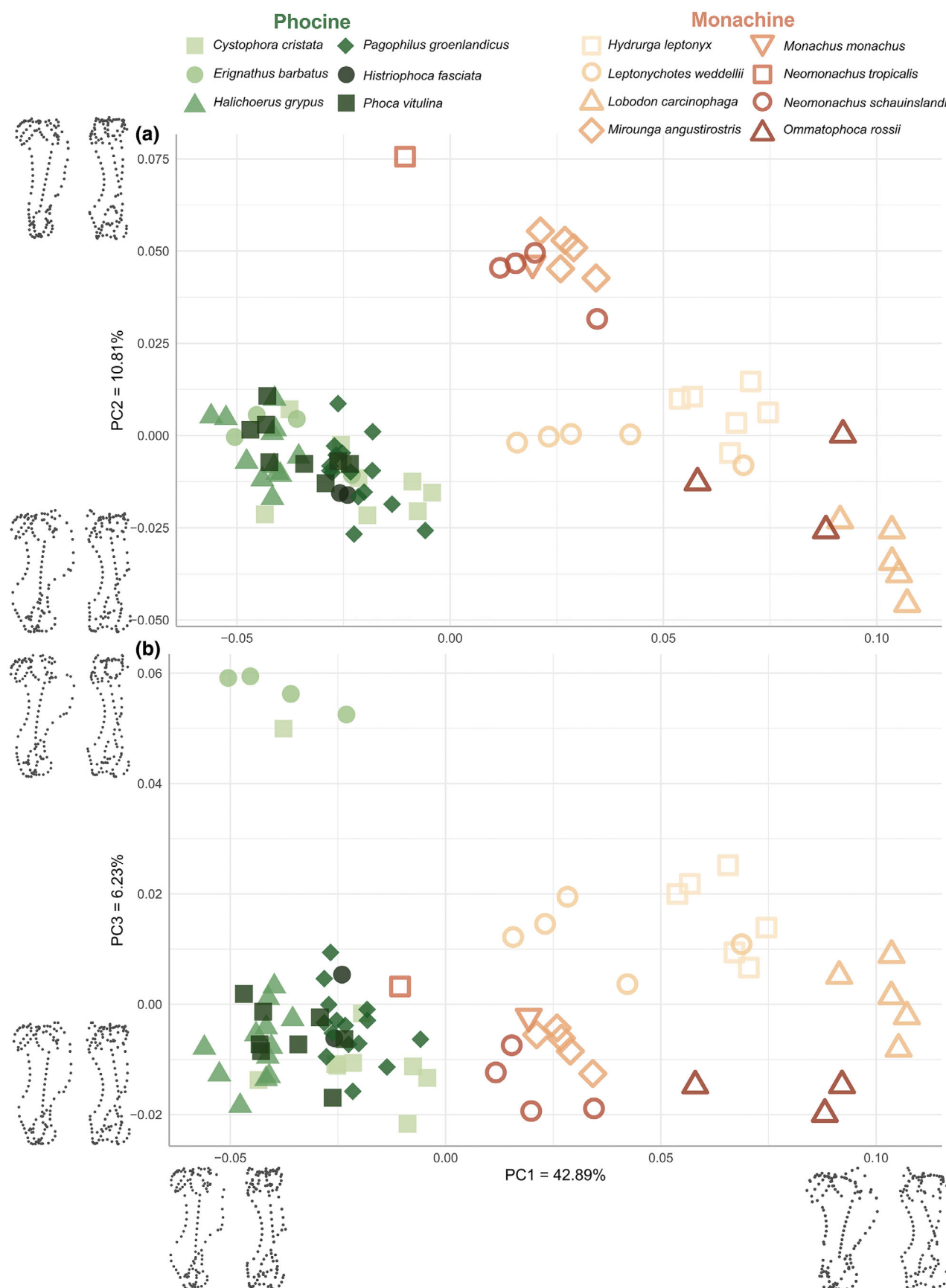


FIGURE 3 Morphospace occupation for the humerus resulting from the PCA. (a) PC 1 versus PC 2; (b) PC 1 versus PC 3.

(Figure 3a), and one specimen of the Weddell seal (*Leptonychotes weddellii*) falling very close to leopard seal (*Hydrurga leptonyx*) humeri in the PC1 versus PC3 plot (Figure 3b). This aligns with the currently understood phylogenetic relationships between *M. monachus* and *N. schauinslandi* as species of the tribe Monachini, and *H. leptonyx* and *L. weddellii* as species of the tribe Lobodontini. It can also be noted from the PC1 v. PC2 morphospace plot that among Monachinae, Lobodontini are separated from other Monachinae along the PC2 axis, that is, having lower values. Lobodontini is the tribe comprising the aforementioned *H. leptonyx*, and *L. weddellii*, as well as the crabeater (*Lobodon carcinophaga*), and Ross seals (*Ommatophoca rossii*).

3.2 | Morphological variation of the humerus

The deltopectoral crest, greater tubercle and humeral head drive most of the humeral shape variation, as variation in size and shape of this crest is visible on the extreme PC shapes of the first three axes (see shape variation on PC axes in Figures 3 and 4).

Highest values on the PC1 (monachines) are associated with a proximally angular deltopectoral crest, a larger and more rounded humeral head, a prominent greater tubercle, and a distal epiphysis that is straighter and larger relative to the diaphysis. On the other hand, the lowest values (phocines) are associated with a thinner, more anteriorly angled distal epiphysis. The deltopectoral crest is less elevated anteriorly. As for the shape variation on PC2, the humerus tends to exhibit a more pronounced supinator crest and a more laterally extended greater tubercle for lower values. Increasing values on PC2 are associated with the reduction of the supinator crest and less pronounced deltopectoral crest and a relatively narrower humerus in both lateral and anterior view.

Shape changes on PC3 include a deltopectoral crest elongated anteroposteriorly and proximally more angular for higher values, shortening and merging smoothly with the diaphysis in the lowest values. Lowest PC3 values are also associated with a slightly more pronounced humeral head, and a more angular deltopectoral epicondyle.

3.3 | Femoral morphospace occupation

The PCA retrieved 65 PCs. The first three PCs explain a total of 54.46% of the variation in the morphology of the femur: PCs 1, 2, and 3 explain, respectively, 36.99%, 9.67%, and 7.8% of the variation (Figure 4). Monachinae

and Phocinae appear closer in terms of femoral shape than humeral shape. Along the PC1 axis, the femora of Phocinae tend to occupy negative values, except for one harp seal (*Pagophilus groenlandicus*) and four *C. cristata* exhibiting positive values. All monachines are found in the positive values of PC1, with the species exhibiting closest values to phocines being *M. monachus* as well as one specimen of *L. weddellii*, which overlaps with the cluster of *C. cristata*. Phocines and monachines largely overlap on both PC2 and PC3.

The distinction at the genus level is not well marked, with only a few species exhibiting peculiar femoral shape: the northern elephant seal (*Mirounga angustirostris*) and *O. rossii* are well distinct from other monachines along the PC1 axis, exhibiting the lowest values. *Hydrurga leptonyx*, *Neomonachus schauinslandi*, and *Leptonychotes weddellii* largely overlap on PC1 but are more spread on PC2. Among Phocinae, *Halichoerus grypus* appears to be the most distinct species, exhibiting the highest values on PC1 and relatively high values for phocines of both PC2 and PC3. The other species largely overlap on both PC2 and PC3.

3.4 | Morphological variation of the femur

The greater trochanter appears to be driving most of the femoral shape variation, followed by the femoral head, the condyles, the diaphysis and the patellar surface (see extreme shape on each axis in Figure 4). Lower PC1 values (monachines) are associated with a robust and straighter femoral shaft, a larger patellar surface, a prominent greater trochanter extending more laterally, and a larger and more rounded femoral head. The medial and lateral epicondyles are more robust and well-developed, contributing to a stronger distal femoral structure. With PC1 values increasing toward phocine values, the femoral shaft becomes narrower, while the patellar surface reduces in size, also becoming more triangular, and the greater trochanter becomes more angular. High PC2 values are characterized by a more extended patellar surface and relatively narrower shaft. The intertrochanteric fossa is also more pronounced. The medial and lateral epicondyles get projected more distally as PC2 values decrease. High PC3 values are associated with a shorter greater trochanter and a wider neck, contributing to a more robust femoral proximal region, with a thicker diaphysis. The lateral and medial epicondyles are also more proximally projected. Lower PC3 values show a femur with a more elongated and medially shifted greater trochanter and a narrower neck, and a smaller femoral head.

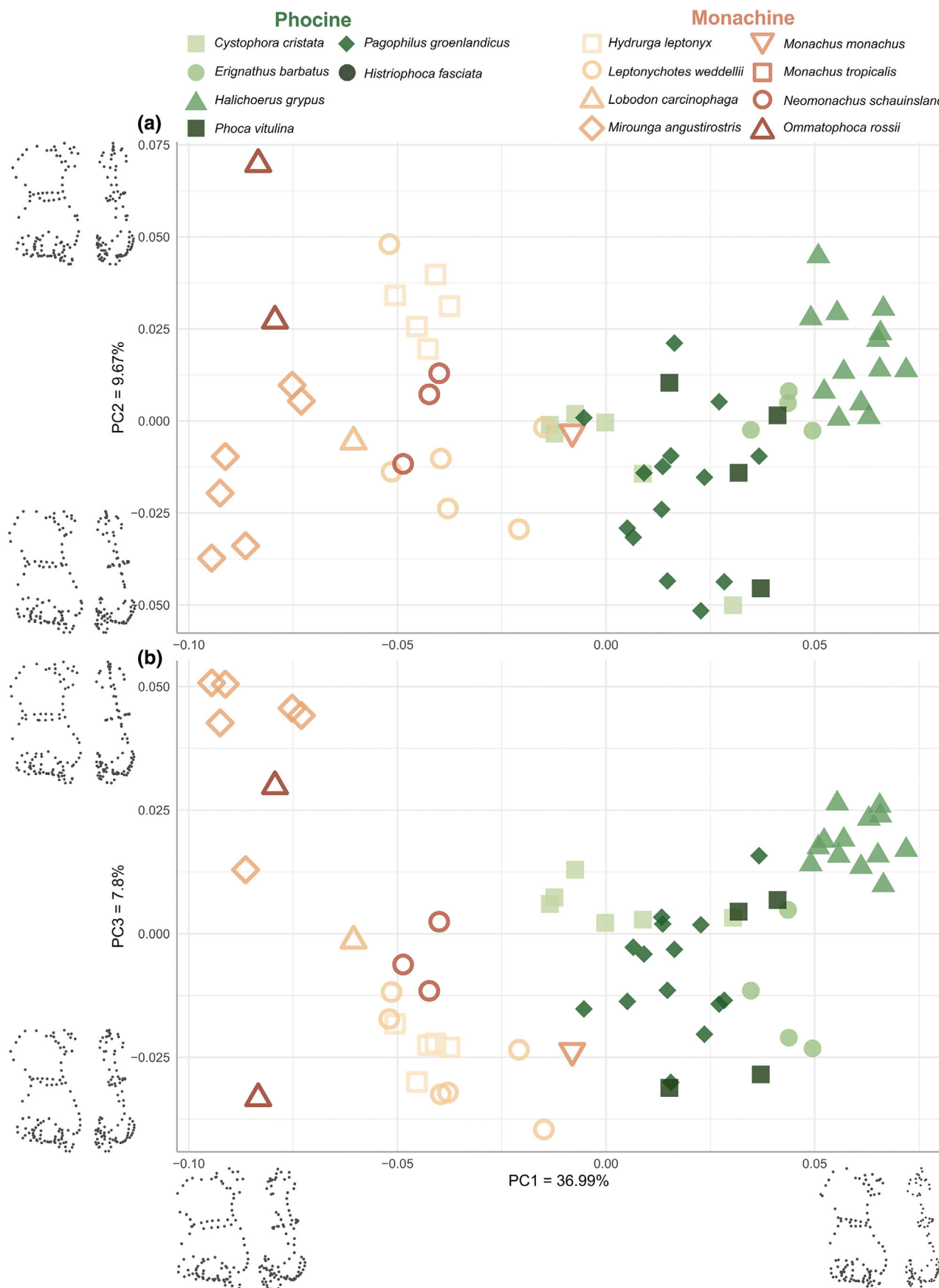


FIGURE 4 Results of the PCA for the femur resulting from the PCA. (a) PC 1 versus PC 2; (b) PC 1 versus PC 3.

3.5 | Classification power of long bones

The results of the CVA analyses (Supplementary Tables S1, S2) indicate high accuracy to differentiate subfamilies based on both femoral (98.46%) and humeral (100%) PC axes. This demonstrates that long bone morphology clearly separates monachines from phocines. Classification accuracy remained quite good at the tribe level based for both the femoral (96.92%) and humeral (98.75%) dataset only misidentifying a single specimen in each specimen, one *Monachini* for the femur dataset (Figure S1), and one *Cystophorini* for the humerus (Figure S3). However, classification accuracy dropped markedly at the genus level (84.13% for the femur and 85% for the humerus), and the corresponding increase in the kappa statistic underscores the reduced reliability of these classifications (Supplementary Tables S1, S2). Several specimens were misclassified during the CVA at the genus level: 10 out of 65 in the femoral dataset and 11 out of 80 in the humeral dataset. Confusion matrices (Supplementary Figures S2 and S4) reveal that, although overall classification performance was reasonable, certain genera were more ambiguous than others: *Ommatophoca* and *Phoca* for the femur, *Ommatophoca* and *Monachus* for the humerus. Overall, these results indicate that while long bone shape efficiently differentiates subfamilies, it remains less reliable for finer taxonomic distinctions, and that some genera seem to bring more noise than others (e.g., *Ommatophoca*). The latter may be due to the existence of multiple morphotypes within an individual species, irrespective of sex and ontogeny, such as has been observed for the extant *Ommatophoca rossii* (James P. Rule, pers. comm), and has tentatively been suggested for the extinct *Homiphoca capensis* from South Africa (Govender et al., 2012). While accuracy remained extremely good at the tribe level, those analyses highlighted the decreasing classification power of the femur and humerus at lower taxonomic ranks.

3.6 | Disparity

Morphological disparity extracted from Procrustes variance using the *morphol.disparity* function shows variation between major clades in both elements. At the subfamily level, *Monachinae* shows higher disparity than *Phocinae* for the femur (0.00556 vs. 0.00386, respectively) and the humerus (0.00442 vs. 0.00245, respectively), supported by a significant *p*-value in both cases (pairwise *p* = 0.001, 999 permutations). At the tribe level, femoral disparity ranges from *Erignathini* (0.00128; lowest) to *Lobodontini* (0.00477; highest), but the only significant pair tested were *Erignathini* versus *Lobodontini*

(*p* = 0.005) and *Erignathini* versus *Phocini* (*p* = 0.038). For the humerus, *Lobodontini* again exhibit the highest disparity (0.00359) and is significantly higher than most tribes (e.g., vs. *Cystophorini* *p* = 0.002, *Erignathini* *p* = 0.001, *Miroungini* *p* = 0.001, *Monachini* *p* = 0.004, *Phocini* *p* = 0.001), with *Miroungini* versus *Phocini* also significant (*p* = 0.019). At the genus level, estimated disparities vary widely but genus-level pairwise results should be interpreted cautiously because most genera are represented by a poor sample size.

4 | DISCUSSION AND CONCLUSIONS

While monachines show large disparity in the shape of the humerus, phocines tend to have humeri with morphometric variation clustering, with intra- and interspecific and -generic variation overlapping considerably. Even if the morphological variation of humerus' shape is larger for the monachines, some morphological similarities, such as overlap for PC2 and PC3, can be found between some taxa, which are more likely representative of their phylogenetic proximity. For the femora, the disparity is more balanced between the two subfamilies.

As a result, this questions the validity of some of the current fossil taxa with isolated femora and/or humeri as type specimens, as already pinpointed by Churchill and Uhen (2019) and Rule et al. (2024). Indeed, whereas our PCA shows a clear separation of morphological variation of humeri and femora of *Phocidae* along PC1 at the subfamily level, this is much less the case for PC2 and PC3, whether it is at the subfamily, genus, or species levels. This is especially true when taking into account that less than 60% of humeral morphometric variation is captured by PC1–3, and less than 55% of femoral morphometric variation. Hence, a considerable amount of morphometric variation is explained by a large number of PCs. Our CVAs highlight that, while long bone shape provides a clear distinction between phocid subfamilies, it remains ambiguous at the genus level.

This strengthens the insights of previous authors (Churchill & Uhen, 2019; Rule et al., 2024) that isolated long bones should no longer be treated as generally diagnostic for *Phocidae*, and that they should no longer be used as type specimens to name new fossil species. However, our CVA, showing that roughly four in five humeri and femora can be identified at the genus level shows that much care is needed when revising the historical fossil record of *Phocidae* based on isolated long bone type material. Nevertheless, an important limitation of our analysis is that most genera are represented by a single species (and often by few specimens), and while there

cannot be a holotype for a genus without a species; our current dataset does not allow us to properly assess the classification accuracy at the species level. As a result, these results do not directly address whether isolated long bones are sufficient to diagnose species-level differences, which is the critical issue for taxonomic practice given that holotypes must ultimately be referable to species, not genera. More compelling tests would require the inclusion of multiple species within the same genus (e.g., *Phoca* or *Pusa*) to evaluate whether closely related species can be reliably distinguished. However, the decreasing classification accuracy at finer taxonomic levels highlighted by our CVAs still suggest caution when attributing a very precise taxonomic attribution to an isolated long bone. A further limitation of our current CVAs is the strongly uneven sampling across genera. While a few genera (notably *Halichoerus* and *Pagophilus*) were represented by a relatively large sample size, most genera include less than five specimens, which might fail to capture their full morphological variability. Consequently, the high classification accuracy observed for well-sampled genera may be due to their disproportionate representation rather than intrinsic diagnosability, whereas classification accuracies for poorly sampled genera should be interpreted with caution. This imbalance, however, largely reflects the genuine scarcity of phocid postcranial material in museum collections and highlights the need for expanded sampling before more robust conclusions about genus- or species-level diagnosability from isolated long bones can be drawn. Whereas many practical problems remain with these species and specimens, such as the difficulty to compare many bones to isolated type long bones, their validity should be reviewed on a case-by-case basis. Multiple fossil phocid seal species, originally named based on isolated long bones, have been re-assessed in the last decade, sometimes after the discovery of additional specimens (e.g., Dewaele, Amson, et al., 2017; Dewaele, Lambert, & Louwye, 2017; Dewaele, Lambert, & Louwye, 2018; Dewaele, Peredo, et al., 2018; Otriazhyi et al., 2025; Rule et al., 2020). Prior to the morphometric studies of Churchill and Uhen (2019) and Rule et al. (2024) stating that isolated long bones are not diagnostic for (fossil) phocid seal species identification, Dewaele, Amson, et al. (2017) presented associated specimens, and provided a robust re-assessment of historical specimens attributed to *Phoca vitulinoides*, renaming it to a new genus: *Nanophoca vitulinoides*. Otriazhyi et al. (2025) presented a detailed description of a skeleton attributed to *Monachopsis pontica*, a fossil taxon from the Miocene of the Paratethys, formerly known from isolated long bones. Dewaele, Lambert, and Louwye (2018) and Rule et al. (2020) erected a new genus, *Noriphoca*, and a new genus and species, *Sarcodectes magnus*,

respectively, to isolated diagnostic fossil seal crania from problematic taxa, namely the genera *Monotherium*, and *Callophoca*, respectively. In contrast, Dewaele, Lambert, and Louwye (2017, 2018); Dewaele, Peredo, et al. (2018) also retained or even created new taxa with isolated long bones as type specimens, the validity of which has since been questioned in multiple studies (Dewaele & de Muizon, 2024; Rule et al., 2024).

While awaiting formal re-assessment, other fossil phocid seal taxa described on isolated long bones should indeed be treated as *nomina dubia*, as posited by Rule et al. (2024). Whereas this partly negates the nuance needed in this debate, it (temporarily) removes these taxa from beta, gamma, and omega taxonomic studies.

AUTHOR CONTRIBUTIONS

Leonard Dewaele: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; writing – review and editing; visualization; formal analysis; project administration; supervision; resources; data curation. **Narimane Chatar:** Investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; software; formal analysis; data curation; resources; supervision; conceptualization. **Jacques Klassen:** Investigation; methodology; validation; visualization; formal analysis; software; data curation. **Mark D. Uhen:** Writing – original draft; writing – review and editing; project administration; resources; supervision; data curation; formal analysis. **Valentin Fischer:** Conceptualization; writing – original draft; methodology; validation; writing – review and editing; formal analysis; data curation; supervision; resources; software.

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SUPPORTING INFORMATION

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